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SPATIAL AND TEMPORAL PATTERN OF TEMPERATURE AND HUMIDITY OF A TROPICAL PREMONTANE RAIN FOREST TREE IN COSTA RICA

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ABSTRACT. In order to correlate epiphyte position and phenology with microclimate, a sensor setup was designed to measure the spatial and temporal pattern of air temperature and relative humidity. The sensor setup featured an automatic measuring device which was installed in a *Ficus jimenezii* tree in the Reserva Biológica Alberto Brenes, Alajuela, Costa Rica. An entire annual data set with a spatial resolution of fourteen locations and a temporal resolution of 20 sec intervals, and a recording time of five minutes, was obtained.

The sensor positions were chosen to analyze the gradient between the ground and the canopy roof and the gradient between the center of the crown and its periphery. A superimposed third gradient occurred between the surface of large branches and the free space between the branches. Generally, temperature and humidity curves were contrary. The gradients' steepness was mainly influenced by humus accumulation on the branches around the sensor position. High accumulations of humus mitigated the gradients considerably. As a consequence, climatic environments close to the branches were similar to those near the ground.

Extreme climatic events, such as low relative humidity and high temperature, were defined. They occurred during less than 1% of total measuring period. The extent and duration of extreme events increased significantly with distance from the ground, from the tree center to the periphery and with distance from large branches. A parallel study showed that these events affect the morphology of different *Columnea* (Gesneriaceae) species and play an important role for epiphyte establishment and fruiting success in this tropical rain forest.

INTRODUCTION

The position of vascular epiphytes in tropical tree canopies can be characterized by architectural features, e.g. branch diameter or height above the forest floor, by features of the substrate, like amount of dead organic matter or pH, and finally by the microclimate, e.g. temperature, humidity, light or wind speed. From the architectural point of view, trees can roughly be divided into the trunk, the branches and the twigs (Schimper 1888). The trunk can be further divided into its basal part and the trunk itself and the crown into equal thirds (Johansson 1974). This zonation is widely accepted (Went 1940, Pócs 1980, Griffiths et al. 1985, Cornelissen & Ter Steege 1986, Freiberg 1989, 1994, Ter Steege & Cornelissen 1989, Benzing 1990). The accumulation of dead organic matter or humus is closely linked to architecture, e.g. branch inclination or diameter (Freiberg 1996). Bilateral dependencies exist between humus accumulation and microclimate (Bohlman et al. 1995). In order to measure the mesometeorology of the forest, the influence of humus and vegetation needs to be minimized, which can be done with the help of towers (Dirmhirn 1961, Cachan 1963, Allen et al. 1972). Measurements near the epiphytes themselves are scarce. Moreover, they often were carried out during short periods or focused on the light regime (Sinclair 1984, Griffiths et al. 1985, Oberbauer et al. 1988, 1989, Smith et al. 1992, Wolf 1993a). However, it has been proposed that the knowledge of the microclimate at the epiphyte position helps to understand epiphyte ecology (e.g. Johansson 1974). During various analyses on epiphytic phenotypes, morphological differences of one species were observed within short distances within a tree. In order to prove influences on epiphytic *Columnea* L. species (Gesneriaceae), microclimate data were collected during a one year period within a *Ficus jimenezii* (Moraceae) with help of an automatic, continuously measuring device (Freiberg 1994). Temporal and spatial pattern on air temperature and relative humidity within this tree and a preliminary model describing gradients around canopy branches are presented.

METHODS

Microclimate data were gathered from June 1991 to June 1992 in a *Ficus jimenezii* tree of 43 m height and 10 to 15 m radius. The tree was located at 870 m above sea level near the biological station of the Reserva Biológica Alberto Brenes (84°35′50″ West, 10°13′15″ North) in the province of Alajuela, Costa Rica. The climate near the station is perhumid almost throughout the year with about 4000 mm of rain and a short dry season from February to April. The branch positions were reached using access methods described elsewhere (Perry 1978, Perry & Wil-

