Anzeiger Abt. I (1999) 135: 3–23

Geographical and Ecological Settings of the Surumoni-Crane-Project (Upper Orinoco, Estado Amazonas, Venezuela)

By

D. Anhuf and H. Winkler

(Vorgelegt in der Sitzung der math.-nat. Klasse am 16. Dezember 1999
durch das k. M. Hans Winkler)

Introduction

Extensive areas of tropical rainforest play an important role in maintaining the diversity of animal and plant communities. They also influence the energy-, water- and carbon-budget on a local, regional, and possibly global scale. Rainforests are increasingly endangered by human interventions such as deforestation and conversion into agricultural land or pasture (Mooney et al. 1980, Wilson 1992). However, assessments of the large-scale impacts are still limited by the limited current knowledge of many of the critical processes involved (Shukla et al. 1990). In part, this deficiency results from fact that the major interface between the biosphere and the atmosphere, the forest canopy, has remained unexplored for a long time because of the difficulties of accessing it.

To investigate the structure and function of a tropical rainforest with special reference to the upper canopy, a cooperative research project of the Austrian Academy of Sciences and the Venezuelan government was established. It was motivated by the realization that canopy research lags far behind research into other hardly accessible environments, and that tower cranes are a flexible, relatively cheap, and safe instrument for canopy research (Parker et al. 1992, Stork et al. 1997). Since November 1995 permanent canopy access has been achieved with the construction of a mobile crane system located near the center of the southernmost Venezuelan state, the Estado Amazonas. The crane is 42 m high with a horizontal jib 40 m long and can move on 120 m long rails. It facilitates direct access for *in situ* observation and experiments in an area of approximately 1.5 ha. The present paper contains first descriptions and analyses of the geographical, ecological, and biological settings of the Surumoni-Crane-Project.

1. Location

The plot of the Surumoni-Crane-Project is located close to the mouth of the Río Surumoni (3°10′ N; 65°40′ W; ca. 105 m a.s.l.), a minor blackwater tributary of the upper Río Orinoco (Fig. 1). Spatially separated from the experimental site, most researchers stay at La Esmeralda, a small village 15 km upstream from the study area.

The region forms a transitional geological zone between the Guayana-Highlands in the north-northeast and the lowlands of the Río Negro–Casiquiare Basin in the south-southwest which extends southward into the central Amazon Basin of Brazil.

The physiography of the landscape is dominated by gently undulating peneplains interrupted only by the striking table mountains (tepuis) in the north. The large and extensive Duida-Marahuaca massif is located some 15 km to the north of the crane site and reaches 2,358 m in elevation at the south-western rim of the Cerro Duida and 2,800 m at the highest point of the northern Cerro Marahuaca.

Industrialized economy and infrastructure are virtually restricted to the northwestern parts of the state. Since the national road system terminates at the state capital Puerto Ayacucho, transport within the state depends on ship- and air-traffic by means of small boats and propeller air-crafts. Due to its isolated and secluded location, together with the lack of industrially useful resources, the Amazonian lowlands of Venezuela have remained largely undisturbed by human interventions. The mainly indigenous population comprises about 14 different ethnic groups and pursues traditional slash-and-burn agriculture and shifting cultivation as well as fishing, hunting and gathering to various degree (Alvarez del Real 1983, Benacchio 1990, Huber 1995a, Müller 1995. Vila 1964).

2. Climate

Due to its location within the inner tropics, the climatic conditions of the study plot are characterized by a mean annual temperature of 25.5–26.5°C with the average diurnal temperature range (5°–10°C) exceeding the

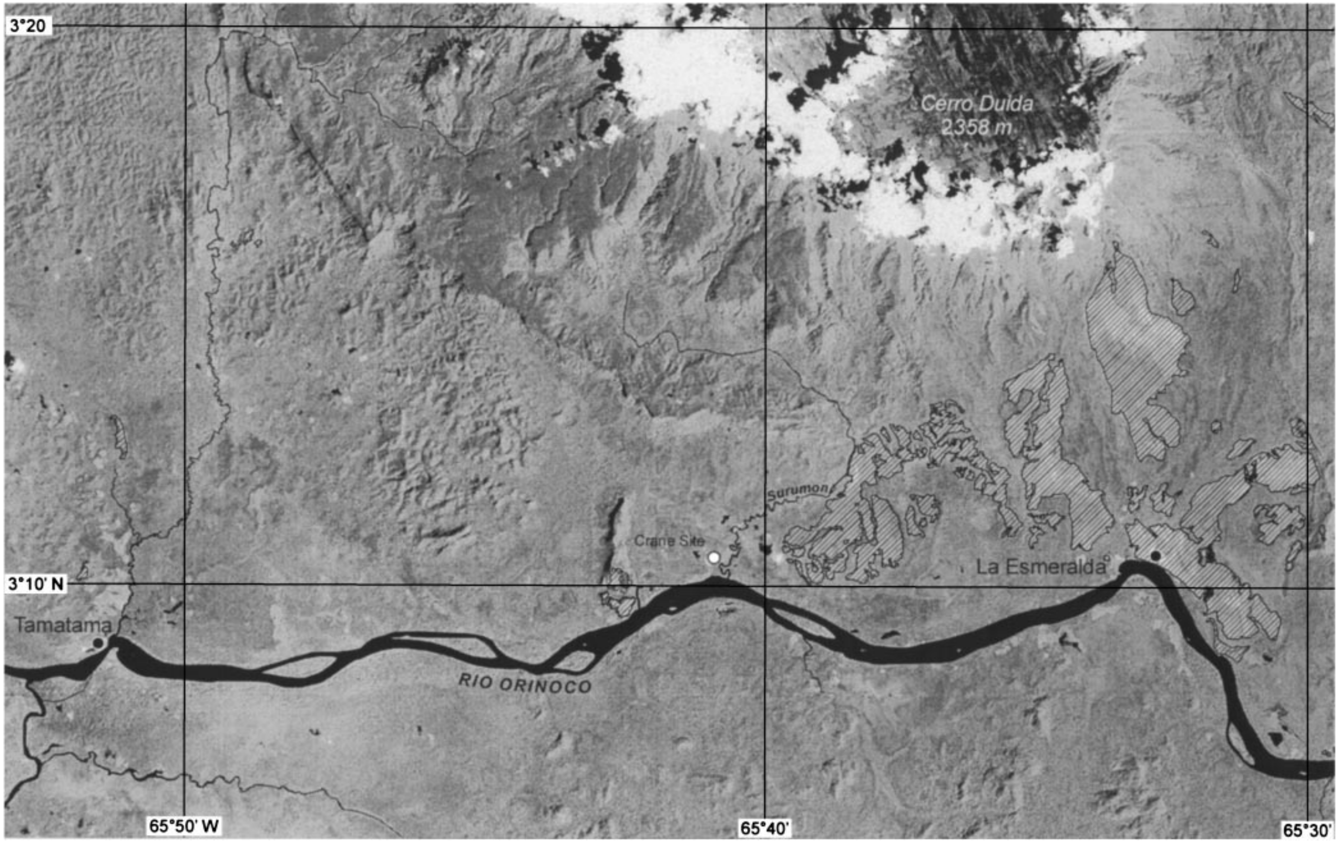

Fig. 1. Section of the Thematic Mapper-scene of 10 November 1986, Mercator projection, ellipsoid WGS84. Contrast enhanced first principal component of channels 1–5 and 7 of the TM-image. The filled white circle designates the crane's position, filled black circles indicate settlements, and the hatched areas represent the savannulas of the area. Prepared by H. Beissmann

