

USING EPIPHYTES AND SOIL TEMPERATURES FOR ECO-CLIMATIC INTERPRETATIONS IN SOUTHERN ECUADOR

With 12 figures, 6 photos and 2 supplements (III, IV)

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Zusammenfassung: Der Nutzen von funktionalen Pflanzentypen und Bodentemperaturen für klimaökologische Interpretationen in Süd-Ecuador

Im Verlaufe der letzten zwanzig Jahre setzte der Autor verschiedene Methoden der Phytoindikation für eine Differenzierung der Humiditäts-Verhältnisse in neotropischen Gebirgsregionen mit erheblichen Wissensdefiziten zum Regionalklima ein. In der vorliegenden Arbeit verbinden sich Ähnlichkeitsanalysen des Epiphytismus als Verfahren zur Beurteilung der Humidität mit einmaligen Temperatur-Messungen in 60 cm Tiefe, um eine genaue Karte der hygro-thermischen Muster in einem komplizierten Relief zu erstellen. Die Abhandlung stellt die methodischen Schritte sowie Teilergebnisse vor. Das Endergebnis und daraus abgeleitete Interpretationsmöglichkeiten zur Rekonstruktion der natürlichen Vegetation sowie zur Erklärung der regionalen Klimazirkulation veranschaulichen beiliegende Karten.

Summary: During the last twenty years the author used various operations of phytoindication to differentiate moisture regimes in neotropical mountain areas showing essential deficits in knowledge of regional climate. In this paper hygric estimations by similarity analyses based on epiphytism are combined with singular measurements of temperatures 60 cm below ground to establish an accurate map of hygro-thermal patterns within a complex relief. The article presents methodical working steps as well as partial results. Supplemented maps demonstrate final outcomes such as derived possibilities of interpretation to reconstruct the former natural vegetation and to explain regional circulation patterns.

1 Introduction

Since form and distribution of natural vegetation are to a great extent influenced by temperature and precipitation bio- or eco-climatic classification intends to explain vegetation patterns. Agro-climatic typecast similarly testifies to the agrarian landscape design. However, reversed interpretations, i.e. the derivation of climate types by natural vegetation or by land-use distribution must be treated cautiously. In the first case, the impact of soil and groundwater conditions, natural disturbance regimes, maturity status (dormancy, growth, senescence), as well as hardly perceptible former human activities must be considered decisive overarching elements for existent plant communities. In the second case, information arising from cultivation or pasturing depends on more or less adequate methods and therefore demands a critical interpretation.

Nevertheless, vegetation remains a helpful tool for climate interpretation as it was true for the global climate classification systems presented by KÖPPEN (e.g. 1923) or TROLL and PAFFEN (1964). More specific modern analyses of vegetation state based on remote sensing indicate ongoing seasonal variations: for example, drought control by regular world-wide surveys of "vegetation health" and of "moisture and thermal conditions" (KOGAN et al., continuously edited) or phenological NDVI synopses (MOULIN et al. 1997; NDVI =

normalised difference vegetation index). At micro- and mesoscale plant functional types can offer information on prerequisites of distinct climate parameters.¹

Functional types or groups are defined as "... a non-phylogenetic classification leading to a grouping of organisms that respond in a similar way to a syndrome of environmental factors" (GITAY a. NOBLE 1997, 5). By comparing various former definitions of the term and related conceptions the same authors point out that the term "functional group" should be confined to "... groups where the response is mediated through the same mechanism" (p. 7). Concerning the methodological approach, they suggest that similarity must be defined by the user according to the type of environmental factors. Thus, it seems in the field of ecological research botanists where the first to assume that "classical taxonomy will have to give way to functional classifications" (HEAL a. GRIME 1991, 21). However, this new trend of ecological interpretation reminds us of "old wine in new bottles" since former functional classification systems also tended to use plants as response groups for environmental factors. Among others, prominent examples are the life-form concept of RAUNKIAER (as specified by MUELLER-DOMBOIS a. ELLENBERG 1974), the growth-form system of BARKMAN (1988), or the leaf-type diversification of VARESCHI (1980). The main difference between the term "functional group" and "indicator group" seems to be a

question of focus. The first is more time-related and above all aims at predicting global change impacts on terrestrial ecosystems (GCTE, a core project of the International Geosphere-Biosphere Programme, IGBP). The second relates to geo-ecological questions of distribution and therefore is space-related. In this paper, the term plant functional group makes sense because epiphytic growth-forms (PFT_{epis}) which are ideal indicators for a hygric differentiation in southern Ecuador might also respond to long-term climate changes.

Similarly, criteria for examining thermal conditions are given by plants too, for example by classification systems based on the degree of hydro- to sclerophyllous structures or on leaf-sizes (RICHTER 1992). Since these attributes are likewise determined by solar irradiation and water availability, directly responding parameters offer a more appropriate tool to depict temperature regimes. As such the quasi-constant soil temperature at -60 cm reveals the mean annual air temperature 2 m above ground in climate huts of the tropics (WINIGER 1981; see below).

Climate maps are normally based on weather station data. Since most of the world's mountain regions present only a wide meshed net of local in situ measurements, information derived automatically by remote sensing (satellites, radar) provides data-sets of higher solution. On the other hand, these data normally reflect momentary situations. In climate surveys such data are transferred into annual means or average amounts of parameters inflicting difficulties since the equivalent procedure must fall back on continuous evaluation. In the following, an operation is introduced to derive a hygro-thermal map of high spatial resolution with the help of epiphytes as indicator and of soil temperature measurements (STP₋₆₀) coupled with weather station data. The method aims to achieve a better understanding of the distribution of former natural vegetation as well as of regional and local circulation systems. A flowchart scheme presents the methodical structure of the paper (Fig. 1).

2 The lack of weather stations – a problem of disproportion in Andean areas

LAUER and FRANKENBERG (1978) produced a hygro-thermal map representing the temperature belts by isothermes and the number of humid months by isohyromenes: their map covers the Central Mexican part of the Veracruz lowlands, the Sierra Madre Oriental and the eastern Meseta up to the Sierra Nevada de México around Popocatépetl and Ixtaccihuatl. Within this area mean annual air temperatures range

from 26.5°C to less than 1°C with three to twelve humid months. To express the complexity of climates the authors had to create a highly differentiated colour scheme. This map, the contents of which are derived by gradient analyses based on altitudinal correlations of 83 weather stations, served as a model for equivalent studies of the author in southern Peru (RICHTER 1981; there 93 weather stations). As both areas cover about 80,000 km² the average station density amounts to approximately one station per 900 km² within rather simply structured mountain terrains (escarpment, high plateau, and high volcanoes).

Although southern Ecuador is not as elevated as Central Mexico and southern Peru, its topography is much more complicated. Here a northern mountain junction called "Nudo de Loja" culminates at 3,800 m a.s.l. in Ferro Urcu and Cerro Chinchilla. From there mountain ranges stretch out towards SW, S and SSE, all three of them interrupted and dissected by valleys and basins between various smaller Inter-Andean Sierras (Fig. 2). This complex orographical region of 25,500 km² holds only 22 weather stations, some of them providing interrupted and insufficient data sets. Additionally, all of the unequally distributed sites within the wide meshed net of one station per 1,160 km² are concentrated on settled valley and slope positions. Only one is located above 2,500 m a.s.l. and none of them on a mountain ridge.

An insufficient net of weather stations makes it difficult to produce exact climate maps in many Andean areas. This is especially true for the wetter parts of the mountain ranges where spontaneous colonisation by squatters is widespread in modern times, particularly on eastern escarpments of the tropical Andes. Another factor prevents data collection in the eastern Cordilleras of southern Ecuador and northern Peru. This rather low section between the northern and Central Andes is affected by extremely high wind speeds and rainfalls resulting from quasi-permanent strong easterlies. Thus these ridges between the depressions of Girón-Paute and of Huancabamba are not even populated.

Experiments with mobile tanks turning against wind verify more than twice as much precipitation as measured with vertical gauges (2,600 mm a⁻¹) situated on the crest of the Páramos de Cajanuma above Loja at 3,400 m a.s.l. Primitive rain collectors near Lagunas de los Compadres signal annual amounts of ca. 6,000 mm a⁻¹ (pers. comm. Dipl.-Hydr. PAUL EMCK, Erlangen), and first radar interpretations give evidence of even higher values in the mountains north of Zamora (pers. comm. Dr. RÜTGER ROLLENBECK, Marburg). Merely 30 km W of both regions the Basin of Catamayo at 1,250 m