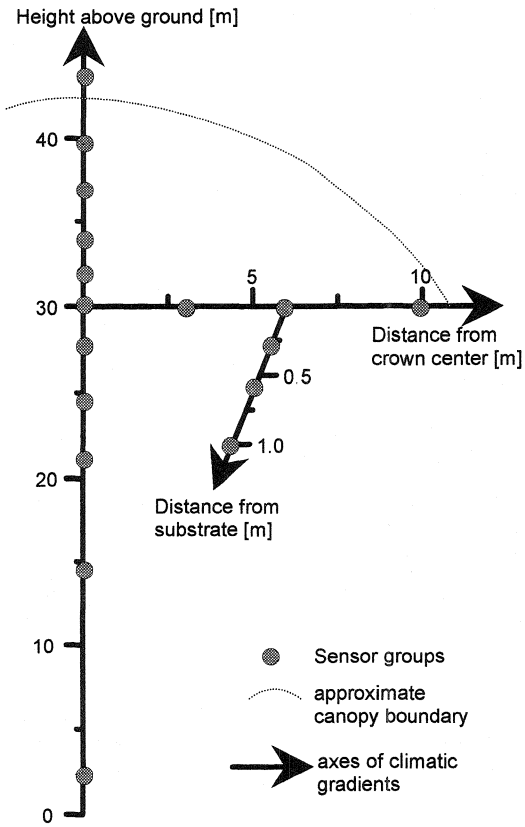

FIGURE 1. Sensor groups in the phorophyte tree of *Ficus jimenezii,* schematic drawing. Notice the different scales of the three gradient axes. Data on air temperature as well as on relative humidity were gathered at each sensor group.

liams 1981). Fourteen sensor groups were installed in the tree along 3 axes: 1) between forest floor and outer canopy, 2) between crown center and canopy periphery 30 m above the forest floor, and 3) between the substrate of the branch and the free space between the branches 30 m above the forest floor and about 6 m from the crown center (FIGURE 1).

The microclimate parameters measured by the sensors were converted into analog data outputs directly at the sensor position and conducted via cable to a central multiplexer. These data were digitized by an 8-Bit A/D transducer (Type ADC 0803 from Analog Device, accuracy ±½ bit), then by serially frequency shift keying modulated and conducted to a computer which transferred the data onto floppy disks. All electronic cases were sealed with silicon rubber. The case of the central data logger was additionally filled with silica gel desiccant.

The precalibrated temperature sensor AD 592 (Analog Device, München) had an absolute accuracy of ±0.3°C. Recalibration of sensor and reference voltage was done every second week. Direct infrared absorption by the black TO 25 case of the sensor was prevented by shielding the sensors with two concentric brass tubes.

The absolute tolerance of the capacitative Humicap-H® Sensor (Vaisela, München) used in this study was given to be 2% below to 90% relative humidity, and 3% above 90% relative humidity. Fungus growth on the sensitive surface was prevented by cleaning it every second week with ethanol. Afterwards, recalibration was done after 6 hours of temperature adjustment over saturated LiCl- and KCl-solutions.

The analog electronics for transferring the climate values to a corresponding analog output were constructed and built at the electronic laboratories of the University of Ulm. The sensor values were determined at intervals of 20 seconds. The mean values of 5 minute periods were calculated and recorded. The equipment worked continuously from June 6, 1991 to June 23, 1992. Two hundred and forty-five million measurements were recorded. Insufficient power voltage of the station was basically responsible for interruptions. Within a month, usually more than 3 weeks of data were collected, both during wet and dry seasons. Regular inspections of the equipment identified spiders and wasps constructing their nests preferably within the brass shields. Larger animals, like monkeys and coati mundi, were cooperative and not interested in damaging the equipment.

In the following sections, the accumulation of dead organic material, bryophytes and other non-vascular plants on the branches are referred to as accumulation of matter. The position, diameter and inclination of all branches larger than 3 cm in diameter as well as the thickness of accumulated matter on the branches was recorded in the tree. The accumulation of matter in the canopy was approximated by summing up the branch surfaces of a stratum at a certain height above the forest floor and the volume of matter on that surface.

RESULTS

Accumulation of matter

The total volume of accumulated matter in the tree was 6.5 m^3. There was nearly no accumulation of matter on the trunk itself and matter on neighboring trees and shrubs was negligibly low. Highest accumulation of nearly 0.7 m^3 was found in the center of the crown between 25 m and 28 m above the ground (FIGURE 2), which corresponds to the main big branches of the tree.