variation of annual means (< 4°C). Relative air humidity is high, usually about 85–90%. Although the absolute content of water vapour remains fairly constant between 15 to 25 g kg^{-1}, relative air humidity experiences greater relative diurnal and seasonal variations due to its temperature dependence. Especially during the El Niño event in 1997–1998, which caused extraordinarily warm and dry conditions in the study region, absolute minima of relative humidity fell below 40% above the forest canopy during the early afternoon, corresponding with saturation deficits of 20 – 25 g kg^{-1}. Wind speeds are generally low (about 2 ± 1 m s^{-1}), with north-easterly or south-easterly wind directions prevailing. The long-term average annual rainfall amounts to 2,700 mm at La Esmeralda (period: 1970–1995; data source: Dirección de Hidrología y Meteorología, Caracas). The rainfall pattern observed in recent years is shown in Fig. 2.

Annual variation in climate is mainly caused by latitudinal shifts of the "intertropical convergence zone" (ITCZ) into which the trade-winds of the Hadley circulation converge. Important climatic features of the ITCZ are cloudiness and rainfall which are mainly due to large-scale convection and the vertical transport of water vapour in association with extensive cloud clusters (GARCIA 1985, McGREGOR & NIEUWOLT 1998). Despite of its location near the equator, the annual rainfall curve exhibits only a single peak. Under the influence of moisture laden south-easterly trade-winds, originating in the Amazon Basin and turning into southerly winds near the equator, the rainy season lasts from April to November with a maximum in June (approximately 400 mm/mouth). Drier and warmer weather conditions prevail from December to March due to north-eastern trade-winds. Nevertheless, monthly precipitation within this drier period amounts to at least 100 mm/month (Fig. 2) (Goldbrunner 1984, Snow 1976).

Regional climatic features, in particular the spatial distribution of precipitation, are considerably influenced by the exposed relief. The steep southern slopes of the Duida-Marahuaca massif stretch from NW to SE and cause orographic uplifting that ultimately leads to appreciable rain showers. This phenomenon explains the pronounced gradient of annual precipitation between the villages La Esmeralda (2,700 mm a^{-1}) and Tama-Tama (3,200 mm a^{-1}) which are only 35 km apart (data period: 1970–1995; Dirección de Hidrología y Meteorología, Caracas). Since the Surumoni site is located approximately halfway between these two villages, we expect an average annual rainfall of 2,900–3,000 mm. A weather station installed by us at La Esmeralda provided further information concerning regional climatic conditions by automatically measuring temperature, humidity, rainfall, wind velocity and direction, and radiation balance.

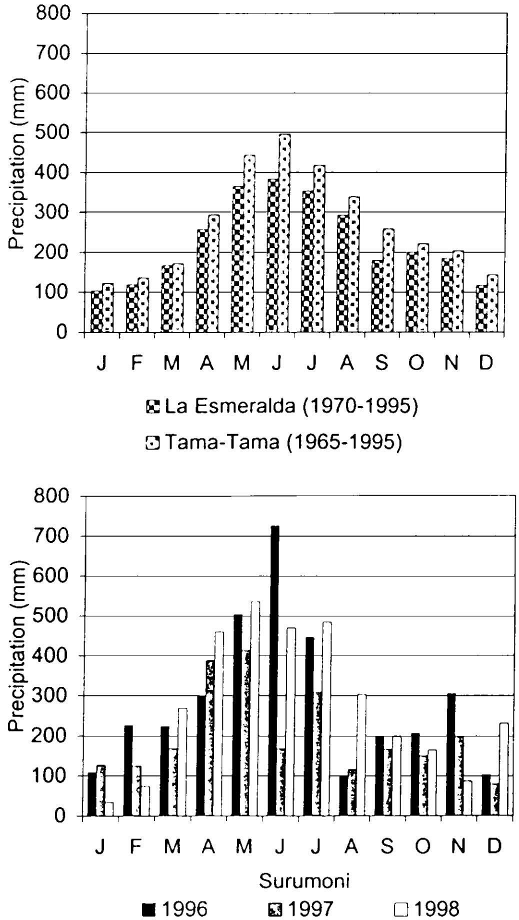

Fig. 2. Mean annual precipitation of La Esmeralda and Tama-Tama (1970–1995) (*top*), and precipitation at Surumoni-site (1996–1998) (*bottom*)

Micrometeorological conditions have been measured within and just above the Surumoni forest to study diurnal fluctuations. The vertical profile of air temperature, humidity, wind speed, photosynthetically active radiation, soil heat budget and soil moisture have been measured with two recording systems at 10 minutes intervals. During daylight hours, the observed gradients of temperature and humidity show that turbulent mixing between the vegetation and the atmosphere is rather efficient in the top two-thirds of the forest, whereas the understory remains partially isolated. At night, however, the canopy often is decoupled from the overlying atmospheric layer due to substantial radiative cooling, causing a stable density stratification above the forest (SZARZYNSKI & ANHUF, in press). These results are similar to those reported from other tropical rainforest sites (FITZJARRALD & MOORE 1995, SHUTTLEWORTH et al. 1985).

Additional research focused on the physical mechanisms that control the exchanges of mass and energy between the biosphere and the atmosphere. Main objectives of these investigations were, first, to determine the component fluxes of the forest energy balance, including the amount of actual evapotranspiration loss, and second, to evaluate different measurement techniques and parameterization models with respect to already existing data sets (DOLMAN et al. 1988, 1991; FITZJARRALD et al. 1990; GASH et al. 1996; ROBERTS et al. 1993; SHUTTLEWORTH 1988, 1989; SHUTTLEWORTH et al. 1984).

3. Hydrography

Extensive river systems exist in the Amazonian lowlands of Venezuela. The major river basins are the northern Orinoco Basin and the southwestern Rio Negro –Amazon Basin. The outstanding hydrographic feature of this area is the Río Casiquiare that drains part of the Upper Orinoco through the famous Orinoco-Casiquiare bifurcation near Tama-Tama to the Rio Negro –Amazonas system (BESLER 1995, HUBER 1995a).

From its source in the *Sierra Parima* (1,047 m A.S.L.), the Río Orinoco runs around the western and northern borders of the Guayana–Highland and finally discharges after about 2,150 km into the Atlantic Ocean at the north-eastern coast of Venezuela (HUBER 1990, PETRÓLEOS de VENEZUELA 1995). The Orinoco is usually considered a white-water river which are characterized by low transparency due to high contents of suspended matter, an average pH-level of 7, and high nutrient concentrations (MEADE et al. 1990, SIOLI 1965, WEIBEZAHN, 1990). However, the headwaters of the Orinoco are strongly influenced by the north-eastern affluents, originating in the Guayana-Highland. In contrast to white-water systems, these rivers have low nutrient and sediment loads (STALLARD 1985). They contain much colored dissolved organic matter (CDOM) as soil humic and fulvic acids, resulting in an extremely low pH in the order 3.8 to 5 (BATTIN 1998, HEDGES et al. 1994). They are called black-water rivers because of their characteristic dark brown color (SIOLI 1965).

