UNIVERSITY OF BAYREUTH

DEPARTMENT OF BIOGEOGRAPHY

# Variation and Distribution of Forest Types on the Southern Foothills of the Cordillera Cahuapanas, Alto Mayo, Peru

Diplomarbeit

**Geoecology**



by

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*There is a theory which states that if ever anybody discovers exactly what the Universe is for and why it is here, it will instantly disappear and be replaced by something even more bizarre and inexplicable. There is another theory which states that this has already happened ...*

DOUGLAS ADAMS

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# ABSTRACT

***The aim of this study was the structural and edaphic classification of primary forests in the upper watershed of the Río Avisado, Alto Mayo Valley, in Northern Peru. Special emphasis was placed on correlations between abiotic environmental factors and the occurrence of distinct vegetation types. The results of this study are intended as a basis for an ecological sensitivity assessment of the area and as a guideline for the development of an integrated management and protection plan for the region.***

Low productivity semi-deciduous forests of the studied area are found on a highly dissected peneplain in the upper Rio Avisado watershed (900 - 1 050 m a.s.l.) and on the southern piedmonts of the Cordillera Cahuapanas (1 000 - 1 150 m a.s.l.) under tropical moist conditions. The highest elevation stands of low-statured heath forests reported in tropical America occur at approx. 1 000 m a.s.l..

Forty-five field plots were chosen in order to characterize all structurally distinguishable forest stands and their geology and topography. In these plots, soils were sampled and the stand structure and dimensions of all woody plants were assessed. The woody above-ground biomass was harvested on ten low-statured heath and on six fern plots.

In order to identify key abiotic factors and to distinguish statistically the different forest types parameter from all sites were analyzed by principal component analysis and hierarchical cluster analysis. This was done separately for soil chemistry, soil texture, biomass distribution, and vegetation structure parameters. For this purpose, soils were analyzed chemically by top and subsoil layers. Above-ground biomass was estimated on the basis of tree dimensions and biomass harvests.

The analysis of physical and chemical soil parameters showed that the white sand soils of the heath forests provide the most adverse edaphic conditions to plant growth due to their high acidity and lack of plant-available nutrients in the mineral soil. "*Shapumbales"* were associated with thick litter layers over different substrates. Soils rich in base cations were mostly associated with stagnant water and thus were likely to be limited by insufficient nitrogen mineralization. All other soils were deficient in phosphorus. A restriction of plant growth through aluminum toxicity was not observed.

The analysis of tree perimeters and heights resulted in the separation of five stand types. With respect to the accumulated above-ground biomass, however, they could only be distinguished significantly into "poor" ($< 50$ t ha$^{-1}$), "moderate" ($\pm 100$ t ha$^{-1}$), and "rich" stands ($> 200$ t ha$^{-1}$).

Statistical analysis of the vegetation resulted in eight forest stand types. A classification scheme for the distinction of these forest types was developed based on selected stand structural and topographic parameters, i. e. stand height and density, canopy cover, leaf morphology, palm proportions, and slope. On white sand plateaus two open and stunted vegetation types were classified as heath forests ("*chamizales*"). The forest type "*shapumbal*" (open forest on steep slopes with dense undergrowth of *Sticherus remotus*) was assumed to be a successional stage on naturally disturbed sites. "*Palm rich rainforests*" dominated by the species *Jessenia bataua* occurred in ravines and in narrow valleys. Wide valleys supported "*premontane rainforests*" which were the only stands exceeding 25 m in height. Along upslope gradients the forest types "*low canopy rainforest*", "*dry rainforest*", and "*impoverished rainforest*" occurred which decrease in tree height but increase in stand density.

A classification of the forest stands in the study area was achieved and a link was established between the geologic and topographic conditions that in turn influence drainage and the variability of soils. Biomass was correlated most positively to the availability of phosphorus, magnesium and potassium in the soil and to parameters indicating rapid nitrogen mineralization. This correlation of vegetation types with abiotic factors provides the base for a subsequent mapping of forest types in the study area.

Site conditions which limit the potential of the studied area for forestry or agricultural use were identified. These risks are soil erosion and land slides on slopes of the upper hill area and limited plant growth on strongly acidic and nutrient poor soils. This study of the edaphic conditions in the Río Avisado area provides a base for further investigation on erosion hazards, water and nutrient balances, and the floristic characterization of the specific vegetation units.

# RESUMEN

***El objetivo del presente trabajo fué el de obtener una clasificación estructural y edáfica de los bosques primarios de la cuenca alta del Río Avisado, valle del Alto Mayo, en el norte del Perú. Se dió énfasis especial a las correlaciones entre los factores abióticos ambientales y la presencia de diferentes tipos de vegetación. Los resultados del presente estudio sirven de base para una evaluación de sensitividad ecológica del área trabajada y como una guía para el desarrollo de un plan de manejo integrado para la región.***

En el área de estudio bosques semi deciduos de baja productividad son encontrados en las regiones fuertemente disectadas de las llanuras de la cuenca del Río Avisado (900 - 1 050 m s.n.m.) y en la parte de sur de los piedmontes de la Cordillera Cahuapanas (1 000 - 1 150 m s.n.m.) bajo condiciones tropicales húmedas. A una altitud aproximada de 1 000 m s.n.m. se encuentran poblaciones de bosque de heath de baja estatura, esta es la mayor elevación registrada para este tipo de bosque en toda América tropical.

Se escogieron 45 parcelas con el fin de caracterizar diferentes tipos estructurales de bosque con relación a condiciones de geología y topografía. Se muestraron los suelos y se evaluó la estructura del bosque y las dimensiones de todas las plantas leñosas. Se colectó la biomasa leñosa aerea de diez parcelas de bosque de heath y de seis parcelas de helechos.

Con el fin de identificar factores abióticos clave y para distinguir estadistícamente, los diferentes tipos de bosque, se hizó un análisis de componentes principales y un análisis jerárquico de clusters de los parámetros de todos los sitios de muestreo. Estos análises fueron hechos en forma separada para los parámetros de características químicas y textura de suelos, distribución de biomasa, y estructura de la vegetación. También, con este propósito, para el análisis químico de los suelos se consideró el suelo superficial y el sub-suelo, y se estimó la cantidad de biomasa aérea a partir de las dimensiones de los árboles y de los datos de la biomasa cosechada.

El análisis de las características físicas y químicas de los suelos mostraron que los suelos de arenas blancas del bosque de heath proporcionan las condiciones edáficas más adversas para el crecimiento de la vegetación, debido a su alto grado de acidez y a la escasez de nutrientes disponibles para las plantas en el suelo mineral. Los "s*hapumbales"* se encontraron asociados a capas profundas de hojarasca sobre diferentes tipos de substrato. Los suelos con un alto nivel de cationes se encontraron asociados a malas condiciones de drenaje y por lo tanto fueron más bien limitados por los bajos niveles de mineralizacion de nitrógeno.Todos los otros suelos presentaron bajos níveles de fósforo. Sin embargo, no se observó una limitación al crecimiento de las plantas debido a niveles tóxicos de aluminio.

Como resultado del análisis de alturas y diámetros de los árboles medidos se obtuvó una separación entre cinco grupos estructurales. Con respecto a la cantidad de biomasa aérea acumulada, sólo se distinguieron tres tipos de parcelas: "pobres" (< 50 t $ha^{-1}$), "moderadas" (± 100 t $ha^{-1}$), y "ricas" (> 200 t $ha^{-1}$).

El análisis estadístico de la vegetación dió como resultado ocho tipos de bosque. Se desarrolló un esquema de clasificación de los tipos de bosque basado en características escogidas de la estructura de las parcelas de bosque y de los parámetros topográficos(altura y densidad de los árboles en la parcela, cobertura del dosel, morfología foliar, ocurrencia de palmeras y nível de pendientes). Se observaron dos tipos de vegetación abierta y truncada que se clasificaron como bosque de heath ("*chamizales*") en las mesetas de arenas blancas. El tipo de bosque "*shapumbal*" (bosque abierto en pendientes fuertes con un sotobosque denso de *Sticherus remotus*) era un estadío sucesional en áreas naturalmente disturbadas. Los bosques lluviosos con alta proporción de palmeras (*Palm rich rainforests*) dominados por la especie *Jessenia bataua* se encuentran en barrancos y valles angostos. Los valles anchos están cubiertos por bosque premontano que está representado por parcelas de más de 25 m de altura. A lo largo de los gradientes de pendientes se encuentran los tipos de vegetación bosque lluvioso bajo (*low canopy rainforest)*, bosque lluvioso seco (*dry rainforest*), y el bosque lluvioso empobrecido (*impoverished rainforest)*. Estos boques muestran una disminución en altura de los árboles y un incremento en la densidad de las parcelas.

Se logró obtener una buena clasificación de las parcelas forestales en el área de estudio, así como también se pudó establecer una conección con las condiciones geológicas y de topografía, que a su vez influencian el patrón de drenaje y la variabilidad entre diferentes tipos de suelo. Se correlacionó de forma positiva el valor estimado de biomasa con los contenidos de fósforo, magnesio, potasio, y los niveles de mineralización rápida de nitrógeno. La correlación entre los diferentes tipos de vegetación y los factores abióticos proporcionan una base para el subsequente mapeo de los tipos de bosque en el área de estudio

Se identificaron las condiciones locales que limitan el uso potencial del área de estudio con fines agrícolas y forestales. Estas son el riesgo de erosión de los suelos y de deslizamientos en zonas de pendiente en la parte alta de la región colinosa y el reducido crecimiento de plantas en suelos fuertemente ácidos y de bajo contenido de nutrientes. Los resultados sobre las condiciones edáficas en el área del Río Avisado deben servir como base para planear futuras investigaciones sobre los peligros de erosión, balance de nutrientes y agua, y la composición florística de los tipos de bosque identificados en la región.

# ZUSAMMENFASSUNG

***Ziel der Untersuchung war die strukturelle und standörtliche Klassifikation von Primärwäldern am Oberlauf des Río Avisado in der Region Alto Mayo, Nordperu. Im Mittelpunkt der Arbeit stand dabei die Erforschung von Zusammenhängen zwischen abiotischen Umweltfaktoren und dem Auftreten bestimmter Vegetationstypen. Die Ergebnisse dieser Studie sollen die Grundlage bilden für die Bewertung der ökologischen Sensibilität des Gebietes und für die Erarbeitung eines integrativen Management- und Schutzplans der Region.***

Im Untersuchungsgebiet finden sich magere, teillaubwerfende Wälder auf einer stark zerklüfteten Rumpffläche im oberen Einzugsgebiet des Río Avisado (900 - 1050 m ü. NN) und am Fuß der Cordillera Cahuapanas (1000 - 1150 m ü. NN) unter feuchttropischem Klima. Auf ca. 1000 m ü. NN liegen die höchstgelegenen niederwüchsigen Heidewälder, die im tropischen Amerika bekannt sind.

Fünfundvierzig Untersuchungsplots wurden ausgewählt, um die vorkommenden Waldbestände auch nach geologischen und topografischen Gesichtspunkten charakterisieren zu können. Auf diesen Plots wurden die Böden beprobt und die Bestandesstruktur und die Dimensionen der verholzenden Pflanzen erhoben. Auf zehn Plots mit niederwüchsigem Heidewald und sechs Plots mit dominierender Farn-Vegetation wurde die oberirdische Biomasse verholzender Pflanzen geerntet.

Um wichtige abiotische Einflussfaktoren zu identifizieren und verschiedene Waldtypen statistisch signifikant auszuweisen, wurden die Daten aller Plots durch Hauptkomponentenanalyse und hierarchische Clusteranalyse ausgewertet. Dies geschah getrennt nach Parametern zu Bodenchemismus und Textur, Biomasseverteilung und Vegetationsstruktur. Die Böden wurden dazu chemisch analysiert und die oberirdische Biomasse wurde anhand von Baumdimensionen und Biomasseernten abgeschätzt.

Die Analyse der physikalischen und chemischen Bodenparameter wies die weißen, stark sauren Sandböden der Heidewälder, die praktisch keine pflanzenverfügbare Nährstoffe im Mineralboden besitzen, als extreme Mangelstandorte aus. „*Shapumbales*“ waren verbunden mit mächtigen Streulagen über verschiedenen Substraten. Basenreiche Böden standen meist unter Stauwassereinfluss und Pflanzenwuchs war daher wahrscheinlich durch unzureichende Stickstoffmineralisation limitiert. In allen anderen Böden war die Phosphorversorgung mangelhaft. Eine Beeinträchtigung des Pflanzenwachstums durch Aluminiumtoxizität konnte allerdings nicht festgestellt werden.

Die Analyse von Stammumfängen und Baumhöhen ergab eine Unterscheidung der Bestände in fünf Gruppen. Bezüglich der gebildeten oberirdischen Biomasse konnten diese Bestände statistisch signifikant allerdings nur in „arm“ ($< 50$ t ha$^{-1}$), „mäßig“ ($\pm 100$ t ha$^{-1}$), und „reich“ ($> 200$ t ha$^{-1}$) eingeteilt werden.

Die statistische Analyse der Vegetation ergab acht Waldtypen. Anhand ausgewählter Parameter zu Bestandesstruktur und Topografie (Bestandeshöhe und -dichte, Kronendeckung, Blattmorphologie, Palmenanteil und Hangneigung) wurde ein Klassifikationsschema zur Unterscheidung dieser Waldtypen entwickelt. Auf Plateaus aus weißen Sanden wurden zwei offene, niederwüchsige Vegetationstypen als Heidewälder klassifiziert („*Chamizales*“). Der Waldtyp „*Shapumbal*“, ein offener Wald in Steillagen mit dichtem Unterwuchs aus *Sticherus remotus*, scheint ein Sukzessionsstadium auf natürlich gestörten Standorten zu sein. „*Palmenreiche Regenwälder*“ kamen in Schluchten und engen Tälern vor und waren dominiert von *Jessenia bataua*. Weite Täler enthielten „*submontane Regenwälder*“, die als einzige Bestände eine Höhe von über 25 m erreichten. Entlang eines hangaufwärts gerichteten Gradienten standen „*niedriger Regenwald*“, „*trockener Regenwald*“ und „*verarmter Regenwald*“ bei abnehmender Baumhöhe und steigender Bestandesdichte.

Eine Klassifikation der Waldbestände wurde erfolgreich durchgeführt und in Zusammenhang gestellt mit edafischen und topografischen Faktoren, die wiederum den Wasserhaushalt und die Variabilität der Böden beeinflussen. Die Biomasse korrelierte positiv am besten mit der Verfügbarkeit von Phosphor, Magnesium und Kalium im Boden sowie mit Parametern, die auf eine rasche Stickstoffmineralisierung hinweisen. Diese Korrelation von Vegetationseinheiten mit abiotischen Faktoren bildet die Grundlage für eine anschließende Kartierung der Waldtypen im Untersuchungsgebiet.

Es wurden die Standortbedingungen beschrieben, die eine wald- und ackerbauliche Nutzung des Untersuchungsgebiets einschränken. Dazu zählt die Gefahr von Bodenerosion und Hangrutschungen im oberen Hügellande sowie limitiertes Pflanzenwachstum auf stark sauren, nährstoffarmen Böden. Die Ergebnisse der vorliegenden Studie zu den edafischen Bedingungen im Río Avisado Gebiet ermöglichen es nun, weitere Untersuchungen zu Erosionsrisiken, zum Wasser- und Nährstoffhaushalt sowie eine floristische Charakterisierung der ausgeschiedenen Vegetationseinheiten zu planen.

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# 1 Introduction

This study attempts to classify the endangered primary rain forests at the foothills of the Cordillera Cahuapanas in the Alto Mayo region of Peru. The aim was to statistically distinguish and describe the different vegetation units in the study area based on data from soil investigation, biometry measurements and vegetation structure determination. The study quantifies stocks of nutrients and biomass, identifies environmental hazards and evaluates the importance of these threatened natural resources.

The situation of the primary forests in the Alto Mayo Valley, in which the study area is located, is typical for the forests of the eastern Andes of Peru. In 1975 the *Carretera Marginal*, a road linking the Amazon lowlands with the central Andes and the Pacific coast, was completed. It initiated a continuous influx of rural settlers from the densely populated Andes. Local preconditions of soils and climate and the sustainable agricultural practices for this region were unfamiliar to the majority of these settlers. By 1998, approximately 140 000 ha of primary forest had been cleared for agricultural use in the Alto Mayo Valley. Almost one-seventh of this area has already been abandoned due to low crop yields (ELLIOT 1998). Along the main roads leading through the flat valley bottom along the Alto Mayo River, forests are now either destroyed or strongly degraded. Primary forests are limited to inaccessible areas above 1 500 m a.s.l or to extremely rugged terrain. Relatively untouched by clear-cutting or agriculture are territories that were recently assigned to indigenous Aguaruna tribes in the area.

Tropical mountains feature a high variability of climates, soils, and relief that host a unique biodiversity in numerous forest types (GENTRY & ORTIZ 1993). YOUNG (1992) proposes an altitudinal zonation of pristine forests covering the eastern slopes of the Peruvian Andes. He describes tropical lowland forests from 200 m a.s.l. to 500 m a.s.l.. Premontane rain forests dominate in 500 m a.s.l. - 1 500 m a.s.l., the montane zone includes a lower montane rain forest from 1 500 m a.s.l. - 2 500 m a.s.l. and an upper montane rain forest from 2 500 m a.s.l. - 3 500 m a.s.l. These forest types vary with respect to their tree species composition, their stand structure and their ecological functions (RICHARDS 1996, GIVNISH 1999). Floristic aspects of tropical forests have been studied for quite some time (WHITMORE 1993). Numerous studies exist on the structural characteristics, since the high diversity of forest species makes taxonomically-based studies difficult (PAULSCH & CZIMCZIK 2001). On a global scale, tropical mountain forests belong to the genetically most diverse ecosystems (GENTRY 1992). Plant structure can be interpreted as an indicator of ecophysiological adaptations closely linked to existing site quality and abiotic conditions (VARESCHI 1980, WERGER et al. 1982, RICHARDS 1996). The complex ecosystem functions of tropical montane forests have been increasingly studied. Focus was often laid on soil preservation and prevention of erosion in steep terrain, the buffering effect for local water cycles, as well as carbon storage in biomass (BRACK & MENDIOLA 2000, BMELF 1999).

Degradation and destruction of tropical forests progresses at a fast pace. However, our understanding of the complex processes and the interactions constituting these ecosystems develops slowly. Primary tropical forests are mainly converted into agricultural land by slashing and burning. Large scale infrastructure and development programs, often in connection with poorly administered timber extraction, contribute to the decrease in forest areas (ALBRECH-STRUCKMEYER 1991, BMELF 1999). Studies by the FAO (1999) show that the loss of tropical forest area from 1990 - 1995 was in the order of 12.5 Mio ha per year. In Peru alone, the annual rate of forest clearing was estimated to be 217 000 ha.

The destruction of the forests has far-reaching ecological and economic consequences. Sustainable agricultural cultivation in the moist tropics is limited to favorable sites, which do not exist in the major part of tropical moist forest regions (BMELF 1999). The soils of the Alto Mayo region have a low potential for long-term agricultural use (ONERN 1982). Continuous degradation of these soils due to inappropriate agricultural cultivation techniques has led to the impoverishment of the rural population and has already reached the subsistence level in many cases. Amelioration of degraded soils by liming or fertilization or increasing crop yields by the use of herbicides is expensive and thus not feasible for the farmers. Instead, degraded soils are commonly abandoned (DEFORPAM 1997, KAUFFMAN et al. 1998, BMELF 1999) which results in mounting pressure on the remaining natural land resources. Abandoned areas are quickly covered by ferns (*Pteridium aquilinum*) forming extended unproductive badlands, locally referred to as *shapumbales*. This vegetation inhibits secondary forest growth for many years. The extension of man-made *shapumbales* in the Alto Mayo Valley in January of 1997 was estimated to be 25 000 ha (DEFORPAM 1997), in March of 1999 more than 30 000 ha (DEFORPAM 1999).

Both the local population and the government land management agencies in Peru generally value forests only for exploitation and agricultural development. Sustenance considerations such as environmental protection and preservation of natural resources are of minor importance compared to the short-term economic gains (BMELF, 1999). In order to advance a sustainable agricultural and forestry development in the region, the German Society for Technical Cooperation (Deutsche Gesellschaft für Technische Zusammenarbeit, GTZ) has supported and consulted the local Peruvian development and management agencies of the *Proyecto Especial Alto Mayo* (PEAM) in Moyobamba through their project *Desarrollo Integral Alto Mayo* (DIAM) since 1997. Special attention has been on the watersheds of the Río Avisado and Río Tioyacu, where contiguous tracts of primary valley rain forests can still be found.

The Forest Ecology and Remote Sensing Group (*FEARS*) at the Ecological Botanical Gardens (*ÖBG*) of the University of Bayreuth has been studying the ecology of this area in cooperation with the *Universidad Nacional de San Martín*, *Facultad de Ecología* in Moyobamba. Until 2003, it is intended to provide data to support management decisions for land use planning and the identification of areas which require special preservation in a natural state. The study

area is characterized by less favorable site conditions such as flooding, poor drainage, susceptibility to slope erosion, or poor soil nutrient status. All studies are designed to serve as a planning tool for the identification of protected forest areas.

The work presented in this study is part of a detailed inventory of the existing forest types and their site conditions and aims to provide a base for the characterization of the watersheds. The classification scheme described within for soil and forest properties combines the analysis of stand structure and quantitative parameters of forest stands with their chemical and physical soil properties.

The forests of the upper watersheds of the Río Tioyacu were classified by DEMPEWOLF (2000), while BÖRNER (2000) investigated the inundated forests in the lower watersheds and the lower hill region. The present study focuses on the upper hill area. This region stretches to the northeast from the last outposts of current settlements towards the southern piedmonts of the Cordillera Cahuapanas. The area supports a significantly different vegetation cover of the upper hill area compared to the lower hill region. The forest stands in this study are all located between approx. 900 and 1 100 m a.s.l. and are premontane forests according to YOUNG (1992). Located at an elevation of approx. 1 000 m a.s.l. near the flanks of the Cordillera Cahuapanas the study region features several small plateaus covered by a stunted and open vegetation formation mainly on poorly drained soils. This vegetation is structurally and floristically similar to the heath forests described for the upper slopes of the Cerro Tambo (DEMPEWOLF 2000, METTE 2001), the *chamizal* vegetation described for the Peruvian Amazon lowlands by RUOKOLAINEN & TUOMISTO (1993), and the white sand savannah for the tropical northeast of South America by COOPER (1979) and by SPECHT (1979) for other tropical regions.

The extremely dissected upper hill region displays a highly variable vegetation cover on a small scale. The pattern of vegetation type distribution may be interpreted either as a random patchwork over the entire upper hill area or bound to site specific factors, e. g. topographic position. It seems likely that a highly variable relief creates differences both in microclimatic conditions as well as soil conditions resulting in different vegetation types on a small scale. If abiotic factors govern the current vegetation distribution patterns, the analysis of topographic and edaphic conditions should result in a good correlation between topography, pedology and vegetation type.

In order to test these assumptions the following four null-hypotheses were formulated to be tested in the study area:

I. **Soil chemistry and soil texture do not vary in the upper Río Avisado watershed.**

   Rejection of this hypothesis would justify an investigation if different edaphic conditions followed topography and if soil status had an effect on the development of the vegetation types.

II. **Above-ground stand biomass is homogeneously distributed within the upper Río Avisado watershed.**

   Rejection of this hypothesis would suggest that based on the biomass of the forest stands there are differences among the vegetation which can be assessed and quantified biometrically.

III. **There are no significant differences in vegetation patterns between different topographic situations.**

   Rejection of this hypothesis would confirm that site topography may influence the development of the vegetation types.

IV. **Separation of the Río Avisado forest types requires comprehensive information on both: edaphic site conditions and stand structure.**

   Rejection of this hypothesis would indicate that there exists a certain proportion of redundancy in the dataset and that omitting these redundant parameters would lead to a streamlined and solid classification scheme for the study area.

The present study intends to provide a baseline for the spatial distribution of different forest types in the upper hill region of the Río Avisado watershed.

# 2 Materials and Methods

## 2.1 Study Area

The following chapter will outline the natural history and current conditions encountered at the study site.

### 2.1.1 Location and History

The study site is located on the eastern slopes of the Andes of North Central Peru at UTM 18S 261056 / 9370052 in the upper Río Mayo Valley, approximately 35 km north of the city of Moyobamba.

Peru covers a territory of 1.28 Mio km2 on the Pacific coast of tropical South America between 0° and 18° S, and from 69° to 81° W. Young (1992) divides the country into three natural regions from west to east: a) the narrow, arid coastal plain of 30 to 60 km width locally termed the “Costa”, b) the Andean highlands (highest peak Mount Huarascarán 6 768 m a.s.l.) called the cordillera or “Sierra”, and c) the region east of the main Andes Cordillera which is potentially covered by tropical rainforest. The latter can be subdivided into the “Selva alta” on the Subandean Belt and the “Selva baja” in the Amazon Basin (Fig. 2.1).




Source: AXION 1997

***Fig. 2.1: Location of the study site indicated on an edited NOAA-AVHRR satellite image of Peru, covering -67° to -83° W and -1° to -18° S.***

*Color coded are the geological units according to YOUNG (1992) from left to right:* ***Coastal Plain*** *(yellow),* ***Cordillera*** *(brown),* ***Subandean Belt*** *(dark green) and* ***Amazonian Plain*** *(green). Coinciding is the local zonation into* **Costa**, **Sierra** *and* **Selva alta** *and* **baja**.

The reason for such a spatially tight sequence of different biomes are the high Andean cordilleras which act as a climatic barrier. The contiguous Peruvian Western Cordillera ("*Cordillera Occidental*") restricts the drought effects of the cold Humboldt current and the impact of irregular decadal events of El Niño to the coastal plains. In addition, the Western Cordillera shields this region from moist air masses from the Amazon basin further inland. The slopes of the Eastern Cordillera ("*Cordillera Oriental*") of Peru are exposed to the humid climate of the Amazon rainforest and are incised by tributaries to the Amazon river.

The term "Alto Mayo" refers to the upper catchment of the Mayo river that belongs to the Río Huallaga-Río Amazonas drainage system. The valley trends NW-SE along the eastern slopes of the Andes on the brink between S*elva alta* and S*elva baja* yet still within the Subandean Belt. The upper Río Mayo is a white water river carrying high sediment loads and is embedded into a broad valley of approx. 50 km width.

The Alto Mayo region covers approx. 40 000 km$^2$, belongs to the department of San Martín. It is divided between the provinces of Rioja and Moyobamba. Total population of the Alto Mayo is estimated to be almost 200 000 (INADE-PEAM 1999).

The study area is framed by the *Cordillera Cahuapanas* mountain ridge in the north. This ridge is part of the *Cordillera Occidental* and which separates the Alto Mayo Valley from the Amazon lowlands (cf. Fig. 2.1). The *Cerro Tambo* massif in the west belongs to the Cordillera Cahuapanas. The study area extends from 800 m a.s.l. in the valley bottoms to approx. 1 840 m a.s.l. in the Cordillera Cahuapanas. It encompasses the watersheds of two left bank tributaries to the Río Mayo, the nutrient poor black water rivers Río Tioyacu and Río Avisado. The Río Tioyacu emerges at 1 050 m a.s.l. north of the Cerro Tambo massif and discharges into the Rio Mayo south of Rafael Belaunde. Its watershed covers approx. 100 km$^2$ (BÖRNER 2000) and is limited to the west by the Río Cachiyacu watershed. The headwaters of the Río Avisado are at 1 200 m a.s.l. on the SE slope of the Cordillera Cahuapanas and flow in southerly direction east of the Río Tioyacu. North of the settlement of Valle de La Conquista, the Río Avisado splits into a system of several meandering branches that reunite near the settlement of Tingana. The Río Avisado finally drains into the Río Mayo in two branches west of Buenos Aires. Its watershed covers approx. 360 km$^2$ (BÖRNER 2000. It is limited by the Río Huascayacu watershed to the east. This study was conducted on the southern slopes of the Cordillera Cahuapanas which include the highly dissected upper hill area (approx 850 - 1 050 m a.s.l.) and the piedmonts of this mountain range between approx. 1 000 and 1 200 m a.s.l. (cf. Fig. 2.11 in chapter 2.1.6).

Until the early 1970's indigenous *Aguaruna* tribes were the only people to make use of the land by hunting and an approximate 10 year cycle of shifting cultivation. The construction of the main road ("*Carretera Marginal*") in the early 1970's connected the northern *Selva* with the coast in 1975 and triggered a tremendous influx of settlers from the overpopulated highlands that continues today. In search for arable land the easily accessible pristine forests of the valley bottom were burnt and logged without control in order to give way for rice terraces (cf. Fig. 2.1 in

chapter 2.1.6). Currently, the land conversion extends into the comparatively less colonized small valleys of the tributaries of the Río Mayo but has slowed down in the last years since the acquisition of new land requires local government permission. In order to prevent further intrusion and illegal colonization by settlers, a large part of the remaining pristine forests was adjudicated in 1999 to the Aguaruna tribes. These tribes now live in a few permanent settlements (*Comunidades Nativas*) and apply modern agriculture. The field work for this study was carried out on the territories of the *Comunidades Nativas Cachiyacu*, *Kusu* and *Shimpiyacu*.

Concurrent with the colonization comes slashing and burning of primary forest to create agricultural areas (cf. Fig. 2.12 in chapter 2.1.6). These areas are often abandoned after a few years due to their diminishing fertility (cf. Fig. 2.9 in chapter 2.1.6). Plantations by the settlers are mostly family-run farms of a few hectares. A small area is always reserved for self sustenance and local trade, e. g. manioc, bananas, potatoes and pineapple. Main cash crops for export are wet and dry rice produced in the valleys and coffee on slopes above 900 m a.s.l.. An estimated 90 % of the rice production covers the Peruvian demand and 10 % is exported. Coffee (mainly *Coffea arabica*) is almost entirely an export product. The coffee plantations replaced earlier plantations of coca (*Erythroxylum coca*), which were given up after governmental enforcement increased in the mid 1990's. Abandoned coca fields are often covered by ferns (*Pteridium aquilinum*, so called *shapumbal*-vegetation) which are a typical component of the region. When the *shapumbales* are not constantly burnt (a common practice without obvious reason, cf. Fig. 2.10 in chapter 2.1.6) secondary forest develops and is recognizable by fast growing Cecropia sp. trees.

Due to reasons of accessibility the bulk of investigation plots were recorded along a ridge in the upper hill area of the eastern Río Avisado watershed. In order to also cover Cretaceous substrate, three plots were examined at comparable altitude near the upper Río Tioyacu (cf. also Fig. 2.1).

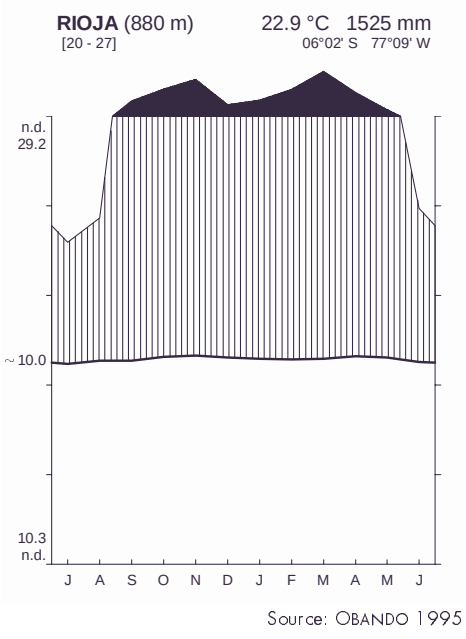
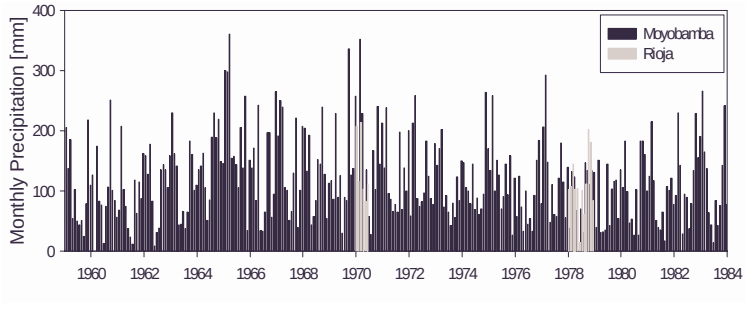



***Fig. 2.2: Climate diagram of Rioja, Alto Mayo, North Central Peru.***
*Rioja is located approx. 30 km SW of the study area. Data was collected 1964 - 83 for temperature and 1964 - 93 for precipitation.*
*The diagram is assembled according to the scheme outlined by WALTER et al. (1975).*

## 2.1.2 Climate

The climatic conditions along the eastern slopes of the Andes vary primarily with orography. Moist air drifting westward from the Amazon basin is blocked by the eastern cordillera where large cloud masses form and rise along the mountain slopes in approx. 1 200 - 2 000 m a.s.l.. The annual mean temperature drops from 25 °C (< 1 000 m a.s.l.) to 9 °C (> 3 500 m a.s.l.), and the annual sum of precipitation drops from 7 000 to 500 mm (YOUNG, 1992). The region is influenced by tropical trade winds that drive moist air masses across the Amazon lowland in westerly direction (KNOCH 1930) and cause two precipitation maxima in November and in March when the inter-tropical low pressure belt (ITC) is centered to the South of the equator (NOBRE et al. 1991). The only pronounced dry season is observed between the months of June and August.

Few data sets exist for precipitation and temperature in this region, and data for sites above 900 m a.s.l. are missing entirely. Continuous measurements for about 20 years are available for a climate station in Rioja (OBANDO 1995) which is located on the right bank of the flat valley bottom of the Río Mayo at 880 m a.s.l. (UTM 18 S: 262020 / 9332641) about 30 km south west of the study area (Fig. 2.2). According to KÖPPEN (1936) the climate of the Alto Mayo Valley is classified as tropical perhumid jungle climate (Afh) since the mean temperature of the coolest month (22.3 °C in July) and the mean annual temperature (22.9° C) in Rioja exceed 18° C and the average minimum precipitation each month is more than 60 mm (average minimum in July 62.6 mm). However, occasional dry spells can be observed when several consecutive months receive less than 50 mm of rainfall. This was the case in 1961 and 1979 (Fig. 2.3). The mean annual precipitation is 1 525 mm. The annual sum of precipitation for areas above 1 000 m a.s.l. is estimated to be much higher between 3 000 and 4 100 mm (ONERN 1982). The reason for the higher precipitation on elevations between 1 200 m a.s.l. and 2 000 m a.s.l. are the eastern Andes

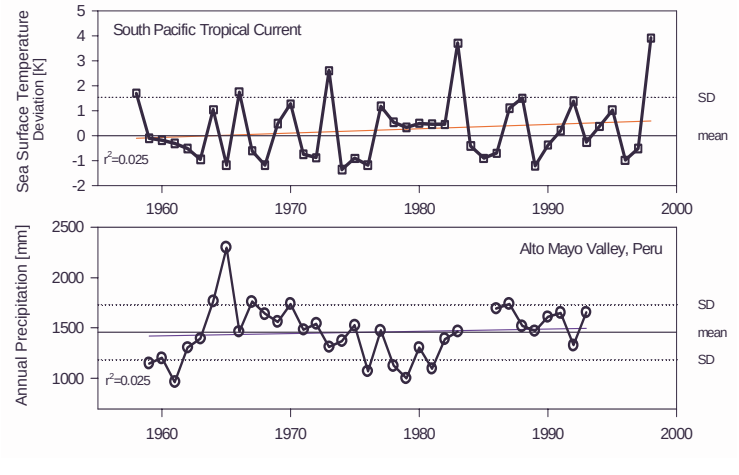



Source: OBANDO 1995

***Fig. 2.3: Monthly sum of precipitation from 1959 to 1984 for two meteorological stations at Moyobamba and Rioja in the Alto Mayo Valley, Northern Peru.***

which block easterly winds carrying moist air from the Amazon basin. Meteorological investigations in the studied watersheds by METTE (2000) showed that precipitation increases towards the slopes of the bordering mountain ranges and reaches 2 200 mm per year at 1 400 m a.s.l. (Cerro Tambo, UTM 18 S: 249017 / 9367930). The dry season is less pronounced and annual mean temperature drops to 19.4 °C. This trend can be assumed to continue in the entire study area towards the slopes of the Cordillera Cahuapanas. Therefore, values recorded at the weather station in Rioja should be considered minimum values for precipitation and maximum values for temperature with respect to the study region.

Interannual variation of precipitation may be tele-connected to large scale global oscillations, like the *El Niño*, (El Niño Southern Oscillation = ENSO) phenomenon. However, it is conceivable that the massive Andean cordilleras act as a shield from coastal climatic events. Therefore, it is not surprising that climatic records from the past 40 years do not display any significant correlations between the annual variability of precipitation in the Alto Mayo Valley and the South Pacific current sea surface temperature deviation (ZIMMERMANN et al. 2002), a parameter commonly used to quantify ENSO activity (MESTAS-NUÑEZ & ENFIELD 2001).




Source: MESTAS-NUÑEZ & ENFIELD 2001, OBANDO 1995

***Fig. 2.4: Comparison of El Niño events to the precipitation situation in the Alto Mayo Valley.***

*Above, the graph describes the mean sea surface temperature deviation (SST) for the South Pacific tropical current from 1958 until 1998.*

*Below, the annual precipitation in the Alto Mayo Valley is plotted, measured in Moyobamba. (Data from 1984 - 1986 are missing due to terrorist problems).*

*Tab. 2.1: Record of major seismic events that affected the Alto Mayo Region over the past 60 years.*

| Date | Magnitude | Epicenter | Reported Damage |
|---|---|---|---|
| 06 Aug **1945** | n.d. | South of Moyobamba | Cracks in ground |
| 10 Nov **1946** | n.d. | Sihuas | Material damage |
| 15 Jun **1954** | n.d. | n.d. | Material damage |
| 19 Jun **1968** | 6.9 | Moyobamba | 15 casualties |
| 29 May **1990** | 6.4 | Rioja | 70 casualties |
| 04 Apr **1991** | 6.2 | Angaiza (Cahuapanas) | 40 casualties |

Source: CUADRA LIÑAN & CHONG CHONG 1991

## 2.1.3 Geology and Geomorphology

The uplifting of the Andes occurred at the western edge of the South American plate due to plate tectonic movements during the middle Cretaceous period (approx. 100 Mio years BP). The last major uplift phase took place during the Pliocene period when the Andes attained close to their current height. On a small scale uplift continues to the present day and is manifested by occasionally recurring seismic activity that also affects the Alto Mayo region (Tab. 2.1).

The Alto Mayo Valley belongs to the Subandean mountain belt which separates the high Andes from the Amazon basin according to YOUNG (1992) (cf. Fig. 2.1). During the Triassic and Cretaceous periods the region was covered from the east by transgressing oceans. This led to the deposition of marine sediments which were folded during the second uplift phase in the mid Miocene until the early Pliocene (Tectonic map of South America 1 : 5 000 000, 1978). The oldest sediment layer is most likely the Triassic-Jurassic limestone formation *Pucará* NW of Rioja (ONERN 1982). All slopes to the west of the Río Mayo consist of limestone formations. High sediment loads make the Río Mayo a white water river. To the east of the Río Mayo the valley is limited by the Cordillera Cahuapanas, a range consisting primarily of sandstones. The valley bottom and areas up to approx. 800 m a.s.l. are covered by relatively young sedimentary deposits of unknown depth.