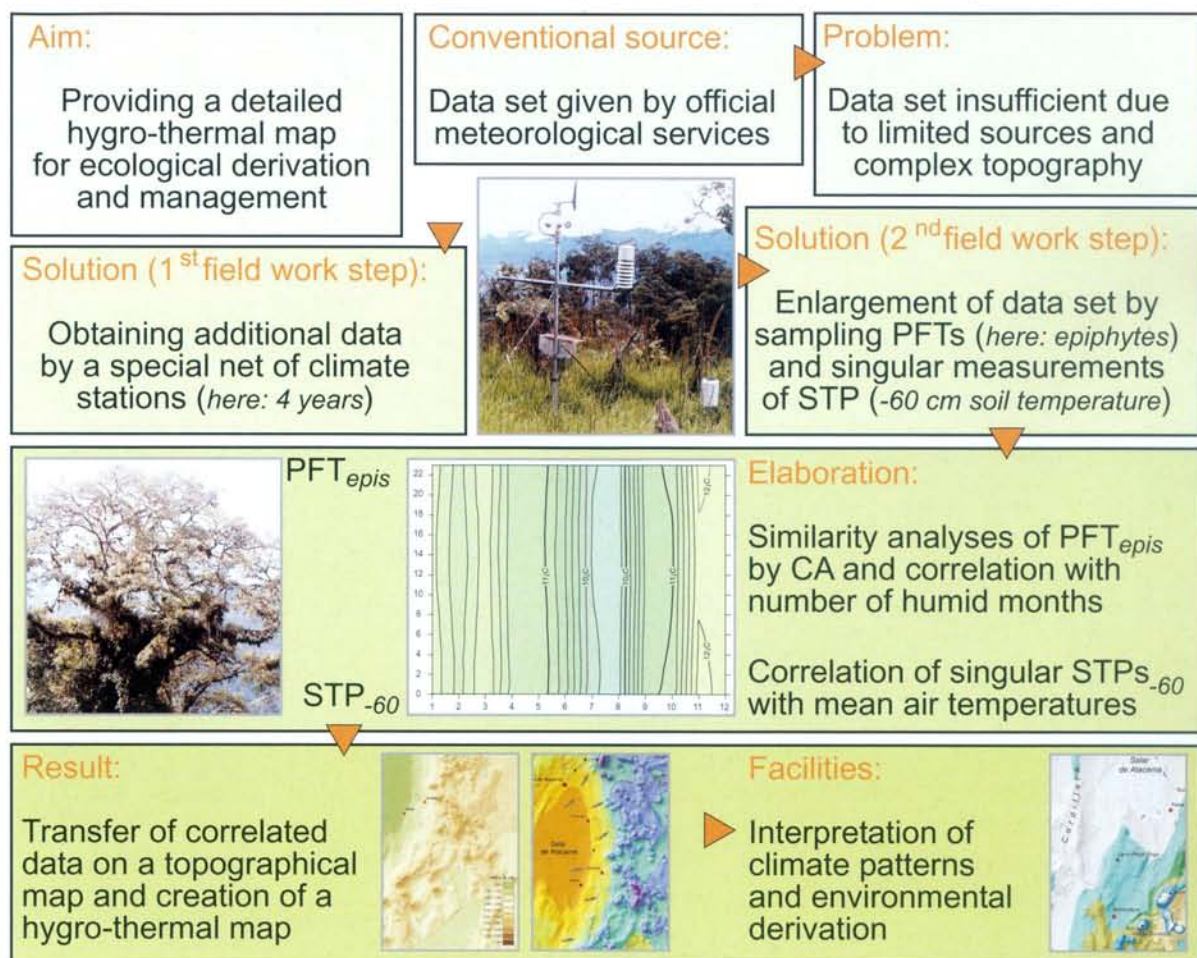


Fig. 1: Concept of the methodical structure

Konzept der methodischen Vorgehensweise in der Arbeit

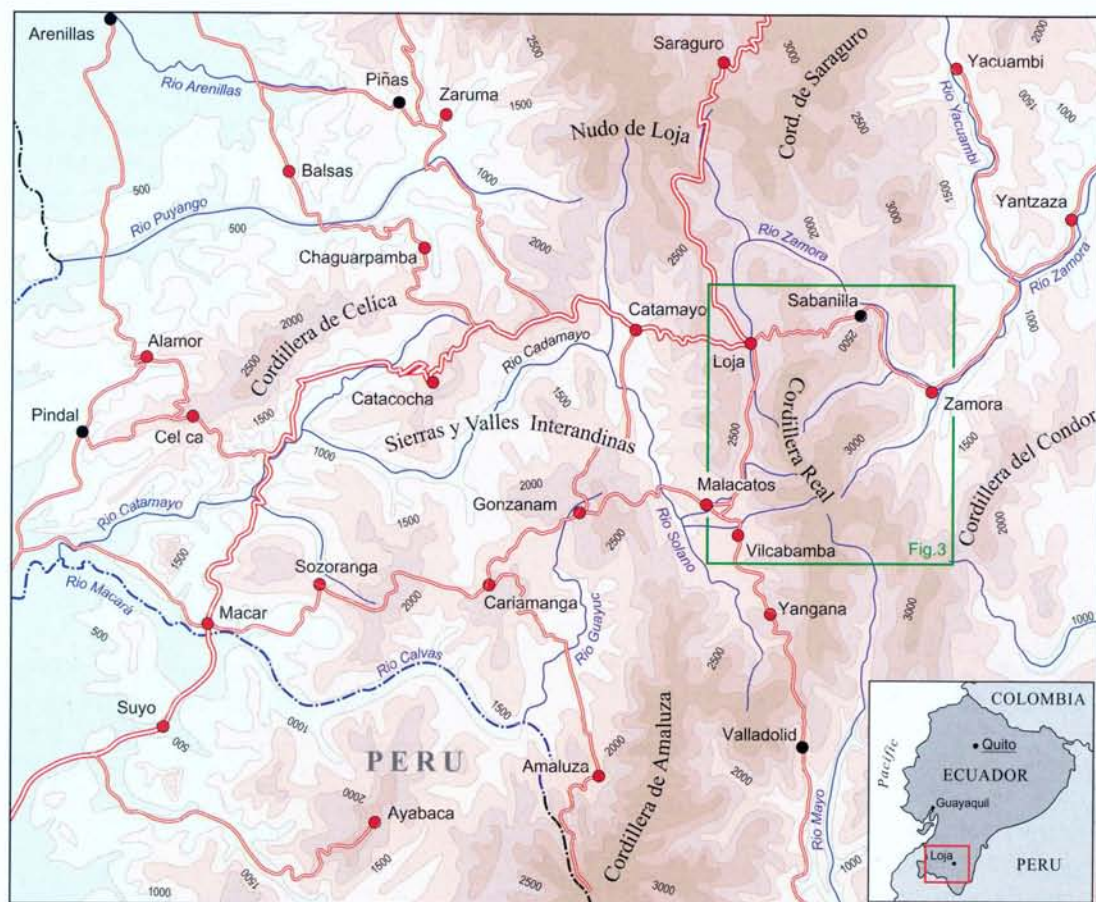
a.s.l. receives only 383 mm a⁻¹ of rainfall! These preliminary results of a current project supported by the DFG (German Research Council) certainly do not only stand for an isolated phenomenon. Instead, there are hints of similar contrasts neighboring a “wet diagonal axis” which is explained by rather stable ITC-positions in the northern Andes crossing the Columbian Cordilleras (analogous term for the “dry diagonal axis” crossing the Cordillera of Atacama). Highly complex structures from xeric to hygric vegetation types within short distance are for example known of Costa Rica, northern Peru, or northern Bolivia. However, these features are not yet climatologically well elucidated.

A rough climatic overview (Fig. 3) highlights deficits in the official weather station net in southern Ecuador. Higher parts of the Cordillera Real are marked by rainfall amounts which were never reflected by authorized services. Precipitation in the mountain area being be-

tween two and four times higher than at wettest low- and midland locations was not expected prior to the recent installation of four DFG-stations in elevations above 2,800 m a.s.l. Thus the crestline of the eastern mountain chain is not only an important climate divide between the moist Oriente and the dry Sierra Interandina but also a poorly known water tower for both environmental types.

3 Looking for better climate information – the installation of a special net

To get more information about the very special, yet unknown climatic conditions in the Cordillera Real east of Loja eight automatic weather stations serve for long-term studies on diversity, dynamic processes, and land use potentials in mountain forest ecosystems of



altitudes in m

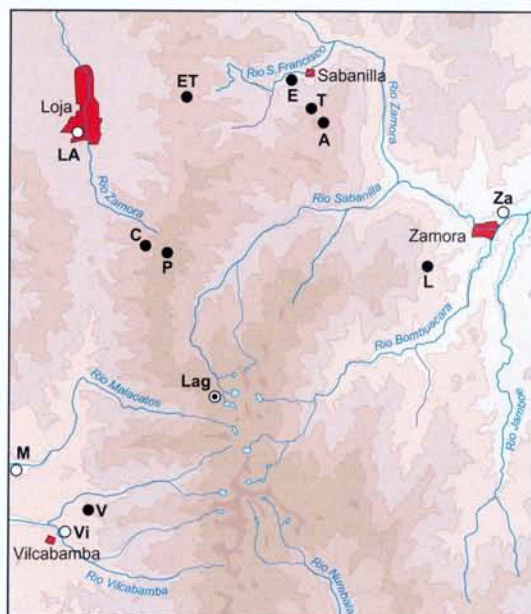
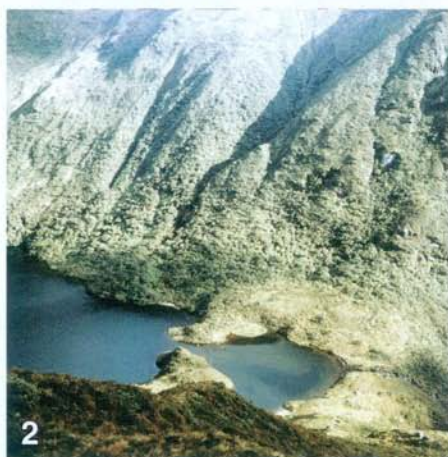


Fig. 2: The area of investigation: The large map indicates the restriction of official weather stations to settled areas while the detailed map enlightens the sites of current DFG- and INAMHI-stations within the Cordillera Real

Das Untersuchungsgebiet: Im großen Kartenbild sind offizielle Wetterstationen auf Siedlungsgebiete beschränkt, während die Ausschnittskarte die Lage der laufenden DFG- und der staatlichen Stationen verdeutlicht



Photos 1, 2, 3: Dry, intermediate, and wet types of widespread landscapes: climatic differences are reflected by natural plant stands. Valle de Naranjo (semiarid Inter-Andean Sierra, 900 m a.s.l.), Sabanilla (semihumid eastern valleys, 1,600 m a.s.l.), Cordillera Real (perhumid Páramos, 3,300 m a.s.l.)

Trockene, mäßig feuchte und feuchte Naturlandschaften



Photos 4, 5, 6: Dry, intermediate, and wet types of widespread landscapes: climatic differences are hidden by land use impacts and the reduction of natural plant stands. Valle de Naranjo (semiarid Inter-Andean Sierra, 1,000 m a.s.l.), Sabanilla (semihumid eastern valleys, 1,600 m a.s.l.), Cordillera de Amaluza (perhumid southern section at the Peruvian borderline, 3,300 m a.s.l.)