One of these typical black-water rivers is the Río Surumoni. It has its source at the southern Cerro Duida and joins the Río Orinoco about 15 km downstream of La Esmeralda. The Surumoni drains a tropical lowland rainforest. During the El Niño event in 1996, as a consequence of well-above-normal rainfall over great parts of northern South America (WMO 1997), total precipitation at the study site amounted to 3,700 mm, resulting in enormous floods which devastated the region in June and July. About one third of the Surumoni research plot close to the river-bank was inundated. However, neither soil conditions (A. MENTLER, pers. comm.) nor the composition of the vegetation (NIEDER et al. 1999) in the section of the crane plot suggest regular annual inundations. Therefore, the floods observed in 1996 were certainly rather exceptional.

4. Geology and Geomorphology

Geologically, the examined area is part of the very old Guayana Shield which strethces from north of the Amazon lowlands in SE Columbia through the Venezuelan Guayana and northern Brazil to the Atlantic coast of Guyana, Suriname, and French Guayana. The Guayana Shield is a kraton consolidated during the Precambrian. According to the classification proposed by HUBER (1995a), the Venezuelan part of the shield consists of three lithologic units:

A magmatic-metamorphic basement of early Proterozoic age,

A clastic sediment cover of the Roraima Formation belonging to the Middle Proterozoic, and a younger intrusive complex, consisting mainly of Paleozoic and Mesozoic stocks and sills.

Additional material from tertiary denudation processes and Quaternary alluvial plain sediments covers the south-western lowland areas. The crystalline basement was formed during repeated orogenetic cycles in the Archean and Proterozoic (about 3.6 billion years ago). The most important Transamazonian orogenesis (2.3–1.9 billion years ago) further consolidated the Guayana Shield. Large-scale plutonic complexes of granitoids and intrusives were formed, and the pre-Transamazonian rock complexes were overprinted with metamorphic rocks, with decreasing age of consolidation towards the south (BOADAS 1983, FITTKAU 1974, GIBBS & BARRON 1993).

Molasse-type sediments were deposited during an extensive uplift and erosion phase between 1.7–1.6 billion years ago, resulting in the sequences of the Roraima Formation (DALTON 1912) which overlie the crystalline basement irregularly. The mainly horizontally layered strata of arkose, sandstone, conglomerate and quartzite are almost undisturbed and only weakly metamorphosed, indicating the long-term tectonic stability of the shield since the Proterozoic. The Roraima Formation, more than 3,000 m thick, is heavily weathered and fragmented by numerous erosion cycles since the late Precambrian leading to the well-known sheer cliffs of the table mountains (tepuis) of the Guayana–Highland, including the Duida-Marahuaca massif (GIBBS & BARRON 1993, HUBER 1995a, KUBITZKI 1989, ZEIL 1986).

The post-Precambrian was dominated by geomorphological processes within a continental environment. Especially the intensive chemical weathering during the warm and humid climates of the Cretaceous and the Tertiary as well as the doming of the Guayana Shield (Upper Cretaceous to Pleistocene) in conjunction with the Andean orogenesis resulted in large-scale denudations and the formation of peneplains (FITTKAU 1974). The denudation debris was deposited in the subsiding areas of the northern Amazon Basin. The large river systems of the Orinoco and the Amazon were formed at the end of the Tertiary (BIGARELLA & FERREIRA 1985, CLAPPERTON 1993).

The Surumoni–Crane plot is located in the Orinoco depression that primarily consists of Pliocene to recent alluvial deposits as well as denudation products of the Guayana-Highland (GONZÁLES de JUANA et al. 1980, GIBBS & BARRON 1993). Within this area the alluvial plains of the Upper Orinoco (*Llanos inundables*) grade into the Casiquiare–Río Negro peneplains (*Peniplanicie baja*) (ALVAREZ DEL REAL 1983, BOADAS 1983).

5. Soils

Long-term chemical weathering processes under the influence of climatic oscillations and a varying vegetation cover produced a complex mosaic of different soils in the Venezuelan Amazon (HUBER 1995a). Even within the boundaries of the Surumoni crane plot, soil structure and texture are remarkably heterogeneous.

In the northern part, soils are ferralic arenosols and notably plinthic-humic ferralsols (FAO-UNESCO 1988). The deeply weathered ferralsols, or oxisols according to the U.S.–Soil Taxonomy, are highly acidic (pH 3.5–5), poor in nutrients and generally characterized by a low cation exchange capacity (CEC) due to the high portion of caolinite (Soil Survey Staff 1975). The latter is the most stable clay mineral under conditions of heavy leaching and high temperatures. Concentrations of ferruginous materials are sparsely distributed, indicating strong eluvial activities resulting from the downward movement of percolating water. Furthermore, hydrated oxides of aluminum and managanese accumulated in the upper layers of the soil, where most of the silica has been removed (LOCKWOOD 1976). Especially toxic aluminum sesquioxides affect the nutrient cycles of the vegetation (FÖLSTER 1986, FRANCO & CABELLO 1972).

Pieces of charcoal are found throughout the plot area, indicating previous burning. Based on tree size distribution, this event was estimated to have occurred about 80 years ago (Horchler, pers. comm.).

In the southern part of the crane plot, close to the Río Surumoni, soils with high sand content predominate. According to the soil atlas of the

Amazonas state (MARNR–ORSTOM 1987), which is based on accurate radar and satellite images combined with detailed field surveys, it represents a transition zone between arenosols and recent entisols (spodic quartzipsamments). southwards, along the river-banks of the Orinoco, entisols together with aquic dystropepts are again widespread extending into the neighbouring alluvial plains (Llanura Aluvial de Orillar). The characteristic savannas around La Esmeralda grow on fine- to coarse-grained orthox quartzipsamments (MARNR–ORSTOM 1987).

6. Vegetation

6.1. General settings

The study region is covered by a mosaic of ombrophilous lowland rainforest, swamp forests, and savannas. The forest at the Surumoni site represents the typical vegetation covering great parts of the Venezuelan Orinoco Basin (HUBER 1995b). Two forest types can be recognized by differences in inundation regimes and soil conditions: flooded and non-flooded (*terra firme*) sites. The forest at the crane site can be classified into three different types (Fig. 3):

Moist evergreen forest (temporarily flooded by black water, 98–103 m a.s.l.),

Transitional evergreen forest (103–104 m a.s.l.), and

Moist evergreen forest (non flooded *terra firme*, >104 m a.s.l.).