The watersheds of the Río Tioyacu and Río Avisado are dominated by Jurassic, Cretaceous, Tertiary and Quaternary sediments (Fig. 2.5). The study area is comprised of predominantly Tertiary and Quaternary sediments although both rivers originate from the piedmonts of the Cordillera Cahuapanas over Jurassic and Cretaceous rocks. The wide river floodplains of the Río Mayo feature primarily Holocene, fluvial, loamy and clayey sediments (Qh-fl) that have been deposited during flooding events. Slightly older alluvial deposits of varying clay and loam layers can be found along the seasonally flooded higher river terraces (Qh-al). Near the southern slopes of the Cordillera Cahuapanas this formation includes patches of deposited white sands containing a thin layer of volcanic material (ONERN 1982) that form extended plateaus. The lower hill region consists of sediments from the *Yahuarango* formation (Tp-y). These are considered to originate

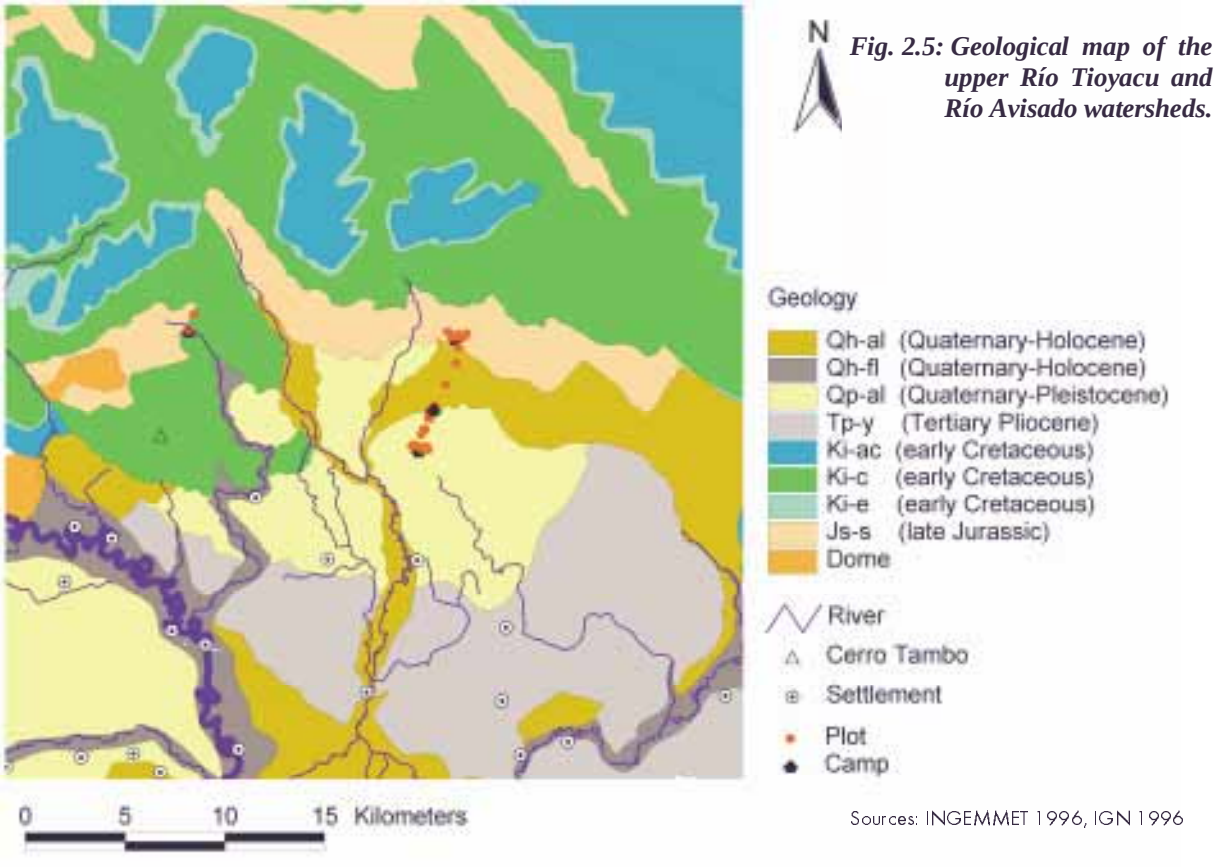
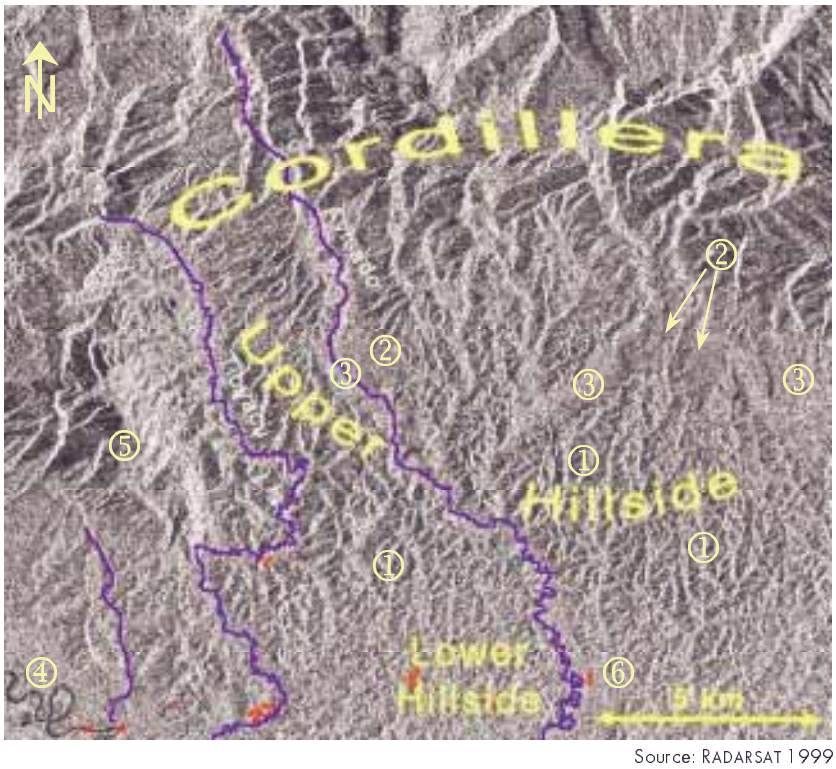



***Fig. 2.5: Geological map of the upper Río Tioyacu and Río Avisado watersheds.***

from the Paleocene to early Eocene periods (INGEMMET 1997) under predominantly fluvial to lacustrine conditions. Lithologically, the formation consists of sandstones with intermittent clay layers and local occurrences of conglomerates. To the north of the settlements of Paz y Esperanza and Gamínedes the lower hill region transforms into the upper hill region which rises to elevations of 1 000 m a.s.l.. The hills consist of alluvial Pleistocene sediments (Qp-al) comprising thin horizontal layers that vary from sands to clays. These layers represent the different uplift phases of the Andean Cordillera during the Pleistocene period.

The main block of the Cordillera Cahuapanas and especially the Cerro Tambo massif at the headwaters of the Río Tioyacu are made up of early Cretaceous rocks of the *Cushatabay* formation (Ki-c). This formation features whitish-gray sandstones of medium to coarse texture which occasionally include micro-conglomerates under inclined, layered stratigraphy with channel structures and varying proportions of loamy sand. This structure led to the conclusion that deposition occurred in a high energy environment as a fluvial delta sediment. Transition to the late Jurassic *Sarayaquillo* formation on the lower slopes of the Cordillera Cahuapanas may be gradual. Rocks of the *Sarayaquillo* formation are described as reddish-brown quartzitic sandstones of fine to medium texture that are firmly packed and crumbly. Sediment structure indicates that sedimentation took place under semiarid conditions into the floodplains of an intra-montane basin (INGEMMET 1997).




Source: RADARSAT 1999

***Fig. 2.6: Radar image of the upper Río Tioyacu and Río Avisado watersheds. Look direction is from the east (right hand side).***
*Settlements are marked red and the rivers Tioyacu and Avisado are outlined in blue. Clearly visible is the dissected and eroded table land of the upper hill area ①. Non-eroded small mesas on the foot of the cordillera ②. Also the younger Quaternary sediments in the river valleys are distinguishable ③. Landmarks are the Mayo River ④, the Cerro Tambo ⑤, and the settlement of Gamínedes ⑥.*

The Tertiary and Pleistocene sediments of the upper and lower hill areas were most likely modified by strong erosion processes during or after the Pleistocene period which created the currently highly dissected and hilly relief (Fig. 2.6) with narrow crests and elevational gradients from 30 to 100 m (cf. digital elevation model in Fig. 3.58). Only a lack of the protective vegetation cover can have permitted such extreme erosion within a short period of time. Since LAUER (1986), VAN DER HAMMEN (1974) and WHITMORE (1991) found that the Pleistocene timberline depression during the last glacial maximum (LGM) did not reach as far down as the floors of the Alto Mayo Valley another explanation for the erosion forms should be sought. Evidence of large scale fires have repeatedly been reported by several authors for the Amazon lowlands during the past 2 000 years (SANFORD et al. 1985, MEGGERS 1994). They link these fires to drought effects by extreme *El Niño* events. However, impacts of such ENSO dynamics were found to be marginal on the study region today. Local scientists report that the entire upper valley of the Río Mayo may have been flooded by a large lake which drained rapidly in up to three stages possibly after decisive seismic events leaving the former lake floor to unimpeded erosion (PERISUTTI, 2002, *pers. communication*). Under these conditions the stability of the geologic substrate may have contributed to the relatively sharp division of the different landforms such as the lower and upper hill regions and the mesas further towards the imaginary shoreline. This would also provide an explanation for the conspicuously even level of the ridgelines which imply an initially plain surface on the bottom of such a sedimentary trough (cf. Fig. 2.11 in chapter 2.1.6).

Approximately 90 % of the watersheds of the Río Tioyacu and Río Avisado are currently covered by dense forests. The stand canopy heights range from 20 to 35 m and effectively

prevent any large scale erosion (cf. aerial photograph in Appendix 9.3.1). Lateral erosion occurs along the creeks during high precipitation events. Also local failures of steep slopes (> 25°) may be fostered by heavy rainfall and by earthquakes (THOMAS 1994).

### 2.1.4 Soils

Soils have been studied with respect to agricultural projects (ONERN 1982, ONERN/PEAM 1989) in some accessible areas of the lower Río Avisado watershed and were classified according to Soil Taxonomy (SOIL SURVEY STAFF 1998).

A clear pedological separation of two units was found for the area. The alluvial and fluvial sediments of river terraces are covered by soils which are influenced by periodic flooding, stagnant water and / or high groundwater levels. Most of them developed to Tropofluvents or Tropaquepts. Tropofluvents are tropical bottomland raw soils of river valley bottoms whereas Tropaquepts occur on alluvial sites with a loamy-clayey texture showing indications of heavy gleys due to high groundwater tables. The $C_{org}$-content is generally high, and layers of undecomposed organic material may be interspersed. The nutrient content is high due to external input by flooding.

In contrast, soil development in the hill region is dominated by topographic position. The slopes of the lower hill region support mainly Dystropepts and dystric Tropudults. Dystropepts are only slightly developed acidic soils with a low base saturation and high $Al^{3+}$ concentrations. Dystric Tropudults are also poor soils that contain a shallow horizon with clay accumulation and a depth of 50 - 75 cm. According to the above studies Troporthents prevail in the upper hill region. These are tropical, generally acidic raw soils on slopes which are easily eroded. BÖRNER (2000) found on a catena of soils in the lower hill region a highly variable texture ranging from clay to loam which reflects the small-scale variability of sedimentary layers of the parent material. On steep slopes the horizon depth and sequence may change within a few meters of elevation. Soils on the slopes are generally well drained. The increased susceptibility for soil erosion, the poor nutrient supply, and an $Al^{3+}$ saturation of generally 40 - 80 % limit these soils for agricultural use.

Source: INRENA 1995

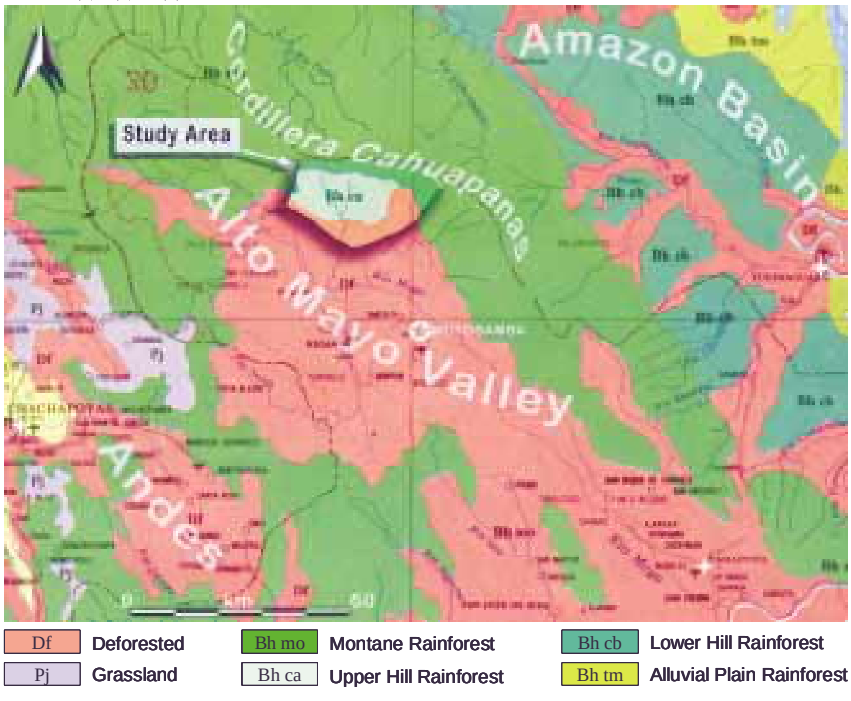



***Fig. 2.7: Location of the study site highlighted on a section of the forest type map of Peru 1 : 1 000 000.***

*Indicated are the four major topographic units: The Andes, the broad Alto Mayo Valley, the Cordillera Cahuapanas and the adjacent Amazon plain. Only the south eastern parts of the study area are classified as deforested areas whereas the remaining part is mainly covered by montane rainforest and upper hill rain forest according to this map. This study focuses on the upper hill rainforest.*

## 2.1.5 Vegetation

The study area belongs to the Neotropis (LAUER 1986). According to the HOLDRIDGE system of life zones, the study area belongs to the premontane moist forest bioclimatic zone with an average temperature between 18 and 24 °C, and average annual precipitation from 1 000 to 2 000 mm that drops below 100 mm for 2 - 4 months (READING et al. 1995).

The biogeographical atlas published by SCHMITHUESEN (1976) shows the Alto Mayo region as tropical montane rain forest. The vegetation map of HUECK & SEIBERT (1981) classifies the forests of the study area as evergreen mountain rain forest, lower level, on the east facing slopes of the medium Andes (*Selva de Yungas*). They are described as rain forests of 30 m in height, having abundant lianas and epiphytes, many palm species (Iriartea, Astrocaryum, Phytelephas, Carludovica), and distinct Cecropias and *Ochroma lagopus*.

According to PRANCE (1989) the study area is covered by lower montane forest 700 - 1 200 m that is considered to be quite similar to lowland rain forest. The species composition gradually changes towards upland forests featuring fewer woody vines, abundant vascular epiphytes, and predominantly mesophyll leaf types.

GRUBB (1974) drew the limit between lower montane forests and lowland rain forest in the Andes between 700 and 1 200 m a.s.l.. The lower montane forests tend to be shorter than their counterparts of adjacent lowland areas, again with fewer woody vines, more vascular epiphytes and predominantly mesophyll leaf types. The upper limit of the lower montane rain forest was observed by GRUBB (1974) between 1 800 and 2 400 m a.s.l. where it transforms into the upper montane forest type of the Andes.

The forest type map of Peru (INRENA 1996) classifies the forests in the lower part of the study area below 1 000 m a.s.l. as *bosque humedo de colinas altas* (*bh ca* = humid upper hill forest). This forest type occupies only 1.4 % of the territory of Peru. Typical slopes are between 15° and 35° in variable topography. Access is generally difficult, maximum tree heights are about 35 m and distinct forest storeys are visible. The canopy height is low on steep slopes and on ridges. The upper part of the study area, including the Cerro Tambo and the Cordillera Cahuapanas, is classified as *bosque humedo de montañas* (*bh mo* = humid montane forest). This type of forest covers 11.7 % of the national territory and basically extends entirely over the eastern flanks of the Peruvian Andes up to 3 200 m a.s.l. in elevation. The relief is typically mountainous and serrated by a web of rivers. A great number of species and life forms (epiphytes, herbs, lianas, bushes and trees) occur in this region (Fig. 2.7).

### 2.1.6 Photographic Survey of the Study Region

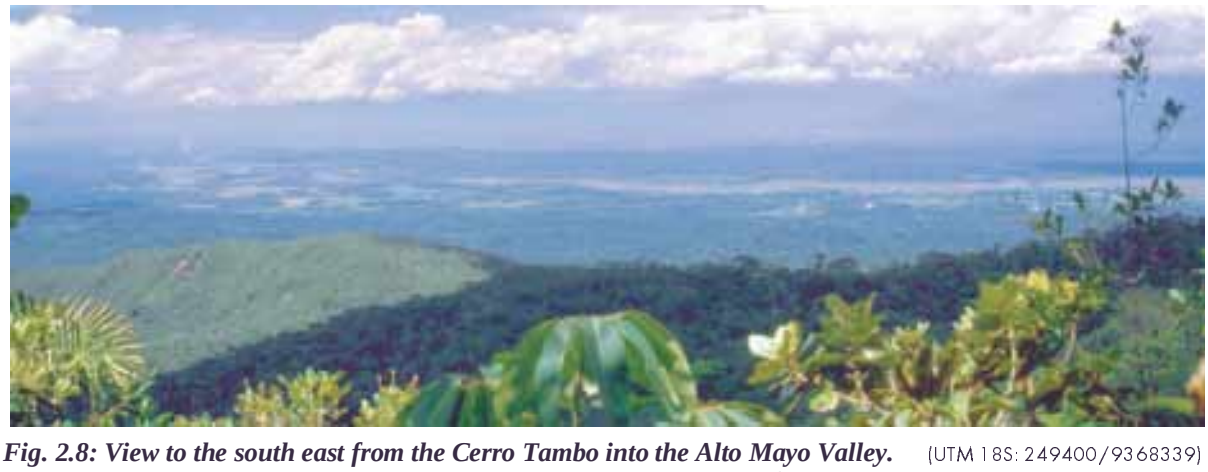


***Fig. 2.8: View to the south east from the Cerro Tambo into the Alto Mayo Valley.*** (UTM 18S: 249400/9368339) *Clearly visible are the closed vegetation cover, the light color of the Cretaceous* Cushatabay *sandstones at landslide edges in the foreground and the extensive patches of cleared ground for rice cultivation on the Alto Mayo plains in the background.*



***Fig. 2.9: Abandoned agricultural clearing at the foot of the Cordillera Cahuapanas near the Río Huascayaquillo.*** (UTM 18S: 262853/9373012)



***Fig. 2.10: Recently burnt vegetation on a ridge east of the Río Avisado showing clear signs of onsetting erosion.*** (UTM 18S: 260549/9366109)



***Fig. 2.11: Panoramic view across the study area towards the ENE from a pre-summit of the Cerro Tambo.*** (UTM 18S: 249099/9367969)
*The left half covers the Río Tioyacu watershed and includes the highest point of the Cordillera Cahuapanas (Pico de Cahuapanas 1 841 m a.s.l.) whereas the right half is dominated by the Río Avisado watershed and the upper hill region.*



***Fig. 2.12: Panoramic view to the ESE of a recently cleared patch of land on a gentle slope in the lower hill area.*** (UTM 18S: 257876/9355037)
*Clearing is done by logging and burning of the vegetation to provide ground for the cultivation of coffee* (Coffea arabica).



***Fig. 2.13: Panoramic view over extended rice fields on the bottom of the Alto Mayo Valley north of the village of Valle de la Conquista.*** (UTM 18S: 256977/9351587)
*Rice cultivation* (Oryza sativa) *is mostly done by hand using gravity irrigation techniques. Center look direction is towards the South.*

## 2.2 Field Data

The data for this study were obtained from August to September 2001 in cooperation with staff from the *Proyecto Especial Alto Mayo* (PEAM) and students of the *Universidad Nacional de San Martín, Facultad de Ecología,* Moyobamba.

### 2.2.1 Plot selection

The dissected upper hill area with its steep slopes, fern thickets, and swampy plateaus and ravines restricts the accessibility of the study site to riverbeds and previously existing trails. These trails connect the isolated clearings of Huascayacu, Paz y Esperanza and Gamínedes with each other and with the marginal road, Yuracyacu - Pueblo Libre, and the banks of the Río Mayo. A few simple trails leading further north towards the cordillera are maintained by indigenous tribes and local hunters. Forty-five plots were chosen mainly along these trails for reasons of accessibility. A representative distribution of plots was selected to cover all the geological formations of the watersheds as displayed in the geological map derived from literature (c.f. Fig. 2.5 in chapter 2.1.3). For that purpose, three plots were arranged along an altitudinal gradient at the headwaters of the Río Tioyacu (plots 1 - 3; for plot coordinates see Appendix 9.4.1) on the early Cretaceous *Cushatabay* formation while nine plots covered the late Jurassic *Sarayaquillo* formation (plots 34 - 42), all primarily on sandstones. Seventeen plots were positioned over Quaternary sediments from the Pleistocene and Holocene periods respectively (plots 4 - 17 and 43 - 45), also primarily sandy substrates. For plot selection, emphasis was laid on distributing plots in all topographical positions, e. g. ridge, ravine, valley bottom, and upper / lower slope. Unique and visually distinct vegetation types (e. g. heath lands, fern thickets) were investigated more thoroughly. Plot selection was done by *a priori* classification of the study site based on available geological information, whereas in the field investigation, sites were chosen based on topographical positions and observations. However, actual plot centers were chosen at random. Sites of evident anthropogenic influence through logging or reported burning were excluded from observation.

Plot sizes differed according to the parameters and the type of vegetation being investigated. Below, Tab. 2.2 illustrates the criteria applied to the respective situations and approaches.

*Tab. 2.2: Plot sizes for individual approaches: biometry, biomass harvest, structure and soil assessment.*

| Approach | Forest | Heath Land | Fern Thicket |
|---|---|---|---|
| **Biometry** | Relascope | Relascope | Relascope |
| **Biomass Harvest** | - | ø 4 m | 2 m × 2 m |
| **Structure*** | 25 m × 25 m | 5 m × 5 m | 15 m × 15 m |
| **Soil**** | 1 pit | 1 pit | 1 pit |

* = Average values (line of sight) ** = Various depths

## 2.2.2 Recorded Parameters

Topographical, structural, biometrical, and soil parameters were assessed by identical methodology for all plots. Mineral soils of plots encountered with a high water table could not be sampled (plots 24, 25, and 27 - 29). Acaulescent individuals of the palm *Jessenia bataua* (Arecaceae) occurred as a common species especially in ravines. Since tree biometry for biomass calculations includes stem diameter and tree height as key parameters, these palms with a thick base of dead leaves would greatly exaggerate the actual biomass. Therefore, a special formula had to be developed in order to adequately consider the contribution to biomass by this species. Three representative leaves were chosen for biomass determination in order to establish a characteristic allometry allowing an improved biomass estimation for this acaulescent palm species which occurred in all tree layers. Additionally, a biomass harvest was conducted on plots where a dense fern layer covered the ground or where the majority of woody individuals did not reach above 1.3 m. This was the case in the heath type vegetation (plots 11, 12 and 20 - 31).

### 2.2.2.1 Site Characteristics

Each plot was documented and characterized by general topographic parameters (Tab. 2.3) as suggested e. g. by RICHARDS et al. (1940).

Plot elevations were determined in the field using two methods. First, measurements were taken with a Global Positioning System (GPS) device (Garmin 12 XL). However, the manufacturer suggests a vertical accuracy of its devices of ± 35 m (HTTP://WWW.GARMIN.COM/SUPPORT/FAQS/8.HTML April 2002). This data range is not satisfactory in order to characterize the elevation situations within the small scale relief of the study area. Secondly, due to the lack of reliable georeferencing points for calibration, elevations were post-determined by processing barometric data recorded by two altimeters (Thommen Classic, Switzerland, 6 000 m and 9 000 m). Barometric data were assessed on site and referenced against values interpolated from five-hourly measurements in Moyobamba (mean distance from investigation plots 43 km). Elevation was calculated using a modified barometric elevation formula by STULL (1995) which is elaborated in equations (1) and (2) (Appendix 9.1.1), Moyobamba was set for 880 m a.s.l. and average temperature for 21 °C.

*Tab. 2.3: General site specific parameters.*

| Category | Parameter | Unit | Annotation | Equipment |
|---|---|---|---|---|
| **General** | Plot number | # | | |
| | Date | dd/mm/yy | | |
| | Time | hh:mm | Begin of recording | |
| | Weather conditions | - | Cloud cover / precipitation | Observation |
| | Plot size | $m^2$ | square or circular | Measuring tape / Sonin ComboPro |
| | Observer(s) | - | Names | |
| **Documentation** | Film number | # | Camera used | Minolta x500 / Yashica 118 |
| | Frame | # | Film used | Agfachrome 100 ASA |
| | Look direction | ° | Compass bearing | Suunto KB 14/360° |
| | Sketch | - | Cross section drawn schematically | Pencil |
| **Location** | Location of plot | - | Placement relative to referece points | Observation |
| | Coordinates | m | UTM, Zone 18 S, Datum WGS-84 | Garmin 12XL |
| | Elevation GPS | m a.s.l. | GPS reading | Garmin 12XL |
| | Elevation Altimeter | m a.s.l. | Altimeter reading | Thommen TX 23 9000m |
| **Topography** | Exposition | ° | Compass bearing | Suunto KB 14/360° |
| | Inclination | % | Inclinometer reading of slope | Suunto PM-5/1520 |
| | Atmospheric pressure | hPa | Barometer reading | Thommen TX 23 9000m |
| | Position on slope | - | top / middle / bottom / ridge / ravine | Observation |
| | Micro Relief | - | even / irregular / very undulated | Observation |
| **Stand** | Brief description of aspect | - | Observations, life forms, stand conditions | Observation |
| | Disturbances | - | Obvious human or natural disturbance | Observation |
| | Dead wood | $m^3$ | In the line of sight (ground / standing) | Estimation |
| | Canopy density | % | Mean of fourfold coverage readings | Estimation |
| **Stratification** | Brief description of layers | - | Anomalies, floristic description | Observation |
| | Number of layers | # | Herb / shrub / 1-3 tree | Observation |
| | Layer properties | - | Diffuse / clearly separable | Observation |
| | Layer height | m | | Estimation |
| | Layer cover | % | In steps of 10 % | Estimation |

### 2.2.2.2 Soils

At each plot one soil pit (approx. 0.5 m × 0.5 m, 0.4 - 1.3 m depth) was dug in order to assess edaphic conditions. A partially superficial water table obstructed sampling of mineral horizons on plots 24, 25, and 27 - 29. Soil horizons were identified, measured and described using German soil nomenclature (AG BODEN 1996). Samples for chemical and soil-physical analyses were seized for each individual horizon. The pH value of each mineral horizon as well as ground water where available was measured using MERCK *Spezialindikator* pH strips (pH 2.5-4.5 / 4.0-7.0). A total of 160 horizons were sampled. Bulk density was determined discontinuously where possible with a steel cylinder of 0.1 $dm^3$ volume. Particle-size distribution was derived from texture classified in the field according to AG BODEN (1996).

For chemical analysis YASIN (2001) suggests extraction with $NH_4NO_3$ (ZEIEN & BRÜMMER 1989) for extractable cations (Ca, Mg, K, Na, Al, Fe, Mn) in acidic soils of montane rainforests in southern Ecuador in order to account fully for potentially high Al concentrations upon analysis by flame atomic-absorption spectroscopy (AAS). Plant-available phosphorus was extracted with

*Tab. 2.4: Soil parameters from field and laboratory analyses.*

| Category | Parameter* | | Unit | Annotation | Equipment | Reference |
|---|---|---|---|---|---|---|
| **Field Analyses** | Ground cover | | % | Estimated in steps of 10 %: bare, litter, moss / lichen | - | - |
| | Parent rock | | - | If recognizable | - | - |
| | Name of horizon | | - | Field name | KA 4 | AG BODEN (1996) |
| | Depth of horizon | | cm | Measurement | Measuring tape | - |
| | Texture | | - | - | KA 4 | AG BODEN (1996) |
| | Aggregates | | - | - | KA 4 | AG BODEN (1996) |
| | Color | | - | - | Munsell color chart | - |
| | Rock content | | % | Rock volume estimated in steps of 10 % | - | - |
| | Rooting intensity | | 0 - 2 | After AG BODEN (1994): W0=(0), W1-3=(1), W4-6=(2 | KA 4 | AG BODEN (1996) |
| | Organic matter content | | 0 - 2 | Estimated from missing (0) to high (2) | - | - |
| | Biological activity | | 0 - 2 | Estimated from missing (0) to high (2) | - | - |
| | Hydromorphic characteristics | | 0 - 2 | Estimated from missing (0) to high (2) | - | - |
| | $pH_{H20}$ | | pH units | Measured in distilled water (v/v approx. 1 : 5) | pH indicator strips, Merck Co. | - |
| **Laboratory Analyses** | Soil density | (± 0.1g) | kg $dm^{-3}$ | Soil cylinder samples (0.1 $dm^3$) dried at 105 °C | Ohaus HP320 | - |
| | $pH_{NH4NO3}$ | (± 0.01) | pH units | Measured in extracted solution | | - |
| | $C_{tot}$ | (80 µg absol.) | % | CHN-Element-Analyzer | | - |
| | $N_{tot}$ | (10 µg absol.) | % | CHN-Element-Analyzer | | - |
| | P | (0.50) | mg $L^{-1}$ | $NaHCO_3$-Extraction, ICP-AEP-Detection | | OLSEN & SOMMERS (1982) modif. |
| | Ca | (0.50) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | ZEIEN & BRÜMMER (1989) modified |
| | Mg | (0.20) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | after YASIN (2001) |
| | K | (0.08) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | |
| | Na | (0.50) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | |
| | Al | (0.05) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | |
| | Fe | (0.02) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | |
| | Mn | (0.50) | mg $L^{-1}$ | $NH_4NO_3$-Extraction, AAS-Detection | | |

* = accuracy and detection limits in parentheses

$NaHCO_3$ (OLSEN & SOMMERS 1982, modified) and consequently analyzed using inductively-coupled plasma-atomic emission spectroscopy (ICP-AES) as demonstrated by YASIN (2001). Total carbon and nitrogen were determined by a CHN-Element-Analyzer. All chemical analyses of soil samples were performed at the laboratory of the Analytic Center of the University of Bayreuth, *BITÖK*. For a complete list of all soil parameters studied see Tab. 2.4.

### 2.2.2.3 Vegetation Structure

A structural classification of the vegetation was attempted since a floristic classification of the study area was not feasible due to the lack of a complete and applicable local flora and time. The term “vegetation structure“ shall be defined as the spatial distribution of vegetation parameters on a stand level. Building on work by AXMACHER (1998), BENZ (1999), and PAULSCH & CZIMCZIK (2001) from montane rain forests of Ecuador, a set of parameters and structural properties was developed which were identifiable in the field (c.f. Tab. 2.5).

This set consists of both area based classification systems like the ones introduced by RICHARDS et al. (1940) and WEBB et al. (1970) and individual plant systems by WERGER et al. (1982). In order to compensate for problems which arise from applying statistical analysis to stand structural data from stands with different layering (BENZ 1999), all stands were separated into a maximum of three tree layers which added up to total stand height. The set of parameters

*Tab. 2.5: List of structural parameters recorded in the field.*

| Parameter | Value | Scale level | Reference |
|---|---|---|---|
| **Crown shape** | Umbrella | Individual | Modified after WERGER & SPRANGER (1982) |
| | Umbel | Individual | |
| | Globe | Individual | |
| | Cylinder | Individual | |
| | Palm tree | Individual | |
| | Cone | Individual | |
| | Irregular | Individual | |
| **Crown status** | Entire | Individual | BENZ (1999) |
| | Inhibited | Individual | |
| | Crippled | Individual | |
| **Crown contact** | Solitary | Individual | BENZ (1999) |
| | Touching | Individual | |
| | Merging | Individual | |
| **Ramification** | Unbranched up to ⅓ of total height | Individual | After WEBB et al. (1970) and |
| | Unbranched up to ⅔ of total height | Individual | WERGER & SPRANGER (1982), modified |
| | Several stems | Individual | |
| **Leaf shape** | Oval | Plot | After RICHARDS et al. (1940) and |
| | Lanceolate | Plot | WERGER & SPRANGER (1982), modified |
| | Elongate | Plot | |
| | Round | Plot | |
| | Palmatifid | Plot | |
| | Palmatisect | Plot | |
| | Bipinnate | Plot | |
| | Other | Plot | |
| **Leaf Size** | 0-4 $cm^2$ | Plot | After RICHARDS et al. (1940), modified |
| | 4-50 $cm^2$ | Plot | |
| | 50-225 $cm^2$ | Plot | |
| | > 225 $cm^2$ | Plot | |
| **Vines / lianas** | Abundance | Ordinal | After RICHARDS et al. (1940), |
| | On stem | Plot | modified after VARESCHI (1980) |
| | In crown | Plot | |
| | Curtain | Plot | |
| **Epihytes** | Abundance | Ordinal | After RICHARDS et al. (1940), modified |
| | On stem | Plot | |
| | On branches | Plot | |
| **Mosses / lichens** | Abundance | Ordinal | After RICHARDS et al. (1940), modified |
| | On stem | Plot | |
| | In crown | Plot | |

was obtained separately for each of the three layers (E1 = upper, E2 = intermediate, E3 = lower layer) estimating on an interval scale in steps of 10 % coverage for plot specific assessment and 10 % share for individual specific assessment. Abundance of special life and forms and taxa (vines, lianas, vascular epiphytes, mosses, lichens) was evaluated using an ordinal scale in three increments simplified after BENZ (1999), CZIMCZIK (1999), BÖRNER (2000), and PAULSCH (2001):

0 no individuals
1 some individuals
2 many individuals

*Tab. 2.6: Biometric parameters recorded in the field.*

| Category | Parameter | Unit | Annotation | Equipment |
|---|---|---|---|---|
| **Dendrometry** | Stand basal area | $m^2$ $ha^{-1}$ | By WZP (BITTERLICH 1984) using scales 1 and 0.5 | BITTERLICH mirror type Relascope |
| | Girth at breast height (GBH)* | cm | Measurement at 1.30 m height on all WZP selected trees | 2 m measuring tape |
| | Angle to tree base | % | For tree height calculation, measured with inclinometer | Suunto PM-5/1520 |
| | Angle to tree top | % | For tree height calculation, measured with inclinometer | Suunto PM-5/1520 |
| | Distance (± 0.01 m) | m | Measured between inclinometer and observed tree | Sonin ComboPro ultrasonic meter |
| **Tree position** | Direction | ° | Compass bearing of tree from plot center | Suunto KB 14/360° |
| | Distance (± 0.01 m) | m | Measured between plot center and observed tree | Sonin ComboPro / measuring tape |
| | Field name | - | From local vernacular nomenclature for selected species | - |
| **Biomass** | Fresh mass green leaf tissue | kg | Total green leaf tissue harvested within plot boundaries | Various spring scales (50 g - 5 kg) |
| | Fresh mass woody tissue | kg | Total woody tissue harvested within plot boundaries | Various spring scales (50 g - 5 kg) |
| | Fresh mass subsample leaf | g | Subsamples taken at random | Ohaus HP320 (± 0.1g) |
| | Fresh mass subsample wood | g | Subsamples taken at random | Ohaus HP320 (± 0.1g) |

* = trees > 1.30 m

### 2.2.2.4 Biometry

For characterization of above-ground biomass distribution a representative number of trees was selected by the angle count method (Winkelzählprobe, WZP) after BITTERLICH using a mirror type relascope with metric scale CP (FOB m.b.H., Austria) using scale unit 1. For thin stemmed stands (e. g. in the heath forests) on plots 2, 17, and 22 - 33, scale unit 0.5 was applied. The WZP is an optical method for quick determination of the basal area and a size-weighted selection of representative trees in forest stands (BITTERLICH 1984). On plots 11, 12, 02, and 21 all trees within a radius of 5 m were recorded. Dendrometric data were acquired for all selected trees (Tab. 2.6).

For descriptive purposes the location of each described tree relative to the plot center was recorded (Tab. 2.6). A biomass harvest was conducted on sites where recorded trees presumably did not constitute the main share of above-ground biomass as suggested by CATCHPOLE (1992). Plot sizes were chosen according to Tab. 2.2. With the exception of palm trees no monocotyledon plants were included in plot measurements. In the case of the acaulescent palm tree *Jessenia bataua* (Arecaceae) wood and leaf tissue fresh weight was determined separately for both fractions based on the assumption that moisture rates differ considerably. Subsamples were taken at random and weighed on site (Tab. 2.6).

## 2.3 Data Processing and Analysis

Raw field data were organized in spreadsheets and files and a multivariate statistical analysis of parameters, plotting and cartographic display of results followed.

### 2.3.1 Data Processing

#### 2.3.1.1 Soils

Soil particle size distribution was derived from texture classified in the field according to the key modified after AG BODEN (1996) in Tab. 9.9, Appendix 9.2.1.4. Missing values for gravimetrical density were compensated with average values from measured horizons of the same type as shown in Tab. 2.7.

Soil element data from laboratory analysis were screened and assigned to each horizon. The exchangeable $H^+$ concentration was calculated from exchangeable $Al^{3+}$ concentrations and the pH value difference in the extraction solution before and after extraction using the $C^{++}$ program *exchHions* by PRENZEL (1995), from the *Institut für Bodenkunde und Waldernährung* at the Georg-August-University of Göttingen. The effective cation exchange capacity ($CEC_{eff}$) was calculated according to BAIZE (1993) as:

$$CEC_{eff} = Ca^{2+} + Mg^{2+} + K^+ + Na^+ + Al^{3+} + H^+$$

Accordingly, the base saturation (BS) in percent was calculated as:

$$BS = (Ca^{2+} + Mg^{2+} + K^+ + Na^+) / (Al^{3+} + H^+) \times 100$$

All cation concentrations were expressed in cmol of cations per kg of dry fine earth ($cmol_c\ kg^{-1}$). Concentrations, pH value and particle size distribution were then calculated separately as sums for topsoil (O and A horizons) and subsoil horizons (up to 60 cm depth) using weighted means over the respective horizon thickness.

***Tab. 2.7: Mean densities derived from actual density measurements for soil horizon classes which were applied to horizons that lacked data for gravimetrical density.***

| Horizon | Mean Density |
|---|---|
| Ah | 0.78 |
| Bhs | 1.25 |
| Bil | 1.19 |
| Bv | 1.20 |
| *n* Bv | 1.53 |
| Cv | 1.32 |

*Tab. 2.8: List of poorly and highly represented structural parameters from the field study.*

| Parameter | Layer | Occurrence | | Relevance for Analysis |
|---|---|---|---|---|
| | | % | plots | |
| Crown cylinder | 3 | 0 | 0 | Eliminated |
| Leaf palmatifid | 3 | 0 | 0 | Eliminated |
| Leaf round | 1 | < 5 | 1-2 | Eliminated |
| Leaf palmatisect | 3 | < 5 | 1-2 | Eliminated |
| Leaf shape other | 1 | < 5 | 1-2 | Eliminated |
| Ramification basal | 3 | < 5 | 1-2 | Eliminated |
| Crown umbrella | 1 | 5-10 | 3 | Remained |
| Leaf shape other | 2 | 5-10 | 3 | Remained |
| Crown shape irregular | 1 | > 95 | 42-45 | Remained |
| Leaf elongate | 1 | > 95 | 42-45 | Remained |
| Leaf size 4-50 $cm^2$ | 1 | > 95 | 42-45 | Remained |

Pools per hectare of all elements were calculated for each sampled horizon by density and thickness. Pools per hectare were then calculated separately as sums for topsoil (0 - 20 cm) and subsoil horizons (20 - 60 cm) using weighted means over the respective horizon thickness. The division was made according to BÖRNER (2000) under the assumption that the root concentration dominates in the upper 20 cm of the mineral soil and therefore the maximum nutrient uptake takes place in this compartment.

### 2.3.1.2 Vegetation Structure

Data describing vegetation structure was first screened for unusually under-represented or over-represented parameters. Consequently parameters that only occurred in < 5 % of all cases (≤ 2 plots) were eliminated from further analysis due to the limited information conveyed. Parameters that occurred in > 90 % of all cases (≥ 42 plots) remained in the analysis as they were all interval scaled parameters with highly variable values still bearing information regarding the variance between plots (Tab. 2.8).

Ordinal values as for epiphyte, liana and moss / lichen abundance were transformed into interval scaled values as follows:

0 = 0 %
1 = 30 %
2 = 60 %

*Tab 2.9: Biomass distribution classes calculated for tree height and girth at breast height as basis for statistical characterization of the investigated stands.*

| | | Class | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Parameter | Unit | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| **Tree Height** | [m] | <2 | 2-5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-30 | >30 |
| **Girth at Breast Height** | [cm] | <10 | 10-50 | 50-100 | 100-150 | 150-200 | >200 | - | - |

### 2.3.1.3 Biometry

Trees were selected for assessment by the relascope method generally using scale 1. For plots with many thin stems scale 0.5 was used. These method allows an upscaling of the stand basal area to square meters per hectare by the “Winkelzählprobe” (WZP) after BITTERLICH (1984) which simply equals the amount of trees observed exceeding the width of scale 1 on the relascope in addition to half the amount of all stems matching the width of relascope unit 1. Growth density expressed in the amount of stems per hectare are computed from relascope measurements in combination with diameter at breast height (dbh) values using equation (7) in Appendix 9.1.4.

For tree height estimation the distance to the observed tree and angles to the tree base and to the tree top were measured in the field. Using the triangulation method corrected for sloped distance measurements (eq. (16), Appendix 9.1.5), actual height of each tree was determined. Biomass distribution within stands was characterized by calculating the abundance of stems in each class for tree height and girth at breast height as listed in Tab 2.9.

#### Tree Biomass

Biomass for trees was calculated from empirically derived allometric equations by OGAWA (1965) from four different tropical forest stands in Thailand. These equations are based on data of diameter at breast height (dbh) and tree height to produce biomass values for the categories stem, branch and foliage. Initially, these equations require the input of the dbh of each individual only. Tree heights are computed from dbh values by using individual factors for each forest stand described (see equations in appendix 9.1.2). In order to test which formula would be the most appropriate for the different stands, tree heights calculated from measured dbh using all four equations by OGAWA (1965) were compared to tree heights derived from field data. Fig. 2.14 suggests that none of the equations is apt to thoroughly describe all trees sampled in the same way. However, the equations by OGAWA were distinguished in order to characterize different forest types. Different forest types were hypothesized to occur in the study area as well. Therefore, it seemed necessary to pre-classify the plots into rough height classes which should be easier to assign to a certain biomass equation by OGAWA (1965).

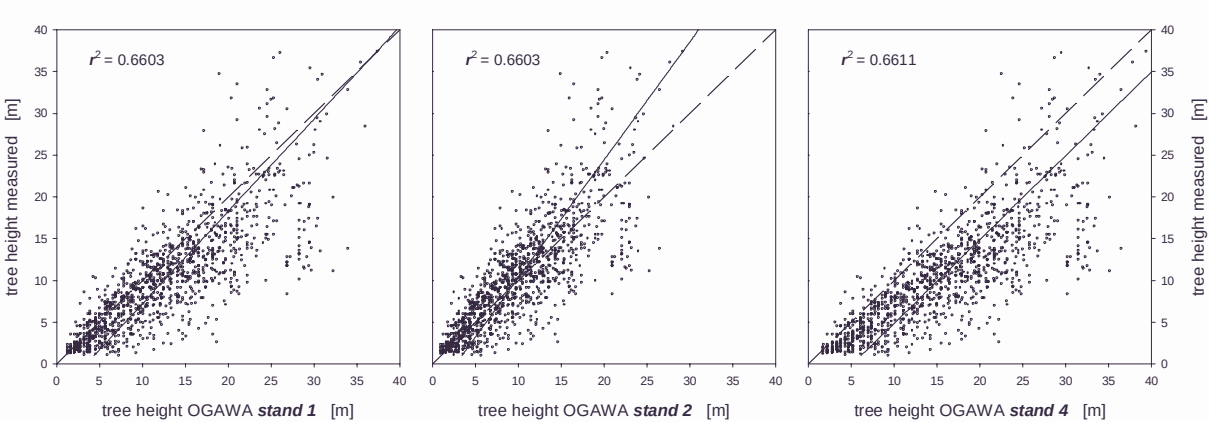



***Fig. 2.14: Comparison of tree height yields from diameter at breast height (dbh) measurements using three different equations by OGAWA (1965) plotted against actual tree heights derived from field measurements.***

Ogawa stand 1 *approaches the 1:1 diagonal only in the upper ranges whereas it over estimates tree heights especially in the lower range.*

Ogawa stand 2 *gets closest to the 1:1 diagonal line in the lower ranges whereas it tends to under estimate heights of taller trees.*

Ogawa stand 4 *seems to over estimate all tree heights systematically based on the data from all assessed trees.*

Measured trees were subsequently grouped in classes ≤ 20 m, 20 - 30 m and > 30 m and again plotted against the OGAWA values for each tree in the respective group from all equations. Fig. 2.15 displays the formulas which appeared to produce the most similar results to the original values and which would therefore be the most appropriate to adequately describe the stand tree biomass.