Trockene, mäßig feuchte und feuchte Agrarlandschaften

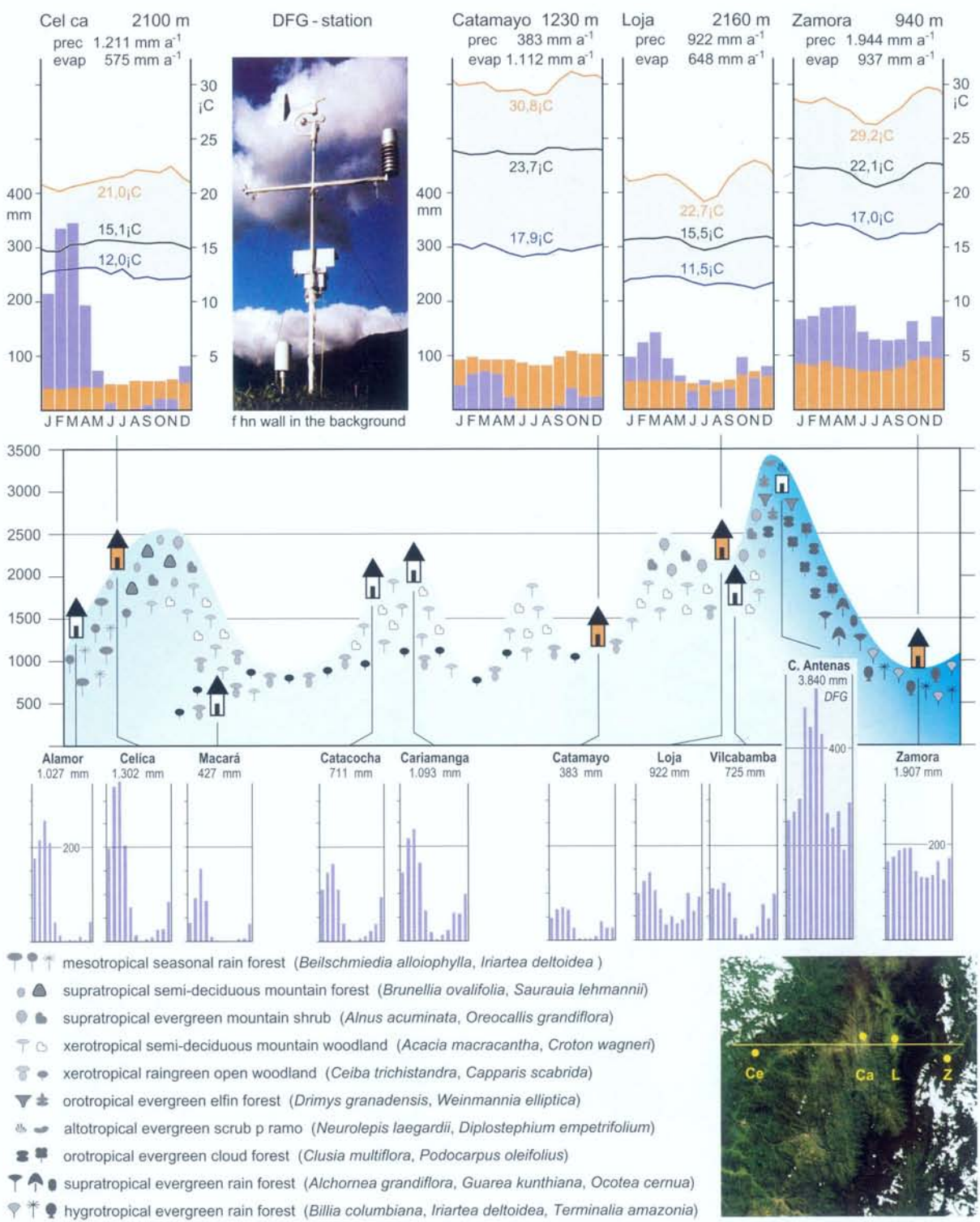


Fig. 3: W-E-transect with climate diagrams of official weather stations in southern Ecuador (apart from own data by the DFG-station at Cerro de las Antenas)¹⁾

W-E-Transekt durch Süd-Ecuador mit Klimadiagrammen staatlicher Wetterstationen und zonale Abfolge natürlicher Pflanzenformationen

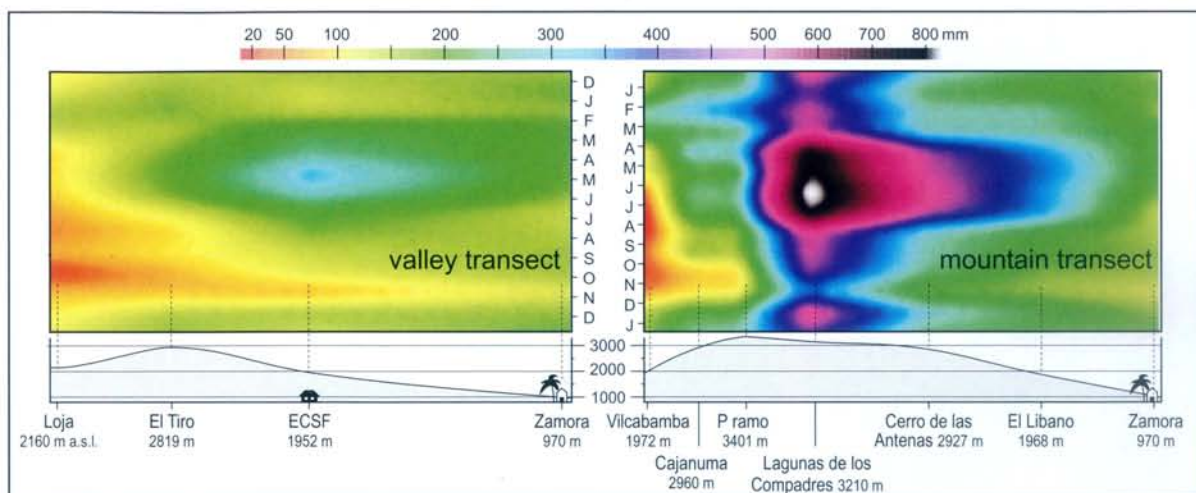


Fig. 4: Time-spatial pluviocomposites passing the Cordillera over a lower profile via Paso El Tiro down through the Rio San Francisco valley and over an upper profile crossing the Cordillera via the crest at Cajanuma. Both profiles extend over 30 km (s. Fig. 3). Data by PAUL EMCK, Erlangen

Raumzeitliche Niederschlagskompositen eines unteren und oberen Profils durch die Cordillera Real

southern Ecuador (Fig. 2). A profile sketch (Fig. 4) illustrates a first climatic feature of the Cordillera Real: precipitation is much lower along a valley transect than along a transect crossing the crest. In the first case, near the scientific station of ECSF, 300 mm per month concentrate on May. In contrast, the windward area around Lagunas de los Compadres a little east of the main crest reveals more than 700 mm per month between April and August. Furthermore, the long dry period of the Inter-Andean section in the west stands out while the eastern escarpment reflects a slight dry peak restricted to November.

Further important differences comprise luff- and rain shadow-effects between Zamora in front of the moist eastern and Vilcabamba at the dry western side of the

escarpment as well as the altitudinal alteration towards the crest of Cajanuma in Podocarpus National Park. These contrasting climates are reflected by figure 5 and summarised in the following per location:

– Comparison of Zamora-El Libano and Vilcabamba, both at 1,970 m a.s.l.: temperatures are around 2.7 K lower (mean annual temperature 15.6° and 18.3°C respectively) and daytime as well as seasonal amplitudes are smaller in the east than in the west. Different moisture regimes are responsible for heat deficiency in the first and a heat surplus in the second case. The configuration of isolines of relative humidity, which is much denser in Vilcabamba than in El Libano, mirrors correspondent relations. At the eastern station mean maxima of 97% occur at around 5 a.m. during the wet period in May, minima of 77% at 2 p.m. during the less moist season in November. Equivalent means in the west amount to 93% at 6 a.m. during the moist February and only 43% at 2 p.m. during late October. The rainfall regimes on both escarpments belong to the equatorial type of precipitation course (TPC) marked by two peaks with a primary maximum from December to April and a second one in October. However, while Vilcabamba is characterised by a pronounced dry season between June and September (TPC 2 according to BENDIX u. LAUER 1992) this period is “filled up” by a third rainy season at Zamora (TPC 3a acc. to the authors). In the same sense, the diurnal course of rainfall is more equally distributed in the east. Highest means of only about 1 mm h⁻¹ occur between 2 and 6 p.m. retarding from March towards July. In the west

¹⁾ The detailed diagrams in the upper part contain mean maximum (red line), average (black), and minimum air temperature (blue) of four locations depicted along a profile illustrated in the satellite image below; red columns represent the average monthly evaporation amounts, blue ones those of precipitation. The latter is presented by further comparative diagrams below the transect sketch. The distribution of natural plant formations is based on own research after consulting lists and maps by SIERRA (1999), commented checklists by MADSEN and ØLLGAARD (1993), ULLOA ULLOA and MØLLER JØRGENSEN (1995), and on papers of GRUBB et al. (1963), GRUBB and WHITMORE (1966), KESSLER (1992), and BUSSMANN (2001)

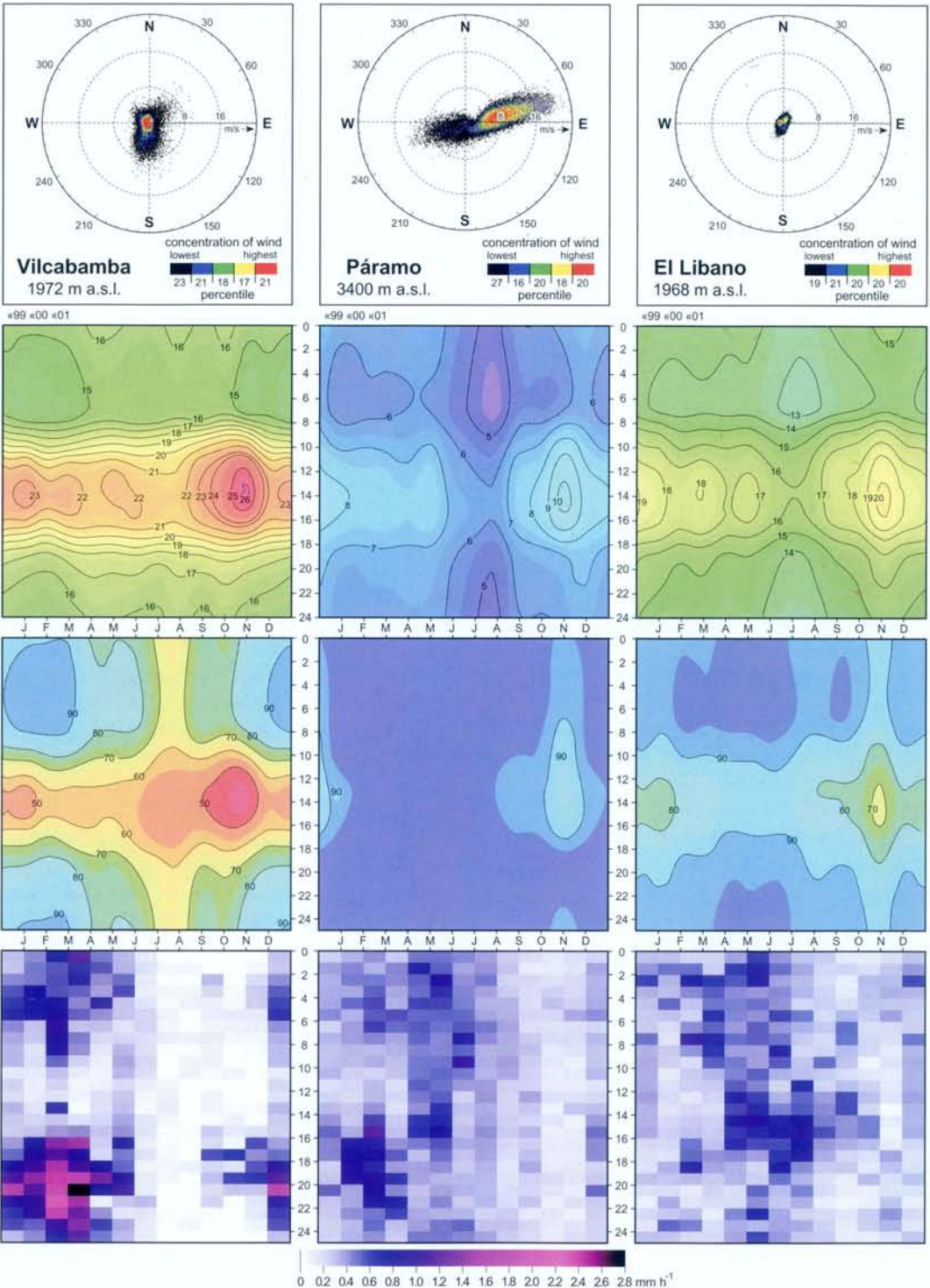


Fig. 5: Climate contrasts in the Cordillera Real, from up to down: Wind speed and direction, isopleths of temperature, relative humidity, and seasonal as well as daytime distribution of rainfall at Vilcabamba (western escarpment), Páramo (crest line), and El Libano (eastern escarpment). All data based on complete sets from Jan. 1999 up to Dec. 2001. Collection, analysis and presentation of data by PAUL EMCK, Erlangen

Klimagegensätze in der Cordillera Real, von oben nach unten: Windgeschwindigkeit und -richtung, Isoplethen der Temperatur und relativen Luftfeuchte sowie jahres- und tageszeitliche Niederschlagsverteilung an drei Stationen

highest means of up to 2.8 mm h^{-1} in the evening between 6 and 11 p.m. hint at strong downpours which continue as persistent advective rains until the early morning from January till May. Winds at El Libano never exceed 4 m/sec and are channelled by the NNE-SSW running valleys of lower Rio Zamora and Rio Bombuscara and, to a lesser extent, by the valley of upper Rio Zamora leaving the main Cordillera and entering the foothills from WNW. In contrast, maximum wind speeds at Vilcabamba amount up to 12 m/sec . Occurring as gusty storms combined with sunshine and dry air, katabatic winds fall down from NE during the wet season, i.e. from the Cordillera Real, or from S during the dry season, i.e. from the linking Paso Tapichalaca towards Cordillera de Amaluza into the Solano Valley.