6.2. Vegetation of the crane plot

Within the crane plot, only the southern part close to the river-bank includes some transitional forest which is floristically distinct in terms of species composition. The remainder of the plot is covered by *terra firme* forest. The 1.5 ha oval plot contains 1,061 marked trees (dbh >10 cm) that may belong to more than 100 species. Among them, only four tree species are deciduous. The mean stem diameter is 19.8 cm and the average stem basal area is 26.2 m^2/ha. Stem density is 650/ha. The forest reaches an average height of about 25 m and is indistinctly stratified into a low shrub layer, understory/subcanopy, and canopy. Emergent trees do not occur in the plot. The topography of the canopy is influenced by the differential growth of the trees causing depressions of occasionally 5–6 m in the vertical vegetation profile (Fig. 4). Furthermore, the canopy is interspersed with a considerable number of gaps that comprise approximately 10% of the plot area (NIEDER et al. 1999). Due to a comparatively low crown density and the indistinct stratification, light penetration is relatively high resulting in a rather dense understory with more than 10,000 stems with

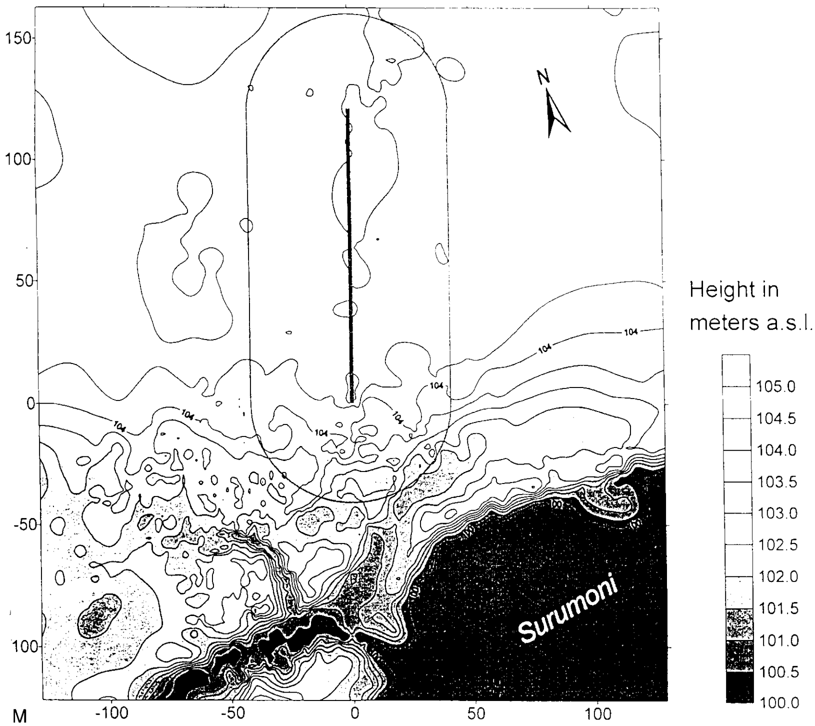

Fig. 3. Digital elevation model of the Surumoni plot (B. Schröder)

diameter above 1 cm per hectare. Typical understorey representatives are Melastomataceae and Arecaceae species.

An intriguing feature of the canopy forest is the high abundance of *Goupia glabra* (Celastraceae), a typical pioneer tree usually frequent in secondary forests growing on barren soils (GENTRY 1993). In the plot, 30% of crown cover is formed by 80 individuals of this species (NIEDER et al. 1999). Other abundant tree species are *Dialium guianense* (Caesalpiniaceae), *Ocotea sp.* (Lauraceae) and *Qualea trichanthera* (Vochysiaceae).

Palms are also abundant, but only few species are present. Most of the 7 species are found in the lower strata of the plot, where they form a considerable portion of the understory (e.g. *Bactris hirta, Geonoma deversa*). *Euterpe precatoria*, on the other hand, is a characteristic canopy component (LISTABARTH, 1999).

Vascular epiphytes have relatively low species richness and abundance, but with a species composition characteristic for a tropical lowland rainforest. The 778 individual epiphytic plants registered within the crane plot

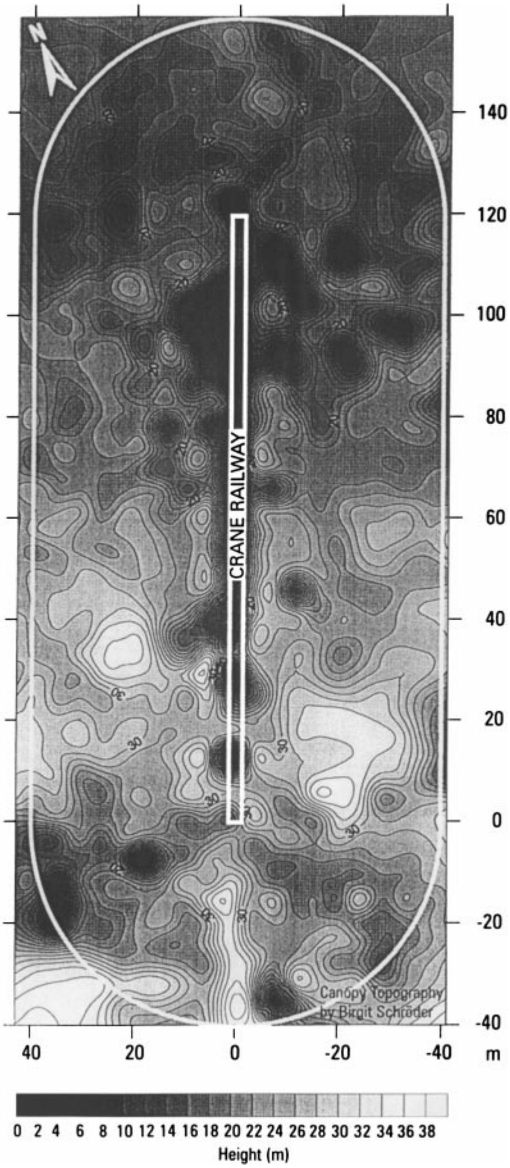

Fig. 4. Forest canopy surface model (B. Schröder)

belong to 53 species in 13 families. The Orchidaceae exhibit the highest species richness (19) followed by the Araceae (14), which have the highest abundance (337 individuals) (NIEDER et al., in press).

6.3. Vegetation of the surrounding area

The forests are interspersed with savannas of various sizes. They are home for characteristic species, e.g. Sabana morrocoy near La Esmeralda, usually growing on sandy and poor soils (HUBER 1990, 1995c). Today, these savannas represent relict communities, but during arid pleistocene phases they covered much larger areas (HASTENRATH 1991, BIGARELLA & FERREIRA 1985, CLAPPERTON 1993). Some savannas may also represent anthropogenic degradational associations, with anthropogenic and natural fires as a regulating factor (EDEN 1968, HARRIS 1968, HITCHCOCK 1947, VILA 1964).

Evergreen riparian forests spread along the banks of the Río Orinoco. Compared with the forest covering the crane plot, they are tall and lush, but the understory is less developed. The genus *Campsiandra* (Caesalpiniaceae) represents one important arboreal element, typically associated with the strikingly flowering *Tabebuia barbata* (Bignoniaceae) and tall individuals of *Ceiba pentandra* (Bombacaceae) (HUBER 1995c). The riverine plants of the area are widely distributed in Amazonia (HOLST & TODZIA 1990).