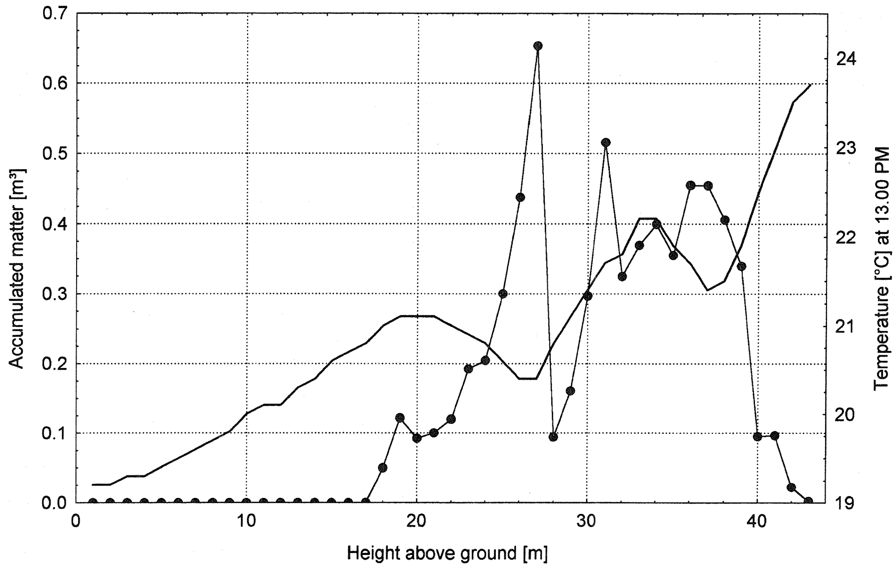

FIGURE 2. Volume of accumulated matter in m^3 of the total phorophyte (left Y-axis) found in a one meter thick layer above the ground (X-axis). The vertical temperature gradient measured at 1:00 p.m. on May 28, 1992 is given on the right Y-axis.

Beyond this peak, accumulation decreased considerably. Although there was a general increase in air temperature from forest floor to upper canopy, the accumulation of matter influenced air temperature, as well as humidity (not shown), on a smaller scale (FIGURE 2).

Air temperature

The mean annual temperature for the San Lorenzo Station, determined according to official meteorological methods, varied between 18.0°C in January and 20.8°C in July. The values for the spatial and temporal variation of air temperature calculated over the total study period 1991/92 are given in FIGURE 3.

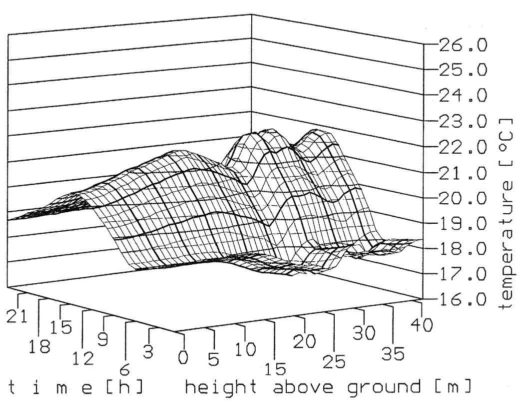

FIGURE 3. Mean annual air temperature over the study period in the phorophyte in its spatial (height above ground) and temporal (time of the day) distribution pattern.

Within the crown, the highest average temperatures (22°C) were usually reached at 33 m height at 2:00 p.m., the lowest (17°C) at 26 m at 5:00 a.m. After sunset, temperature decreased slowly until midnight. In the first three hours, this decrease was less than 1°C. The average temperature difference between the ground and the upper canopy was 2°C at 2:00 p.m. and about 0.5°C in the early morning hours.