– Situation at Páramo de Cajanuma, $3,400 \text{ m a.s.l.}$: the aforementioned clear foehn effect results from strong easterly airflows acting as motor for moist air masses supported by trades towards the eastern escarpment. Thus the crest of the Cordillera Real is mostly wrapped in a typical foehn wall. Within these rather shallow clouds strong winds from ENE with maximum speeds of up to 22 m/sec and an average speed of about 8 m/sec prevail by far. Nevertheless, during the transition between the dry and wet period in the Inter-Andean area, i.e. between October and December, westerlies of up to 14 m/sec may occur during phases of one to ten days. Usually they provide the páramos, which are constantly wet during easterly impact, with rare fine and dry weather situations. Thus relative humidity is permanently high (mean values over 90%) apart from a short period in November (TPC 4 acc. to BENDIX u. LAUER 1992). Rainfalls are equally distributed with less precipitation and with maxima in the evenings between January and March. Inputs do not surmount means of 0.8 mm h^{-1} (measured by standard, i.e. vertically installed rain gauges). Noon temperature exceeds 10°C only in November and drops to a minimum mean of 4.2°C in the mornings of early August; freezing was not observed during the three year-period 1999–2001. The unusual harsh weather conditions of the crest region are expressed by phenomena atypical for the tropics and by diurnal temperature amplitudes being smaller than annual ones. As a conclusion, the extraordinary weather of the Cordillera Real prevents settlement and land use and therefore explains the existence of a pure natural páramo ecosystem. These completely untouched sites are a unique feature restricted to the Andean mountain areas north and south of the border between Ecuador and Peru.

Hence the exemplary data of the DFG-stations once again point out the lack of respective information for

remote mountain areas (first step of solution in Fig. 1). However, even a greater number of climate stations could hardly express the climate complexity in a region where open cactus shrub and moss-packed elfin forests are found within a range of not even five kilometers. In addition, the existence of a rather low belt of maximum precipitation in tropical high mountains (WEISCHET 1965; LAUER 1976) does not seem to be applicable for the research area.

4 Looking for additional information – phytoindication and soil temperature

Figure 6 comprises the different hygro-thermal climate types governing southern Ecuador. The ordination is based on data of mean annual temperature and of the number of humid months given by eight DFG-stations and 21 official INAMHI-stations (+ 1 by Peruvian SENAMHI). Additionally, the distribution schemes of main vegetation types provide enlightenment on the climate ecological relations. For most of southern Ecuador the sketch should be a provisory basement for climate assignment by phytoindication through representative plant communities. However, map 2 (Suppl. III) hints at scattered relicts of natural vegetation and at a land use coverage of more than 80%. This is specially true for the dry Inter-Andean valleys serving since long as areas of settlement. Vaster parts of natural vegetation are evidently restricted to the wet and harsh climates of the eastern Cordilleras. Thus modern vegetation only insufficiently reflects the climate conditions as demonstrated by the comparison of photo 1, 2 and 3 with photo 4, 5, and 6.

Climate can be interpreted directly and indirectly by phytoindication. Direct techniques base on an immediate connection between climate and vegetation expressed by phytomorphological aspects. For the Neotropical Cordillera the author presented various procedures taking examples from Mexico to Northern Chile (RICHTER 1992, 1996). Among various analyses those of leaf-consistence or leaf-size of all species of plant-stands are only of limited value since they mirror microclimatic rather than meso- or macroclimatic prerequisites. On the other hand, the leaf-size method might be suitable if restricted to defined indicator taxa, e.g. to the Melastomataceae in the Neotropical Cordilleras. Most of the appertaining family members are confined to open environments including sites of human impact. They normally allow precise conclusions concerning the hygric situation within their distribution area (less than six arid months). While evaluations in Bolivia and Chiapas proved significant results (GRILL

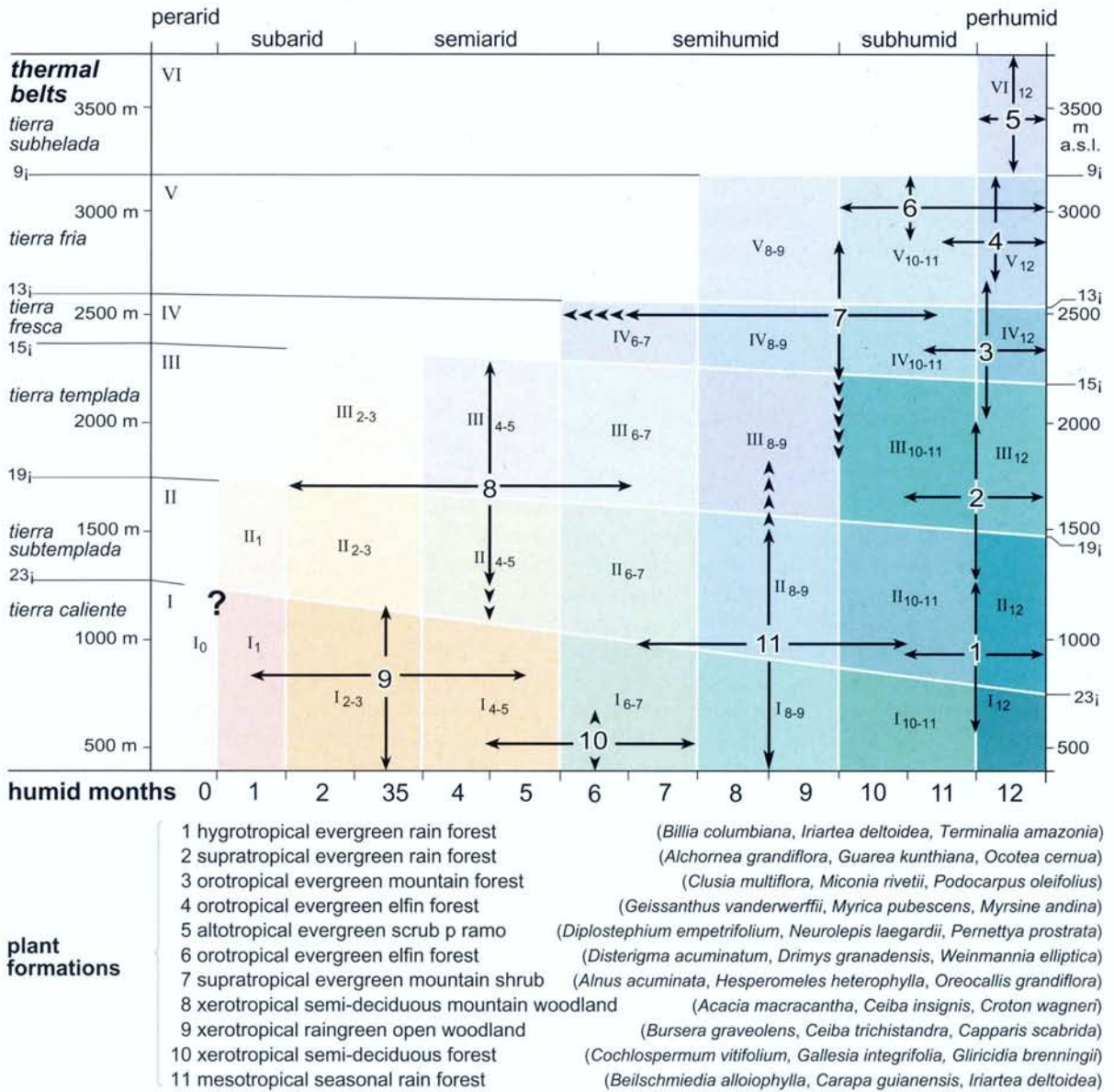


Fig. 6: Ordination of climate types and of the main plant formations in southern Ecuador. The coloured section indicates climates to be found in the area of investigation. Nomenclature of altitudinal belts according to RICHTER (2001), nomenclature and allocation of hygro-thermal types according to LAUER (1973)

Ordination der Klimatypen und wesentlichen Pflanzenformationen Süd-Ecuadors

2002; RICHTER u. LAUER 1987; SCHULZ 1997), southern Ecuador seems to be an exception because of unsatisfactory results. Thus none of the mentioned direct methods, neither those adapted to arid regions like analyses of life-form spectra or of plant coverage, are useful in the present case.

