The Spatio-Temporal Distribution of Fog in French Guiana as a Precondition for the Appearance of a new Vegetation Type - the Tropical Lowland Cloud Forest

kumulative Dissertation
zur Erlangung des Doktorgrades
der Naturwissenschaften
(Dr. rer. nat.)

dem Fachbereich Geographie
der Philipps-Universität Marburg
vorgelegt von

André Obregón Flores
aus Düsseldorf

Marburg / Lahn 2015

Vom Fachbereich Geographie
der Philipps-Universität Marburg als Dissertation
am 13. Januar 2016 angenommen.

Erstgutachter:	Prof. Dr. Jörg Bendix
Zweitgutachter:	Prof. Dr. Georg Miehe

Tag der mündlichen Prüfung: 27. April 2016

Morning Fog in Les Nouragues Nature Reserve, French Guiana
Cover Photo of Ecotropica 18 (2012)

For Lionel

Preface

The fog is finally lifting after years of devoting parts of my life to this work. Finalization of this thesis could not have been achieved without the utmost support of my supervisor Jörg Bendix to whom I am very grateful for his counsel and confidence in me throughout all these years. He and Rob Gradstein have made this project possible and I thank them for giving me the opportunity of becoming a part of it. Funding by the German Research Foundation under grants BE 1780/13-1 and GR 1588/12-1 is gratefully acknowledged. I am also much obliged to Jan Cermak for giving me guidance and motivation in an early stage of this work.

This endeavour would not have been possible without my co-workers in French Guiana. Rütger Rollenbeck provided tremendous help with setting up the climate station and I benefitted substantially from his scientific and technical expertise. Sebastian Achilles is thanked for his enthusiasm and tireless support during several field campaigns under challenging working conditions. I thank Christine Gehrig for providing her botanical expertise to this work and her help in the field, together with Felix Normann and Patrick Weigelt, who have been excellent company during our field campaign in Saül. I am very grateful to Philippe Gaucher (CNRS Guyane) for logistic help in French Guiana and maintenance of the COPAS climate station. I also express my gratitude to Alex Pardow and Michael Lakatos for our fruitful cooperation and their assistance in the field.

The people of French Guiana are thanked for their friendliness and help they offered during this time. I am grateful for having been given the chance to live and work in a nearly pristine tropical rain forest ecosystem for several months which enabled me to appreciate even more the true beauty of nature.

I thank my former colleagues at the Laboratory for Climatology and Remote Sensing for the beautiful working environment and all the time that we spent together in and outside the office. With special gratitude I thank Helga Nitsche, Peer Hechler, Andrea Kaiser-Weiss and Frank Kaspar from the German Meteorological Service (DWD) for facilitating my pursuit of this thesis during my time at DWD. Also, I wish to thank my current Director Barbara Ryan and my

colleagues at the Group on Earth Observations (GEO) Secretariat in Geneva. I thank Gary Geller for his constructive advice.

Special thanks go to my friends and family for their backing and support whenever needed. I thank my mother for her never ending faith in my capability to reach my objectives.

Finally, I thank my beloved wife Karol. Without her unconditional encouragement and support this thesis could not have been written. I also wish to express my heartfelt love to my son Lionel to whom I dedicate this work.

Geneva, December 2015 André Obregón

Contents

List of Figures

List of Tables

List of Acronyms and Symbols

AVHRR	Advanced Very High Resolution Radiometer
CALIOP	Cloud-Aerosol Lidar with Orthogonal Polarization
COPAS	Canopy Operating Permanent Access System
dbh	diameter at breast height [cm]
DEM	Digital Elevation Model
ERA	ECMWF Reanalysis
FAO	Food and Agriculture Organization
FAR	False Alarm Ratio
FG	French Guiana
FLS	Fog / Low Stratus
GOES	Geostationary Operational Environmental Satellite
IR	Infrared
ITCZ	Intertropical Convergence Zone
LBA	Large-Scale Biosphere-Atmosphere Experiment in Amazonia
LCF	Tropical Lowland Cloud Forest
Lidar	Light detection and ranging
LRF	Tropical Lowland Rain Forest
LST	Local Solar Time
LUT	Lookup Table
LWC	Liquid Water Content [g m$^{-3]}$
LWD	Leaf Wetness Duration [h]
MCF	Tropical Montane Cloud Forest
MIR	Mid Infrared
MODIS	Moderate Resolution Imaging Spectroradiometer
NCEP-NCAR	National Centers for Environmental Prediction / National Center for Atmospheric Research
NOAA	National Oceanic and Atmospheric Administration
PCA	Principal Component Analysis
PFI	Potential Fog Index
POD	Probability of Detection

Radar	Radio detecting and ranging
RH	Relative Humidity [%]
ROC	Receiver Operating Characteristics
RTC	Radiative Transfer Calculations
sd	Specific saturation deficit [g kg^{-1}]
SRTM	Shuttle Radar Topographic Mission
SZA	Satellite Zenith Angle
TMCF	Tropical Montane Cloud Forest
TPI	Topographic Position Index
TPW	Total Precipitable Water
USGS	United States Geological Survey
UTM	Universal Transverse Mercator
VIS	Horizontal Visibility [m]
VPD	Vapour Pressure Deficit [hPa]
WMO	World Meteorological Organization
ΔT	Temperature difference IR-MIR band

1 Introduction

1.1 Fog in tropical lowland forests

Cloud forests are a type of rainforest which is under the permanent or regular influence of clouds. They are mainly associated with tropical mountain regions, being well-known as Tropical Montane Cloud Forests (TMCFs) (Bruijnzeel et al. 2010), but they are also found in subtropical and temperate regions (Weathers 1999).

When a cloud is in direct physical contact with the underlying surface, it is meteorologically referred to as fog. Several definitions of fog are found in the literature, either defining fog by thresholds of horizontal visibility or as a physical phenomenon (Cermak 2006). The World Meteorological Organization defines fog as a suspension of very small, usually microscopic water droplets in the air reducing the horizontal visibility at the Earth´s surface to less than 1 km (WMO 1992). In synoptic reporting, fog is generally treated as an obstruction to visibility. Most international studies follow the definition of fog by horizontal visibility. Glickman (2000) extended this definition by introducing the condition of small cloud droplets (diameter below 200 μm) being present.

Physically, a fog consists of very small water droplets with a diameter ranging from 1 to 40 µm, with fall velocities below 5 cm s^{-1} (WMO 2010). Fog can form via different meteorological processes, involving either cooling of surface air or evaporation from a warm and moist surface, or a combination of both. Air humidity close to saturation, low wind velocities and a reduction of turbulence are important prerequisites of fog formation (Findlater 1985, Schilling 1991, Pasricha et al. 2003). Related to the meteorological processes involved in the formation of fog, a broad variety of definition of fog types exist. Bruijnzeel et al. (2005) proposed seven types of fog, which are named according to the meteorological process (radiation fog, sea fog, steam fog, advection fog) or to the geographic location (coastal fog, valley fog, mountain fog). However, a sharp separation remains difficult, e.g. valley fog is typically a radiation fog and coastal fog an advection fog.

Radiation fog is one of the most common fog types related to cooling of air temperature below the saturation point. It is predominantly formed in valleys and basins due to nocturnal outgoing radiation and cooling of the boundary layer air, often promoted by katabatic flows. A*dvection fog* occurs when humid air is transported over a colder surface leading to cooling of the air mass and condensation (Roach 1995). Cooling of an air mass can also occur by forced lifting along mountain slopes until reaching a condensation level which leads to *orographic fog,* also known as *mountain fog* or *cloud fog*. Since this fog type refers to all kind of fogs at high elevation it is not necessarily a stratus or stratiform cloud (Eugster 2008).

Fog as a research object is extensively studied by different research communities comprising a multiplicity of fields, ranging from meteorological studies (e.g. nowcasting), socio-economical applications (e.g. water harvesting) and ecological studies (e.g. biodiversity). Reviews on past achievements and future perspectives of fog research are found in Gultepe et al. (2007) and Eugster (2008). While fog is often associated with negative attributes (e.g. for traffic and human well-being) it has remarkable positive interrelations with the biotic and abiotic environment (Bendix et al. 2011). Although meteorologists are generally more concerned with fog as an obstruction to visibility, it is important to note that fog water deposition to surfaces is a form of precipitation (WMO 2008) which can be of great ecological value.

From a hydrological perspective, cloud moisture input can make a considerable contribution to the water balance of tropical watersheds (Stadtmüller & Agudelo 1990). The crucial role of fog as an additional water supply source, in particular for epiphytic plants, is widely accepted (Bruijnzeel et al. 2011). The process of fog water deposition is also known as fog drip, horizontal precipitation, cloud water interception, cloud stripping, lateral cloud filtering or occult precipitation. Regarding the role of fog in plant ecology it should be stressed that tropical montane cloud forest trees are capable to absorb cloud water directly through their leaves - a process which is described as foliar uptake (Goldsmith et al. 2013).

In addition to canopy moistening, other effects of cloud immersion that are beneficial for epiphytic vegetation that rely on moist environments and water supply from the air include the reduction of solar radiation, vapour deficit and evapotranspiration (Hamilton 1995). Hence, fog occurrence is regarded as the single most important microclimatic feature affecting the distribution and function of TMCF plants (Oliveira et al. 2014), and particularly as a major precondition for high epiphyte diversity (e.g. Bruijnzeel et al. 2011). Richards et al. (1996) and many others thereafter showed that TMCF may harbour more species of epiphytes than any other forest type.

Since meteorological conditions creating a foggy environment are not restricted to mountainous areas, cloud forest can occur at virtually any elevation. In fact, their occurrence is also documented for lowlands in temperate regions, e.g. at the coast of California (Dawson 1998) and in northern Chile (Aravena et al. 1989). However, lowland cloud forests in the tropics have remained largely under-investigated.

It is a general assumption that montane forests are richer in species than lowland forests (e.g. Richards 1984, Hamilton & Bruijnzeel 2000). However, botanic inventories of non-vascular epiphyte diversity (bryophytes, lichens) in tropical lowland and montane forests across the Neotropics give reason to call this into question. For example, in a moist lowland forest in Guyana, five trees yielded 88 moss species (50 liverworts) and in Saül (French Guiana), 40 species of moss and 60 species of liverwort were found on only four trees. One single tree yielded up to 50 bryophyte species (Cornelissen & Gradstein 1990, Montfoort & Ek 1990, Gradstein 1995, 2006). These figures are the highest worldwide reported for tropical lowland rain forest. Species richness of epiphytic liverworts in French Guiana has reported to be three times higher than in Amazonian lowland forest at Surumoni (Venezuela) (Gradstein 2006) and up to 1.5 times higher than in moist submontane and montane forest in the tropical Andes (Wolf 1993, Acebey et al. 2003).

The causes of high species richness in Guyana and French Guiana have been unclear because elevation and annual precipitation are similar for instance to the Surumoni site which has lower epiphyte richness and abundance (Gradstein 1995, Anhuf & Winkler 1999). Gradstein (2006) pointed at the high incidence of fog in French Guiana which is absent at Surumoni as a potential reason. The high species richness was hence explained by the favourable air moisture regime caused by fog which allows poikilohydric species to thrive in the hot lowland forest. Fog during day times may prevent desiccation and allow these plants to achieve positive net photosynthesis in spite of high temperatures (Gradstein 2006).

To date, no comprehensive studies on either the spatio-temporal occurrence of tropical canopy fog or on the meteorological processes leading to fog formation have been conducted in tropical lowland forest areas. The role of fog in the distribution of tropical lowland forest types remains poorly understood. Investigations are made more difficult by the fact that measurements of horizontal visibility at the surface/above the canopy in tropical forest are rarely available. Therefore, it is unknown which fog type might foster the epiphyte-rich lowland forest in valleys of central French Guiana.

Prior to describing the objectives of the present study and the conceptual approach of this work in subsequent sections, the next section gives a brief overview of the study area.

1.2 Study area

French Guiana is located on the northeastern coast of South America. It lays upon the easternmost part of the Guiana Shield, a cratone of the South American plate, which comprises the whole of French Guiana, Suriname and Guyana as well as parts of Venezuela, Brazil and Colombia. The Guiana Shield extends roughly between the Orinoco River in the west and the Amazon River in the south. It is one of the least populated areas of the world and large areas are covered with almost undisturbed rain forests (Hammond 2005a).

Hammond (2005b) distinguished five large landforms for the Guiana Shield of which the "Precambrian Rolling Hills" account for almost all of French Guiana. This landform describes an undulating granitoid landscape that has been created through synclinal folding and differential weathering (Hammond 2005b). The terrain in French Guiana is undulating throughout the country; in particular, the central part is hilly and considerably dissected. The elevation of hills, ridges and small river valleys varies between 50 and 300 m a.s.l. (refer to figure. 1.1).

According to the Global Forest Resources Assessment 2010 (FAO 2010), French Guiana has a total forest area of around 8 million hectares and its relative forest cover ranks among the highest worldwide. 98% of the land area is covered by forests, of which 95% are classified as old-growth or primary forests. Between 1990 and 2010 total forest extent decreased by 1.3 % and primary forest decreased by 3.9%. Above-ground biomass and carbon stock per land area in French Guiana are among the highest worldwide (Saatchi 2011).

French Guiana has a tropical climate, with annual mean daily temperatures between 25° and 27°C. Annual rainfall ranges from around 2,500 mm in the west to 3,500 mm at the Atlantic Coast with a bimodal seasonal precipitation cycle. The main dry season is between August and November. A less pronounced dry period occurs in February and March. Bovolo et al. (2011) give an overview of the fine-scale regional climate in the Guianas using ERA-40 reanalysis data for 1958-2001.

In terms of meteorological measurements, the entire Guiana Shield is one of the poorest monitored regions in the world (Hammond 2005b). In French Guiana, Météo France operates six meteorological stations of which five are located close to the Atlantic coast. The station Maripasoula is located at the border to Suriname, 50 km up the Maroni River. There are no official inland stations in French Guiana.

However, long-term meteorological measurements for research purposes have been conducted in the Nouragues Natural Reserve, around 100 km inland from the Atlantic coast. Grimaldi & Riera (2001) give a summary of these measurements for November 1987 to December 1996 (refer also to chapter 3.2.1 of the present study).

Figure 1.1 gives a topographic overview of the study area. The two sites where field work has been conducted are briefly described in the following:

1) COPAS site:

The Canopy Operation Permanent Access System (COPAS) (refer to next chapter) is located close to the research station Saut Pararé, within the uninhabited Nouragues Natural Reserve (4° 2' 30'' N, 52° 40' 30''W, 75 m a.s.l.). It is situated in the valley of the Arataye river, 350 m away from the edge of the river. The site is ca. 100 km inland from Atlantic coast. Elevation varies from 50 to 200 m a.s.l.. The area comprises high forest, slope forest and forest growing on hydromorphic soil. Canopy trees reach up to approximately 50 m.

2) Saül site:

The secondary site is 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. The area is hilly and considerably dissected, with small river valleys at about 200–250 m and hills to about 400m in elevation. 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).

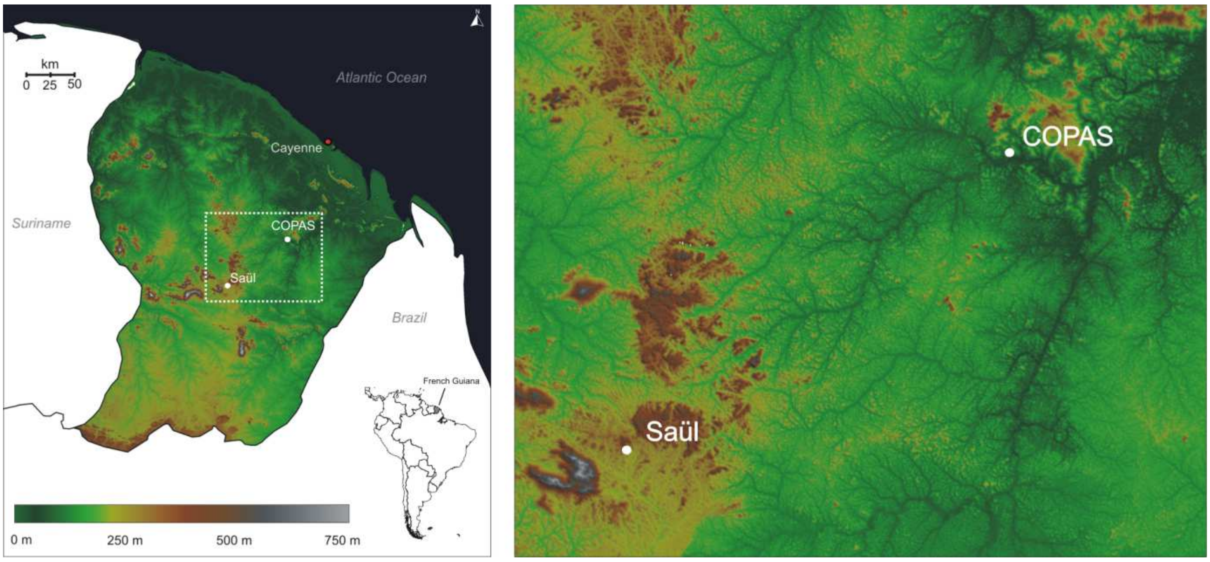

Figure 1.1. Map of the study area. The dotted rectangle marks the inner study area, which comprises the Saül and COPAS sites

The study sites have been selected for their representativeness (each site harbouring nearly undisturbed valley and hill forests) and due to their sufficient distance to the coast (to avoid confusion with coastal fog). For detailed descriptions of the study sites the reader may refer to the individual chapters of this thesis.

1.3 Aims of this work and outline

The present work is part of a collaborative study between the University of Göttingen and the University of Marburg. The primary goal of this collaboration is to investigate the relationship between climate, especially fog, and epiphyte vegetation in French Guiana. The underlying presumption of the study is the existence of a novel type of tropical lowland cloud forest (LCF), which is caused by frequent fog occurrence and characterized by high epiphyte diversity.

Hitherto, no systematic investigation has been available on the interaction of energy balance, local breeze pattern and fog occurrence in tropical lowland forests. The knowledge of temporal and spatial fog dynamics in the tropical lowland is generally poor. The main goal of this thesis is therefore to provide an in-depth study of the fog phenomenon and its spatiotemporal dynamics in French Guiana and to assess its implications on the formation of cloud forest in the tropical lowland.

Two main hypotheses will be tested within this work:

H1 Radiation fog occurs frequently in valleys of French Guiana and is supported by nocturnal katabatic flows. Valley fog is a regularly occurring phenomenon in space.

H2 Valley forest is characterized by high epiphyte diversity, abundance and biomass due to a favourable canopy microclimate. The occurrence of fog thus spatially determines the new vegetation unit Tropical Lowland Cloud Forest.

Following from these hypotheses, the aims of the presented work are:

- To analyse the underlying meteorological processes leading to fog formation
- To investigate microclimatic differences between forest in valleys and ridges
- To shed light on the relation between fog occurrence and epiphyte species richness in LCF
- To reveal the spatio-temporal dynamics of night-time fog throughout French Guiana and, with this, to provide evidence for potential LCF habitats

The investigation should shed light on current knowledge deficits:

- Fog formation has never been studied in depth in tropical lowland forests and therefore its spatial occurrence and role in these habitats is poorly understood
- The spatio-temporal distribution of fog can only be detected with weather satellite data. However, fog in French Guiana is hypothesized to be a small-scale phenomenon, frequently restricted to narrow river valleys which often lie in the sub-pixel detection range even of polar-orbiting weather satellites with relatively high spatial resolution (mostly 1 km). A subpixel fog/low stratus detection scheme is necessary which can only rely on IR satellite data for night/early morning time applications.

Figure 1.2 presents an outline of this work. It starts in chapter 2 with the description of the conceptual design including an overview of the work packages and the technical preparation. The implementation of the work packages is embedded in four publications: The underlying meteorological processes of fog formation in French Guiana are presented in the publication Obregon, Gehrig-Downie, Gradstein, Rollenbeck & Bendix 2011: Canopy Level Fog Occurrence in a Tropical Lowland Forest of French Guiana as a Prerequisite for High Epiphyte Diversity, Agricultural and Forest Meteorology, doi: 10.1016/j.agformet.2010.11.003 (chapter 3.). The investigation of canopy microclimate in different habitats and the impacts on the epiphytic vegetation are embedded in two publications: Gehrig-Downie, Obregon, Bendix, Gradstein 2011, Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana, Biotropica, doi: 10.1111/j.1744-7429.2010.00745.x (chapter 4) and Gehrig-Downie, Marquardt, Obregon, Bendix, Gradstein 2012, Diversity and Vertical Distribution of Filmy Ferns as a Tool for Identifying the Novel Forest Type "Tropical Lowland Cloud Forest", Ecotropica, 18, 35-44 (chapter 5). Finally, the development of an algorithm to detect the spatio-temporal fog dynamics in French Guiana is presented in the publication Obregon, Gehrig-Downie, Gradstein & Bendix 2014: The potential distribution of tropical lowland cloud forest as revealed by a novel MODIS-based fog/low stratus night-time detection scheme, Remote Sensing of Environment, doi: 10.1016/j.rse.2014.09.005 (chapter 6). A short summary of the results and an outlook provided in chapter 7 conclude this thesis.

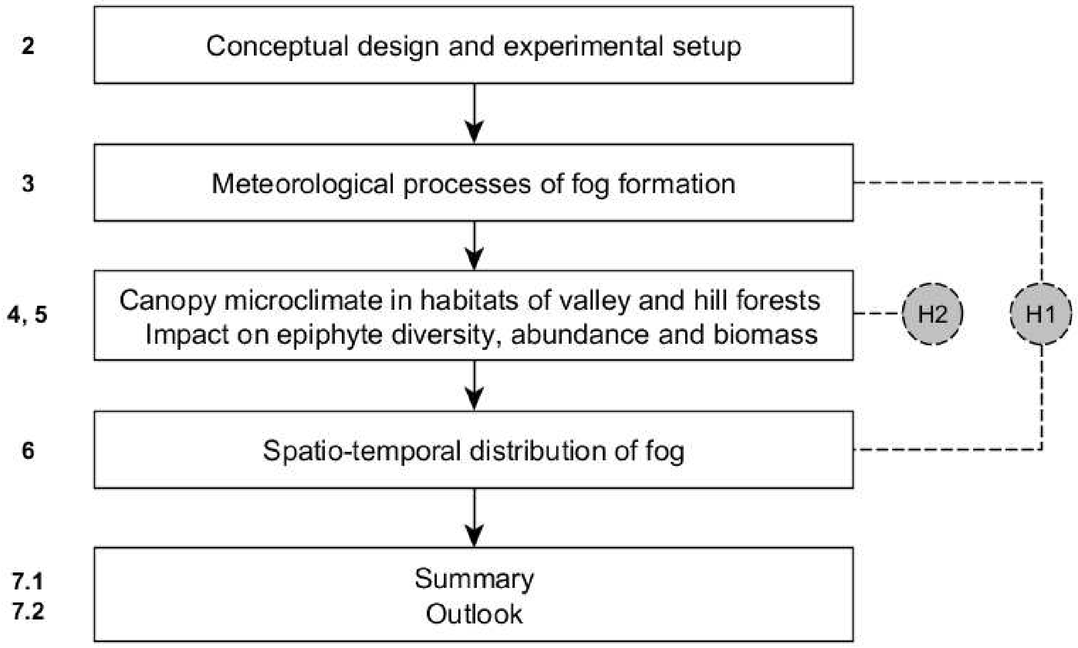

Figure 1.2. Outline of this work (indicating chapters and hypotheses)

References

Acebey, A., Gradstein, S.R., Kromer, T., 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of Tropical Ecology 19, 9-18.

Aravena, R., Suzuki, O., Pollastri, A., 1989. Coastal fog and its relation to groundwater in the IV region of northern Chile. Chemical Geology: Isotope Geoscience section 79, 83-91.

Bendix, J., Eugster, W., Klemm, O., 2011. Fog - boon or bane? Erdkunde 65, 229-232.

Bovolo, C.I., Pereira, R., Parkin, G., Kilsby, C., Wagner, T., 2012. Fine-scale regional climate patterns in the Guianas, tropical South America, based on observations and reanalysis data. International Journal of Climatology 32, 1665-1689.

Bruijnzeel, L.A., Eugster, W., Burkard, R., 2005. Fog as a hydrologic input, in: Anderson, M.G. (Ed.), Encyclopedia of Hydrological Sciences. John Wiley, Chichester, UK, pp. 559-582.

Bruijnzeel, L.A., Kappelle, M., Mulligan, M., Scatena, F.N., 2010. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, UK, pp. 691-740.

Bruijnzeel, L.A., Mulligan, M., Scatena, F.N., 2011. Hydrometeorology of tropical montane cloud forests: emerging patterns. Hydrological Processes 25, 465-498.

Cermak, J., 2006. SOFOS – A New Satellite-based Operational Fog Observation Scheme, Philipps-Universitat Marburg, Germany.

Cornelissen, J.H.C., Gradstein, S.R., 1990. On the occurrence of bryophytes and macrolichens in different lowland rain forest types of Mabura Hill, Guyana. Tropical Bryology 3, 29-35.

Dawson, T.E., 1998. Fog in the California redwood forest: Ecosystem inputs and use by plants. Oecologia 117, 476-485.

de Granville, J.J., 1986. Flore et vegetation. Saga, Cayenne, French Guiana.

de Granville, J.J., 2001. Végétation, in: Barret, J. (Ed.), Altlas illustré de la Guyane. IRD Editions, Paris, France, pp. 52-55.

Eugster, W., 2008. Fog Research. Erde 139, 1-10.

FAO, 2010. Global Forest Resources Assessment 2000, Rome, Italy.

Findlater, J., 1985. Field investigations of radiation fog formation at outstations. Meteorological Magazine 114, 187-201.

Gehrig-Downie, C., Marquardt, J., Obregon, A., Bendix, J., Gradstein, S.R., 2012. Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type “tropical lowland cloud forst”. Ecotropica 18, 35-44.

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, S.R., 2011. Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana. Biotropica 43, 591-596.

Glickman, T.S., 2000. Glossary of meteorology. 2nd edition. American Meteorological Society, Boston.

Goldsmith, G.R., Matzke, N.J., Dawson, T.E., 2012. The incidence and implications of clouds for cloud forest plant water relations. Ecology Letters, n/a-n/a.

Gradstein, S., 1995. Diversity of Hepaticae and Anthocerotae in montane forests of the tropical Andes, in: Churchill, S.P., Balslev, H., Forero, E., Luteyn, J.L. (Eds.), Biodiversity and Conservation of neotropical Montane Forests. New York Botanical Garden Press, New York, pp. 321-343.

Gradstein, S.R., 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. Cryptogamie Bryologie 27, 141-152.

Grimaldi, M., Riéra, B., 2001. Geography and Climate, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 9-18.

Gultepe, I., Tardif, R., Michaelides, S.C., Cermak, J., Bott, A., Bendix, J., Mueller, M.D., Pagowski, M., Hansen, B., Ellrod, G., Jacobs, W., Toth, G., Cober, S.G., 2007. Fog research: A review of past achievements and future perspectives. Pure and Applied Geophysics 164, 1121-1159.

Hamilton, L.S., 1995. Mountain Cloud Forest Conservation and Research: A Synopsis. Mountain Research and Development 15, 259-266.

Hamilton, L.S., Bruijnzee, L.A., 2000. Decision Time for Cloud Forests. UNESCO Division of Water Sciences, Paris.

Hammond, D.S., 2005a. Ancient land in a modern world, in: Hammond, D.S. (Ed.), Tropical forests of the Guiana shield: ancient forests in a modern world. CABI Publishing, Wallingford, pp. 1-14.

Hammond, D.S., 2005b. Biophysical features of the Guiana shield, in: Hammond, D.S. (Ed.), Tropical forests of the Guiana shield: ancient forests in a modern world. CABI Publishing, Wallingford, pp. 15-194.

Montfoort, D., Ek, R., 1990. Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana, Institute of Systematic Botany, Utrecht.

Mori, S.A., Boom, B.M., 1987. The forest, in: Mori, S.A. (Ed.), The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana, pp. 9-29.

Obregon, A., Gehrig-Downie, C., Gradstein, S.R., Bendix, J., 2014. The potential distribution of tropical lowland cloud forest as revealed by a novel MODIS-based fog/low stratus night-time detection scheme. Remote Sensing of Environment 155, 312-324.

Obregon, A., Gehrig-Downie, C., Gradstein, S.R., Rollenbeck, R., Bendix, J., 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. Agricultural and Forest Meteorology 151, 290-300.

Oliveira, R.S., Eller, C.B., Bittencourt, P.R.L., Mulligan, M., 2014. The hydroclimatic and ecophysiological basis of cloud forest distributions under current and projected climates. Annals of Botany 113, 909-920.

Pasricha, P.K., Gera, B.S., Shastri, S., Maini, H.K., John, T., Ghosh, A.B., Tiwari, M.K., Garg, S.C., 2003. Role of the water vapour greenhouse effect in the forecasting of fog occurrence. Boundary-Layer Meteorology 107, 469-482.

Richards, P.W., 1984. The ecology of tropical forest bryophytes, in: Schuster, R.M. (Ed.), New manual of bryology. Hattori Botanical Laboratory, Nichinan, Japan, pp. 1233-1270.

Richards, P.W., Walsh, R.P.D., Baillie, I.C., Greig-Smith, P., 1996. The tropical rain forest an ecological study (2nd edition). Cambridge University Press, Cambridge.

Roach, W.T., 1995. Back to Basics: Fog: Part 2 - The formation and dissipation of land fog. Weather 50, 7-11.

Saatchi, S.S., Harris, N.L., Brown, S., Lefsky, M., Mitchard, E.T.A., Salas, W., Zutta, B.R., Buermann, W., Lewis, S.L., Hagen, S., Petrova, S., White, L., Silman, M., Morel, A., 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. Proceedings of the National Academy of Sciences of the United States of America 108, 9899-9904.

Schilling, V.K., 1991. A Parameterization For Modeling the Meteorological Effects of Tall Forests - A Case-study of A Large Clearing. Boundary-Layer Meteorology 55, 283-304.

Stadtmuller, T., Agudelo, N., 1990. Amount and variability of cloud moisture input in a tropical cloud forest. International Association of Hydrological Sciences Publication 25-32.

Weathers, K.C., 1999. The importance of cloud and fog in the maintenance of ecosystems. Trends in Ecology & Evolution 14, 214-215.

WMO, 1992. International Meteorological Vocabulary, WMO 182. World Meteorological Organization: Geneva, Switzerland, Geneva, Switzerland.

WMO, 2008. Guide to Meteorological Instruments and Methods of Observation, 7th ed. World Meteorological Organization, Geneva, Switzerland,.

WMO, 2010. CIMO Guide. World Meteorological Organization, Geneva, Switzerland,.

Wolf, J.H.D., 1993. Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. Annals of the Missouri Botanical Garden 80, 928-960.

2 Conceptual Design

The scientific issues and hypotheses outlined in the previous chapter require a sequence of work packages (WP), which are designed with the following specific aims:

WP1 Analysing the causes of fog formation in tropical lowland forests and the underlying meteorological processes. The aim is to reveal the physical conditions involved in the fog formation, including fog type, fog persistence, fog frequency, and to determine the meteorological parameters triggering the process of fog development.

WP2 Characterizing the microclimatological properties in tropical lowland rain forest (LRF) on slopes and hills, and LCF habitats in valleys and comparing results to the botanical studies. The objective is to confirm the different microclimates of LRF and LCF and to elaborate the impacts for epiphytic vegetation.

WP3 Mapping the spatio-temporal distribution of fog. The purpose is to clarify whether fog formation in tropical lowlands is a local phenomenon or if it is widely distributed in space.

A specific experimental design is needed to address the challenges described above. This specific setup is illustrated in figure 2.1. In the following, the design of each work package including the technical preparation will be described.

Work package 1. The tower system COPAS (Canopy Operation Permanent Access System) at the site Saut Pararé is freely accessible to the international research community (Charles-Dominque et al. 2002) and provides an ideal infrastructure to conduct meteorological measurements with sophisticated instruments directly above the forest canopy at 45 m height. Testing H1 requires the installation of a permanent and automatically operating meteorological station on one platform of the COPAS system to consider the meteorological conditions at canopy level where fog formation is hypothesized to occur.