During day time, there was always a profound positive temperature gradient from the ground to the upper canopy. This gradient was most profound between high noon and 2:00 p.m.. Daily temperature changes were slower near the ground than at the top, where maximum values were kept during a longer period. Only a few days were identified to have a temperature gradient between forest floor and canopy roof of up to 6°C (e.g. May 28, 1992, FIGURE 4). Local maxima and minima of air temperature within the crown were detected for single days as well as for the whole year (vertical gradient, FIGURES 3 and 4). The minima interrupting the otherwise gradual increase towards the upper canopy were at 26 m and 36 m above ground, which roughly corresponds to the maxima of substrate accumulation (FIGURE 2). During night time, temperature at these sites in the canopy was lower than

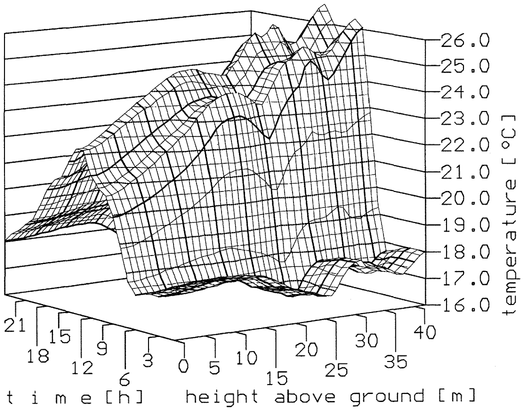

FIGURE 4. Air temperature in the phorophyte measured on May 28, 1992 in its spatial (height above ground) and temporal distribution pattern. Data reduced to means of 1 hour periods. At 9:00 a.m. the temperature gradient between forest floor and upper canopy was 6°C.

temperature at the ground (FIGURE 3), leading to negative gradients or temperature sinks. In the wet season, these sinks were even more distinct.

The sensor groups within the canopy (FIGURE 1) revealed the existence of two more gradients, one from crown center to outer canopy (horizontal gradient, FIGURE 5) and the other between the surface of branches with accumulated matter and the space between the branches (substrate gradient, FIGURE 6). The inclination of the substrate gradient was highest for the first decimeter. The horizontal gradient, measuring 40 cm aside the branches, was less profound than the corresponding gradient for the last 12 m of the

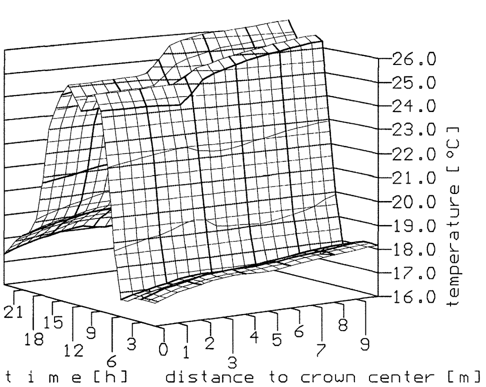

FIGURE 5. Air temperature in the phorophyte measured on May 28, 1992 along the horizontal canopy axis (distance to crown center) and time of the day. Data reduced to means of 1 hour periods. At 9:00 a.m. the temperature gradient between center of the crown and periphery was ≈2°C.

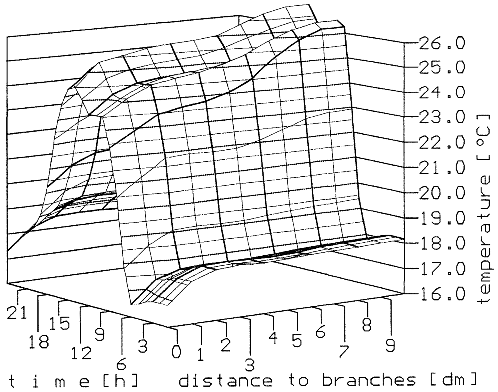

FIGURE 6. Air temperature in the phorophyte measured on May 28, 1992 along a substrate axis of 1 m, in 6 m distance to the crown center and time of the day. Data reduced to means of 1 hour periods. At 9: 00 a.m. the temperature close to the substrate of the branch was 22.5°C while the temperature 1 m below the branch was 26.2°C, leading to a gradient of more than 3.5°C.

canopy. The quality of both gradients followed the gradient between ground and upper canopy. During the driest and hottest day, the substrate gradient along 1 m of canopy volume reached 3.5°C (FIGURE 6), when the vertical gradient reached 6°C along 43 m of the total tree height (FIGURE 4).