Indirect techniques take into account the indication of significant taxa (active or passive monitoring) or species groups. Assessment of climate by epiphytism

(second step of solution in Fig. 1) can be methodically enlarged by adding characteristic growth-forms such as pinnated or non-pinnated leaves within the fern-group, absence or presence of bulbs among orchids, or subdivisions of lichen-forms. Bromeliads evidence even more growth-types which stand for different hygric (and thermal) types as demonstrated in figure 7. Using a system based on the combination of growth-forms and taxonomic features admittedly is systematically in-

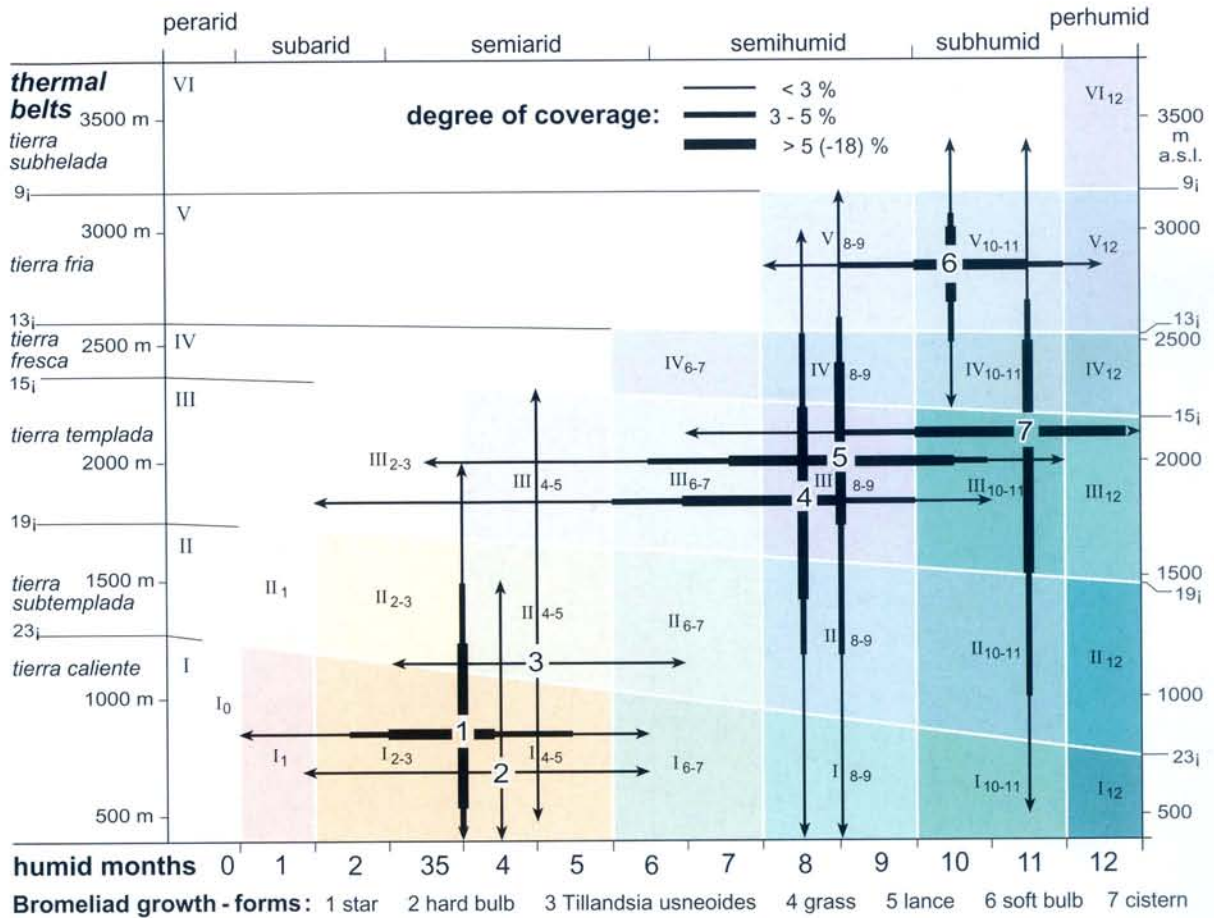


Fig. 7: Climate ordination with a superimposed distribution of various growth forms of Bromeliads (colours according to Fig. 6). *T. usneoides* represents an "azonal" species restricted to moist micro-climates (e.g. riversides, foggy environs)

Klimaordnung und Verteilung verschiedener Bromelien-Wuchsformen

correct. On the other hand, the aim is an environmental rather than a systematic classification – and therefore just the end justifies the mean. Since in the present case the aim is a characterisation of climate an investigation of epiphytism must be concentrated on the upper reaches of tree crowns (stratum 5 according to JOHANSSON 1974) where the outer biosphere layer is directly linked to radiation, water vapour and precipitation of the open atmosphere. Only solitary trees or small open tree stands guarantee proper habitats. Upper branches of low trees can be climbed in order to estimate epiphytic cover; higher exemplars are checked with a binocular; the "out-of-touch procedure" prevents ongoing and probably useful differentiation of mosses into Anthocerotae, Hepaticae, and Musci.

While statistical analyses based on epiphytism are a useful tool for hygric characterisation that does not deny thermal and radiation impacts measurement of soil temperatures in a depth of 60 cm had been exam-

ined as an ideal indicator for temperature regimes. WALTER and MEDINA (1969) were among the first to point out quasi-constant soil temperatures in this level as a phenomenon of the tropics. WINIGER (1981) refined the method and recommended various techniques to optimise the results. In order to receive comparable data, measurements are conducted under forest stands, where correlation between soil and mean annual air temperature is highest (second step of solution in Fig. 1). Furthermore, data collecting must be concentrated on sites of similar exposure and inclination to diminish effects of soil-moisture differences. If site conditions vary considerably, for example caused by the absence of suitable forests or big trees, interpolation procedures must be considered. Measurements within open plant formations usually lead to a necessary reduction of values. However, in the case of Ecuador the correction factor is slight since long term studies by BENDIX and RAFIQPOOR (2001) as well as own comparisons hint at

Species:

- 1 = *Tillandsia ionochroma* (Bromeliac.)
- 2 = *Bomarea distichifolia* (Amaryllidac.)
- 3 = *Pernettya prostrata* (Ericac.)
- 4 = *Oxalis subintegra* (Oxalidac.)
- 5 = *Hymenophyllum fucoides* (Hymenophyllac.)
- 6 = *Polypodium curvibasis* (Polypodiac.)
- 7 = *Anthurium brevicaule* (Arac.)
- 8 = *Nephrolepis crassifolia* (Polypodiac.)
- 9 = *Pleurothallis spec.* 5 (Orchidac.)
- 10 = *Pleurothallis cauliflora* (Orchidac.)
- 11 = *Macleania rupestris* (Ericac.)
- 12 = *Elaphoglossum latifolium* (Lomariopsidac.)
- 13 = *Clusia elliptica* (Clusiace.)
- 14 = *Tillandsia stenoura* (Bromeliac.)

Growth-forms of all 5 sites for CA-Classification:

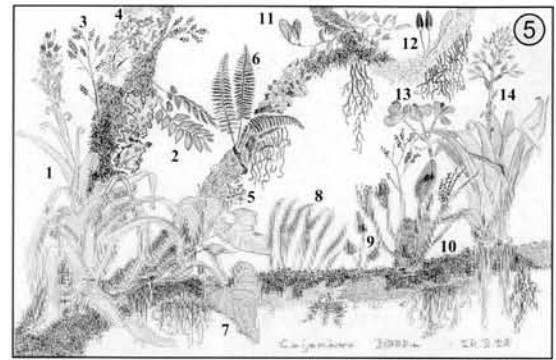
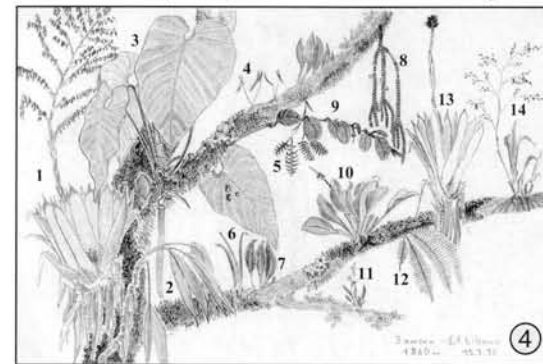
5	Mosses	95%
	crust lichens	5%
	pinnated ferns	3%
	non-pinnated ferns	10%
	Hymenophyllaceae	3%
	Orchid (with bulb)	1%
	Orchid (without bulb)	5%
	Bromeliad (cistern)	2%
	Araceae	1%
	Ericaceae	8%
	others	2%
	total coverage	= 135%

Growth-forms of all 5 sites for CA-Classification:

4	Mosses	70%
	crust lichens	20%
	shrub lichens	5%
	pinnated ferns	3%
	non-pinnated ferns	3%
	Hymenophyllaceae	2%
	Orchid (with bulb)	6%
	Orchid (without bulb)	8%
	Bromeliad (cistern)	12%
	Araceae	4%
	Ericaceae	3%
	Melastomataceae	1%
	Palmae	1%
	Peperomiaceae	3%
	others	6%
	total coverage	= 139%

Species:

- 1 = *Tillandsia triplinata* (Bromeliac.)
- 2 = *Asplundia heteranthera* (Cyclanthac.)
- 3 = *Anthurium formosum* (Arac.)
- 4 = *Pleurothallis spec.* 3 (Orchidac.)
- 5 = *Dichaea spec.* (Orchidac.)
- 6 = *Campyloneurum angustifolium* (Polypodiac.)
- 7 = *Elaphoglossum lingua* (Lomariopsidac.)
- 8 = *Disterigma pentandra* (Ericac.)
- 9 = *Macleania coccoloboides* (Ericac.)
- 10 = *Cephaelis spec.* (Orchidac.)
- 11 = *Cichneinfia cf. suarezii* (Orchidac.)
- 12 = *Pecluma curvans* (Polypodiac.)
- 13 = *Guzmania acuminata* (Bromeliac.)
- 14 = *Oliveriana brevifolia* (Orchidac.)

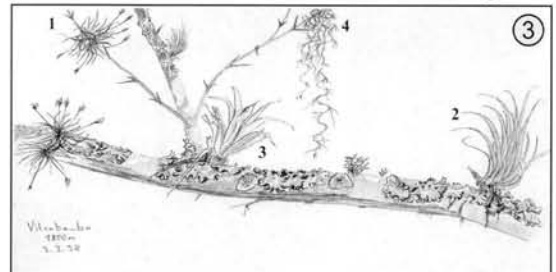


Species:

- 1 = *Tillandsia recurvata* (Bromeliac.)
- 2 = *Tillandsia purpurea* (Bromeliac.)
- 3 = *Tillandsia multiflora* (Bromeliac.)
- 4 = *Tillandsia usneoides* (Bromeliac.)

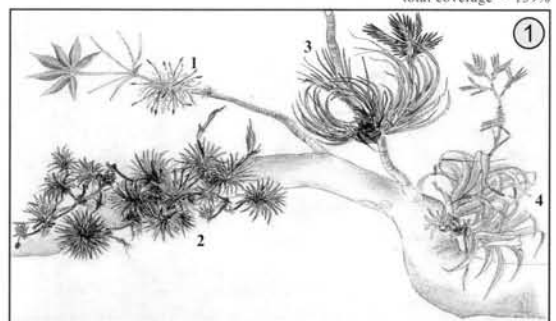
Growth-forms of all 5 sites for CA-Classification:

3	Mosses	1%
	crust lichens	60%
	shrub lichens	15%
	Bromeliad (cistern)	2%
	Bromeliad (grass)	1%
	Bromeliad (star)	3%
	Bromeliad (beard)	1%
	total coverage	= 85%



Growth-forms of all 5 sites for CA-Classification:

2	Mosses	70%
	crust lichens	20%
	shrub lichens	5%
	pinnated ferns	3%
	non-pinnated ferns	3%
	Hymenophyllaceae	2%
	Orchid (with bulb)	6%
	Orchid (without bulb)	8%
	Bromeliad (cistern)	12%
	Araceae	4%
	Ericaceae	3%
	Melastomataceae	1%
	Palmae	1%
	Peperomiaceae	3%
	others	6%
	total coverage	= 139%



Growth-forms of all 5 sites for CA-classification:

1	crust lichens	15%
	Bromeliad (lance)	2%
	Bromeliad (grass)	1%
	Bromeliad (star)	4%
	total coverage	= 22%

Fig. 8: Epiphytic communities reflecting different climate conditions in southern Ecuador

1 El Enpalme (940 m, subarid), 2 Zamora (980 m, perhumid), 3 Vilcabamba (1,800 m, semiarid), 4 El Libano (1,860 m, perhumid), 5 Cajanuma (3,000 m, perhumid)

Epiphyten-Gemeinschaften subarider, semiarider und perhumider Standorte in Süd-Ecuador

differences of only 1 to 2 K between grass and forest stands. More important are corrections influenced by seasonal variation. The eight DFG-stations in the Cordillera Real show temperature deviations of up to 3 K in the given soil level during the year and hence require seasonal corrections of singular measurements at further check points.