7. Fauna

The commonly held belief at the onset of canopy research was that faunal diversity, particularly arthropod diversity, was especially high in the upper canopy (ERWIN 1983, PARKER et al. 1992). However, recent surveys indicate that species richness in the upper layers is, if at all, only moderately higher than in the lower strata (e.g. HAMMOND et al. 1997). None of our projects was devoted solely to this question. Therefore, we possess little information on stratification of faunal diversity, except for birds for which a rather distinct stratification of species was observed (see below).

7.1. Ants

Ants undoubtedly constitute an important component in any rain forest ecosystem. Preliminary results obtained with thuna baits suggest that, at heights between 10–35 m, about 20–30 species dominate, mainly representing the subfamilies Myrmicinae, Formicinae, and Dolichoderinae (SCHMUCK et al. 1997, T. SCHMUCK, pers. comm.). Ants are not usually restricted to one stratum. However, ants of the genus *Pseudomyrmex* are a possible exception since they were only found in the upper canopy. The ant fauna at the ground level is much more diverse than the arboreal one.

Ant gardens are another conspicuous feature of the Surumoni site. They are most abundant in the more open parts of the crane plot. Five epiphyte families were found in the gardens, with *Anthurium gracile* (Araceae) being the most abundant species. The gardens were used by many species of ants representing at least 9 genera. A study of the relationships between ants and plants at our site revealed that the garden plants benefit not only from their seeds being transported into the gardens, but also from nitrogen fixating cyanobacteria that are dispersed by the ants together with the seeds (CEDEÑO et al. 1999).

7.2. Herpetofauna

Amphibians are poorly represented at the crane plot. Only 15 species have been found so far, while about 44 species were recorded in the La Esmeralda area (C. SENARIS, unpubl. data). Dominant species in the crane plot are *Bufo margaritifer (=typhonius), Hyla boans, H. parviceps, Osteocephalus taurinus*, and *leptodactylus wagneri*.

Reptiles are a conspicuous sight at the crane plot with 8 recorded species of iguanas and lizards. The most abundant species are *A. ameiva, P. plica*, and *Uracentron azureon (=Tropidurus werneri)* (A. Amézquita, N. Ellinger, W. Hödl, pers. comm.). Snakes are the other dominant reptile faction. They are represented with 17 species at the crane plot of which *Bothrops atrox* appears to be the most abundant one. Other reptiles of the region include *Caiman crocodilus* and *Chelus fimbriatus*.

7.3. Birds

Tropical rain forests are home of great numbers of bird species. Among these, Neotropical rain forests are especially species rich as the South American continent is inhabited by more species (about 4000) than any other continent. High species richness is partially due to resources unique to tropical rain forests and ecologically specialized species not found in other forest types (MARRA & REMSEN 1997). The avifauna of the area belongs to the Amazonian one (see biogeographical analysis below). With about 270 species observed on 5 ha at the crane it compares well with two Amazonian sites (264 and 271 species have been reported from a *terra firme* area north of Manaus and Manu National Park, respectively; see COHN–HAFT et al. 1997). Also, the cumulative number of species (37) resulting from 100 captures in the understory agrees well with numbers at other Neotropical sites (LOVEJOY 1974, KARR 1980, KARR et al. 1990). A total of about 440 bird species has been recorded in the area around La Esmeralda.

An analysis of stratum use of 185 abundant species revealed that 43% of the species are confirmed to the canopy, 31% use the interior, and the remaining 27% can be found in either zone.

Carnivorous species comprise 41% of the avifauna. They are mainly found in the interior. Frugivores (36%) and omnivores (39%) are the dominant groups in the 79 canopy species.

The extensive use of epiphytes (NADKARNI & MATELSON 1989) does not contribute to the bird species diversity of the Surumoni site.

Although passerine migrants preferably occupy the forest canopy or edge (LEVEY & STILES 1992) and should therefore have beeen readily observed during the observations from the crane, migrants comprise only a small portion of the forest avifauna (less than 2% of the species). This feature distinguishes the Surumoni site from Middle American sites (e.g. GREENBERG 1981, LOISELLE 1987). Furthermore, austral migrants are about as frequent as northern ones.

7.4. Mammals

No systematic studies of the mammalian fauna were carried out so far. However, some data accumulated in the course of the zoological activities at the site and in La Esmeralda. Bats clearly form the most species rich group, followed by rodents. 12 species of bats have been identified at the crane site so ar. Dolphins (*Ina geoffrensis*) are regularly seen in the Surumoni and occasionally in the Orinoco. Jaguars occur in the area even though they are hunted and despite large prey, such as paca, aguti, and peccaris, being under strong pressure from local hunters. primates are relatively rare. Night Monkey (*Aotus trivirgatus*), Brown Pale-fronted Capuchin (*Cebus albifrons*), Weeper Capuchin (*C. nigrivittatus*), Red Howler Monkey (*Alouatta seniculus*) and Wolly Monkey (*Lagothrix lagotricha*) have been identified. Two more primate species were observed at the riverbank south of the Orinoco.

8. Biogeography

Various authors still disagree about details of the biogeographical division of South America. We follow one of the most recent and widely accepted attempts (DINERSTEIN et al. 1995). According to the analyses presented in that survey, the Surumoni area belongs to the Japura/Negro moist forests ecoregion that extends from Brazil to southern Venezuela, Colombia, and Peru.

A comparative analysis of the palm flora (C. Listabarth, in prep.) confirmed that view. The inventories of 9 *terra firme* plots throughout the Amazon basin and Guyana were compared. The Surumoni area was most similar (Jaccard coefficient, see Sneath & Sokal 1973) to a plot at the upper Río Negro. These two sites were loosely connected with a cluster formed by sites from central and eastern Amazonian, the Guyana sites, the lower Río Negro and Puerto Ayacucho. The two western Amazonian (lower Ucayali) sites were clearly separated from these sites.

Comparative analyses of the anuran and bird faunas were also conducted. Northern South America was divided by Haffer (1974, 1985) into 7 endemicity regions. Ron (1995) used this classification to analyze phylogeographic relationships of anuran faunas, adding Central American regions. For our analysis, we used this regional data set (Ron 1995, Appendix 2) separately adding species from La Esmeralda as well as species found in the Estado Bolivar (Duellman 1997), both belonging to the Guiana area of endemism (see also Prum 1988). A cluster analysis of the 11 regions showed that "Guiana" (in Ron's 1995 data), La Esmeralda and Bolivar formed one cluster that was most closely related to "Belem", Rondonia, Napo, and Inambari, respectively. The Chocó and the Central American sites formed another distinct cluster, and the Serra do Mar region was well separated from the two other major clusters.

Ornithologists have recognized 13 areas of endemism in southern America (Haffer 1974, 1985, Cracraft & Prum 1988, Prum 1988). The Guiana area of these studies includes the Guianas and the area east of the Rio Negro to the Atlantic coast, and extends to the Amazon which forms its southern border. We analyzed (Walther et al., in prep.) species lists of 9 lowland rain forest sites and found that Surumoni and La Esmeralda, together with a site south of Porto Ayacucho have close affinities to the Manaus area, and are well separated from east slope Andean and south Amazonian sites. Thus, the avifauna too shows close affinities with the Manaus area and belongs to the Guiana area.

