Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica), with the first vegetation map of the area

Diversidad de ecosistemas en el Parque Nacional Piedras Blancas y áreas adyacentes (Costa Rica), con la primera presentación de una mapa vegetacional

Anton Weissenhofer, Werner Huber, Tatjana Koukal, Markus Immitzer, Eva Schembera, Susanne Sontag, Nelson Zamora & Anton Weber

Abstract: The Golfo Dulce region is botanically one of the most diverse areas in Central America. During the last 15 years, research plots have been established in the Piedras Blancas National Park and its surroundings, for the investigation of species composition, vegetation structure, growth patterns, reproductive ecology and forest dynamics. This paper presents an overview of the vegetation units that have so far been recognised in the region. Altogether, 28 ecosystems, ranging from untouched primary to secondary and anthropogenic vegetation, can be distinguished. Of these, 15 can be classified as natural, 5 as semi-natural and 8 as anthropogenic. For each ecosystem, a brief description of species diversity, vegetation structure and significance/abundance in the region is given. For the first time, a detailed vegetation map based on aerial photo interpretation is presented.

Key words: Costa Rica, Golfo Dulce, Piedras Blancas National Park, ecosystems, vegetation diversity, land use, vegetation map.

Resumen: La región del Golfo Dulce es uno de las áreas vegetacionales más diversas de América Central. Durante los últimos 15 años de investigación se han establecido parcelas de investigación en el Parque Nacional Piedras Blancas y sus alrededores, para la investigación de la composición de las especies, estructura de la vegetación, patrones de crecimiento, ecología reproductiva y dinámica del bosque. Este trabajo presenta un panorama de las unidades de vegetación que han sido reconocidas hasta ahora en la región. En total, se pueden distinguir 28 ecosistemas, que abarcan desde vegetación primaria sin perturbaciones hasta la vegetación secundaria y antropogénica. De ellos, 15 pueden clasificarse como naturales, 5 como seminaturales y 8 como antropogénicos. Para cada ecosistema se entrega una breve descripción acerca de la diversidad de especies, la estructura de la vegetación y la importancia y abundancia en la región. Por primera vez se presenta un mapa detallado de la vegetación.

Palabras clave: Costa Rica, Golfo Dulce, Parque Nacional Piedras Blancas, ecosistemas, diversidad vegetacional, uso del suelo, mapa vegetacional.

Introduction

Though tropical rainforests cover only 7% of the earth's land surface, they encompass more than half of the world's plant and animal species (Wilson 1988). Costa Rica can serve as an extreme example: it covers only 0.03% of the global land surface, but it is estimated that it harbors about 3.9% of the living species on earth (Kapelle et al. 2003). The southern zone around the Golfo Dulce is particularly rich in species (Hammel et. al. 2004, Lobo & Bolaños 2005). It is definitely the richest area in Costa Rica and represents one of the most speciose areas in the neotropics. The vegetation consists mainly of "tropical lowland wet forest" (in the classification of Holdridge et al. 1971, Gomez 1986), which is among the most threatened, yet least studied, vegetation types.

The forests represent the last tropical lowland wet forests along Central America's pacific coast. So far, 2.662 species of vascular plants out of 187 families have been recorded (INBio Database ATTA 2008).

In recent decades, several vegetation studies have been performed in the Golfo Dulce area. By 1981, thirteen major ecosystems had been distinguished (Tosi 1975, Boza & Mendoza 1981, Vaughan 1981),

Stapfia **88**, zugleich Kataloge der oberösterreichischen Landesmuseen Neue Serie **80** (2008): 65-96

Fig. 1: View over the Piedras Blancas National Park with its hills, ridges and ravines.

whereas HARTSHORN (1983) estimated the actual number to be 25 to 30.

The recently established "Ecomaps" project, a cooperation between the National Institute of Biodiversity (INBio) and the National Systems of Conservation Areas of Costa Rica (SINAC), aims to map all the ecosystems in Costa Rica, in order to get more information about the vegetation and to allow decisions to be made about conservation and inventory efforts. In 1998, the project started in the Área de Conservación Osa (ACOSA), which includes 17 protected areas within the range from Dominical to Osa Península and Punta Burica. About 44.7% of the area is covered by natural forests, with a concentration in the Corcovado and Piedras Blancas national parks. The studies have been performed at a rather rough scale and do not consider small ecosystems and ecotones.

Our studies mainly focus on the Piedras Blancas National Park, also known as the Esquinas forest, and adjacent areas. This forest is well structured, but heterogeneous due to the varied relief (presence of many hills, ridges and gorges), causing different ecological conditions. Fertile flood plains along the larger rivers allow permanent agriculture. Many of the flat areas were logged in the 1950s when the United Fruit Company (UFCO) entered the region for banana cultivation. In 1986, when the UFCO left the region, plantations were abandoned or converted into pastures or rice plantations. Recently, the African oil palm was used to substitute the old banana plantations.