Consequently, all tree biomasses of plots featuring trees with a maximum height of ≤ 20 m

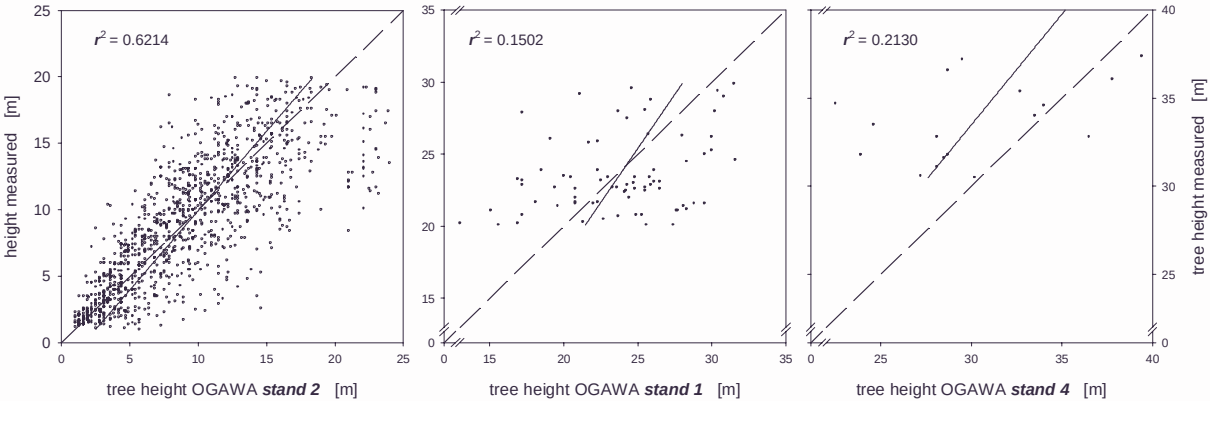



***Fig. 2.15: Tree height yields from diameter at breast height (dbh) measurements using three different equations by OGAWA (1965) plotted against actual tree heights derived from field measurements in the ranges ≤ 20 m, 20 - 30 m and > 30 m.***

Ogawa stand 2 *equation was subsequently assigned to all plots with a maximum measured tree height of ≤ 20 m.*

Ogawa stand 1 *equation was subsequently assigned to all plots with a maximum measured tree height of 20 - 30 m.*

Ogawa stand 1 *equation was subsequently assigned to all plots with a maximum measured tree height of > 30 m.*

were calculated using stand 2 equation. Tree biomasses of plots featuring trees with maximum height of 20 - 30 m were calculated using stand 1 equation. Tree biomasses of plots featuring trees with maximum height of > 30 m were calculated using stand 3 equation.

Eventually the computed biomass was multiplied by the abundance per hectare of each individual tree. The sum of all tree biomasses recorded on a plot expressed the total above-ground biomass.

**Palm Biomass**

As mentioned in chapter 2.2.2.4 the palm species *Jessenia bataua* was represented in many plots in large numbers yet lacked a stem that was conform with the biomass equations above. These plants comprised of many leaves that were made up of a strong rib and many dissected leaf lobes and reached from their bases until the canopy top. In the field, each individual was characterized as well by its girth at breast height and its overall height of the tallest leaf. Three representative leaves of different sizes were harvested and weighed for biomass. Sub-samples were taken for the determination of dry biomass in the laboratory. The following formula was derived based on the data obtained (cf. eqs. (3) - (6), Appendix 9.1.3):

$$w_L = h^{2.4} \cdot (0.33135 \cdot gbh + 23.95449)$$

with $w_L$ = total leaf biomass in kg
$h$ = height of tallest leaf in m
$gbh$ = girth at breast height in cm

**Harvested Biomass**

Biomass was harvested on plots, where trees did not comprise the main proportion of the above-ground biomass. This situation occurred where either a dense fern layer covered the ground (plots 11, 12, 20 and 21) or where the majority of woody individuals did not reach above 1.3 m which was the case in the heath type vegetation (plots 22 - 31).

All ferns (*Sticherus remotus* and *Gleichenella pectinata*, both Gleicheniaceae) were harvested on a plot of 2 m x 2 m, divided into green leaves and brown stalks, weighed and sampled separately. Likewise, all woody individuals on heath forest plots (Ø 4 m) were separated into wood and foliage fractions, weighed and sampled separately and scaled up to the hectare.

Biomass values for larger trees obtained on these plots by OGAWA-calculations were subsequently added to the harvested biomass for total stand biomass.

## 2.3.2 Statistical Analysis

For better comparison with previous studies from the project, soil data and biometrical parameters were first evaluated in separate statistical approaches according to BÖRNER (2000). Eventually all parameters were combined for an analysis of the total data as demonstrated by DEMPEWOLF (2000) and DIETZ et al. (2002).

All methods of statistical analysis, which were applied, are described in detail in BACKHAUS et al. (1996) and BROSIUS (1999) for further reference. Nomenclature was adopted from these authors and from SPSS software (cf. definitions in chapter 7).

Before the cluster analysis, all data were Z-standardized to remove the distortion by variables measured in different dimensions (BROSIUS 1999). After standardization, all variables have a mean of 0 and a standard deviation of 1.

### 2.3.2.1 Spearman's Correlation Coefficient

The first method for the reduction of a dataset by statistical analysis was the screening of the data for highly correlated parameters using Spearman's correlation coefficient. This was done to test for redundant information since one variable of a correlated pair should be expelled from further analysis. Exclusion threshold was set for a correlation coefficient of $r \geq \left| 0.9 \right|$.

### 2.3.2.2 Principal Component Analysis

The second method to reduce a dataset was to submit it to Principal Component Analysis (PCA). Principal Component Analysis is a robust method which accepts even the input of highly correlated variables which makes a screening for Spearman's correlation coefficient unnecessary. This analysis helps to reduce the complexity of a dataset to only a few synthesized, mutually independent parameters which can be handled and interpreted more easily (BROSIUS 1999).

Input data for PCA must be scaled metrically or at least by intervals. Therefore, abundance classes were translated into intervals. All available variables of a dataset were then tested for their suitability to Principal Component Analysis. This was done by computing the "Measure of Sampling Adequacy" (MSA) for each variable by SPSS software. All variables with "unacceptable" to "mediocre" MSA below 0.7 were eliminated from further analysis (Tab. 2.10). Like the MSA for a single variable the KAISER-MAYER-OLKIN (KMO) measure expresses the total sampling adequacy of an entire set of variables for Principal Component Analysis. The same ratings from Tab. 2.10 apply.

***Tab. 2.10: Rating of "Measure of Sampling Adequacy" (MSA) for the suitability of a parameter for Principal Component Analysis.***
*(KAISER & RICE in BACKHAUS et al. 1996).*

| **MSA Range** | < 0.5 | ≥ 0.5 | ≥ 0.6 | ≥ 0.7 | ≥ 0.8 | ≥ 0.9 |
|---|---|---|---|---|---|---|
| **Rating** | "unacceptable" | "poor" | "mediocre" | "fairly good" | "respectful" | "marvelous" |

Principal Component Analysis tries to explain the total variance within a dataset iteratively with mutually independent variables (= factors) in the multidimensional space. As this procedure is done iteratively the first extracted factor explains the majority of the variance, the second factor explains the majority of the remaining variance and so on with decreasing portions of explained variance. The eigenvalue is a measure for the amount of the variance which is explained by a factor. As variables are Z-standardized to a mean of 0 and a standard deviation of 1 before analysis each variable therefore has a variance of 1. Consequently, a factor with an eigenvalue $< 1$ is not significant as it describes less variance within the dataset than there is within each variable itself. For this reason only factors with an eigenvalue $> 1$ are considered ("KAISER criterion"). In order to optimize the solution for interpretability by Hierarchical Component Analysis it is attempted to apportion the eigenvalues more evenly to the factors by rotating them in virtual space without changing the overall variance explained.

In order to characterize and interpret a factor *post-hoc* with respect to the initial variables the factor loadings are commonly used. Factor loadings indicate the proportion to which each variable contributes to a certain factor.

As mentioned above, the extracted factors can be considered to be new variables describing the variance within all submitted variables in a set of cases (plots). In other words: A factor score is the degree to which a certain plot is described by the extracted factors. Factor scores, however, can only be determined by regressional techniques and are repeated as a case-factor matrix by SPSS software.

#### 2.3.2.3 Hierarchical Cluster Analysis

The Hierarchical Cluster Analysis (HCA) is a technique to visualize similarities and dissimilarities by joining most similar cases (in our case the individual plots) into a decreasing number of clusters on the basis of independent variables. Consequently, the datasets must be previously cleared of all correlated variables. This was done by testing for Spearman's correlation coefficient. Factors from Principal Component Analysis are mutually independent by definition and therefore suitable for HCA.

According to BACKHAUS et al. (1996) every Cluster Analysis is sensitive to outliers. Consequently, a procedure for detection of such outliers was necessary. BACKHAUS et al. (1996) recommend a cluster analysis using the Single Linkage method, which links individual objects

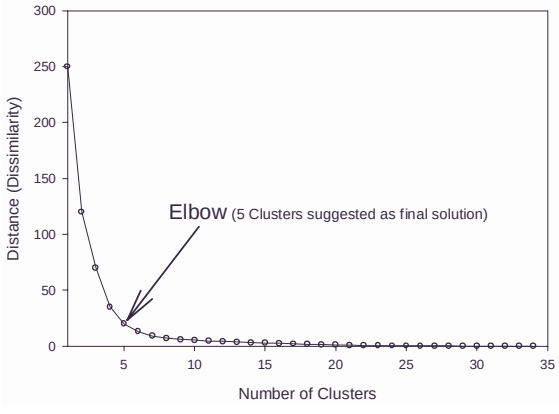



***Fig. 2.16: Hypothetical curve of the number of clusters plotted against the employed distance measure (BACKHAUS et al. 1996).***
*The suggested cluster solution is marked by a sudden "elbow" in the line to the right of which the distance (as a measure of dissimilarity) between each additional cluster shows no more significant increase. From this point the dissimilarity rises sharply with decreasing number of clusters.*
*Based on this principle a solution with up to five distinguished clusters would be justifiable in this case.*

with very different properties as single clusters to the dendrogram. The corresponding dendrograms are documented in Appendix 9.2.

For the final Cluster Analysis after elimination of obvious outliers Ward's method was chosen. It uses a different algorithm for joining those objects that minimize the increase of scatter within a group. This leads to the creation of homogeneous clusters (BACKHAUS et al. 1996). SPSS recommends for this procedure as measure of proximity the squared Euclidean distance. The elbow criterion was consulted for the decision on the amount of clusters for the final solution (BACKHAUS et al. 1996). In this procedure the squared Euclidean distance is plotted against the respective number of clusters. This plot allows the graphical detection of the point at which the heterogeneity between the clusters increases which is indicated by a steep rise of the slope to the left of the "elbow" of the plotted curve. At the same time, the heterogeneity within the clusters remains minimal which is expressed by the relatively small and constant rise of the slope to the right of the "elbow" (Fig. 2.16). Appendix 9.2 shows all dendrograms of the final clustering of data.

BACKHAUS et al. (1996) propose the calculation of a modified t-value for characterizing each cluster (see eq. (17), Appendix 9.1.6). Positive t-values indicate an over-representation of a particular variable within each group relative to the other values, negative t-values indicate an under-representation. The higher the absolute t-value for a particular variable, the more this variable contributes to the separation of one cluster from others. t-values were calculated for all datasets of the different approaches, all of their clusters and all of their variables in order to identify the variables that cause the separation of clusters. For the plots which had been identified as outliers the means of their properties were compared with the respective means of the clusters and the plots were reintegrated into the clusters if appropriate.

#### 2.3.2.4 One-Way ANOVA Analysis

One-way ANOVA Analysis is a procedure to compare different groups by their means. This is done in SPSS Software by computing means and variation of a certain variable within given groups. These values are then weighted for varying group sizes and compared to the mean and

variance of the respective variable over all cases. Differences between groups are rated for significance levels but not specified for the individual groups. So called *post-hoc* tests explicitly reveal these significant differences between groups. By the STUDENT-NEWMAN-KEULS-test subsets are formed at a significance level of $\alpha = 0.05$. Groups represented in each subset are arranged to be homogeneous, i. e. they do not differ significantly by their mean whereas groups represented in different subsets can be distinguished from each other significantly. As groups are commonly of unequal sizes harmonic means are used.

### 2.3.3 Image Processing

Two radar satellite images (JERS-1, L-Band, resolution 100 m) were available from 1996 and 1997. No significant patterns for the vegetation could be detected for the study area on these coarsely resolved images. All examined LANDSAT scenes (acquisition dates from 1996 until 1999: 9/64 1997, 9/64 1999, 8/64 1996, 8/64 1999) showed considerable cloud cover over the study area near the Cordillera Cahuapanas and could not be used for vegetation analysis. Panchromatic, stereographic aerial photographs of the study region were available from October 17, 1992 at the *Instituto Geográfico Nacional* in Lima. Image quality was sufficient. However, the acquisition date of 1992 did not reflect the current situation of clearings and vegetation disturbance patterns (fire, landslides) nine years later.

#### 2.3.3.1 Aerial Photography

The geo-referencing of an aerial photograph (IGN Lima; Roll 17: Strip 335: No. 65) was performed in ENVI 3.4 using conspicuous landmarks as reference points which had been described by GPS measurements in the field. This photograph was used to derive information for common characteristics of classified vegetation units under the assumption that the current vegetation situation resembles the one nine years ago.

#### 2.3.3.2 Digital Elevation Model Processing

From a pair of stereoscopic aerial photographs (IGN Lima; Roll 17: Strip 335: No. 64 & 65) with a stereoscopic overlap of approx. 60 % a digital elevation model (DEM) was created. It covers approx. 2 300 ha of the sampled core section of the study site from the upper hill area to the foot hills of the Cordillera Cahuapanas. Digitizing of the DEM was performed at the *Geographische Institut* of the Friedrich-Schiller-University in Jena using an electronic mirror-stereoscope (P 33, Planicomp, Zeiss, Germany). The elevation of the visible surface was digitized with a horizontal grid, mesh size 50 m; vertical resolution was approx. 2 m. The final product is a surface model including the height of the vegetation which was the only visible surface in the densely forested area.

From the DEM the slopes were computed using Geographic Information System (GIS) software. In ArcView, 3D-Analyst (ESRI, Redlands, Ca., USA) a map of slope classes was computed for the DEM section. The DEM, the slope class map, and an overview map are shown in chapter 3.4.3 and in Appendix 9.3.2.

### 2.3.4 Software

Word processing was done using MS Word 2000. Graphs and tables were generated with SigmaPlot 2000 and MS Excel 2000. Statistical analyses were conducted in SPSS 10. Images were enhanced and processed using Adobe PhotoShop 6, ACDSee 3.0, GIMP 1.2.3 and PanoramaFactory 2.0. Stereoscopic images were digitized with AutoCAD 13. Georeferencing for scanned maps was done using Fugawi 2.17, for aerial photography and satellite images using ENVI 3.4. Mapping was performed with ArcView 3.2.

# 3 Results

## 3.1 Soils of the Study Area

Soils of the study area were sampled at each investigated plot and were subsequently analyzed for texture and chemical properties. This was done to test the first null-hypothesis which claims edaphic conditions to be homogeneous in the upper hill area. Data were used for classification of soil status by statistical methods. TIESSEN et al. (1994) reports that in poor soils in the Amazon basin 95 % of all roots are found in the upper 30 cm of the mineral soil. It was demonstrated by BÖRNER (2000) that the rooting depth of trees in these tropical soils is confined to the uppermost 20 cm of the mineral soil. As this study investigates correlative relationships between soil and vegetation, it focuses on element and nutrient status of the topsoil (0 - 20 cm depth) and subsoil compartments (> 20 cm depth). Conventional soil classification schemes (e. g. Soil Taxonomy, SOIL SURVEY STAFF (1998) or KA 4, AG BODEN (1996)) include aspects like soil genesis and the function of the parent material which are considered only supplementary in this study.

### 3.1.1 Statistical Classification

For each plot, data on 108 soil parameters were obtained. The dataset was prepared to be expressed through mutually independent variables by Principal Component Analysis. Independent variables were a pre-requisite for a subsequent Hierarchical Cluster Analysis. First, tests were performed to identify highly suitable parameters for Principal Component Analysis. Variables with a computed “Measure of Sampling Adequacy” (MSA) of less than 0.7 are considered “mediocre” on the KAISER scale (cf. Tab. 2.10 in 2.3.2.3) and were therefore excluded.

***Tab. 3.1: Soil parameters and their “Measure of Sampling Adequacy” (MSA) expressing their suitability for Principal Component Analysis. All parameters listed were selected to represent the individual plots in a Principal Component Analysis.***
*The parameters are divided into three categories: general soil properties, nutrient status and exchangeable cations.*

| General | | | Macro-Nutrients | | | Cations | | |
|---|---|---|---|---|---|---|---|---|
| **Parameter** | **Code** | **MSA** | **Parameter** | **Code** | **MSA** | **Parameter** | **Code** | **MSA** |
| pH topsoil | PH_TS | **0.902** | C/N ratio topsoil | CN_TS | **0.821** | $Al^{3+}$ conc. topsoil | ALC_TS | **0.854** |
| Sand topsoil | SAND_TS | **0.820** | $C_{tot}$ conc. topsoil | CC_TS | **0.697** | $Al^{3+}$ conc. subsoil | ALC_SS | **0.898** |
| Sand subsoil | SAND_SS | **0.859** | $N_{tot}$ pool subsoil | NP_SS | **0.753** | $Al^{3+}$saturat. ratio topsoil | ALCE_TS | **0.744** |
| Clay subsoil | CLAY_SS | **0.905** | $N_{tot}$ conc. topsoil | NC_TS | **0.585** | $Al^{3+}$saturat. ratio subsoil | ALCE_SS | **0.783** |
| - | - | - | $N_{tot}$ conc. subsoil | NC_SS | **0.789** | $Al^{3+}$saturat. ratio total pit | ALCE_TOT | **0.777** |
| - | - | - | $K^+$ conc. subsoil | KC_SS | **0.782** | $Fe^{3+}$ conc. subsoil | FEC_SS | **0.884** |
| - | - | - | $K^+$ pool upper 20 cm | KP_20 | **0.877** | $Mn^{3+}$ conc. topsoil | MNC_TS | **0.706** |
| - | - | - | $K^+$ pool subsoil | KP_SS | **0.752** | - | - | - |
| - | - | - | $Mg^{2+}$ conc. subsoil | MGC_SS | **0.700** | - | - | - |

**Overall KMO-Value for 20 Parameters: 0.814 = "*respectful*"**

***Tab. 3.2: Eigenvalues of the three factors extracted by Principal Component Analysis.***
*The three mutually independent factors together explain over 81 % of the variance within the dataset. Factors from Principal Component Analysis were extracted to be mutually independent, iteratively explaining a maximum of the variance within a dataset in a multidimensional space. Since variables were Z-standardized to a mean of 0 and a standard deviation of 1 before analysis each variable therefore has a variance of 1. Consequently, a factor with an eigenvalue of < 1 is not significant since it describes less variance within the dataset than there is within each variable itself. For this reason only factors with an eigenvalue of > 1 are considered. Rotation of the factors in space (with their relative position to each other maintained) apportions the explained variance more evenly to the factors.*

| | Initial Eigenvalues | | | Rotated Values | | |
|---|---|---|---|---|---|---|
| **FACTOR** | **Total** | **Variance explained** | **Cumulative** | **Total** | **Variance explained** | **Cumulative** |
| | | % | | | % | |
| **1** | 11.03 | 61.28 | 61.28 | 6.50 | 36.11 | 36.11 |
| **2** | 2.37 | 13.17 | 74.44 | 4.25 | 23.61 | 59.72 |
| **3** | 1.22 | 6.77 | 81.21 | 3.87 | 21.49 | 81.21 |

The initial dataset was reduced to the 20 parameters listed in Tab. 3.1. It can be seen that all aspects of soil quality (e. g. texture, pH value, nutrients, and cation status) were still represented. An achieved KAISER-MEYER-OLKIN (KMO) value of 0.814 for the factor model rated it “respectful” according to KAISER & RICE in BACKHAUS et al. (1996). Three factors were extracted using the KAISER criterion (BACKHAUS et al. 1996) and were subsequently VARIMAX rotated (see regression values for factor scores in Tab. 9.2 in Appendix 9.2.1.1). These three factors together explained more than 81 % of the total variance in the data set (Tab. 3.2).

Examination of factor loadings (Tab. 9.3 in Appendix 9.2.1.2) suggested that none of the factors clearly represented a certain category of parameters. Sets of parameters which were eventually used to describe differences between the soils groups could already be ascribed vaguely to the individual factors: Factor 1 contained parameters such as sandy texture, pH value, and nitrogen content which points to acidic, sandy soils with high humus content such as podzols or peaty soils in the area. Factor 2 is dominated by nutrient parameters with aluminum values being under-represented suggesting a connection to more base saturated, nutrient rich soils. High factor loadings for clay and aluminum were found for factor 3. These three sets of parameters were therefore most suitable to characterize the different soils of the study region.

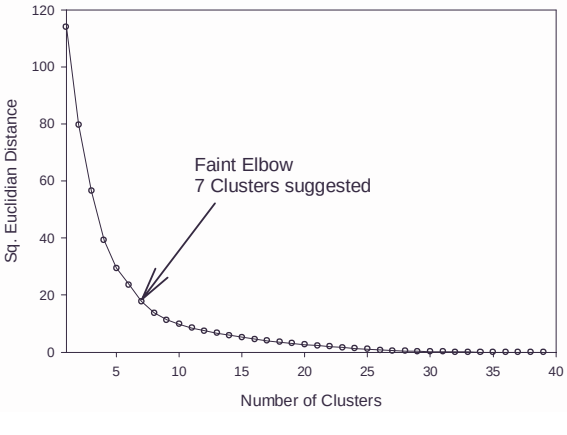



***Fig. 3.1: Soil analysis: Number of clusters plotted against the employed distance measure: squared Euclidean distance (BACKHAUS et al. 1996).***
*The initial cluster solution is marked by an “elbow” in the line where the distance between each additional cluster does not increase significantly any more.*

Regression scores of the three factors which had been extracted by Principal Component Analysis were subsequently submitted to a Hierarchical Component Analysis. Outliers were identified by a Hierarchical Component Analysis using the Single Linkage method. Six plots were excluded by this criterion (P01, 13, 39, 40, 41, and 42). Data for the remaining 39 plots were clustered using Ward's method. The "elbow" criterion was used to decide on the number of final clusters. A maximum of seven clusters were justified (Fig. 3.1). However, only five clusters were separated because the seven-cluster solution would have required a statistically confirmed distinction within Cluster 1 and Cluster 5 which could not be achieved with the available dataset.

The clusters roughly belong to three super-ordinate groups characterized by their main texture: very sandy, sandy and clayey. Investigation of common properties of soils in each group was done by calculating t-values (BACKHAUS et al. 1996) for each soil parameter (see Tab. 9.4 - Tab. 9.8 in Appendix 9.2.1.3 for tabled t-values). In order to reflect the individual soil types the represented clusters were labeled ***Acidic Sand*** soils (subsoil sand > 80 % and topsoil pH < 3.1), ***Litter*** soils (thickness of O horizons > 20 cm on slopes > 10°), soils with a dark ***Carbon***

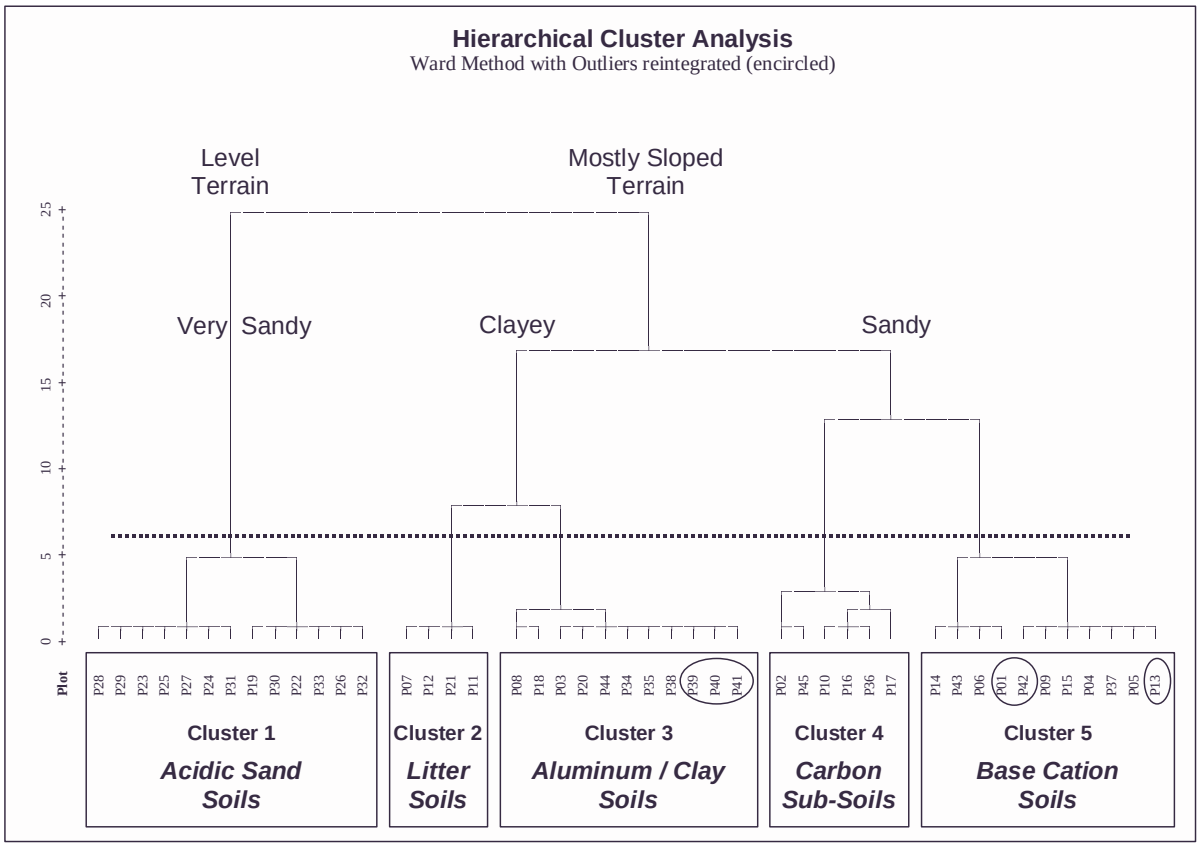



***Fig. 3.2: Dendrogram of soil clusters generated by Hierarchical Cluster Analysis using Ward's Method.***

*Six outlier plots were re-integrated into the five clusters based on their similar properties. The outlier plots P01, 13, 39, 40, 41, and 42 of the initial statistical analysis are encircled.*

*Distinction of clusters was confirmed by statistical analysis (cf. t-values in Appendix 9.2.1.3 and ANOVA statistics in Appendix 9.2.2.4) on the basis of topographic position and texture. Soil units are described by common texture, and / or element characteristics*

*Squared Euclidean distances used in the analysis were rescaled to a maximum of 25.*

***Subsoil*** horizon (subsoil $C_{tot}$ concentration > 1.0 % on slopes > 10°), soils rich in ***Aluminum and Clay*** ($Al^{3+}$ saturation > 50 % and subsoil clay > 40 %), and soils rich in ***Base Cations*** and nutrients (topsoil base saturation > 10 % and $P_{Olsen}$ measurable in the subsoil > 10 ppm). The six outlier plots were *post-hoc* assigned to the cluster to which they showed greatest similarity. Fig. 3.2 shows the cluster combination on the modified dendrogram for the analysis. Outliers are re-integrated into the pattern and marked by circles. All previous analytical steps can be reproduced with dendrograms in Fig. 9.2 and Fig. 9.3 in Appendix 9.2.1.2.

## 3.1.2 Results of Soil Analysis

For each classified soil unit, descriptive statistics were calculated over all plots contained. Characteristic soil properties were compared between soil units. Complete soil data are documented in Appendix 9.5.1.

Texture composition was examined for the grain size fractions of sand, silt and clay of the bulk soil (Fig. 3.3 for topsoil and Fig. 3.4 for subsoil). In some cases, variability within the average pedon of a soil unit from topsoil to subsoil was greater than differences between individual soil units. Generally, the proportion of the silt fraction decreased in the subsoil in favor of both sand and clay. *Acidic sand soils* contained the largest amount of sand primarily in the subsoil, highest sand content in the topsoil show the often strongly leached soils from the *carbon sub-soil* unit. *Litter soils* as well as *aluminum / clay soils* had the highest clay fraction both in topsoil and subsoil.

Observed $pH_{H_2O}$ values of 2.8 - 4.1 are generally low for all soils sampled (Fig. 3.5). Topsoils are slightly more acidic throughout, probably caused by higher concentrations of organic acids. This may also be the reason for litter soils having a slightly lower pH than all other non-sandy soils. Very consistent pH values in this soil group could be caused by the thick litter layer

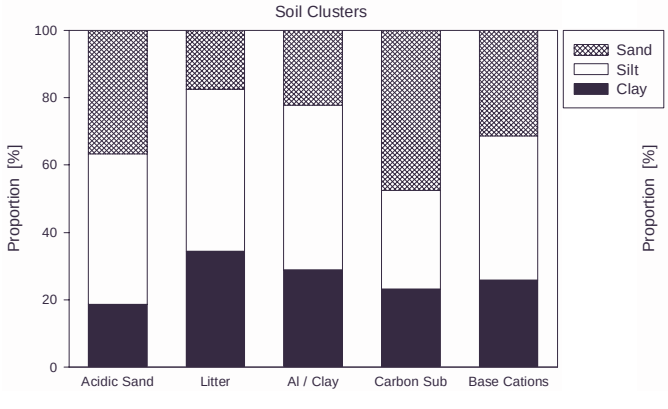



***Fig. 3.3: Topsoil texture composition of the fractions sand, silt, and clay of the soil units.***

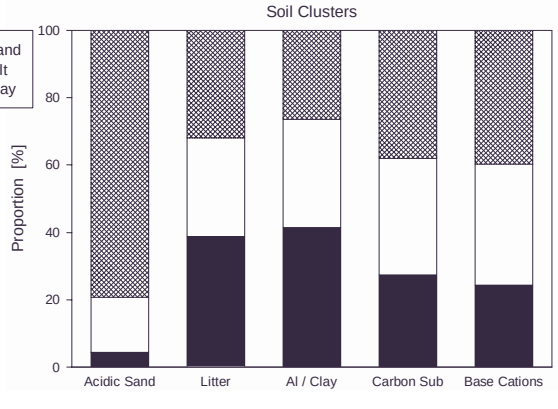



***Fig. 3.4: Subsoil texture composition of the fractions sand, silt, and clay of the soil units.***

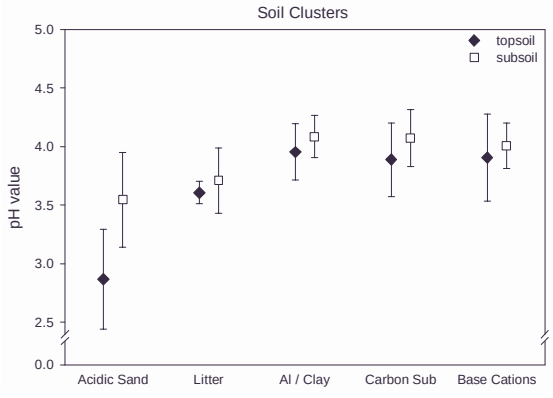



*Fig. 3.5: The pH values of the soil units.*

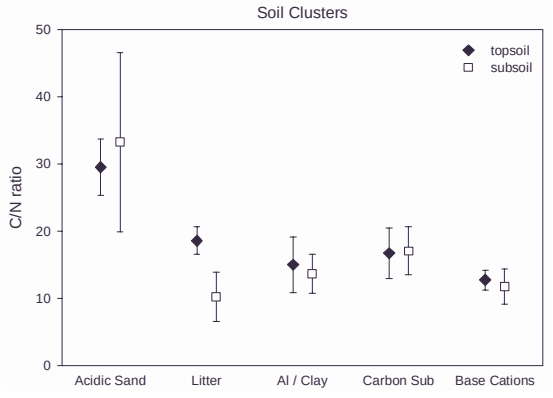



*Fig. 3.6: Distribution of C/N ratio in the soil units of the study area.*

influencing the leachate to be similar for each soil. *Acidic sand soils* display significantly lower topsoil pH than all other units. Subsoil pH, however, is relatively high. Highest subsoil concentrations for calcium were also measured for the *acidic sand soils* (cf. Fig. 3.15).

The C/N ratios of topsoils and subsoils generally range between 10 and 20 (Fig. 3.6). Values for topsoils vary little in comparison to corresponding subsoils. Exceptions are *litter soils* with an unusually narrow C/N ratio in the subsoil both absolute and relative to the topsoil. The C/N ratio in the *acidic sand soil* group is significantly wider. Subsoil C/N ratio varies greatly. This may be influenced by restrictions in sampling of moist sites due to a high ground water table. Sample size is small for this sub-unit. The C/N ratios around 30 rather reflect properties of fulvic substances than of humic matter as it seems likely for all other soils which are better drained.

Total carbon contents ($C_{tot}$) are significantly higher in the topsoil than in the subsoil. No significant difference was found soils with a *carbon subsoil* horizon where subsoil carbon content is highest among all units (Fig. 3.7). Subsoil carbon content and total carbon pools for topsoil and subsoil are lowest in litter soils. Although subsoil carbon contents for *acidic sand soils* are average, topsoil concentration is highest of all. Low microbial activity resulting in low mineralization rates under waterlogged and strongly acidic conditions may provide an explanation.

Total carbon concentration and total carbon pools show similar trends (Fig. 3.8). Although carbon concentrations are higher in topsoils, subsoil carbon pools are larger due to significantly denser subsoil horizons. Exceptions are litter soils and acidic sand soils where differences between topsoil and subsoil concentrations were large.

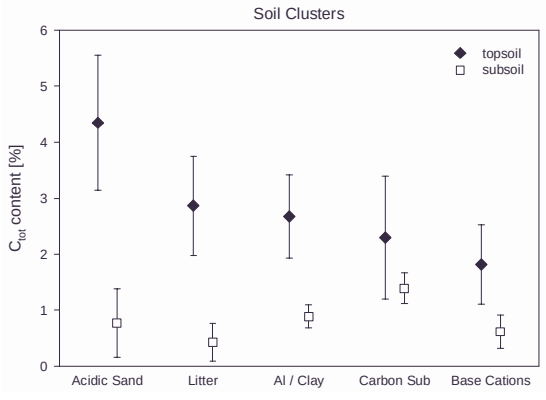



*Fig. 3.7: Distribution of $C_{tot}$ concentration in the soil units.*

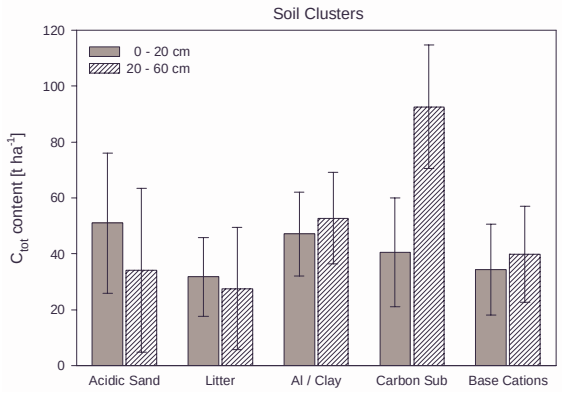



*Fig. 3.8: Distribution of $C_{tot}$ pools in the soil units.*

The situation for total nitrogen ($N_{tot}$) is similar to carbon. Both elements are closely linked as chief constituents of soil organic matter (SOM). The variability of the nitrogen concentrations is very large (Fig. 3.9). Highest nitrogen concentrations are found in the topsoil of *aluminum / clay soils* whereas lowest concentrations are in the subsoil of *acidic sand soils*. *Acidic sand* soils are poorest in total nitrogen both in concentration and in pools. For *carbon sub-soils* highest nitrogen pools were calculated (Fig. 3.10).

The nutrient status of the soils is reflected in exchangeable potassium ($K^+$). Concentrations in topsoils exceed those in subsoils (Fig. 3.11) but larger potassium pools are found in the subsoils (Fig. 3.12). The extreme variability within the topsoils of *aluminum / clay soils* is notable. Generally, exchangeable potassium pools are highest for the *base cation soils* (206 kg ha$^{-1}$ topsoil / 591 kg ha$^{-1}$ subsoil) and on the lower end for *carbon sub-soils* (114 kg ha$^{-1}$ topsoil / 273 kg ha$^{-1}$ subsoil). There is practically no exchangeable potassium stored in *acidic sand soils* (26 kg ha$^{-1}$ topsoil plus subsoil) probably due to their shallow dimensions.

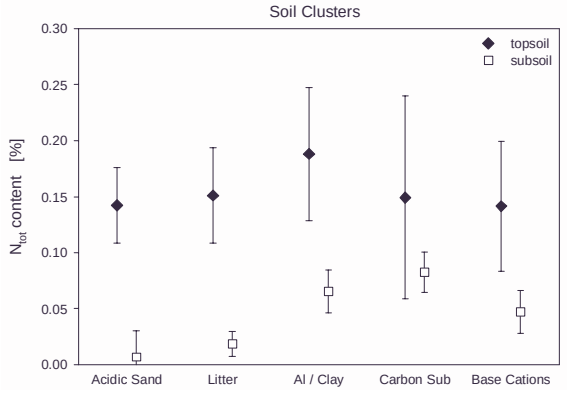



*Fig. 3.9: Distribution of $N_{tot}$ concentration in the soil units.*

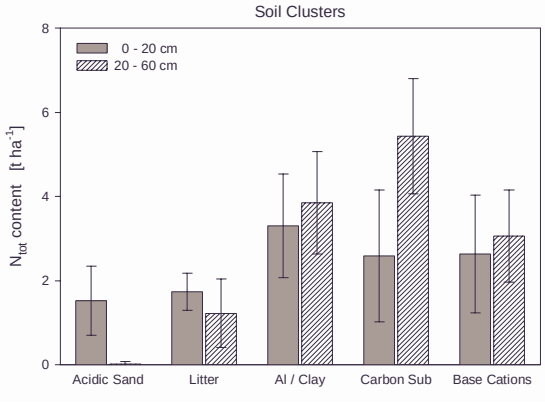



*Fig. 3.10: Distribution of $N_{tot}$ pools in the soil units.*

***Values for each soil pit are means weighted for horizon thickness. Displayed are means and their standard deviation for each soil unit.***

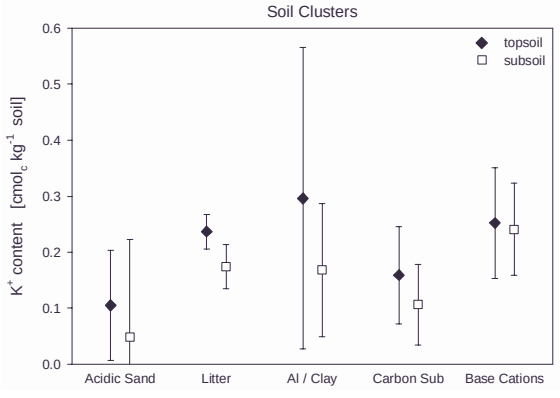



***Fig. 3.11: Distribution of exchangeable $K^+$ concentration in the soil units.***

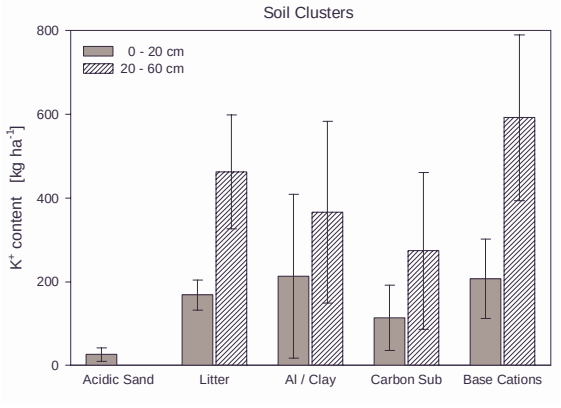



***Fig. 3.12: Distribution of exchangeable $K^+$ pools in the soil units.***

The phosphorus ($P_{Olsen}$) shown supposedly accounts for the plant-available portion of soil phosphorus. Detection limits for analysis were high. Phosphorus concentrations below 10 ppm of fine earth could not be detected by the analysis tools therefore zero values from analysis for phosphorus may in reality still be considerable in dense and thick horizons but would not be accounted for in the data. No plant-available phosphorus was found in subsoils, therefore Fig. 3.13 displays only topsoil P pools. In many topsoils, irrespective of any soil units, and in most *litter soils* no phosphorus was detected which resulted in high variation within the soil units. Nevertheless, a continuous rise in P supply from 9.7 to 27 kg $ha^{-1}$ can be proposed for the series *carbon sub-soils*, *aluminum / clay soils* to *base cation soils*. A plant-available phosphorus supply of only 0.8 kg $ha^{-1}$ was found for topsoils of *acidic sand soils*. This supports the hypothesis that heath forests, which were exclusively found on *acidic sand soils*, are suffering from P-limitation (OZANNE & SPECHT 1979).