Relative humidity

The mean annual relative humidity during night time was always close to 100%, although even then there was a small gradient between

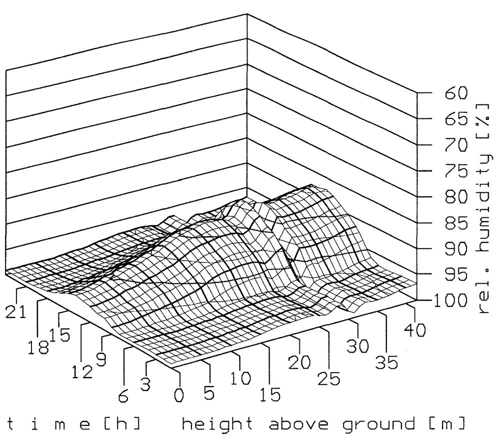

FIGURE 7. Mean annual relative humidity over the study period in the phorophyte in its spatial (height above ground) and temporal (time of the day) distribution pattern.

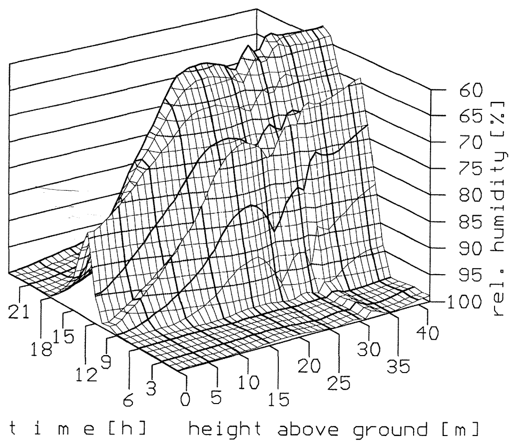

FIGURE 8. Relative humidity in the phorophyte measured on May 28, 1992 in its spatial (height above ground) and temporal distribution pattern. Data reduced to means of 1 hour periods. At 9:00 a.m. the humidity gradient between forest floor and upper canopy was 27%.

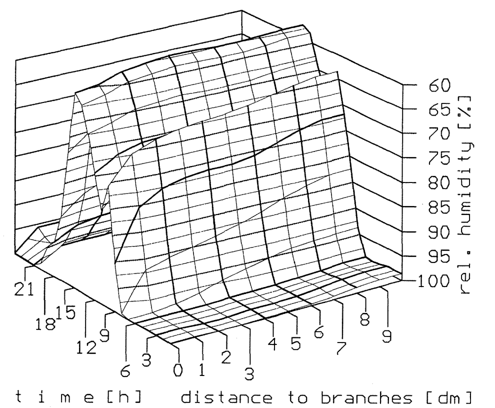

FIGURE 9. Relative humidity in the phorophyte measured on May 28, 1992 along a substrate axis of 1 m, in 6 m distance to the crown center and time of the day. Data reduced to means of 1 hour periods. At 9:00 a.m. the humidity close to the substrate of the branch was 90% while the humidity 1 m below the branch was 72%, leading to a gradient of nearly 20%.

forest floor and upper canopy (FIGURE 7). During the study period, the hourly mean did not reach values below 85%, concerning both, the temporal and spatial scale (FIGURE 7). A negative humidity gradient was most profound between the ground and about 20 m. From there to the upper canopy the gradient was present but less distinct. Duration as well as velocity of daily humidity reduction increased with distance to the ground, which is demonstrated most obviously for single days (FIGURE 8). Local maxima and minima of relative humidity within the crown overlapped with those of air temperature (FIGURE 4) and coincided with substrate accumulation (FIGURE 2).

The lowest value of relative humidity during the study period (57%) was measured on May 28, 1992 at 2:00 p.m. in the upper part of the crown (FIGURE 8). This day was the brightest and hottest day, too. At noon, the saturation deficit (calculated from air temperature and relative humidity with standard formulas) reached 12 mbar. Even plants in the understory suffered visibly from drought stress. On the driest day, there was a gradient from up to 20% relative humidity within a distance of 1 meter from the branch (FIGURE 9). The horizontal gradient (FIGURE 10) is similar to the substrate gradient, but it differs in the spatial scale.

Hours exceeding values of 70% relative humidity, 25°C and 10 mbar saturation deficit are defined "event hours." Days exceeding all these values during more than 1 hour are defined "event days." During events, the vertical temperature difference was greater than 4°C and the humidity difference greater than 20%. The highest frequency of event hours per month in May does not coincide with the dry season from January to March (FIGURE 11). Highest saturation deficits occurred in May at the beginning of the wet season.