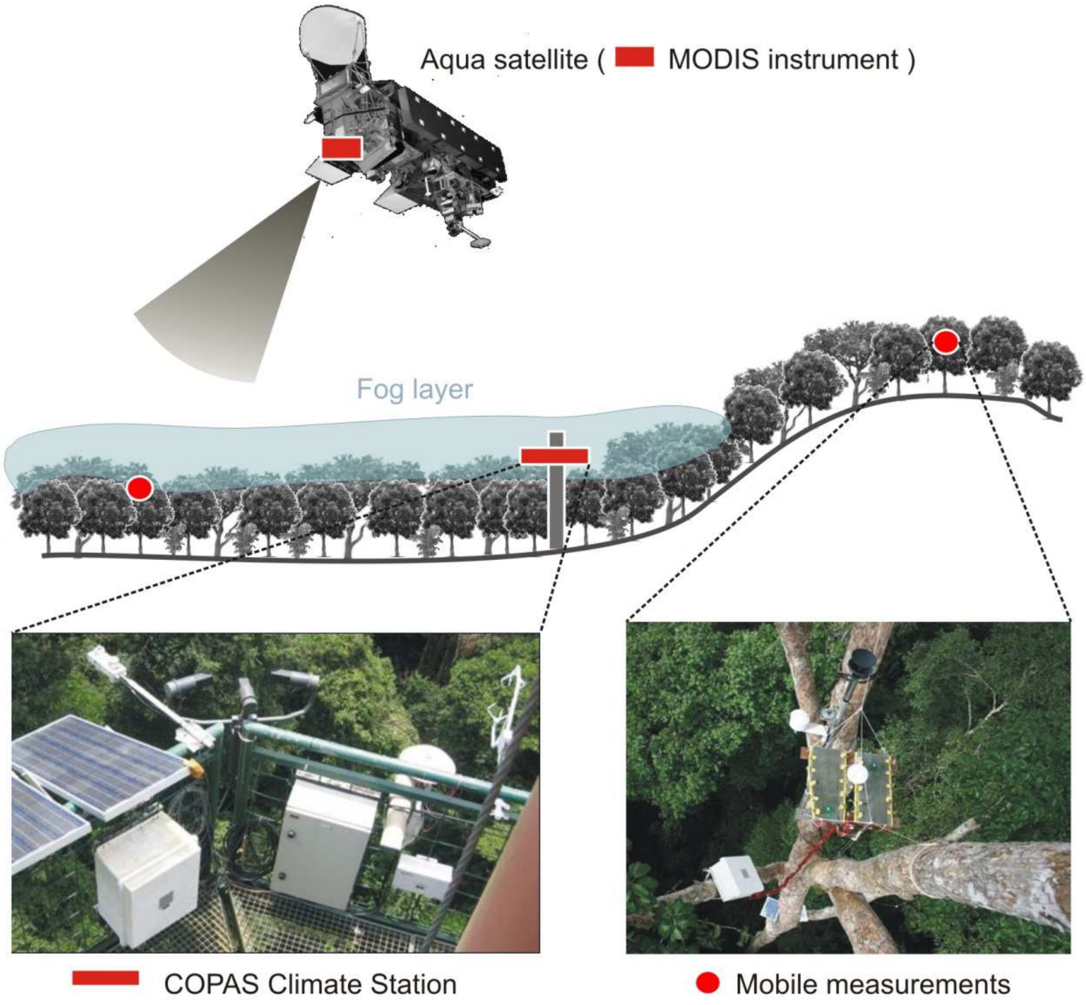

Figure 2.1. Experimental setup for the work packages (WP1: COPAS Climate Station, WP2: Mobile measurements, WP3: Remote sensing data)

The climate station encompasses a set of sophisticated instruments which are designed for accurate measurements under extreme weather conditions. The short-wave and thermal radiation balance is gathered by a net radiometer. A 3D-sonic anemometer is installed to detect low wind velocities at night associated with potential nocturnal drainage flows in order to reveal to what extent katabatic flows play a role in the fog formation process. Further, this type of sensor delivers information about turbulence conditions and stability. Since air humidity is expected to be close to saturation at night, the measurement of humidity is conducted by using a psychrometer. This instrument allows for the accurate calculation of relative humidity close to 100 per cent. The core instrument of the installation is a visibility and present weather sensor. A backscatter receiver enables the calculation of horizontal visibility (and thus fog occurrence) and the detection of precipitation type (fog, haze, drizzle etc.) and liquid water content. Since dewfall may serve as another potential water source for epiphytes when fog occurrence or rainfall does not take place, a leaf wetness sensor is installed in addition to the described instruments.

The overall measurement configuration facilitates a full picture of condensation tendencies, fog dynamics and the boundary conditions involved in the fog formation process (wind fields, turbulence). All instruments are operated by solar and battery power and are connected to a data logger computing 5-min averages from 60-s sampling intervals. The wind measurements are conducted more frequently to account for turbulence. All meteorological instruments are listed in figure 2.2.

The measurements are used to build a comprehensive and robust set of statistics, including means and deviations for different time periods, as well as diurnal courses for all relevant parameters. Case studies are performed by considering various types of weather conditions. Based on the visibility data, statistics of fog occurrence are built. Fog duration is calculated for each day and for different periods during a day. Fog events are classified into different fog density classes. A regression analysis is performed between fog duration and various meteorological parameters to reveal the atmospheric parameters involved in the entire fog formation process. For a detailed description of the data analyses refer to chapter 3.2.3.

The variables derived from the scatterometer measurements also feed into the fog detection algorithm in work package 3.

Work package 2. To reveal the meteorological conditions in ridge and valley locations and to address H2, parallel measurements with mobile climate stations mounted in canopy trees are conducted. The single rope technique is used to access the tree crowns (Mitchell et al. 2002).

Upper slopes and hills are expected to be free of fog and hence covered by ordinary tropical rain forest. Cold air pools likely form at night in these areas. In contrast, valley locations of putative lowland cloud forest are supposed to be frequently exposed to fog. The meteorological instruments are directly installed into trees to investigate the canopy microclimate. In order to derive the microclimatological information related to the different zonation of epiphytic plants, the instruments are placed in two height zones (inner tree crown, outer canopy). These height zones are ecologically relevant because of general differences in epiphyte diversity; see Johansson (1974) and Gradstein et al. (2003).

Air temperature, relative humidity and global radiation are measured in both height zones to analyse the climatic coupling between these zones and to elaborate the different living conditions for epiphytes. At the interface between the forest canopy and the atmosphere, wind speed and wind direction are derived by a 2D-sonic anemometer. Rainfall is measured with a rain gauge.

In combination with the fog measurements at COPAS, the additional vertical information of the mobile measurements in the valley helps to reveal the fog dynamics by showing to what extent the canopy is decoupled from the tree crown during times of potential fog formation. The comparison between the measurements at the hill site is important since a different canopy microclimate is expected.

At the sites where mobile meteorological measurements are undertaken, the trees are sampled for epiphyte biomass, abundance and diversity. This work is carried out by the University of Göttingen and the derived botanical inventories are used for the interpretation of the meteorological results. A principal component analysis is performed in order to elaborate the relationship among relative humidity, air temperature and epiphyte diversity.

Work package 3. Remotely-sensed imagery from satellites can provide full spatio-temporal coverage which is needed to reveal fog occurrence throughout French Guiana. Testing H1 requires the development of a satellite-based fog-detection algorithm capable of detecting fog in tropical lowland forests.

Since fog in the study area is hypothesized to occur only at night and early morning, night-time satellite data providing infrared channels have to be used. Over the past decades, specific algorithms have been developed for the detection of fog during night-time (e.g. Bendix, 2002; Eyre et al., 1984; Turner et al., 1986). The basis for most of these schemes are differences in the emissivity of small droplet water clouds in the wavelength around 3.9 µm versus the emissivity around 10.8 µm. Brightness temperature differences can be used to detect pixels of low stratiform cloudiness.

The existing algorithms have been developed for regions in the mid and high latitudes and have to be adapted for the detection of fog over tropical lowlands. In particular, the algorithm has to be adapted for fog detection at sub-pixel levels in order to account for the small-scale nature of fog in the study area. The reliable detection of small patches of fog in sub-pixel regions is generally considered to be difficult (e.g. Cermak et al. 2009). The region of French Guiana serves as a test case for a novel fog detection scheme.

To address these challenges, data from the MODIS instrument, flying on-board the polar orbiting Aqua satellite, is used. It offers a 1 km resolution for the infrared channels for wavelengths at 3.660 - 3.840 µm, 10.780 - 11.280 µm and 11.770 - 12.270 µm, which are essential for fog detection.

Four years of MODIS Level 1b calibrated radiances are used, corresponding to the period of meteorological measurements. In addition, the fog detection scheme requires the MODIS Level 2 Total Precipitation Water product and a Digital Elevation Model derived by SRTM data. Radiative transfer calculations

(RTC) are conducted to derive thresholds functions for varying TPW amounts and sub-pixel cloudiness. A discriminant analysis is performed for the assessment of these functions. Basis for the validation of the classification results are the scatterometer measurements at the study site. The algorithm development including the preprocessing of the satellite data is presented in chapter 6.3.

The novel fog detection scheme is used to derive the first fog frequency maps of French Guiana. The analysis of fog dynamics in French Guiana is expected to answer whether lowland fog development, and hence the precondition for the formation of lowland cloud forest, is a local phenomenon or if it occurs throughout the country. figure 2.2 gives an overview on the instruments, data and methods used in this thesis.

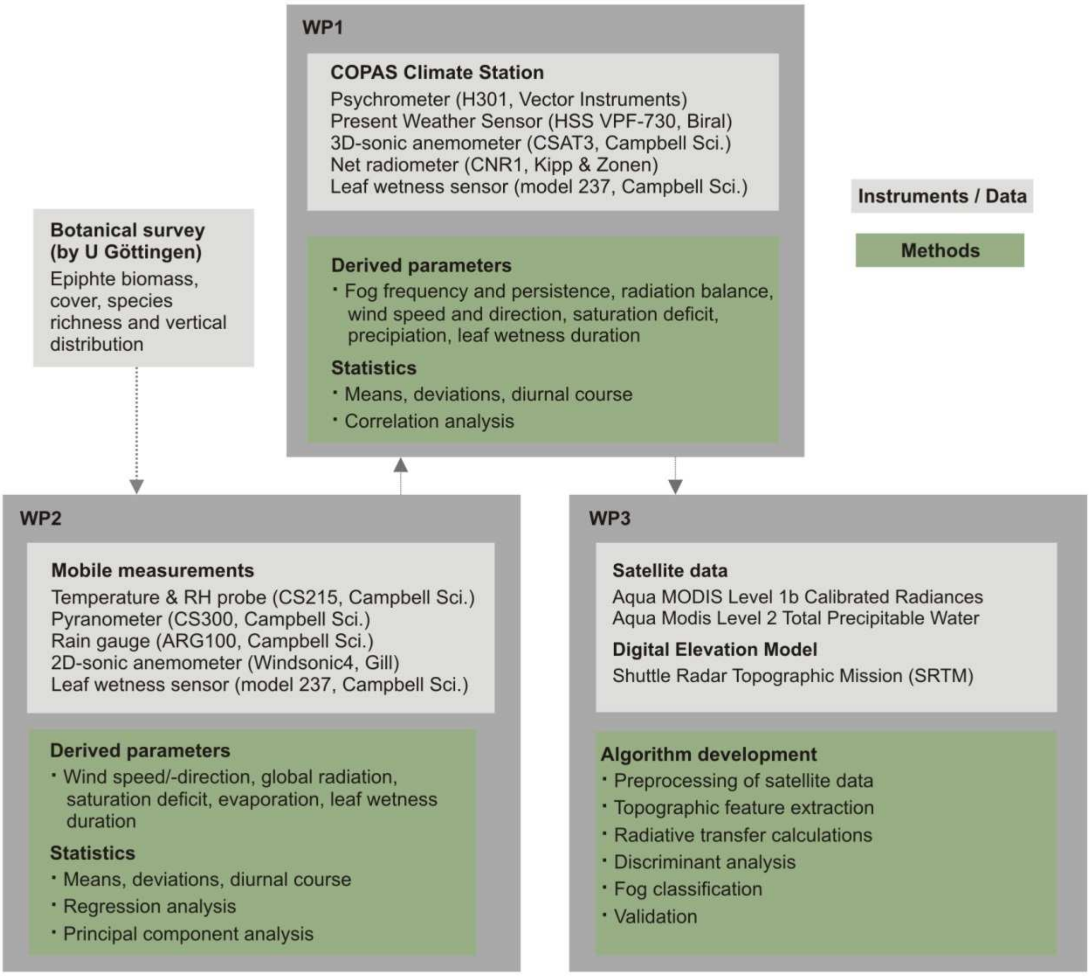

Figure 2.2. Overview on instruments, data and methods used for Work Packages 1-3

References

Bendix, J., 2002. A satellite-based climatology of fog and low-level stratus in Germany and adjacent areas. Atmospheric Research 64, 3-18.

Cermak, J., Eastman, R.M., Bendix, J., Warren, S.G., 2009. European climatology of fog and low stratus based on geostationary satellite observations. Quarterly Journal of the Royal Meteorological Society 135, 2125-2130.

Charles-Dominique, P., Gottsberger, C., Freiberg, M.S., A.D., 2002. COPAS: a new permanent system to reach the forest canopy, in: Mitchell, A.W., Secoy, K., Jackson, T. (Eds.), The Global Canopy Handbook. Global Canopy Programme, Oxford, pp. 91-96.

Eyre, J.R., Brownscombe, J.L., Allam, R.J., 1984. Detection of fog at night using Advanced Very High-Resolution Radiometer (AVHRR) Imagery. Meteorological Magazine 113, 266-271.

Gradstein, S.R., Nadkarni, N.M., Kromer, T., Holz, I., Noske, N., 2003. A Protocol for Rapid and Representative Sampling of Vascular and Non-Vascular Epiphyte Diversity of Tropical Rain Forest. Selbyana 24, 105-111.

Johansson, D., 1974. Ecology of vascular epiphytes in West African rain forest.

Mitchell, A.W., Secoy, K., Jackson, T., 2002. The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford.

Turner, J., Allam, R.J., Maine, D.R., 1986. A Case Study of the Detection of Fog at Night Using Channel 3and 4 On the Advanced Very High Resolution Radiometer (AVHRR). Meteorological Magazine 115, 285-290.

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

This chapter is published in *Agricultural and Forest Meteorology*, 151, 290-300 (2011).
Received: 4 February 2010 / Accepted: 31 October 2010

http://dx.doi.org/10.1016/j.agrformet.2010.11.003

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

Obregon, A. (1), Gehrig-Downie, C. (2), Gradstein, S.R.(2), Rollenbeck, R. (1), and J. Bendix (1)

(1) Laboratory for Climatology and Remote Sensing, Department of Geography, University of Marburg, Germany
(2) Department of Systematic Botany, Institute of Plant Sciences, University of Goettingen, Germany

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.

3.1 Introduction

Fog as defined by a horizontal visibility of ≤1km (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 & Kunz 1983, Bendix 2002, Gultepe et al. 2007, Cermak & Bendix 2008, Eugster 2008) and for tropical montane cloud forests (e.g. Hamilton & 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 & 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 & 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 & 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 habitate 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).

3.2 Materials and methods

3.2.1 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 (figure 3.1a).

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. 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 (figure 3.2, 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.

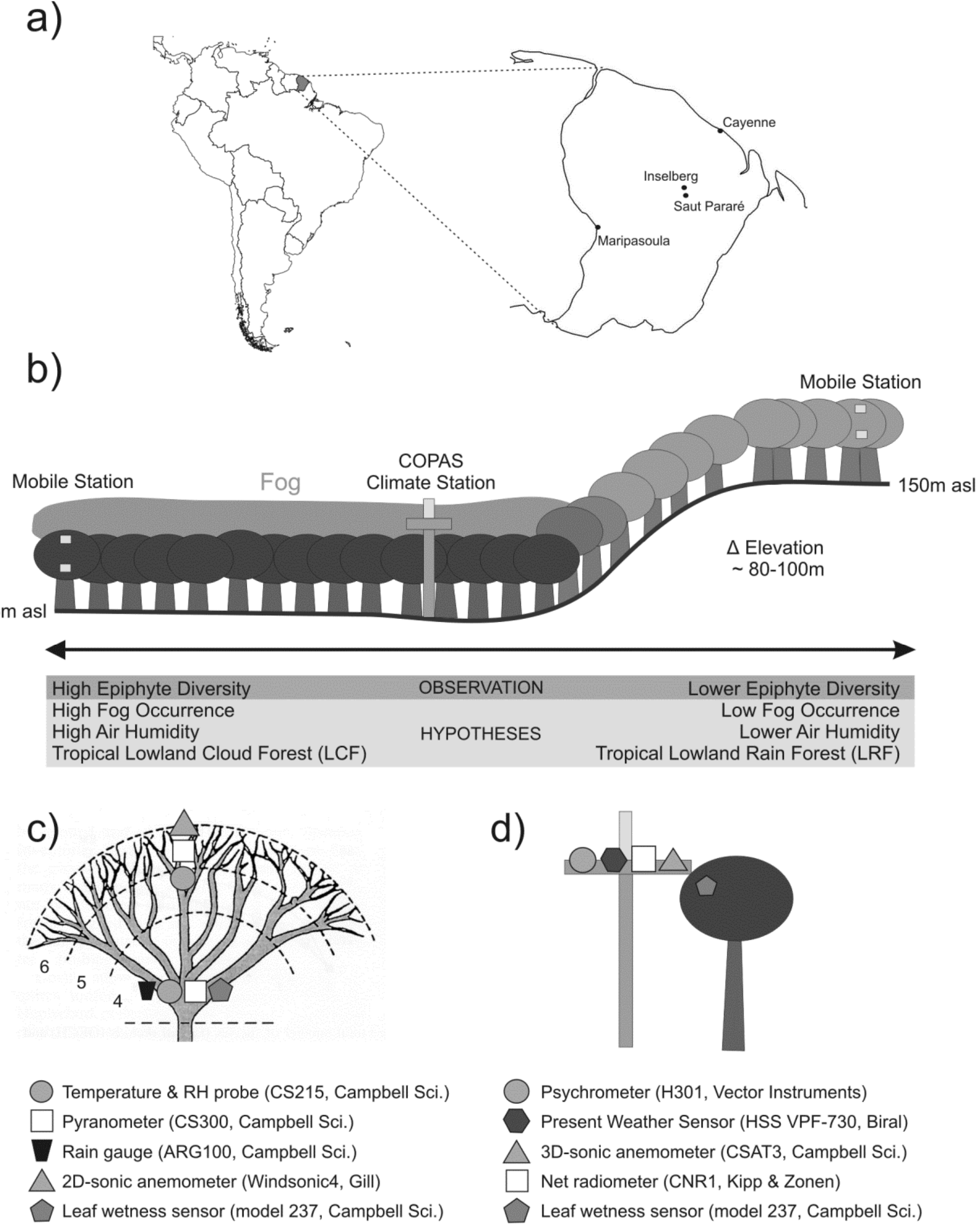

Figure 3.1. Measurement approach at the study site. (a) Location of the study site; (b) layout and visualization of hypothesis; (c) placement of mobile sensors in the canopy; (d) permanent measurements on COPAS platform

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 & 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.

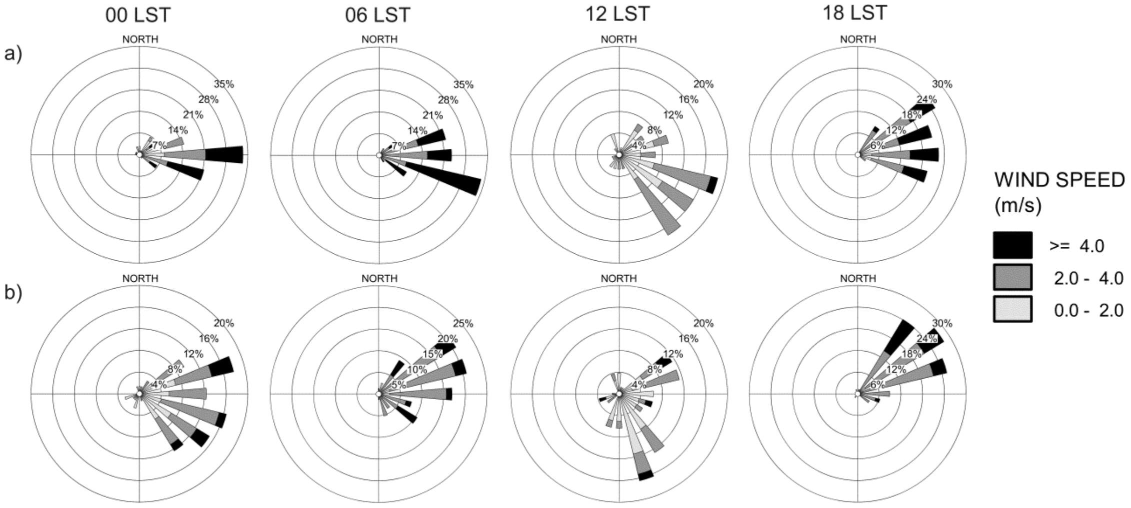

Figure 3.2. General streamflow patterns in 10m (sigma-995 level) from NCEP reanalysis data at different times of day for a) dry season (August–October 2007) and b) rainy season (May–July 2008)

3.2.2 Experimental setup

The measurement approach is illustrated in figure 3.1. 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.; figure 3.1d) (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 (figure. 3.1c). 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 & 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.

3.2.3 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 & 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.

3.3 Results

3.3.1 Fog frequency and fog density

Fog frequency at canopy level is presented in figure 3.3a. The data show that fog is a common phenomenon in the Aratay e 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 (figure 3.3a). 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 (figure 3.3b). 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.

The frequency of fog density classes, as a parameter for liquid water content (LWC), is shown in figure 3.4. 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 3.5 underpins the significant relation between mean visibility and fog persistence.

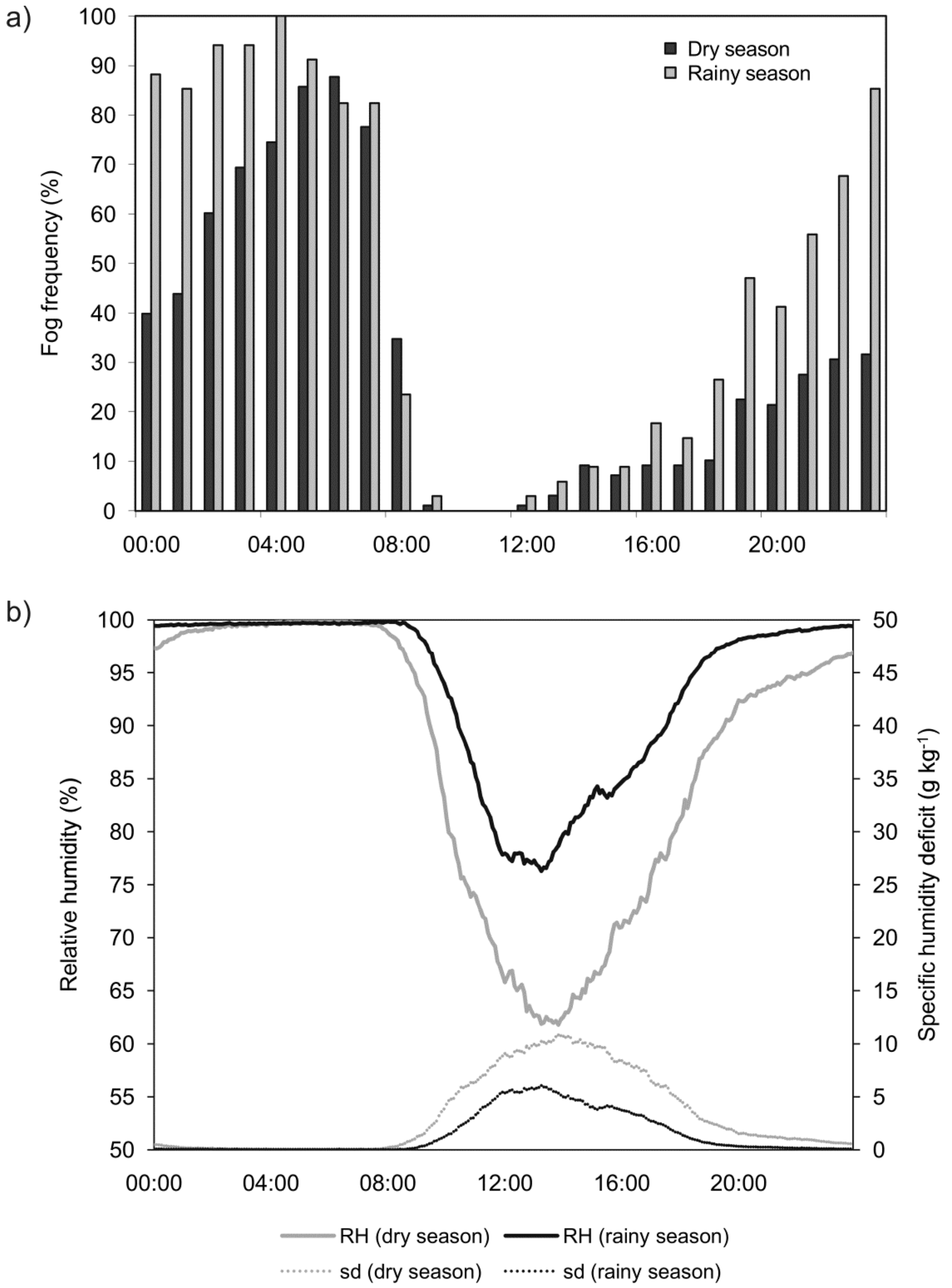

Figure 3.3. (a) Diurnal course of fog frequency in the dry (mid-August until mid-November 2007) and rainy (mid-June until mid-July 2008) season at the study site (present weather sensor) (b) diurnal course of average relative air humidity (RH) and specific saturation deficit (sd) for the rainy and dry season, both at the canopy–atmosphere interface level

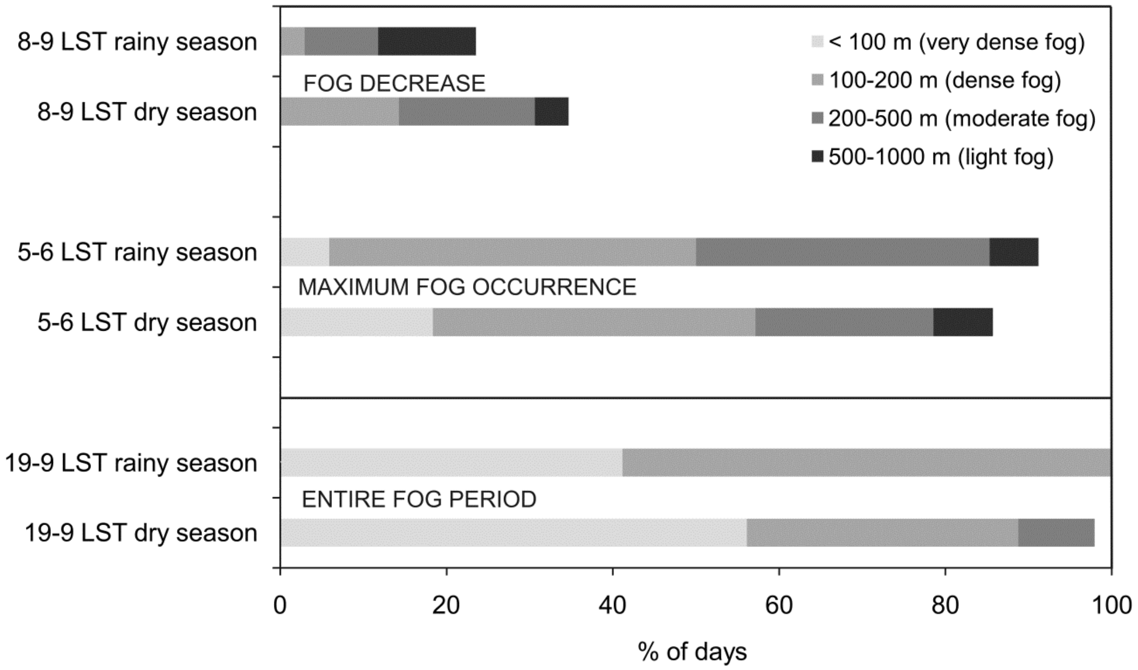

Figure 3.4. Frequency of visibility classes for the fog at the study site (present weather sensor) at canopy–atmosphere interface level

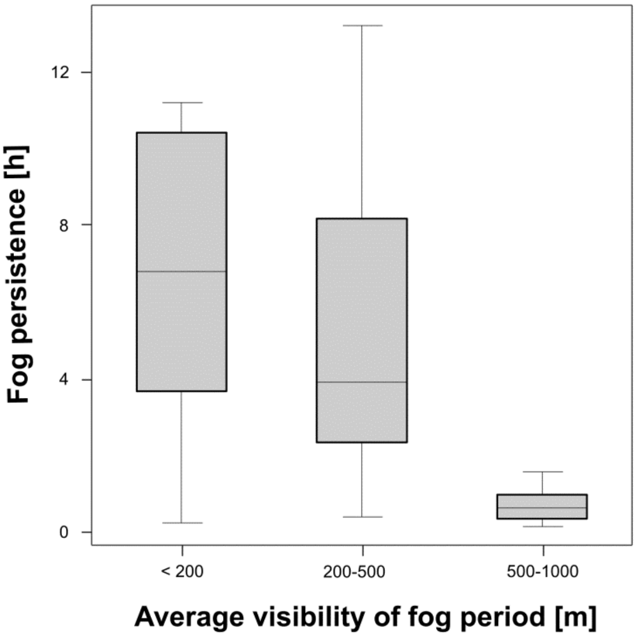

Figure 3.5. Box–Whisker plots of fog persistence shown for three fog density classes (dense fog: visibility <200 m, moderate fog: visibility between 200 and 500 m, light fog: visibility between 500 and 1000 m) in the dry season. Fog density (mean visibility) is calculated for each corresponding fog period

Median global radiation during morning fog is linearly correlated to corresponding values during fog-free morning hours (figure 3.6). 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).

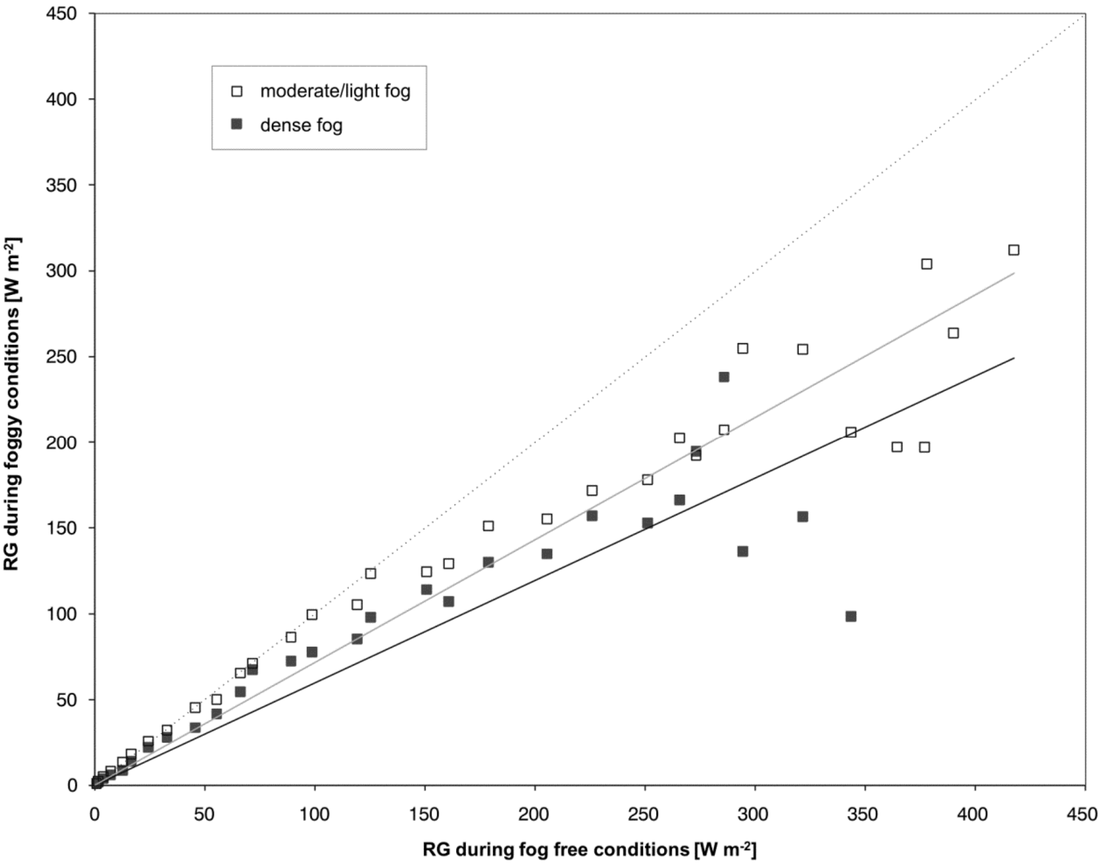

Figure 3.6. Median values of global solar radiation (RG) under foggy and fog-free conditions in the dry season. Data shown for 5-min intervals for the morning period from 6 to 9 LST (dotted line: 1:1 bisection); black line: regression line ($r^2 = 0.822$) for dense fog (visibility <200 m); grey line: regression line ($r^2 = 0.937$) for light and moderate fog (visibility 200–1000 m)

3.3.2 Relevant meteorological parameters of fog persistence

Significant correlations between atmospheric parameters and fog persistence were found for the dry season (table 3.1). 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 3.1. 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; $\alpha = 5\%$. Observation period 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 3.2). 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 (figure 3.3b). Also, no significant relationships between average fog density (visibility) and atmospheric parameters were found, neither for the rainy season nor for the dry season.