5 Using epiphytism as indicator for the number of humid months

According to BENZING (1987) epiphytic bromeliads and orchids are subject to accelerated evolutionary progress caused by short regeneration cycles. Due to their generative power they may react genetically flexible to stressful environments to compensate for mortality imposed by disturbance. GENTRY and DODSON (1987) give an example by stating natural in situ speciation of various Ecuadorian *Scelochilus*-orchids in as little as 15 years. In the same context, they point out nine local endemics of 14 *Telipogon*-orchids, each found in a single valley or on a single slope in the South Ecuadorian cordilleras. Other taxa are also prominent members of the manifold epiphytic communities. Figure 8 illustrates their impressive variability in southern Ecuador by exemplary sketches of places at 900 m a.s.l. and at 1,860 m a.s.l. in moist and dry climates and at 3,000 m a.s.l. within a mostly cloud and rain induced elfin-forest. Visual comparison of the pictured diversity evokes the idea to use similarity analyses for a statistical determination of obvious differences and to relate them with climate impacts. However, phytodiversity among southern Ecuador's epiphytes is too high for numerical analyses based on the species level. Correct identification would take much time and require tree-climbing. Even more important, detailed determination of each species would lead to overfilled data sets contributing to a confusing variety of "climate-indicators" since many species are restricted to only a few sites. Over-information is not helpful in this case as it prevents general interpretation which is much easier on the basis of clearly arranged synoptic groups of plant functional types. Species names are therefore only added to figure 8 for floristically interested readers. Instead, the listed epiphytic groups of combined family-classes and growth-forms correspond to the applied data elaboration for the hygric map in this paper (map 3, Suppl. III). The sketches represent five types out of 156 relevés obtained during various field trips in late March between 1998 and 2002.

The subdivision of epiphytic groups was created during and after initial field checks and took into consi-

deration own former experiences from Mexico, Guatemala, Costa Rica, Panamá, Venezuela, Colombia, Peru and Bolivia. Each of the 156 relevés composed out of five samples on neighbouring trees covers a total branch-length of 15 ± 3 m. In many cases lichens and mosses form closed carpets around the branch which provide basic substrates for the growth of erect, winding, or descendant vascular plants. Thus cover values of more than 100 % are common. Percent coverage of each element (taxon alone or taxa with specific growth-form differentiation) was estimated. Root-transformed calculations of plant-coverage of distinct epiphytic groups figure as an appropriate tool for similarity analyses based on multivariate correlation. Instead presence/absence analyses would result in a less detailed differentiation while cover values hide abundant small associates but emphasise less abundant big community-members or large carpets of individuals. The transformed percent values supply the basement for following correspondence analysis (here: normalised relevés; agglomeration rule: minimum variance; similarity ratio: van der Maarel).

Each of the sample sites is allocated by GPS; priority check points are chosen near INAMHI- and all DFG-weather stations in order to use them as "information-centers" for the number of humid months at places of medium- to long-term evaluation of climatic parameters. The stations provide necessary precipitation and temperature data to calculate mean evaporation rates with the formula of Papadakis (SCHMIEDECKEN 1979). Adding 126 samples to those near the 22 official and 8 DFG-weather stations leads to a more than four-fold enlargement of the data that are available to establish the detailed hygric map shown in supplement III. The eight subdivisions listed by the legend of map 3 can be derived from the scatter plot in figure 9 (step of elaboration in Fig. 1). The diagram illustrates the wide pattern of epiphytic communities comprising those of perhumid areas located on the upper left and of perarid regions on the right side of the plot. Numbers indicate the humid months next to those dots related to respective nearby weather stations. Between black dots marking wet sites and white dots marking dry sites the grey dots in the center and at the bottom of the horseshoe-formed distribution curve reflect intermediate locations of semihumid to semiarid climates. Isolines dividing the regimes of humid months are added by hand. Numbers that do not coincide with the isolines and the colours of the dots originate from weather stations with long fog seasons and are not revealed by the original precipitation data. Instead, the real number of humid months at these sites is therefore higher than depicted in figure 9. The last step comprises the transfer of the

statistically elaborated hygric situation at any epiphyte location to the topographical map and the integration of all data into a system of isohyromenes.

A synthetic description of five main epiphytic clusters based on the same data set is presented by structural components in figure 10. At first glance, lichens and mosses seem to be of decisive importance since outstanding high cover values determine all the diagrams. However, the significant role of smaller percentages of vascular plants should not be neglected. Various quantities of Bromeliad growth-forms can make a great difference in grouping after their indicator value has been emphasised by the mentioned root transformation. This becomes obvious in comparing cluster 1 and 5 with hygric Bromeliad types on the one and xeric types on the other hand. Therefore, the supposedly obvious importance of lichens and mosses should not result in disregarding vascular epiphytes.

The essential hygric patterns on map 3 are summarised as follows:

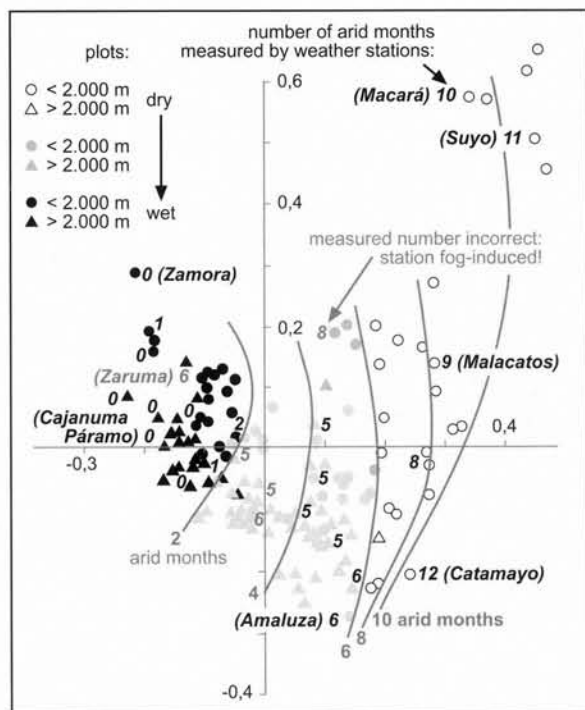


Fig. 9: CA-analysis for discrimination of similarity degrees of epiphytism added by numbers of arid months at weather stations situated close to some of the 156 sample sites in southern Ecuador

CA-Analyse zur Trennung der Ähnlichkeitsverhältnisse des Epiphytismus mit Zahl der humiden Monate in der Nähe einiger der 156 Aufnahmen in Süd-Ecuador

– The eastern part up to the crests of the Cordillera de Amaluza, Cord. Real, and Cord. de Saraguro are characterised by humid climates triggered by the constant impact of trades.

– The central intermediate zone of valleys and ranges is determined by complex hygric conditions. While downpours during the wet season provide rainfall in higher elevations the same events do not necessarily touch the lower areas due to high evaporation rates. Furthermore, convective processes caused by effects of mass elevation result in higher and more frequent precipitation in summit areas ("Merriam effect", RICHTER 1996).

– The western part is once again marked by heterogeneous rainfall patterns, but to a lesser extent than the center since the Pacific lowlands are not as dry as the interior valleys. The crest-areas are less humid than those of the eastern Cordilleras.

– A conspicuous "wet spot" that has been unknown until today is located NW of Piñas and does not at all coincide with registrations of any nearby weather station (Zaruma 4, Balsas 5 humid months!). The reason for sub- to perhumid hygric prerequisites signaled by an epiphytism similar to that of the Zamora region east of Cordillera Real is clearly induced by frequent fogs during the dry season.

– A conspicuous "dry spot" is centered around the Basin of Catamayo. Annual means of precipitation (383 mm a^{-1}) are slightly lower than in Macará located 800 m below (427 mm a^{-1}) and a little higher than in Zapotillo (368 mm a^{-1}). Both stations are situated in the lowlands at the Peruvian border. Nevertheless, the wettest month in Catamayo still proves water deficits contrasting to at least one humid month in Macará and Zapotillo.

The general summary elucidates the extremely diverse hygric conditions ranging between perarid and perhumid. Finally, it must be highlighted that the distance between the driest and the wettest spot comprises less than 30 km (383 mm a^{-1} versus probably more than $6,000 \text{ mm a}^{-1}$)!

6 Using soil temperature as indicator for air temperature means

For the thermal differentiation 244 holes of 50 cm depth had been dug for immediate temperature checks with stab thermo-sensors 10 cm below, thus corresponding to the required soil temperature at a depth of 60 cm . Once again, sites near INAMHI-weather stations serve for comparison. Since soil temperature amplitudes of $2\text{--}3 \text{ K}$ were typical in the annual course and since the specific field work covered the rainy season

from December 1998 to April 1999, seasonal adjustment was obligatory. The same is true for interannual variations. At the time of field measurements all weather stations still indicated sustaining positive anomalies produced by after-effects of El Niño 1997/98: Temperatures on elevated crests were around 1 K and in Inter-Andean valleys up to 3 K higher than in non-ENSO years. Seasonal correction is obtained by continuous measurements of the DFG-stations as well as of six mini loggers (temperature hobos) in the respective -60 cm-level since January 1998 (step of elaboration in Fig. 1). Interannual deviations are eliminated for each site by correcting data of nearby INAMHI- and DFG-stations.