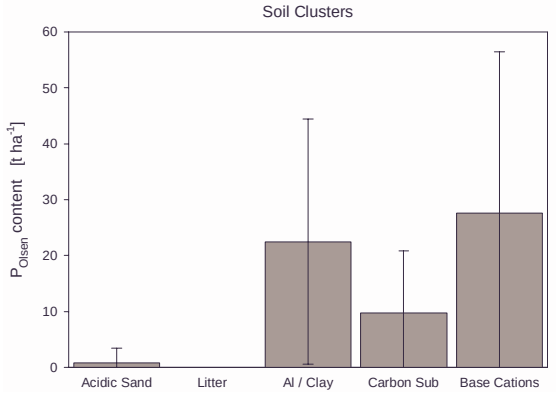



***Fig. 3.13: Distribution of plant-available $P_{Olsen}$ pools in the topsoil of the soil units.***

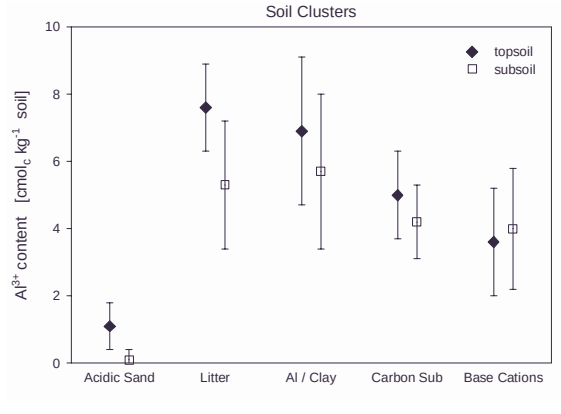



***Fig. 3.14: Distribution of exchangeable $Al^{3+}$ concentration in the soil units.***

*Values for each soil pit are means weighted for horizon thickness. Displayed are means and their standard deviation for each soil unit.*

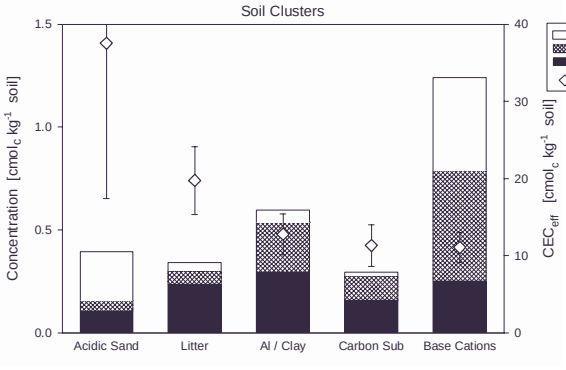



***Fig. 3.15: Topsoil contribution of the exchangeable portion of bases ($K^+$, $Ca^{2+}$, and $Mg^{2+}$) to the effective cation exchange capacity ($CEC_{eff}$) of the soil units.***

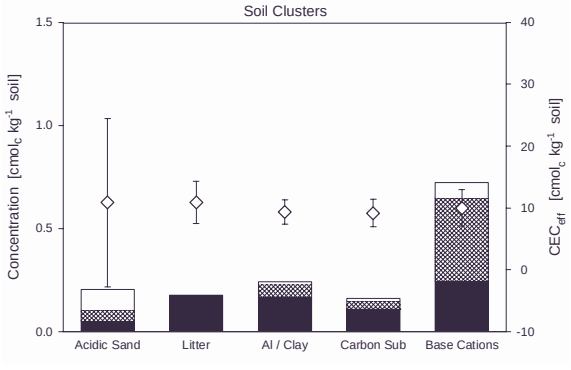



***Fig. 3.16: Subsoil contribution of the exchangeable portion of bases ($K^+$, $Ca^{2+}$, and $Mg^{2+}$) to the effective cation exchange capacity ($CEC_{eff}$) of the soil units.***

*Values for each soil pit are means weighted for horizon thickness. Displayed are means and their standard deviation for each soil unit.*

Exchangeable aluminum ($Al^{3+}$) concentrations were highly variable (Fig. 3.14). Highest concentrations were found in topsoils of *litter soils* and *aluminum / clay soils* which may be due to the higher clay content of the parent materials. The exchangeable aluminum concentrations in the *acidic sand soils* were surprisingly low. A possible explanation might be that most aluminum is chelated permanently to organic complexes at extremely low pH (SCHEFFER et al. 1998).

Soil nutrient status is also characterized by the base cation micro-nutrients calcium ($Ca^{2+}$) and magnesium ($Mg^{2+}$). Fig. 3.15 and Fig. 3.16 show the mean cumulative concentration of the base cations calcium, magnesium, and potassium for topsoils and subsoils. *Base cation soils* show the highest values in both topsoil and subsoil with only calcium decreasing substantially in the subsoil. The most prevalent cation in these soils is magnesium.

As a general trend, concentrations of plant nutrients in the study area are very low and show a relatively uniform and proportional decrease in base cation concentration with depth. With the exception of *acidic sand soils* and *base cation soils* where calcium or magnesium dominate respectively, all other soil units contain potassium as main fraction. In *carbon subsoil soils* calcium is under represented. Subsoils of the *litter* unit contain potassium only. Nevertheless, the effective cation exchange capacity ($CEC_{eff}$) is highest for the acidic sand soils as exchangeable proton ($H^+$) contribution is high at such low pH levels.

Topographic effects were not included in the soil analysis but were analyzed and evaluated subsequently (Tab. 3.3). Only inclination (slope) which is presumably a driving force for soil and element displacement caused recognizable differences between the clusters. *Acidic sand soils* were distinguished from all other units. *Litter soils* were significantly distinguished from *base cation* and *acidic sand soils* by One-Way ANOVA-Analysis which uses a harmonic group mean.

| Soil Unit | Inclination ° | Elevation m | xposition ° |
|---|---|---|---|
| Litter Soils | 27[a] (10) | 969 (15) | 133 (147) |
| Carbon Sub-Soils | 20[a] (15) | 1009 (108) | 286 (75) |
| Al / Clay Soils | 17[b] (8) | 1038 (74) | 201 (69) |
| Base Cation Soils | 15[b] (12) | 982 (38) | 157 (72) |
| Acidic Sand Soils | 1[c] (2) | 985 (15) | 179 (111) |

***Tab. 3.3: Mean slope, elevation above sea level, and exposition as used to evaluate the topographical situation of the five soil units.***
*Soil units are arranged by increasing inclination. Standard deviations are given in parentheses.*

## 3.1.3 Description

The following chapter briefly summarizes and discusses the most conspicuous characteristics of the classified soil units and assesses their implications for plant growth.

### 3.1.3.1 Soil Units

#### Acidic Sand Soils

The most remarkable soils in the study area are combined in the *acidic sand soil* unit. These soils are exclusively found on level plateau sites within the Quaternary-Holocene sediments of the upper hill region. The sites are covered with distinctly low and open tropical heath vegetation (SPECHT 1979). The substrate originates from bright white sand layers of approximately 2 - 3 m thickness (cf. COOPER 1979). These soils may be subdivided into a) well drained, more profound soils which mostly occur towards the rim of the plateaus and b) into poorly drained or permanently waterlogged soils over a duripan horizon displaying peat-like properties. Previous studies by ONERN (1982) suggest that the impenetrable duripan is caused by cementing substrate of volcanic origin. The subsoil texture is clearly dominated by the sand fraction. Although the topsoil shows significantly less sand this trend may be blurred by the effect of large amounts of organic material in the topsoils. In field assessment of texture, organic material is known to simulate clay. The soils of this unit are the most acidic found in the area. Topsoils reach pH values down to 2.8 probably due to a high concentration of organic acids. Subsoils are less acidic at pH values about 3.5. C/N ratios of both topsoil and subsoil are significantly higher, around 30 and are a consequence of anaerobic and acidic conditions. High variability within the unit is driven by different properties between dry and wet sites. Due to accumulation of organic substances the carbon concentration is highest, but the low horizon densities result in comparable $C_{tot}$ pools to other soils. Nitrogen values in the topsoil are slightly below average.

Generally the nutrient situation of *acidic sand soils* is extremely poor. Except for some calcium in the topsoil there are very few nutrients available and negligible plant-available phosphorus (0.8 kg per hectare) was found. Subsoil nitrogen and potassium were marginal. The exchangeable aluminum was surprisingly low and is probably chelated with organic matter. If volcanic material (as mentioned by the soil survey by ONERN 1982) was actually present in the substrate, high amounts of aluminum and iron would be expected paired with little phosphorus which would be permanently bound. Indeed, the soils contain little phosphorus and relatively high amounts of iron. Because analysis was not conducted for the identification of the characteristic fractions for allophanes the volcanic origin seems plausible but could not yet be confirmed.

**Litter Soils**

Litter soils were named after a thick layer of litter which accumulated under a dense cover of *Sticherus remotus* and *Gleichenella pectinata*. These soils can only be found on upper slopes on Quaternary-Pleistocene sediments of the upper hill area. The soils are characterized by a distinct change in texture from a silty topsoil with little sand to a subsoil with a relatively high clay content. Topsoil pH varies little between 3.5 and 3.7 which is probably an effect of a similar composition of litter leachate under this homogeneous fern cover. C/N ratio in the topsoil is approximately 20. Significant differences in C/N between topsoil (19) and subsoil (10) suggests that there is probably no connection between processes in topsoil and subsoil. Exchangeable aluminum concentrations are among the highest found in the area which may also be a reason why no plant-available phosphorus was detected. Concentrations of exchangeable base cations were low with potassium dominating especially in the subsoil horizons. All soils which were assigned to this unit were strikingly different in appearance. Topsoils varied from dark colors caused by black carbon to hydromorphic colors which was due to obstructed lateral flow. Similar soil genesis could not be inferred but all soils were found in sites recently disturbed by either fire or gravitational mass transport by landslides.

**Aluminum / Clay Soils**

*Aluminum / clay soils* occurred on all geologic formations studied. They were most frequently found on the late Jurassic substrate at the foothills of the Cordillera Cahuapanas on almost all topographical positions with the exception of the immediate river plains. One site each was located on gently sloped terrain over Quaternary-Holocene sediments and over early Cretaceous rocks. In the upper hill area on Quaternary-Pleistocene sediments these soils were confined to ridges and upper slopes. Although these soils showed the highest clay content in the subsoil, their topsoil texture varied. Base cation status was highly variable. The soil reaction was about pH 4, which is in the range of aluminum buffering, and the exchangeable aluminum concentrations were high.

### Carbon Subsoil Soils

Soils of the *carbon subsoil* unit were characterized by a black subsoil horizon with high concentrations of carbon. These soils were found on gently to moderately sloped terrain but never on lower slopes or in valleys and ravines. No distinction was made as to whether the carbon allocation had occurred either by illuviation as in podzols (which seemed likely in most cases) or as topsoil horizons buried in situ. In general, these soils showed the highest sand content in the topsoil which is a common prerequisite for the formation of podzols fostered by low pH values of approx. 4. Not surprisingly, subsoil carbon concentrations were highest among all soils sampled and the $C_{tot}$ pools were highest due to fairly thick and dense subsoil horizons. Because nitrogen and carbon are closely linked in soil organic matter, $N_{tot}$ dynamics follow those of $C_{tot}$. concentrations and pools of exchangeable potassium which is leached easiest were lowest compared to all other soil units. Plant-available phosphorus was present but with approx. 10 kg per hectare very low. Also, the concentration of exchangeable base cations was lowest in this unit both for topsoil and subsoil.

### Base Cation Soils

*Base cation soils* were found almost exclusively on lower slopes and in depressions, other locations were on river plains. All sites appeared to have a supply of nutrients through seepage or fluvial deposition but great differences exist in the moisture regime of these soils. Well drained sites of rather sandy texture on river plains are included as well as permanently waterlogged soils on the bottom of ravines. These soils did not show any other conspicuous properties other than being rich in nutrients. The aluminum concentration was quite low and nutrients such as phosphorus and potassium were sufficiently supplied. Nitrogen values are similar to all other sites sampled. In the topsoil the concentrations of exchangeable calcium and magnesium were high which might suggest the occurrence of magnesium deficiency due to antagonistic effects during mineral uptake.

## 3.1.3.2 Summary of Soil Analysis

The most distinct soil units in the study area supported vegetation formations with low and open canopy like *chamizales* and *shapumbales* and appeared to be linked to certain geological situations.

### Geological Effects

The nutrient poor sandy plateaus which are covered by *chamizales* are restricted to the Quaternary-Holocene formations of the study area. No distinction, however, was achieved by statistical analysis between the waterlogged soils and the better drained and more profound soils.

Alluvial sand deposits are subject to land slides during heavy rains, especially when deposited over clay layers. This situation is common on Quaternary deposits in the hill region. Land slides can be triggered by earthquakes (BAILLIE 1996), which occasionally occur in the study area (cf. Tab. 2.1 in chapter 2.1.3). *Shapumbales* on *litter soils* are found exclusively over Quaternary sediments where landslides regularly produce bare and fresh patches ready for colonization. Burnt snags and black carbon in the topsoil were encountered in *shapumbales* indicating fires occurring on these slopes. Following intense fires the protective vegetation cover for soils on such steep slopes may be largely destroyed and give rise to soil degradation by erosion and small scale bulk soil displacement. This fire hypothesis is supported by significantly different pH values for topsoils and subsoils which may indicate the separation of young pedogenetic processes in the mineral subsoil from a high activity in the organic compartment. Together with an unusually thick litter layer the discrepancy between the C/N ratios is the only common characteristic for all *litter soils.* This suggests that not soil type but rather disturbance conditions cause the extensive cover by thick fern layers. All other soil units in the Río Avisado area were found independent of geological conditions.

**Topographic Effects**

Topographic aspects seem important for *litter soils* which are assumed to follow landslides. Slopes become unstable on slopes > 25° (THOMAS 1994). Therefore, these sites may appear more susceptible to landslides. Higher exposure to solar radiation and drainage by lateral flow may create drier stand conditions and favor fires. These slopes seem the most disturbance prone.

*Base cation soils* were characterized by high concentrations of nutrients. The water regime of these soils was not considered in the analysis, but these soils were always found in narrow ravines and valleys as well as in fluvial plains near rivers where water dynamics are high. The favorable nutrient supply found on these sites is typically accumulated by lateral flow from upslope and maintained by stagnant water in the case of ravines or by seasonal fluvial deposition near larger rivers.

*Carbon subsoil soils* are found in all geological and topographical positions. The criterion of a common dark carbon subsoil horizon is of little significance for interpretation. Such humus rich horizons can be found as a secondary carbon allocation by illuviation on poor sandy podzolic soils or constitute a buried organic horizon with fresh overlying material deposited by erosion processes. Only knowledge about these processes would allow an interpretation of these soils for plant growth. The abundance of tree ferns on these sites (cf. Fig. 3.20 in chapter 3.2.2) can either be attributed to poor nutrient conditions or indicates a young stand age.

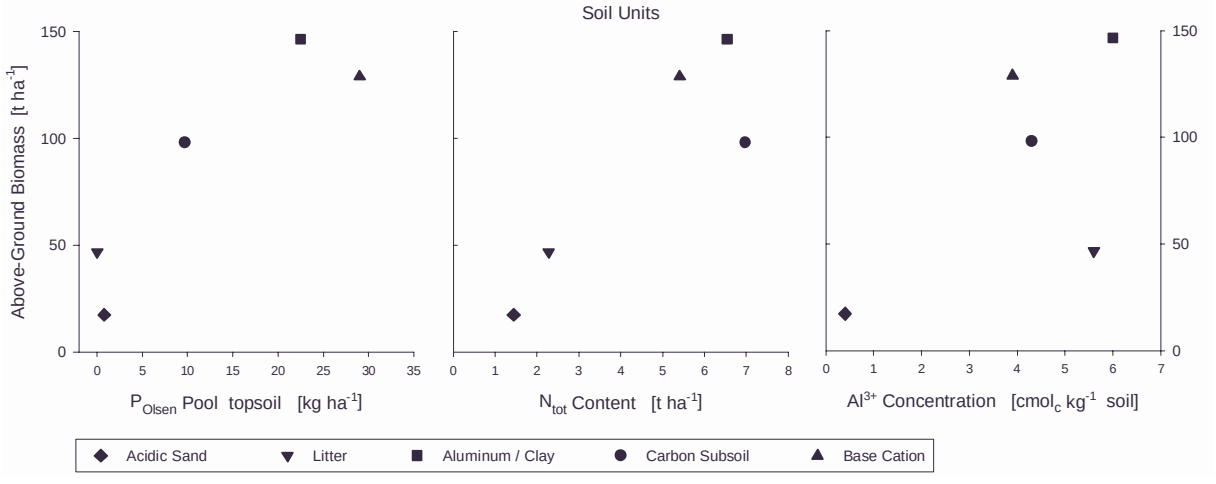



***Fig. 3.17: Relation between soil chemistry and biomass for the respective soil units.***
*Plotted are soil nutrient pools of plant-available phosphorus and total nitrogen, and the total concentration of exchangeable aluminum ($Al^{3+}$) against the biomass values calculated for the stands of each soil unit. Variability for the values given is high throughout.*

Findings of different soil texture suggest that texture drives the soil development on the slopes of the upper hill area into podzols (*carbon subsoils*) or *Al / clay soils*. If this was true, then the finely layered deposits would make it impossible to predict differences in soil from topography.

### 3.1.3.3 Statistical Evaluation

Soil clusters could be significantly distinguished and classified based on their texture and element composition as Tab. 9.20 in Appendix 9.2.2.4 demonstrates. Parameters were examined by One-Way ANOVA to find significant differences of their means over each soil unit. A classification sequence was suggested in order to unanimously identify each cluster. This was possible for each parameter set and implies that vegetation reflects the edaphic conditions of the site.

With respect to biomass, a characteristic feature of vegetation types, soil units could only be grouped into two vague groups: 1) stands of higher biomass (> 100 t $ha^{-1}$) as yielded by *carbon subsoils*, *Al / clay soils* and *base cation soils*, and 2) low formations of little biomass (< 50 t $ha^{-1}$) as found over *acidic sand soils* and *litter soils* (Fig. 3.17). A dependence of biomass on soil nutrient status is suggested for both phosphorus and nitrogen. However, phosphorus was distributed unevenly over the study area. Many mineral soils especially in the upper hill region did not contain any detectable plant-available phosphorus. Variability for phosphorus values was therefore very high. On the other hand, the biomass accumulation pattern with respect to the total aluminum concentration and to aluminum toxicity was indifferent.

***Tab. 3.4: Comparison of means for all classified soil units in respect to thickness of topsoil, pH, and nitrogen, potassium, and phosphorus pools and concentrations.***

| | Thickness | pH | | $N_{tot}$ | | | | | $K_2O$* | | | | | $P_2O_5$** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | pool | | | concentration | | pool | | | concentration | | pool | conc. |
| | cm | | | t $ha^{-1}$ | | | % | | kg $ha^{-1}$ | | | $cmol_c$ $kg^{-1}$ soil | | kg $ha^{-1}$ | ppm |
| | topsoil | topsoil | subsoil | topsoil | subsoil | total | topsoil | subsoil | topsoil | subsoil | total | topsoil | subsoil | topsoil | topsoil |
| **Acidic Sand Soils** | 17 | 2.9 | 3.5 | 1.4 | 0.0 | 1.4 | 0.14 | 0.01 | 26 | 0 | 26 | 0.11 | 0.05 | 1 | 1 |
| **Litter Soils** | 9 | 3.6 | 3.7 | 1.1 | 1.2 | 2.3 | 0.15 | 0.02 | 71 | 462 | 532 | 0.24 | 0.17 | 0 | 0 |
| **Al / Clay Soils** | 15 | 4.0 | 4.1 | 2.7 | 3.8 | 6.5 | 0.19 | 0.07 | 187 | 365 | 552 | 0.30 | 0.17 | 22 | 16 |
| **Carbon Sub-Soils** | 11 | 3.9 | 4.1 | 1.5 | 5.4 | 7.0 | 0.15 | 0.08 | 66 | 273 | 339 | 0.16 | 0.11 | 10 | 6 |
| **Base Cation Soils** | 16 | 3.9 | 4.0 | 2.3 | 3.1 | 5.4 | 0.14 | 0.05 | 165 | 591 | 756 | 0.25 | 0.24 | 29 | 12 |

* = $NH_4NO_3$-Extraction ** = $NaHCO_3$- Extraction

Variation within the plots is generally extremely high which leads to the conclusion that soils grouped according to this approach are not suitable to explain different vegetation patterns. Soil units include stands which are not at similar developmental stages. The spectrum of forest types stocking on soils within one particular unit is broad. For example *base cation soils* as well as *Al / clay soils* both include very tall stands rich in biomass as well as short stands rich in unproductive palms. They create a high variation of biomass characteristics within the soil unit and therefore yield similar mean values for biomass of many soil units. Classifying stands based on the soil units alone will mask the actual variation of biomass between stands and thus obviously different vegetation types will not be distinguished.

An overview of mean pool values and concentrations for the macro-nutrients nitrogen, potassium, and phosphorus in topsoil and subsoil of all soil units is given in Tab. 3.4.

## 3.2 Stand Biometrical Analysis

An inventory of biomass and dimensions of all woody individuals (> 1.3 m) which were selected by the relascope method was conducted at each plot in order to test the second null-hypothesis. This hypothesis assumes a homogeneous distribution of stand biomass within the study area. Basal area in the stands was assessed by the angular count method (*Winkelzählprobe,* WZP) by BITTERLICH (1984). Trees were measured for height and stem girth at breast height (1.3 m). Recorded individuals were also marked in the categories dead, inclined, tree fern, palm, and liana. Species were named in the field by their local vernacular name.

From the data above-ground biomass was determined for each plot using equations by OGAWA (1965) as specified in chapter 2.3.1.3. Stem abundance was calculated for each individual tree. Classes were formed for tree height and girth in combination with abundance data. These classes characterize patterns of the distribution of biomass and consequently are a measure for vegetation growth patterns (cf. Tab 2.9).

### 3.2.1 Statistical Classification

The biometrical classes were examined for their correlations but no highly significant correlations (> |0.9|) were found (Tab. 3.5). Thus, values from all computed biomass distribution classes were submitted to a Hierarchical Cluster Analysis.

The “elbow” criterion was used in order to decide on the number of final clusters. A number of six clusters was suggested (Fig 3.18), but after thorough analysis of the cluster dendrogram eventually only five clusters were separated because the sixth cluster would have been made up of plot P01 only (Fig 3.19).

***Tab. 3.5: Spearman’s correlation coefficient matrix generated for all biometric classes calculated from measurements.***
*No extremely high values (> |0.9|) were observed therefore all of the parameters shown were submitted to a Hierarchical Cluster Analysis.*

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **ba2_025** | 0.23 | | | | | | | | | | | | | | | | **18 Parameters used** | |
| **ba2_050** | 0.04 | 0.31 | | | | | | | | | | | | | | | | |
| **ba2_075** | -0.32 | 0.15 | 0.59 | | | | | | | | | | | | | | | |
| **ba2_100** | -0.33 | 0.08 | 0.42 | 0.47 | | | | | | | | | | | | | | |
| **ba2_250** | -0.41 | 0.34 | 0.36 | 0.65 | 0.67 | | | | | | | | | | | | | |
| **ba2_500** | -0.39 | -0.03 | 0.32 | 0.60 | 0.56 | 0.67 | | | | | | | | | | | | |
| **ba2_1000** | -0.61 | -0.02 | 0.00 | 0.24 | 0.44 | 0.52 | 0.58 | | | | | | | | | | | |
| **ba2_2000** | -0.48 | -0.31 | -0.13 | 0.15 | 0.18 | 0.18 | 0.56 | 0.72 | | | | | | | | | | |
| **ba2_max** | -0.48 | -0.32 | -0.19 | 0.10 | 0.13 | 0.12 | 0.53 | 0.69 | 0.78 | | | | | | | | | |
| **hitea02** | 0.56 | -0.14 | -0.16 | -0.48 | -0.43 | -0.57 | -0.44 | -0.48 | -0.36 | -0.30 | | | | | | | | |
| **hitea05** | 0.58 | 0.58 | 0.14 | -0.07 | -0.17 | -0.06 | -0.29 | -0.46 | -0.61 | -0.56 | 0.25 | | | | | | | |
| **hitea10** | -0.23 | 0.47 | 0.69 | 0.63 | 0.70 | 0.72 | 0.53 | 0.35 | 0.05 | 0.01 | -0.54 | -0.02 | | | | | | |
| **hitea15** | -0.39 | 0.12 | 0.28 | 0.57 | 0.61 | 0.67 | 0.78 | 0.70 | 0.56 | 0.53 | -0.50 | -0.36 | 0.62 | | | | | |
| **hitea20** | -0.49 | -0.17 | -0.06 | 0.31 | 0.30 | 0.44 | 0.68 | 0.81 | 0.87 | 0.76 | -0.44 | -0.48 | 0.20 | 0.72 | | | | |
| **hitea25** | -0.35 | -0.31 | -0.13 | 0.17 | 0.07 | 0.21 | 0.41 | 0.59 | 0.77 | 0.51 | -0.40 | -0.49 | 0.02 | 0.32 | 0.71 | | | |
| **hitea30** | -0.28 | -0.29 | -0.08 | 0.13 | 0.06 | 0.08 | 0.30 | 0.49 | 0.68 | 0.57 | -0.31 | -0.44 | -0.03 | 0.22 | 0.60 | 0.83 | | |
| **hiteamax** | -0.27 | -0.33 | -0.14 | 0.03 | -0.04 | 0.04 | 0.27 | 0.37 | 0.58 | 0.51 | -0.25 | -0.41 | -0.08 | 0.11 | 0.48 | 0.71 | 0.86 | |
| | **ba2_010** | **ba2_025** | **ba2_050** | **ba2_075** | **ba2_100** | **ba2_250** | **ba2_500** | **ba2_1000** | **ba2_2000** | **ba2_max** | **hitea02** | **hitea05** | **hitea10** | **hitea15** | **hitea20** | **hitea25** | **hitea30** | |

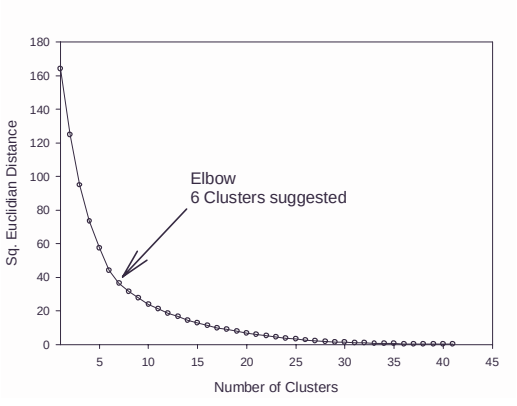



***Fig 3.18: Number of clusters plotted against the squared Euclidean distance (BACKHAUS et al. 1996).***

When including canopy density Clusters 1 to 5 could already be distinguished roughly by the parameters biomass and tree height. Two groups had an average canopy cover < 60 %. The first of these groups featured taller stands with a maximum height > 5 m and was called *"**Open Woodland**"* (Cluster 1) whereas stands which did not reach 5 m were assigned to the *"**Shrubland**"* (Cluster 2). The group of plots with closed canopy (cover > 60 %) and tall trees

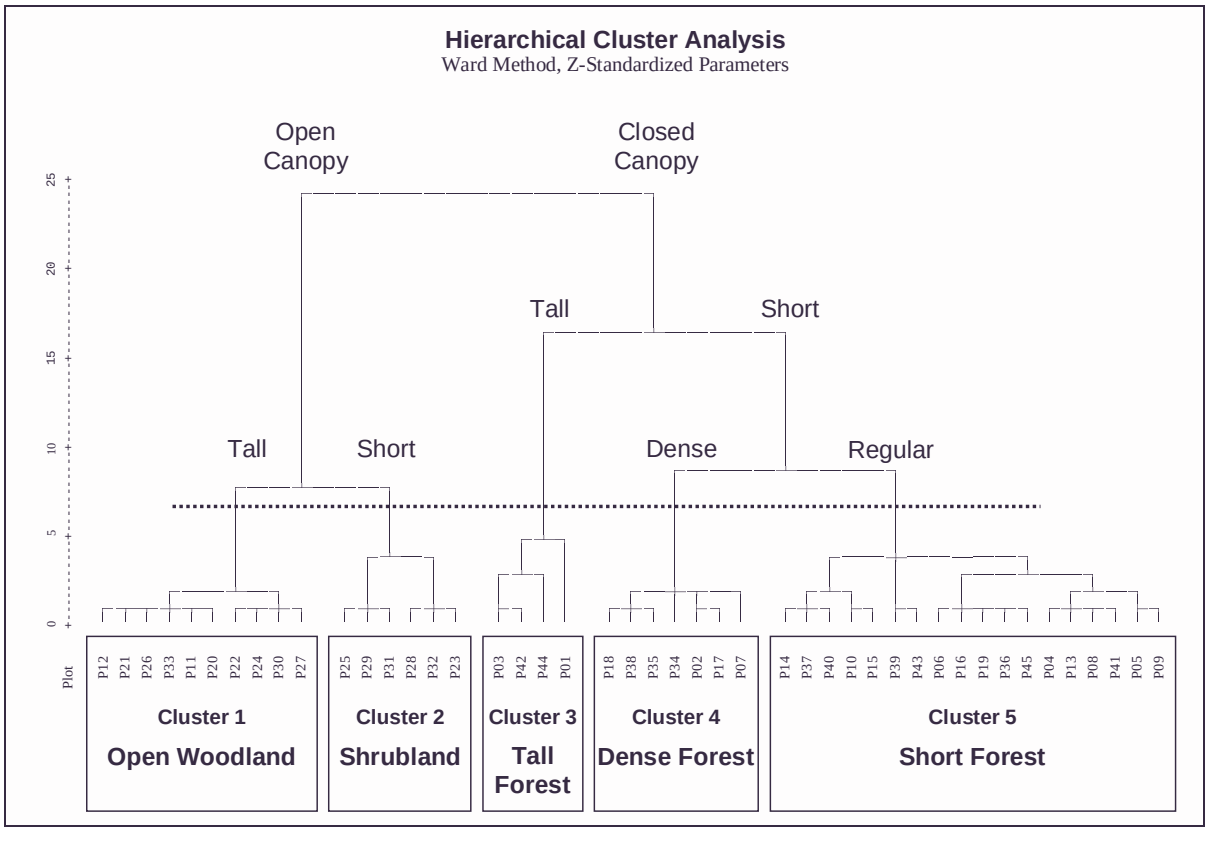



***Fig 3.19: Dendrogram generated by Hierarchical Cluster Analysis using Ward's method for the extraction of clusters with maximum similarity.***

*Z-standardized values are used from 18 parametersdescribing the stand biometrical properties of 45 plots as shown in Tab. 3.5.*

*Clusters names correspond to the stand types predominantly found in each cluster.*

*Distances used in the analysis were rescaled to a maximum of 25.*

***Tab. 3.6: t-values calculated after BACKHAUS et al. (1996) for all biomass parameters found in the individual biometric clusters.***

*High t-values indicate a parameter being relatively over-represented within a group with respect to the entire dataset. t-values (> │0.8│) are marked bold. Units are arranged according to increasing tree height.*

| | Class | t-Values | | | | |
|---|---|---|---|---|---|---|
| | | Shrubland | Open Woodland | Dense Forest | Short Forest | Tall Forest |
| Girth (breast height) | <10 cm | **2.23** | -0.07 | -0.23 | -0.49 | -0.55 |
| | 10-50 cm | -0.56 | -0.54 | **1.71** | 0.01 | **-0.81** |
| | 50-100 cm | **-1.13** | **-1.12** | 0.69 | 0.52 | **0.96** |
| | 100-150 cm | -0.61 | -0.61 | -0.45 | 0.23 | **2.18** |
| | 150-200 cm | -0.54 | -0.54 | -0.54 | 0.48 | **0.97** |
| | >200 cm | -0.38 | -0.38 | -0.38 | -0.14 | **2.80** |
| Tree Height | <2 m | **1.90** | -0.01 | -0.40 | -0.38 | -0.41 |
| | 2-5 m | **1.57** | -0.02 | 0.04 | -0.41 | -0.54 |
| | 5-10 m | -0.69 | -0.60 | **1.83** | -0.03 | -0.53 |
| | 10-15 m | **-0.89** | **-0.89** | 0.26 | **0.72** | -0.11 |
| | 15-20 m | -0.62 | -0.62 | -0.55 | 0.48 | **1.26** |
| | 20-25 m | -0.37 | -0.37 | -0.37 | -0.20 | **3.03** |
| | 25-30 m | -0.31 | -0.31 | -0.31 | -0.18 | **2.58** |
| | >30 m | -0.18 | -0.18 | -0.18 | -0.18 | **1.84** |

(maximum height > 30 m) was called "***Tall Forest***" (Cluster 3) whereas closed canopy stands of lower maximum height (< 30 m) were distinguished by their growth density. "***Dense Forests***" (Cluster 4) with > 5 000 stems per hectare are significantly denser than "***Short Forests***" (Cluster 5) with < 5 000 stems per hectare.

All common properties within the stands of each group were analyzed by calculating t-values (BACKHAUS et al. 1996) for each biomass distribution class (Tab. 3.6). The analysis of these values showed that the *shrubland* vegetation is characterized by very thin and short individuals. No domination of any parameter could be found in the *open woodland* unit which combines two open but evidently different vegetation types. This class features merely an under-representation of thicker stems (girth 50 - 100 cm) and higher trees (> 10 m) which is both similar to the *shubland* unit. Only the very short and thin stems are missing. Forests of the *dense forest* unit are dominated by thin stems (girth 10 - 50 cm) and short trees (5 - 10 m) whereas forests of the *short forest* unit are characterized by slightly taller trees (10 - 15 m). No further unique characteristics could be observed for this unit. As it is the largest group ($n = 18$) uniting several different plots it is the least homogeneous showing highest variability between its constituents. *Tall forests* are dominated by large trees throughout.

## 3.2.2 Results of Biometrical Analysis

For each classified biometric unit the means and standard deviations of all plots contained were calculated. Characteristic properties of stand biometry were compared. The overall biometric data are documented in Tab. 9.23 in Appendix 9.2.3.1.

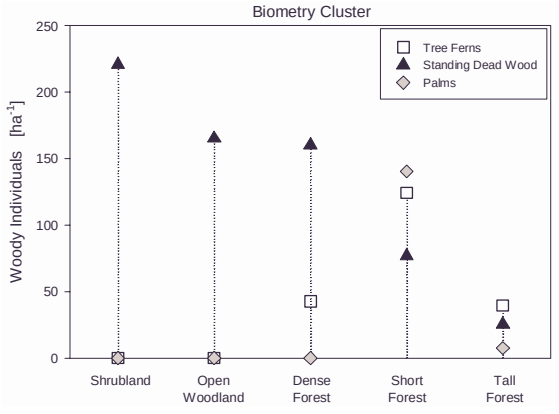



***Fig. 3.20: Means of non-tree woody individuals (palms, tree ferns) and standing dead wood plotted as individuals per hectare for each biometric unit.***

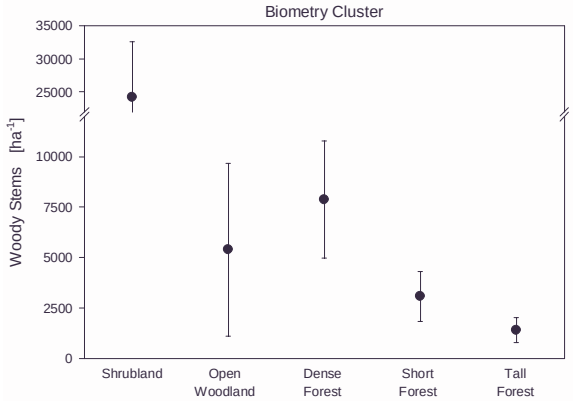



***Fig. 3.21: Growth density means (expressed in stems per hectare) plotted for each biometric unit with standard deviations.***

Woody individuals were recorded in four categories: Living trees, dead trees, palms and tree ferns (stand characters) in order to readily describe specific site conditions. Dead trees were excluded from biomass calculations because their wood density values and the contribution to the total above-ground biomass was uncertain. Fig. 3.20 shows the spectrum of all non-tree woody individuals including standing dead wood for each biometric unit. No tree ferns or palms were encountered in the *shrubland* and *open woodland* units, both of which have a very open canopy. However, these stands abound in standing dead woody individuals. The number of standing woody individuals is also high in the *dense forest* unit but tree ferns occur there as well. Most tree ferns and palms can be found in the *short forest* unit which has considerably less standing dead wood than *dense forests*. This unit is comprised of a large number of plots mostly within the upper hill area slopes and ravines, therefore variability is high. The number of palms may indicate moister site conditions. For *tall forests* with fairly moist climate it is not surprising that both dead wood as well as palm and tree ferns are present but only at low abundance since overall growth density is fairly low in this unit (Fig. 3.21). The lowest overall density of living woody individuals was found in *tall forests* and only the *shapumbales* in the *open woodland* unit can be compared to *tall forests* with respect to growth density. Growth density is significantly higher in *dense forests* and the highest density rates were found for *shrubland* with about 25 000 individuals per hectare.

Examination of tree growth patterns was done by plotting their diameter at breast height (dbh) against the respective tree height. Fig. 3.22 shows the scatter of values from 1 209 woody individuals. Most individuals were less than 20 m high and less than 30 cm thick at breast height. Heights of up to 35 m were recorded with stem thickness varying from 30 to 80 cm. Individuals of heights between 5 and 15 m covered the whole spectrum of stem thickness from 3 to > 80 cm. A common relation was calculated at $r^2 = 0.63$ but the overall scatter was great. Growth patterns in terms of the relationship between tree height and stem size were similar as the fits showed similar curvature (Fig. 3.23). However, stands could be divided roughly into three groups:

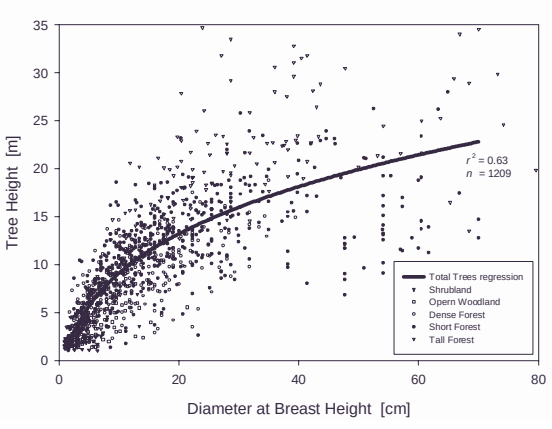



***Fig. 3.22: Regression fitted to the diameter at breast height vs. tree height plot for all 1 209 assessed trees > 1.3 m.***

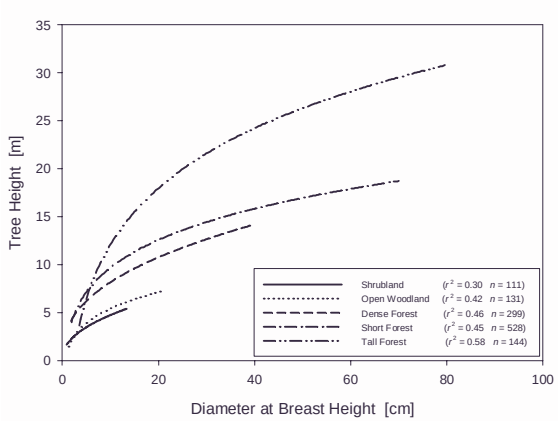



***Fig. 3.23: Regressions fitted to the diameter at breast height vs. tree height plots for each biometric unit.***

*Shrubland* and *open woodland* have low vegetation with fairly thick stems. *Dense* and *short forest* types developed taller trees at similar stem size. *Tall forests* had the tallest trees at similar dbh with *dense* and *short forest* but lacked very thin stems in their stands.

Mean diameter at breast height for all biometry units rises from the *shubland* (2.9 cm) continuously to *tall forests* (30.9 cm). Fig. 3.24 suggests that stem sizes (expressed as girth at breast height) for the *dense forest* remained quite uniform whereas the *short forest* showed very high variation. The fact that the *short forest* unit also includes all ravine forests which are rich in thick palms, like *Jessenia bataua*, may account for this high variability. A similar trend to mean stem sizes can be seen for tree heights of all biometric units (Fig. 3.25).

In order to visualize the distribution of biomass in terms of stem size the basal area was computed for each woody individual assuming circular cross-sections for each stem. Individuals were then divided into nine groups. According to Fig. 3.26 both *shrubland* and *open woodland* units abound in the smallest girth classes with the *shrubland* still significantly exceeding the *open woodland* with 22 900 vs. 4 100 stems per hectare of < 10 $cm^2$ basal area. Stem abundance for the *dense forest* also peaks in the smallest two basal area classes, yet this stand type features trees of all sizes and actually shows most trees of 100 - 200 $cm^2$ basal area over all units. Similar proportions were calculated for the *short forest*. Still, trees were distributed more evenly over all classes with the smallest class being far less dominant. In *tall forests* barely any thin trees were found and the overall stem abundance in *tall forests* was low and concentrated in the classes of 25 - 50 $cm^2$ and 100 - 250 $cm^2$ basal area.

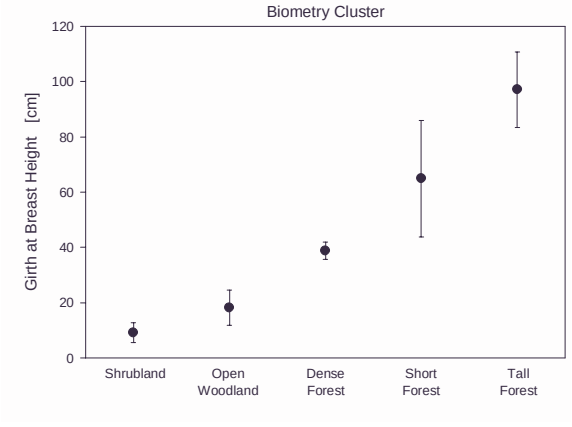



*Fig. 3.24: Girth at breast height means plotted for each biometric unit with standard deviations.*

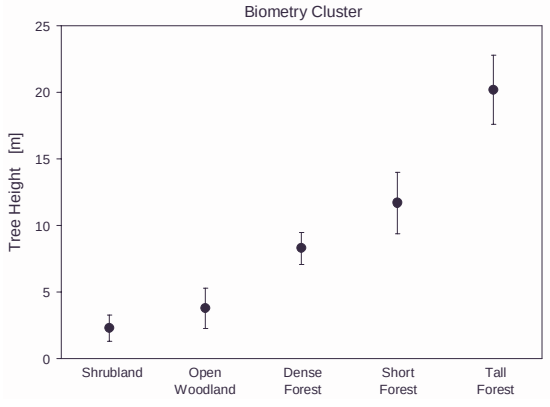



*Fig. 3.25: Tree height means plotted for each biometric unit with standard deviations*

A similar approach was taken for tree heights (Fig. 3.27). Eight height classes were formed. *Shrublands* were dominated by individuals < 2 m (13 900 individuals per hectare) whereas *open woodlands* had most individuals between 2 and 5 m in height. In both units no trees > 10 m were recorded. In the *dense forest* the tallest trees were 15 - 20 m, trees 5 - 10 m were most abundant, and trees < 2 m hardly existed. In the *short forest* the tallest trees reached heights of 25 - 30 m, but most trees (especially palms) were only 5 - 10 m high. In *tall forests* no trees < 2 m were recorded and trees of heights 5 - 20 m were quite evenly distributed. Tallest individuals exceeded 30 m in height.

A measure integrating stem abundance and density is the basal area for an entire stand (Fig. 3.28). On this basis only *shrubland* and *open woodland* (< 10 $m^2$ per hectare) could be distinguished significantly from all other units (> 20 $m^2$ per hectare).