3.3.3 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 (figure 3.7).

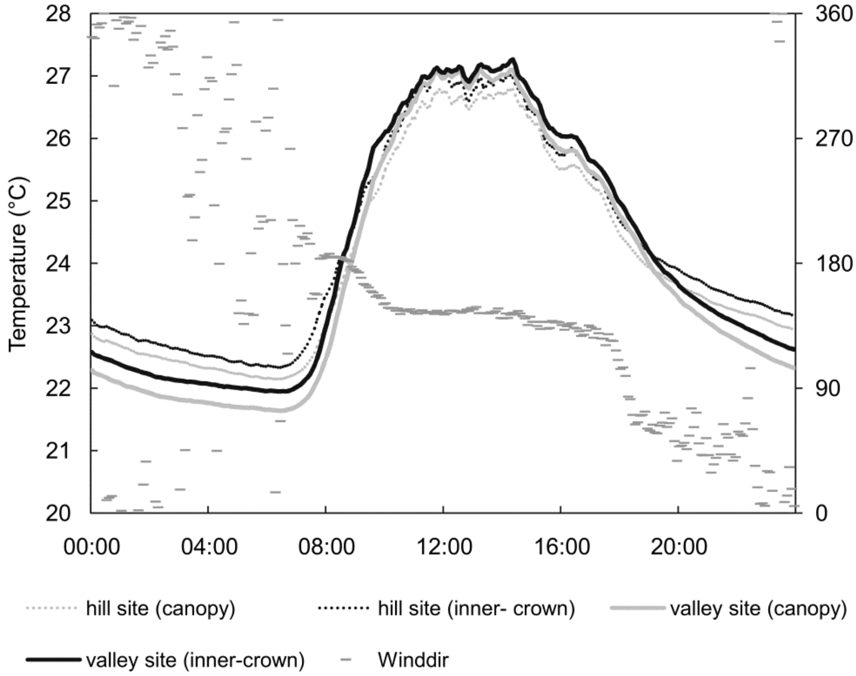

Figure 3.7. Average diurnal course of air temperature in two tree levels (canopy, innercrown) and wind direction (COPAS tower) on hill and in valley at the study site (field campaign March–April 2008)

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 innercanopy 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 figure 3.2). 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 figure 3.8). 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 ($>90\% < 0.5\mathrm{ms}-1$) 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 (figure 3.8) 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.

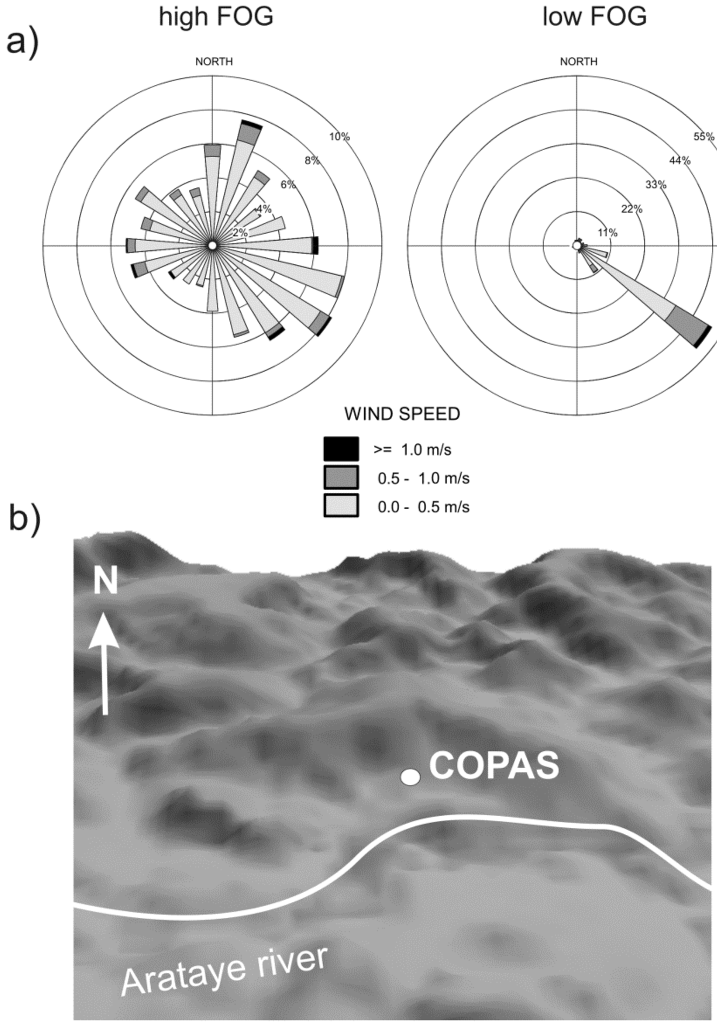

Figure 3.8.. a) Distribution of wind directions (COPAS tower) in dry season for days of long (>6 h, high fog) and short fog persistence (<2 h, low fog) in the evening hours (19:00–00:00 LST) and b) terrain map of the surroundings

3.3.4 Fog dynamics

Figure 3.9 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. All events show some clear similarities: (i) Fog formation is related to equally reduced air temperature leading to saturation, (ii) low wind speed (<0.2ms^{-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.

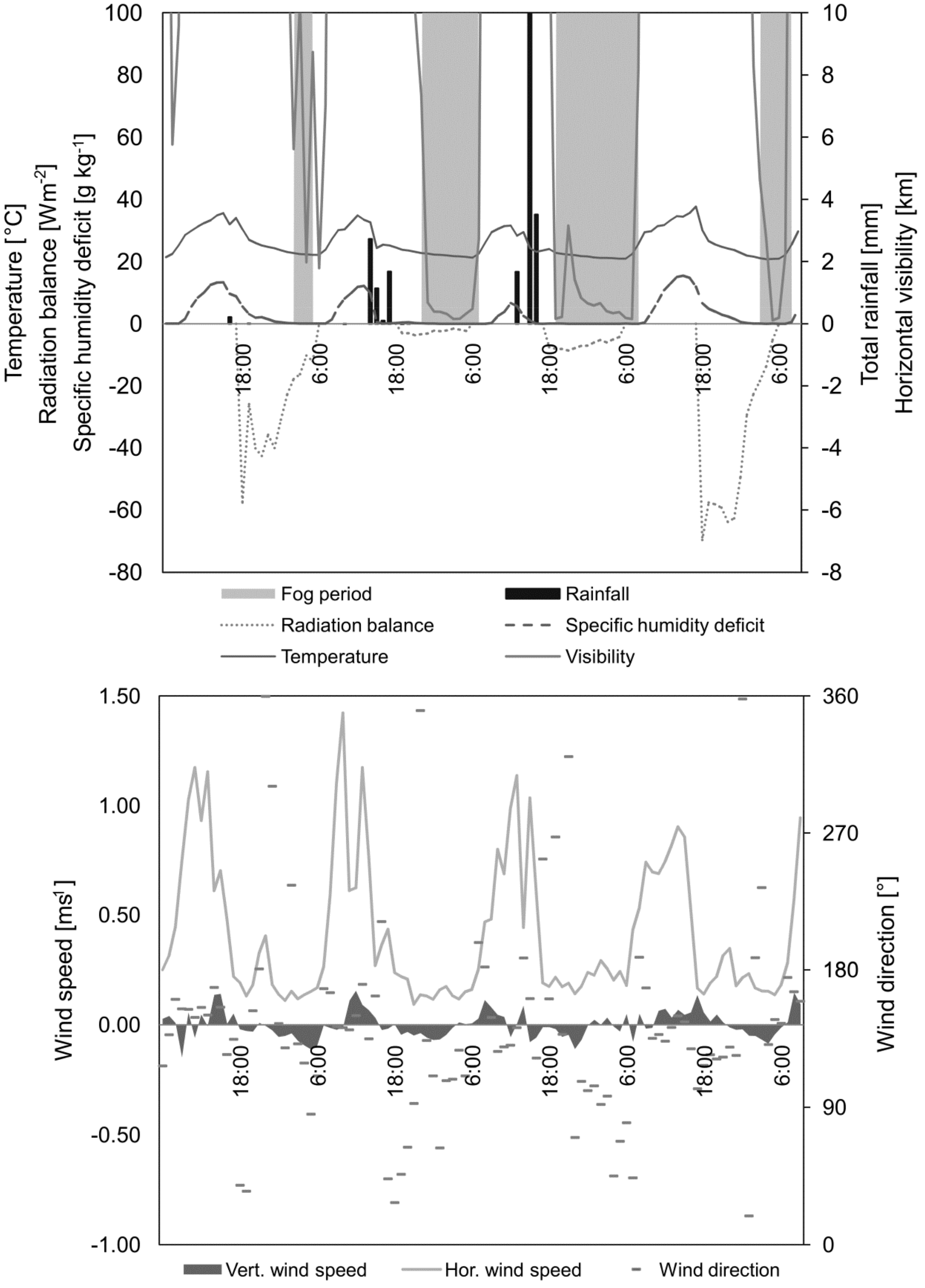

Figure 3.9. Fog dynamics for the period of 20–24 October 2007

3.3.5 Fog occurrence and species richness at LCF and 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 3.2). The valley forest is generally characterized by higher RH, lower temperatures and lower wind speed.

Table 3.2. 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 (8 trees per site). No visibility data (*) was available for the hill 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 (figure 3.10). 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.

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.

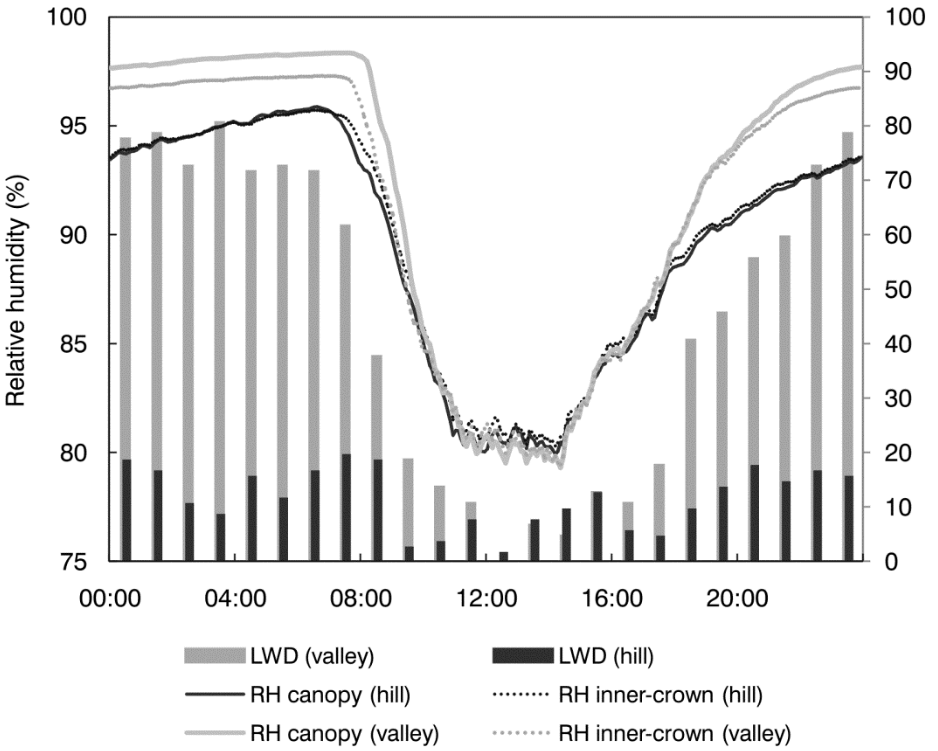

Figure 3.10. Mean diurnal course of relative humidity in two tree levels (canopy, inner crown) and leaf wetness duration (percentage of time per hour) on hill and in valley at the study site (field campaign March–April 2008)

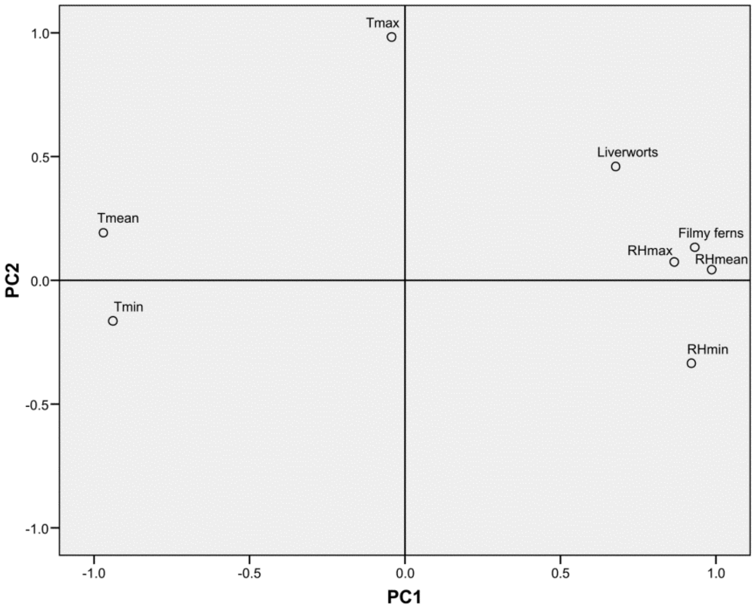

Figure 3.11. Component plot for the principal component analysis using air temperature, relative humidity and epiphyte diversity parameters

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 3.3 and the component plot is shown in figure 3.11. 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 3.3. 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

3.4 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 1000m 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 & 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 $<$ 100m) 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 & 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 & 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 & 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 awell-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 (Hoelscher 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 (750m 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 500m 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 & 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 visibily data. The future use of a fog collector (e.g.

Schemenauer & 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).

Acknowledgements

This project is funded by the German Research Foundation (DFG grants BE 1780/13-1 and GR 1588/12-1). We are very grateful to Philippe Gaucher (CNRS Guyane) for logistic help in French Guiana and maintenance of the COPAS Climate Station. Without his kind assistance the work could not have been realized. For field work assistance we thank Sebastian Achilles (University of Marburg), Felix Normann, Patrick Weigelt (University of Göttingen), and Michael Lakatos and Alexandra Pardow (University of Kaiserslautern). We thank two anonymous reviewers for valuable comments and suggestions.

References

Anhuf, D., Motzer, T., Rollenbeck, R., Schröder, B., Szarzynski, J., 1999. Water Budget of the Surumoni Crane Site (Venezuela). Selbyana 20, 179-185.

Ataroff, M.S., 1998. Importance of cloud-water in Venezuelan Andean cloud forest, in: Schemenauer, R.S., Bridgman, H.A. (Eds.), Proceedings of the First International Conference on Fog and Fog Collection. IDRC, Ottawa, Canada.

Bastable, H., Shuttleworth, W.J., Dallarosa, R.L.G., Fisch, G., Nobre, C.a., 1993. Observations of climate, albedo, and surface radiation over cleared and undisturbed amazonian forest. International Journal of Climatology 13, 783-796.

Bendix, J., 2002. A satellite-based climatology of fog and low-level stratus in Germany and adjacent areas. Atmospheric Research 64, 3-18.

Bendix, J., Rollenbeck, R., Goettlicher, D., Naubss, T., Fabian, P., 2008. Seasonality and diurnal pattern of very low clouds in a deeply incised valley of the eastern tropical Andes (South Ecuador) as observed by a cost-effective WebCam system. Meteorological Applications 15, 281-291.

Betts, A.K., Jakob, C., 2002. Evaluation of the diurnal cycle of precipitation, surface thermodynamics, and surface fluxes in the ECMWF model using LBA data. Journal of Geophysical Research-Atmospheres 107.

Bruijnzeel, L., 2001. Hydrology of tropical montane cloud forests: a reassessment. Land use and water resources research 1, 1-18.

Bruijnzeel, L.A., Eugster, W., Burkard, R., 2005. Fog as a hydrologic input, in: Anderson, M.G. (Ed.), Encyclopedia of Hydrological Sciences. John Wiley, Chichester, UK, pp. 559-582.

Cavelier, J., Goldstein, G., 1989. Mist and fog interception in elfin cloud forests in Colmbia and Venezuela. Journal of Tropical Ecology 5, 309-322.

Cereceda, P., Osses, P., Larrain, H., Farias, M., Lagos, M., Pinto, R., Schemenauer, R.S., 2002. Advective, orographic and radiation fog in the Tarapaca region, Chile. Atmospheric Research 64, 261-271.

Cermak, J., Bendix, J., 2008. A novel approach to fog/low stratus detection using Meteosat 8 data. Atmospheric Research 87, 279-292.

Chang, S.C., Lai, I.L., Wu, J.T., 2002. Estimation of fog deposition on epiphytic bryophytes in a subtropical montane forest ecosystem in northeastern Taiwan. Atmospheric Research 64, 159-167.

Charles-Dominique, P., 2001. The field station, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 1-8.

Charles-Dominique, P., Gottsberger, C., Freiberg, M.S., A.D., 2002. COPAS: a new permanent system to reach the forest canopy, in: Mitchell, A.W., Secoy, K., Jackson, T. (Eds.), The Global Canopy Handbook. Global Canopy Programme, Oxford, pp. 91-96.

Ehleringer, J.R., Dawson, T.E., 1992. Water uptake by Plants: perspectives from stable isotope composition. Plant Cell and Environment 15, 1073-1082.

Eldridge, R.G., 1971. The Relationship Between Visibility and Liquid Water Content in Fog. Journal of the Atmospheric Sciences 28, 1183-1186.

Eugster, W., 2008. Fog Research. Erde 139, 1-10.

Eugster, W., Burkard, R., Holwerda, F., Scatena, F.N., Bruijnzeel, L.A., 2006. Characteristics of fog and fogwater fluxes in a Puerto Rican elfin cloud forest. Agricultural and Forest Meteorology 139, 288-306.

Fedorova, N., Levit, V., Fedorov, D., 2008. Fog and stratus formation on the coast of Brazil. Atmospheric Research 87, 268-278.

Findlater, J., 1985. Field investigations of radiation fog formation at outstations. Meteorological Magazine 114, 187-201.

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, S.R., 2011. Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana. Biotropica 43, 591-596.

Gillespie, T.J., Kidd, G.E., 1978. Sensing Duration of Leaf Moisture Retention Using Electrical Impedance Grids. Canadian Journal of Plant Science 58, 179-187.

Gordon, C.A., Herrera, R., Hutchinson, T.C., 1994. Studies of fog events at two cloud forests near Caracas, Venezuela-I. frequency and duration of fog. Atmospheric Environment 28, 317-322.

Goulden, M.L., Miller, S.D., da Rocha, H.R., 2006. Nocturnal cold air drainage and pooling in a tropical forest. Journal of Geophysical Research-Atmospheres 111.

Gradstein, S.R., 2006. The lowland cloud forest of French Guiana – a liverwort hotspot. Cryptogamie Bryologie 27, 141-152.

Gradstein, S.R., Nadkarni, N.M., Kromer, T., Holz, I., Noske, N., 2003. A Protocol for Rapid and Representative Sampling of Vascular and Non-Vascular Epiphyte Diversity of Tropical Rain Forest. Selbyana 24, 105-111.

Gradstein, S.R., Obregon, A., Gehrig, C., Bendix, J., 2010. Tropical lowland cloud forest: a neglected forest type, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 329-338.

Grimaldi, M., Riéra, B., 2001. Geography and Climate, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 9-18.

Grubb, P.J., Whitmore, T.C., 1966. A Comparison of Montane and Lowland Rain Forest In Ecuador .2. Climate and Its Effects On Distribution and Physiognomy of Forests. Journal of Ecology 54, 303-&.

Gultepe, I., Tardif, R., Michaelides, S.C., Cermak, J., Bott, A., Bendix, J., Mueller, M.D., Pagowski, M., Hansen, B., Ellrod, G., Jacobs, W., Toth, G., Cober, S.G., 2007. Fog research: A review of past achievements and future perspectives. Pure and Applied Geophysics 164, 1121-1159.

Hamilton, L.S., Bruijnzee, L.A., 2000. Decision Time for Cloud Forests. UNESCO Division of Water Sciences, Paris.

Hamilton, L.S., Juvik, J.O., Scatena, F.N., 1995. Tropical Montane Cloud Forests. Springer Verlag, New York.

Hammond, D.S., 2005. Biophysical features of the Guiana shield, in: Hammond, D.S. (Ed.), Tropical forests of the Guiana shield: ancient forests in a modern world. CABI Publishing, Wallingford, pp. 15-194.

Harris, P.P., Huntingford, C., Cox, P.M., Gash, J.H.C., Malhi, Y., 2004. Effect of soil moisture on canopy conductance of Amazonian rainforest. Agricultural and Forest Meteorology 122, 215-227.

Holscher, D., Kohler, L., van Dijk, A., Bruijnzeel, L.A., 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. Journal of Hydrology 292, 308-322.

Johansson, D., 1974. Ecology of vascular epiphytes in West African rain forest.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R., Joseph, D., 1996. The NCEP/NCAR 40-year reanalysis project. Bulletin of the American Meteorological Society 77, 437-471.

Kamara, S.I., 1989. Diurnal and seasonal variations of fog over Sierra Leone. Singapore Journal of Tropical Geography 10, 160-169.

Klockow, D., Targa, H.J., 1998. Performance and results of a six-year German Brazilian research project in the industrial area of Cubatao/SP, Brazil. Pure and Applied Chemistry 70, 2287-2293.

Koehler, L., Tobon, C., Frumau, K.F.A., Bruijnzee, L.A., 2007. Biomass and water storage dynamics of epiphytes in old-growth and secondary montane cloud forest stands in Costa Rica. Plant Ecology 193, 171-184.

Komatsu, H., Yoshida, N., Takizawa, H., Kosaka, I., Tantasirin, C., Suzuki, M., 2003. Seasonal trend in the occurrence of nocturnal drainage flow on a forested slope under a tropical monsoon climate. Boundary-Layer Meteorology 106, 573-592.

Kruijt, B., Malhi, Y., Lloyd, J., Norbre, A.D., Miranda, A.C., Pereira, M.G.P., Culf, A., Grace, J., 2000. Turbulence statistics above and within two Amazon rain forest canopies. Boundary-Layer Meteorology 94, 297-331.

Kumagai, T., Saitoh, T.M., Sato, Y., Takahashi, H., Manfroi, O.J., Morooka, T., Kuraji, K., Suzuki, M., Yasunari, T., Komatsu, H., 2005. Annual water balance and seasonality of evapotranspiration in a Bornean tropical rainforest. Agricultural and Forest Meteorology 128, 81-92.

Lee, Y.H., Mahrt, L., 2005. Effect of stability on mixing in open canopies. Agricultural and Forest Meteorology 135, 169-179.

Liang, Y.-L., Lin, T.-C., Hwong, J.-L., Lin, N.-H., Wang, C.-P., 2009. Fog and Precipitation Chemistry at a Mid-land Forest in Central Taiwan. Journal of Environmental Quality 38, 627-636.

Liu, W.J., Liu, W.Y., Li, P.J., Gao, L., Shen, Y.X., Wang, P.Y., Zhang, Y.P., Li, H.M., 2007. Using stable isotopes to determine sources of fog drip in a tropical seasonal rain forest of Xishuangbanna, SW China. Agricultural and Forest Meteorology 143, 80-91.

Liu, W.J., Wang, P.Y., Liu, W.Y., Li, J.T., Li, P.J., 2008. The importance of radiation fog in the tropical seasonal rain forest of Xishuangbanna, south-west China. Hydrology Research 39, 79-87.

Lyons, T.J., 2002. Clouds prefer native vegetation. Meteorology and Atmospheric Physics 80, 131-140.

Mahrt, L., Lee, X.H., Black, A., Neumann, H., Staebler, R.M., 2000. Nocturnal mixing in a forest subcanopy. Agricultural and Forest Meteorology 101, 67-78.

Mitchell, A.W., Secoy, K., Jackson, T., 2002. The Global Canopy Handbook. Techniques of Access and Study in the Forest Roof. Global Canopy Programme, Oxford.

Nadkarni, N.M., 1984. Epiphyte Biomass and Nutrient Capital of a Neotropical Elfin Forest. Biotropica 16, 249-256.

Nadkarni, N.M., 2010. Potential effects of global climate change on epiphytes in a tropical montane cloud forest: an experimental study from Monteverde, Costa Rica, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 557-565.

Oliveira, A.P., Fitzjarrald, D.R., 1993. The Amazon River breeze and the local boundary layer: I. Observations. Boundary - Layer Meteorology 63, 141-162.

Oliveira, A.P., Fitzjarrald, D.R., 1994. The Amazon River breeze and the local boundary layer: II. Linear analysis and modelling. Boundary - Layer Meteorology 67, 75-96.

Olivier, J., 1995. Spatial-distribution of Fog In the Namib. Journal of Arid Environments 29, 129-138.

Osses, P., Barria, C., Farias, M., Cereceda, P., 2005. La nube estratocumulo an Tarapaca, Chile. Validacion de imagenes GOES mediante observacion en tiempo real. Rev. de Geogr. Norte Grande 33, 131-143.

Pasricha, P.K., Gera, B.S., Shastri, S., Maini, H.K., John, T., Ghosh, A.B., Tiwari, M.K., Garg, S.C., 2003. Role of the water vapour greenhouse effect in the forecasting of fog occurrence. Boundary-Layer Meteorology 107, 469-482.

Poncy, O., Sabatier, D., Prevost, M.F., Hardy, I., 2001. The lowland forest: structure and tree species diversity, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 31-46.

Proctor, M.C.F., 2003. Comparative ecophysiological measurements on the light responses, water relations and desiccation tolerance of the filmy ferns Hymenophyllum wilsonii Hook. and H. tunbrigense (L.) Smith. Annals of Botany 91, 717-727.

Pypker, T.G., Unsworth, M.H., Bond, B.J., 2006. The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 36, 809-818.

Richards, P.W., Walsh, R.P.D., Baillie, I.C., Greig-Smith, P., 1996. The tropical rain forest an ecological study (2nd edition). Cambridge University Press, Cambridge.

Ritter, A., Regalado, C.M., Aschan, G., 2009. Fog reduces transpiration in tree species of the Canarian relict heath-laurel cloud forest (Garajonay National Park, Spain). Tree Physiology 29, 517-528.

Roach, W.T., 1994. Back to basics: Fog: Part 1 - definitions and basic physics. Weather 49, 411-415.

Rollenbeck, R., 2002. Wasser- und Energiehaushalt eines neotropischen Tieflandregenwaldes. Mannh. Geogr. Arb 55, 1-173.

Rollenbeck, R., Fabian, P., Bendix, J., 2006. Precipitation dynamics and chemical properties in tropical mountain forests of Ecuador. Advances in Geosciences 6, 73-76.

Sabatier, D., Prevost, M.F., 1990. Quelques données sur la composition floristique et la diversité des peuplements forestiers de Guyane francaise. Bois et Forets des Tropiques 219, 31-56.

Schemenauer, R.S., Cereceda, P., 1994. A Proposed Standard Fog Collector For Use In High-elevation Regions. Journal of Applied Meteorology 33, 1313-1322.

Schilling, V.K., 1991. A Parameterization For Modeling the Meteorological Effects of Tall Forests - A Case-study of A Large Clearing. Boundary-Layer Meteorology 55, 283-304.

Sentelhas, P.C., Dalla Marta, A., Orlandini, S., Santos, E.A., Gillespie, T.J., Gleason, M.L., 2008. Suitability of relative humidity as an estimator of leaf wetness duration. Agricultural and Forest Meteorology 148, 392-400.

Sentelhas, P.C., Gillespie, T.J., Santos, E.A., 2007. Leaf wetness duration measurement: comparison of cylindrical and flat plate sensors under different field conditons. International Journal of Biometeorology 51, 265-273.

Shanyengana, E.S., Henschel, J.R., Seely, M.K., Sanderson, R.D., 2002. Exploring fog as a supplementary water source in Namibia. Atmospheric Research 64, 251-259.

Shuttleworth, W.J., 1977. The exchange of wind-driven fog and mist between vegetation and the atmosphere. Boundary-Layer Meteorology 12, 463-489.

Stewart, D.A., Essenwanger, O.M., 1982. A survey of fog and related optical propagation characteristics. Reviews of Geophysics 20, 481-495.

Stuntz, S., Simon, U., Zotz, G., 2002. Rainforest air-conditioning: the moderating influence of epiphytes on the microclimate in tropical tree crowns. International Journal of Biometeorology 46, 53-59.

Szarzynski, J., Anhuf, D., 2001. Micrometeorological conditions and canopy energy exchanges of a neotropical rain forest (Surumoni-Crane Project, Venezuela). Plant Ecology 153, 231-239.

Van der Meer, P.J., Bongers, F., 2001. Tree-falls and canopy gaps: patterns of natural disturbance, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 243-250.

Van der Molen, M.K., 2002. Meteorological impacts on land use change in the maritime tropics. Free University of Amsterdam.

Veneklaas, E.J., Zagt, R.J., Vanleerdam, A., Vanek, R., Broekhoven, A.J., Vangenderen, M., 1990. Hydrological Properties of the Epiphyte Mass of A Montane Tropical Rain-forest, Colombia. Vegetatio 89, 183-192.

Villegas, J.C., Tobon, C., Breshears, D.D., 2008. Fog interception by non-vascular epiphytes in tropical montane cloud forests: dependencies on gauge type and meteorological conditions. Hydrological Processes 22, 2484-2492.

Wanner, H., Kunz, S., 1983. Climatology of fog and cold air layers in the swiss prealpine basins using weather satellite pictures. Archives for Meteorology Geophysics and Bioclimatology Series B-Theoretical and Applied Climatology 33, 31-56.

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

This chapter is published in *Biotropica*, 43, 591-596 (2011).
Received: 25 February 2010 / Accepted: 26 September 2010

http://dx.doi.org/10.1111/j.1744-7429.2010.00745.x

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

Gehrig-Downie, C. (1), Obregon, A. (2), J. Bendix (2) and Gradstein, S.R. (1,3)

(1) Department of Systematic Botany, Institute of Plant Sciences, University of Goettingen, Germany
(2) Laboratory for Climatology and Remote Sensing, Department of Geography, University of Marburg, Germany
(3) Museum Naturelle d'Histoire Naturelle, Dept. Systematique et Evolution, Paris, France

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.

4.1 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.

4.2 Methods

4.2.1 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).

4.2.2 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.

4.2.3 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.

4.2.4 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.

4.2.5 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 SS-levels of significance were recognized: $P<0.05$, $P<0.01$, and $P<0.001$.