After an improvement of all soil temperature data gradient analyses are derivable. In figure 11 the study sites are split up according to the three main sub-regions. The grey triangles standing for the mean air temperatures of available weather stations are disregarded in the correlation. The regression formula evidence conspicuously distinguished lapse rates. Trade rainfalls prevail along the eastern escarpments of the eastern Cordilleras and lead to wet adiabatic conditions expressed by a vertical decrease of 0.59 K / 100 m. The theoretical mean 0°C-line ought to be found around 4,700 m a.s.l., i.e. nearly 1,000 m above the highest

peaks. In contrast, the lapse rate calculated for the Inter-Andean valleys and ranges is characterised by dry conditions reflected by a vertical decrease of 0.71 K / 100 m. In fact, the steep angle once again mirrors the important altitudinal alteration of climate processes. While the tierra caliente gives evidence of hot basins and valley grounds in elevations of up to 1,000 m a.s.l., more frequent rainfalls and fogs cause cooling effects at mountain tops. Thus, lower areas of heat surplus are overlain by heat deficits in summit areas with a theoretical mean 0°C-line lowered to around 4,350 m a.s.l. Finally, the western escarpment and southern reaches of the Cordillera de Celica, which tapers off towards the north Peruvian desert, are marked by a surprisingly low lapse rate of 0.45 K / 100 m. Such values correspond to findings of especially small gradients typical for tropical "moist air deserts" (LAUER 1995; WEISCHET 1996). Although upwelling of cold water usually no longer touches the Pacific coast of southern Ecuador cool winds crossing the coastal Sechura desert of Peru still strike out along the foothills of the Cordillera de Celica. LETTAU (1976) highlights the suppression of sea breezes in this area by strongly divergent winds parallel to the western mountain chain. This S-N trade explains lower temperatures from the lowlands up to fog induced levels, which range between 1,000 and 2,400 m

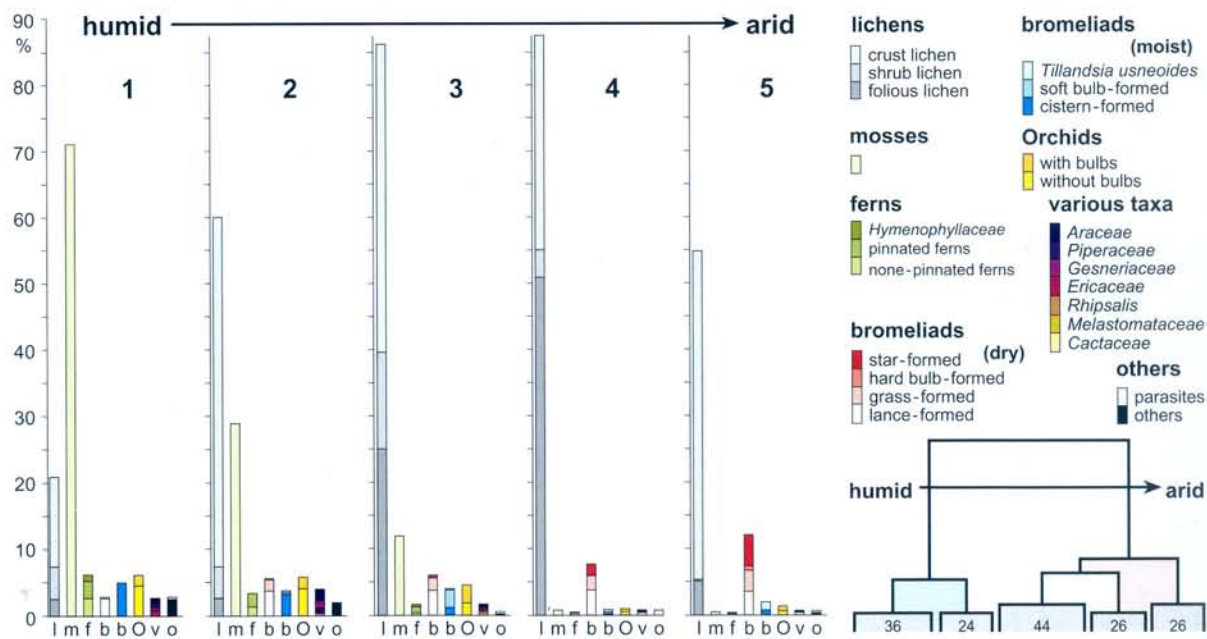


Fig. 10: Classes of epiphytism derived from a cluster analysis indicated in a simplified form by a dendrogram at the right bottom of the sketch (numbers = relevés). The classification system relates to numerical analyses of the investigated plant groups

Klassen der Epiphytismus, abgeleitet aus einer (vereinfachten) Cluster-Analyse unten rechts

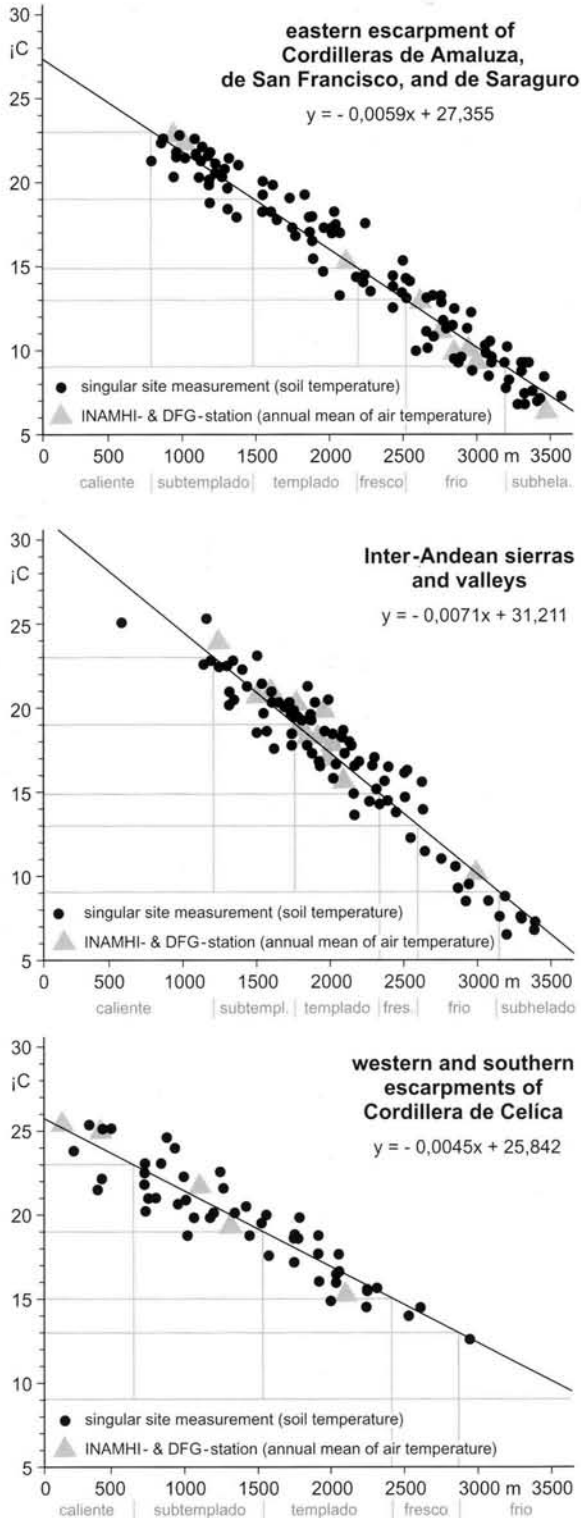


Fig. 11: Gradient analyses of –60 cm soil temperatures in the three subregions of southern Ecuador

Gradientanalysen der –60 cm-Bodentemperaturen in den drei Teilregionen Süd-Ecuadors

a.s.l. according to season and daytime. As orographical fog impact is reduced at higher altitudes, summit areas surmount the cool advective air masses and form relatively warm islands above the inversion layer. The given gradient leads to a theoretical position of the mean 0°C-line in 5,600 m a.s.l. – which, at least in this case, casts a doubt on its arithmetical derivation.

Different gradients also imply complex temperature regimes. Analyses of temperature residuals prove asymmetric distributions of the “tierras” for southern Ecuador as depicted by their vertical extents annotated below each scatter plot in figure 11. Taking the western part of the research area as an example, the tierra caliente is reduced to a shallow layer up to only 680 m a.s.l. due to the mentioned cooling impact. The same belt reaches up to 1,200 m a.s.l. within the Inter-Andean section. The different spatial extents of thermal regimes are considered in map 4 (Suppl. III). Areas with positive temperature residuals transgressing +2 K are concentrated around the Basin of Catamayo and along the valleys south of Gonzanamá sheltered by manifold ranges and influenced by strong foehn winds descending from the Cordillera de Amaluza. In contrast, the wettest area along the crest of the Cordillera Real and especially in the northern part of Podocarpus NP between Loja and Zamora as well as the quasi-permanently fog induced “wet spot” NW of Piñas are characterised by negative temperature residuals of more than –2 K. Once again, “hottest” and “coldest spot” are situated close to each other and coincide with the aforementioned “driest” and “wettest spot” which underlines the thermal relation to water deficient and water excessive areas.

7 Ongoing interpretations derived from hygro-thermal climate patterns

Placing the two maps one upon the other results in even smaller hygro-thermal patterns (here added by the rather flat, northernmost part of Peru). The vastly destroyed natural vegetation (DODSON a. GENTRY 1991) might be reconstructed with the help of the detailed reproduction of climate complexes within the three subregions (“facilities” in Fig. 1). Furthermore, genetic aspects responsible for the hygric and thermal structure become more obvious if accompanied by weather observations during various seasons.

Derived from the hygro-thermic map 5 (Suppl. IV) that one of the potential natural vegetation (map 6 in Suppl. IV) distinguishes twelve plant formations. There are many more in reality because several smaller ranges split from the “Nudo de Loja” towards SE and SW,

which complicates the regional climatic and phytogeographical zonation. However, not only climatic differentiation but also vegetation history and different disturbance regimes cause an extraordinary plant diversity and complexity of communities. In this context another important point should be looked at. Upon arrival in their new environment, immigrating species often find insurmountable climatic conditions to establish themselves as potential participants of novel communities since they, for example, may prefer humid environments but must cross dry "sinks". However, if such an establishment is successful, these species become founder populations and give impulses for vivid adaptive radiation. GENTRY and DODSON (1987) provide evidence for speciation associated with rapid genetic transience in large evolutionary plastic genera such as *Anthurium*, *Piper*, and *Cavendishia* ("evolutionary explosion" according to GENTRY 1982). The authors also point out micro-site differentiation that is typical for diverging mountain chains as crucial triggers for genetic diversification. Thus the divergence zone of the ranges south of the "Nudo de Loja" provides best prerequisites for species diversity because it includes a wide variety of wet and dry habitats close to each other due to extremely rough terrain with slopes of different wind aspects. Furthermore, mountain crossings combined with regimes of frequent and different sized disturbances (crown breakage, landslides, drought, and fire) can be considered optimum spots for a high rate of genetic exchange as consequence of micro-geographic niche partitioning. Consequently, the specific structure of the Cordilleras as foundation for historical plant migration leads to extraordinary physiological plasticity of many genera.

Large-distance pathways along the crest-lines, the heterogeneity of infiltration areas, the topographic structure with many niches and different disturbance regimes mainly contribute to the extremely accelerated adaptive diversity and community richness in higher elevations of the region. Best examples are the narrow altitudinal belts of the eastern elfin forests and the upwards following páramos from where BUSSMANN (2002) reports an extreme high community complexity. In contrast, the dry valley areas of the Inter-Andean section are characterized by widespread semi-deciduous mountain bush and deciduous open woodland, the latter extending towards the dry lowlands of northern Peru. Speciation rates as well as community differentiation are smaller there because climate heterogeneity, niche structure, and probably also natural disturbances have presumably been of limited importance in the semiarid areas for a long time. Some species such as *Acacia macracantha*, *Cordia lutea*, *Croton wagneri*, *Erythrina*

edulis, and *Tabebuia chrysantha* are distributed from sea level to at least 2,000 m a.s.l. suggesting the ability to delimitate their habitat against potential competitors. Finally, it must be mentioned that the fog induced exuberant forests on the western escarpment of the Cordillera de Celica are the last southern outposts of the perhumid evergreen rainforests from the Chocó in northern Pacific Ecuador and Colombia.