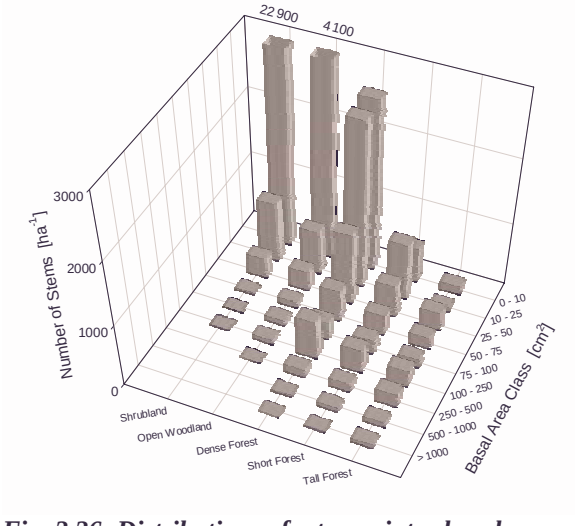



*Fig. 3.26: Distribution of stems into basal area classes for the classified biometric units.*

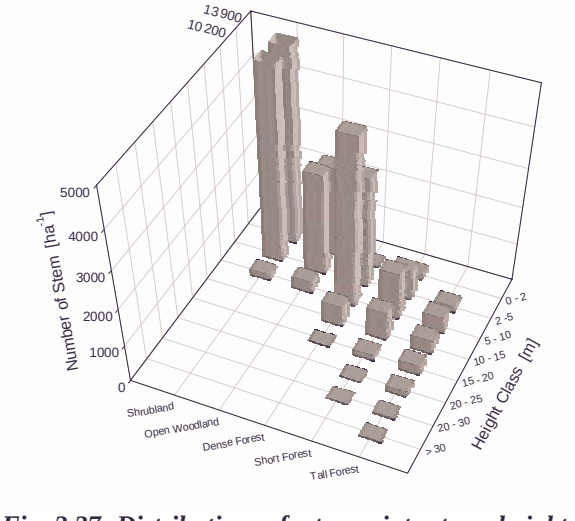



*Fig. 3.27: Distribution of stems into tree height classes for the classified biometric units.*

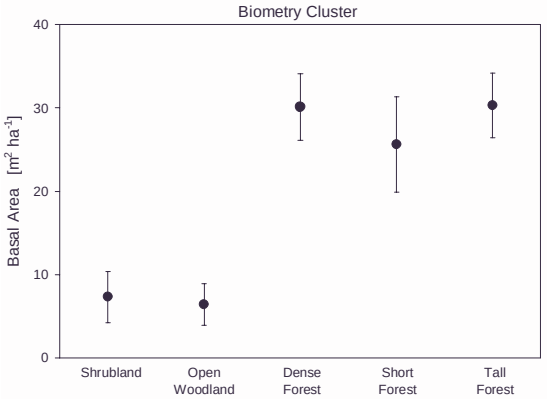



*Fig. 3.28: Basal area means with standard deviations of the biometric units.*

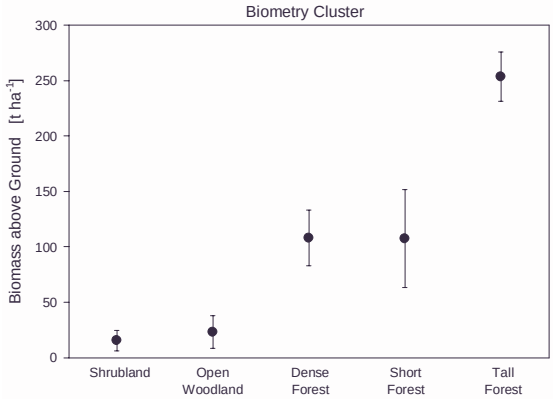



*Fig. 3.29: Standing above ground biomass means with standard deviations of the biometric units*

Total above-ground biomass was calculated as the most comprehensive parameter for each stand (Fig. 3.29). *Shrubland* and *open woodland* were lowest in biomass (both < 50 t per hectare). The *dense* and *short forests* showed values quite similar to each other (slightly > 100 t per hectare), but variability was high within the *short forest* unit. The variability can be ascribed to an abundance of palm trees in many ravine sites which are relatively low in biomass. Biomass of the *tall forest* generally exceeded 250 t $ha^{-1}$.

## 3.2.3 Description

The following chapter briefly summarizes and discusses the most conspicuous characteristics of each classified biometric unit and their relation to soil nutrient status.

### 3.2.3.1 Biometry Units

**Tall Forest** (Valley)

*Tall forests* were confined to the level river plains and terraces found in wider valleys. These valleys were formed by larger rivers than the one existing within the upper hill area. The tallest individuals (40.5 m) as well as some of the thickest trees (diameter 70 cm) were found in these forests whereas very short individuals (< 2 m) were rare and only very few thin stems (< 25 $cm^2$ basal area) were recorded. This indicates competition for light under favorable growth conditions in terms of slope, moisture regime, and nutrient availability. In spite of the lowest stem density overall (averaging 1 404 stems per hectare), the highest biomass stocks were developed in these forests (253 t per hectare). Also, the highest rate of tree ferns was encountered in these forests.

**Short Forest**

The *short forest* unit is by far the largest group in terms of documented plots that are included. These forests were typically found on lower slopes or bottoms of ravines under various soil moisture and nutrient conditions but also on less exposed upper slopes and ridges. This unit combined a large variety of stands. For example the stand featuring the largest individual (dbh 144 cm, height 37.4 m) and an above-ground biomass of 197 t per hectare was assigned to this unit as well as the stand with the highest palm abundance (1 515 individuals per hectare). Low biomass developed by palms accounted for the low biomass stock of 107.6 t per hectare. Tree ferns were also found frequently indicating rather moist and cool stand conditions. Mean tree diameter was highly variable in the *short forest*, but lower than in the *tall forest* and higher than in the *dense forest*. This was also caused by the large number of thick palms dominating waterlogged sites. On average, tree height was significantly lower than in the *tall forest* but in some cases exceeded 20 m.

**Dense Forest**

*Dense forests* are typically found on well drained and nutrient poor upper slopes and ridges which are both well exposed to intense radiation. No palms and only few tree ferns were recorded. Stands of this unit are rather uniform in terms of biomass allocation. They are characterized by a high growth density of 7 900 stems per hectare which is more than twice as much as in the *short forest*. These stands were dominated by thin stems (basal area < 25 $cm^2$), and trees did not reach 20 m in height. The overall mean biomass of 108.1 t per hectare was comparable to biomass stocks of *short forests* (107.6 t $ha^{-1}$).

**Open Woodland** (Shapumbal & Open Chamizal)

The *open woodland* unit combines two very distinct vegetation types which shared an open canopy (expressed by low values for basal area) without palms and tree ferns and only few trees taller than 5 m. However, *shapumbales* were only encountered on steep upper slopes on Quaternary-Pleistocene substrate. Trees reached no more than 10 m in height. Growth density was low at 600 - 2 300 stems per hectare compared to the *chamizal* plots and relatively higher in standing dead wood yielding biomass values between 20 and 50 t per hectare. On the other hand, *chamizales* were restricted to the better drained rims of level plateaus of Quaternary-Holocene origin. Vegetation rarely exceeded 5 m in height and reached growth densities of up to 13 500 stems per hectare. Biomass values were low at 7 - 27 t per hectare.

**Shrubland** (Dense Chamizal)

The most conspicuous vegetation type found in the study area is classified here as *shrubland*. Like the *chamizales* represented in the *open woodland* unit, the *shrubland* occurred only on level plateaus formed by Quaternary-Holocene sediments but under waterlogged conditions. This formation was characterized by a dense cover of up to 36 200 short, shrub-like individuals per hectare of heights less than 10 m. Above-ground biomass was low with an average of 15.6 t per hectare.

### 3.2.3.2 Summary

*Shrublands* were easily identified for their dense cover with thin stems in the shrub layer. However, *shapumbales* and *chamizales* of more open nature were combined in the *open woodland* unit based on their similar stand characteristics: open canopy and short trees of height < 10 m. Biomass was also fairly similar for both types.

*Dense forests* were found on well drained and nutrient poor ridges of different slopes throughout the study area. They were characterized by low-statured trees and dominated by a dense growth of thin individuals. However, biomass was not significantly lower than in *short forests*.

*Short forests* represented the largest cluster combining a wide variety of stands within the study area. Therefore, due to this high variation among the plots contained, it was difficult to characterize these stands well. *Barranco* vegetation, rich in palms and low in stem density, is included as well as plots from ridges and slopes of different stand height, growth density and composition of stand characters.

*Tall forests* featured highest biomass stocks allocated in tall and thick trees but at low stand density. They are found not only near rivers but also in broad valleys or on terraces of only gentle inclination. All sites were well drained and provided with phosphorus and nitrogen in the mineral soil.

### 3.2.3.3 Statistical Evaluation

The units could be roughly divided into three groups based on their living above-ground biomass (Fig. 3.30). *Shrubland* and *open woodland* units represent the lowest stands which are also lowest in biomass. Medium values for biomass were calculated for both *dense* and *short forest* types from the upper hill area although the *dense* version showed lower stand height. *Tall forests* were highest in biomass.

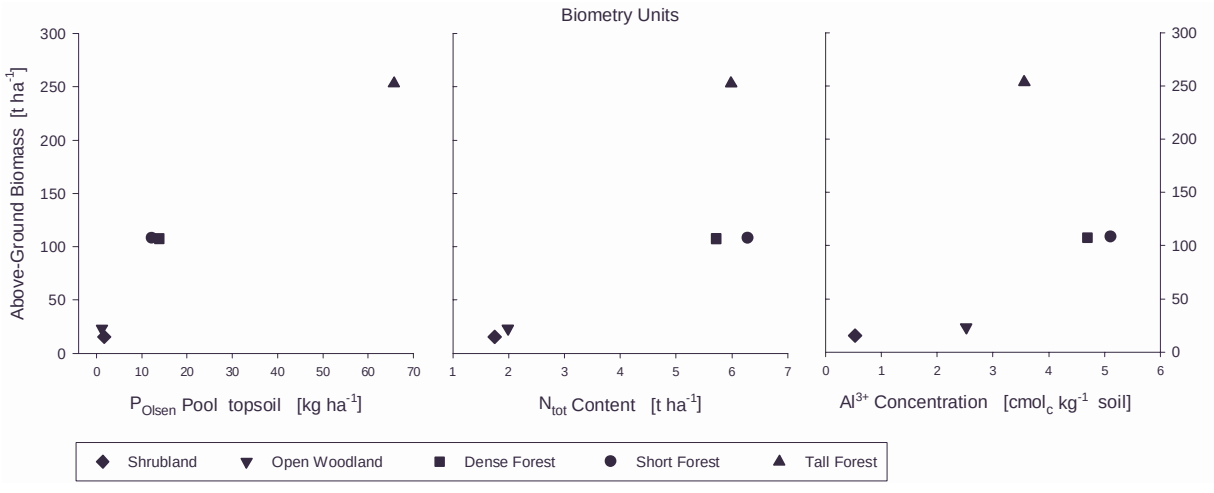



***Fig. 3.30: Relation between soil chemistry and biomass for the respective biometry units.***
*Plotted are soil nutrient pools of plant-available phosphorus and total nitrogen, and the total concentration of exchangeable aluminum ($Al^{3+}$) against the biomass values calculated for the stands of each biometry unit. Variability for the values given is high throughout.*

Fig. 3.30 shows soil parameters most likely to influence plant growth. No toxic effects of aluminum were indicated since aluminum concentrations did not show an inverse relationship with biomass. However, the nutrients and phosphorus showed a similar correlation with plant growth. Phosphorus seems most likely to be the limiting factor since nitrogen supply in all "*forests*" is similar yet only the combination of high phosphorus and nitrogen supply seems to permit the development of high biomass as in *tall forests*. Vegetation of *shrubland* and *open woodland* must obviously receive their share of phosphorus and nitrogen largely from the organic layer since supply of these nutrients in the mineral soil is minute.

Statistical analysis of the biometry clusters revealed that soil parameters were not sufficient to distinguish equally between all units. However, the application of strictly structural parameters also lead to a reasonable differentiation (cf. One-Way ANOVA results in Appendix 9.2.2.4).

***Tab. 3.7: Significant Spearman's correlation coefficients (values $> |0.7|$) between soil parameters and structural parameters assessed in the upper hill area of the Rio Avisado.***

| Vegetation Parameter | Soil Parameter | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $CEC_{eff}$ topsoil | C/N topsoil | pH topsoil | $Mg^{2+}$ conc. subsoil | $P_{Olsen}$ pool topsoil | $K^+$ conc. subsoil | $K^+$ pool subsoil | Thickness undecom-posed | Thickness organic horizons |
| Girth Median | **-0.75** | **-0.78** | | | | | | | |
| Girth Mean | **-0.76** | **-0.80** | | | | **0.71** | **0.70** | | |
| Height Median | **-0.77** | **-0.83** | **0.72** | **0.72** | **0.73** | **0.72** | **0.70** | **-0.70** | **-0.74** |
| Height max | **-0.74** | **-0.82** | | | **0.70** | | | | **-0.73** |
| Biomass $ha^{-1}$ | **-0.73** | **-0.79** | **0.74** | | **0.72** | | | | |
| Basal area 500-1000 $cm^2$ | **-0.70** | | | | | | | | |
| Basal area 1000-2000 $cm^2$ | | | | **0.74** | | | | | |
| Leaf 225 $cm^2$ layer1 | | **-0.76** | | | | | | | |

*Tab. 3.8: Comparison of all classified biometric units in respect to tree height, diameter at breast height, basal area, stem density, biomass and stand characters.*

| | Stand Biometry | | | | | | | Stand Characters | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Biometric Unit | Tree Height Mean | Tree Height Max | Diameter Mean* | Basal Area | Amount Stems** total | Amount Stems** > 10 cm gbh | Bio-mass*** | Stand. Dead Wood | Palms | Tree Ferns |
| | m | | cm | $m^2\ ha^{-1}$ | $ha^{-1}$ | | $t\ ha^{-1}$ | $ha^{-1}$ | | |
| **Shrubland** | 2.3 | 4.1 | 2.9 | 7.3 | 24219 | 1396 | 15.6 | 221 | 0 | 0 |
| **Open Woodland** | 3.8 | 6.2 | 5.8 | 6.4 | 5391 | 1495 | 23.1 | 165 | 0 | 0 |
| **Dense Forest** | 8.3 | 14.7 | 12.3 | 30.1 | 7871 | 5276 | 108.1 | 160 | 0 | 42 |
| **Short Forest** | 11.7 | 20.3 | 20.7 | 25.6 | 3070 | 2575 | 107.6 | 77 | 140 | 124 |
| **Tall Forest** | 20.2 | 35.7 | 30.9 | 30.3 | 1404 | 1404 | 253.3 | 25 | 8 | 39 |

* = Derived from girth measurements at breast height (1.3 m)
** = Calculated using the angle count method after BITTERLICH (1984)
*** = Calculated using own biomass harvest combined with calculations after OGAWA (1965)

On plot basis, biometric results correlated positively with soil parameters only for phosphorus which is considered a macro-nutrient and thus may well influence plant growth (cf. Tab. 3.7). Strong negative correlation effects were found for topsoil C/N and effective cation exchange capacity ($CEC_{eff}$). The C/N ratio is a measure for microbial activity in the soil and consequently for mineralization dynamics. Low C/N ratios imply high microbial activity and therefore a rapid nutrient cycling. In this case, $CEC_{eff}$ includes protons ($H^+$) and $Al^{3+}$ ions which contributed most to the $CEC_{eff}$ in the studied soils. Thus, high values of $CEC_{eff}$ also suggest highly acidic conditions and / or high aluminum saturation which are both considered unfavorable for plant growth.

An overview of biometric parameter means is given in Tab. 3.8 for all units.

***Tab. 3.9: Assessed parameters and their "Measure of Sampling Adequacy" (MSA) expressing their suitability for Principal Component Analysis. All parameters listed were selected to represent the individual plots in a Principal Component Analysis.***
*The parameters are divided into three categories: Soil properties, biometric properties and structural properties.*

| Soil | | | Biometry | | | Structure | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Parameter** | **Code** | **MSA** | **Parameter** | **Code** | **MSA** | **Parameter** | **Code** | **Layer** | **MSA** |
| $Al^{3+}$/ CEC ratio subsoil | ALCE_SS | **0.904** | Height stand. dev. | HCOR_STD | **0.898** | Leaf 4 $cm^2$ layer1 | BL2CM1 | 1 | **0.871** |
| $Fe^{3+}$ conc. topsoil | FEC_SS | **0.903** | Cover layer2 | COVLAY2 | **0.886** | Number of layers | LAYNO | total | **0.847** |
| C/N ratio topsoil | CN_TS | **0.889** | Stems $ha^{-1}$ | STEM_HA | **0.877** | Moss abundance | MFVIEL2 | 2 | **0.781** |
| $Al^{3+}$ conc. subsoil | ALC_SS | **0.872** | Height mean | HCOR_MEN | **0.863** | Leaf 50 $cm^2$ layer3 | BL7CM3 | 3 | **0.751** |
| Clay subsoil | CLAY_SS | **0.853** | Diameter median | DIAM_MED | **0.858** | Liana abundance | LIVIEL1 | 1 | **0.735** |
| $K^+$ pool subsoil | KP_SS | **0.835** | Height layer1 | HITELAY1 | **0.855** | - | - | - | - |
| $K^+$ pool upper 20 cm | KP_20 | **0.829** | Height max | HCOR_MAX | **0.853** | - | - | - | - |
| pH topsoil | PH_TS | **0.786** | Basal area | BAS_AREA | **0.838** | - | - | - | - |
| $Al^{3+}$ conc. topsoil | ALC_TS | **0.784** | Biomass $ha^{-1}$ | BMEX_HA | **0.837** | - | - | - | - |
| pH total pit | PH_TOT | **0.775** | Diameter mean | DIAM_MEN | **0.821** | - | - | - | - |
| $N_{tot}$ conc. subsoil | NC_SS | **0.762** | Height layer2 | HITELAY2 | **0.819** | - | - | - | - |
| pH subsoil | PH_SS | **0.759** | Canopy cover | PLOTCOV | **0.800** | - | - | - | - |
| C/N ratio total pit | CN_TOT | **0.672** | Diameter max | DIAM_MAX | **0.781** | - | - | - | - |
| - | - | - | Height layer3 | HITELAY3 | **0.723** | - | - | - | - |

**Overall KMO-Value for 32 Parameters: 0.825 = "*respectful*"**

## 3.3 Combined Approach

Topography often influences pedogenesis and conditions of stand microclimate which in turn affect the composition of vegetation. In order to elucidate relationships between soil and vegetation, which are associated with topographical properties, all recorded parameters of stand structure were combined with parameters describing the biomass distribution of the stands and characteristic soil parameters. If such correlations existed, the third null-hypothesis could be rejected.

### 3.3.1 Statistical Classification

For each plot data were available in form of 282 parameters from three categories: soil texture and chemistry (edaphic condition), biomass distribution (biometric data), and vegetation structure. The dataset was prepared to contain only mutually independent variables by Principal Component Analysis. This was required for subsequently submitting the data to a Hierarchical Cluster Analysis. Tests were performed to identify highly suitable parameters for Principal Component Analysis. All variables with a computed "Measure of Sampling Adequacy" (MSA) of less than 0.7 are considered "mediocre" on the KAISER scale (cf. Tab. 2.10 in chapter 2.3.2.2) and were excluded from further analysis. The initial dataset was reduced to 32 parameters listed in Tab. 3.9. All three categories: edaphic conditions, biometric characteristics and structure parameters were still represented. The achieved KAISER-MEYER-OLKIN (KMO) value of 0.825 for the factor model rated it "respectful" according to KAISER & RICE in BACKHAUS et al. (1996). Four factors were extracted using the KAISER criterion and were then VARIMAX rotated (see regression

***Tab. 3.10: Eigenvalues of the four factors extracted by Principal Component Analysis.***

*The four mutually independent factors together explain over 79 % of the variance within the dataset. Factors from Principal Component Analysis were extracted to be mutually independent, iteratively explaining a maximum of the variance within a dataset in a multidimensional space. Since variables were Z-standardized to a mean of 0 and a standard deviation of 1 before analysis each variable therefore has a variance of 1. Consequently a factor with an eigenvalue of < 1 is not significant since it describes less variance within the dataset than there is within each variable itself. For this reason only factors with an eigenvalue of > 1 are considered. Rotation of the factors in space (with their relative position to each other maintained) apportions the explained variance more evenly to the factors.*

| | Initial Eigenvalues | | | Rotated Values | | |
|---|---|---|---|---|---|---|
| FACTOR | Total | Variance explained | Cumulative | Total | Variance explained | Cumulative |
| | | % | | | % | |
| **1** | 18.6 | 58.2 | 58.2 | 8.3 | 26.0 | 26.0 |
| **2** | 3.0 | 9.5 | 67.7 | 7.1 | 22.2 | 48.2 |
| **3** | 2.4 | 7.6 | 75.2 | 6.8 | 21.1 | 69.4 |
| **4** | 1.3 | 4.0 | 79.2 | 3.2 | 9.9 | 79.2 |

values for factor scores in Tab. 9.10 in Appendix 9.2.2.1). The resulting four factors together explained over 79 % of the total variance in the data set (Tab. 3.10).

Examination of factor loadings (Tab. 9.11 in Appendix 9.2.2.2) suggested that only factor 3 clearly represented one certain category of parameters. Only soil parameters loaded high on this factor. Biometry parameters were of minor importance to the composition of factor 4.

As expected for factors of a Principal Component Analysis the first factor loaded high on only few parameters, but from all categories. The parameters a) potassium in the subsoil, b) tree diameter and c) layering of the stands appeared suitable to express the majority of the variance within the dataset. Structural parameters describing layering, epiphyte situation and canopy quality combined with biomass and growth density characterized factor 2. Factor 3 was loaded exclusively with soil characteristics. Epiphytes and soil pH influenced factor 4 the most.

Regressional scores of all four factors which had been extracted by Principal Component Analysis were subsequently submitted to a Hierarchical Component Analysis. Outliers were first identified by Hierarchical Component Analysis using the Single Linkage method (Fig. 9.4 in Appendix 9.2.2.2). Three plots were excluded by this criterion (P11, 12, and 41). Data for the

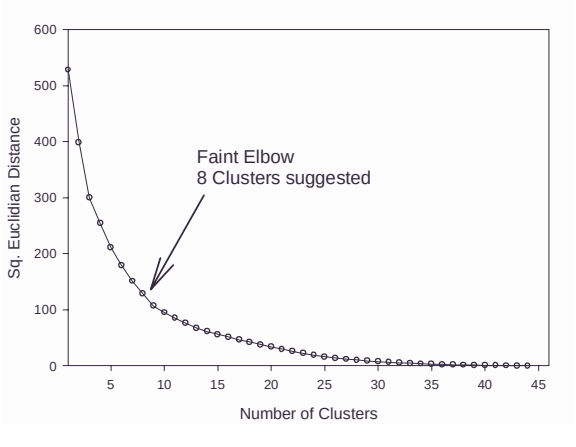



***Fig. 3.31: Combined analysis: Number of clusters plotted against the employed distance measure: squared Euclidean distance (BACKHAUS et al. 1996).***

*The initial cluster solution is marked by an "elbow" in the line where the distance between each additional cluster does not increase significantly any more.*

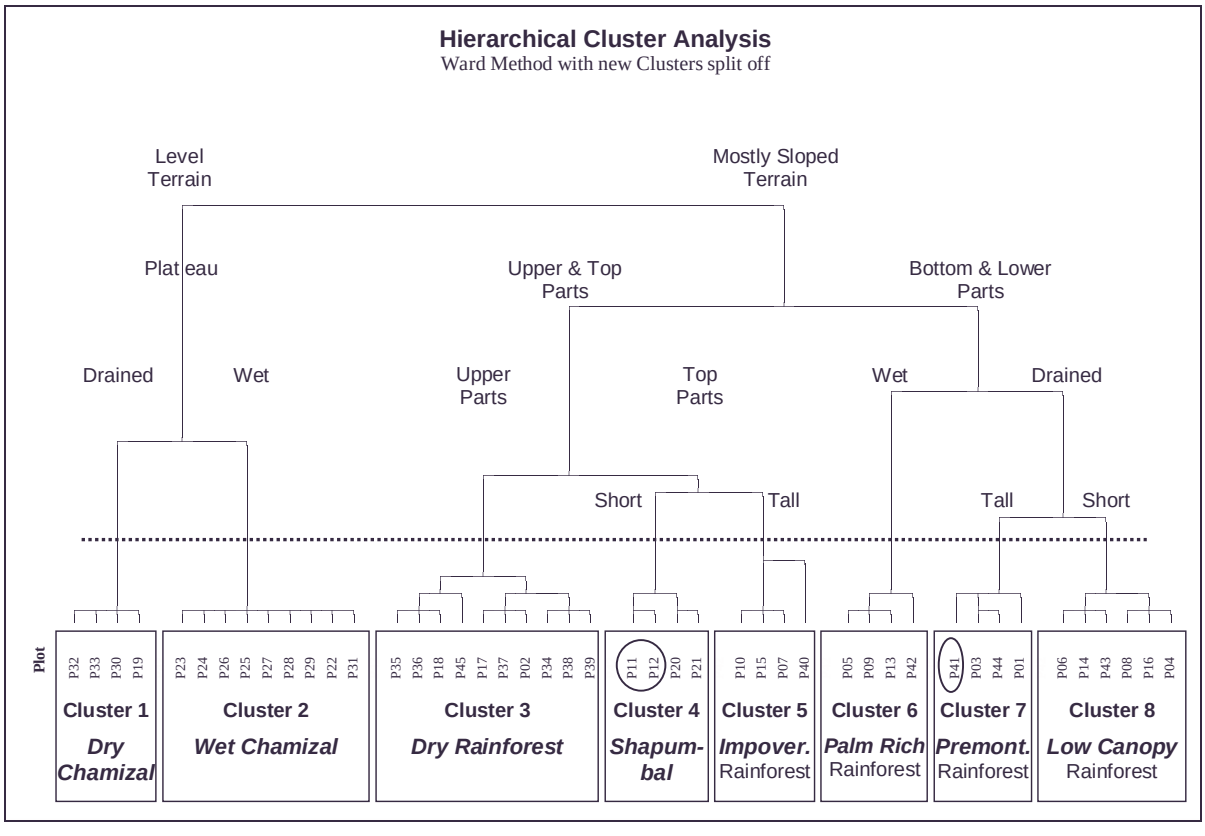



***Fig. 3.32: Dendrogram generated by Hierarchical Cluster Analysis using Ward's Method.***
*Three outlier plots were re-integrated into the clusters based on their similar properties.*
*The outlier plots P11, 12, and 41 of the initial statistical analysis are encircled.*
*Distinction of clusters was confirmed by statistical analysis (cf. ANOVA-Analysis) on the basis of topographic and moisture situation of the sites, and stand height.*

remaining 42 plots were clustered using Ward's method. The "elbow" criterion was used to decide on the number of final clusters. Eight clusters were suggested (

Fig. 3.31), however, after further analysis of the cluster dendrogram only six clusters were chosen (cf. Fig. 9.5 in Appendix 9.2.2.2). A separation into eight clusters would have resulted in plot P40 representing a single cluster. This plot had previously not been identified as outlier and therefore interpretation of this cluster solution was limited. The seventh cluster was essentially composed of *premontane rainforest* plots but merged with the neighboring cluster on a similar level as plot P40. Eventually, this cluster was split off from the super-ordinate arrangement *post-hoc* (Fig. 3.32).

Investigation of common structural properties within each group was conducted by calculating t-values (BACKHAUS et al. 1996) for each parameter (see Tab. 9.12 - Tab. 9.19 in Appendix 9.2.2.3 for tabled t-values). Three outlier plots were *post-hoc* assigned to the cluster to which they showed greatest similarity. Fig. 3.32 shows the cluster combination of the modified dendrogram where re-integrated outliers are marked by circles. Clusters 1 and 3 as well as clusters 5 and 6 had been separated out of one initial cluster based on different morphological

***Tab. 3.11: Terrain inclination, elevation above sea level, and slope exposition as used to characterize the topographical situation for the classified units.***
*Units are arranged by their position within the hill area from top to bottom. Standard deviations are given in parentheses.*

| Vegetation Unit | Inclination | | Elevation | | Exposition | |
|---|---|---|---|---|---|---|
| | ° | | m | | ° | |
| **Wet Chamizal** | **0** | (1) | **985** | (16) | **9** | (28) |
| **Dry Chamizal** | **2** | (2) | **985** | (16) | **210** | (113) |
| **Impoverished Rainforest** | **17** | (16) | **961** | (51) | **98** | (89) |
| **Shapumbal** | **29** | (9) | **977** | (8) | **193** | (134) |
| **Dry Rainforest** | **20** | (13) | **1063** | (97) | **253** | (76) |
| **Low Canopy Rainforest** | **17** | (8) | **972** | (17) | **201** | (88) |
| **Palm Rich Rainforest** | **10** | (2) | **971** | (15) | **138** | (72) |
| **Premontane Rainforest** | **13** | (9) | **1013** | (12) | **156** | (57) |

properties of the stands (e. g. stand height). All analytical steps can be reproduced with dendrograms in Fig. 9.4 and Fig. 9.5 in Appendix 9.2.2.2.

The cluster combinations could be explained by the topographic position of the combined plots. Two groups could be found on level terrain (inclination < 5°) which could be identified as plateau position from field observations. This branch splits into the *"**Dry Chamizal**"* (Cluster 1) on drained sites and the *"**Wet Chamizal**"* (Cluster 2) on sites frequently affected by stagnant water. For groups on sloped terrain (inclination > 5°) it was again possible to ascribe them to specific topographic positions in the next step. Plots from upper slopes were combined in the *"**Dry Rainforest**"* (Cluster 3) whereas plots encountered on the top parts of slopes were further divided into short stands of maximum tree heights < 10 m which corresponded to *"**Shapumbales**"* (Cluster 4) and taller stands with tree heights > 10 m which represented the *"**Impoverished Rainforest**"* (Cluster 5). Plots found on lower slopes and valley bottoms were also distinguished further. Plots on wet sites characterized the *"**Palm Rich Rainforest**"* (Cluster 6). Drained sites featured tall stands with trees > 30 m in height and were combined in the *"**Premontane Rainforest**"* (Cluster 7) whereas the cluster containing plots of lower stand height (< 30 m) was termed *"**Low Canopy Rainforest**"* (Cluster 8).

## 3.3.2 Results of Combined Analysis

The rationale for this classification approach was to identify possible topographic factors controlling the development of different forest types. Tab. 3.11 lists mean values of the recorded topographical parameters a) slope of terrain (inclination), b) elevation above sea level and c) exposition for the units classified by this approach. Little significant information could be derived from this analysis. Both *chamizal* types are found on least inclined sites, whereas slopes of *shapumbal* sites are steepest. Slopes of *palm rich rainforest* sites are most consistent and slopes of *impoverished rainforest* sites most variable since these include steep to level sites. It may also be noted that *premontane rainforests* are not necessarily restricted to level terrain.

Results of the combined analysis will be presented separately for soil, biomass and structural characteristics of the units which were chosen.

### 3.3.2.1 Soil

Within each classified unit, means and standard deviations were calculated for all plots contained. Characteristic soil properties were compared between units.

In terms of soil texture the *palm rich rainforest* featured the highest proportion of clay in the topsoil and highest silt and lowest sand in the subsoil (Fig. 3.33 and Fig. 3.34). Relatively high subsoil clay contents were found in *impoverished rainforests* and in *shapumbales*. Subsoils in the *premontane rainforests* contained up to 50 % sand. *Dry chamizales* contained the highest proportion of sand in the topsoil and were almost exclusively made up of sand in the subsoil. Topsoil texture composition for *wet chamizales* was average although the high organic matter content may have disguised higher sand content as discussed in chapter 3.1.2. Subsoils of *wet chamizales* were also rich in sand.

Soil pH was in the aluminum buffer range (between 3.5 and 4.5) for most topsoils and subsoils (Fig. 3.35). The only exceptions were *wet chamizales* and the topsoil of *dry chamizales.*

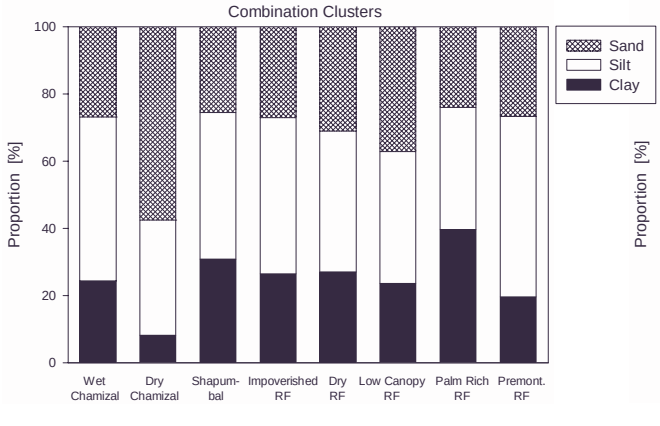



*Fig. 3.33: Topsoil texture composition of the fractions sand, silt, and clay of the classified units of the study area.*

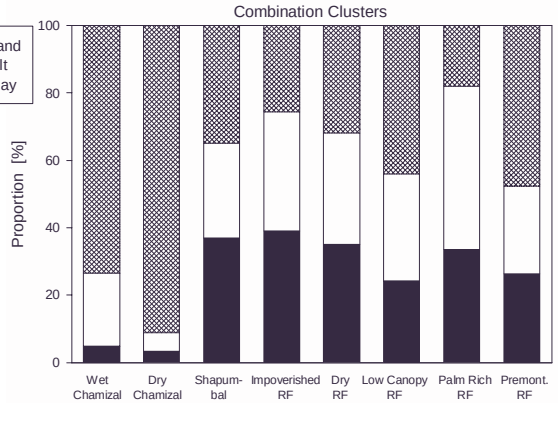



*Fig. 3.34: Subsoil texture composition of the fractions sand, silt, and clay of the classified units of the study area.*

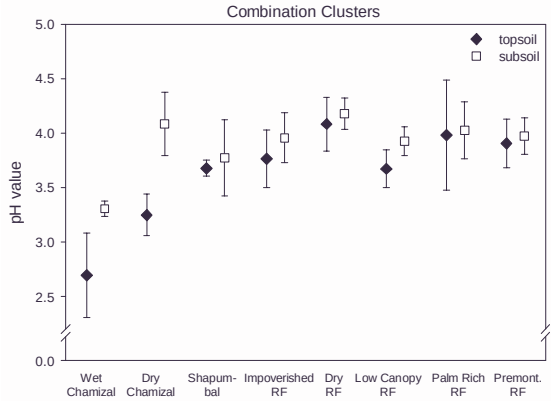



*Fig. 3.35: The pH values in the classified units.*

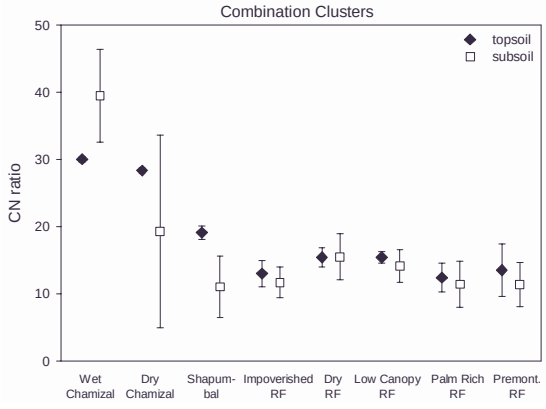



*Fig. 3.36: Distribution of C/N ratio in the classified units of the study area.*

For *chamizales* a large discrepancy between lower topsoil and higher subsoil pH was observed. However, the pH of *dry chamizales* was always higher than of *wet chamizales* which is a clear effect of high concentrations of organic acids involved.

The C/N ratios showed high and consistent values of approx. 30 for the topsoils of both *chamizal* types (Fig. 3.36). It is remarkable that C/N ratios for *wet chamizales* were even wider at approx. 40 in the subsoil, whereas subsoils of the dry types featured narrower but highly variable C/N ratios of approx. 20. Also, C/N ratios for topsoil and subsoil of *shapumbal* soils differed significantly as it was observed previously.

Carbon ($C_{tot}$) concentrations were always significantly higher in topsoil than in subsoil, except on lower slopes (Fig. 3.37). Variation was highest for $C_{tot}$ in topsoils of the *premontane rainforests* and lowest in the *low canopy rainforest*. Highest $C_{tot}$ concentrations in the subsoil were found for the *dry rainforests* where podzols were present and in the topsoil for *wet chamizales*. Subsoil carbon pools were highest in both *dry* and *low canopy rainforests* which might not only indicate

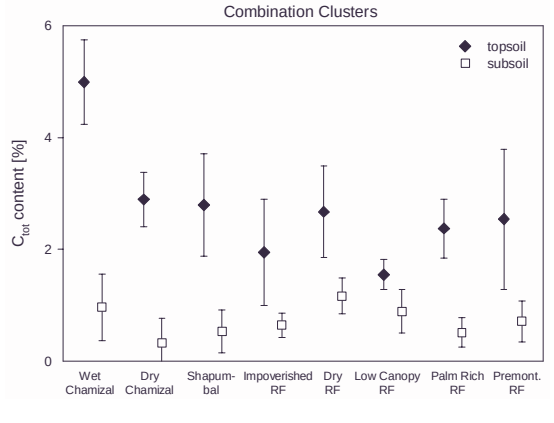



*Fig. 3.37: Distribution of $C_{tot}$ concentration in the respective classified units.*

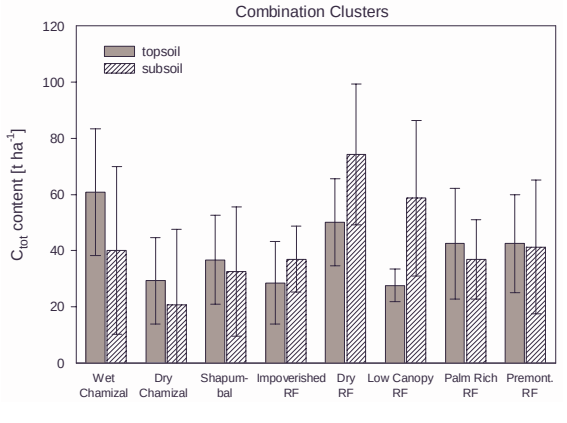



*Fig. 3.38: Distribution of $C_{tot}$ pools in the respective classified units.*

*Values for each soil pit are means weighted for horizon thickness. Displayed are means and their standard deviation for each soil unit.*

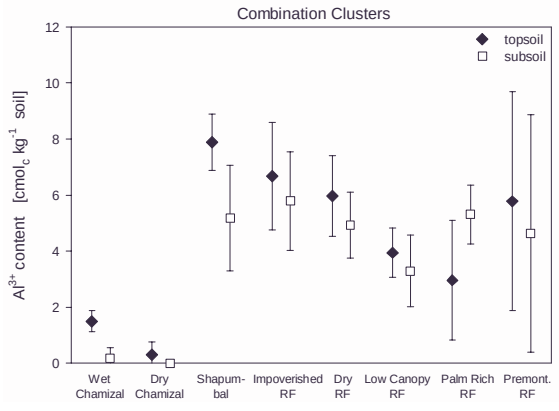



***Fig. 3.39: Distribution of exchangeable $Al^{3+}$ concentration.***

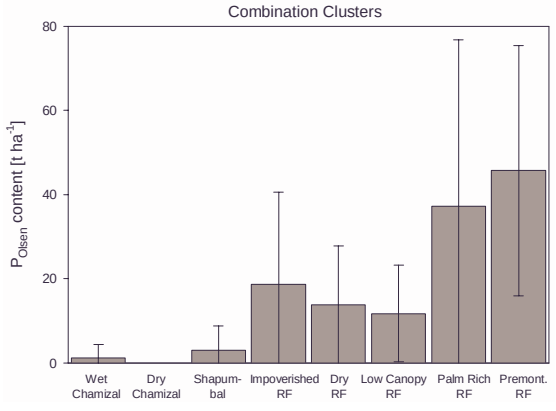



***Fig. 3.40: Distribution of $P_{Olsen}$ pools in the topsoil.***

the presence of podzols but also that buried organic horizons existed after mass transport (landslides). Highest topsoil C-pools were calculated for *wet chamizales* with profound organic horizons (Fig. 3.38).

Concentrations of exchangeable aluminum ($Al^{3+}$) were lowest in the *heath forests* (Fig. 3.39). Highest concentration in the topsoils were calculated for *shapumbales*. A slight trend for rising $Al^{3+}$ concentrations in the topsoil with rising position on the slope can be observed. Variation for $Al^{3+}$ concentration is high throughout all non-*chamizal* units, especially in the *premontane rainforest*. Therefore, no predictions can be made for these units in terms of aluminum status.