9. Paleoecology

A number of research projects concerning changes in vegetation cover have shown that even tropical regions were affected by the enormous climatic oscilltions of the last 20,000 years (Anhuf 2000). It is still uncertain whether the forest was separated into different pockets (refugia) as the Kongo Basin was. Around 18,000 BP, aridity reached its climax and savanna vegetation exhibited its maximum extension (Latrubesse 2000). In comparison with the Congo Basin, the Amazon Basin has received much more rain. Thus, it seems plausible that the rain forest survived in larger areas than in central Africa. Paleoecological information for the region is largely limited to the Holocene period from 6,000 BP onwards. Palynological records from peat samples collected at various depths have been obtained from the Chimanta massif, the Auyán tepui, and the Cerro Guaiquinima. They showed that a series of more or less intensive climatic oscillations have occurred (RULL 1991). These changes coincided with Holocene changes reported by van der HAMMEN (1982) for the northern Andes. They were documented through the alternating dominance of pollen from herbs and pollen from forests. Such vegetational changes took place repeatedly on the Chimanta Massif and the Auyan-Tepui (HUBER 1995a).

10. Conservation

The region of the upper Orinoco lies in an area judged by the WWF as fairly stable in terms of conservation. To protect the natural environment and the resident population the establishment of National Parks and Biosphere Reserves recently became an important tool in the Venezuelan conservation policy. The *Alto Orinoco-Casiquiare Biosphere Reserve* within the framework of the UNESCO-program "Man and Biosphere" (MaB), was establisheded by presidential decree in June 1993. It covers the whole catchment area of the Upper Orinoco (0°45′–4°17′ N, 63°20′–66°34′ W) in an elevation range between 100–800 m and represents with its area of 87,000 km^2 the largest such reserve within the tropics (HUBER 1995c).

Acknowledgements

The Surumoni-Crane-Project is a multidisciplinary, collaborative research project founded by the Austrian Academy of Science (AAS) and the Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR) in Venezuela. It was initiated by W. MORAWETZ when he headed the research centre for Biosystematics and Ecology of the Austrian Academy of Sciences. German contributions to this project were financially supported by the Deutsche Forschungsgemeinschaft, the Austrian ones by the Fonds zur Förderung der wissenschaftlichen Forschung. All of them are gratefully recognized. The authors are pleased to acknowledge the generous support of the Venezuelan ambassador E. Becker-Becker and his staff from the embassy in Bonn. Essential information on the chapter of vegetation was provided by the Botanical Institute in Bonn (W. BARTHLOTT, S. ENGWALD, J. NIEDER), the Botanical Institute in Leipzig (W. MORAWETZ, D. SATTLER, J. WESENBERG), and C. LISTABARTH.

The basic studies in climatology and hydrology were carried out by N. Szarzynski, R. Rollenbeck and Th. Motuv, holding out for months at the crane site, collecting data which will be available soon after publication of their PhD thesis. The latter helped greatly with his comments during the preparation of the manuscript. In particular we would like to thank O. Huber (Caracas) for various supports in Venezuela, P. Rothe (Mannheim) for reviewing the chapter on geology and geomorphology, as well as the Dirección de Hidrología y Meteorología (Caracas) for providing important climatological data W. Hödl greatly helped with data and literature on the herpetofauna. C. Listabarth, H. Beissmann and B. Walther did much to substantially improve the quality of the manuscript.

References

Alvarez del Real, M. E. Libro: Atlas de Venezuela. Caracas (1983).

Anhuf, D.: Vegetational history and climate changes in Africa north and south of the Equator (10 N–10 S) during the Last Glacial Maximum (18,000–15,000 BP). pp. 226–43 *in* Smolka, P. P. & Volkheimer, W. (eds.): Southern Hemisphere Paleo- and Neoclimates, Berlin (2000).

Anhuf, D., Motzer, T., Rollenbeck, R., Schröder, B. & Szarzynski, J.: Water budget of the Surumoni crane site (Venezuela). Selbyana **20**, 179–185 (1999).

Battin, T.: Dissolved organic matter and its optical properties in a blackwater tributary of the Upper Orinoco River, Venezuela. Organic Geochemistry **28**, 9/10, 561–69 (1998).

Benacchio, S.: El potencial agriocola del Territorio Federal Amazonas - Una perspectiva. pp. 407–29 *in* Weibezahn, F. H., Alavarez, H. & Lewis, W. M. Jr. (eds.). El Río Orinoco como ecosistema. Caracas (1990).

Besler, H.: Beobachtungen zum Casiquiare-Problem. Erdkunde **49**, 152–56 (1995).

Bigarella, J. J. & Ferreira, A. M. M.: Amazonian Geology and the Pleistocene and the Cenozoic Environments and Paleclimates. pp. 49–71 *in* Prance, G. T., & T. E. Lovejoy. (eds.). Amazonia. Oxford (1985).

Boadas, A. R.: Geografía del Amazonas venezolano. Collección Geografía de Venezuela nueva no. 15. Caracas (1983).

Cedeño, A., Mérida, T. & Zegarra, J.: Ant gardens of Surumoni, Venezuela. Selbyana **20**, (1999).

Clapperton, C.: Quaternary Geology and Geomorphology of South America. Amsterdam (1993).

Cohn-Haft, M., Whittaker, A. & Stouffer, P. C.: A new look at the "species-poor" central Amazon: the avifauna north of Manaus, Brazil. Ornithological Monographs **48**, 205–35 (1997).

Cracraft, J. & Prum, R. O.: Patterns and processes of diversification: speciation and historical congruence in some Neotropical birds. Evolution **42**, 603–20 (1988).

Dalton, L. V.: On the geology of Venezuela. Geological Magazine or Monthly Journal of Geology **9**, 203–10 (1912).

Dezzeo, N. & Huber, O.: Tipos de bosques sobre el Cerro Duida, Guayana Venezolana. pp. 149–58 *in* Churchill, S.P. (ed.). Biodiversity and conservation of neotropical montane forests. New York (995).

DINERSTEIN, E., OLSON, D. M., GRAHAM, D. J., WEBSTER, A. L., PRIMM, S. A., BOOKBINDER, M. P. & LEDEC, G.: A conservation assessment of the terrestrial ecoregions of Latin America and the Caribbean. Washington, D.C. (1995).

DOLMAN, A. J., STEWART, J. B. & COOPER, J. D.: Predicting forest transpiration from climatological data. Agricultural and Forest Meteorology **42**, 339–53 (1988).

DOLMAN, A. J., GASH, J. H. C., ROBERST, J. & SHUTTLEWORTH, W. J.: Stomatal and surface conductance of tropical rainforest. Agricultural and Forest Meteorology **54**, 303–18 (1991).

DUELLMAN, W. E.: Amphibians of La Escalera region, southeastern Venezuela: taxonomy, ecology, and biogeography. Sci. Papers Nat. Hist. Mus. Univ. Kansas **2**, 1–52 (1997).