4.3 Results

4.3.1 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: x̄= 3.3 g/m^2, SD= 11.1 g/m2). The difference was significant for trunks (*P*<0.01) and crowns (*P*<0.001).

4.3.2 Epiphyte cover

Throughout all height zones, total epiphyte cover in LCF exceeded that in LRF significantly (figure 4.1, *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 (figure 4.2, lichens: *P*<0.01; bryophytes: *P*<0.001; angiosperms: *P*<0.001).

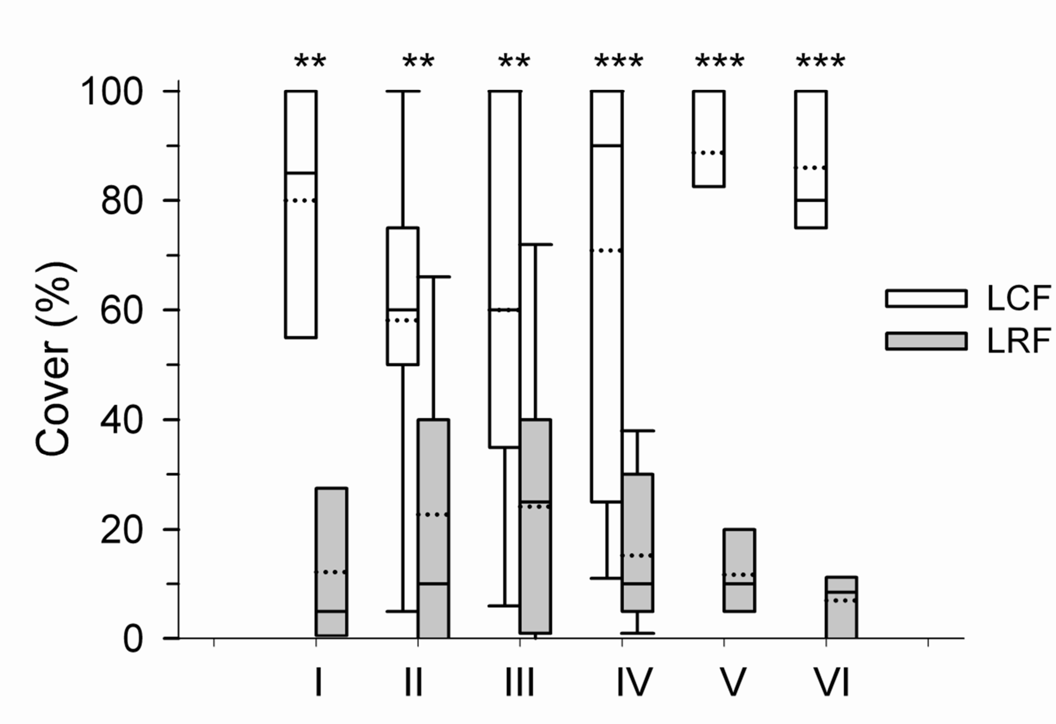

Figure 4.1. Abundance of all epiphytes in percentage of bark coverage in lowland cloud forest (LCF) (white) and lowland rain forest (LRF) (gray) in different height zones (I–VI) on the tree; N= 24 trees per forest type. Boxes indicate upper and lower quartile of data, unbroken line gives the median, 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

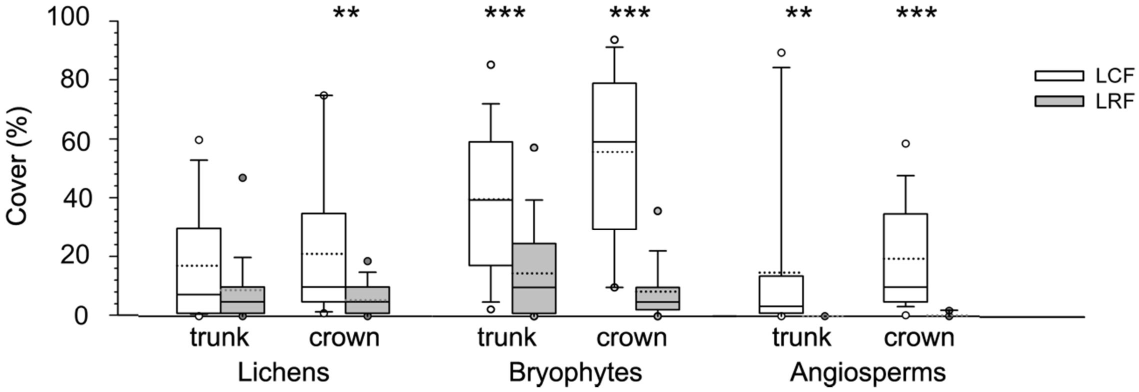

Figure 4.2. Abundance of epiphytic lichens, bryophytes, and angiosperms in percentage of bark coverage on trunks (zones I–III) and crowns (zones IV–VI) in lowland cloud forest (LCF) (white) and lowland rain forest (LRF) (gray); N= 72 estimates per forest type. Boxes indicate upper and lower quartile 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, *$P<0.05$, **$P<0.01$, ***$P<0.001$

4.3.3 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 4.1). 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 ($T_{\mathrm{LCF}} = 26$°C; $T_{\mathrm{LRF}} = 27$°C; $\mathrm{RH}_{\mathrm{LCF}} = 74\%$; $\mathrm{RH}_{\mathrm{LRF}} = 72\%$). Temperature was lowest around 0400 h ($T_{\mathrm{LCF}} =22$°C; $T_{\mathrm{LRF}} = 21$°C) when air humidity was highest ($\mathrm{RH}_{\mathrm{LCF}} = 97\%$; $\mathrm{RH}_{\mathrm{LRF}} = 95\%$). 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 (figure 4.3).

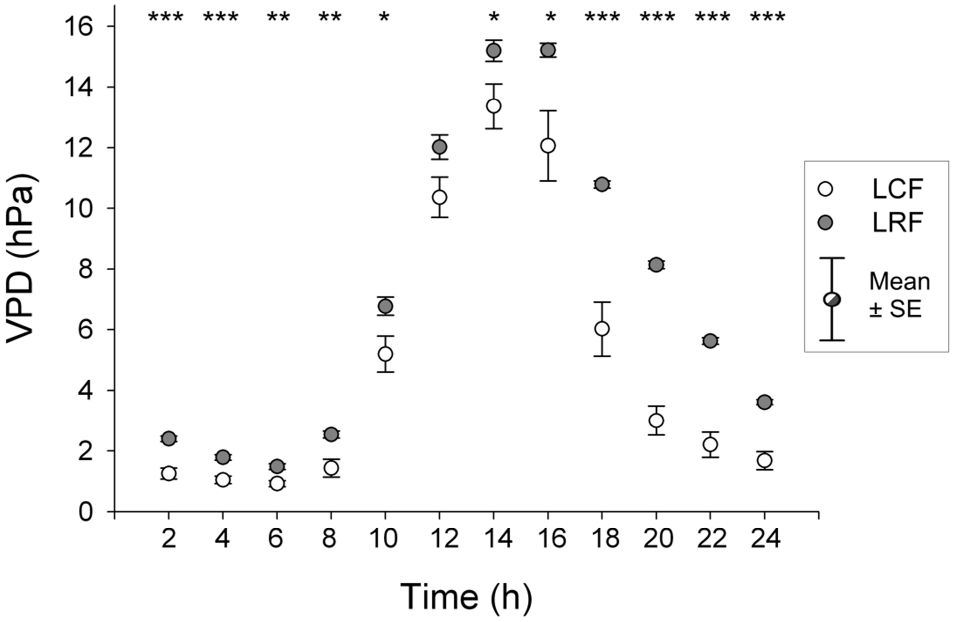

Figure 4.3. Diurnal course of vapor pressure deficit (VPD), calculated using hourly mean temperature and air humidity during 48 d of the dry season in lowland cloud forest (LCF) (white circles) and lowland rain forest (LRF) (gray circles). Levels of significance are obtained with unpaired t-tests and shown by asterisks, (*P<0.05, **P<0.01, ***P<0.001

Table 4.1 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

4.3.4 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 (figure 4.4). 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.

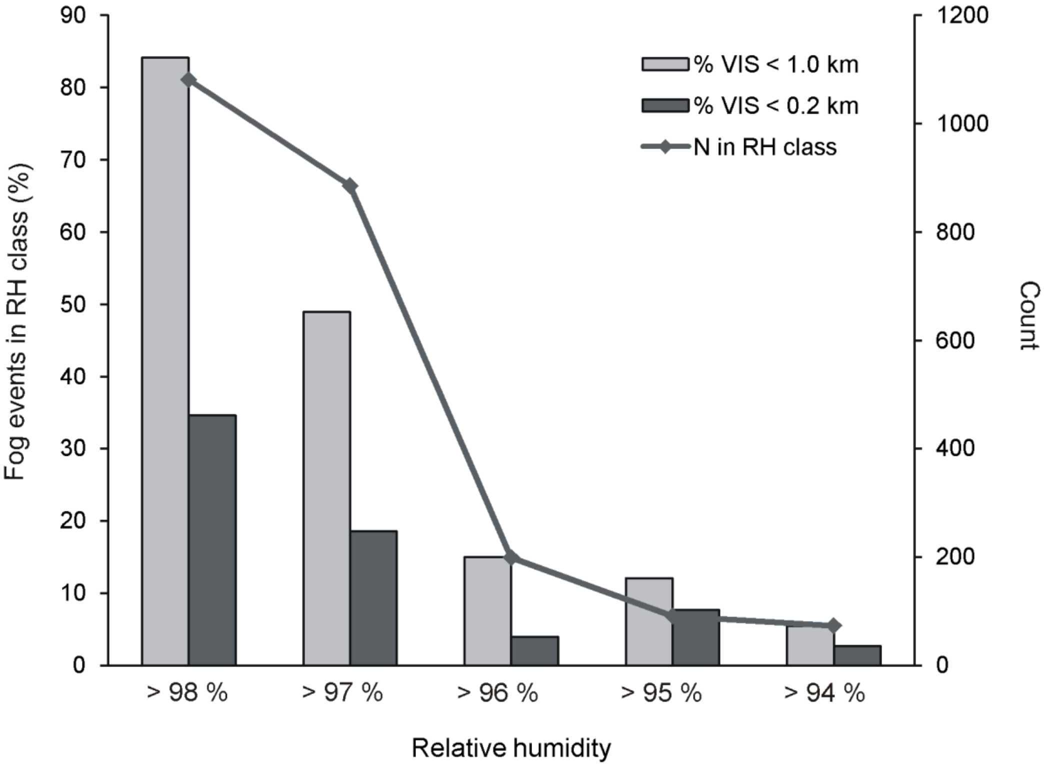

Figure 4.4. Relative (in percentage) and absolute (in N= number of total events) occurrence of light fog (visibility<1 km, light gray) and dense fog (visibility<0.2 km, dark gray) for classes of high relative humidity (RH) in lowland cloud forest at Canopy Operating Permanent Access System station, June–July 2008

4.4 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.

Acknowledgements

We are very grateful to Dr. Jean-Jacques de Granville (IRD France) and Philippe Gaucher (CNRS Guyane) for logistic support, to Dr. Michael Kessler (University of Zürich) for methodological advice, and to Dr. Maike Bader (University of Oldenburg) for references. For fieldwork assistance, we kindly acknowledge Felix Normann, Patrick Weigelt and Monika Hofstaetter-Müncheberg (University of Göttingen), and Dr. Rütger Rollenbeck and Sebastian Achilles (University of Marburg). This project is funded by the German Research Foundation (DFG grants GR 1588/13–1 and BE 1780/ 13–1).

References

Bayton, H.W., 1969. The ecology of an elfin forest in Puerto Rico. 2. The microclimate of Pico del Oeste. J. Arnold Arbor 49, 419-430.

Bruijnzeel, L.A., Eugster, W., Burkard, R., 2005. Fog as an input to the hydrological cycle, in: Anderson, M.G., McDonnell, J.J. (Eds.), Encyclopedia of hydrological sciences. John Wiley, Chichester, UK, pp. 559-582.

Coxson, D., Nadkarni, N.M., 1995. Ecological roles of epiphytes in nutrient cycles of forest ecosystems, in: Lowman, M., Nadkarni, N.M. (Eds.), Forest canopies. Academic Press, San Diego, California, pp. 495-546.

de Granville, J.J., 1986. Flore et vegetation. Saga, Cayenne, French Guiana.

de Granville, J.J., 1988. Phytogeographical characteristics of the Guinan forests. Taxon 37, 578-594.

de Granville, J.J., 2001. Végétation, in: Barret, J. (Ed.), Altlas illustré de la Guyane. IRD Editions, Paris, France, pp. 52-55.

Frahm, J.P., 1990. Bryophyte phytomass in tropical ecosystems. Botanical Journal of the Linnean Society 104, 23-33.

Frahm, J.P., Gradstein, S.R., 1991. An altitudinal zonation of tropical rain forests using bryophytes. Journal of Biogeography 18, 669-678.

Freiberg, M., Freiberg, E., 2000. Epiphyte diversity and biomass in the canopy of lowland and montane forests in Ecuador. Journal of Tropical Ecology 16, 673-688.

Gradstein, S.R., 2006. The lowland cloud forest of French Guiana - a liverwort hotspot. Cryptogamie Bryologie 27, 141-152

Gradstein, S.R., Nadkarni, N.M., Kromer, T., Holz, I., Noske, N., 2003. A Protocol for Rapid and Representative Sampling of Vascular and Non-Vascular Epiphyte Diversity of Tropical Rain Forest. Selbyana 24, 105-111.

Gradstein, S.R., Obregon, A., Gehrig, C., Bendix, J., 2010. Tropical lowland cloud forest: a neglected forest type, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 329-338.

Green, T.G.A., Nash III, T.H., Lange, O.L., 2008. Physiological ecology of carbon dioxide exchange, in: Nash III, T.H. (Ed.), Lichen biology. Cambridge University Press, Cambridge, UK, pp. 152-181.

Grubb, P.J., Whitmore, T.C., 1966. A comparison of montane and lowland rain forest in Ecuador: II. The climate and its effects on the distribution and physiognomy of the forests. Journal of Ecology 54, 303-&.

Hietz-Seifert, U., Hietz, P., Guevara, S., 1996. Epiphyte vegetation and diversity on remnant trees after forest clearance in southern Veracruz, Mexico. Biological Conservation 75, 103-111.

Hofstede, R.G.M., Wolf, J.H.D., Benzing, D.H., 1993. Epiphyte biomass and nutrient status of a Colombian upper montane rain forest. Selbyana 14, 3-11.

Holscher, D., Kohler, L., van Dijk, A., Bruijnzeel, L.A., 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. Journal of Hydrology 292, 308-322.

Hosokawa, T., Odani, N., Tagawa, T., 1964. Causality of the distribution of corticulous species in forests with special reference to the physio-ecological approach. Bryologist 67, 396-411.

Ingram, S.W., Nadkarni, N.M., 1993. Composition and Distribution of Epiphytic Organic Matter in a Neotropical Cloud Forest, Costa Rica. Biotropica 25, 370-383.

Lambers, H., Chapin III, F.S., Pons, T.L., 1998. Plant physiological ecology. Springer, New York.

Lange, O.L., Budel, B., Heber, U., Meyer, A., Zellner, H., Green, T.G.A., 1993. Temperate rain forest lichens in New Zealand: high thallus water content can severely limit photosynthetic Co2 exchange. Oecologia 95, 303-313.

Lange, O.L., Budel, B., Meyer, A., Zellner, H., Zotz, G., 2000. Lichen carbon gain under tropical conditions: water relations and CO2 exchange of three Leptogium species of a lower montane rainforest in Panama. Flora 195, 172-190.

Mori, S.A., Boom, B.M., 1987. The forest, in: Mori, S.A. (Ed.), The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana, pp. 9-29.

Nadkarni, N.M., 1981. Canopy roots: Convergent evolution in rainforest nutrient cycles. Science 214, 1023-1024.

Nadkarni, N.M., 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16, 249-256.

Nadkarni, N.M., Longino, J.T., 1990. Invertebrates in Canopy and Ground Organic Matter in a Neotropical Montane Forest, Costa Rica. Biotropica 22, 286-289.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S.R., Sipman, H.J.M., Obregon, A., Bendix, J., 2010. Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators 10, 1111-1118.

Proctor, M.C.F., 2000. Physiological ecology, in: Shaw, A.J., Goffinet, B. (Eds.), Bryophyte biology. Cambridge University Press, Cambridge, UK, pp. 225-247.

Richards, P.W., 1984. The ecology of tropical forest bryophytes, in: Schuster, R.M. (Ed.), New manual of bryology. Hattori Botanical Laboratory, Nichinan, Japan, pp. 1233-1270.

Richards, P.W., Walsh, R.P.D., Baillie, I.C., Greig-Smith, P., 1996. The tropical rain forest an ecological study (2nd edition). Cambridge University Press, Cambridge.

Schimper, A.F.W., 1888. Die epiphytische Vegetation Amerikas, Jena.

Seifriz, W., 1924. The altitudinal distribution of lichens and mosses on Mt Gedeh, Java. Journal of Ecology 12, 307-313.

Sillett, S.C., Antoine, M.E., 2004. Lichens and bryophytes in forest canopies, in: Lowman, M.D., Rinker, H.B. (Eds.), Forest canopies (2nd edition). Academic Press, New York, pp. 151-174.

van Reenen, G.B.A., Gradstein, S.R., 1983. Studies on Colombian Cryptograms XX. A transect analysis of the bryophyte vegetation along an altitudinal gradient on the Sierra Nevada de Santa Marta, Colombia. Acta Botanica Neerlandica 32, 163-175.

Veneklaas, E.J., Vanek, R., 1990. Rainfall interception in two tropical montane rain forests, Colombia. Hydrological Processes 4, 311-326.

Veneklaas, E.J., Zagt, R.J., Vanleerdam, A., Vanek, R., Broekhoven, A.J., Vangenderen, M., 1990. Hydrological properties of the epiphyte mass of a montane tropical rain forest, Colombia. Vegetatio 89, 183-192.

Wolf, J.H.D., 1993. Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. Annals of the Missouri Botanical Garden 80, 928-960.

Yanoviak, S.P., Nadkarni, N.M., Solano-J, R., 2007. Arthropod assemblages in epiphyte mats of Costa Rican cloud forests. Biotropica 39, 202-210.

Zotz, G., Budel, B., Meyer, A., Zellner, H., Lange, O.L., 1998. In situ studies of water relations and CO2 exchange of the tropical macrolichen, Sticta tomentosa. New Phytologist 139, 525-535.

Zotz, G., Schultz, S., Rottenberger, S., 2003. Are tropical lowlands a marginal habitat for macrolichens? Evidence from a field study with Parmotrema endosulphureum in Panama. Flora 198, 71-77.

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

This chapter is published in *Ecotropica*, 18, 35-44 (2012).

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

Gehrig-Downie, C. (1), Marquardt, J. (2), Obregon, A.(3),
J. Bendix (3) and Gradstein, S.R. (1,4)

(1) Department of Systematic Botany, Institute of Plant Sciences, University of Goettingen, Germany
(2) Biocenter Martinsried, University of Munich, Germany
(3) Laboratory for Climatology and Remote Sensing, Department of Geography, University of Marburg, Germany
(4) Museum Naturelle d'Histoire Naturelle, Dept. Systematique et Evolution, Paris, France

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.

5.1 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.

5.2 Methods

5.2.1 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.

5.2.2 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 5.1).

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.*

Table 5.1. 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	

5.2.3 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.

5.2.4 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.

5.3 Results

5.3.1 Species richness

On 32 trees we collected in total 9 species of Hymenophyllaceae (2 genera), 9 in LCF and 4 in LRF (table 5.2). *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 5.2. 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

5.3.2 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.

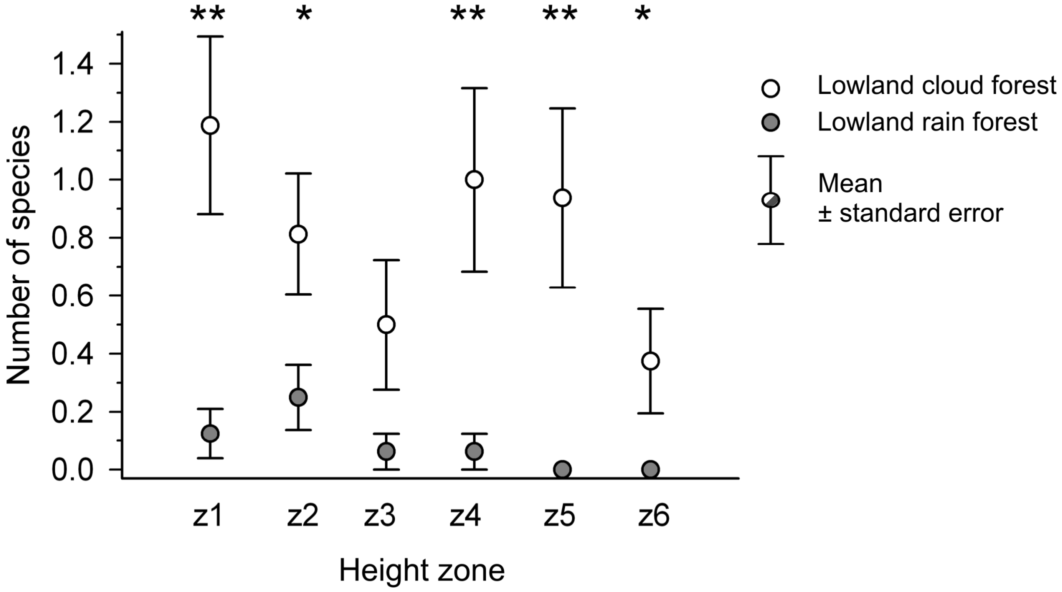

Figure 5.1. Number of epiphytic Hymenophyllaceae species per height zone in lowland cloud forest and lowland rain forest; n = 16 trees per forest type. Asterisks indicate level of probability calculated with unpaired t-test (* $p<0.05$, ** $p<0.01$). z1 = trunk base, z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy

5.3.3 Vertical distribution

The vertical distribution of the species on trees in the two forest types was remarkably different (figure 5.1). 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*).

5.3.4 Canopy microclimate

During 60 days in the dry season the diurnal mean relative humidity (RH) was positively correlated with species diversity of filmy ferns (figure 5.2; $r^2 = 0.81$, $P<0.001$). Estimated mean daily evaporation was highest in the outer canopy in LRF, while smallest values were related to the inner crown in LCF (figure 5.3). 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 (figure 5.4). Average daily wind speed was 0.65 m s^{-1} in LRF and 0.17 m s^{-1} in LCF.

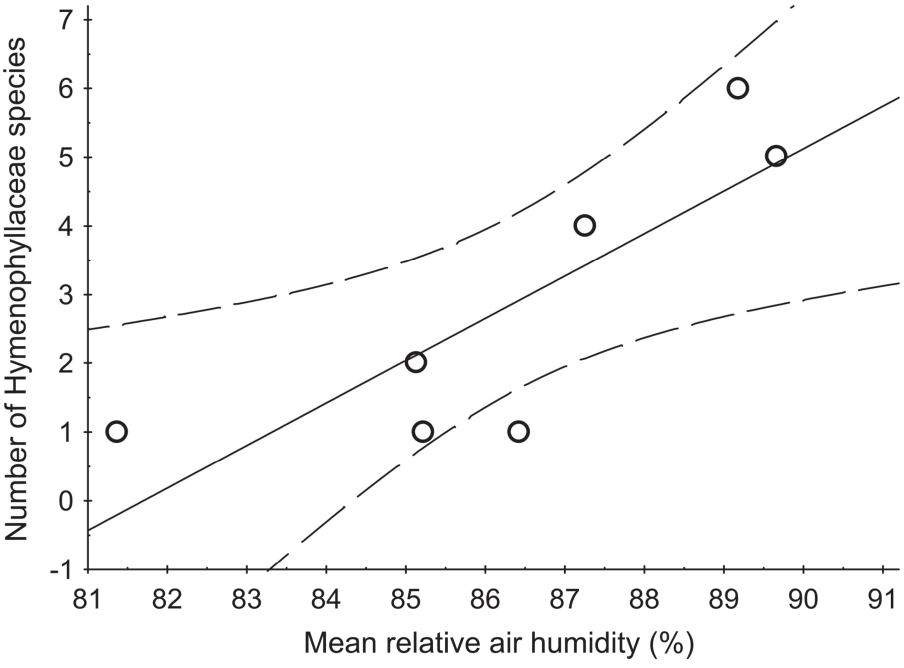

Figure 5.2. Correlation between number of Hymenophyllaceae species per tree and mean diurnal relative air humidity for 60 days of the dry season in the canopy of 7 trees in lowland cloud forest. Unbroken line indicates the regression, dotted line the 0.95 confidence interval. $R = 0.82$, $P<0.05$

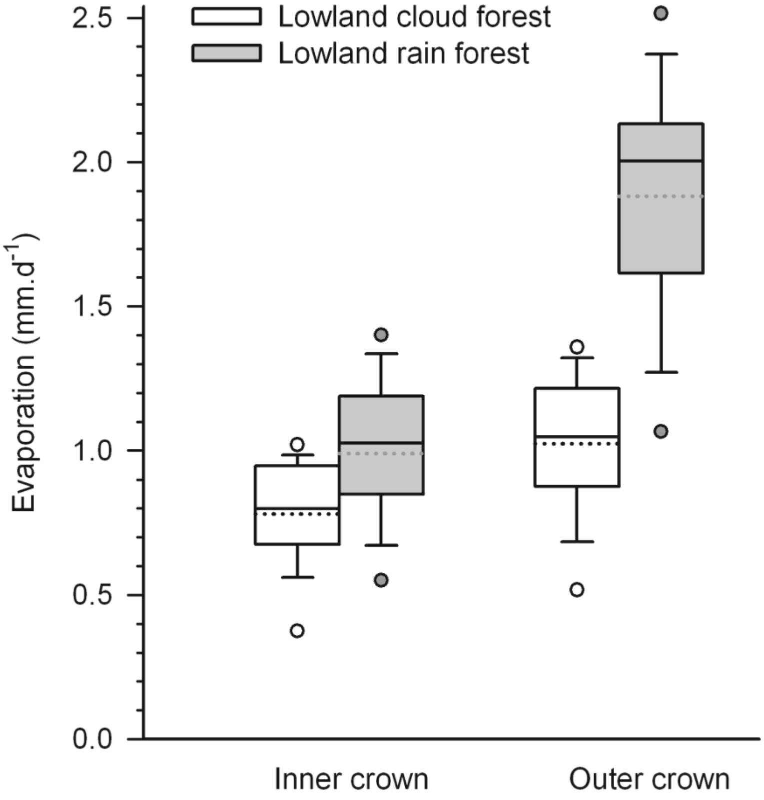

Figure 5.3. Evaporation per day in the inner and outer canopy of lowland cloud forest and lowland rain forest, calculated using a simplified version of the Penman equation provided by Valiantzas (2006), incorporating daily global radiation, relative humidity, air temperature and the latitude of the site. 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

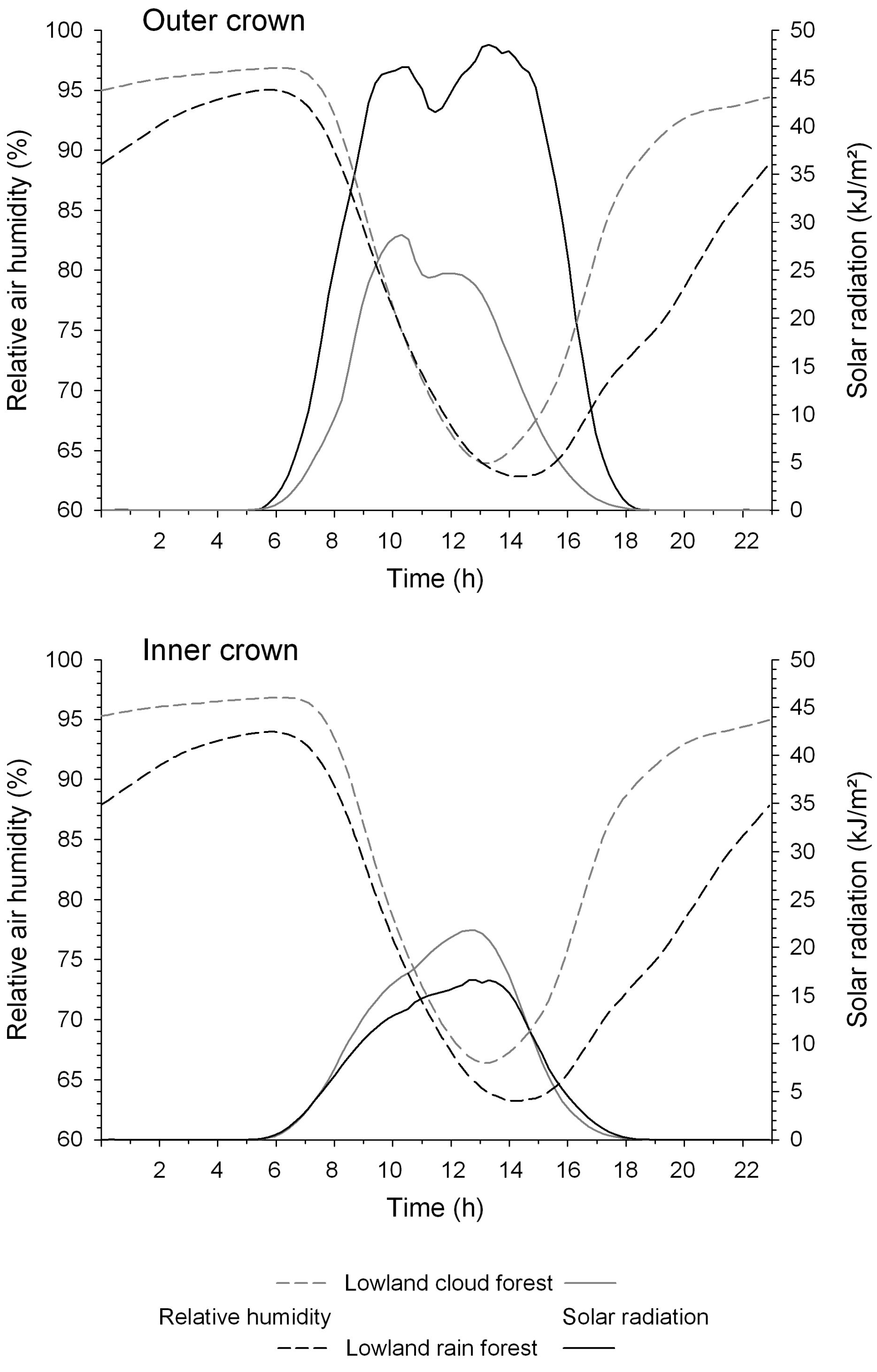

Figure 5.4. Mean diurnal course of global radiation and relative humidity in lowland cloud forest and lowland rain forest in the inner and outer canopy during 22 September – 24 October 2007

5.4 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 (figure 5.1). 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 5.1).

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 (figure 5.2).