Pools of plant-available phosphorus are shown for topsoils in Fig. 3.40. Again, variation is high. Classified units can be divided into three different groups: Most phosphorus is found in *premontane rainforest* and *palm rich rainforest* soils. Some phosphorus is available in soils on the slopes under low *canopy*, *dry* and *impoverished rainforest*. Lowest pools were calculated for

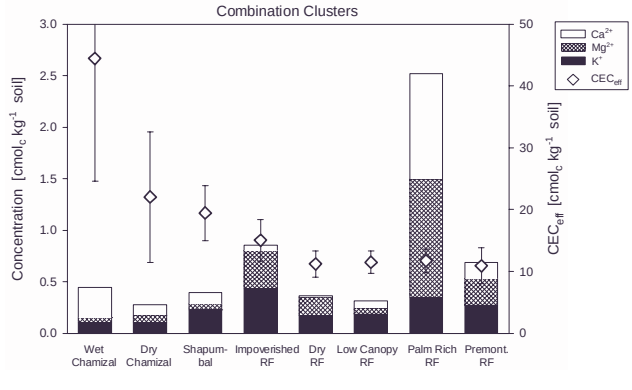



***Fig. 3.41: Topsoil contribution of the exchangeable portion of bases ($K^+$, $Ca^{2+}$, and $Mg^{2+}$) to the effective cation exchange capacity ($CEC_{eff}$).***

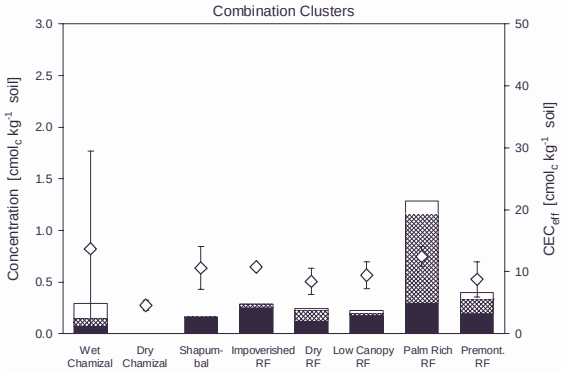



***Fig. 3.42: Subsoil contribution of the exchangeable portion of bases ($K^+$, $Ca^{2+}$, and $Mg^{2+}$) to the effective cation exchange capacity ($CEC_{eff}$).***

*Values for each soil pit are means weighted for horizon thickness. Displayed are means and their standard deviation for each soil unit.*

***Tab. 3.12: Comparison of all classified units by the combined approach in respect to thickness of topsoil, pH, and nitrogen, phosphorus and potassium pools and concentrations.***

| | Thickness | pH | | $N_{tot}$ | | | | | $K_2O$* | | | | | $P_2O_5$** | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | pool | | | concentration | | pool | | | concentration | | pool | conc. |
| | | | | t $ha^{-1}$ | | | % | | kg $ha^{-1}$ | | | $cmol_c$ $kg^{-1}$ soil | | kg $ha^{-1}$ | ppm |
| | topsoil | topsoil | subsoil | upper 20 cm | subsoil | total | topsoil | subsoil | upper 20 cm | subsoil | total | topsoil | subsoil | upper 20 cm | topsoil |
| **Wet Chamizal** | 19 | 2.7 | 3.3 | 1.8 | 0.0 | 1.8 | 0.16 | 0.01 | 28 | 0 | 28 | 0.10 | 0.00 | 1 | 1 |
| **Dry Chamizal** | 12 | 3.3 | 4.1 | 0.9 | 0.1 | 0.9 | 0.10 | 0.00 | 21 | 0 | 21 | 0.11 | 0.00 | 0 | 0 |
| **Shapumbal** | 11 | 3.7 | 3.8 | 1.9 | 1.7 | 3.0 | 0.15 | 0.03 | 168 | 412 | 494 | 0.23 | 0.16 | 3 | 3 |
| **Impoverished Rainforest** | 14 | 3.8 | 4.0 | 2.3 | 2.7 | 4.7 | 0.15 | 0.05 | 320 | 578 | 835 | 0.43 | 0.25 | 19 | 8 |
| **Dry Rainforest** | 14 | 4.1 | 4.2 | 3.4 | 4.7 | 7.1 | 0.18 | 0.07 | 130 | 292 | 386 | 0.17 | 0.12 | 14 | 10 |
| **Low Canopy Rainforest** | 12 | 3.7 | 3.9 | 1.9 | 3.9 | 5.1 | 0.11 | 0.06 | 141 | 447 | 536 | 0.19 | 0.18 | 12 | 8 |
| **Palm Rich Rainforest** | 17 | 4.0 | 4.0 | 3.5 | 2.9 | 6.3 | 0.19 | 0.04 | 276 | 710 | 953 | 0.35 | 0.29 | 33 | 10 |
| **Premontane Rainforest** | 16 | 3.9 | 4.0 | 3.0 | 3.5 | 6.1 | 0.19 | 0.06 | 191 | 402 | 587 | 0.27 | 0.19 | 46 | 28 |

* = $NH_4NO_3$-Extraction ** = $NaHCO_3$- Extraction

*shapumbales* and *wet chamizales*. *Dry chamizales* are virtually devoid of any plant-available phosphorus.

In terms of exchangeable micro-nutrients the *palm rich rainforest* soils show the highest concentrations of base cations both in topsoils and subsoil (Fig. 3.41 and Fig. 3.42). However, in topsoils of *palm rich rainforests* an unfavorable ratio between calcium and magnesium was found, possibly leading to magnesium shortage due to an antagonistic process with calcium. The overall micro-nutrient situation in topsoils and subsoils seems most favorable in *premontane rainforest* soils, in spite of lower base cation concentrations. Topsoil content of base cations is surprisingly high under the *impoverished rainforest*. Subsoils of *dry chamizales* are devoid of any exchangeable base cations which are probably rapidly leached under conditions of good drainage. This is in contrast to *wet chamizales*. Potassium is found in all soils, with the highest values occurring under the *impoverished rainforest*.

Tab. 3.12 compares all units from the combined analysis based on the soil nutrient status.

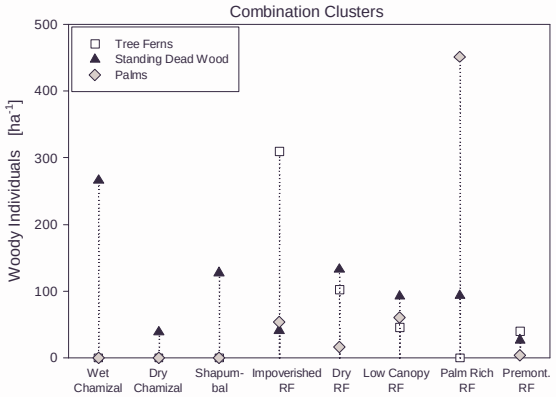



***Fig. 3.43: Density of non-tree woody individuals (tree ferns, palms) and standing dead wood for each classified unit.***

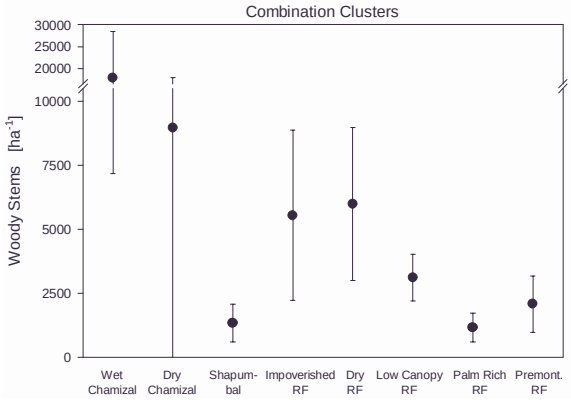



***Fig. 3.44: Growth density means (expressed in stems per hectare) plotted for each classified unit with standard deviations***

### 3.3.2.2 Biometry

For each biometric unit derived from combined analysis the means and standard deviations were calculated for all plots. In this chapter the values for characteristic biometrical properties are compared between these units.

Examination of the stand characteristics within the units shows that the number of tree ferns decreases steadily downward on the slopes from the *impoverished rainforest* to the *palm rich rainforest* (Fig. 3.43). In relation to total stem density, however, tree ferns are most abundant in the *premontane rainforest*. No tree ferns were found in vegetation types with open canopy such as the *chamizales* and the *shapumbal*. Palms abound in *palm rich rainforests* and *low canopy rainforests*. They can be found in the undergrowth also in *impoverished rainforests*. No palms were recorded for *shapumbales* and *chamizales* although some individuals of *Mauritiella peruana* were observed protruding the *wet chamizal* vegetation. Most stems of standing dead wood were found in *wet chamizales*. However, due to their thin nature they did not contribute much to total biomass. The least standing dead wood occurred in *premontane rainforest* but overall stem

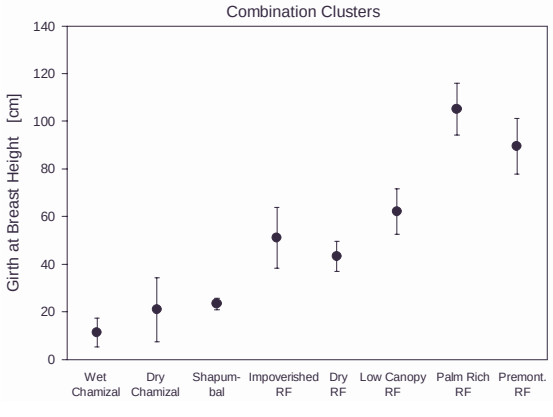



***Fig. 3.45: Girth at breast height means plotted for each classified unit with standard deviations.***

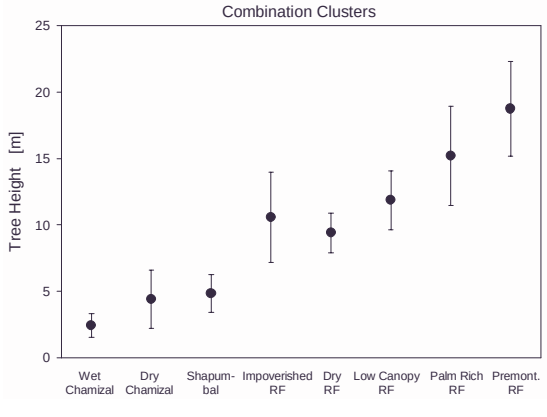



***Fig. 3.46: Tree height means plotted for each classified unit with standard deviations.***

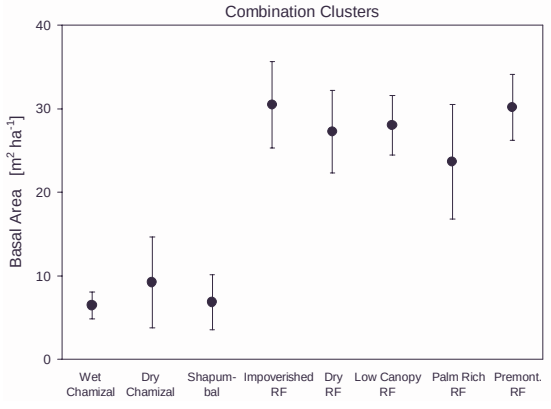



***Fig. 3.47: Basal area means plotted for each classified unit with standard deviations.***

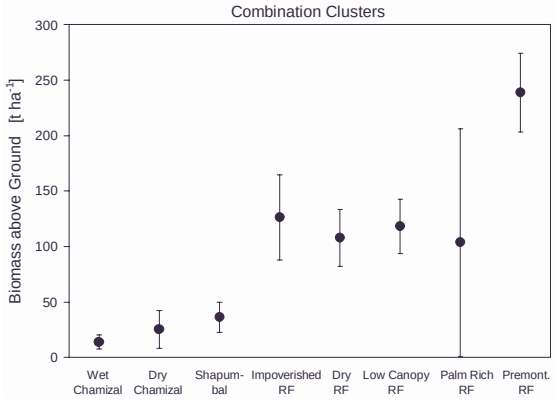



***Fig. 3.48: Standing above ground biomass means plotted for each classified unit with standard deviations.***

density was also low (Fig. 3.44). In relative terms, the highest rates of standing dead wood were calculated for *shapumbales*.

Lowest growth density was found in *palm rich rainforests* and *shapumbales* with less than 1 500 stems per hectare. In *premontane rainforest* an average of approx. 2 000 stems per hectare were recorded. Significantly denser were *dry* and *impoverished rainforests* with up to 6 000 stems per hectare. Highest rates were found for *chamizales* with an average density of approx. 9 000 and 18 000 stems per hectare for *dry* and *wet chamizales* respectively.

A tendency of stem thickness to decrease with the topographic position upward on the slope could be observed (Fig. 3.45). Exceptions were the *impoverished* and *lower canopy rainforests* where thick palm trees raised the mean diameter of the plots. *Shapumbales* show very little variation in stem thickness suggesting that the plots are stocked with similar individuals.

Tree height tends to decrease steadily on slopes from bottom to top (Fig. 3.46). Only *impoverished rainforests* on the ridges display trees of heights similar to *low canopy rainforests* on lower slopes. This might be caused by these regions being less frequently affected by landslides, and taller individuals are more likely to survive recurring fires.

Based on values for basal area the vegetation units could only be divided into two groups: a) closed canopy formations with high basal area of approx. 30 $m^2$ per hectare and b) open canopy formations like *shapumbal* and both *chamizales* with basal area less than 10 $m^2$ per hectare (Fig. 3.47).

The biomass values suggest a grouping into a) high, b) moderate and c) low biomass groups (Fig. 3.48). The *premontane rainforest* exceeded all other units significantly at 238.7 t per hectare. Lowest in above-ground biomass were the open canopy formations *shapumbal* with 36.4, *dry chamizal* with 25.1 and *wet chamizal* with 13.9 t per hectare. All other units developed a total biomass of slightly over 100 t per hectare. *Palm rich rainforests* showed a very high standard

*Tab. 3.13: Comparison of all classified units by the combined approach in respect to tree height, diameter at breast height, basal area, stem density, biomass and stand characters.*

| | Stand Biometry | | | | | | | Stand Characters | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Tree Height Mean | Tree Height Max | Diameter Mean* | Basal Area | Amount Stems** total | Amount Stems** > 10 cm gbh | Bio-mass*** | Stand. Dead Wood | Palms | Tree Ferns |
| | m | | cm | $m^2$ $ha^{-1}$ | $ha^{-1}$ | | $t$ $ha^{-1}$ | $ha^{-1}$ | | |
| **Wet Chamizal** | 2.4 | 4.2 | 3.6 | 6.4 | 17805 | 1284 | 13.9 | 266 | 0 | 0 |
| **Dry Chamizal** | 4.4 | 7.7 | 6.6 | 9.2 | 8966 | 2262 | 25.1 | 39 | 0 | 0 |
| **Shapumbal** | 4.9 | 7.6 | 7.4 | 6.8 | 1337 | 1241 | 36.4 | 127 | 0 | 0 |
| **Impoverished Rainforest** | 10.6 | 18.8 | 16.3 | 30.5 | 5541 | 4348 | 126.4 | 41 | 53 | 309 |
| **Dry Rainforest** | 9.4 | 16.2 | 13.8 | 27.3 | 5985 | 4169 | 107.7 | 132 | 16 | 102 |
| **Low Canopy Rainforest** | 11.9 | 20.4 | 19.8 | 28.0 | 3115 | 2588 | 118.2 | 93 | 60 | 45 |
| **Palm Rich Rainforest** | 15.2 | 23.5 | 33.4 | 23.6 | 1175 | 1175 | 103.5 | 93 | 451 | 0 |
| **Premontane Rainforest** | 18.7 | 36.4 | 28.5 | 30.1 | 2081 | 1835 | 238.7 | 27 | 4 | 39 |

* = Derived from girth measurements at breast height (1.3 m)
** = Calculated using the angle count method after BITTERLICH (1984)
*** = Calculated using own biomass harvest combined with calculations after OGAWA (1965)

deviation in biomass which was caused by one plot that had been assigned to this cluster for reasons of similar soil moisture conditions but had an unusually high biomass of 255 t per hectare. Otherwise biomass stock in this unit would be far below 100 t per hectare.

Tab. 3.13 compares the mean values of biometric stand parameters for all units from the combined classification.

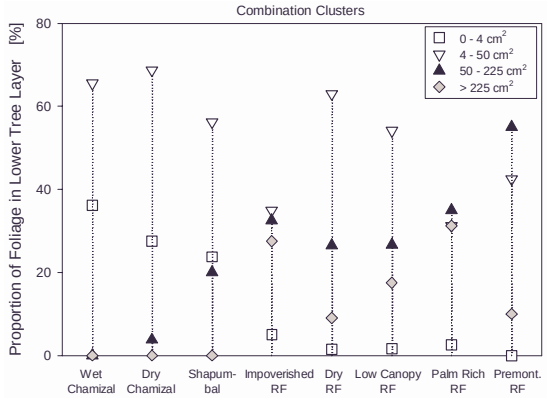



***Fig. 3.49: Proportional leaf size distribution in the lower tree layer (1).***

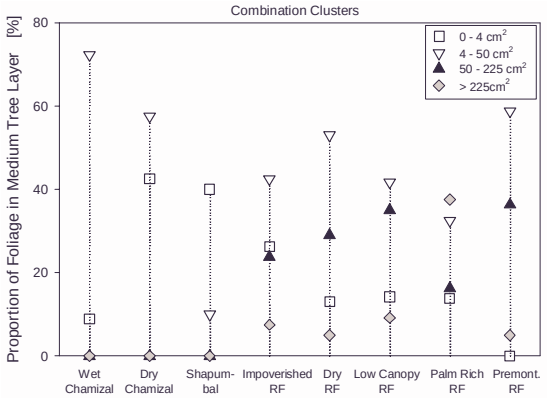



***Fig. 3.50: Proportional leaf size distribution in the medium tree layer (2).***

*Four leaf size classes were recorded in each layer.*
*Shown are mean estimated proportions of these leaf size classes for each classified unit.*

### 3.3.2.3 Structure

In this chapter values for characteristic properties of stand structure are compared between units. For each unit derived from combined analysis the means and standard deviations were calculated over all plots contained.

Leaf sizes may reflect stand climatic conditions (RICHARDS 1983). Therefore, special attention was paid to leaf sizes recorded in the field. Underestimation of leaf size might be caused when measurements occur during the dry season and foliage from deciduous trees is under-represented. Four leaf size classes were separated in each canopy layer. Fig. 3.49 shows the distribution of leaf sizes of the lower tree layer within the vegetation units. Thus, totals of the proportions displayed may exceed 100 %. Remarkable is the presence of very small leaves (0 - 4 $cm^2$) in this layer only in open canopy formations. For all other units the contribution of these small leaves is marginal in this layer. Medium sized leaves (4 - 50 $cm^2$) dominate this layer both in open canopy formations and on slopes. In *impoverished* and in *palm rich rainforests* all leaf sizes larger than 4 $cm^2$ are represented equally. Highest proportions of large leaves (> 225 $cm^2$) were encountered in *impoverished* and in *palm rich rainforests* indicating either the presence of large leaved Melastomataceae or palms. Leaves of 50 - 225 $cm^2$ dominate in the lower tree layer of premontane rainforests.

In most *shapumbal* and *chamizal* stands the medium tree layer (2) constituted the actual top layer (Fig. 3.50). Whereas the proportion of smallest leaves increased slightly for the *dry chamizales*, medium sized leaves (4 - 50 $cm^2$) made up almost the entire foliage in the *wet chamizales* indicating permanently good water availability even under high insolation. *Shapumbales* showed highest proportions of small leaves in the medium layer, suggesting high water stress on these sites. The largest leaf class of more than 225 $cm^2$ (i. e. palms) was well represented in *palm rich rainforests*.

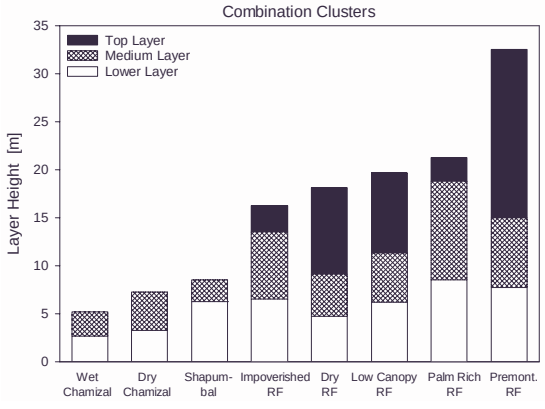



***Fig. 3.51: Cumulative canopy height chart.***
*A maximum of three canopy layers was distinguished at each plot. Shown are mean estimated heights of these layers for each classified unit.*

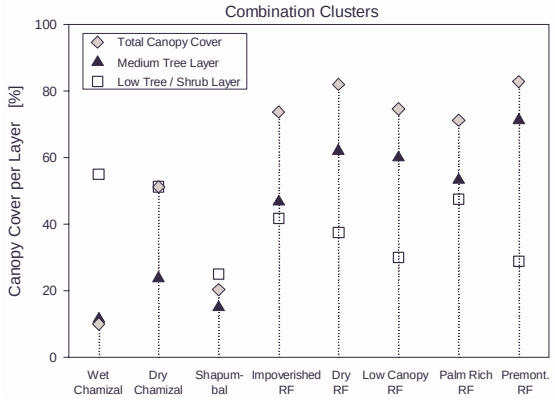



***Fig. 3.52: Canopy cover by each individual layer.***
*Layer (1) includes all woody individuals on the ground up to the top of this relative layer. Layer (2) includes all trees between layer (1) and the top canopy layer. Total canopy cover was measured > 1.3 m.*

Canopy layering may allow conclusions to be made about light availability in a forest stand. Heights of all identified canopy layers were recorded and the vertical layer structure was compared for all units (Fig. 3.51). For open canopy formations only two canopy layers were identified. In *chamizales* the height of the lower layer is similar, yet the upper layer is slightly higher in *dry chamizales*. In *shapumbales* the distinction between a fairly high lower layer to the short upper layer was difficult. Layer proportions on the slopes are similar with a distinct upper layer clearly separated in height from the medium layer. Conditions are similar in the *impoverished rainforest* yet the height I greater overall. The layering structure for *palm rich* and *impoverished rainforests* was comparable because both lower and medium layers were relatively tall.

The contribution of the individual layers to the total canopy cover expresses the horizontal layer structure and may also indicate the gradient for available light within the stand. In Fig. 3.52 the estimated cover of the lower layer (including shrubs) and of the medium layer is compared to recorded total canopy cover. Because total canopy cover was assessed above 1.3 m (this distinction was not made for the shrub layer) the cover of the shrub layer may exceed the total canopy cover. Total canopy cover was high for all units of the hill area. Within this group, proportional cover by the lower tree layer was highest in *palm rich rainforest* which abounded in small palms and was lowest in the *low canopy rainforest* which may be an indication for poor light availability at the bottom of these stands. Lowest canopy cover was recorded in *wet chamizales* and *shapumbales* whereas *dry chamizales* showed medium canopy cover values. The shrub layer was dense in *wet chamizales* whereas cover of all layers was low in the *shapumbal* accounting for the thick and impenetrable layer of ferns strongly suppressing the re-growth of other species. Total canopy cover in *dry chamizales* reached approx. 50 % and was significantly higher than in the *wet chamizales* (10 %).

## 3.3.3 Description

The following chapter briefly summarizes the most conspicuous characteristics of the classified soil units and assesses their implications for plant growth. The prevalent topographic situation where plots of each unit was found is mentioned in parentheses.

### 3.3.3.1 Vegetation Units

**Wet Chamizal** (Plateau)

*Wet chamizales* occur often adjacent to *dry chamizales* on the same plateaus but cover waterlogged sites. Soils were composed of white sands and were very acidic, especially in the organic topsoil with widest C/N ratios in the subsoil. Drainage was always obstructed by an impenetrable layer of sediments (hard pan). Carbon pools were highest in the topsoil. Aluminum and nutrient concentrations were very low. The upper shrub layer cover exceeded the cover by trees. Trees were short (< 5 m) and bore almost exclusively leaves of 4 - 50 $cm^2$. Growth density was extremely high with approx. 17 800 stems per hectare. The stand biomass was lowest at an average of 13.9 t per hectare.

**Dry Chamizal** (Drained Plateau)

*Dry chamizales* were found exclusively on the drained portions on rims of plateaus formed by Quaternary-Holocene sediments. Soils were mainly composed of sand and very acidic especially in the topsoil. C/N ratios were approximately 30. Aluminum concentrations as well as pools for all nutrients were very low in the mineral soils. Although medium sized leaves (4 - 50 $cm^2$) dominated the upper layer, *dry chamizales* showed the same amount of small leaves < 4 $cm^2$ as the *shapumbal* vegetation suggesting occasional water stress. Overall stem density was variable but high with a remarkably small dead wood proportion. Trees did not reach 10 m and biomass averaged 25.1 t per hectare.

**Shapumbal** (Steep Upper Slopes)

*Shapumbales* were confined to steep upper slopes on Quaternary-Pleistocene sediments. These sediments are highly susceptible to landslides. *Shapumbales* are open stands of few stunted and small leaved trees with a thick and impenetrable understorey of the ferns *Sticherus remotus* and *Gleichenella pectinata*. Burnt snags and considerable amounts of charcoal in the soil were found at some sites. Common soil characteristics were a thick organic litter layer formed by the ferns, fairly high contents of clay and aluminum. Soils in general were highly variable. Nutrients such as phosphorus were very low and C/N ratios varied significantly from topsoil to subsoil. Neither palms nor tree ferns were found. Canopy cover in both recorded tree layers was low and the upper layer is almost exclusively made up of leaves < 4 $cm^2$. Stem density is low with slightly over 1 300 stems per hectare but the proportion of standing dead wood is high. The

conspicuously twisted trees reach heights between 5 and 10 m. Biomass was low with an average of 36.4 t per hectare.

**Impoverished Rainforest** (Ridges)

*Impoverished rainforest* developed over all geological formations in the study area. They were, however, found both on steep slopes close to narrow crests as well as on wide and level ridge tops. Subsoils are relatively often rich in clay and high in exchangeable potassium. Except for the smallest leaves (0 - 4 $cm^2$) all other sizes were equally represented in the lowest layer and the boundary between medium and top layer is not pronounced. The highest number of tree ferns was found in these forests. Woody individuals were slightly taller and thicker than in the *dry* and *low canopy rainforests*. This may be caused either by reduced susceptibility of these sites to landslides and thus longer growth periods or by the fact that these trees are more likely to survive recurrent fires. Biomass was calculated to be 126.4 t per hectare.

**Dry Rainforest** (Upper Slopes)

*Dry rainforests* were mostly found at the slopes of the Cordillera Cahuapanas on late Jurassic substrate. Soil parameters did not allow any significant distinctions to the *low canopy rainforest*. Only pH values and carbon pools in the subsoil tended to be slightly higher. The fact that fewer palms but more tree ferns were recorded might indicate a cooler and possibly even moister micro-climate which is likely especially at the slopes of the Cordillera Cahuapanas. Higher rates of precipitation were found there by METTE (2001). Stand height is even shorter than in *low canopy rainforest*. Stems are thinner and more abundant. Biomass at approx. 107 t per hectare is comparable to values from the *low canopy rainforest*.

**Low Canopy Rainforest** (Lower Slopes)

The largest portion of the upper hill region, especially the very finely layered and unstable Quaternary-Pleistocene section is made up of sloped terrain. Landslides are frequent in this area therefore vegetation must be adapted to highly dynamic edaphic situations. Stand conditions on lower slopes are slightly more favorable since this part is better sheltered from adverse climatic conditions, moister in stand climate and better supplied with nutrients due to accumulation from above. Soils are highly variable under these conditions. Furthermore the low canopy rainforests feature soils from different geological substrate of Tertiary and late Jurassic material. Thus, no distinctions for characteristic soil properties in this unit can be made. Stands were slightly shorter than in *palm rich rainforests* but with clearer layer structure, less palms and more tree ferns present. Calculated biomass was 118 t per hectare which was slightly higher than in *palm rich rainforests*.

**Palm Rich Rainforest** (*Barrancos* / Ravines)

*Barrancos*, where *palm rich rainforests* were found primarily, are rather steep ravines or narrow valleys primarily found in the dissected landscape on Quaternary-Pleistocene sediments. *Palm rich rainforests* were characterized by a large number of palms which indicated stagnant and wet soils. Slope inclination ranged from almost level to greater than 10°. Due to a low overall stem density, slender trees and relatively unproductive palms biomass is rather low for these stands. One plot, structurally belonging to the *premontane* type, was assigned to the *palm rich rainforests* for its soil conditions and thus disguised the lower biomass value of this unit. Medium and top tree layers were not well separated and lianas were most frequent in the lowest layer. Clay content, phosphorus and base cation concentrations in the topsoil were high and were likely due to accumulation from upslope. Both magnesium and calcium concentrations were high which may cause magnesium deficiency due to competition between both.

**Premontane Rainforest** (Valleys / Terraces)

The *premontane rainforests* stocked on drained sites which occur either on gently sloped terrain, not necessarily close to rivers, but also on higher terraces where natural disturbances by landslides or fire are unlikely to occur. No *premontane rainforests* were found on Quaternary-Pleistocene substrate which is too dissected to form wider valleys or broad ridges. In the *premontane rainforests* trees grew tallest (> 30 m) with a distinct top canopy layer and produced most biomass (238.7 t $ha^{-1}$) although the number of stems per hectare was relatively low. The top tree layer abounded in lianas and epiphytes. Leaf size domination shifted from large leaves (50 - 225 $cm^2$) in the lowest layer to medium leaf size (4 - 50 $cm^2$) in the top layer. Soils were moist but always well drained sandy fluvisols or clayey oxisols. Phosphorus pools in *premontane rainforest* soils were the highest found among all vegetation units.

### 3.3.3.2 Summary

**Geologic Effects**

Geology determined the occurrence of *shapumbales* which were restricted to Quaternary sediments (chapter 3.1.3.2). Valleys of sufficient width to provide relatively level ground for tall vegetation had never formed on Quaternary-Pleistocene substrate in the Río Avisado area. *Palm rich rainforest* dominated the narrow valleys instead. Both *chamizal* types were only found on plateaus of Quaternary-Holocene origin. *Low canopy*, *dry* and *impoverished rainforest* types occurred independent of geological preconditions.

### Topographic Effects

Characteristic topographic positions could be ascribed to all vegetation units formed. *Chamizales* were restricted to plateaus. *Shapumbales* were found on steep upper slopes. *Premontane rainforests* occurred on sheltered plains, terraces or gently sloped, wide ridges. *Palm rich rainforests* developed in steep ravines or on the bottom of narrow valleys. *Low canopy rainforests* occurred on sites of moderate slopes which were mainly found towards the foot of slopes but could also be found on moderately sloped parts further uphill. Especially in the more dissected hill area *dry rainforests* covered sites of similar quality as *shapumbales*. Also on the lower foothills of the Cordillera Cahuapanas exclusively *dry rainforests* were found. *Impoverished rainforests* were confined mostly to sharp ridges and therefore also found on steeply sloped terrain neighboring the ridgeline.

### Moisture Effects

Vegetation units of badly drained sites were *wet chamizales* and *palm rich rainforests*. Permanently moist but drained were soils of the *premontane rainforest*. Variable drainage conditions were assumed for all vegetation units of the slopes. However, higher precipitation rates at the foothills of the Cordillera Cahuapanas may provide forests there with slightly more water. Well drained and climatically dry conditions were found for *dry chamizales*. No distinct predictions for water regime under *shapumbales* could be made.

### Erratic Effects

A misarrangement caused plot P 42 to be assigned to the *palm rich rainforest* type. With a maximum tree height of 37 m and a total biomass of 255 t per hectare it was more likely to belong to the *premontane* unit. However, intense hydromorphic properties of the soil may have caused it to be grouped to the *palm rich rainforest*. This shows that soil properties may not only have a disguising effect for biomass as shown in chapter 3.1.3.3 but also may be misleading for the classification of vegetation types. This error caused a high variability within the *palm rich rainforest* unit and led to an overestimate of tree height and biomass values for this unit. A similar effect was observed for *impoverished rainforests*. Plot P 40 was recorded on a ridge similar to most plots within the *impoverished rainforest* unit. However, it was located on level ground near the Cordillera Cahuapanas. Geological and stand climatic conditions there were different compared to the sharp ridges of the upper hill area where the remaining plots of this unit were described. This plot featured trees and biomass values higher than the average for this unit even though soil conditions and vegetation structure differed less.

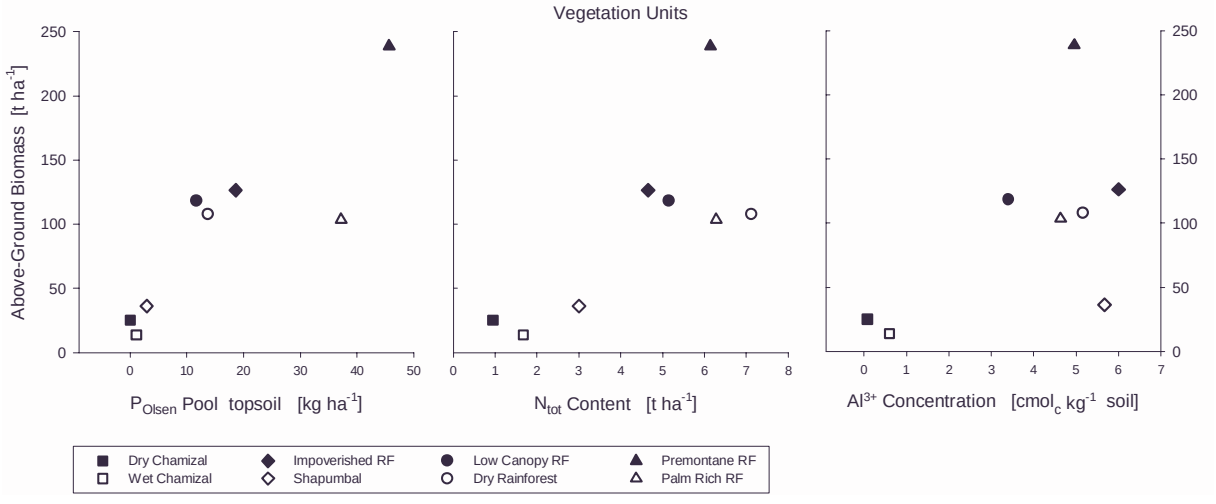



***Fig. 3.53: Relation between soil chemistry and biomass for the respective biometry units.***
*Plotted are soil nutrient pools of plant-available phosphorus and total nitrogen, and the total concentration of exchangeable aluminum ($Al^{3+}$) against the biomass values calculated for the stands of each biometry unit. Variability for the values given is high throughout.*

### 3.3.3.3 Statistical Evaluation

As Fig. 3.53 demonstrates, a trend for increasing biomass development can be observed in the series of vegetation units from top to bottom of the slopes (left to right). This is not surprising as moisture regimes may be more favorable and certain sheltering effects from adverse climatic and disturbance conditions can be expected on lower slopes (*low canopy rainforest*) and in valleys (*premontane rainforest*) allowing a more luxuriant vegetation to develop. Statistical analysis confirms that the vegetation units can be grouped into three categories by their biomass stock (cf. One-Way ANOVA in Appendix 9.2.2.4). Observing the phosphorus supply, the trend follows the biomass values closely with the exception of the *palm rich rainforest*. In spite of relatively rich nutrient pools similar to the premontane rainforest, little biomass develops. While the shortage of nutrients other than P and N may be a possible explanation for the low biomass, it is likely that the permanently wet soils may prevent an efficient conversion of the nutrients into biomass. In addition to possible water stress, phosphorus limitation probably inhibits the production of more biomass in *dry rainforests* and *shapumbales*. Aluminum concentration, although high in many soils, does not seem to affect the biomass growth adversely. An arrangement of species tolerant to high aluminum concentrations in the premontane rainforest has been suggested but could not be evaluated from this data.

## 3.4 Spatial Distribution of Vegetation

In order to detect and describe common patterns in the spatial distribution of vegetation in the study area it was necessary to use remote sensing data (BÖRNER & ZIMMERMANN 2002, READING et al. 1995). Together with topographic data that had been obtained in the field it was possible to waive cost intensive satellite images in order to produce an adequately accurate model of the topographic situation in the study area from aerial photographs.

### 3.4.1 Image Data

Radar images (RADARSAT (C-Band), and JERS-1 (L-Band) with pixel resolution 100 m) available from 1996 and 1997 were of insufficient spatial resolution for such small scale vegetation patterns of the study region (Fig. 3.54). Foreshortening effects caused by terrain with high relief energy disturb all radar images which are not interferometrically available and processed. The highly dissected relief of the study area also caused a small scale scatter variation, which made a radiometric and terrain correction impossible. These effects are detrimental to a comprehensive set of information as signals of only certain slope aspects can be detected and evaluated depending on the image azimuth.

Cloud cover near the foothills of the Cordillera Cahuapanas is nearly continuous due to the condensation of moist air masses ascending at this mountain range. Thus, all examined LANDSAT$^{TM}$ scenes (acquisition dates from 1996 until 1999) were covered by low clouds over the study area (Fig. 3.55). The only useful data source were panchromatic, stereographic aerial photographs of the study region, available from October 1992 (scale 1 : 80 000). However, the acquisition date of 1992 did not reflect the current situation of clearings and vegetation disturbance patterns (fire, landslides) nine years later.

### 3.4.2 Topographic Data

A topographic map (1-IGN J631 1459 (12-i), scale 1 : 100 000) was available from the *Instituto Geográfico Nacional* in Lima. The data provided by this map were insufficient since the 50 m contour lines did not resolve the hills in the area (Fig. 3.56). GPS reference points were therefore taken in the field and later used to reference two stereoscopic panchromatic aerial photographs (Fig. 3.57; IGN 1992). These photographs served as basis to compute a digital elevation map (DEM) with a surface elevation resolution of 2 m of the core region of the study area (cf. also Fig. 9.6 - Fig. 9.8 in Appendix 9.3).

### 3.4.3 Spatial Arrangement and Analysis

The analysis of the vegetation in the study area also considered connections to edaphic factors such as underlying geology and topographical effects. In addition to the existing

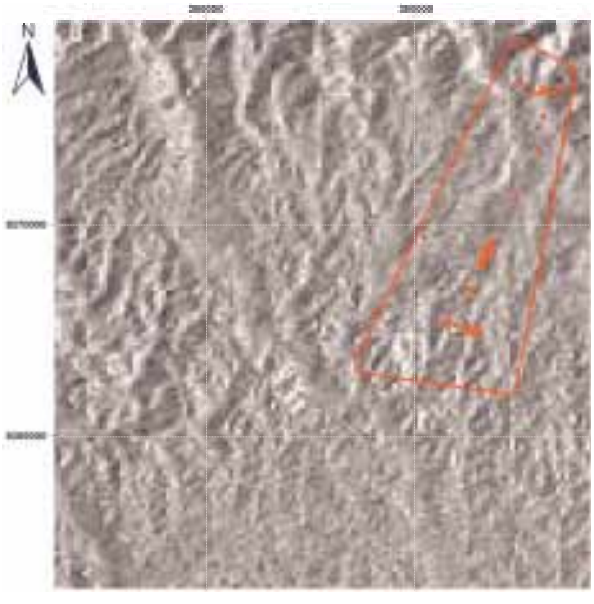


***Fig. 3.54: JERS-1 radar image (L-Band) of the study area showing coarse spatial resolution and intense foreshortening due to ridges.***
*The contours of the DEM and plot locations are indicated. Pixels are re-sampled from 18 m to 100 m resolution.*
Source: JERS-1 Tile 116, October 1995, courtesy of GLOBAL RAINFOREST MAPPING PROJECT, NASDA/MITI

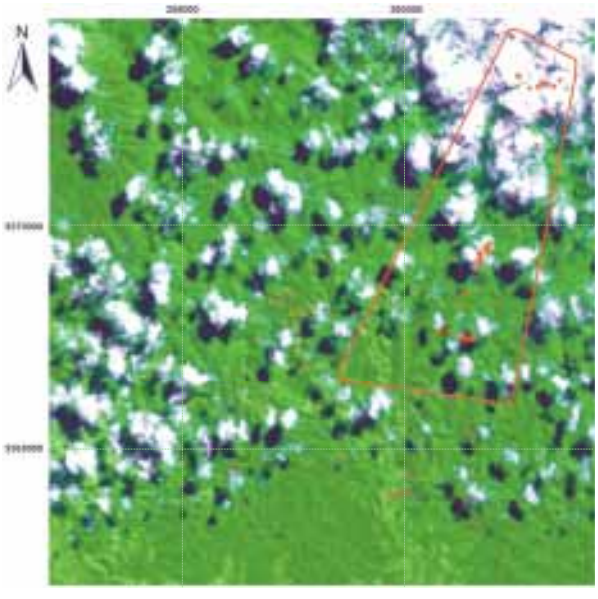


***Fig. 3.55: LANDSAT-7 (Enhanced Thematic Mapper) image of the study area showing high cloud cover.***
*The contours of the DEM and plot locations are indicated. Channels 7, 4 & 1 (RGB) are used, 30 m pixel resolution.*
Source: LANDSAT-7 ETM+, July 11, 1999 (Path8, Row64)

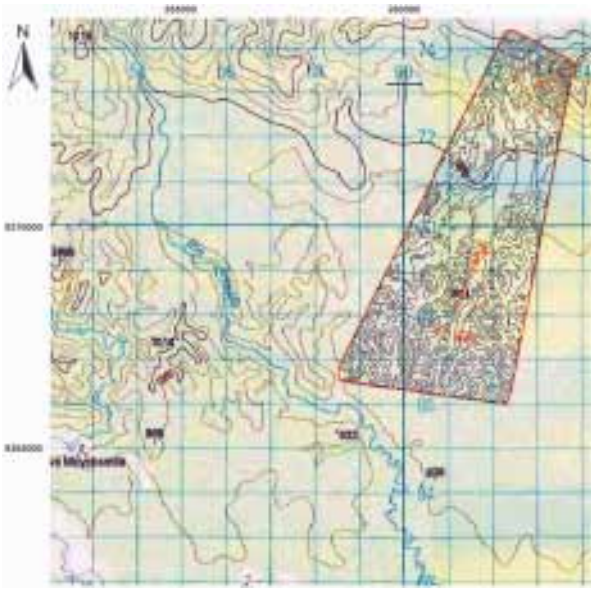


***Fig. 3.56: Topographic map (1 : 100 000) of the study area showing low vertical resolution.***
*The 20 m contours of the DEM and plot locations are superimposed.*
Source: IGN Lima, Topographical Map 1 : 100 000 *Nueva Cajamarca*, 1-IGN J631 1459 (12-i)

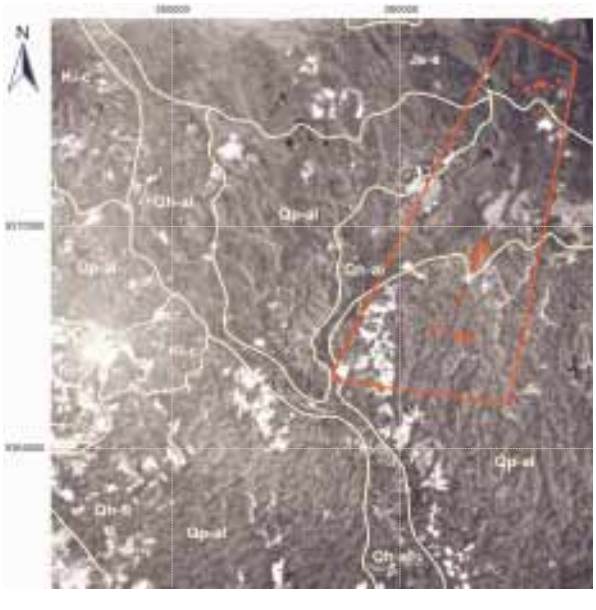



***Fig. 3.57: Panchromatic aerial photograph of the study area from October 17, 1992.***
*The outlines of geological formations, 25 m contours of the DEM and plot locations are superimposed.*
***Qh-al/fl*** *(Quaternary-Holocene),* ***Qp-al*** *(Quaternary-Pleistocene),* ***Ki-c*** *(early Cretaceous),* ***Js-s*** *(late Jurassic)*
Source: IGN Lima; Roll 17: Strip 335: No. 64

geological data the digital elevation map (DEM) of the visible surface of the terrain was used to assess relative position of the plots within the landscape as well as relief properties (Fig. 3.58).