EDEN, M. J.: Geographers on the Orinoco. Geographical Magazine **41**, 107–109 (1968).

ERWIN, T. L.: Tropical forest canopies: the last biotic frontier. Bull. Ent. Soc. Am. **29**, 14–19 (1983).

FAO-UNESCO Soil map of the world. Revised legend. Food and Agriculture Organization, Rom (1988).

FITTKAU E. J.: Zur ökologischen Gliederung Amazoniens. 1. Die erdgeschichtliche Entwicklung Amazoniens. Amazoniana **5**, 77–134 (1974).

FITZJARRALD, D. R. & MOORE, K. E.: Physical mechanisms of heat and mass exchange between forests and the atmosphere. p. 45–72 *in* Lowman, M. D., & N. M. Nadkarni (eds.). Forest canopies. San Diego (1995).

FITZJARRLD, D. R., MOORE, K. E., CABRAL, O., SCOLAR, J., MANZI, A. O. & DE ABREU Sá, L. D.: Daytime turbulent exchange between the Amazon forest and the atmosphere. J. Geophys. Res. **95** (D10), 16825–38 (1990).

FÖLSTER, H.: Forest-savanna dynamics and desertification processes in the Gran Sabana. Interciencia **11**, 311–16 (1986).

FRANCO, W. & CABELLO, O.: Evaluación y manejo de los suelos de la región Amazonica (Venezuela-Brasil). Revista forestal Venezolana **15** (22), 103–62 (1972).

GARCIA, O.: Atlas of Highly Reflective Clouds (HRC) for the global tropics. 1971–83. NOAA-ERL Atlas, No.7. Boulder, Colorado (1985).

GASH, J. H. C., NOBRE, C. A., ROBERTS, J. M. & VICTORIA, R. L.: Amazonian deforestation and climate. Chichester, New York (1996).

GENTRY, A. H.: Woody plants of northwest South America. Washington D.C. (1993).

GIBBS, A. K. & BARRON, C. N.: The Geology of the Guiana Shield. Oxford (1993).

GOLDBRUNNER, A. (ed.): Atlas Climatológica. Periodo 1951–70. Maracay (1984).

GONZÁLES de JUANA, C., ITURRALDO de AROZENA, J. M. & PICARD CADILLAT, X. (eds.): Geología de Venezuela y de sus cuencas petrolíferas. –Tomo I/II. Caracas (1980).

GREENBERG, R.: The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. Biotropica **13**, 241–51 (1981).

HAFFER, J.: Avian speciation in tropical South America. Publ. Nuttall Ornithol. Club **14**, 1–390 (1974).

HAFFER, J.: Avian zoogeography of the Neotropical lowlands. Ornithol. Monogr. **36**, 113–46 (1985).

HAMMEN, T. van der: Paleoecology of tropical South America. pp. 60–66 *in* Prance, G. T. (ed.). Biological diversification in the tropics. New York (1982).

HAMMOND, P. M., STORK, N. E. & BRENDELL, M. J. D.: Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. pp. 184–223 *in* Stork, N. E., Adis, J., & R. K. Didham (eds). Canopy arthropods. London (1997).

HARRIS, D. (1968): Venezuela's empty rain forests. Geographical Magazine **41**, 216–20.

HASTENRATH, S. T.: Climate Dynamics of the Tropics. Dordrecht (1991).

HEDGES, J. L., COWIE, G. L., RICHEY, J. E., QUAY, P. D., BENNER, R., STROM, M. & FORSBERG, B. R.: Origins and processing of organic matter in the Amazon River as indicated by carbohydrates and amino acids. Limnol. Oceanogr. **39**, 743–61 (1994).

HITCHCOCK, C. B.: The Orinoco-Ventuari Region, Venzuela. The Geographical Review **37**, 525–66 (1947).

HOLST, B. K. & TODZIA, C. A.: L éon Croizat's plant collctions from the Franco-Venezuelan expedition to the headwaters of the Rio Orinoco. Ann. Missouri Bot. Gard. **77**, 483–516 (1990).

HUBER, O.: Estado actual de los conocimientos sobre la flora y vegetación de la región Guayana, Venezuela. pp. 337–386 *in* Weibezahan, F. H., Alavarez, H., & W. M. Lewis Jr. (eds.). El Río Orinoco como ecosistema. Caracas (1990).

HUBER, O.: Geographical and Physical Features. pp. 1–61 *in* Steyermark, J. A., Berry, P. E., & B. K. Holst (eds.). Flora of the Venezuelean Guayana, Vol. 1: Introduction. Portland (1995a).

HUBER, O.: Vegetation. pp. 97–159 *in* Steyermark, J. A., Berry, P. E., & B. K. Holst (eds.). Flora of the Venezuelean Guayana, Vol. 1: Introduction. Portland (1995b).

HUBER, O. & RIINA, R. (eds.): Glosario Fitoecológico de las Américas. Vol. 1: América del Sur: países hispanoparlantes. Caracas (1997).

HUBER, O. Conservation of the Venezuela Guayana. pp. 193–218 *in* STEYERMARK, J. A. BERRY, P. E. & B. K. HOLST (eds.). Flora of the Venezuelean Guayana, Vol. 1: Introduction. Portland (1995a).

KARR, J. R.: Geographical variation in the avifaunas of tropical forest undergrowth. Auk **97**, 283–98 (1980).

KARR, J. R., ROBINSON, S. K., BLAKE, J. G., BIERREGAARD, R., Jr.: Birds of four neotropical forests. pp. 237–251 *in* Gentry, A. H. (ed.), Four Neotropical Rainforests. New Haven & London (1990).

KUBITZKI, K.: Amazonas-Tiefland und Guayana-Hochland (historische und ökologische Aspekte ihrer Florenentwicklung). Amazoniana **XI** (1), 1–12 (1989).

LATRUBESSE, E. M.: The Pleistocene in Amazonia: A paleoclimatic approach. p. 208–225 *in* Smolka, P. P. & Volkheimer, W. (eds.). Southern Hemisphere Paleo- and Neoclimates, Berlin (2000).

LEVEY, D. J. & STILES, F. G.: Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. Am. Nat. **140**: 447–76 (1992).

LISTABARTH, C.: The palms of the Surumoni area (Amazonas, Venezuela). I. Assemblage composition and survey of pollination strategies. Acta Bot. Venez. **22**, 141–51 (1999).

LOCKWOOD, J. G.: The Physical Geography of the Tropics. Oxford (1976).

LOISELLE, B. A.: Migrant abundance in a Costa Rican lowland forest canopy. J. Tropical Ecol. **3**, 163–68 (1987).

LOVEJOY, T. E.: Bird diversity and abundance in Amazon forest communities. Living Bird **13**, 127–91 (1974).

MARRA, P. P. & REMSEN, J. V., Jr.: Insights into the maintenance of high species divesity in the Neotropics: habitat selection and foraging behavior in understory birds of tropical and temperate forests. Orn. Monogr. **48**, 445–83 (1997).

MCGREGOR, G. R. & NIEUWOLT, S. (1998): Tropical Climatology. 2. Ed. Chichester.