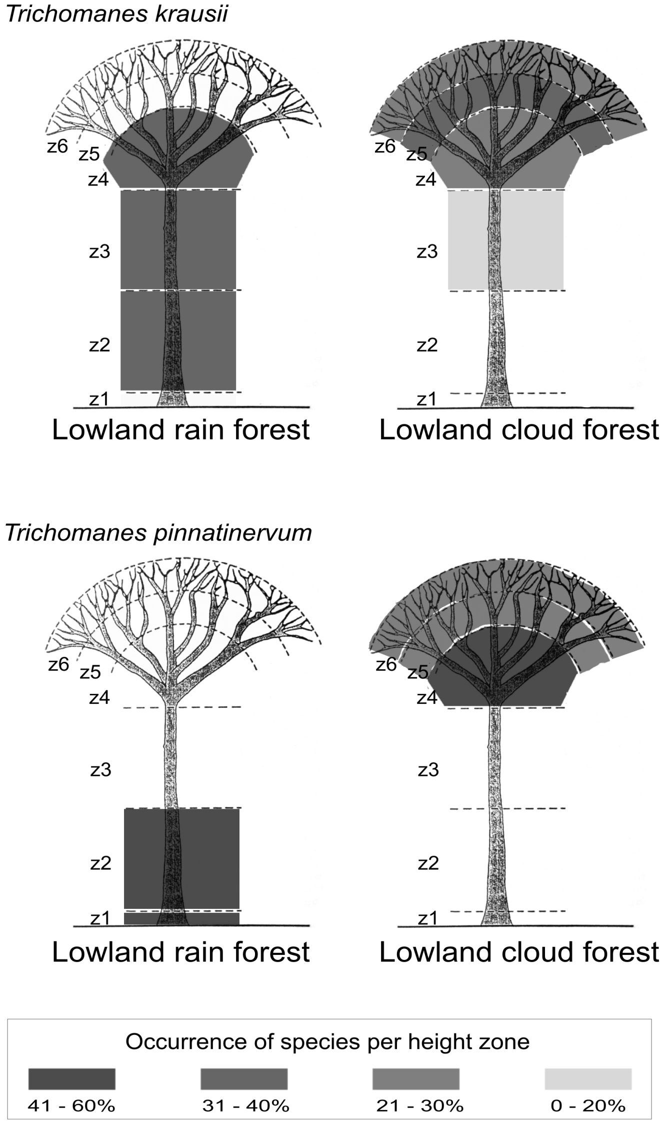

Figure 5.5. Vertical distribution of two Hymenophyllaceae species in lowland rain forest and lowland cloud forest, expressed by percent occurrence per zone as compared with occurrence on whole trees. z2 = lower trunk, z3 = upper trunk, z4 = lower canopy, z5 = middle canopy, z6 = outer canopy

Interestingly, we found that species restricted to trunks in the understory of LRF occurred in the canopy of LCF (table 5.1; figure 5.5). 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.

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.

Acknowledgments

We are very grateful to Dr. Jean-Jacques de Granville (IRD France) and Philippe Gaucher (CNRS Guyane) for logistic support and to Dr. Michael Kessler (University of Zürich) for methodological advice and help with identification of species. For field work assistance we kindly acknowledge Felix Normann, Patrick Weigelt and Monika Hofstaetter-Müncheberg (University of Göttingen). This project was funded by the German Research Foundation (DFG grants GR 1588/13-1 and BE 1780/13-1).

References

Acebey, A., Gradstein, S.R., Kromer, T., 2003. Species richness and habitat diversification of bryophytes in submontane rain forest and fallows of Bolivia. Journal of Tropical Ecology 19, 9-18.

Banaticla, M.C.N., Buot, I.E., 2005. Altitudinal zonation of pteridophytes on Mt. Banahaw de Lucban, Luzon Island, Philippines. Plant Ecology 180, 135-151.

Benzing, D.H., 1990. Vascular Epiphytes. Cambridge University Press, Cambridge.

Buck, W.R., 2003. Guide to the plants of Central French Guiana: Part 3. Mosses.

Cardelús, C.L., 2007. Vascular epiphyte communities in the inner-crown of Hyeronima alchorneoides and Lecythis ampla at La Selva Biologial Station, Costa Rica. Biotropica 39, 171-176.

Cardelus, C.L., Chazdon, R.L., 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. Biotropica 37, 238-244.

Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. Ecology Letters 8, 148-159.

Cornelissen, J.H.C., Tersteege, H., 1989. Distribution and ecology of epiphytic bryophytes and lichens in dry evergreen forest of Guyana. Journal of Tropical Ecology 5, 131-150.

Cremers, G., 1997. Hymenophyllaceae, in: Mori, S.A., Cremers, G., Gracie, C.A., de Granville, J.J., Hoff, M., Mitchell, J.D. (Eds.), Guide to the vascular plants of central French Guiana. Pteridophytes, Gymnosperms, and Monocotyledons, pp. 103-114.

de Granville, J.J., 1986. Flore et vegetation. Saga, Cayenne, French Guiana.

de Granville, J.J., 2001. Végétation, in: Barret, J. (Ed.), Altlas illustré de la Guyane. IRD Editions, Paris, France, pp. 52-55.

Dubuisson, J.Y., Hennequin, S., Rakotondrainibe, F., Schneider, H., 2003. Ecological diversity and adaptive tendencies in the tropical fern Trichomanes L. (Hymenophyllaceae) with special reference to climbing and epiphytic habits. Botanical Journal of the Linnean Society 142, 41-63.

Evans, G.B., 1964. Studies on the autecology of the British species of Hymenophyllum, T. wilsonii HK and H. tunbrigense (L.) Sm., University of Wales, UK.

Freiberg, M., 1997. Spatial and temporal pattern of temperature and humidity of a tropical premontane rain forest tree in Costa Rica. Selbyana 18, 77-84.

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, S.R., 2011. Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana. Biotropica 43, 591-596.

Gessner, F., 1940. Die Assimilation der Hymenophyllaceen. Protoplasma 34, 102-116.

Gradstein, S.R., 2006. The lowland cloud forest of French Guiana - a liverwort hotspot. Cryptogamie Bryologie 27, 141-152.

Gradstein, S.R., Ilkiu-Borges, A.-L., 2009. Guide to the plants of Central French Guiana. Part IV. Liverworts and hornworts, 76 ed.

Gradstein, S.R., Nadkarni, N.M., Kromer, T., Holz, I., Noske, N., 2003. A Protocol for Rapid and Representative Sampling of Vascular and Non-Vascular Epiphyte Diversity of Tropical Rain Forest. Selbyana 24, 105-111.

Gradstein, S.R., Obregon, A., Gehrig, C., Bendix, J., 2010. Tropical lowland cloud forest: a neglected forest type, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 329-338.

Grimaldi, M., Riéra, B., 2001. Geography and Climate, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 9-18.

Hietz, P., Hietzseifert, U., 1995. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. Journal of Vegetation Science 6, 719-728.

Iwatsuki, K., 1990. Hymenophyllaceae, in: Kubitzki, K. (Ed.), The families and genera of vascular plants. Vol I, Pteridophytes and Gymnosperms. Springer Verlag, Berlin, pp. 157-163.

Johansson, D., 1974. Ecology of vascular epiphytes in West African rain forest.

Johnson, G.N., Rumsey, F.J., Headley, A.D., Sheffield, E., 2000. Adaptations to extreme low light in the fern Trichomanes speciosum. New Phytologist 148, 423-431.

Kelly, D.L., 1985. Epiphytes and climbers of a Jamaican rain forest: vertical distribution, life forms and life histories. Journal of Biogeography 12, 223-241.

Kessler, M., Parris, B.S., Kessler, E., 2001. A comparison of the tropical montane pteridophyte floras of Mount Kinabalu, Borneo, and Parque Nacional Carrasco, Bolivia. Journal of Biogeography 28, 611-622.

Köster, N., 2002. Räumliche Diversitätsmuster der Epiphyten zweier amazonischer Tieflandregenwälder im Vergleich: Tiputini (Ecuador) und Surumoni (Venezuela). Nees Institute for Biodiversity of Plants, University of Bonn, Bonn.

Kreft, H., Koster, N., Kuper, W., Nieder, J., Barthlott, W., 2004. Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuni, Ecuador. Journal of Biogeography 31, 1463-1476.

Krömer, T., Kessler, M., 2006. Filmy ferns (Hymenophyllaceae) as high-canopy epiphytes Ecotropica 12, 57-63.

Krömer, T., Kessler, M., Gradstein, S.R., 2007. Vertical stratification of vascular epiphytes in submontane and montane forest of the Bolivian Andes: the importance of the understory. Plant Ecology 189, 261-278.

Lellinger, D.B., 1994. Hymenophyllaceae, in: Gorts-Van Rijn, A.R.A. (Ed.), Flora of the Guianas, Series B: ferns and fern allies, Fascicle 3. Koeltz Scientific Books, Königstein, Germany.

Magurran, A.E., 2004. Measuring biological diversity. Blackwell, Oxford, UK.

Meinzer, F.C., Goldstein, G., 1996. Scaling up from leaves to whole plants and canopies for photosynthetic gas exchange, in: Mulkey, S.S., Chazdon, R.L., Smith, A.P. (Eds.), Tropical forest plant ecology. Chapman & Hall, New York, pp. 114-138.

Mori, S.A., Boom, B.M., 1987. The forest, in: Mori, S.A. (Ed.), The Lecythidaceae of a Lowland Neotropical Forest: La Fumee Mountain, French Guiana, pp. 9-29.

Mori, S.A., Cremers, G., Gracie, C.A., de Granville, J.J., Heald, S.V., Hoff, M., Mitchell, J.D., 2002. Guide to the vascular plants of central French Guiana. Dicotyledons.

Mori, S.A., Cremers, G., Gracie, C.A., de Granville, J.J., Hoff, M., Mitchell, J.D., 1997. Guide to the vascular plants of central French Guiana. Pteridophytes, Gymnosperms and Monocotyledons.

Nieder, J., Engwald, S., Klawun, M., Barthlott, W., 2000. Spatial distribution of vascular epiphytes (including hemiepiphytes) in a lowland amazonian rain forest (Surumoni crane plot) of southern Venezuela. Biotropica 32, 385-396.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S.R., Sipman, H.J.M., Obregon, A., Bendix, J., 2010. Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators 10, 1111-1118.

Obregon, A., Gehrig-Downie, C., Gradstein, S.R., Rollenbeck, R., Bendix, J., 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. Agricultural and Forest Meteorology 151, 290-300.

Parra, M.J., Acuna, K., Corcuera, L.J., Saldana, A., 2009. Vertical distribution of Hymenophyllaceae species among host tree microhabitats in a temperate rain forest in Southern Chile. Journal of Vegetation Science 20, 588-595.

Perez Peña, A., Krömer, T., 2011. Qué pueden aportar los acahuales y las plantaciones de cítricos a la conservación de las epífitas vasculares en Los Tuxtlas, Veracruz?, in: Reynoso, V.H., Coates, R. (Eds.), Avances y perspectivas en la investigación de bosques tropicales y sus alrededores: Los Tuxtlas. Instituto de Biologia, Universidad Nacional Autonoma de Mexico, Mexico.

Pos, E.T., Sleegers, A.D.M., 2010. Vertical distribution and ecology of vascular epiphytes in a lowland tropical rain forest of Brazil. Bol. Mus. Para. Emilio Goeldi. Cien. Nat., Belém 5, 335-344.

Proctor, M.C.F., 2003. Comparative ecophysiological measurements on the light responses, water relations and desiccation tolerance of the filmy ferns Hymenophyllum wilsonii Hook. and H. tunbrigense (L.) Smith. Annals of Botany 91, 717-727.

Pryer, K.M., Smith, A.R., Hunt, J.S., Dubuisson, J.Y., 2001. rbcL data reveal two monophyletic groups of filmy ferns (Filicopsida : Hymenophyllaceae). American Journal of Botany 88, 1118-1130.

Richards, P.W., 1972. Hymenophyllum. Journal of Ecology 60, 245-&.

Ter Steege, H., Cornelissen, J.H.C., 1988. Collecting and studying bryophytes in the canopy of standing rain forest trees, in: Glime, J.M. (Ed.), Methods in Bryology. Hattori Botanical Laboratory, Nichinan, Japan, pp. 285-290.

ter Steege, H., Cornelissen, J.H.C., 1989. Distribution and Ecology of Vascular Epiphytes in Lowland Rain Forest of Guyana. Biotropica 21, 331-339.

Valiantzas, J.D., 2006. Simplified versions for the Penman evaporation equation using routine weather data. Journal of Hydrology 331, 690-702.

Zotz, G., Büche, M., 2000. The epiphytic filmy ferns of a tropical lowland forest - species occurence and habit preferences. Ecotropica 6, 203-206.

6 The potential distribution of tropical lowland cloud forest as revealed by a novel MODIS-based fog/low stratus night-time detection scheme

This chapter is published in *Remote Sensing of Environment*, 155, 312-324 (2014)
Received: 11 March 2014 / Accepted: 5 September 2014

http://dx.doi.org/10.1016/j.rse.2014.09.005

The potential distribution of tropical lowland cloud forest as revealed by a novel MODIS-based fog/low stratus night-time detection scheme

Obregon, A. (1), Gehrig-Downie, C. (2), Gradstein, S.R.(2) and J. Bendix (1)

(1) Laboratory for Climatology and Remote Sensing, Department of Geography, University of Marburg, Germany
(2) Department of Systematic Botany, Institute of Plant Sciences, University of Goettingen, Germany
(3) Museum Naturelle d'Histoire Naturelle, Dept. Systematique et Evolution, Paris, France

Abstract Fog is a crucial driver of epiphyte richness in tropical montane cloud forests but its spatial occurrence and role in tropical lowland areas is poorly understood. Recent studies in French Guiana have reported high epiphyte richness in previously undescribed “tropical lowland cloud forest” (LCF) due to radiation fog. Here, we analyze the spatial extent of fog/low stratus (FLS) in lowland forests of French Guiana using the frequency distribution by means of night-time MODIS (Moderate Resolution Imaging Spectroradiometer) satellite data for the years 2007–2010. The analysis is based on a newly developed dynamic threshold-test method relying on brightness temperature differences between thermal and mid-infrared bands. Individual thresholds for the discrimination between fog/low stratus and cloud-free pixels were retrieved by radiative transfer calculations and validated using discriminant analysis. The thresholds dynamically depend on total precipitable water (TPW) and the terrain-induced maximum possible sub-pixel fog coverage. The results of the new retrieval were validated using in-situ data and compared to results from existing fog detection algorithms, showing an improvement of the new detection scheme regarding the capability to detect sub-pixel fog coverage under varying TPW. FLS frequency maps derived from the novel fog classification scheme indicate a widespread distribution of night-time fog in river valleys, marking a multitude of potential areas for LCF throughout French Guiana. LCF is probably not only a local phenomenon but also may be widely distributed in river valleys in the lowland tropics, with significant consequences for biodiversity mapping in tropical lowland areas.

6.1 Introduction

Tropical cloud forests are generally associated with mountainous regions where they are termed "Tropical Montane Cloud Forests", abbreviated as TMCF (Hamilton et al. 1995, Stadtmüller 1987, Zadroga 1981). They account for 1.4% of all tropical forests worldwide and for 6.6% of all tropical mountain forests (Kapos et al. 2000). The American continent harbors 40.8% of the global TMCF area (Bruijnzeel et al. 2010). TMCFs are widespread in the tropics above 500 m a.s.l. (Hamilton et al. 1995), usually occurring between 2000 and 3000 m. Their elevation varies depending on vegetation zonation and mountain size, commonly described as the "telescoping" effect (Scatena et al. 2010, Whitmore 1998).

TMCFs have been recognized for their high biodiversity and as providers of high-quality freshwater (Bruijnzeel et al. 2011). Their unique ecology is threatened by habitat fragmentation and climate change. TMCFs are therefore warranted for protection (Bubb et al. 2004). They are in particular characterized by the abundance and high species richness of epiphytes (bryophytes, lichens, ferns, flowering plants; Frahm and Gradstein 1991, Richards 1984, Wolf, 1993). TMCFs generally differ from lowland rain forests in structure and functioning. The similarity of TMCFs and, at the same time, their most striking difference to lowland rain forests is the frequent occurrence of ground-touching clouds (Bruijnzeel & Veneklaas, 1998) which are in contact with the forest canopy and are perceived as fog at the surface. Dynamically, fog water immersion at windward mountain slopes by clouds is generally generated by advective clouds touching the ground which is different from radiation fog normally occurring at night due to radiation processes (Richter et al., 2013).

Despite the dynamic fog type, the effect of cloud immersion is a reduction of solar radiation and vapor deficit, canopy moistening and reduction of evapotranspiration (Hamilton, 1995) which in particular is beneficial for epiphytic plants. A significant proportion of gross precipitation comes from canopy interception of fog water and/or occult precipitation. Thus, the crucial role of fog as a major precondition for high epiphyte diversity in tropical montane cloud forests is widely accepted (e.g. Bruijnzeel et al., 2011).

In contrast, epiphyte-rich cloud forests were hitherto considered to be absent in tropical lowland areas due to the lack of ground-touching advection clouds. Recent studies in tropical lowland forests of French Guiana, however, indicate that cloud forests are not limited to tropical mountain areas but also occur in lowland areas well below 500 m a.s.l., with high epiphyte richness resembling TMCFs (Gehrig-Downie et al., 2011, 2012, 2013, Gradstein et al. 2010, Normann et al. 2010, Obregon et al. 2011, Pardow & Lakatos 2013, Pardow et al. 2012, refer to table 6.1).

Table 6.1. Summary of field investigations regarding performance of canopy epiphytes in lowland cloud forest (LCF) and lowland rain forest (LRF) for the two sites marked in figure 6.1. The data are compiled from Gehrig-Downie et al. (2011, 2012 & 2013).

		Saül		COPAS	
		LCF	LRF	LCF	LRF
Biomass (g/m²)	Total	58.5	34.5	-	-
	Bryophytes & lichens	53.4	33.4	-	-
	Pteridophytes	1.3	0.1	-	-
	Angiosperms	3.8	1.1	-	-
Cover (%)	Total	65	6	83	25
	Lichens	17	2	23	11
	Bryophytes	42	4	55	17
	Vascular plants	5	0.1	19	0.1
Diversity (species per tree)	Cyanolichens	4.5	1.5	-	-
	Filmy ferns	1.8	0.3	0.6	0
	Liverworts	31.6	24	38.3	27.6

The question which clouds might foster an epiphyte-rich lowland forest was addressed by a study of Obregon et al. (2011) in lowland valleys of central French Guiana. It turned out that recurring nocturnal radiation fog formation in the river valleys might be the reason for the occurrence of the hitherto undescribed, epiphyte-rich "tropical lowland cloud forest" (LCF).

Based on the local study in central French Guiana, we hypothesize that radiation fog occurrence potentially leading to LCF is a wider phenomenon covering greater parts of French Guiana and beyond, maybe being a global general phenomenon of tropical lowlands.

Unfortunately, fog formation over tropical lowland forests is hardly documented in the scientific literature. There are only a few local studies giving reason to expect that radiation fog occurrence might be distributed throughout the tropical lowlands, as e.g. central Amazonia (Baars 2012, De Araújo 2009), SW China (Liu et al. 2008) and West Africa (Kamara 1989). However, detailed knowledge on the spatial distribution of fog in the tropical lowland is lacking, but would be an essential precondition for mapping potential LCF habitats, which are potentially biodiversity hotspots of e.g. bryophytes (Pardow & Lakatos 2013).

Due to this lack of knowledge, the current study aims on mapping the spatial extent and frequency of tropical lowland fog as a precondition for LCF over the Guianas. Unfortunately, in-situ data from operational meteorological stations providing horizontal visibility over the canopies are not available for French Guiana and are also extremely rare in tropical lowland forests worldwide. The availability of remotely sensed imagery from satellites can compensate for this shortcoming by providing full spatiotemporal coverage, presupposing a proper fog/low stratus (FLS) detection technique is available.

For several decades, different schemes for the detection of fog and low stratus from operational weather satellite data have been developed for day and night (Cermak & Bendix 2007, 2008, 2011, Gultepe et.al 2007). Many approaches exist for the detection of fog during night-time (e.g. Bendix 2002, Eyre et al. 1984, Turner et al. 1986) which started with the development of retrieval techniques based on data of polar orbiting satellites (NOAA-AVHRR). Most solutions are threshold-based methods relying on the brightness temperature differences (ΔT) between the thermal (10.8 µm) and mid-infrared bands (3.9 µm), due to the reduced emissivity of small-droplet clouds in the mid-IR (Bendix & Bachmann 1991). However, most satellite-based studies mentioned above are conducted in the mid and high latitudes. To our knowledge there are no space-borne studies on fog detection over tropical lowlands. The region of French Guiana is an optimal test case but at the same time imposes three major challenges:

i. The high water vapor content (total precipitable water, TPW) of the tropical atmosphere might require dynamic alterations to thresholds of well-established fog detection algorithms.
ii. Fog in French Guiana is hypothesized to be a small-scale phenomenon, frequently bound to narrow river valleys which often lie in the sub-pixel detection range even of polar-orbiting weather satellites with relatively high spatial resolution (mostly 1 km), as e.g. provided by the Moderate Resolution Imaging Spectroradiometer (MODIS) onboard the Terra and Aqua platforms (Savtchenko et al. 2004).
iii. Fog in French Guiana is mainly a nocturnal / early morning phenomenon (Obregon et al. 2011), which means that a detection scheme must solely rely on IR satellite data.

As a consequence, a novel fog detection scheme based on MODIS night-time data is presented which has the capability to detect small-scale fog in the sub-pixel range with night-time IR data under varying amounts of TPW. The overall goal of this study is to reveal the spatial distribution of night-time fog frequencies throughout French Guiana and, with this, to provide evidence for potential habitats of tropical lowland cloud forests.

6.2 Study area

French Guiana is located on the northeastern coast of South America and belongs to the Guiana Shield (Gibbs & Barron 1993). The terrain is undulating throughout most of the country. In particular, central French Guiana is hilly and considerably dissected, with a series of hills, ridges and small river valleys in an altitudinal range between 50 m (valleys) and 300 m (ridges) a.s.l. (see figure 6.1). Hammond (2005) describes this landform which accounts for almost all of French Guiana as “Precambrian Rolling Hills”. According to Obregon et al. (2011) this hilly relief plays a crucial role in the formation of night-time valley fog through nocturnal pooling and cold air drainage flow from the hills.

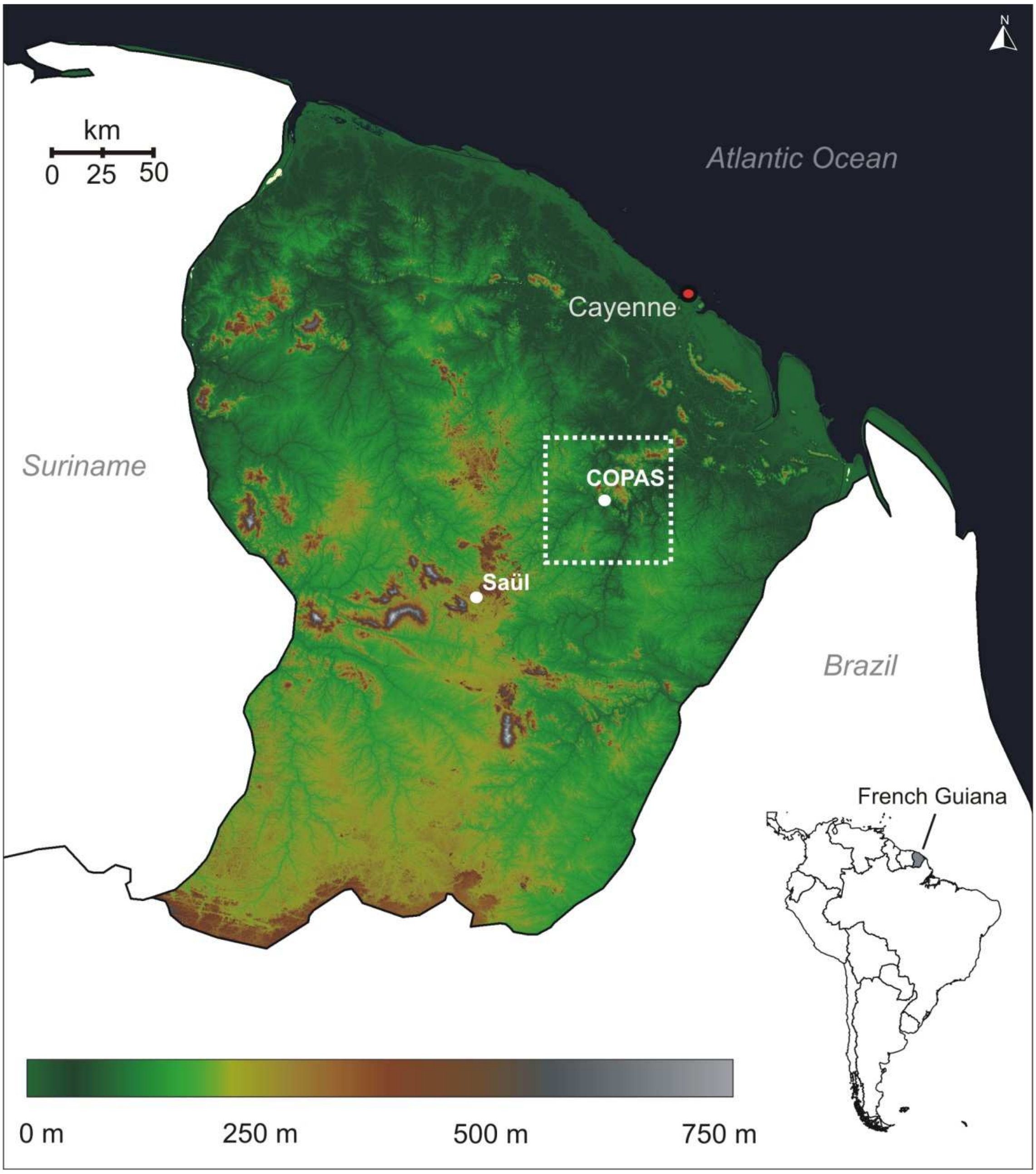

Figure 6.1. Terrain map of French Guiana and the inner study area (dotted rectangle, refer to figure 6.3 for details). Digital Elevation Model derived from the Shuttle Radar Topographic Mission (USGS 2006).The marked dots represent two study sites (COPAS, Saül) intensively investigated regarding climate and epiphytic diversity

Except for the coastal region, where mangrove forests and swamps occur, virtually all of French Guiana is covered by tropical lowland rain forest. Gond et al. (2011) using remote sensing data distinguished five forest classes, with “high forest with regular canopy” being dominant in the northern half of the country and “mixed high and open forest” in the south. Pennec et al. (2011) described a north-south gradient with several forest types consisting of fast-growing and drought-tolerant species occurring in the south. The rain forest is generally characterized by considerable biodiversity and is almost pristine. Epiphytic diversity was studied in tree canopies in the river valleys and nearby ridges of the two sites marked in figure 6.1 (for the study design see Gehrig-Downie et al. 2011, 2013, Obregon et al. 2011). It was clearly shown that there is a significant increase in diversity, abundance and biomass in the valleys where the LCF was hypothesized to occur.

The climate of French Guiana is of tropical monsoon type according to the Köppen-Geiger classification (Peel et al. 2007), with annual mean daily temperatures between 25° and 27°C and annual rainfall ranging from around 2500 mm in the west to 3500 mm at the Atlantic Coast. The precipitation regime depends on the position of the intertropical convergence zone (ITCZ) which moves over French Guiana twice a year. The seasonal precipitation cycle is bimodal with a main dry season between August and November when the ITCZ is farthest to the north, and a less pronounced dry period occurring in February and March when the ITCZ is farthest to the south (Bovolo et al. 2011). Onset and end of the dry period vary considerably throughout the years (Grimaldi & Riéra 2001).

The topoclimate was intensively investigated between 2007 and 2010 at the COPAS site (figure 6.1). Fog occurrence was measured above the canopy. It could be shown that radiation fog occurs very frequently (>90% of nights during dry season and 100% of nights during rainy season) in valleys of the lowland forest while the adjacent hill slopes remain nearly unaffected. Comparably high fog frequencies are only reported from tropical montane cloud forests (e.g. Bendix et al. 2008). Fog frequency showed a clear diurnal cycle, with a maximum before sunrise. Average fog duration at night (7 p.m. to 8 a.m.) was 4.6 h, but ranged from 4.4 h in the dry season to 6.2 h in the rainy season. The main trigger of fog development in the lowland forest seemed to be precipitation, leading to higher soil moisture, greater evapotranspiration, thus lowering saturation vapor pressure deficit of the above-canopy 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, underlined a clear influence of katabatic flows on fog formation (Obregon et al. 2011).

6.3 Data and methods

In this section, the methods used for the satellite-based valley fog detection approach are described. figure 6.2 shows the outline of the workflow which is presented in more detail in the following subchapters related to the single processing steps.

Generally, scatterometer measurements at the study site are the basis for validation of the fog retrieval. After preprocessing the MODIS data, an SRTM-based digital elevation model is used to determine the orographic landform of a pixel. After that, radiative transfer calculations (RTC) are used to derive functions for threshold-based fog detection including sub-pixel fog. A discriminant analysis is performed for the assessment of the RTC-derived threshold functions. Finally, fog classification and validation of the new technique are conducted and discussed.

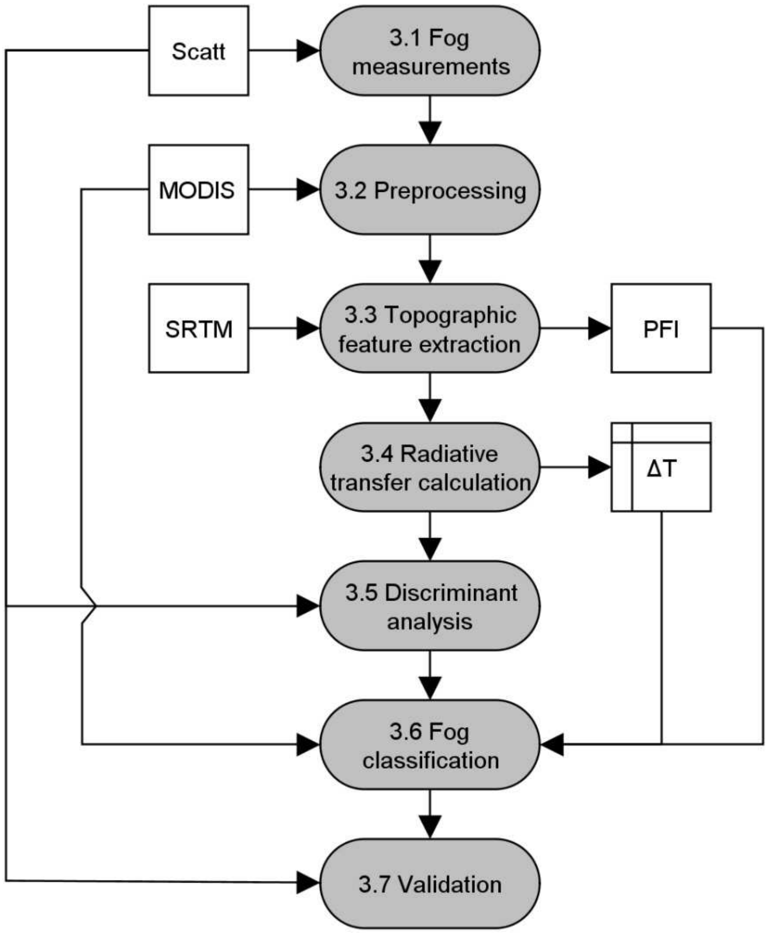

Figure 6.2. Flowchart of methodology showing methods with the corresponding sections (grey) and input data (white). Scatt = Scatterometer data, PFI = Potential Fog Index, ΔT = temperature difference IR-MIR band).

6.3.1 Fog measurements for training and validation

We carried out meteorological measurements including horizontal visibility above the canopy between the years 2007 and 2010 at two locations in central French Guiana: a) at research station Saut Pararé in the Nouragues Natural Reserve (4°02'30"N, 52°40'30"W) and b) in the vicinity of the village Saül (3°37'20"N, 53°12'31"W) (for locations refer to figure 6.1). For details of the experimental setup the reader may refer to Obregon et al. (2011).

Fog (visibility) data were available for five periods at the COPAS site only: a) Aug-Nov 2007, b) Mar-Apr 2008, c) Jun-Jul 2008 d) Oct 2008-Jan 2009, e) Feb-Apr 2010. During our measurement campaigns, 48 % of days in the dry season were without any rain but fog occurred on more than 90% of days during night and early morning.

For the validation of the MODIS-derived fog classification, the mean horizontal visibility between 2 and 3 a.m. was calculated for all days (averaging 12 measurements of 5-min each), matching the overpass time of the Aqua satellite in French Guiana (ranging around 2.30 a.m.). Hourly means of horizontal visibility below 1 km were classified as fog, indicating a stable fog layer during this period.