The three-dimensional view of the study area (Fig. 3.58, lower image) reflects the landforms described in the previous chapters. The foreground is dominated by almost parallel trending ridges (crests are shaded in yellow) of the dissected upper hill area. These ridges eventually

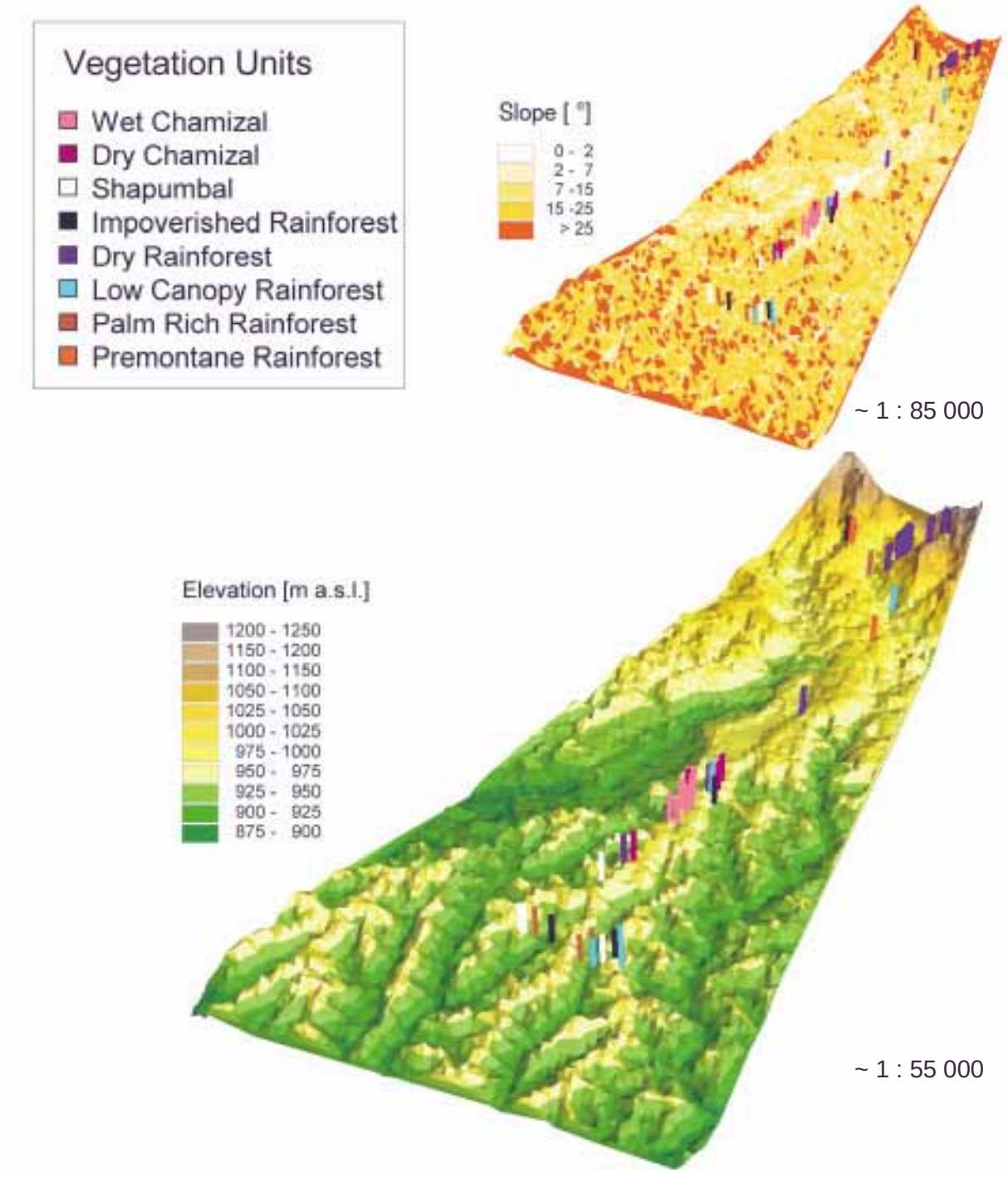



***Fig. 3.58: Spatial distribution of vegetation types as classified by combined analysis.***
*Plots are colored by corresponding vegetation type and pictured* **(below)** *on the surface of a 3-dimensional aspect of the study area to demonstrate topographical position and* **(above)** *on the same view expressing the slope situation for each plot. Vertical distances are exaggerated three-fold. Plots P01 - P03 are not pictured.*

***Tab. 3.14: Slope distribution in the study area.***
*Slopes were derived from a 2 300 ha sample DEM in five distinct classes with a grid resolution of 10 m.*

| Slope | Area | |
|---|---|---|
| ° | ha | % |
| 0- 2 | 65 | 3 |
| 2- 7 | 387 | 17 |
| 7-15 | 838 | 36 |
| 15-25 | 785 | 34 |
| > 25 | 226 | 10 |
| *total* | *2302* | *100* |

extend to the oblong plateau of the studied *chamizales*. To the left of this plateau the wider valley of a tributary to the Río Avisado unfolds outward of the section. The landscape in the background is characterized by wider and gentler ridges before these rise at the far end to form the Cordillera Cahuapanas. The gradual rise of the projected terrain surface becomes obvious in this aspect.

Additionally, a map of slope classes was computed from the DEM in order to determine the slope situations which indicate the susceptibility to erosion or landslides in the study area (Fig. 3.58). Classes were chosen to distinguish level sites (slope 0 - 2°) which are primarily characteristic for the plateaus where *chamizales* are found but also broad ridges and alluvial valley bottoms (of which the upper canopy surface was mapped) featured such level areas occasionally. These areas constitute only 3 % of the mapped area. Together with the portion of gentle slopes (2 - 7°) which concentrate in similar areas these account for 20 % of the digitalized area. The bulk area of the study side is of sloped terrain. Most prominent are areas of the slope the classes 7 - 15° and 15 - 25° which cover 36 and 34 % of the total assessed area respectively. Steep slopes (> 25°) which are most likely susceptible to erosion such as landslides and thus might be indicative for the occurrence of *shapumbales* account for 10 % of the area.

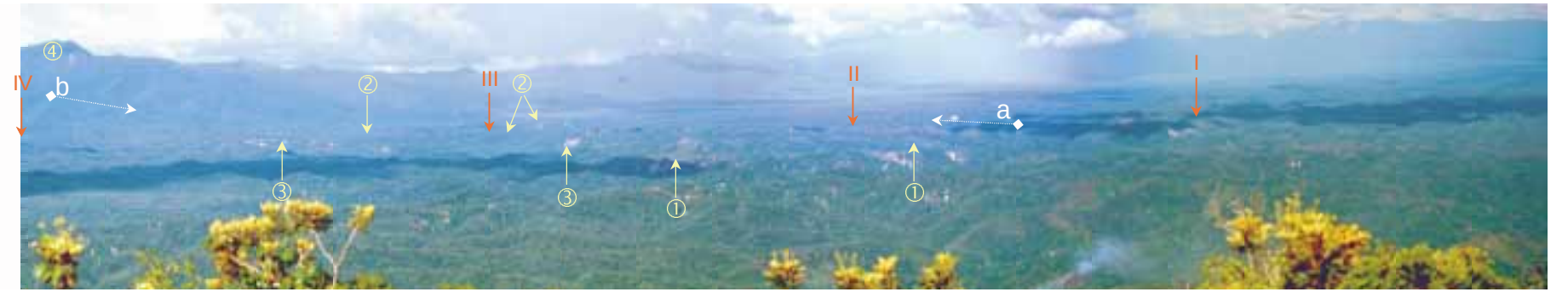



***Fig. 3.59: Panoramic view across the upper hill area towards the East (center) from a pre-summit of the Cerro Tambo.*** (UTM 18S: 249400/9368339)
*Indicated in yellow are sites of vast* shapumbal *cover (primarily after fire)* ①, chamizal *plateaus* ②, *recent landslides* ③, *and the Pico de Cahuapanas (1 841 m a.s.l.)* ④.
*Marked in red are the positions of* Gamínedes (**I**), *Camp 2* ("Burnt Camp", **II**), *Camp 3* ("Chamizal Camp", **III**), *and Camp 4* ("Cahuapanas Camp" **IV**).
*White arrows indicate the look direction of Fig. 3.60* (**a**), *and Fig. 3.61* (**b**).



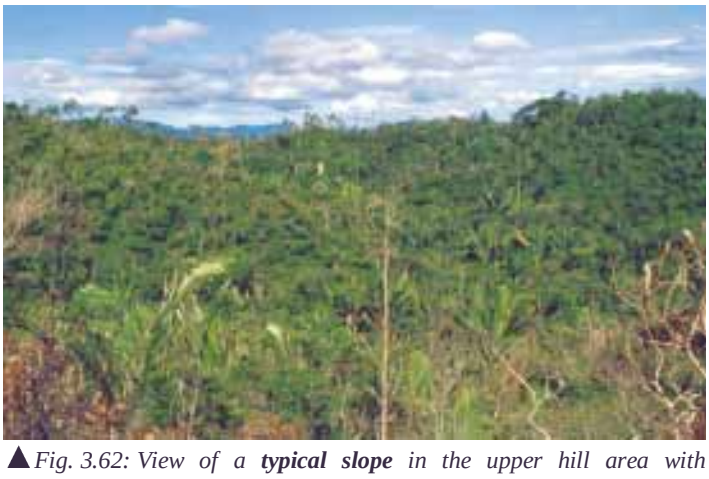
***Fig. 3.60: Panoramic view across the study area northward towards the Cordillera Cahuapanas in the Río Avisado watershed.*** (UTM 18S: 260281/9365725)
*Recognizable is the semi-deciduous vegetation covering the upper slopes and ridges of the upper hill region* (dry *and* impoverished rainforest) *in the center.*
*To the left, vast* shapumbal *areas can be seen. The Pico de Cahuapanas is to the right.*




***Fig. 3.61: Black and white panoramic view across the upper hill area southward from the foothills of the Cordillera Cahuapanas.*** (UTM 18S: 263575/9373270)
*Clearly visible are the plateaus covered by* chamizales ① *in the background left, the broad valleys covered by premontane rainforest* ② *in the foreground, and abandoned agricultural clearings* ③ *on the right.*

## 3.4.4





▲*Fig. 3.62: View of a **typical slope** in the upper hill area with vegetation of decreasing growth density and height towards the ridge top.* (UTM 18S: 261034/9367396)

◀*Fig. 3.63: View into a valley with the palm* Jessenia bataua *along the **ravines** and on the bottom.* (UTM 18S: 260281/9365725)

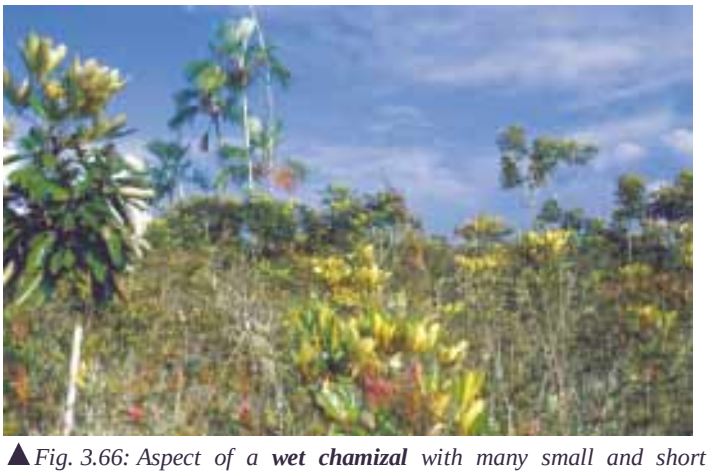




▲*Fig. 3.64: Close view of an upper slope with light green colored **shapumbal** ground cover.* (UTM 18S: 261177/9368208)

◀*Fig. 3.65: View of a **shapumbal** slope, easily recognizable with many bright and shiny stems visible.* (UTM 18S: 261846/9369502)





▲*Fig. 3.66: Aspect of a **wet chamizal** with many small and short stemmed individuals and a group of tall individuals of* Mauritiella peruana. (UTM 18S: 261692/9369297)

◀*Fig. 3.67: Aspect of a **dry chamizal** with considerably higher vegetation.* (UTM 18S: 261586/9369220)

## Proposed Mapping Criteria

In this chapter guidelines will be presented for the distinction of vegetation characteristics based on mapped information.

### 3.4.4.1 Vegetation Types

Based on characteristics of the vegetation types which were classified in chapter 3.3 the following criteria were proposed for subsequent mapping of the vegetation cover in the study area:

- ***Premontane Rainforests*** are found in broad valleys of late Jurassic and early Cretaceous geology where signature on the aerial photograph is coarsely structured by large crowns protruding the canopy. This type also includes forests on wide ridges at > 1 050 m a.s.l. on Quaternary-Holocene substrate which bear a similar signature.
- ***Palm Rich Rainforests*** in the study area are only found on both Quaternary formations. They stock on relatively narrow depressions of less than 200 m width on slopes < 15° and in narrow ravines leading down from the ridges on steeper slopes.
- ***Low Canopy Rainforests*** occur on both Quaternary formations as well. Straight slopes of up to 25° which are not incised by ravines bear this forest type.
- ***Dry Rainforests*** cover all slopes > 15° on late Jurassic and early Cretaceous formations.
- ***Impoverished Rainforests*** are found on all geologic formations on ridges of slopes up to 15°.
- ***Shapumbales*** cannot be mapped from aerial photography as no distinct signature could be derived which links current field data to the image situation nine years ago. Indications from site analysis, however, suggested that this vegetation type occurs on frequently disturbed sites. These may be slopes greater then 25° on the Quaternary-Pleistocene formation. Therefore, all areas matching this criterion must be considered potential *shapumbal* sites.
- ***Dry*** and ***wet chamizales*** cannot be easily distinguished in aerial photos. They occur both on strictly flat plateaus of Quaternary-Pleistocene origin. Dynamics within these formations may be high which is suggested by the nine-year-old aerial photograph which shows two contrasting signatures for currently similar vegetation types. *Dry chamizales* exhibit a darker and coarser signature in the photograph compared to *wet chamizales*. *Wet chamizales* are found on strictly flat plateaus of Quaternary-Pleistocene origin. They are very light and smooth in signature.

#### 3.4.4.2 Biomass

This study finds that above-ground biomass in forests varies little between *low canopy*, *dry* and *impoverished rainforests*, and between *wet* and *dry chamizales*. Therefore, it appears justifiable to simplify the mapping scheme for biomass to the classes *valley, barranco*, *hill area rainforests*, and *chamizal*:

- ***Valley*** type forests (*premontane rainforests*) are found in broad valleys of late Jurassic and early Cretaceous geology where signature on the aerial photograph is coarsely structured by large crowns protruding the canopy. This type also includes forests on wide ridges > 1 050 m a.s.l. on Quaternary-Holocene substrate which bear a similar signature.
- ***Barranco*** type forests (*palm rich rainforests*) are only found on both Quaternary formations occurring in the study area. They stock on relatively narrow depressions of less than 200 m width on slopes < 15° and in narrow ravines that stretch downwards from the ridges on steeper slopes.
- ***Hill area*** forests (*low canopy*, *dry* and *impoverished rainforests*) occur on all sloped areas in the study region that do not belong to the barranco class up to an elevation of 1 200 m a.s.l..
- ***Chamizales*** occur strictly on flat plateaus of Quaternary-Holocene origin.
- The ***shapumbal*** biomass unit can be classified only as a potential formation for visible landslides or all other sloped areas > 25° on Quaternary-Pleistocene substrate.

# 4 Discussion

This chapter discusses four hypotheses in order to identify factors that cause the variation and distribution of forest types in the Río Avisado region. Special attention will be given to the occurrence of heath forests and brief comments will be made on the environmental implications for human land use in the area.

## 4.1 Classification Approaches

To test for differences in soil properties, biomass allocation, and the influence of topography on the vegetation three different classification approaches were chosen. All field data were evaluated statistically using Principal Component Analysis and / or Hierarchical Cluster Analysis (cf. chapter 3). Results of the three classification approaches are compared in Fig. 4.1, where all 45 investigation plots are grouped by the vegetation types reached by the combination of all data (X-axis). Assignments of each plot to soil classes (A) and biometry classes (B) are plotted along

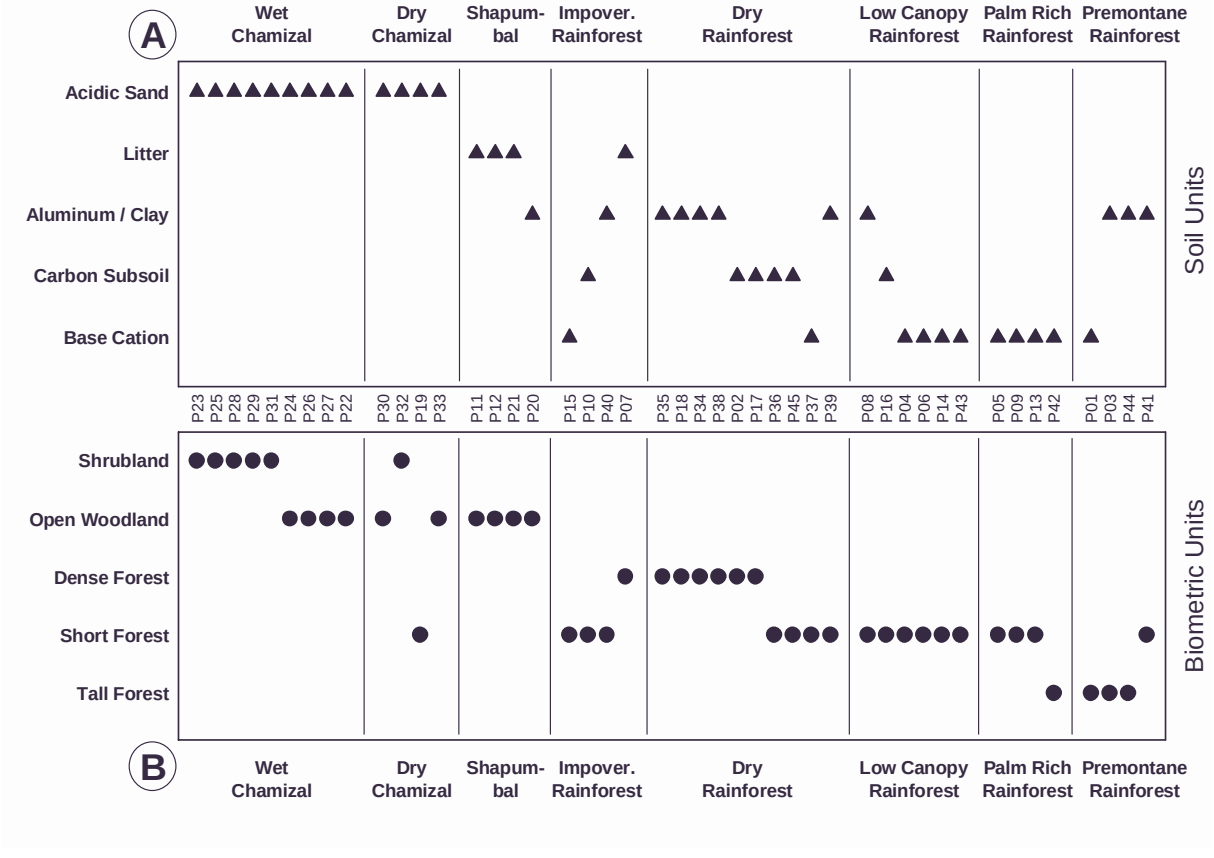



***Fig. 4.1: Overview of relationships between statistical classification units generated by the soil, biometric and combined approach.***

*All plots studied are grouped by the forest types to which they were assigned through statistical classification combining information from soil, biometric and structure parameters. Units are arranged by topographic position on slopes from top to bottom.*

*The upper chart (A) demonstrates the different soil units represented in each vegetation unit (solid triangles). The lower chart (B) demonstrates the different biometric units in each vegetation unit (solid circles).*

the Y-axis. Results from One-Way ANOVA Analysis of the vegetation types were used to reduce significant parameters. From this reduced set of parameters a classification scheme was developed for the forest types of the study area.

### 4.1.1 Soil Chemistry and Texture

**NULL-HYPOTHESIS I**

**Soil chemistry and soil texture do not vary in the upper Río Avisado watershed.**

Five soil clusters were formed based on parameters expressing soil texture, soil reaction, and element composition (cf. Fig. 3.3 - Fig. 3.16 in chapter 3.1.2). These clusters were also clearly separated by statistical analyses *post-hoc* (cf. ANOVA results; Tab. 9.20 in Appendix 9.2.2.4). Therefore, hypothesis I must be rejected.

Tropical soils are largely known for their poor nutrient status (RICHARDS 1996). It is a common belief that the limitation of tropical plant growth by phosphorus (P) affects mainly lowland rainforest whereas with altitude nitrogen (N) limitation becomes increasingly influential (GRUBB 1989, LAURANCE et al. 1999, SILVER 1994, TANNER et al. 1998, VITOUSEK 1984). Such large scale generalizations are difficult since N and P conditions in tropical soils are highly variable in terms of the concentration of their exchangeable fraction as well as in overall supply (CUEVAS & MEDINA 1988). Due to this variability conclusions as to the limiting effect of either N or P can only be drawn on regional level. TANNER et al. (1998) conducted fertilizer experiments in several tropical forests where they found montane plant growth to be limited by N only in Venezuela and in Costa Rica. In Jamaica both P and N were shown to limit plant growth whereas Hawaiian montane forests were P deficient. Hawaiian soils are almost entirely of volcanic origin and contain high amounts of allophanes which fix P permanently (HINTERMAIER-ERHARD & ZECH 1997, SANCHEZ 1989). A similar situation could arise in the case of *acidic sand soils* of the Río Avisado area if volcanic material was identified in the upper horizons as proposed in a previous investigation by ONERN (1983).

In tropical montane forests many species have developed physiological adaptations to low phosphorus levels (SILVER 1994) or reduce growth according to the P supply (CHAPIN 1983). The efficiency of mycorrhiza in enhancing the P uptake for plants at minute concentrations is pointed out by BAILLIE et al. (1987), SILVER (1994), and WILD (1989). Such strategies may explain the absence of chloroses and necroses as deficiency symptoms in the vegetation of the study area. In contrast to nitrogen, the exclusive sources for plant-available phosphorus in soils are the mineralization from organic matter and the weathering of primary minerals if soils are not yet

deeply weathered and P supplies become inaccessible to plant roots (SILVER 1994). CUEVAS & MEDINA (1988) and LAURANCE et al. (1999) discuss the reduced P availability due to high concentrations of aluminum (Al), especially within the range of Al buffering (pH < 5.5; WILD 1989). According to their studies, P is not only fixed as aluminum phosphate or adsorbed onto sesquioxide nodules but the high Al levels also inhibit mycorrhizal activity. Deeply weathered and dystrophic soils with high Al saturation are characteristic for the Río Avisado area. Plant-available P was restricted to topsoil horizons with high humus content. This suggests that the P supply in the soils of the study area is closely linked to organic matter. Confirmation might come from TIESSEN et al. (1994) who found up to 70 % of phosphorus in soil organic matter (SOM) of the Venezuelan Rio Negro region. Evaluation of soil P and N status in relation to the actual above-ground biomass (cf. Fig. 3.17 in chapter 3.1.3.3) revealed that nitrogen was sufficiently supplied with the exception of *acidic sand* and *litter soils* and that biomass strongly correlated with the variation of phosphorus. In the hills of the Río Avisado region, BÖRNER (2000) found a correlation of low pH and low P levels in soil to small stems which could be confirmed in this study, yet on a less significant basis.

Nitrogen is biologically fixed from the atmosphere and mineralized from organic matter by microbial activity. Limitation of plant growth by nitrogen in tropical lowlands has been reported only in a few instances, e. g. the terra firme forests over geologically very old bedrocks along the Rio Negro (TIESSEN et al. 1994). The estimation of the actual amount of nitrogen (N) available to plants by mineralization appears to be an essential parameter besides the determination of total nitrogen pools. In some cases literature reports considerable discrepancies between the N-pool in the soil and nitrogen concentration in the vegetation (GRUBB 1989). In these cases the nutrient supply to plants was much lower than suggested by the soil N-pool. Generally, nitrogen is readily available under tropical warm and moist climate (VITOUSEK 1984) because favorable conditions for mineralization exist in terms of soil reaction, soil texture, soil water, and especially temperature. Soil temperature is one of the limiting factors to N-mineralization at higher elevations (WILD 1989, SILVER 1994). Nitrogen-mineralization in lowlands is inhibited in waterlogged, anaerobic or strongly acidic soils. This situation applies to the *base cation* and *acidic sand soils* of the Río Avisado area. Due to the short period of investigation, mineralization rates were not assessed. However, parameters which influence mineralization like the C/N ratio and pH in soils were measured (BAILLIE 1989).

Additionally, the element composition of the organic layers may be of significance for plant nutrition beacause the majority of nutrient cycling in tropical forest soils takes place in these soil compartments (CUEVAS & MEDINA 1986, SWIFT & ANDERSON 1989). The exchangeable contents of the nutrients phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) were determined for the sampled soils using standard methods that had been developed to characterize the short-term availability of nutrients to crops. Regarding the characterization of the nutrient situation of tropical forests, WILD (1989) points out the shortcomings of these methods.

Especially in forest soils, long-term availability of nutrients may be supplemented by the weathering of primary minerals and seasonal fluvial deposition (BAILLIE 1989, BAILLIE et al. 1987). WILD (1989) proposed an analysis of total nutrient stock and a measurement or estimation of the rate of mineralization in addition to the analysis of easily exchangeable nutrient contents (see also BAILLIE 1989). For this purpose a mineralogical analysis of the soil might be useful to determine total potassium which is considered the most mobile nutrient (CUEVAS & MEDINA 1988) and thus easily leached in the mostly sandy soils of the study area. TANNER et al. (1989) emphasize multiple interactions between nutrients resulting in a limitation of plant growth. Various antagonistic effects exist between cations competing in root uptake processes (BAILLIE 1996, HINTERMAIER-ERHARD & ZECH 1997). Limitation in the growth rates of a forest stand is not necessarily caused by a low nutrient pool in the soil or a limited availability but imbalances in the proportions of the absorbed nutrients may be of significance (LINDER 1995). A crucial role in vegetation development is ascribed to magnesium (BAILLIE et al. 1987, CUEVAS & MEDINA 1988). Especially podzols which are represented in the *acidic sand* and *carbon subsoil soils* in the Río Avisado region but also *litter soils* were low in Mg (SCHACHTSCHABEL et al.1989, VAN WAMBEKE 1992). For a better assessment of existing nutrient deficiencies a combined sampling of nutrient contents in soil and plants is required as well as an estimation of the mineralization of nutrients and weathering of primary minerals.

BAILLIE (1989) advocates the existence of open nutrient cycles under conditions of good nutrient supply which is indicated by deeply rooted vegetation. Deepest rooting in the study area was observed in *Al / clay soils*. The root systems are generally shallow under vegetation with a closed nutrient cycle where nearly all nutrients are confined to organic matter and no near-surface weathering of nutrient rich substrate occurs. In the upper hill region BÖRNER (2000) observed a concentration of roots in the upper 20 cm of the solum. This was confirmed by the present study suggesting rather poor lithogenic nutrient supply and closed nutrient cycles, especially for the *acidic sand soils* of the Río Avisado region.

It was possible to prove in this study that soils differed significantly within the upper hill region and adjacent areas (cf. Fig. 4.1). Soil units were in some instances linked to topographic position. This is the case for *acidic sand soils* on plateaus, *litter soils* on steep slopes and *base cation soils* in ravines, on lower slopes, and in valleys. But soils especially along the slopes of the upper hill area vary on a small scale reflecting fine layers of contrasting substrate (BÖRNER 2000). Although soil units alone were not able to characterize or explain the vegetation distribution some strong correlations existed.

### 4.1.2 Above-Ground Biomass

**NULL-HYPOTHESIS II**

**Above-ground stand biomass is homogeneously distributed within the upper Río Avisado watershed.**

Five biometry clusters were formed based on parameters expressing the allocation of biomass in terms of stand density and tree dimensions. (cf. Fig. 3.20 - Fig. 3.29 in chapter 3.2.2). Biomass itself was not directly entered into analysis because it was derived from the data on stand density and tree dimensions. Nevertheless, all five clusters were clearly separated by statistical analysis *post-hoc* (cf. ANOVA results; Tab. 9.21 in Appendix 9.2.2.4). Therefore, hypothesis II must be rejected.

Biomass estimates for tropical rainforests vary greatly over the tropical belt (HOUGHTON et al. 2001). Many different estimation techniques have been applied leading to different results when scaled up to regional levels and beyond (CATCHPOLE & WHEELER 1992, HOUGHTON et al. 2001). Direct comparability of the results remains questionable due to different approaches and local variation of abiotic factors (FEARNSIDE et al.1993). In this regard, special attention should be paid to small scale variation of stands within each region. LAURANCE et al. (1999) hold mainly edaphic factors responsible for such variation on two accounts: a) Biomass on different soils varies due to altered species composition featuring different growth rates and b) the enhanced growth rates of a similar floristic set under more favorable soil nutrient status. In the hill region of the Río Avisado area patterns of highly variable stand biomass were first reported by BÖRNER (2000). Like in this study, BÖRNER (2000) surveyed her plots by the relascope technique choosing representative random samples of trees.

Regular techniques of forest inventory fail in low scrub vegetation since most methods include the stem diameter at a tree height (dbh) of 1.3 m. This height was rarely reached by the thin stems of this dense vegetation. Therefore, a biomass harvest was conducted for all above-ground parts of woody individuals. Monocotyledonous plants which frequently form a dense undergrowth as well as mosses or lichen were not included in order to comply with the approach taken in the forests. Thus biomass values in the *shrubland* and *open woodland* units must be considered to be minimal values.

In the upper hill region of the Río Avisado almost all recorded stands contain more than 1 000 stems per hectare (gbh > 10 cm), the average is 3 411 stems per hectare. The highest value is 7 519 stems per hectare on a ridge in the upper hill region. These findings are only slightly higher than in the study by BÖRNER (2000) who reported an average of 2 239 stems with a maximum of 5 347 stems per hectare for the upper and lower hill areas together. The study area of DEMPEWOLF (2000) is located to the west of the area considered here. Even higher counts of

up to 9 108 stems per hectare were found there. Stands with a large number of stems but moderate stand height were described by TANNER (1980) in the Blue Mountains in Jamaica. As possible reasons for this a limited supply of the nutrients N, P, K and Ca (cf. also TANNER 1985), low pH-values or moderate radiance were identified. Water stress as a reason was ruled out by TANNER (1977) in the Blue Mountains on the basis of long-term soil moisture measurements. METTE (2001) drew similar conclusions from moisture measurements at the Cerro Tambo near the study area.

Phosphorus supply is frequently critical in impoverished tropical soils. Contrary to C or N, no biological fixation or absorption from the atmosphere is possible. The P pool is nourished by the parent material of the soil (VITOUSEK 1984, WILD 1989). Positive correlations were found between the amount of litterfall and P concentrations in the litter of tropical lowland forests which indicated P limitation rather than N limitation in these forests (VITOUSEK, 1984). At low pH-values of 3.5 - 4.0 and high Al concentrations in the soil solution P forms aluminum phosphate complexes and is thus immobilized.

In the *short* and *dense forests* of the Río Avisado area P limitation is evident (cf. Fig. 3.30 in chapter 3.2.3.3). This is expressed by relatively low biomass values under conditions of high N pools but low P concentration in the soils. Better supply of phosphorus combined with similar N pools in the *tall forests* yielded significantly higher biomass. Both N and P supply and thus biomass were low in *shrubland* and *open woodland* accounting for the extremely low biomass there.

There was evidence that other edaphic factors did influence stand structure as well. Besides a strong correlation between biomass and topsoil P statistical analysis revealed further evidence for plant growth to be influenced by other nutrients which was already suggested by BAILLIE et al. (1987) and CUEVAS & MEDINA (1988) (cf. Tab. 3.7 in chapter 3.2.3.3). In this study, undecomposed litter, low pH values, and wide C/N ratios in the topsoil were negatively correlated to tree size indicating that mineralization was a strong estimator for plant nutrition (BAILLIE 1989, LAURANCE et al. 1999, WILD 1989). Exchangeable concentrations of magnesium and potassium in the subsoil correlated positively to tree size which also implies the significance of these nutrients to growth patterns in these forests.

In the investigation by BÖRNER (2000) aluminum concentrations only correlated significantly with the occurrence of smaller stems but no significant relationship was found between Al concentration and biomass. This is supported by the indifferent reaction of biomass to varying aluminum concentrations in this study. Fig. 3.30 in chapter 3.2.3.3 shows no clear trend because the highest biomass was produced by *tall forests* under fairly aluminum rich conditions whereas low aluminum saturation in the *open woodlands* yielded only about 10 % of the biomass from *tall forests* which surprisingly show high P levels together with high Al concentrations. Aluminum saturation of soils seems not to be an important limiting factor to plant growth.

It was demonstrated that biomass production and soil conditions were correlated. It can be concluded that results from biometric measurements lacked a distinct grouping for vegetation types. For example, in the *open woodland* unit and the *short forest* unit several structurally different stands were combined. However, stands of different nature and growth strategies achieved similar pools of overall biomass. Thus, biomass alone is not suitable as a criterion to describe vegetation types with fairly low forest biomass below 130 t per hectare. Although assignment of plots to biometric units did not yield uniform groups in terms of vegetation types it was possible to demonstrate and explain general trends in growth.

In conclusion, it is proven that above-ground stand biomass is not homogeneously distributed within the Río Avisado area.

### 4.1.3 Topography

**NULL-HYPOTHESIS III**

**There are no significant differences in vegetation patterns between different topographic situations.**

Both classification approaches could not characterize vegetation patterns in the Río Avisado at the desired resolution. In both cases units were synthesized which still combined vegetation types that were evidently different in their stand structure. In order to account for these differences a third classification approach was chosen to attain a more complete separation of the studied vegetation into robust units. For this purpose all parameters for soil and biometry were combined with recorded parameters describing stand structure (e. g. epiphyte and liana abundance, layering of the canopy, leaf sizes). Eight vegetation units were formed which were successfully linked to topographic positions by evaluating field observations on topography and a digital elevation map (cf. Fig. 3.58 in chapter 3.4.3). Therefore, hypothesis III must be rejected.

On a large regional scale, GRUBB (1989) describes altitudinal gradients in stand structure. He finds forests decreasing in stand height and being composed of more and slimmer individuals with increasing altitude. Stands of low stature in the moist tropical lowlands are generally ascribed to nutrient deficiencies. Similarly, TANNER et al. (1998) argue that, besides regular stands in tropical lowlands of heights 20 - 40 m, stunted forests shorter than 10 m occur on acidic soils at all altitudes. These stands suffer exclusively from nitrogen and / or phosphorus deficiency. Topography is held accountable for disturbance hazards (GRUBB 1989), for the difference in soil water and soil nutrient status (TIESSEN et al. 1994), and consequently for floristic and biomass variation (KLINGE & HERRERA 1983, LAURANCE et al. 1999).

In this chapter the implications of topography on the development and distribution of soils, on biomass and ultimately on vegetation will be discussed for all closed canopy forest formations of the Río Avisado region. Since the topographic and edaphic conditions of the *wet* and *dry chamizales* differed completely from all other sites the occurrence of these heath forest types will be discussed separately later in this chapter.

## Soil

Most authors consider the altitude of 1 000 m a.s.l. to be within the transitional zone between tropical lowland and montane vegetation (CAVELIER 1996, FUKAREK et al. 1995, GENTRY 1992, HUECK 1966, INRENA 1996, READING et al. 1995, WHITMORE 1991, YOUNG 1992). Therefore, no assumptions could be made whether lowland conditions expressed by P limitation (N readily available due to good mineralization but too acidic for P to be plant-available) or montane conditions expressed by N limitation (due to inhibited mineralization at lower temperatures) would prevail (cf. GRUBB 1989, LAURANCE et al. 1999, VITOUSEK 1984). DEMPEWOLF (2000) found an accumulation of organic material in soils with increasing elevation on a vertical 600 m transect west of the study area suggesting an increasing limitation by nitrogen due to slow mineralization (CÔUTEAUX et al. 2002).

The altitudinal gradient within the Río Avisado area of this study was negligible. Thus, focus was on small scale variation of topography and soils. In Fig. 4.1 (A) (page 85, above) the vegetation types are arranged according to their topographic position in the hill area. The topographic gradient from upslope positions downwards is seen in the arrangement of vegetation types from left to right. Soils found under *shapumbales*, *palm rich rainforests* and *premontane rainforests* were fairly consistent whereas several different soil types were combined in the vegetation units on slopes (*impoverished*, *dry*, and *low canopy rainforest*). This may be due to the fact that geological substrate varies greatly and drives variation in texture of the parent material in the upper hill region. This was confirmed by BÖRNER (2000) who examined a soil catena on a slope gradient of 70 m in the lower hill area. The nutrient dynamics of the upper hill area seem to resemble lowland conditions (cf. chapter 3.3) since the plant growth is obviously limited by phosphorus rather than by nitrogen (cf. Fig. 3.17, Fig. 3.30 & Fig. 3.53). An exception to this are frequently waterlogged soils of the *palm rich rainforests* where both exchangeable P concentrations in the mineral soil and total N concentrations are comparable with *premontane rainforests* but biomass of the *palm rich* type is less than half of that of the *premontane rainforest* (cf. Fig. 3.53). The high P concentration in comparison with all other forest types of the upper hill region can be explained by the flushing of nutrients from upslope (GRUBB 1989) and by the constantly high water content which causes reducing soil conditions. TIESSEN et al. (1994) claim that such reducing soil conditions suppress the accretion of sesquioxide cementations which are

known to have a high P-sorption capacity due to their large surface area. Thus, the exchangeable P fraction in such water saturated soils may be high whereas the anaerobic conditions inhibit any microbial mineralization of the organic matter that accounts for the high $N_{tot}$ values. It can be concluded that *palm rich rainforests* are the only forest type in the study area suffering from N limitation.

No direct symptoms of aluminum toxicity were found. Most biomass was developed by the *premontane rainforests* under conditions of equally high aluminum saturation as in any other forest types of the upper hill region. Investigations by BÖRNER (2000) showed that several plant species occurred in the natural forests of the study area that are known to be extremely tolerant to high levels of aluminum. METTE (2001) found extremely high Al concentrations in leaves of Melastomataceae which can be shed in order to dispose of such excess toxic elements. This is a known strategy to cope with toxicity (GRUBB 1989).

## Biomass

In the previous paragraph, a close relation was recognized between topography and soil fertility. LAURANCE (1999) reports a close link between nutrients and biomass. In his study in the Amazon lowlands, soil fertility accounts for one third of the biomass variation. He found positive correlations between biomass and total nitrogen, base cations and clay whereas aluminum and sand influenced biomass negatively. Of his conclusions, only the positive effect of base cations on biomass can be affirmed by this study.

In Fig. 4.1 (B) (page 85, above) biometric units follow the decreasing slope gradient quite strictly which is another direct indication for a link between biomass and topography. ONe exception is the biometric units assigned to the *impoverished rainforest,* which are predominantly associated with ridge positions. There, a return from the *dense* to the *short forest* is observed. In this case, however, nomenclature is misleading since individuals of the *impoverished rainforest* tend to be slightly larger than in the forest types further downslope (cf. Fig. 3.26 and Fig. 3.27 in chapter 3.2.2). This is in accordance with observations by GRUBB (1989) who stated that stands on ridges are higher than on slopes especially for unstable soils which are found particularly in the upper hill region.

According to values for biomass the vegetation units can be merged into three groups (cf. Fig. 3.29 in chapter 3.2.2): a) productive stands with biomasses above 200 tons per hectare (*impoverished rainforests*), b) all stands on impoverished soils in the *hill region* with biomasses slightly above 100 t $ha^{-1}$, and c) unproductive stands such as the *chamizal* and *shapumbal* vegetations with biomasses below 50 t $ha^{-1}$.