The following derivation of regional circulation systems, which are influenced by tropical large scale air streams, provide the spatial distribution of the hygro-thermal patterns and is accompanied by regular weather observations. Map 7 and 8 (Suppl. IV) give an idea of frequent situations during the dry and the wet season, which are additionally expressed by block diagrams in figure 12. The inset maps of surface air streams agree roughly but not in detail with equivalent overviews delivered by KREUELS et al. (1975), LETTAU (1976), BENDIX a. LAUER (1992), and WEISCHET (1996). They rather try to combine personal observances of regional circulation systems with vast aerological systems over the whole of South America in an optimal way. This means, for example, that the occurrence of monsoon effects on the west coast or of convective processes in propagation of thermally induced sea breezes coupled with up-slope winds (BENDIX 2000; "sea-mountain wind system" acc. to RICHTER u. SCHMIDT 2002) can be considered a frequent but not a dominant phenomenon during February (green streamlines in Fig. 12 and map 8). The same air stream oppresses the prevailing trade winds originating from the high pressure system of the southeastern Pacific which normally pour into the coastal plains west of the Cord. de Celica (blue streamlines in Fig. 12 and in map 7 a. 8).

Stormy easterlies are obviously responsible for rainy weather between May and December at the elevated parts of the eastern Cordilleras. These strong currents are the principal motor for uplifts of air masses that diverge from the trades. The trades themselves pass east of the mountain chain over the Amazon foreland from N to S in the southern summer and from S to N in the southern winter (red streamlines in Fig. 12 and in map 7 a. 8). The same air flows cause flat whirl-clouds in the summit region of the Cordilleras which release a latent heat flux and strong fall winds into the Inter-Andean valley region. Desiccating foehns are especially efficient in the areas of Loja, Malacatos, Vilcabamba, and Yanguana (yellow and orange arrows). However, the crest clouds seldom extend into the middle troposphere. Hence thunderstorms are rare events in the eastern mountainous area. On the contrary, super-radiation with values far above the solar constant is a short but

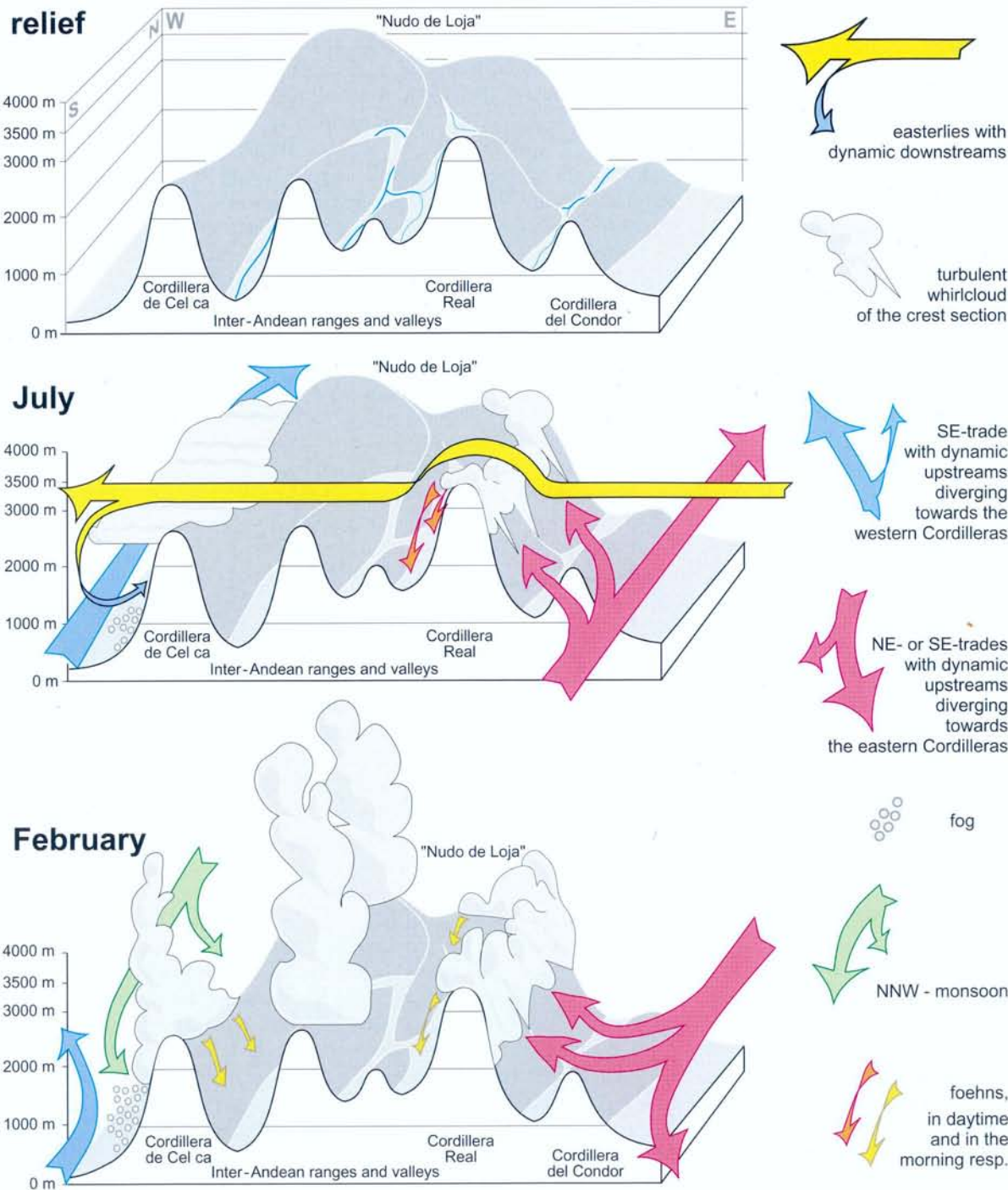


Fig. 12: Block profile indicating observed cloud patterns and reconstructed air flows derived from map 7 and 8 in Suppl. IV
Blockprofil mit beobachteten Wolkenmustern und abgeleiteten Windströmen

frequent phenomenon when clouds rip open and direct as well as reflective radiation hit the ground (pers. comm. PAUL EMCK, Erlangen). The eastern Cordilleras are characterised by rainfalls, the Inter-Andean Sierras

by a dry leeward situation during easterlies, but circumstances on the western escarpment of the western Cordillera are completely different. Here, the shallow S to N air flow along the coastal plain and foothills is

superimposed by the easterly air stream. This results in a low-level-jet with helical air fluxes creating an inversion layer around 1,200 to 2,400 m. Orographical fogs are cut off at this point by the strong easterlies and form a dense cloud carpet bordering upon the western slopes or overlap the lower parts of the crest-lines (Fig. 12).

The easterlies providing the Amazon escarpment with rain dominate year-round but weaken during the wet season between December and April. Then cloud walls may cross the western Cordillera from the Pacific side towards east and release foehns into the interior valleys in the morning. Thunderstorm clouds eventually start to tower up over the Inter-Andean ranges around noon. They are the only rainfall sources for the central section of the study area and can be assigned to one of the southernmost positions of the ITC when crossing the Andes. In ENSO-years this situation becomes strengthened which explains rainfalls being more frequent west of the Cordillera Real than east of it contrasting to non-ENSO years. A third weather event, namely "no-rain-at all", is restricted to the period from October till April reaching the highest frequency during late October and November ("veranillo del niño", corresponding to the short dry period crossing over towards Amazonia). First interpretations of NCEP / NCAR-Reanalysis plots by NOAA-CIRES indicate vast indifferent pressure fields over the Gulf of Guayaquil with no winds or slight flows changing from north to west.

Finally, two special features go along with the special situation of high rainfalls in the crest areas of the eastern Cordilleras: The Andean depression results in a low modern timberline at altitudes of around 3,100 m a.s.l. \pm 200 m and in late glacial deposits already found at 2,800 m a.s.l. It also conducts excessive foehns in the eastern Inter-Andean section which are by far not as strong or do not occur at all further north where the Andes build up closed walls against the easterly moisture input.

8 Conclusions

The reconstruction of natural vegetation and an improved knowledge of climate circulation patterns are two of various objectives to provide hygro-thermal maps. Apart from purely scientific themes the content aims at questions of agricultural, environmental, or medicinal application. Information on weed-susceptibility, crop-sensibility, and intensities of soil erosion (HAGEDORN 2002) on the potential distribution of parasitic and infectious diseases as well as planning of adapted land-use, forest management, and pest-control

are facilitated by a better perception of regional climate patterns. Nevertheless, few disadvantages given by the part of plant functional types within the combined method should not be denied:

- Regional restriction: the plant functional groups used in this paper must not be considered as an inevitably fixed composition. Regional adjustment remains unavoidable since taxonomic and growth-form features change according to the area of investigation. This is especially true for the Paleotropis where vascular epiphytism is much lower than in the Neotropis (e.g. South America contains sevenfold more than Africa, WOLF 1991).

- Subjective rating: estimations of the percentage cover of epiphytic groups differ from those of terrestrial groups since the distance between observer and object is greater. Thus the degree of exactness depends on the elaborating person. This means that relevés by different observers are not necessarily comparable. A region of interest therefore ought to be investigated by one researcher alone to avoid different error ratios.

On the other hand, it must be pointed out that further studies achieved by equivalent operations prove excellent results in the southernmost section of the Sierra Madre de Chiapas (Grill 2002). The main advantages of the method are summarised as follows:

- Time factor: establishing hygric and thermal maps of the given quality and spatial dimension requires only five weeks of field work. In the present case this net time is based on 300 km of hiking and 500 km of driving.

- Expense factor: an enlarged net of weather stations for long-term measurements managed by additional operation staffs is not necessarily needed. For decisive data lacks caused by special relief features few additional climate stations located at spots of special interest (i.e. summits or crests, centres of basins etc.) might be helpful. Concentrated measurement of around three years is sufficient for matching of data with those of long-term stations.

- Improvement factor: in comparison with conventional procedures based solely on station data an extension by indicator values considerably increases the exactness of resulting maps.

These decisive advantages document the high degree of effectiveness of the method. They should encourage geographers, ecologists, and biologists to look for better climatic resolution to explain spatially controlled scientific phenomena. Moreover, they provide a convincing bases of professional judgement for political decision makers and experts who look for climate-based optimisation of land-use in tropical areas. The demonstrated technique is of special value for meso-scale documents

of average situation and may be an ideal link to macro-scale analyses based on remote sensing.

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