6.3.2 Satellite data and preprocessing

Daily Aqua MODIS Level 1b Calibrated Radiances at 1 km resolution (MYD021KM) from 2007 to 2010 encompassing 1295 images were selected (Savtchenko et al. 2004), which covered the field campaigns. The overpass time of the Aqua satellite over French Guiana is between 2 and 3 a.m. local time in descending (night-time) node. Preprocessing of the satellite data was done by using the operational MODIS processing scheme MOPS (Nauss & Bendix 2005). The brightness temperatures were derived for MODIS channels 20 (3.660 - 3.840 µm), 31 (10.780 - 11.280 µm) and 32 (11.770 - 12.270 µm), which are crucial for the fog detection scheme (see chapter 3.6). The satellite zenith angle (SZA) was also extracted and all pixels with SZA $>$ 50° were not considered in any further analysis. All data were re-projected onto a 1 km Universal Transverse Mercator (WGS84) grid subset covering French Guiana.

Because fog classification thresholds must be adjusted for TPW in the atmosphere during the image acquisition date, the corresponding MODIS TPW Level 2 products (Gao & Kaufmann 2003, Seemann et al. 2003) at 1 km resolution (MYD05) were obtained and re-projected on the same grid. An average TPW value was calculated for the whole study domain during classification by averaging all available land pixels for each scene, yielding an average daily TPW value for the FG domain. Pixel-specific TPW values could not be used since

MODIS TPW data are often not available for all pixels. A comparison with ERA-Interim TPW data (Dee et al. 2011) for the grid box covering French Guiana showed a good agreement for most days (Pearson correlation > 0.9).

6.3.3 Extraction of topographic features

Because fog classification thresholds must be adjusted regarding different degrees of fractional fog coverage in a MODIS pixel, the classification needs some pre-information on the potential maximum of fractional fog coverage. Thus, a potential fog index (PFI) is introduced which is derived from a digital elevation model in a two-step procedure: (Step 1) Calculation of a topographic position index (TPI) and (step 2) subsequent aggregation towards the 1 km resolved PFI. Based on ground observations (Obregon et al. 2011), this approach follows the premise that particularly valleys and lower slope positions (i.e. hillslopes forming the inner surface at the slope base) are considered as potential fog areas.

Step 1: A SRTM (Shuttle Radar Topography Mission, USGS 2006) derived digital elevation model (DEM) was used at 90 m resolution (figure 6.3a). Several SRTM tiles were stitched to cover French Guiana and resampled to a 100 m UTM grid with borders matching the MODIS data. The topographic position index (TPI) was calculated for each pixel using the MATLAB-based framework tool Mirone (Luis 2007) implementing an algorithm after Wilson et al. (2007). TPI is increasingly used for topographic slope position measurements and automated landform classification (De Reu et al. 2013). It was introduced by Weiss (2001) following Guisan et al. (1999) and describes the difference between the elevation of a grid cell and the mean elevation of a surrounding area given by a predefined radius:

$$TPI[scalefactor] = DEM - focalmean(DEM, circle, r) \qquad (1)$$

where DEM is the SRTM-derived raster grid and $focalmean$ is the mean value of grid values within the circle of radius r (Wilson et al. 2007).

Positive TPI values indicate higher elevation compared to the surroundings (e.g. ridges) while negative TPI values indicate the opposite (e.g. valleys). TPI is scale-dependent with a specified radius defining whether to capture small-scale features or larger-scale variations. Several radii from 3 to 60 pixels were tested in an iterative process and a window radius of 30 pixels (equivalent to a scalefactor of 3000 m) gave the most reliable results for the topographic position. The slope position was then derived by thresholding the standard deviation of TPI values and classifying into six slope position classes (table 6.2 and figure 6.3b).

Step 2: For the MODIS-based fog detection approach the slope position had to be resampled on a 1 km grid with information for each pixel of the potential fog coverage. Therefore, the Potential Fog Index (PFI) was derived by calculating the ratio between potential fog pixels (slope position classes 4-6) and potential fog free pixels (slope position classes 1-3) for each 1 km grid cell:

$$PFI = \sum_{i=1}^{n} \frac{slpos(4,5,6)}{slpos(1,2,3)} \tag{2}$$

where n is the number of pixels within an 1 km moving window and *slpos* the slope position class in table 6.2.

PFI indicates the maximum possible sub-pixel fog extent, ranging from 1 for broad valleys of ≥ 1 km width and 0 for upper slopes and ridges that fill one entire pixel (figure 6.3c).

Table 6.2. Classification of topographic position index (TPI) values into slope position classes using thresholds derived by the standard deviation (SD) of TPI.

Slope position	TPI threshold
(1) Ridge	TPI > 1.0 SD
(2) Upper slope	0.5 SD < TPI <= 1.0 SD
(3) Middle slope	-0.5 SD < TPI <= 0.5 SD; slope > 5 deg
(4) Flat	-0.5 SD < TPI <= 0.5 SD; slope <= 5 deg
(5) Lower slope	-1.0 SD < TPI <= -0.5
(6) Valley	TPI < -1.0 SD

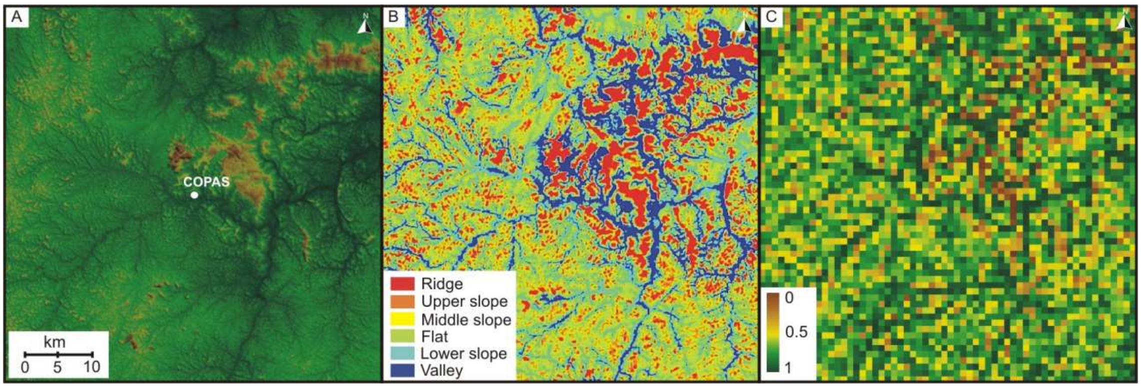

Figure 6.3. Digital Elevation Model for the inner study area (A), slope position classes derived by the Topographic Position Index for the COPAS area at 100 m resolution (B), and the Potential Fog Index at 1 km resolution (C).

6.3.4 Radiative transfer calculations

As a previous step to the fog classification scheme (refer to figure 6.2 for the processing steps) thresholds of ΔT had to be estimated for the discrimination between FLS and cloud-free surfaces. A radiative transfer model was used to simulate these thresholds. Radiative transfer calculations (RTC) were performed with the *Streamer* code, which can be used for computing radiances for a variety of atmospheric and surface conditions (Key & Schweiger 1998). Brightness temperatures were simulated for the MODIS channels 20 (3.9 µm) and 31 (10.9 µm) for a ground-touching cloud layer with a geometrical thickness of 30 m. Effective radius was set as 4 µm and cloud fraction (i.e. fog cover) was varied from 0.2 to 1.0. Total column amount of water vapor was specified according to Tomasi et al. (1998) using 0.85 cm for the Mid-latitude Winter model, 2.92 cm for the Mid-latitude Summer model and 4.12 cm for the Tropical model. These standard atmospheric profiles are used to reveal the general influence of TPW on the FLS threshold. A background tropospheric aerosol was set as vertical profile. Gaseous absorption and Rayleigh scattering was turned on. The optical thickness is determined by the radiative transfer model using the inputs for cloud geometrical thickness, water content and effective radius. The threshold functions for the fog classification were then derived by a regression model of the simulated ΔT vs. TPW using an exponential fit.

6.3.5 Discriminant analysis

For the verification of the RTC derived threshold functions, a discriminant analysis (DA) was performed in a sample of 100 days using data of MODIS-derived ΔT and TPW. Values below a ΔT of -3 K in the satellite images were discarded from the discriminant analysis since they are contaminated by mid or high level clouds. The samples were classified into fog (VIS $<$ 1 km), and no-fog (VIS $>$ 1 km), using data of mean horizontal visibility between 2 and 3 a.m. at the COPAS climate station (section 3.1).

In order to test the feasibility of the RTC-determined thresholds for a range of PFIs, discrimination analyses were performed using the COPAS collocated pixel (PFI=0.8) and corresponding pixels in the vicinity of the COPAS site. For the COPAS pixel, a direct assessment of the RTC-derived functions is possible due to the availability of ground truth data (scatterometer measurements). The assessment of adjacent pixels is based on the assumption that fog measured at the COPAS climate station implies fog occurrence in the adjacent valley pixels which is supported by visual observations in the field.

6.3.6 Fog detection scheme

The proposed fog classification scheme (figure 6.4) is a modification of the night-time approach presented by Bendix et al. (2004) for a tropical mountainous regions, which followed Saunders (1986), Saunders & Kriebel (1988) and Kriebel et al. (2003). The scheme consists of three tests for the detection of different cloud types (including FLS) and the identification of cloud-free pixels if all tests pass. The tests make use of brightness temperature differences between the MODIS infrared channels 20 ($T_{3.9}$), 31(T_{11}) and 32 (T_{12}):

- $\Delta T_{3.9\text{-}12}$: ΔT between the 3.9 μm channel and the 12 μm channel
- $\Delta T_{11\text{-}12}$: ΔT between the 11 μm channel and the 12 μm channel
- $\Delta T_{11\text{-}3.9}$: ΔT between the 11 μm channel and the 3.9 μm channel

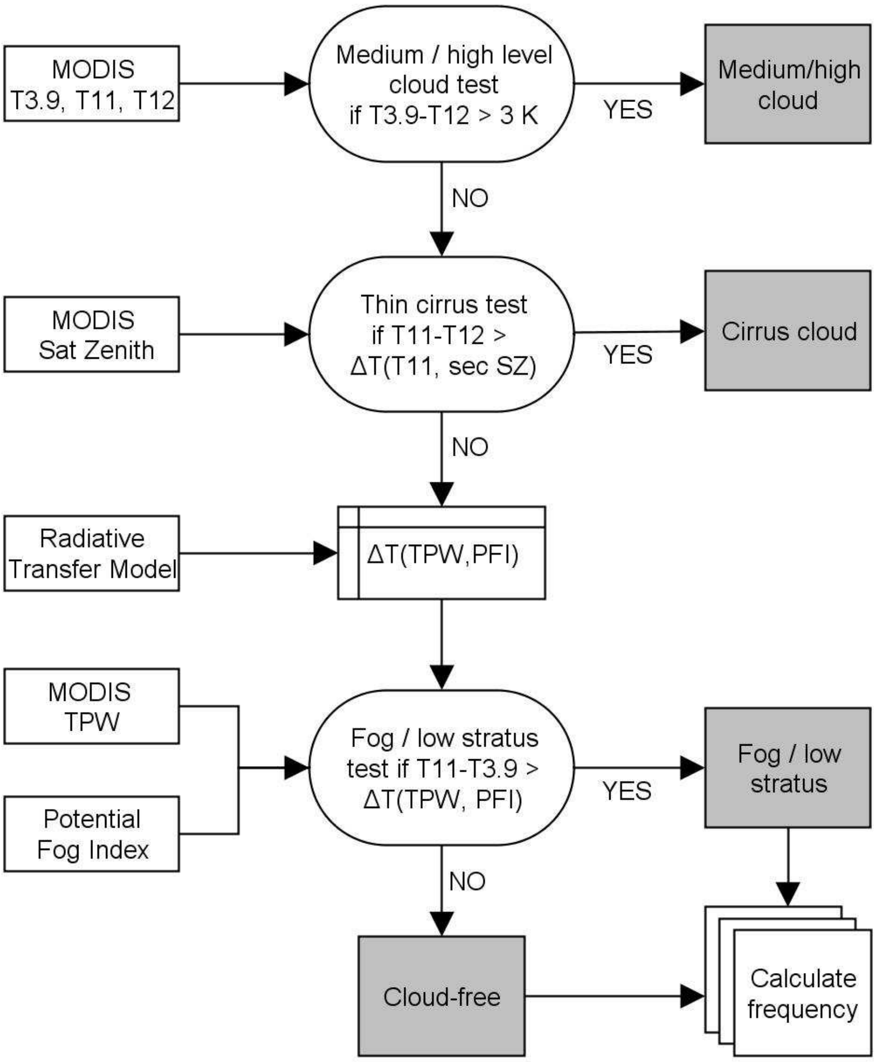

Figure 6.4. Proposed fog/low stratus detection scheme.

The first test is applied for the detection of middle and high level clouds. The temperature differences between $T_{3.9}$ and T_{12} can be used due to different cloud emissivity at both wavelengths. The AVHRR-based threshold of 1 K, published by Saunders & Kriebel (1988) and Kriebel et al. (2003) and the adjusted threshold of 1.5 K proposed by Bendix et al. (2004) have proven to be too sensitive for the MODIS channels in the study area. Thus, a modified threshold of 3 K was chosen based on visual inspection of the classification results.

The second test for the detection of thin cirrus clouds follows Saunders & Kriebel (1988) and is based on temperature differences of the split window channels T_{11} and T_{12}. The lookup table (LUT) presented by Saunders & Kriebel (1988) for $\Delta T_{11\text{-}12}$ thresholds depending on satellite zenith angle and T_{11} is used. $\Delta T_{11\text{-}12}$ temperature differences larger than the corresponding LUT threshold are flagged as cirrus-contaminated.

For pixels passing the two previous tests a final test is applied which forms the core element of the proposed scheme. The final FLS test uses brightness temperature differences of channels 31 and 20 ($\Delta T_{11\text{-}3.9}$) and introduces some major modifications compared to previous approaches by Saunders & Kriebel (1988), Kriebel et al. (2003) and Bendix et al. (2004). To discriminate pixels contaminated by FLS from cloud-free pixels the following steps are conducted:

i. Thresholds functions are derived beforehand by radiative transfer calculations for different TPW and PFI values (see section 3.4).

ii. Brightness temperature differences $\Delta T_{11\text{-}3.9}$ of the MODIS data are compared to the result of the RTC-derived threshold functions using TPW values during satellite overpass and corresponding PFI values.

iii. Pixels are flagged as FLS for MODIS $\Delta T_{11\text{-}3.9}$ being larger than the simulated thresholds; otherwise pixels are flagged as cloud-free.

In a last step, relative fog frequencies are calculated using *n* pixels classified as “fog/low stratus” and *m* pixels classified as “cloud-free surface” for all time steps:

$$Freq = \sum_{i=1}^{n} fog \Bigg/ \left(\sum_{i=1}^{n} fog + \sum_{j=1}^{m} surface \right)$$

Pixels flagged as cirrus or mid/high level clouds were discarded for the fog frequency calculation since no information on underlying ground fog or cloud-free surface can be retrieved. Fog frequencies were calculated for the whole time period (2007-2010), for single years and for individual and multi-year dry and rainy seasons.

6.3.7 Validation approach

The last element of the workflow depicted in figure 6.2 is the validation of the fog classification. Scatterometer measurements of horizontal visibility between 2 and 3 a.m. at the COPAS climate station (described in section 3.1) were used as ground-truth data. Since the threshold functions are retrieved solely by radiative transfer calculation the visibility measurements at the COPAS site represent an independent data source.

In total, 299 days of scatterometer measurements were available between 2007 and 2010 (with most succeeding days of 99 during dry season 2007). 211 days had a MODIS coverage for the COPAS site. For the validation, 131 days had to be discarded due to missing TPW values, high SZ angles or possible mid/high level cloud contamination. Out of 80 remaining days, 17 days were characterized by a mean visibility between 2 and 3 a.m. below 1 km, indicating a stable fog situation.

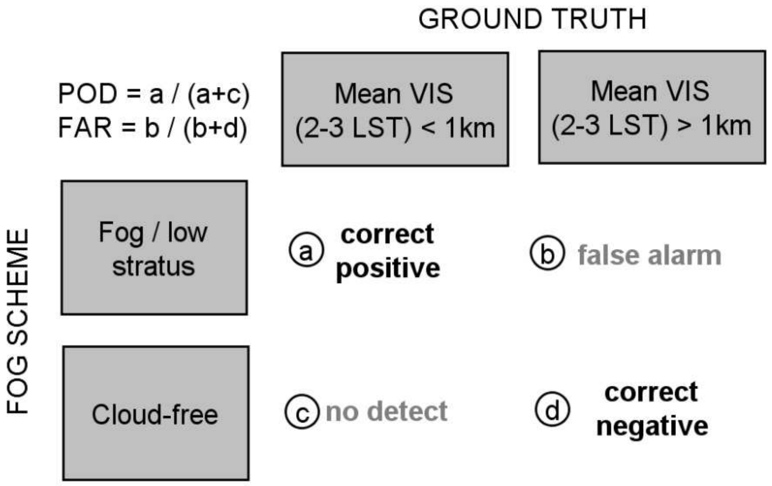

Figure 6.5. Confusion matrix and definition of skill scores used for the validation.

The *probability of detection* (POD), also known as hit rate, was calculated, representing the number of correctly classified fog events divided by the number of total ground-truth fog events. The *false alarm rate* (FAR), also known as probability of false detection, was calculated, representing the number of fog classifications when no ground-truth fog occurred (false alarms) divided by the number of all fog-free events (figure 6.5). FAR might not be confused with the *false alarm ratio*, which represents the ratio of false alarms to the number of all fog classifications (refer to Barnes et al. (2009) for clarification). POD and FAR were used for receiver operating characteristic (ROC) calculations (refer also to Bendix et al. (2005)). Validation was conducted for the pixel representing the COPAS site (PFI=0.79) during the dry season of 2007 (13 Aug – 16 Nov). In total, 29 scenes of either fog or cloud-free surface at the validation site could be used and 80 days for the whole period from 2007 to 2010.

6.4 Results

6.4.1 Suitability of thresholds

The simulated brightness temperature differences ($\Delta T_{11\text{-}3.9}$) show significantly lower values for the tropics as compared to the midlatitudes, which is indicated by a strong negative bias ranging between-1.5 and -2 (figure 6.6). The theoretical calculations indicate that thresholds for the detection of shallow valley fog must be kept dynamical because:

i. Thresholds are generally modified by atmospheric loading of water vapor (TPW).

ii. In the tropics, thresholds become negative for an optical depth below 1.5.

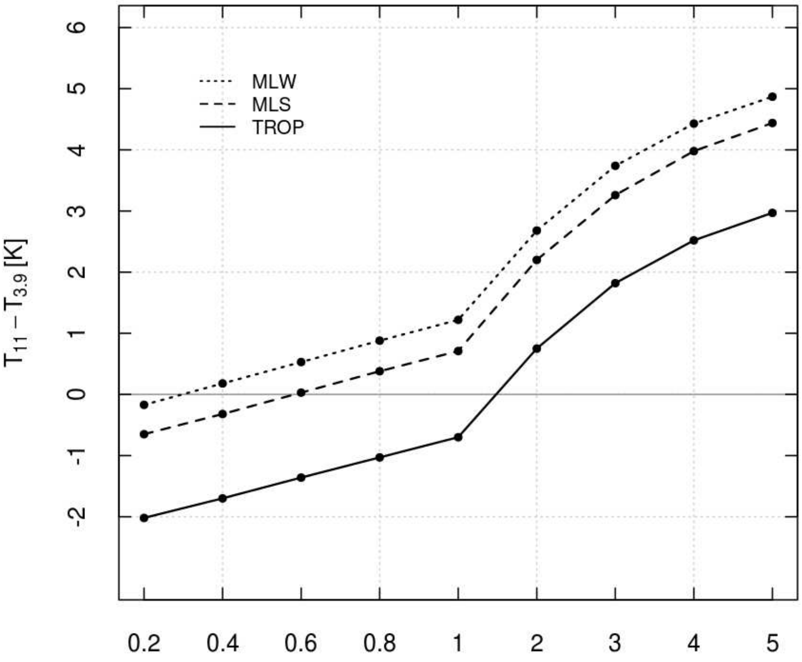

Figure 6.6. Radiative transfer calculations for a ground-touching fog layer with different optical thicknesses. Brightness temperature differences ($\Delta T_{11\text{-}3.9}$) are shown for three standard atmospheres (MLW=midlatitudes winter, MLS=midlatitudes summer, TROP=tropics). The simulated fog layer in the study area corresponds to an optical thickness of around 1.

Table 6.3. Results for brightness temperature differences ($\Delta T_{11\text{-}3.9}$ µm) from radiative transfer calculations for a constant effective radius of 4 µm (= fog) and a geometrical thickness of 30 m for different potential fog coverages (expressed as PFI) and three standard atmospheres (MLW=midlatitudes winter, MLS=midlatitudes summer, TROP=tropics).

Standard	Fractional fog cover = Potential Fog Index (PFI)					
atmosphere	0	0.2	0.4	0.6	0.8	1
MLW	-0.5	-0.17	0.17	0.52	0.87	1.22
MLS	-0.78	-0.49	-0.19	0.11	0.4	0.71
TROP	-2.07	-1.8	-1.53	-1.25	-0.98	-0.7

The second potential modification of the temperature threshold is expected due to varying fractional fog cover per pixel. Table 6.3 shows the simulated brightness temperature differences for the simulated fog layer in the study area (tropical standard atmosphere) with different sub-pixel fog extents, ranging from 1.0 (= full fog cover) to 0.2 (only 20% covered by fog). A maximum threshold of -0.7 is calculated for pixels of full fog extent (=large valleys) in the tropics. The radiative transfer calculations indicate that thresholds for separating fog from fog-free surfaces decrease with increasing total precipitable water and decreasing fog coverage. Table 6.4 and figure 6.7 (left) present the corresponding functions to derive the ΔT threshold from TPW for different PFIs.

Figure 6.7 (right) shows the assessment of the separability of fog and no-fog events using the proposed classification approach. The discrimination line derived by linear discrimination analysis for the COPAS pixel describes the optimal separability between the two groups, indicating that a separation is generally possible. The RTC-derived function which is used for high PFI in the FLS detection scheme shows a good separability of the groups and coincides rather well with the corresponding discrimination line, in particular for TPW values between 3 and 6. In detail, the discriminant analysis using equal prior probabilities for the COPAS pixel indicates a proportion of 81% of correctly separated cases.

Discriminant lines for adjacent pixels with lower PFI show a slightly lower separability and a negative bias for higher TPW values, along with a clock-wise rotation of the discriminant functions. This implies, in contrast to the RTC calculations, a positive bias of thresholds for TPW values below approximately 4 cm. From figure 6.7 (right) it can be seen that fog formation below a TPW of 4 cm does almost not occur, which holds also true when using a larger sample. Hence, a decrease of thresholds for lower PFIs, as suggested by the RTC calculations, would introduce larger errors in the classification scheme due to higher amount of misclassifications (non-fog pixels being classified as fog). As a consequence, the classification scheme would largely overestimate fog in areas of potential sub-pixel fog occurrence. For a more robust classification, threshold functions for PFI below 0.8 are therefore only applied for TPW values higher than 4 cm. The proposed FLS classification scheme uses four PFI groups (high, middle, low, very low) according to table 6.4.

Table 6.4. Functions of ΔT and TPW derived by radiative transfer calculations for different cloud fractions using an exponential fit. Corresponding PFI classes are shown.

Cloud fraction	Radiative transfer calculation	PFI classification
0.8	$\Delta T = -0.282TPW^2 + 0.837TPW + 0.362$	1.00 – 0.75 (high)
0.6	$\Delta T = -0.286TPW^2 + 0.880TPW - 0.021$	0.75 – 0.50 (middle)
0.4	$\Delta T = -0.288TPW^2 + 0.913TPW - 0.397$	0.50 – 0.25 (low)
0.2	$\Delta T = -0.286TPW^2 + 0.925TPW - 0.749$	0.25 – 0.00 (very low)

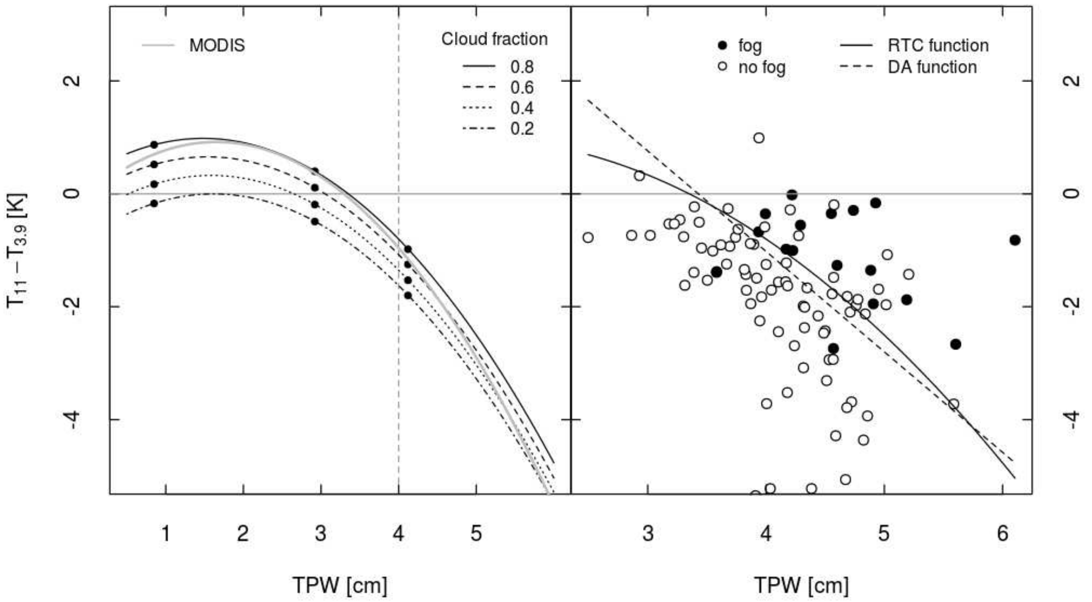

Figure 6.7. (Left): RTC-derived functions of brightness temperature differences vs. total precipitable water for different cloud fractions. Points indicate the values derived by the radiative transfer calculations. An exponential fit was used for the regression lines. The gray line shows the empirical relationship between $\Delta T_{11-3.9}$ and TPW using CALIOP clear vs. cloudy determinations and MODIS radiance data (taken from Ackermann et al. 2010). The function is calculated as $\Delta T = -0.0077+1.1234*TPW+(-0.3403*TPW^2)$. The vertical line marks the TPW value (=4 cm) of which above modified PFI functions are used. (Right): Threshold functions for the separation of fog and fog-free pixels (according to the in-situ fog measurements) derived by radiative transfer calculations (table 6.4, PFI=0.8) and discriminant analysis (discriminant line: $\Delta T = -1.77TPW+6.1$). $\Delta T_{11-3.9}$ values of MODIS data of all days with validation data are shown for the corresponding MODIS-derived TPW values.

6.4.2 Validation of the novel FLS classification scheme

To assess the validity of the developed classification scheme, three different threshold sets with increasing complexity are applied to the classification scheme in figure 6.4:

A) Technique hitherto used: Fixed threshold, tested for values from -1.5 to +1.

B) First improvement: Dynamic threshold depending on TPW using a fixed PFI function (high).

C) Expected optimum skill: Dynamic threshold depending on both, TPW and PFI classes.

Validation results for sets A) and C) for different fixed and dynamic thresholds are shown in figure 6.8.

The fixed threshold method A shows a rather weak performance. A threshold of +1, which is generally suitable and often applied for the midlatitudes, fails in detecting fog in the study area while a low threshold of -1.5 leads to a highly erroneous overestimation of fog. An optimal fixed threshold is found around -0.5 which corresponds to the threshold calculated by using the 100 % PFI function with the median TPW for the study area (ca. 4.0 cm) for the dry season.

However, the fixed threshold approach is clearly outperformed by the dynamic threshold technique C. Best agreement is reached for PFI between 1.0 and 0.6, coinciding well with the PFI for the COPAS pixel (=0.79). Using functions for PFI below 0.6, the probability of detection increases but results in higher false alarm rates. Using the threshold function calculated for a fog cover of 80%, the POD for the COPAS pixel during dry season is 0.78 with a FAR of 0.15. Using a fog cover of 100% instead, POD decreases to 0.67 while FAR also decreases to 0.05. The validation results for the dry season are generally better than for the whole period where POD slightly decreases and FAR at the same time increases.

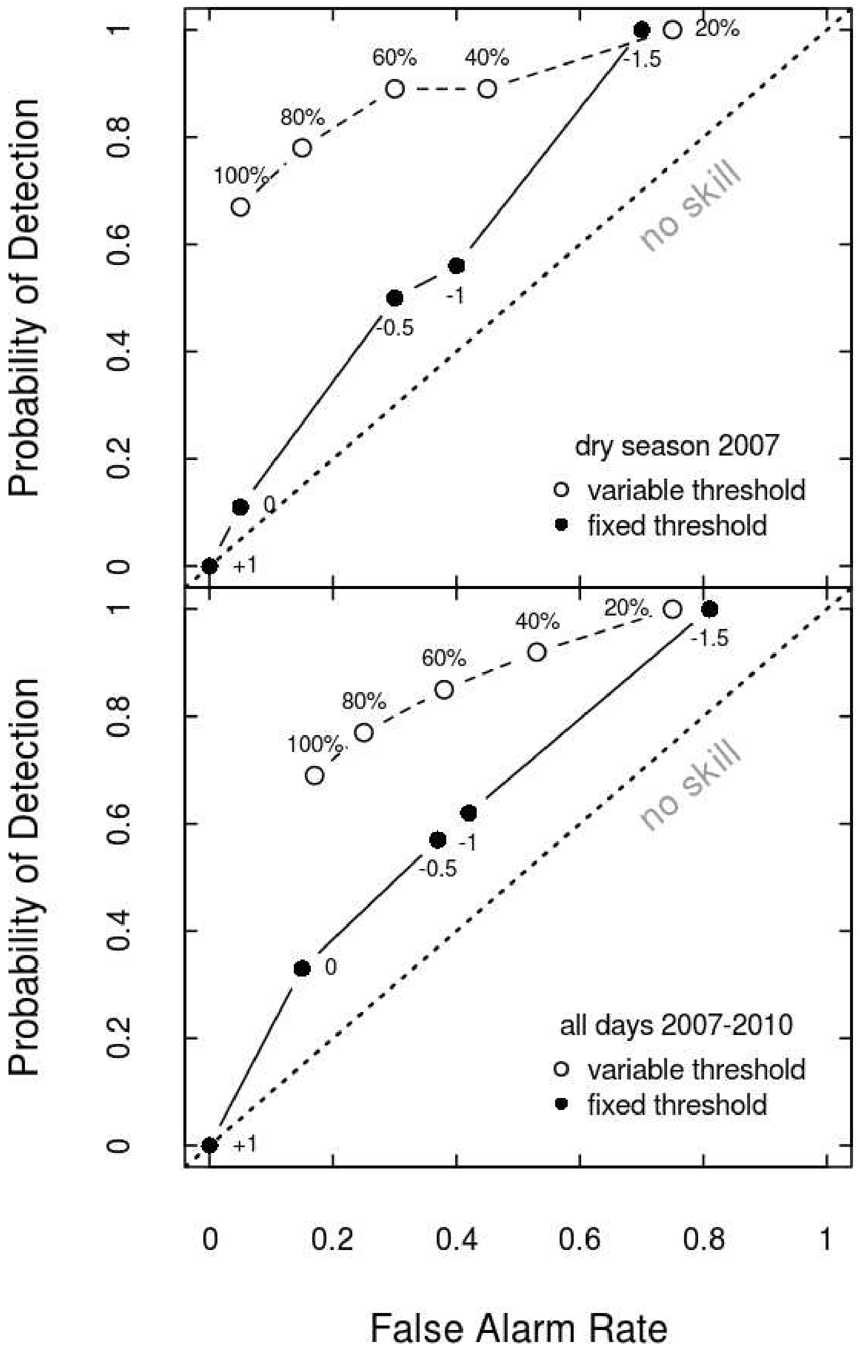

Figure 6.8. ROC diagrams showing validation results for the COPAS pixel (PFI=0.79) for the dry season 2007 (N=29) (top) and all available validation days (N=80) (bottom). The dashed lines indicate retrievals with variable thresholds depending on TPW using different RTC-derived PFI functions (PFI in %). The solid lines indicate fixed thresholds between -1.5 and +1. Since the fog detection scheme is a discrete classifier, POD and FAR correspond to a single point in ROC space.