MEADE, R. H., WEIBEZAHN, F. H., LEWIS, W. M., Jr & HERNÁNDEZ, D. P.: Suspended-Sediment budget for the Orinoco River. pp. 55–79 *in* Weibezahn, F. H., Alavarez, H. & W. M. Lewis Jr. (eds.). El Río Orinoco como ecosistema. Caracas (1990).

Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR) – Office de la Recherche Scientifique et Technique Outre Mer (ORSTOM). Atlas del inventario de tierras del Territorio Federal Amazonas. MARNR, DGSIIA, Caracas (1987).

MOONEY, H. A., BJORKMAN, O., HALL, A. E., MEDINA, E., & TOMLINSON, P. B.: The study of the physiological ecology of tropical plants: current status and needs. BioScience **30**, 22–26 (1980).

MÜLLER, W.: Die Indianer Amazoniens. München (1995).

NADKARNI, N. M. & MATELSON, T. J.: Bird use of epiphyte resources in neotropical trees. Condor **91**, 891–907 (1989).

NIEDER, J., ENGWALD, S., KLAWUN, M. & BARTHLOTT, W.: Spatial Distribution of Vascular Epiphytes in a Lowland Amazonian Rain Forest (Surumoni Crane Plot) in Southern Venezuela. Plant Ecology (in press).

OCHSENIUS, C.: Quaternario en Venezuela.- Introducción a la paleoecología en el Norte de Suramerica. Cuadernos Falcionados **3**, 1–68 (1980).

PARKER, G. G., SMITH, A. P. & HOGAN, K.P.: Access to the upper forest canopy with a large tower crane. BioScience **42**, 664–70 (1992).

PETRÓLEOS de VENEZUELA (ed.): Imagen de Venezuela - Unavisión espacial. 3. Ed. Caracas (1995).

PRUM, R. O.: Historical relationships among avian forest areas of endemism in the neotropics. Acta XIX Congr. Int. Ornithol.: 2562–72 (1988).

ROBERTS, J., CABRAL, O. M. R., FISCH, G., MOLION, L. C. B., MOORE, C. J. & SHUTTLEWORTH, W. J.: Transpiration from an amazonian rainforest calculated from stomatal conductance measurements. Agricultural and Forest Meteorology **65**, 175–96 (1993).

RON, S. R.: Biogeographic area relationships of lowland Neotropical rainforests based on cladistic analysis of anurans. PhD thesis, University of Kansas (1998).

RULL, V. Contribución a la paleoecología de Pantepui y la Gran Sabana (Guayana Venezolana). Scientia Guaianae 2, **i–xxii**, 1–133 (1991).

SCHMUCK, T., VERHAAGH, M. & MORAWETZ, W.: Strategien der Ressourcen-Nutzung von Ameisen in der Baumkronenregion eines südvenezolanischen Regenwaldes. In: Soziale Insekten IUSSI-Tagung Graz 1997 (K. Crailsheim & A. Stabentheiner eds.), 84 (1997).

SHUKLA, J., NOBRE, C. & SELLERS, P.: Amazon deforestation and climate change. Science **247**, 1322–25 (1990).

SHUTTLEWORTH, W. J., GASH, J. H. C., LLOYD, C. R., MOORE, C. J., ROBERTS, J., MARQUES, A. de O., FISCH, G., SILVA, V. de P., RIBEIRO, M. N. G., MOLION, L. C. B., de ABREU Sa, L. D., NOBRE, J. C., CABRAL, O. M. R., PATEL, S. R. & de MORAES, J. C.: Eddy correlation measurements of energy partition for Amazonian forest. Quart. J. R. Meteorol. Soc. **110**, 1143–62 (1984a).

SHUTTLEWORTH, W. J., GASH, J. H. C., LLOYD, C. R., MOORE, C. J., ROBERTS, J., MARQUES, A. de O., FISCH, G., SILVA, V. de P., RIBEIRO, M. N. G., MOLION, L. C. B., de ABREU Sa, L. D., NOBRE, J. C., CABRAL, O. M. R., PATEL, S. R., & de MORAES, J. C.: Daily variations of temperature and humidity within and above Amazonian forest. Weather **40**, 102–108 (1984b).

SHUTTLEWORTH, W. J.: Evaporation from Amazonian rain forest. Proc. R. Soc. London, B **233**, 321–46 (1988).

SHUTTLEWORTH, W. J.: Micrometeorology of temperate and tropical forest. Phil. Trans. R. Soc. London, B **324**, 299–34 (1989).

SIOLI, H.: Bemerkungen zur Typologie amazonischer Flüsse. Amazoniana **1**, 74–83 (1965).

SNEATH, P. H. A. & SOKAL, R. R.: Numerical taxonomy. San Francisco (1973).

SNOW, J. W.: The climate of Northern South America. pp. 295–379 *in* Schwerdtfeger, W. (ed.). World Survey of Climatology, Vol. 12. Amsterdam (1976).
Soil Survey Staff. Soil taxonomy. Agricultural Handbook No. 436, Soil Conservation Service. U.S. Dept. of Agriculture, Washington D.C (1975).
STALLARD, R.: River chemistry, geology, geomorphology, and soils in the Amazon and Orinoco basins. pp. 293–316 *in* Drever, J.I. (ed.). The chemistry of weathering (1985).
STORK, N. E., WRIGHT, S. J. & MULKEY, S. S.: Craning for a better view: the Canopy Crane Network. Trends Ecol. Evol. **12**, 418–20 (1997).
SZARZYNSKI, J. & ANHUF, D.: Micrometeorological conditions and canopy energy exchanges of a neotropical rainforest (Surumoni-Crane-Project, Venezuela). Plant Ecology (in press).
VILA, M.-A.: Aspectos geográficos del Territorio Federal Amazonas. Caracas (1964).
WEIBEZAHN, F. H.: Hidroquimica y solidos suspendidos en el Alto y Medio Orinoco. pp. 151–210 *in* Weibezahn, F. H., Alavarez, H. & Lewis, W. M., Jr. (eds.). El Río Orinoco como ecosistema. Caracas (1990).
WILSON, E. O. (ed.): Ende der biologischen Vielfalt? Der Verlust an Arten, Genen und Lebensräumen und die Chancen für eine Umkehr. Heidelberg (1992).
WINKLER, H. & PRELEUTHNER, M.: The ecological role of birds in tropical rain forests canopies. Plant Ecology (in press).
World Meteorological Organisation (WMO) (ed.) WMO statement on the status of the global climate in 1996. WMO-No. 858. Genf (1997).
ZEIL, W.: Südamerika. Geologie der Erde Vol. 1. Stuttgart (1986).
ZIMMERMANN, G.: Floristische und strukturelle Differenzierung der Wälder von La Esmeralda (Estado Amazonas, Venezuela). Unpubl. Masters Thesis, University of Vienna, Austria (1997).

Authors' address: PD Dr. Dieter Anhuf, Department of Physical Geography, University of Mannheim, L9, 1-2, D-68131 Mannheim, Germany; Prof. Dr. Hans Winkler, Konrad Lorenz-Institute for Comparative Ethology, Austrian Academy of Sciences, Savoyenstraße 1A, A-1160 Vienna, Austria.