***Tab. 4.1: Biomass, stand height, and basal area of tropical rainforests.***

*Findings from this study are compared in respect to their stand biometry to potentially corresponding rainforests types from literature to a) Premontane rainforests, b) impoverished rainforests, and c) heath forests.*

| Forest type | Location | Elevation m a.s.l. | Above-ground biomass t ha$^{-1}$ | Stand Height m | Basal area m² ha$^{-1}$ | Source |
|---|---|---|---|---|---|---|
| **a) PREMONTANE RAINFORESTS** | | | | | | |
| Terra firme forest | Rio Xingu, Brazil | - | 254 | - | - | HEINSDIJK (1958) [1] |
| Tropical forest | Sao Miguel de Guama, Brazil | - | 253 | - | - | GLERUM & SMIT (1962) [1] |
| Dry monsoon-rain forest | Chiang Mai Province, Thailand | 500 | 267 | < 26 | 35.4 | OGAWA et al. (1965) |
| Lower montane rain forest | Luquillo Natl. Forest, Puerto Rico | 510 | 146.5-246.7 | 30 | 36.0-41.0 | OVINGTON et al. (1970) [1] |
| Tropical moist forest | Panama | - | 269 | - | - | GOLLEY (1975) [1] |
| Tropical seasonal evergreen forest | Magdalena Valley, Colombia | - | 252 | - | - | FÖLSTER et al. (1976) [1] |
| Lower montane rain forest | Sierra de Chamá, Guatemala | 900 | 457-499 | < 40 | 46.0 | KUNKEL-WESTPHAL et al. (1979) [5] |
| Tropical montane wet forest | India | - | 457 | - | - | RAI (1981) [2] |
| Productive broadleaf forest | Tropical America | - | 155 | - | - | BROWN & LUGO (1984) |
| Tropical evergreen submontane forest | Brazil | - | 268 | - | - | KAUFFMAN et al. (1995) [1] |
| Tropical montane wet forest | San Carlos de Rio Negro, Venezuela | - | 314 | - | - | DELANEY et al. (1997) [1] |
| Tropical lower montane moist forest | San Carlos de Rio Negro, Venezuela | - | 346 | - | - | DELANEY et al. (1997) [1] |
| Valley forest | Alto Mayo, Peru | 830-980 | 240 | < 30 | 40.0 | DEMPEWOLF (2000) |
| Lower slope rainforest | Alto Mayo, Peru | 850-1000 | 192 | < 30 | 35.2 | BÖRNER (2000) |
| **Premontane rainforest** | **Alto Mayo, Peru** | **920-1100** | **239** | **< 36** | **30.1** | **DIETZ (2002)** |
| **b) IMPOVERISHED RAINFORESTS** | | | | | | |
| Low Amazon Caatinga | San Carlos de Rio Negro, Venezuela | - | 170 | < 11 | - | KLINGE & MEDINA (1979) |
| Tropical premontane moist forest | - | - | 170 | - | - | DEANGELIS et al. (1981) [2] |
| Unproductive broadleaf forest | Tropical America | - | 89 | - | - | BROWN & LUGO (1984) |
| Premonate tropical forest | Bajo Urubamba, Peru | - | 124 | - | - | ONERN (1990) [1] |
| Tropical evergreen forest | San José de Cabitu, Beni, Bolivia | - | 166 | - | - | KUDRENECKY (1993) [1] |
| Dense tropical moist forest | Amazonia, Brazil | - | 226 | - | - | HIGUCHI et al. (1994) [1] |
| Dense tropical moist forest | Amazonia, Brazil | - | 185 | - | - | HIGUCHI et al. (1994) [1] |
| Hill forest | Alto Mayo, Peru | 870-1300 | 202 | > 25 | 36.0 | DEMPEWOLF (2000) |
| Upper slope hill forest | Alto Mayo, Peru | 850-1000 | 138 | < 20 | 33.2 | BÖRNER (2000) |
| **Semi-deciduous hill forest** | **Alto Mayo, Peru** | **900-1000** | **107** | **< 20** | **27.5** | **DIETZ (2002)** |
| **c) HEATH FORESTS** | | | | | | |
| Muri heathland | Coastal Guyana | - | - | 1.8-4.5 | - | FANSHAWE (1952) [6] |
| Heath forest | Kampuchea, Cambodia | - | 145 | - | - | HOZUMI et al. (1969) [4] |
| Swamp forest | Kampuchea, Cambodia | - | 11 | - | - | HOZUMI et al. (1969) [4] |
| Padang heathland | Bako Natl. Park, Sarawak, Borneo | - | - | 0.5-7 | - | SPECHT & WORMERSLEY (1979) |
| Campina | Rio Negro, Brazil | - | - | 1.5-15 | - | KLINGE & MEDINA (1979) |
| Bana forests | San Carlos de Rio Negro, Venezuela | - | - | - | 20-31 | BRÜNIG et al. (1979) [3] |
| Open forest | Tropical America | - | 33-77 | - | - | BROWN & LUGO (1984) |
| Heath forest | Alto Mayo, Peru | 900-1400 | 5-162 | < 18 | 5-35 | DEMPEWOLF (2000) |
| Heath forest | Alto Mayo, Peru | 1200-1400 | 7-50 | 3.5-9 | 15-40 | METTE (2001) |
| **Chamizal** | **Alto Mayo, Peru** | **980** | **7-32** | **2-8** | **4-13** | **DIETZ (2002)** |

[1] from HOUGHTON et al. (2001) [2] from BROWN & LUGO (1984) [3] from BRÜNIG (1983) [4] from GOLLEY (1983) [5] from CANNELL (1982) [6] from COOPER (1979)

Above-ground biomass estimates for *premontane rainforests* after OGAWA et al. (1965) were comparable to values from literature listed in Tab. 4.1. Values for unproductive semi-deciduous forests in wet tropical regions are rare. Average above-ground biomasses for the impoverished upper *hill region* are relatively moderate compared to other studies. They agree best with biomasses found by ONERN (1990, cited in HOUGHTON et al. 2001) at the lower Urubamba River

of Peru, where forests were also classified as “moist forest of the upper hills” by INRENA (1996). Little information is available on above-ground biomass of heath forests. Compared with values provided by literature stand characteristics of *chamizales* are comparable but biomass is low relative to other tropical heath forests. However, above-ground biomass of the *chamizal* vegetation is within the range reported previously for heath forests in the study area (DEMPEWOLF 2000, METTE 2001).

## Vegetation

Studies in the dipterocarp rainforests of Sarawak led BAILLIE et al. (1987) to the conclusion that the profundity of soils and topography determined the diversity and physiognomy of the vegetation. In the study area, it was possible to arrange the vegetation units shown in Fig. 4.1 (page 85, above) along a downslope gradient of their topographical position. The best match between vegetation type and topography was seen for the *chamizales* on plateaus and will be discussed later in this chapter.

*Shapumbales* constitute an exceptional and presumably dynamic vegetation formation found frequently in the upper hill area. A “*Gleichenia* thicket ecotone” is reported for warm temperate zones at 2 400 m a.s.l. in Sumatra (READING et al. 1995) but *Sticherus remotus* has also been observed as a dominant colonizing species in the Peruvian lowlands (PINO GARAY 2002, *pers. communication*). The occurrence of these fern dominated woodlands is difficult to ascribe to edaphic site conditions since this vegetation type seems closely linked to natural disturbances which are difficult to predict. Potential *shapumbal* sites could be only identified by instable geology and steep upper slopes (cf. Fig. 3.58 in chapter 3.4.3). Tree canopy of this vegetation type as seen from vertical projection is still dense and obstructs clear identification of these stands by optical remote sensing techniques. On the ground, *shapumbales* can be recognized by the high amount of stems visible from a lateral perspective.

The pronounced dry season between June and August apparently leads to the formation of semi-deciduous forest types in the study area. Investigation began within these months when all forest types with the exception of the *palm rich forests* and the *chamizales* clearly showed deciduous individuals in their stands. This was especially pronounced in the *dry rainforest* indicating a temporary water shortage within the area during the dry period which was confirmed by METTE (2001) who found that forest stands on the Cerro Tambo exhaust all soil water during the dry season.

*Impoverished rainforests* are primarily found on ridges where soils are poorest in nutrients. These sites are frequently characterized by deeply weathered podzols with a low water retention capacity due to their sandy texture. GRUBB (1989) mentions the susceptibility of soils to drought in

such topographic positions. *Dry rainforests* occur on upper slopes where asandy substrate still prevails but some input of moisture and nutrients is provided by lateral flow. Species richness and the density of slender stems increases under these conditions (GRUBB 1989, LAURANCE et al. 1999). *Low canopy rainforests* on the lower slopes suffer from inherently poor soil conditions but profit from nutrients flushed in from upslope (TIESSEN et al. 1994) which can be better retained in soils containing higher amounts of clay. Their stature of rich understoreys up to 10 m high and a single canopy at 20 - 25 m resembles the description by READING et al. (1995) for lower montane rainforests. *Palm rich rainforests* are found in ravines (*barrancos*) or tight valleys of the upper hill area on permanently wet soils or along small streams. Theses stands were dominated by the palm *Jessenia bataua* which is characteristic of seasonally waterlogged soils of mixed tropical rainforest on hills (KLINGE & HERRERA 1983). *Premontane rainforests* are restricted to wide valleys or gentle slopes on rather clayey but well drained soils which BAILLIE et al. (1987) considers to be prerequisites for the formation of productive lowland rainforest. Stand structural properties combine characteristics of tropical evergreen rainforest and tropical lower montane rainforest in the sense of WHITMORE (1991).

In the forest type map of Peru (INRENA 1995) the entire upper hill region is classified as “bosque humedo de las colinas altas” (moist forest on upper hills). This forest type is not very common covering only 1.4 % of the territory of Peru. It is described to be stratified clearly up to a height of 35 m on moderately dissected terrain. Based on this study this classification is questionable. A list of characteristic timber species for this forest type is provided by INRENA (1996) but floristic data are lacking in this study. However, the underlying relief must be described as highly dissected (cf. Fig. 3.59 in chapter 3.4.3). Clear strata were not found (cf. Fig. 3.51 in chapter 3.3.2.3) and stand heights of 35 m were never reached within the upper hill region. The same forest type occurs also along the lower Río Urubamba in the south of Peru. Investigations at the lower Río Urubamba reported a similarly low biomass stock as found in the Río Avisado area (cf. Tab. 4.1).

***Tab. 4.2: Occurrence and classification of tropical heath forests.***
*Findings from this study are compared in height to sclerophyllous closed scrub formations and heathlands of different nomenclature which are described from other tropical regions of Asia and South America.*

| Formation | Soil Moisture | Borneo | Guyanas | Rio Negro / Amazon River | Peruvian Amazon | Alto Mayo |
|---|---|---|---|---|---|---|
| Sclerophyllous closed scrub | Excessively drained | Padang scrub<br>2 - 7 m | Muri scrub<br>2 - 3 m | Low campina / bana<br>3 - 10 m | Varillal<br>10 m | **Dry chamizal**<br>**< 10 m** |
| Heathland | Waterlogged | Padang heathland<br>< 2 m | Bush islands<br>< 1.5 m | Low campina / bana<br>1.5 - 3 m | Chamizal<br>< 3 m | **Wet chamizal**<br>**< 4.5 m** |
| | References | SPECHT & WORMERSLEY (1979) | COOPER (1979) | KLINGE & MEDINA (1979) | RUOKOLAINEN & TUOMISTO (1993) | **DIETZ (2002)** |

## Heath Forest

The most conspicuous and locally best defined vegetation types in the Río Avisado area were the open and stunted scrubs and woodlands of the *wet* and *dry chamizales*. Similar formations have been described under the general name of heath forests in literature. Due to their unique soil and vegetation properties these vegetation types will be discussed here as a whole.

Heath forests occur as locally well defined vegetation formations throughout the humid tropical lowlands although local names and scientific nomenclature varies (Tab. 4.2). Other reported sites of heath forests closest to the study region are located in the lowlands of eastern Peru (PRANCE 1989, RUOKOLAINEN & TUOMISTO 1993).

This formation is commonly characterized as a xeromorphic or sclerophyllous scrub community (COOPER 1979, RICHARDS 1996, SPECHT & WORMERSLEY 1979) of perhumid tropical lowlands (WHITMORE 1995). According to SPECHT & WORMERSLEY (1979) the occurrence of tropical heath forests has a distinct gap between lowlands and subalpine regions; only in Borneo they can also be found at elevations between 1 000 - 2 000 m a.s.l. (RICHARDS 1995). All heath forest types are exclusively found on slightly elevated sites featuring extremely nutrient poor, leached, white sandy soils which are drained by black water rivers (BRÜNIG 1983, COOPER 1979, METTE 2001, PRANCE 1989, SPECHT & WORMERSLEY 1979, WHITMORE 1995). Those soils form either on mostly Pliocene / Pleistocene alluvial or litoral sand deposits or are bleached *in situ* as ground water podzols resulting in substrates of almost pure quartzitic sand (BRÜNIG 1983, SARMIENTO & MONASTERIO 1975, SPECHT & WORMERSLEY 1979). Heath forests developing in seasonal savannas or peat swamps on mesa-like outcrops of sandstone, where a hardpan at the place of an ancient water table impedes drainage, are well described for South America by SARMIENTO & MONASTERIO (1975) and for Asia by BRÜNIG (1983). Although it seems questionable

to assume lowland conditions for the study region all the above characteristics of heath forests correspond to observations made during this study.

Most authors consider heath forests as pedobiomes or rather peinobiomes in the sense of WALTER & BRECKLE (1984) since extremely adverse edaphic conditions are held responsible for the reduced plant growth (FERRI 1960 in KLINGE & MEDINA 1979, KLINGE et al. 1990). Soils are described to be either of coarse texture with a low water retention capacity or mostly waterlogged due to a shallow duripan (BRÜNIG 1983, KLINGE & MEDINA 1979, RICHARDS 1996, SARMIENTO & MONASTERIO 1979). Heath forest soils are commonly strongly acidic reaching toxic levels of hydrogen ions (WHITMORE 1989) below the range of aluminum buffering (pH < 4) and are inherently low in sesquioxides (RICHARDS 1996) although SPECHT & WORMERSLEY (1979) report fairly high iron concentrations which were confirmed in the *chamizales* of the study area. Macro-nutrients such as N and P are low in all white sand soils (CUEVAS & MEDINA 1986, 1988, SPECHT & WORMERSLEY 1979, VITOUSEK 1984, cf. also Tab. 3.4 in chapter 3.1.3.3). Due to the extreme scarcity of nutrients special strategies for phosphorus conservation have been reported in such plants (VITOUSEK 1984). Symbiontic relationships with termites as mentioned by WHITMORE (1991) were also observed in the study area on waterlogged sites. RICHARDS (1996) points out that precious nutrients stored in evergreen leaf tissue are protected from herbivory by the production of toxic phenols which in turn requires an efficient mycorrhizal activity since microbial mineralization of leaf litter is reduced by these substances (WHITMORE 1989). Slow mineralization in the study area is indicated by the build-up of peat-like organic layers with wide C/N ratios (cf. Fig. 3.36 in chapter 3.3.2.1).

Although water stress is not considered to be crucial in the development of *campinas* (KLINGE & MEDINA 1979) or in the heath forests on the slopes of the Cerro Tambo (METTE & ZIMMERMANN 2002) short dry spells of 6 - 8 days or even a short dry season may occur. According to BRÜNIG (1983), water stress under either poor or excessive drainage is the key factor for the development of heath forest vegetation. Both situations are found on the white sand plateaus in the Río Avisado area. Waterlogged conditions are found in the center whereas soils toward the rim of the plateaus drain deeply.

Indications for nutrient and moisture conditions which mutually enhance their restrictive effects on plant growth can be found in the *chamizales* of the study area. It was observed that rooting depth in these soils was extremely shallow and concentrated in the organic horizons due to nutrient scarcity in the mineral soil (cf. chapter 4.1.1). Waterlogged conditions prevailed in *wet chamizales* due to impeded drainage by a shallow hardpan less than 40 cm below the mineral soil surface. However, roots were observed reaching not further than 10 cm into the mineral horizon possibly due to an extremely low pH. In this case, a minimal drop of the ground water level may have a significant impact on the water supply for the vegetation. Therefore, edaphically induced restrictions of the root system may limit the water uptake from such soils.

***Tab. 4.3: Floristic elements linking the*** chamizales ***of the Alto Mayo with other tropical heath forests.***
*Plant families, genera and/or species listed are taken from literature where they were considered to be characteristic for certain heath forest types. All floristic elements listed were also encountered on the* dry *and/or* wet chamizales *in the study area during an incomplete, preliminary floristic inventory.*

| Family | Genus | Species | Heath Forest Location | Reference |
|---|---|---|---|---|
| Evergreen sclerophyllous | | | all tropics | KLINGE & MEDINA (1979), RICHARDS (1996), SPECHT & WORMERSLEY (1979) |
| Ericaceae | | | all tropics | PRANCE (1989), |
| Lycopodiaceae | *Lycopodium* | | all tropics | KLINGE & MEDINA (1979) |
| Sphagnaceae | *Sphagnum* | | all tropics | KLINGE & MEDINA (1979) |
| Cyperaceae | *Carex* | ssp. | all tropics | PRANCE (1989), RICHARDS (1996) |
| Humiriaceae | *Humiria* | *balsamifera* | South America | PRANCE (1989), RICHARDS (1996) |
| Melastomataceae | *Graffenrieda* | sp. | Chamizal, Peruvian Amazon | RUOKOLAINEN & TUOMISTO (1993) |
| Arecaceae | *Mauritiella* | sp. | Chamizal, Peruvian Amazon | RUOKOLAINEN & TUOMISTO (1993) |
| Clusiaceae | | | Varillal, Peruvian Amazon | RUOKOLAINEN & TUOMISTO (1993) |
| Clusiaceae | *Clusia* | ssp. | Campina / Bana, Rio Negro Muri, Guyana | PRANCE (1989), RICHARDS (1996), SPECHT & WORMERSLEY (1979) |
| Melastomataceae | *Miconia* | ssp. | Campina, Brazil | KLINGE & MEDINA (1979) |
| Nyctaginaceae | *Neea* | sp. | Campina, Brazil | KLINGE & MEDINA (1979) |
| Orchidaceae | | | Campina, Brazil Padang, Borneo | PRANCE (1989), SPECHT & WORMERSLEY (1979) |
| Arecaceae | *Mauritia* | sp. | Bana, Venezuela | RICHARDS (1996) |
| | *Cladonia* | | Bana, Venezuela | PRANCE (1989) |

Heathland vegetation is genuinely evergreen (RICHARDS 1996, SPECHT & WORMERSLEY 1979) but BRÜNIG (1969, cited in WHITMORE 1991) found for eight heath forest species in Borneo that heath forest species are as sensitive to desiccation due to water shortage as rainforest species. Thus, given a low water supply, a number of strategies must be sought to minimize evaporation. Many examples are given in literature which applied to the *chamizales* of the study region as well. Among such strategies are the avoidance of direct insolation by nearly vertical positions of the leaves (BRÜNIG 1983, KLINGE & MEDINA 1979, PRANCE 1989, SPECHT & WORMERSLEY 1979, WHITMORE 1991) or avoidance of heating of their shiny and light colored leaves (WHITMORE 1991). According to WHITMORE (1991) *"other adaptations reduce water loss from the heath forest as a whole. These are the clustering of leaves, the clustering of leafy twigs into dense subcrowns, and perhaps also the very uniform forest canopy top surface which by its smoothness reduces turbulent mixing of air"*. A smooth and even canopy structure of heath forests can be easily recognized from the air (RICHARDS 1996, SPECHT & WORMERSLEY 1979). This is particularly true for the *chamizal* sites of the study area which were identifiable by their smooth texture in aerial photographs (see Fig. 3.61 in chapter 3.4.3 and Fig. 9.6 in Appendix 9.3.1).

Palms were reported to occur in the chamizales of the upper Amazon river (RUOKOLAINEN & TUOMISTO 1993) and in Neotropical peat swamps (SARMIENTO & MONASTERIO 1975). Palms were observed on patches within the *wet chamizal* (see Fig. 3.66 in chapter 3.4.3) which suggest locally permanent water saturation of the soil. Thus, differences in soil moisture created small scale patterns within the stand. These patterns could be reinforced due to a higher resistance of such permanently wet sites to fires which occasionally affect heath forests (COOPER 1979, KLINGE & MEDINA 1979, SPECHT & WORMERSLEY 1979). Edaphic conditions are also held accountable for the gradual transition from well drained sites supporting higher vegetation to more stunted stands on waterlogged soils which is also reflected in the floristic composition of the higher and lower formations (cf. Tab. 4.2 and Tab. 4.3). This is, however, in contrast to observations by METTE (2001) who documented sharp transitions between heath forests and bordering rainforests on the slopes of the Cerro Tambo west of the study area. Heath forests of similar floristics occur there on slopes of white sandstone instead of sandy deposits. Due to the inclination of the terrain waterlogged sites do not exist there. Instead of differences in moisture regime of the soils only different depths were encountered under heath and rainforest on the Cerro Tambo. It may be hypothesized that heath forests on such slopes occupy shallow initial soils of former landslide locations. This hypothesis should be tested by further investigations.

## Conclusion

The combined analysis and classification approach resolved the vegetation patterns better than all previously performed approaches. It was modified and refined *post-hoc* according to structural and topographical aspects. Erratic effects were observed indicating that it was difficult to find common characteristics for the entire study region. Two plots which were assigned to supposedly inappropriate units were recorded in the region of the Cordillera Cahuapanas where geological and microclimatic conditions differ from the upper hill region (METTE 2001). The influence of soil parameters in the presented classification approach appears to be high since questionable assignments could be reproduced best if considering edaphic factors. Fertilizer experiments as well as further investigations on foliar nutrients (VITOUSEK 1984) and the mineralization dynamics are required to verify these assumptions. Although indications were found that plant growth is limited by phosphorus deficiency on most sites, soils appear to be only one factor behind the development of different vegetation types. Topographic and consequently stand climatic factors are likely to influence the distribution of all vegetation types.

Quantitative approaches such as soil and biomass assessment alone are not able to produce a robust distinction between vegetation types (cf. Fig. 4.1). Nevertheless, for evaluations on a larger scale, biomass as a descriptive parameter may serve well to characterize an entire ecosystem such as the upper hill area although stand height, at higher resolution than presented, would be a much better estimator to describe the observed vegetation patterns. Stand biomass

*per se* does not permit a non-ambiguous separation of vegetation types (e. g. *low canopy*, *dry* and *impoverished rainforests*, or *dry chamizal* and *shapumbal*) which pursue different strategies of biomass allocation within the stand but yield similar overall biomass.

### 4.1.4 Simplified Classification

**NULL-HYPOTHESIS IV**

**Separation of the Río Avisado forest types requires comprehensive information on both: edaphic site conditions and stand structure.**

A vegetation classification scheme was developed excluding of soil parameters. The idea was to create a straight forward guideline for assessing the vegetation in the upper Río Avisado area based on parameters which are easy to determine in the field. Seven parameters were chosen from the dataset which showed statistically most significant differences between the groups that were separated in each step (cf. ANOVA results; Tab. 9.22 in Appendix 9.2.2.4). Fig. 4.2 depicts the decision pattern for this classification scheme. Since it was shown that a robust classification could be achieved under the exclusion of soil parameters, hypothesis IV must be rejected.

Initially, it is differentiated between open and closed canopy formations to account for the low biomass and low tree formations such as *shapumbal* and *chamizales*. As a measure of crown cover the proportion of small leaves in the lowest layer is used. It was the parameter which most significantly separated both groups. A high proportion of small leaves (≤ 4 $cm^2$) in the shrub and lower canopy layers (> 10 %) reflects the lack of a protective shield by a dense canopy layer. Stands of the open canopy group are eventually examined for the number of woody individuals shorter than 2 m. High rates (> 3 000 stems $ha^{-1}$) indicate shrub land or *wet chamizal*. Low stand densities of up to 3 000 stems $ha^{-1}$ are characteristic for woodland types. Distinction is made between *dry chamizal* on moderately sloped terrain (≤ 5°) and *shapumbal* on steep slopes (> 5°). Stands of the closed canopy group are distinguished based on their number of tall trees (> 20 m). If the number of tall trees exceeds 50 individuals per hectare tall stands of alluvial plains and terraces will be identified as *premontane rainforest* vegetation. All stands with less than 50 tall individuals per hectare are attributed to sloped terrain of the hill areas or the foothills of the Cordillera Cahuapanas. In the next step the number of palms is evaluated. High palm abundance (> 100 individuals $ha^{-1}$) indicates moist conditions and therefore *palm rich rainforest* vegetation. In all remaining stands the number of thick stems greater than 70 cm in diameter is assessed. Several stems of such dimensions (> 4 per hectare) point to better and more stable growth conditions which can be found in *low canopy rainforest*. The final distinction between *dry* and

*impoverished rainforest* is made based on the proportion of small leaves (≤ 4 $cm^2$) in the top tree layer which was the only statistically valid parameter to distinguish between these units. High proportions of leaves of this class (> 20 %) indicate *dry rainforest*.

It turns out that all parameters applied for separation can be interpreted to be functional for each corresponding unit or super-ordinate group. Thus, it proved possible to classify the vegetation of the study area with statistical significance by simple means of field observation.

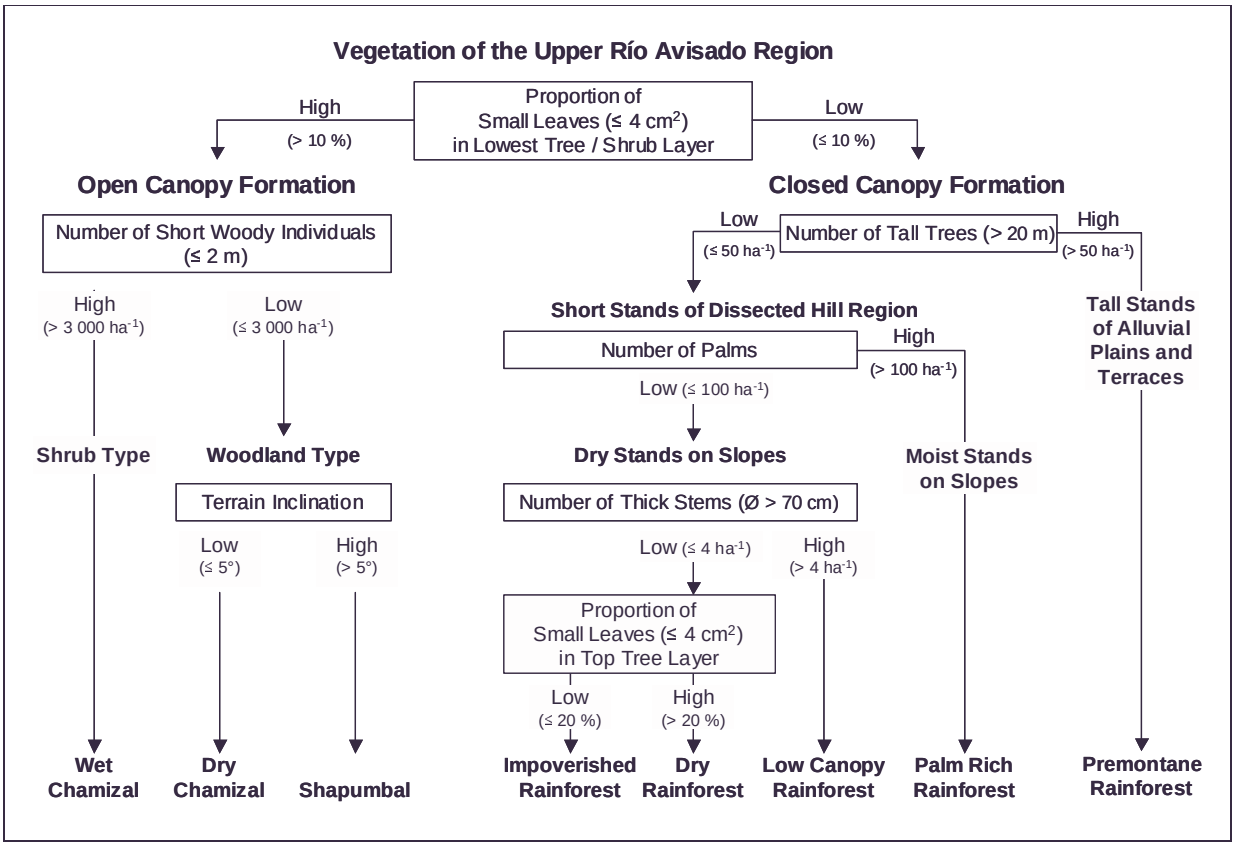



***Fig. 4.2: Proposed key for ground based classification of vegetation units in the study area.***
*The units were produced by combined analysis of all assessed parameters. The classification scheme is based primarily on significantly different parameters of above-ground biometric, structural and topographic site characteristics.*

## 4.2 Ecological Evaluation

Soils in the highly dissected upper hill region at the Río Avisado are inherently poor in nutrients. On the dystric soils of the region, closed nutrient cycles exist which are particularly sensitive to disturbance (SARMIENTO & MONASTERIO 1975). Given the predominantly steep relief which affects soil water conditions and landslide hazards, these soils are not sustainable for any land use (TIESSEN et al. 1994). Since the loss of vegetation leads to rapid soil degradation when the scarce nutrients are quickly mineralized from organic material under higher soil temperature due to direct insolation. The lack of root mats and the predominantly sandy texture of the soils yield a low water retention capacity, increased leaching of nutrients and soil erosion are the result on the steep relief (see Fig. 2.10 in chapter 2.1.6). Secondary growth would be forced to re-establish a structure of intact nutrient cycles (TIESSEN et al. 1994). Successful re-growth of vegetation after land use is unlikely on the soils in the upper hill region. This area is limited for agricultural use *per se* due to their infertility, strong acidity, poor water holding capacity, and high aluminum content (LAURANCE et al. 1999, VAN WAMBEKE 1992). High aluminum saturation was found to be influential on the phosphorus dynamics and would render fertilization ineffective unless soil pH and texture were improved simultaneously. Such soil treatment is not economically feasible under the topographic and edaphic preconditions in the upper Río Avisado area. Aluminum toxicity obviously does not directly harm the natural vegetation of the upper hill area since species occurring naturally on these sites are adapted to high aluminum levels (METTE 2001). However, crop plants quickly suffer from nutrient deficiency (GRUBB 1989). LAURANCE et al. (1999) point out that the damage of pasture use of such infertile soils is both immediate and irreversible. He proposes that the natural forest is the only sustainable plant cover under such edaphic conditions.

The forests of the upper hill region do not possess biomass stocks for suitably economic timber exploitation. Large trees are very rare and accessibility to this remote area is difficult. Also, forest growth rates and productivity are too low to support forestry (ZIMMERMANN et al. 2001). Forest stands producing considerable timber for extraction are only found in wider valleys near the flanks of the Cordillera Cahuapanas. However, the same problems of accessibility also apply there. The forests of the study area are classified as "*bosques humedos de las colinas altas*". This forest type is suggested to be subject to ecological protection (INRENA 1996).

Protection is particularly recommended for the *chamizal* areas of the Río Tioyacu and Río Avisado watersheds. WHITMORE (1989) concluded that heath forests are truly fragile ecosystems which cannot sustain agriculture. Also SARMIENTO & MONASTERIO (1975) claim such hydromorphic soils to be unfavorable for plant growth in general and consider them the *"poorest soils of tropical America"*. PRANCE (1989) found a rate of endemism greater than 50 % in Venezuelan *muri* vegetation. If similar rates can be confirmed for *chamizales,* the need for the conservation of this unique and fragile vegetation form will be evident in order to the protect the biodiversity in the region.

## 4.3 Outlook

The short investigation period available for this study required a concisely recorded data set. In some instances during the evaluation, a richer dataset would have been desirable. Some results of this study remain tentative at this point and will require confirmation by further investigation. However, based on the results of this study several approaches to further investigation seem promising in order to enhance the dataset for the intended ecological evaluation:

- A soil inventory of the Río Avisado region has been conducted by BÖRNER (2000) and by the present study. However, data on nutrient cycling are still lacking. METTE (2001) looked at nutrient distribution in biomass, but his investigation was restricted to a small area within the studied region and included only two contrasting vegetation types.
- In order to fully understand the nutrient budgets of the study area and to confirm indications on nutrient limitations, representative measurements for below-ground biomass, mineralization rates, nutrient storage in biomass, and leaf area should be considered.
- The generation of a high-resolution digital elevation model from stereoscopic aerial photography proved successful. A GIS based overlay of derived topographical data in combination with geology and readily available data on biomass and water budgets should be implemented as a proper tool to characterize, survey and model the ecological implications of anthropogenic influences on the studied watersheds.
- Further hypotheses can now be formed on different succession dynamics in the landscape to explain the occurrence of heath forests on the slopes of the Cerro Tambo or the *shapumbal* vegetation in the upper hill region. Attempts to characterize vegetation dynamics should be supported by specific investigations and inventories of the floristic diversity of the region.

# 5 Summary

- Eight forest types were classified in the Río Avisado and Río Tioyacu region using Principal Component Analysis and subsequent Hierarchical Cluster Analysis for data describing soil, biomass and vegetation structure. Most forest types could be ascribed to certain topographic features.
- Soils of the upper hill area are generally strongly acidic and poor in nutrients. The vegetation of the upper hill area tends to be limited by phosphorus deficiency. Links between topographic situation and soil properties exist, but soils alone are not suitable to completely characterize the variation and distribution of forest types.
- Forest biomass stocks within the upper hill region of the Río Avisado and on the piedmonts of the Cordillera Cahuapanas are remarkably low compared to rates published for productive lowland and premontane rainforests.
- A simple regression formula based on height and girth was established for the prediction of biomass for the palm *Jessenia bataua* (Arecaceae).
- The highest stands of low statured heath forests reported in tropical America, besides the paramo vegetation, were found at 1 000 m a.s.l., and a biomass harvest was conducted to establish the living above-ground biomass.
- Due to their extremely fragile nutrient cycles and a presumably high rate of floristic endemism, patches of heath forest vegetation (*chamizales*) are recommended for protection for permanent conservation.
- Natural disturbances (landslides and / or fires) occur and probably trigger a conspicuously open woodland (*shapumbales*) with a dense undergrowth of ferns (predominantly *Sticherus remotus* and *Gleichenella pectinata*, both Gleicheniaceae).
- The soils and vegetation of the Río Avisado region are not suitable for economically and ecologically sustainable land use.

# 6 Literature


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# 7 Glossary

**Anthropogenic Influence**
Is defined hereby as direct and intentional actions by humans in order to change the characteristics of their environment such as burning of vegetation or felling of trees as well as measures for redirecting or creating water bodies (e. g. for irrigation). Not included are secondary effects such as atmospheric element immissions or changed floristic compositions due to the lack of extinct browsers or predators.

**Barranco**
Spanish for *ravine*. In local vernacular language the term applies to steep and narrow ravines which are characteristic for the highly dissected upper hill area of the Río Avisado watershed and constitute a portion of the slopes leading form the ridges down toward the valleys. Barrancos often display small creeks of moister soil conditions than the plain slopes in the vicinity.

**Biomass**
If not indicated otherwise *biomass* in this study always refers to the dry above-ground biomass of all woody species > 1.3 m in height. This includes foliage weight, branch weight and stem weight but excludes root biomass.

**Biometry**
Refers to all quantifiable parameters of living plant individuals. In this case these are height, stem diameter at breast height (dbh) and growth density as well as derived parameters such as ↗ biomass. No estimation (without prior statistical evaluation in case of empirical allometries) is involved.

**Carretera Marginal**
Spanish for *Marginal Road*. Built in the 1970's this road leads across the Andes massif connecting the northern Pacific Coast of Peru (↗ Costa) with the Amazon Basin (↗ Selva).

**Case**
For statistical analysis a *case* is referred to as the complementary term to ↗ variable in a data matrix. In this study a *case* always represents a ↗ plot.

**Chamizal** (*pl.* chamizal**es**)
Locally referred to a shrub-like vegetation type with short, stunted trees and xeromorphic / peinomorphic leaves. The term is derived from a cluster of representative species (e. g. *Brachyotum* sp., Melastomatacea; *Bertieria* sp., Rubiaceae and *Cavendishia* sp., Ericaceae) all uniformly named "*Chamizo*" (↗ Heath).

**Cluster**
In statistical terms a *cluster* is referred to as an association of ↗ cases, grouped by a Hierarchical Cluster Analysis as long as the represented cases have not been interpreted further.

**Comunidad Nativa**
Largely self-governing community of indigenous tribes on granted territory. Nowadays, the territory is marked and protected against intruding settlers. All indigenous tribes of the study area belong to the *Aguaruna* group.

**Cordillera (Occidental / Oriental)**
Spanish term describing any given *mountain range* which needs to be specified further. The *Cordillera Occidental* and *Cordillera Oriental* refer to the western and eastern range of the Peruvian Andes, respectively, which constitute the ↗ Sierra.
The study site is located at the piedmonts of the *Cordillera* Cahuapanas which forms the easternmost range of the Andes in northern Peru south of the Solimões.

**Costa**
Spanish for *coast*. It describes the arid, narrow coastal plains of an average width of 60 km which stretch along the Pacific Ocean.

**Disturbance**
Complementary to ↗ anthropogenic influence the term *disturbance* is applied to natural abiotic effects destroying vegetation such as natural fires, floods, storms, earthquakes and landslides. Herbivoral damage is not included.

**Factor**
In statistical terms a *factor* is referred to as a synthetic and abstract ↗ variable extracted by a Principal Component Analysis.

**Forest**
The arrangement of woody individuals > 1.3 m in height (mostly trees but also tree ferns and palms) on an area of > 0.1 ha. This does also include only shrub-like vegetation with occasionally emergent trees.

**Group**
In this study a *group* is defined as a ↗ cluster which has already been interpreted for distinctive properties between each other.

**Heath**
This refers to a stunted, shrub-like sclerophyllous vegetation type commonly described for nutrient poor (white) sandy soils of the humid tropics (COOPER 1979, SPECHT 1979a, SPECHT & WORMERSLEY 1979, RUOKOLAINEN & TUOMISTO 1993). Heath forests have also been described in the study area on sloped terrain by DEMPEWOLF (2000) and METTE (2001). Heath forests in this study are comparable to the latter in terms of floristic composition and general substrate but occur on level terrain. For distinction, these shall be termed ↗ *chamizales*.

**Layer**
This refers to a subjectively chosen unit. It describes one vegetation height zone with its upper boundary characterized by an obvious accumulation of individuals of similar height. An herb layer, a shrub layer, and a maximum of three tree layers were described at each plot.

**Parameter**
A *parameter* is one particular property of the investigated entity (e. g. soil pH, tree height, liana abundance) which is used to describe the variation between sites.

**Plot**
Generally, in this work a *plot* does not refer to a graphic chart but rather describes a particular investigation site which was chosen in order to represent a certain type of ↗ forest stands.

**Selva (Alta / Baja)**
Spanish for *forest*. This term is used to describe the eastern zones of Peru which potentially support tropical rainforest. This region is subdivided into two biomes: The *Selva Alta (Upper Rainforest)*, which covers the Subandean Belt and the *Selva Baja (Lowland Rainforest)* in the Amazon Basin.

**Settler**
Non-indigenous farmer who arrived after 1950 and who cultivates recently cleared, formerly pristine forest areas.

**Shapumbal** (*pl.* shapumbal**es**)
Locally refers to badlands exclusively covered by ferns. Ferns of the first successional stages following cultivation are generally *Pteridium aquilinum*. In this study the term *shapumbal* specifically applies to a vegetation type with very open canopy and a dense fern thicket of *Sticherus remotus* and *Gleichenella pectinata*, Gleicheniaceae, of considerable height (≤ 2 m).

**Sierra**
Spanish term locally referring to the Andean highlands of Peru between the ↗ Cordillera Occidental and the ↗ Cordillera Oriental.

**Stand Characters**
For reasons of rapid assessment an assortment of conspicuous characteristics among woody plants were chosen which were assumed to be indicative of certain stand properties such as microclimate, soil moisture regime, and nutrient status. Therefore, the abundance of the *stand characters* palms, tree ferns, standing dead wood and shrubs (≤ 1.3 m) was assessed separately.

**Structure**
According to BARKMAN (1979) structure is understood as the horizontal and vertical arrangement of vegetation. In this case it also includes the differentiation into different ↗ stand characters.

**Swamp**
A pedological unit with nearly constant water logging or inundation of the mineral and organic soil with an ombrogenic water regime.

**Unit**
In this case, a *unit* (e. g. soil unit) refers to a ↗ group of plots which have already been characterized in respect of their common properties and which have been labeled accordingly.

**Variable**
A *variable* represents the complete set of all values of a ↗ parameter over all ↗ cases (= ↗ plots) as used in statistical processes.

# 8 Abbreviations

| | |
|---|---|
| AAS | flame Atomic-Absorption Spectroscopy |
| $Al^{(3+)}$ | Aluminum (cation) |
| a.s.l. | above sea level |
| approx. | approximately |
| AVHRR | Advanced Very High Resolution Radiometer |
| BITÖK | Bayreuther Institut für terrestrische Ökosystemforschung |
| BMELF | Bundesministerium für Ernährung, Landwirtschaft und Forsten |
| BP | Before Present |
| BS | Base Saturation |
| C | Celsius |
| $C_{(tot)}$ | Carbon (total) |
| $Ca^{(2+)}$ | Calcium (cation) |
| cbh | circumference at breast height (1.3 m) |
| $CEC_{(eff)}$ | Cation Exchange Capacity (effective) |
| cf. | confer |
| cm | centimeter |
| $cmol_{(c)}$ | centimol (of cations) |
| conc. | concentration |
| dbh | diameter at breast height (1.3 m) |
| DEFORPAM | Desarrollo Forestal Participativo en la Región del Alto Mayo |
| DEM | Digital Elevation Map / Model |
| DIAM | Desarrollo Integral Alto Mayo |
| $dm^3$ | cubic decimeter |
| E | East |
| Ed(s). | Editor(s) |
| e. g. | for example |
| ENSO | El Niño Southern Oscillation |
| Eq. | Equation |
| et al. | and others |
| ETM | Enhanced Thematic Mapper |
| FAO | Food and Agricultural Organization |
| $Fe^{(3+)}$ | Iron (cation) |
| FEARS | Forest Ecology and Remote Sensing Group |
| Fig. | Figure |
| fl. | fluvial |
| g | gram |
| gbh | girth at breast height (1.3 m) |
| GIS | Geographic Information System |
| GTZ | Gesellschaft für technische Zusammenarbeit |
| h | height / hour |
| $H^{(+)}$ | hydrogen (cation) |
| $H_20$ | water |
| ha | hectare |
| hPa | hectoPascal |
| ICP-AES | Inductively-Coupled Plasma-Atomic Emission Spectroscopy |
| i. e. | that means |
| IGN | Instituto Geográfico Nacional |
| INADE | Instituto Nacional de Desarrollo |
| INGEMMET | Instituto Geológico Minero y Metalúrgico |
| INRENA | Instituto Nacional de Recursos Naturales |
| JERS-1 | Japanese Earth Remote Sensing Satellite |
| K | Kelvin |
| $K^{(+)}$ | Potassium (cation) |
| KA4 | Kartieranleitung (AG BODEN 1996) |
| kg | kilogram |
| km | kilometer |
| $km^2$ | square kilometer |
| KMO | KAISER-MEYER-OLKIN |
| L | liter |
| LGM | Last Glacial Maximum |
| m | meter |
| $m^2$ | square meter |
| max | maximum value |
| mg | milligram |
| $Mg^{(2+)}$ | Magnesium (cation) |
| min | minimum value |

| | |
|---|---|
| min | minute |
| Mio | million |
| mm | millimeter |
| $Mn^{(2+)}$ | Manganese (cation) |
| Modif. | modified |
| MSA | measure of Sampling Adequacy |
| N | North |
| $N_{(tot)}$ | Nitrogen (total) |
| $Na^{(+)}$ | Sodium (cation) |
| $NaHCO_3$ | Sodium bicarbonate |
| n.d. | no data |
| $NH_4NO_3$ | Ammonium nitrate |
| no. | number |
| NOAA | National Oceanic and Atmospheric Administration |
| ÖBG | Ökologisch Botanischer Garten |
| ONERN | Oficina Nacional de Evaluación de Recursos Naturales |
| $P_{(Olsen)}$ | Phosphorus (plant-available) |
| PEAM | Proyecto Especial Alto Mayo |
| ppm | parts per million |
| Q. | Quaternary |
| RF | rainforest |
| S | South |
| s.n.m. | sobre nivel del mar |
| SOM | Soil Organic Matter |
| sp. | Species |
| SST | Sea Surface Temperature |
| stdev | standard deviation |
| t | metric ton |
| Tab. | Table |
| tot | total |
| UTM | Universal Transverse Mercator Grid System |
| vs. | versus |
| W | West |
| WGS | World Geodetic System |
| WZP | Winkelzählprobe (angle count plot sampling) |
| x | multiplied by |
| µg | microgram |
| π | pi |
| Ø | diameter |
| # | number |
| % | percent |
| & | and |
| < | less than |
| = | equal to |
| > | greater than |
| ° | degree |
| 2-D | two dimensional |
| 3-D | three dimensional |

# 9 Appendix

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