6.4.3 Spatial fog occurrence in French Guiana

The hitherto used fog retrieval with a fixed ΔT threshold shows generally low fog frequencies in the COPAS area (figure 6.9a). A distinction of higher frequencies in major river valleys and lower frequencies in adjacent ridges is revealed but gradients are, however, rather low. A fixed threshold of -0.5 was used in figure 6.9a which corresponds to the RTC-derived function for a PFI of 1.0 using the median TPW for the dry season (4.0 cm). This threshold represents the optimum value for the fixed threshold approach as shown by the validation. With even higher fixed thresholds, commonly used for the midlatitudes (i.e. thresholds between 0 and 1), almost no fog is detected by the retrieval throughout the inner study area (not shown).

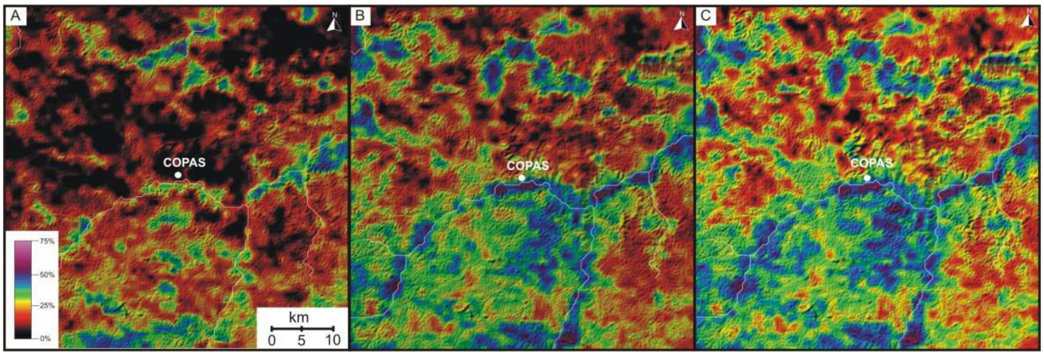

Figure 6.9. Fog frequency maps for the three different retrievals in the COPAS area: A) fixed threshold of -0.52; B) variable TPW and fixed PFI; C) variable TPW and variable PFI. The dry season 2007 is presented, which has the best coverage of validation data. Hillshading is enabled using SRTM data.

The modified approach using a dynamic threshold based on variable TPW and a fixed PFI (high) reveals some major differences (figure 6.9b). Fog frequencies are generally higher in river valleys with frequencies exceeding 50% in the COPAS area, approaching the values obtained by scatterometer measurements in the field. The general spatial distribution of fog frequencies gives a more realistic result with all river valleys characterized by frequent fog filling and a stronger gradient towards lower frequencies in ridge positions.

Additionally incorporating different sub-pixel fog covers (PFI) gives further information of possible fog occurrences in sub-pixel areas (figure 6.9c). While areas of high PFI (major river valleys) are showing identical frequencies due to using the same algorithm for this PFI class, some areas of middle and lower PFI result in higher fog frequencies. The area south of the COPAS site which is considerably dissected and undulating (compare to DEM in figure 6.3a) reveals high fog frequencies in all PFI classes compared to lower frequencies in the north which is characterized by higher mountain ridges (and some inselbergs) and a generally less hilly topography.

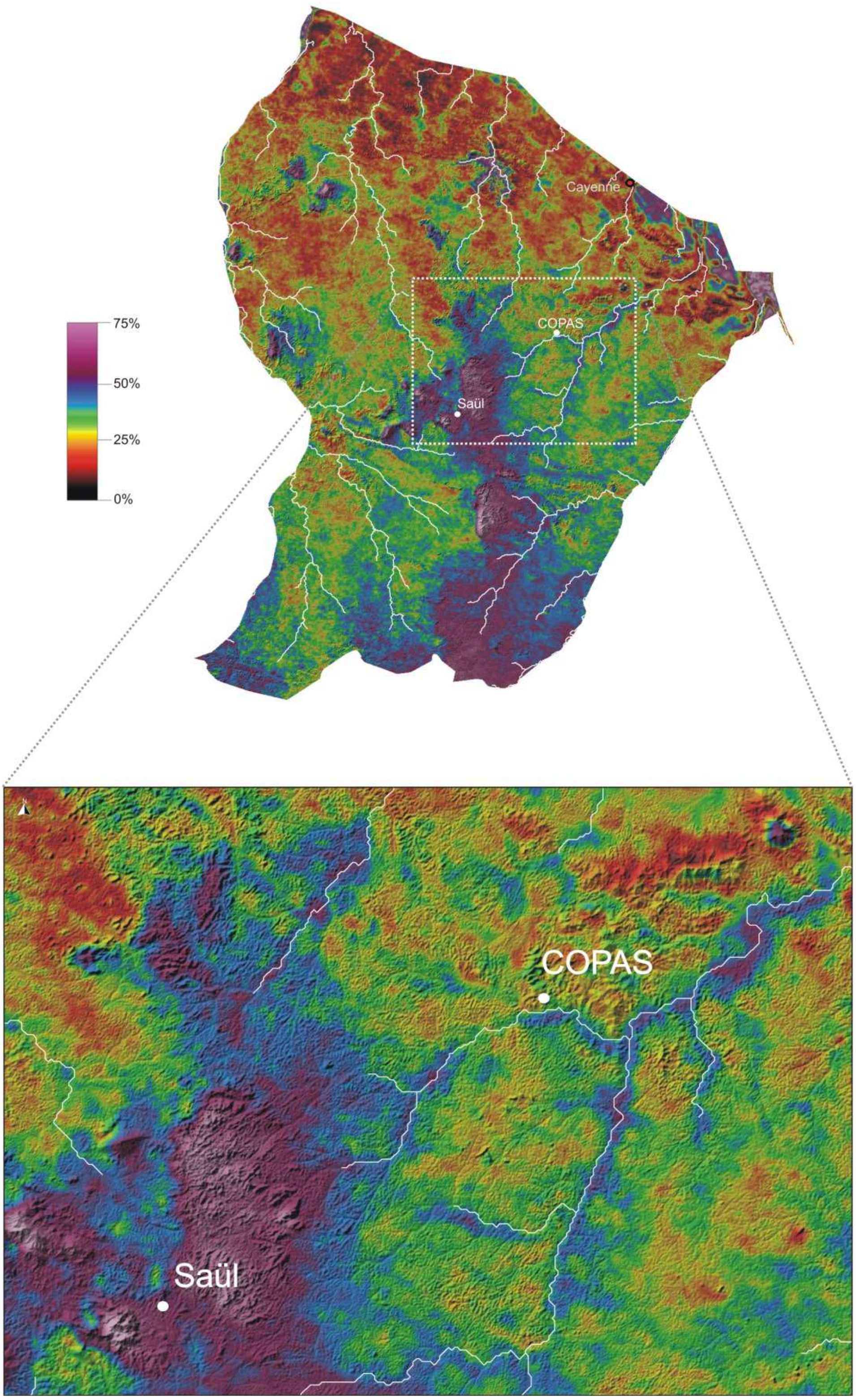

Figure 6.10. Fog frequency map for August, September, October (dry season) from 2007 till 2010 encompassing a detailed inset of the inner area covering the sites of the field measurements. A dynamical threshold based on variable TPW and variable PFI was used. SRTM data was applied for hillshading.

Fog frequency during the dry season (2007-2010) in the entire country of French Guiana shows a heterogeneous spatial pattern with four distinct clusters (figure 6.10):

i. The coastal area up to 50 km inland. This area is characterized by low fog frequencies except for the Kaw swamp, the eastern coast of Oyapock estuary and a large water reservoir west of Cayenne.

ii. Major river valleys and areas of more undulating terrain and small ravines. These areas are associated with higher fog frequencies as compared to adjacent slopes and small hills (greenish and blueish areas along the rivers).

iii. The central highlands and isolated mountains. Characterized by high fog frequencies which increase with elevation, partly exceeding 75%.

iv. Southern and southeastern French Guiana. A spatially rather homogeneous area of high fog frequencies without clear dependency on topography (blueish and violetish areas).

6.5 Discussion and Conclusions

This is the first study revealing spatiotemporal frequency of fog in a tropical lowland moist forest area using satellite imagery. We developed a novel FLS detection algorithm by accounting for the sensitivity of $\Delta T_{11\text{-}3.9}$ µm thresholds to the spatially restricted sub-pixel fog extent and atmospheric loading of TPW. The thresholds are defined dynamically depending on TPW and the terrain-induced maximum possible sub-pixel fog coverage. Test thresholds are functions of TPW because atmospheric moisture loading has a large impact on $\Delta T_{11\text{-}3.9}$ µm relative to the small expected changes between clear and cloudy skies (Ackermann et al. 2010).

The presented relationship between TPW and ΔT is supported by several lines of evidence which are based on three independent assessments (all functions displayed in figure 6.7):

i. Theoretical calculation by means of a radiative transfer model and regression analysis using an exponential fit (this paper)

ii. Discriminant analysis using satellite brightness temperatures and in-situ scatterometer measurements (this paper)

iii. Empirical relationship between MODIS thresholds and CALIOP cloud and cloud-free determinations (Ackermann et al. 2010)

The discriminant analysis confirms the theoretical assumptions derived from RTC and thus, validates the simulated threshold functions.–The relationship between TPW and ΔT proposed by Ackermann et al. (2010) remarkably resembles the RTC-derived functions (figure 6.7, left). The proposed method results in good classification accuracies and is effective in separating fog and fog-free areas, significantly outperforming fixed-threshold approaches. Hence, we state that a proper FLS classification at night in tropical lowland forests with low-earth orbiting satellite data (here MODIS) requires information on TPW and sub-pixel fog cover. Since most existing threshold-based FLS detection schemes have been developed or applied for the outer tropics with lower atmospheric moisture loading (e.g. Bendix 2002, Eyre et al. 1984, Turner et al. 1986 for NOAA AVHRR, Ellrod 1995, Underwood et al. 2004 for GOES, Cermak & Bendix 2008 for Meteosat), the effect of TPW on the $\Delta T_{11\text{-}3.9}$ µm threshold has been widely neglected so far. Therefore, the paper gives reason to rethink common threshold-based approaches when being applied to areas of higher atmospheric moisture loading.

The FLS frequency maps derived from the novel fog classification scheme indicate a widespread distribution of night-time fog in river valleys throughout French Guiana, marking a multitude of potential areas for tropical lowland cloud forest.

The higher fog frequency in river valleys as compared to adjacent slopes and hills is particularly prominent on the windward side of the central highlands and is very distinct in the valley of the Approuague River valley (figure 6.10). The high prevalence of fog in river valleys can be explained by radiation fog (Obregon et al. 2011) being primarily controlled by the balance between radiative cooling, which encourages fog, and turbulence, which inhibits it (Roach et al. 1976). It only occurs in supportive conditions, which are defined by vertical mixing of heat and moisture, wind structure, radiative cooling rate profiles and surface conditions (Fitzjarrald & Lala 1989). Radiation fog often forms in hollows, where it can be attributed to additional moisture and drainage flow of cold air (Golding 1993). The Approuague River valley provides ideal preconditions for fog formation which might be attributed to all before-mentioned factors, since radiation fog is often a combination of different processes (Duynkerke 1991). The demand for sufficient moisture is satisfied by the permanent advection of moist air masses through the northeastern and southeastern trade winds. Thus, the region of frequent occurrence of radiation fog (valley fog) in French Guiana must be regarded as the optimum habitat for lowland cloud forest even though the formation of cloud forests depends on the amount of cloud water intercepted by vegetation, and not only on the persistence of fog (Gomez-Peralta et al. 2008).

The highest frequencies of fog/low stratus occurrence in French Guiana occur in the central highlands and on isolated mountains. The mountain ranges in central French Guiana, which are also known as *massif central guyanais* reach up to 851 m a.s.l. close to Saül (Montagnes Bellevue de l'Inini) and 830 m at the southern extension of the highlands (Sommet Tabulaire). The observed high values of FLS frequency in this area is probably due to low-level stratus clouds and/or advection fog. The processes leading to the stratiform cloudiness could be manifold. Advection processes are supposed to play a key role in the formation of the low-level clouds in the central highlands, either through trade wind advection or due to extended sea breeze and local wind systems. Processes may also be combinations of sea breeze and upslope breeze. Orographic clouds generally form when moist air is topographically forced to rise due to the prevailing winds blowing against higher mountains which force the incoming air masses to ascend and cool the near-surface moist air by adiabatic expansion (Beniston 2005, Gultepe et al. 2007, Scholl et al. 2011). When condensation level is reached, water vapor is converted to fine liquid water particles that become visible in the form of mist, fog or clouds (Beniston 2005). At the surface, this condensation is generally described as upslope fog or orographic fog (Cereceda et al. 2002). The more humid the uplifted air, the lower the altitude of condensation onset (Foster 2010). Hence, at smaller mountains close to the coast condensation tends to happen at lower altitudes than further inland (Jarvis & Mulligan 2010).

The formation of stratiform clouds in French Guiana may be initiated at the coast from where they are advected further inland and forced to rise along the slopes of the central highlands and inselbergs. This leads to further cooling and condensation and hence the formation of orographic fog at higher altitudes (Bruijnzeel et al. 2005). Most of French Guiana is generally under the influence of the trade easterlies, which provide permanent moisture supply from the Atlantic Ocean. The formation of orographic fog is also known for the eastern coast of Mexico where the eastern prevailing winds gather humidity over the Gulf of Mexico and are orographically forced to ascend to higher altitudes (Garcia-Garcia & Zarraluqui 2008).

The discrimination between very low stratus and ground fog remains a major challenge of satellite-based fog retrievals although some studies have proposed solutions to this for daytime data from polar orbiting and geostationary satellites (Bendix et al. 2005, Cermak & Bendix 2011). For the presented algorithm, no estimation of the cloud base height can be made and hence no statement about the presence of ground-touching clouds in the central highlands.

Fog in local valleys close to Saül (figure 6.1) was reported by Montfoort & Ek (1990) and could also be observed during the field work of this study. In contrast, slopes and small hills around Saül are generally free of fog. Gehrig et al. (2011) revealed the differences in humidity between valleys and adjacent hills. De Granville (1991) reported the formation of orographic fog with increasing altitude in this area, promoting the growth of vascular epiphytes in the canopy. After De

Granville (1991), the higher elevations are covered by a low cloud forest with garlands and mats of bryophytes, most typically on the edges of plateaus on the leeward side. De Granville (1999) applied the term "submontane cloud forests" to these forests.

The occurrence of ground-touching clouds above 400 – 500 m a.s.l. marks the transition from regular lowland rain forests to submontane cloud forests. From the literature and observations in the field, it seems that most stratiform clouds detected by the FLS scheme do not reach the ground. Hence, an additional moisture input to the epiphytic vegetation can be only be expected to occur in forests at higher elevation and in small valleys and ravines. Unfortunately, the FLS retrieval is not able to detect the shallow valley fog around Saül due to overlying stratus cloud fields and due to the small-scale nature of fog in this area.

The area of high abundance of fog or low stratus in southern French Guiana is neither related to high elevations nor clearly aligned to river valleys. Since no literature or field observations are available for this area, it remains uncertain whether ground fog or low-level stratus is the main contributor there.

In conclusion, the fog frequency maps give reason to distinguish between three main forest types in French Guiana, associated with different topographic, meteorological and ecological environments:

i) Lowland cloud forest (LCF), occurring below 100 (-200) m, or even above depending on the relative topography, in major river valleys as well as in small ravines and basins, due to frequent formation of radiation fog/valley fog, being the major driver for high epiphyte-richness. Due to the type of cloud, the term "lowland fog forest" (LFF) may be used as a synonym for LCF.

ii) Submontane cloud forest occurring above 400-500 m associated with mountain ridges of the central highlands and isolated hills due to frequent occurrence of orographic fog. Only most exposed sites may be frequently covered by ground-touching stratiform clouds and characterized by high epiphyte-richness, resembling those in TMCFs.

iii) Regular tropical lowland rainforest, restricted to habitats between LCF and submontane cloud forests. Precipitation is the main source of humidity, while water uptake by vascular epiphytes due to fog and mist does not play a significant role.

The environmental processes that have led to the formation of submontane cloud forests in French Guiana might be similar to those in tropical montane cloud forests, where the coincidence of fog and high diversity is well documented (e.g. Hamilton et al. 1995, Richards et al. 1996), as well as the importance of fog in the water budget (e.g. DeLay & Giambelluca 2010, Scholl et al. 2011). In contrast, radiation fog formation in tropical lowland forests follows different physical processes, which have been hitherto only studied more thoroughly by Obregon et al. (2011). Further investigations on fog microphysics and meteorological process enhancing fog formation should therefore be conducted in future studies. Data collected at other Amazonian study sites, such as the flux towers in Paracou, French Guiana (Gourlet-Fleury et al. 2004) and at various sites of the Large Scale Biosphere Atmosphere Experiment in Amazonia (LBA) (Keller et al. 2009) may contribute valuable information.

The spatial distribution of fog frequency in French Guiana shows no correlation with the pattern of average precipitation which is highest in NE areas and lower towards inland. Some rather vague consistencies are found with the map of remotely-sensed forest landscape types in French Guiana (refer to figure 1 in Gond et al. 2011). The area of high valley fog in the windward side of the central mountains coincides with the region of high forest with regular canopy, while the area in the south, where no clear distinction between valley fog and low stratus can be made, is associated with ”mixed high and open forest”. The higher potential of LCF in COPAS-like areas and the less pronounced pattern in the southern part of French Guiana might also be reflected by the north-south gradient of more drought-tolerant species described by Pennec et al. (2011).

The ecological benefits of fog in cloud forests are manifold. The major role plays the additional water supply for the ecosystems (Bruijnzeel et al. 2005). Trees benefit by fog incidence via foliar uptake and prevention of dehydration (Burgess & Dawson 2004, Ponette-Gonzalez et al. 2010), while vascular epiphytic plants in tropical cloud forests, in particular, benefit from the interception of fog water (Hölscher et al. 2004, Nadkarni 1984, Villegas et al. 2008). Since canopy epiphytes heavily depend on atmospheric water deposition and are particularly stressed in the dry season by lower humidity and higher temperature causing high evapotranspiration, the surplus of moisture is of crucial importance (Benzing 1990, Zotz & Hietz 2001). The presence of fog leads to a delayed onset of the stress period and prevents epiphytes from desiccation. The attenuation of global radiation by morning fog may reduce evaporative demand and transpirational losses (Ewing et al. 2009, Ritter et al. 2009). Hence, the fog layer might function as a climatic shelter against unfavourable weather conditions for epiphytes (Obregon et al. 2011).

The role of tropical lowland cloud forests may be especially important when analyzing major drought events and their implications for climate change. Two major droughts have affected the Amazon region in recent years, one in 2005 (Marengo et al. 2008) and another in 2010 (Lewis et al. 2011, Marengo et al. 2011). Generally, global climate models indicate an increase in frequency, intensity and severity of drought events in the Amazon region in this century (Lewis et al. 2011). In particular, it is expected that the dry season will extend in length and increase in intensity, leading to a drying of Amazon forests potentially accelerating climate change through carbon losses and changed surface energy balances (Philips et al. 2009). A significant change of dry season characteristics would in particular effect epiphytic vegetation in LCF due to their strong dependence on meteorological conditions. Epiphytes are very sensitive to environmental changes (Nadkarni & Solani 2002) and have therefore a high significance as bioindicators for climate change (e.g. Benzing 1998, Richter 2003). The mapping of fog frequency in the Amazon region may therefore be of great importance since it can help to identify the putative distribution of LCF, harbouring important bioindicators for a future drying of the Amazon region. Our approach should be taken as a first step towards the accurate mapping of LCF habitats. Further improvements of the retrieval could be realized by incorporating pixel-wise information on TPW, which had to be calculated as an average for the whole domain. Since the proposed scheme does not distinguish between ground-touching clouds (i.e. fog at the ground) and low stratiform clouds, ground fog occurrence may be overestimated and partly attributed to low stratus cloudiness without ground contact. It must also be taken into account that this study was conducted for satellite overpasses between 2 and 3 a.m., where fog formation has not reached its mature stage yet. Therefore, it must be expected that incorporating satellite data covering the time period between 6 a.m. and 7 a.m. would lead to higher fog frequency since fog is most frequent and densest shortly before sunrise (Obregon et al. 2011).

Overall, the paper highlights the need for a thorough understanding of fog dynamics in the tropical lowland. The results indicate that tropical lowland fog and thus, LCF is not only a local phenomenon but could be widely distributed particularly throughout river valleys and basins of the lowland tropics worldwide, with significant consequences for biodiversity mapping in tropical lowland areas. Generally, the findings provide strong evidence for the existence of the “Lowland Cloud Forest“ (LCF) and confirm the assertions of Gehrig-Downie et al. (2011, 2012), Gradstein et al. (2010) and Obregon et al. (2011). Although some caveats remain, the presented fog detection scheme opens up a new route toward the global mapping of tropical lowland cloud forests.

Acknowledgements

This study was performed within the project “Fog climate and epiphyte diversity of the tropical lowland cloud forest of French Guiana”, generously funded by the German Research Foundation (DFG grants BE 1780/13-1 and GR 1588/12-1). We are very grateful to Philippe Gaucher (CNRS Guyane) for logistic help in French Guiana and maintenance of the COPAS climate station. For field work assistance we thank Sebastian Achilles, Rütger Rollenbeck

(University of Marburg), Felix Normann and Patrick Weigelt (University of Göttingen). We also express our gratitude to Michael Lakatos and Alexandra Pardow (University of Kaiserslautern) for fruitful cooperation in the study of the lowland cloud forest of French Guiana.

References

Ackerman, S., Frey, R.A., Strabala, K., Liu, Y., Gumley, L., Baum, B., Menzel, P., 2010. Discriminating clear sky from clouds with MODIS, Algorithm Theoretical Basis Document (MOD35), Version 6.1., available at: http://modis-atmos.gsfc.nasa.gov/reference_atbd.html (last access: 8 March 2014).

Baars, H., Ansmann, A., Althausen, D., Engelmann, R., Heese, B., Muller, D., Artaxo, P., Paixao, M., Pauliquevis, T., Souza, R., 2012. Aerosol profiling with lidar in the Amazon Basin during the wet and dry season. Journal of Geophysical Research-Atmospheres 117.

Barnes, L.R., Schultz, D.M., Gruntfest, E.C., Hayden, M.H., Benight, C.C., 2009. CORRIGENDUM: False Alarm Rate or False Alarm Ratio? Weather and Forecasting 24, 1452-1454.

Bendix, J., 2002. A satellite-based climatology of fog and low-level stratus in Germany and adjacent areas. Atmospheric Research 64, 3-18.

Bendix, J., Bachmann, M., 1991. Ein operationell einsetzbares Verfahren zur Nebelerkennung auf der Basis von AVHRR-Daten der NOAA-Satelliten. Meteorologische Rundschau 43, 169-178.

Bendix, J., Rollenbeck, R., Göttlicher, D., Nauß, T., Fabian, P., 2008. Seasonality and diurnal pattern of very low clouds in a deeply incised valley of the eastern tropical Andes (South Ecuador) as observed by a cost-effective WebCam system. Meteorological Applications 15, 281-291.

Bendix, J., Rollenbeck, R., Palacios, W.E., 2004. Cloud detection in the Tropics - a suitable tool for climate-ecological studies in the high mountains of Ecuador. International Journal of Remote Sensing 25, 4521-4540.

Bendix, J., Thies, B., Cermak, J., Nauß, T., 2005. Ground Fog Detection from Space Based on MODIS Daytime Data—A Feasibility Study. Weather and Forecasting 20, 989-1005.

Beniston, M., 2005. Mountain climates and climatic change: An overview of processes focusing on the European Alps. Pure and Applied Geophysics 162, 1587-1606.

Benzing, D.H., 1990. Vascular Epiphytes. Cambridge University Press, Cambridge.

Benzing, D.H., 1998. Vulnerabilities of Tropical Forests to Climate Change: The Significance of Resident Epiphytes. Climatic Change 39, 519-540.

Bovolo, C.I., Pereira, R., Parkin, G., Kilsby, C., Wagner, T., 2012. Fine-scale regional climate patterns in the Guianas, tropical South America, based on observations and reanalysis data. International Journal of Climatology 32, 1665-1689.

Bruijnzeel, L.A., Eugster, W., Burkard, R., 2005. Fog as a hydrologic input, in: Anderson, M.G. (Ed.), Encyclopedia of Hydrological Sciences. John Wiley, Chichester, UK, pp. 559-582.

Bruijnzeel, L.A., Kappelle, M., Mulligan, M., Scatena, F.N., 2010. Tropical montane cloud forests: state of knowledge and sustainability perspectives in a changing world, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, UK, pp. 691-740.

Bruijnzeel, L.A., Mulligan, M., Scatena, F.N., 2011. Hydrometeorology of tropical montane cloud forests: emerging patterns. Hydrological Processes 25, 465-498.

Bruijnzeel, L.A., Veneklaas, E.J., 1998. Climatic conditions and tropical, montane forest productivity: The fog has not lifted yet. Ecology 79, 3-9.

Bubb, P., May, I., Miles, L., Sayer, J., 2004. Cloud Forest Agenda. UNEP-WCMC, Cambridge, UK.

Burgess, S.S.O., Dawson, T.E., 2004. The contribution of fog to the water relations of Sequoia sempervirens (D. Don): foliar uptake and prevention of dehydration. Plant Cell and Environment 27, 1023-1034.

Cereceda, P., Osses, P., Larrain, H., Farias, M., Lagos, M., Pinto, R., Schemenauer, R.S., 2002. Advective, orographic and radiation fog in the Tarapaca region, Chile. Atmospheric Research 64, 261-271.

Cermak, J., Bendix, J., 2007. Dynamical nighttime fog/low stratus detection based on meteosat SEVIRI data: A feasibility study. Pure and Applied Geophysics 164, 1179-1192.

Cermak, J., Bendix, J., 2008. A novel approach to fog/low stratus detection using Meteosat 8 data. Atmospheric Research 87, 279-292.

Cermak, J., Bendix, J., 2011. Detecting ground fog from space - a microphysics-based approach. International Journal of Remote Sensing 32, 3345-3371.

De Araújo, A.C., 2009. Spatial variation of CO 2 fluxes and lateral transport in an area of terra firme forest in Central Amazonia. VU University Amsterdam, Netherlands.

De Granville, J.-J., 1991. Remarks on the Montane Flora and Vegetation Types of the Guianas. Willdenowia 21, 201-213.

De Granville, J.-J., 1999. Palms of French Guiana Diversity, distribution, ecology and uses. Acta Botanica Venezuelica 22, 109-125.

De Reu, J., Bourgeois, J., Bats, M., Zwertvaegher, A., Gelorini, V., De Smedt, P., Chu, W., Antrop, M., De Maeyer, P., Finke, P., Van Meirvenne, M., Verniers, J., Crombe, P., 2013. Application of the topographic position index to heterogeneous landscapes. Geomorphology 186, 39-49.

Dee, D.P., Uppala, S.M., Simmons, A.J., Berrisford, P., Poli, P., Kobayashi, S., Andrae, U., Balmaseda, M.A., Balsamo, G., Bauer, P., Bechtold, P., Beljaars, A.C.M., van de Berg, L., Bidlot, J., Bormann, N., Delsol, C., Dragani, R., Fuentes, M., Geer, A.J., Haimberger, L., Healy, S.B., Hersbach, H., Holm, E.V., Isaksen, L., Kallberg, P., Kohler, M., Matricardi, M., McNally, A.P., Monge-Sanz, B.M., Morcrette, J.J., Park, B.K., Peubey, C., de Rosnay, P., Tavolato, C., Thepaut, J.N., Vitart, F., 2011. The ERA-Interim reanalysis: configuration and performance of the data assimilation system. Quarterly Journal of the Royal Meteorological Society 137, 553-597.

DeLay, J.K., Giambelluca, T.W., 2010. History of fog and cloud water interception research in Hawaii, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 332-341.

Duynkerke, P.G., 1991. Radiation Fog: A Comparison of Model Simulation with Detailed Observations. Monthly Weather Review 119, 324-341.

Ellrod, G.P., 1995. Advances in the Detection and Analysis of Fog at Night Using GOES Multispectral Infrared Imagery. Weather and Forecasting 10, 606-619.

Ewing, H.A., Weathers, K.C., Templer, P.H., Dawson, T.E., Firestone, M.K., Elliott, A.M., Boukili, V.K.S., 2009. Fog Water and Ecosystem Function: Heterogeneity in a California Redwood Forest. Ecosystems 12, 417-433.

Eyre, J.R., Brownscombe, J.L., Allam, R.J., 1984. Detection of fog at night using Advanced Very High-Resolution Radiometer (AVHRR) Imagery. Meteorological Magazine 113, 266-271.

Fitzjarrald, D.R., Lala, G.G., 1989. Hudson Valley Fog Environments. Journal of Applied Meteorology 28, 1303-1328.

Foster, P., 2010. Changes in mist immersion, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 57-66.

Frahm, J.-P., Gradstein, S.R., 1991. An Altitudinal Zonation of Tropical Rain Forests Using Byrophytes. Journal of Biogeography 18, 669-678.

Gao, B.C., Kaufman, Y.J., 2003. Water vapor retrievals using moderate resolution Imaging spectroradiometer (MODIS) near-infrared channels. Journal of Geophysical Research-Atmospheres 108, 10.

Garcia-Garcia, F.G., Zarraluqui, V., 2008. A Fog Climatology for Mexico. Erde 139, 45-60.

Gehrig-Downie, C., Marquardt, J., Obregon, A., Bendix, J., Gradstein, S.R., 2012. Diversity and vertical distribution of filmy ferns as a tool for identifying the novel forest type “tropical lowland cloud forst”. Ecotropica 18, 35-44.

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, R., 2013. Diversity and vertical distribution of epiphytic liverworts in lowland rain forest and lowland cloud forest of French Guiana. Journal of Bryology 35, 243-254.

Gehrig-Downie, C., Obregon, A., Bendix, J., Gradstein, S.R., 2011. Epiphyte Biomass and Canopy Microclimate in the Tropical Lowland Cloud Forest of French Guiana. Biotropica 43, 591-596.

Gibbs, A.K., Barron, C.N., 1993. The geology of the Guiana Shield. Oxford University Press, New York.

Golding, B.W., 1993. A Study of the Influence of Terrain on Fog Development. Monthly Weather Review 121, 2529-2541.

Gomez-Peralta, D., Oberbauer, S.F., McClain, M.E., Philippi, T.E., 2008. Rainfall and cloud-water interception in tropical montane forests in the eastern Andes of Central Peru. Forest Ecology and Management 255, 1315-1325.

Gond, V., Freycon, V., Molino, J.F., Brunaux, O., Ingrassia, F., Joubert, P., Pekel, J.F., Prevost, M.F., Thierron, V., Trombe, P.J., Sabatier, D., 2011. Broad-scale spatial pattern of forest landscape types in the Guiana Shield. International Journal of Applied Earth Observation and Geoinformation 13, 357-367.

Gourlet-Fleury, S., Guehl, J.M., Laroussinie, O., 2004. Ecology and management of a neotropical rainforest : lessons drawn from Paracou, a long-term experimental research site in French Guiana. Elsevier, Paris.

Gradstein, S.R., Obregon, A., Gehrig, C., Bendix, J., 2010. Tropical lowland cloud forest: a neglected forest type, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 329-338.

Grimaldi, M., Riéra, B., 2001. Geography and Climate, in: Bongers, F., Charles-Dominique, P., Forget, P.-M., Théry, T. (Eds.), Nouragues: Dynamics and Plant-Animal Interactions in a Neotropical Rainforest. Kluwer, Dordrecht, The Netherlands, pp. 9-18.

Guisan, A., Weiss, S.B., Weiss, A.D., 1999. GLM versus CCA spatial modeling of plant species distribution. Plant Ecology 143, 107-122.