DISCUSSION

A climatic gradient between the forest floor and the canopy roof persisted more or less throughout the year. The continuity of this gra-

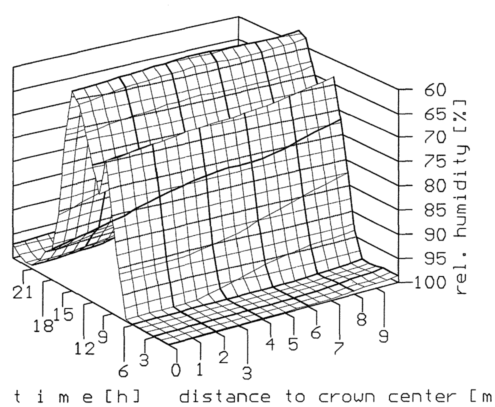

FIGURE 10. Relative humidity in the phorophyte measured on May 28, 1992 along the horizontal canopy axis (distance to crown center) and time of the day. Data reduced to means of 1 hour periods. At 9:00 a.m. the humidity gradient between center of the crown and periphery was nearly 10%.

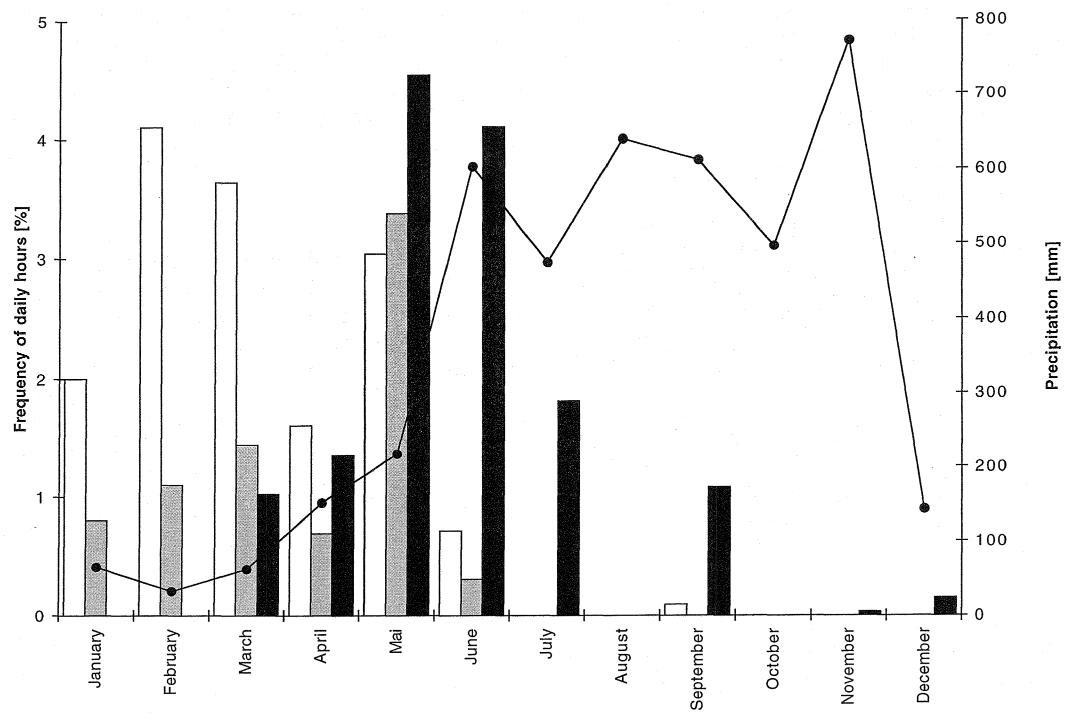

FIGURE 11. Monthly precipitation during study period (line) and the frequency as percentage of "event hours" during day time (bars). One hundred per cent equals the total number of sampled hours during day time. White bars: frequency of hours with relative humidity <70%, black bars: frequency of hours with air temperature >25°C, grey bars: frequency of calculated saturation deficit >10 mbar.