Gultepe, I., Tardif, R., Michaelides, S.C., Cermak, J., Bott, A., Bendix, J., Muller, M.D., Pagowski, M., Hansen, B., Ellrod, G., Jacobs, W., Toth, G., Cober, S.G., 2007. Fog research: A review of past achievements and future perspectives. Pure and Applied Geophysics 164, 1121-1159.

Hamilton, L.S., 1995. Mountain Cloud Forest Conservation and Research: A Synopsis. Mountain Research and Development 15, 259-266.

Hamilton, L.S., Juvik, J.O., Scatena, F.N., 1995. Tropical Montane Cloud Forests. Springer Verlag, New York.

Hammond, D.S., 2005. Biophysical features of the Guiana shield, in: Hammond, D.S. (Ed.), Tropical forests of the Guiana shield: ancient forests in a modern world. CABI Publishing, Wallingford, pp. 15-194.

Hölscher, D., Köhler, L., van Dijk, A.I.J.M., Bruijnzeel, L.A., 2004. The importance of epiphytes to total rainfall interception by a tropical montane rain forest in Costa Rica. Journal of Hydrology 292, 308-322.

Jarvis, A., Mulligan, M., 2010. The climate of cloud forests, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 39-56.

Kamara, S.I., 1989. Diurnal and seasonal variations of fog over Sierra Leone. Singapore Journal of Tropical Geography 10, 160-169.

Kapos, V., Rhind, J., Edwards, M., Ravilious, C., Price, M.F., 2000. Developing a Map of the Worlds Mountain Forests, in: Price, M.F., Butt, N. (Eds.), Forests in a Sustainable Mountain Environment: A state of knowledge report for 2000. CAB International, Wallingford, pp. 4-9.

Keller, M., Bustamante, M., Gash, J., Silva Dias, P., 2009. Amazonia and Global Change. AGU Press.

Key, J.R., Schweiger, A.J., 1998. Tools for atmospheric radiative transfer: Streamer and FluxNet. Computers & Geosciences 24, 443-451.

Kriebel, K.T., Gesell, G., Kastner, M., Mannstein, H., 2003. The cloud analysis tool APOLLO: improvements and validations. International Journal of Remote Sensing 24, 2389-2408.

Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M.F., Nepstad, D., 2011. The 2010 Amazon Drought. Science 331, 554-554.

Liu, W.J., Wang, P.Y., Liu, W.Y., Li, J.T., Li, P.J., 2008. The importance of radiation fog in the tropical seasonal rain forest of Xishuangbanna, south-west China. Hydrology Research 39, 79-87.

Luis, J.F., 2007. Mirone: A multi-purpose tool for exploring grid data. Computers & Geosciences 33, 31-41.

Marengo, J.A., Nobre, C.A., Tomasella, J., Oyama, M.D., Sampaio de Oliveira, G., de Oliveira, R., Camargo, H., Alves, L.M., Brown, I.F., 2008. The Drought of Amazonia in 2005. Journal of Climate 21, 495-516.

Marengo, J.A., Tomasella, J., Alves, L.M., Soares, W.R., Rodriguez, D.A., 2011. The drought of 2010 in the context of historical droughts in the Amazon region. Geophysical Research Letters 38, L12703.

Montfoort, D., Ek, R., 1990. Vertical distribution and ecology of epiphytic bryophytes and lichens in a lowland rain forest in French Guiana, Institute of Systematic Botany, Utrecht.

Nadkarni, N.M., 1984. Epiphyte Biomass and Nutrient Capital of a Neotropical Elfin Forest. Biotropica 16, 249-256.

Nadkarni, N.M., Solano, R., 2002. Potential effects of climate change on canopy communities in a tropical cloud forest: an experimental approach. Oecologia 131, 580-586.

Nauss, T., Bendix, J., 2005. An operational MODIS processing scheme for PC dedicated to direct broadcasting applications in meteorology and earth sciences. Computers & Geosciences 31, 804-808.

Normann, F., Weigelt, P., Gehrig-Downie, C., Gradstein, S.R., Sipman, H.J.M., Obregon, A., Bendix, J., 2010. Diversity and vertical distribution of epiphytic macrolichens in lowland rain forest and lowland cloud forest of French Guiana. Ecological Indicators 10, 1111-1118.

Obregon, A., Gehrig-Downie, C., Gradstein, S.R., Rollenbeck, R., Bendix, J., 2011. Canopy level fog occurrence in a tropical lowland forest of French Guiana as a prerequisite for high epiphyte diversity. Agricultural and Forest Meteorology 151, 290-300.

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.

Pardow, A., Lakatos, M., 2013. Desiccation Tolerance and Global Change: Implications for Tropical Bryophytes in Lowland Forests. Biotropica 45, 27-36.

Peel, M.C., Finlayson, B.L., McMahon, T.A., 2007. Updated world map of the Koppen-Geiger climate classification. Hydrology and Earth System Sciences 11, 1633-1644.

Pennec, A., Gond, V., Sabatier, D., 2011. Tropical forest phenology in French Guiana from MODIS time series. Remote Sensing Letters 2, 337-345.

Phillips, O.L., Aragão, L.E.O.C., Lewis, S.L., Fisher, J.B., Lloyd, J., López-González, G., Malhi, Y., Monteagudo, A., Peacock, J., Quesada, C.A., van der Heijden, G., Almeida, S., Amaral, I., Arroyo, L., Aymard, G., Baker, T.R., Bánki, O., Blanc, L., Bonal, D., Brando, P., Chave, J., de Oliveira, Á.C.A., Cardozo, N.D., Czimczik, C.I., Feldpausch, T.R., Freitas, M.A., Gloor, E., Higuchi, N., Jiménez, E., Lloyd, G., Meir, P., Mendoza, C., Morel, A., Neill, D.A., Nepstad, D., Patiño, S., Peñuela, M.C., Prieto, A., Ramírez, F., Schwarz, M., Silva, J., Silveira, M., Thomas, A.S., Steege, H.t., Stropp, J., Vásquez, R., Zelazowski, P., Dávila, E.A., Andelman, S., Andrade, A., Chao, K.-J., Erwin, T., Di Fiore, A., C, E.H., Keeling, H., Killeen, T.J., Laurance, W.F., Cruz, A.P., Pitman, N.C.A., Vargas, P.N., Ramírez-Angulo, H., Rudas, A., Salamão, R., Silva, N., Terborgh, J., Torres-Lezama, A., 2009. Drought Sensitivity of the Amazon Rainforest. Science 323, 1344-1347.

Ponette-Gonzalez, A.G., Weathers, K.C., Curran, L.M., 2010. Water inputs across a tropical montane landscape in Veracruz, Mexico: synergistic effects of land cover, rain and fog seasonality, and interannual precipitation variability. Global Change Biology 16, 946-963.

Richards, P.W., 1984. The ecology of tropical forest bryophytes, in: Schuster, R.M. (Ed.), New manual of bryology. Hattori Botanical Laboratory, Nichinan, Japan, pp. 1233-1270.

Richards, P.W., Walsh, R.P.D., Baillie, I.C., Greig-Smith, P., 1996. The tropical rain forest an ecological study (2nd edition). Cambridge University Press, Cambridge.

Richter, M., 2003. Using epiphytes and soil temperatures for eco-climatic interpretations in southern Ecuador. Erdkunde 57, 161-118.

Richter, M., Beck, E., Rollenbeck, R., Bendix, J., 2013. The study area, in: Bendix, J., Beck, E., Bräuning, A., Makeschin, F., Mosandl, R., Scheu, S., Wilcke, W. (Eds.), Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador. Springer, Berlin, Heidelberg, New York, pp. 3-18.

Ritter, A., Regalado, C.M., Aschan, G., 2009. Fog reduces transpiration in tree species of the Canarian relict heath-laurel cloud forest (Garajonay National Park, Spain). Tree Physiology 29, 517-528.

Roach, W.T., Brown, R., Caughey, S.J., Garland, J.A., Readings, C.J., 1976. The physics of radiation fog: I – a field study. Quarterly Journal of the Royal Meteorological Society 102, 313-333.

Saunders, R.W., 1986. An automated scheme for the removal of cloud contamination from AVHRR radiances over western Europe. International Journal of Remote Sensing 7, 867-886.

Saunders, R.W., Kriebel, K.T., 1988. An improved method for detecting clear sky and cloudy radiances from AVHRR data. International Journal of Remote Sensing 9, 123-150.

Savtchenko, A., Ouzounov, D., Ahmad, S., Acker, J., Leptoukh, G., Koziana, J., Nickless, D., Burrows, J.P., Thompson, A.M., 2004. Terra and aqua MODIS products available from NASA GES DAAC. Trace Constituents in the Troposphere and Lower Stratosphere 34, 710-714.

Scatena, F.N., Bruijnzeel, L.A., Bubb, P., Das, S., 2010. Setting the stage, in: Bruijnzeel, L.A., Scatena, F.N., Hamilton, L.S. (Eds.), Tropical Montane Cloud Forests: Science for Conservation and Management. Cambridge University Press, Cambridge, pp. 3-12.

Scholl, M., Eugster, W., Burkard, R., 2011. Understanding the role of fog in forest hydrology: stable isotopes as tools for determining input and partitioning of cloud water in montane forests. Hydrological Processes 25, 353-366.

Seemann, S.W., Li, J., Menzel, W.P., Gumley, L.E., 2003. Operational retrieval of atmospheric temperature, moisture, and ozone from MODIS infrared radiances. Journal of Applied Meteorology 42, 1072-1091.

Stadtmüller, T., 1987. Cloud Forests in the Humid Tropics: A Bibliographic Review. United Nations University Press.

Tomasi, C., Vitale, V., De Santis, L.V., 1998. Relative optical mass functions for air, water vapour, ozone and nitrogen dioxide in atmospheric models presenting different latitudinal and seasonal conditions. Meteorology and Atmospheric Physics 65, 11-30.

Turner, J., Allam, R.J., Maine, D.R., 1986. A Case Study of the Detection of Fog at Night Using Channel 3and 4 On the Advanced Very High Resolution Radiometer (AVHRR). Meteorological Magazine 115, 285-290.

Underwood, S.J., Ellrod, G.P., Kuhnert, A.L., 2004. A multiple-case analysis of nocturnal radiation-fog development in the Central Valley of California utilizing the GOES nighttime fog product. Journal of Applied Meteorology 43, 297-311.

USGS, 2006. Shuttle Radar Topography Mission, 3 Arc Second, Filled Finished-A 2.0, WRS-2 Tiles. Global Land Cover Facility, University of Maryland, College Park, Maryland.

Villegas, J.C., Tobón, C., Breshears, D.D., 2008. Fog interception by non-vascular epiphytes in tropical montane cloud forests: dependencies on gauge type and meteorological conditions. Hydrological Processes 22, 2484-2492.

Weiss, A.D., 2001. Topographic position and landforms analysis, ESRI Users Conference, San Diego, CA.

Whitmore, T.C., 1998. An Introduction to Tropical RainForests (2nd Edition). Clarendon Press, Oxford.

Wilson, M.F.J., O'Connell, B., Brown, C., Guinan, J.C., Grehan, A.J., 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. Marine Geodesy 30, 3-35.

Wolf, J.H.D., 1993. Diversity Patterns and Biomass of Epiphytic Bryophytes and Lichens Along an Altitudinal Gradient in the Northern Andes. Annals of the Missouri Botanical Garden 80, 928-960.

Zadroga, F., 1981. The hydrological importance of a montane cloud forest area of Costa Rica, in: Lal, R., Russell, E.W. (Eds.), Tropical Agricultural Hydrology. John Wiley, New York, pp. 59-73.

Zotz, G., Hietz, P., 2001. The physiological ecology of vascular epiphytes: current knowledge, open questions. Journal of Experimental Botany 52, 2067-2078.

7 Summary and Outlook

7.1 Summary

Tropical cloud forests are characterized by high epiphyte diversity and abundance with a crucial driver for this being the frequent occurrence of fog that constitutes an additional water source for epiphytic vegetation. The ecological value of fog in these ecosystems is widely recognized and although tropical cloud forests in montane regions are known to be biodiverse and abundant in epiphytes, recent work indicates similar levels of both diversity and abundance in tropical lowland systems. An important question is whether fog plays a similar role in lowland systems as it does in montane areas, particularly since the physical mechanisms for fog formation in the tropical lowland are not well understood.

The major aim of the present study was to provide an in-depth investigation of the fog phenomenon in French Guiana, including the spatio-temporal fog dynamics, and with this, to enhance the understanding of the impact of fog on epiphytic vegetation in tropical lowland forests. The main hypotheses suggest the frequent occurrence of radiation fog in valley forests throughout French Guiana, supported by nocturnal katabatic flows, and the formation of the epiphyte-rich "tropical lowland cloud forest" (LCF) as a new vegetation unit, which is restricted to areas frequently affected by fog.

Testing these hypotheses required a specific experimental setup, an interdisciplinary approach and the development of a novel fog detection scheme. The objectives and results of the three work packages are as follows:

1. First, the causes of fog formation in the tropical lowland and the underlying meteorological processes were analysed. The main subject of the study was to reveal the physical conditions involved in the fog formation, including fog type, fog persistence, fog frequency, and to determine the meteorological parameters triggering the process of fog development. Measurements of the meteorological conditions at canopy level gave evidence of the frequent occurrence of radiation fog in the study area. It could be demonstrated that fog is a regularly occurring phenomenon at night time and early morning, with a clear

diurnal course and a maximum before sunrise. Fog formation was primarily caused by strong cooling at night due to longwave radiation losses leading to saturation of air and triggered by nocturnal cold air drainage and the provision of moisture through precipitation events the day before. The frequent occurrence of heavy rain is expected to lead to water-logging in valleys, and hence higher soil moisture, greater evapotranspiration and higher water content of air, fostering the formation of fog. Additional factors that have been identified to contribute to the fog formation include negligible wind speed, very low turbulence at night, a generally undulating terrain with many hills and small river valleys supportive of the formation of katabatic flows, and the proximity to the Atlantic coast, facilitating a constant moisture supply.

2. Next, the microclimatic differences between forest in valleys (LCF) and ridges (LRF) were investigated with the objective to reveal the impacts of fog formation on epiphytic vegetation. The microclimate data gathered in this study showed that during both wet and dry seasons mean diurnal relative air humidity was higher in LCF than in LRF at night and early morning. A strong correlation between fog events and RH, and large differences in leaf wetness duration in LCF and LRF indicate that fog is a rare phenomenon for elevated terrain. Further, it could be demonstrated that the interface between the tropical forest canopy and the atmospheric boundary layer seems to foster the formation of radiation fog since the dense canopy of the tropical lowland forest inhibits cold air diffusion to lower canopy levels. Microclimatic conditions correlated with epiphyte diversity, biomass and abundance, with LCF featuring significant higher values as compared to adjacent LRF. Some species restricted to the understory of LRF showed an upward shift in distribution towards the canopy in LCF.

   The ecological benefits of fog for the epiphytes in LCF are manifold. At first, the occurrence of fog constitutes a direct additional input of liquid water for epiphytes. Furthermore, fog events lead to a prolonged availability of high air humidity and facilitate a surplus of moisture. A result is a delayed onset and significant shortening of the stress period, which is of particular importance in the dry season. It is suggested that this goes along with a shortening of the periods of photosynthetic inactivity and desiccation. The persistence of high RH after sunrise was significantly longer in LCF and favours epiphytes in their establishment and growth. The fog layer itself may also provide a protection against radiation and hence evaporative loss, preventing epiphytes from desiccation. In contrast, it was evident that microclimatic conditions on hill sites are generally less suitable for epiphytes due to higher wind speed, higher evaporation caused by more open canopies, and the resulting lack of fog events.

3. Finally, a novel algorithm for the detection of fog/low stratus in tropical lowland forests was developed based on MODIS satellite data. The objective of this study was to reveal the spatio-temporal dynamics of fog in French Guiana and thereby to identify potential habitats of the epiphyte-rich tropical lowland cloud forest. The proposed scheme is based on previous algorithms relying on brightness temperature differences between thermal and mid-infrared bands. Major challenges for a proper detection scheme for the study area included the small-scale nature of fog and the varying atmospheric moisture conditions. Theoretical calculations by means of a radiative transfer model, as well as a discriminant analysis using ground truth measurements, demonstrated the dependency of thresholds of brightness temperature differences on total precipitable water (TPW) and the terrain-induced maximum possible sub-pixel fog coverage. The novel scheme accounts for dynamical thresholds depending on moisture conditions and potential fog extent for each pixel and satellite scene. The proposed method has shown effective in discriminating fog from fog-free areas. Validation with ground fog measurements indicated that fixed-threshold methods were clearly outperformed by the novel detection scheme in terms of the capability to detect sub-pixel fog coverage under varying TPW. The derived maps of fog/low stratus frequency in French Guiana indicate a widespread distribution of night-time fog in river valleys throughout the country.

The first hypothesis concerning the frequent spatio-temporal occurrence of valley fog could be verified by the statistical assessments of the meteorological data derived in the field and the results of the satellite-based fog-detection scheme. The identified meteorological processes confirm the hypothesised mechanism of radiation fog formation and demonstrated that katabatic flows play a role. Therefore, nocturnal cold air drainage, typical in complex terrains of the midlatitudes, should also be regarded as a trigger of fog formation in the tropical lowland.

The integrative assessment of canopy microclimate and epiphyte parameters verifies the second hypothesis. It was demonstrated that epiphyte diversity, abundance and biomass are significantly higher in valley forest as a consequence of a more favourable canopy microclimate due to frequent fog episodes. These findings provide strong evidence for the existence of the hitherto neglected tropical lowland cloud forest as a novel forest type. Thus, the results indicate that LCF and LRF should no longer be viewed as a single formation. Epiphyte diversity and distribution in LCF and LRF may represent useful characteristics for discriminating these forests. Further, the results indicate that the region of frequent occurrence of radiation fog in French Guiana can be regarded as optimum habitat for tropical lowland cloud forests.

Overall, both hypotheses of this study can be confirmed. The investigations of the presented work have shown that fog formation is a regularly occurring phenomenon in space and time in French Guiana with significant impacts for epiphytic vegetation.

7.2 Outlook

This study has enhanced the understanding of the role of fog in tropical lowland forests and paved the way towards future studies. The work on the meteorological processes leading to fog formation could be complemented by future systematic research on physical and chemical fog properties as well as on the role of fog in the local and regional water cycle. Direct measurements of liquid water content and fog droplet distributions could be conducted to estimate fog water fluxes. Direct sampling of fog water, e.g. by the use of a fog collector, would be a means to study fog chemistry. Measuring plant weight increase would enable the estimation of fog deposition rates. Environmental isotope analysis could be used as a tool to quantify the portion of fog and rain water as a resource for epiphytic vegetation.

The sensitivity of epiphytes to humidity and fog water supply has been underlined in this study and indicates that a closer investigation of their role as bioindicactors for climate change may have value. Observations over recent decades indicate an increased dry-season length in the Amazon region and suggest a drying trend, in particular in the southern parts (Fu et al. 2013). The vegetation canopy of the Amazon rainforest is highly sensitive to changes in precipitation patterns and vegetation greenness across large parts of Amazonia has already diminished (Hilker et al. 2014). Global climate models predict that the Amazon region will experience an increase in frequency, intensity and severity of drought events in this century (Lewis et al. 2011). Epiphytes are known for their vulnerability to global climate change (Benzing 1998, Zotz & Bader 2009) and it can be expected that they will be among the first group to be affected by an ongoing drying trend. The fragile ecology means they are generally ill equipped to deal with the changing climate. The observed differences in diversity and distribution of epiphytic bryophytes, lichens and filmy ferns in LCF and LRF highlight their potential use as indicators of tropical lowland cloud forest. More generally, indicator taxa of the tropical lowland cloud forest could serve as bioindicators for a future drying of the Amazon region.

Lastly, the current work has produced a satellite-based fog detection scheme which has laid the groundwork for improving algorithms for the detection of valley fog. Improvements of the provided technique in the short term are expected to be achieved by selecting satellite data with overpass times that match the mature stage of fog development in the early morning, when fog is most frequent and dense. Incorporating pixel-wise information on TPW is expected to have a positive effect on accuracy. Information on the cloud base height would be crucial to identify the presence of fog at the ground. In the long term, new technologies such as sensors with higher spatial resolution or new methods such as data fusion with radar and lidar observations or model data will improve the discrimination between low stratiform and ground-touching clouds and contribute to a more reliable detection of ground fog in tropical lowland forests. Thus, it must be expected that the accurate detection of small-scale fog in the tropical lowland and hence the mapping of potential habitats of the tropical lowland cloud forest will become feasible on a global scale.

References

Benzing, D.H., 1998. Vulnerabilities of Tropical Forests to Climate Change: The Significance of Resident Epiphytes. Climatic Change 39, 519-540.

Fu, R., Yin, L., Li, W., Arias, P.A., Dickinson, R.E., Huang, L., Chakraborty, S., Fernandes, K., Liebmann, B., Fisher, R., Myneni, R.B., 2013. Increased dry-season length over southern Amazonia in recent decades and its implication for future climate projection. Proceedings of the National Academy of Sciences of the United States of America 110, 18110-18115.

Hilker, T., Lyapustin, A.I., Tucker, C.J., Hall, F.G., Myneni, R.B., Wang, Y., Bi, J., Mendes de Moura, Y., Sellers, P.J., 2014. Vegetation dynamics and rainfall sensitivity of the Amazon. Proceedings of the National Academy of Sciences of the United States of America 111, 16041-16046.

Lewis, S.L., Brando, P.M., Phillips, O.L., van der Heijden, G.M.F., Nepstad, D., 2011. The 2010 Amazon Drought. Science 331, 554-554.

Zotz, G., Bader, M.Y., 2009. Epiphytic Plants in a Changing World-Global: Change Effects on Vascular and Non-Vascular Epiphytes. Progress in Botany 70 70, 147-170.

Zusammenfassung

Tropische Nebelwälder sind gekennzeichnet durch hohe Diversität und Abundanz von Epiphyten. Ein wichtiger Faktor ist hierfür das häufige Auftreten von Nebel, der eine zusätzliche Wasserquelle für die epiphytische Vegetation darstellt. Der ökologische Wert von Nebel in diesen Ökosystemen ist allgemein anerkannt. Obwohl Nebelwälder in tropischen Bergregionen für ihre Biodiversität und Abundanz an Epiphyten bekannt sind, weisen neuere Studien auf ein ähnlich hohes Niveau an Diversität und Abundanz in tropischen Tiefland-Systemen hin. Eine wichtige Frage ist hierbei, ob Nebel in Tiefland-Systemen eine ähnliche Rolle wie in Bergregionen spielt, insbesondere da die physikalischen Prozesse der Nebelbildung im tropischen Tiefland bisher wenig verstanden sind.

Hauptziel der vorliegenden Arbeit war eine umfassende Untersuchung des Nebelphänomens in Französisch-Guyana, einschließlich der raum-zeitlichen Nebeldynamik, und somit ein besseres Verständnis der Auswirkung von Nebel auf die epiphytische Vegetation in tropischen Tieflandwäldern. Die Hypothesen dieser Arbeit umfassen das häufige Auftreten von Strahlungsnebel in Tieflandwäldern in Französisch-Guyana, unterstützt von nächtlichen Kaltluftabflüssen, sowie die Bildung des epiphytenreichen „Tieflandnebelwaldes“ (LCF) als neue Vegetationseinheit, beschränkt auf Gebiete unter häufigem Nebeleinfluss.

Die Überprüfung der Hypothesen erforderte ein spezifisches Messdesign, einen interdisziplinären Ansatz sowie die Entwicklung eines neuartigen Verfahrens zur Nebelerkennung. Die Ziele und Ergebnisse der drei Arbeitspakete sind im Einzelnen:

1. Zunächst wurden die Ursachen der Nebelbildung im tropischen Tiefland und die zugrundeliegenden meteorologischen Prozesse analysiert. Das Ziel der Studie war die Identifizierung der physikalischen Bedingungen im Zusammenhang mit der Nebelbildung, einschließlich Nebeltyp, Nebeldauer, Nebelhäufigkeit und die Bestimmung der meteorologischen Parameter, die für die Auslösung der Nebelbildung verantwortlich zeichnen. Messungen der meteorologischen Bedingungen auf Niveau des Kronendaches belegten das häufige Auftreten von Nebel im Untersuchungsgebiet. Es konnte gezeigt werden, dass Nebel ein regelmäßig auftretendes Phänomen in

der Nacht und am frühen Morgen ist, mit einem deutlichen zeitlichen Verlauf und einem Maximum kurz vor Sonnenaufgang. Die Nebelbildung war hauptsächlich verursacht durch starke nächtliche Abkühlung aufgrund langwelliger Strahlungsverluste und wurde begünstigt durch nächtliche Kaltluftabflüsse sowie die Verfügbarkeit von Feuchte durch Niederschlagsereignisse am Vortag. Es wird angenommen, dass das häufige Auftreten von Starkniederschlägen zu Staunässe in Tälern führt, und somit zu höherer Bodenfeuchte, einer höheren Verdunstung und einem höheren Wassergehalt der Luft, welches die Bildung von Nebel fördert. Als zusätzlich zur Nebelbildung beitragende Faktoren wurden identifiziert: eine sehr geringe nächtliche Windgeschwindigkeit und geringe Turbulenz, ein generell welliges Relief mit vielen Hügeln und kleinen Flusstälern, das die Bildung katabatischer Flüsse ermöglicht, sowie die Nähe zur Atlantischen Küste, die einen permanenten Feuchtezufluss gewährleistet.

2. Anschließend wurden die mikroklimatischen Unterschiede zwischen Wäldern in Tallagen (LCF) und auf den Randhöhen (LRF) untersucht, mit dem Ziel, den Einfluss der Nebelbildung auf die epiphytische Vegetation zu bestimmen. Die in dieser Studie erhobenen Daten zum Mikroklima zeigten eine höhere mittlere relative Luftfeuchtigkeit in der Nacht als auch am frühen Morgen in LCF im Vergleich zu LRF, sowohl für die Trockenzeit als auch für die Regenzeit. Eine hohe Korrelation zwischen Nebelereignissen und relativer Luftfeuchtigkeit, sowie große Unterschiede der Blattfeuchtedauer in LCF und LRF weisen darauf hin, dass Nebel ein seltenes Phänomen in höheren Lagen ist. Darüber hinaus konnte gezeigt werden, dass der Schnittstellenbereich zwischen tropischem Kronendach und der atmosphärischen Grenzschicht die Bildung von Strahlungsnebel begünstigt, da das dichte Kronendach des tropischen Tieflandwaldes das Eindringen kalter Luft in tiefere Bereiche des Kronendaches hemmt. Mikroklimatische Bedingungen korrelierten mit Epiphytendiversität, -abundanz und -biomasse, mit signifikant höheren Werten in LCF als in angrenzendem LRF. Einige Arten, die auf den Unterwuchs in LRF beschränkt sind, zeigten eine Verschiebung der Verteilung in Richtung des Kronendaches in LCF.
   Der ökologische Nutzen von Nebel für Epiphyten in LCF ist vielfältig. Zunächst stellt der Nebel eine direkte, zusätzliche Quelle an Flüssigwasser für die Epiphyten dar. Darüber hinaus führen Nebelereignisse zu einer verlängerten Verfügbarkeit hoher relativer

Luftfeuchtigkeit und ermöglichen ein zusätzliches Feuchteangebot. Das Ergebnis ist ein verzögertes Einsetzen und somit Verkürzung der Stressperiode, welches insbesondere in der Trockenzeit von Bedeutung ist. Es liegt nahe, dass dies mit einer verkürzten Phase photosynthetischer Inaktivität und Austrocknung einhergeht. Die Andauer hoher relativer Luftfeuchtigkeit nach Sonnenaufgang war signifikant höher in LCF und begünstigt die Etablierung und das Wachstum der Epiphyten. Die Nebelschicht selbst kann ebenfalls ein Schutz gegen Strahlung und somit vor Verdunstungsverlusten darstellen, der die Epiphyten vor Austrocknung bewahrt. Im Gegensatz dazu konnte belegt werden, dass die mikroklimatischen Bedingungen auf den Randhöhen generell weniger günstig für Epiphyten sind aufgrund höherer Windgeschwindigkeit, höherer Verdunstung durch ein offeneres Kronendach und das daraus resultierende Fehlen von Nebelereignissen.

3. Abschließend wurde ein auf MODIS-Satellitendaten basierendes, neuartiges Verfahren für die Detektierung von Nebel/niedgrigem Stratus entwickelt. Ziel dieser Studie war die Untersuchung der raum-zeitlichen Nebeldynamik in Französisch Guyana und somit die Identifizierung möglicher Habitate des epiphytenreichen tropischen Tieflandnebelwaldes. Das entwickelte Verfahren baut auf bisherigen Algorithmen auf, die auf Unterschieden der Helligkeitstemperatur zwischen Kanälen im thermalen und nahen Infrarot basieren. Herausforderungen für ein geeignetes Verfahren im Untersuchungsgebiet stellten die generell kleinräumige Nebelstruktur und die schwankenden atmosphärischen Feuchtezustände dar. Theoretische Berechnungen anhand von Strahlungstransfermodellen sowie eine Diskriminanzanalyse basierend auf Bodenmessungen, zeigten die Abhängigkeit der Schwellenwerte der Helligkeitstemperatur-Unterschiede vom maximal niederschlagbaren Wasser (TPW) und von der topographie-abhängigen maximal möglichen Nebelausdehnung im Subpixel-Bereich. Das neue Verfahren berücksichtigt dynamische Schwellenwerte je nach Feuchtezustand der Atmosphäre und möglicher Nebelausdehnung für jedes Pixel und Satellitenszene. Mit dem vorgelegten Verfahren konnte die effektive Trennung von Nebel und Nebel-freien Gebieten demonstriert werden. Die Validierung anhand von Bodennebel-Messungen zeigte deutlich bessere Ergebnisse des neuen Verfahrens im Vergleich zu Methoden basierend auf festen Schwellenwerten hinsichtlich der Erkennung von Nebel im Subpixelbereich unter schwankendem TPW. Die

> abgeleiteten Karten der Häufigkeit von Nebel/niedrigem Stratus zeigen ein landesweites Vorkommen von nächtlichem Nebel in Flusstälern Französisch-Guyanas.

Die erste Hypothese, hinsichtlich der hohen raum-zeitlichen Frequenz von Talnebel konnte anhand der statistischen Auswertungen der meteorologischen Daten sowie der Ergebnisse des satelliten-basierten Nebelerkennungs-Verfahrens verifiziert werden. Die herausgearbeiteten meteorologischen Prozesse bestätigen den vermuteten Mechanismus der Bildung von Strahlungsnebel und zeigten, dass katabatische Flüsse eine Rolle spielen. Daher sollten nächtliche Kaltluftabflüsse, welche typisch in komplexem Gelände der Mittelbreiten sind, auch als ein Auslöser der Nebelbildung im tropischen Tiefland betrachtet werden.

Die integrative Bewertung von Mikroklima im Kronenbereich und der epiphytischen Parameter verifizieren die zweite Hypothese. Es wurde belegt, dass Epiphytendiversität, -abundanz und –biomasse signifikant höhere Werte in Wäldern in Tallagen aufweisen infolge eines günstigeren Mikrolimas im Kronenbereich aufgrund häufiger Nebelereignisse. Die Resultate liefern einen deutlichen Beleg für die Existenz des bisher vernachlässigten tropischen Tieflandnebelwaldes als neuer Waldtyp. Demzufolge belegen die Ergebnisse, dass LCF und LRF nicht länger als zusammengehörige Einheit betrachtet werden sollten. Epiphytendiversität und – verteilung in LCF und LRF könnten nützliche Eigenschaften darstellen, um zwischen diesen beiden Waldtypen zu differenzieren. Ferner zeigen die Befunde, dass Gebiete mit häufiger Bildung von Strahlungsnebel als optimale Habitate für tropische Tieflandnebelwälder betrachtet werden können.

Zusammengefasst können die beiden zentralen Hypothesen dieser Arbeit bestätigt werden. Die Untersuchungen der vorgelegten Studie haben gezeigt, dass Nebelbildung ein regelmäßig in Raum und Zeit auftretendes Ereignis in Französisch-Guyana darstellt mit erheblichen Auswirkungen auf die epiphytische Vegetation.