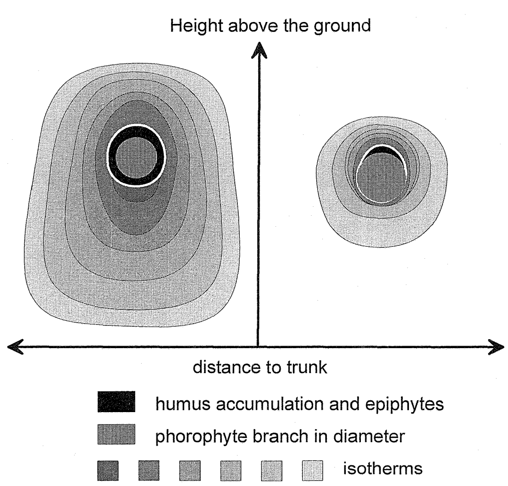

FIGURE 12. A preliminary sketch of a model presenting isothermic or isohydric lines around a canopy branch with equal diameter but either large (left) or small (right) accumulation of matter.

dient was only disrupted by branches with large humus accumulations.

A positive temperature gradient between the forest floor and the canopy roof, that is increasing temperature towards the canopy, has already been detected in other studies (Allen et al. 1972, Johansson 1974, Wolf 1993a, 1993b). In the present investigation, between forest floor and canopy roof a negative temperature gradient of 1°C to 2°C could be observed additionally during the colder season and the early morning hours. This was probably due to the capacity of the understory vegetation to store warm air during the night, while the upper layers cooled down rapidly during cloudless nights.

The results show that standardized meteorological measurements do not reflect the microclimatic variation within tree crowns. The microclimate at heights between 1.5 m and 2.0 m above forest floor was much more constant than within the crown. Moreover, fluctuations within the crown close to large branches were smaller than in the free space between the branches. Accumulations of humus and bryophytes in the canopy, especially in mountain forests, can be quiet extensive (Klinge 1966, Pócs 1982, Nadkarni 1984, 1986). In this study, the climate gradients within the crown can be explained by accumulations of up to 8 cm humus and 5 to 10 cm bryophyte mats. Depending on the branch diameter, the inclination, the layers of humus, and the types of epiphytes growing on the branch, a specific microclimatic gradient developed around the branches, basically during daytime. Probably bryophytes play the most important role due to their ability to store water a multifold of their dry weight (Pócs 1982). The distribution of accumulated matter in the canopy shown in FIGURE 2 gives strong evidence for its influence on otherwise perhaps gradual microclimate gradients. Moreover, it can be proposed that the ecological importance of canopy matter to mitigate microclimatic extremes is most important during the dry season and the unpredictable occurring days at the beginning of the wet. Then the water saturation deficit is high in the free space, whereas due to accumulated matter it is relatively low close to the branches.

A microclimatic model of a tropical rain forest tree must reflect a spatially and temporally highly structured habitat. Isothermic and isohydric lines exist concentrically around the branches. Gradients on the upper side are probably steeper than on the lower side. A preliminary sketch of such a model is given in FIGURE 12. The shape of the isoclimates around a particular branch further depends on the influence of wind and light. The upper sides of the branches heat up quickly, especially in the upper canopy. Places sheltered from the wind and prolonged exposure to sunlight by canopy openings become warmer and drier than wind-exposed places above the canopy.

Besides general gradients, the absolute extremes and the duration of extreme values is important to life in the canopy (Buckley et al. 1980). Extreme values of high saturation deficits (high temperature, low humidity) were most frequent during the dry season, but also occurred during the wet season (FIGURE 11). Suffering of the vegetation began for values <70% relative humidity, >25°C and saturation deficits >10 mbar, respectively. The days reaching these values for more than 1 hour were defined "event days."

In order to detect extreme microclimatic events in the canopy, it is necessary to measure microclimatic data continuously and over prolonged time periods. Such events, like the driest day in the wet season, are unpredictable. The importance of event days for tropical vegetation in Malaysia was discussed by Buckley et al. (1980), while it is generally known to be important for temperate vegetation (Walter & Straka 1970). Phenomorphological studies on epiphytic *Columnea* species (Freiberg 1994) already showed the susceptibility of epiphytes to such events, which may be an important selection pressure. Further investigations are necessary to facilitate the interpolation of events on a larger scale.

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