The extensive primary forests, the different forest (sub)types, the current variety of land uses and the recent changes in land use makes the region ideal for studying the diversity of natural and anthropogenic ecosystems according to soil, climatic and geological conditions as well as for conservation biology.

The outcome of the present study is the first detailed vegetation map, with a minimum mapping unit of 0.5 ha. The map covers all natural and anthropogenic ecosystems within the study area, and is intended to serve as a basis for further studies on vegetation diversity, conservation efforts and sustainable development in one of the most interesting areas in Costa Rica.

Methods

The study area covers the Piedras Blancas National Park (140.4 km²), the Golfito Forest Reserve (28.7 km²) and adjacent areas. In total, an area of 255.5 km² was investigated. The borders of the Piedras Blancas National Park and of the Golfito Forest Reserve were adopted from MADRIGAL (2007). The borders of the study area are artificial and were defined as follows: North: Inter-American highway, East: forest road running from Alto for some kilometres in the direction of Golfito, South: coastline of the Golfo Dulce, West: the road from Chacarita to Rincón and then following a forest road in a southerly direction to the coast. All coordinates classified in the paper refer to UTM (zone 17 N).

The period of investigation and data collection was from 1993 to 2008. The Tropical Station La Gamba (E 257756, N 962502, altitude: 78 m) was used as scientific basis for the studies. Different forest sites and ecosystems were selected by empirical assessment and with the help of aerial photographs.

In every ecosystem, a plot was defined. Sizes ranged from 0.01 ha to 1 ha. All trees ≥ 10 cm diameter at breast height (d.b.h.) were recorded. In some selected plots, all plants of ≥ 2.5 cm stem diameter were recorded. Voucher specimens of all species were collected and deposited at the Herbario Nacional (CR), in the herbarium of the University of Vienna (WU), and in the Biology Center Linz (LI).

Growth form, d.b.h., height, crown diameter and phenological aspects of flowering and fruiting were recorded in all plants recorded. At selected study sites, profile diagrams of appropriate length and 10 m width were established, which included all trees ≥ 10 cm d.b.h. The reference to families follows APG II (2003).

The delineation and identification of vegetation units was done by the method of photogrammetry using aerial photographs (colour-infrared, mean photo scale 1:45.000) acquired within the framework of CARTA (Costa Rican Airborne Research and Technology Applications) project in March 2003. Due to substantial cloud cover in some areas, an additional set of aerial photographs (true colour, mean photo scale 1:40.000,

taken in December 1998, project TERRA 97/98) was used to fill the gaps.

The images, provided in digital format, were orientated using GPS-measured ground control points by the Soft Copy Station "LPS (Leica Photogrammetric Suite, Leica Geosystems)". The delineation and visual interpretation of vegetation units was performed with stereoscopic (three-dimensional) viewing using the software "Stereo Analyst for ArcGIS". The stereoscopic view proved essential for the discrimination of primary and secondary forest as well as for the identification of forest types that are specifically related to topography (e.g. forest on hill tops, forest on slopes). All vegetation units with a minimum size of 0.5 ha (5.000 m^2) were registered in the map. Smaller units were exceptionally considered in the map, if they differed significantly from the surrounding (e.g. settlements surrounded by pasture). The visual interpretation was supported and complemented by expert knowledge of various botanists and by on-site data collection. Preliminary mapping results and the final vegetation map were controlled by field checks.

(A) Vegetation map and ecosystem diversity

For the first time, a detailed vegetation map of the Piedras Blancas National Park, Golfito Forest Reserve and adjacent areas is presented here (see appendix). It is based on aerial photographs (for details see "Methods") and covers all vegetation units with a minimum size of 0.5 ha. The vegetation map presents the state of 2003 and in some areas the state of 1998 due to clouds in the imagery of 2003. Available information on the current state has knowingly not been considered in order to avoid inconsistencies between well-known areas and areas where detailed information on the current land cover is missing.

The ecosystems range from primary forests through riverine vegetation, mangroves, coastal and beach vegetation to secondary and anthropogenic vegetation. Further rivers, gravel banks, lagoons and sea are considered in the map and cover 1,6% of the study area. In total, 28 ecosystems are distinguished. They can be classified into natural (15), semi-natural (5) and anthropogenic (8) systems. In the following, a detailed hierarchical classification is presented (B), and subsequently the particular systems are described in detail (C).

(B) Ecosystem classification

1. Primary vegetation

1.1. Primary forests and riverine vegetation

1.1.1. Forest on plains

1.1.2. Forest on hill tops and ridges

1.1.3. Forest on inland slopes

1.1.4. Forest on coastal slopes

1.1.5. Forest in ravines

1.1.6. Riverine vegetation

1.1.6.1. Riverine forest along slow to medium flowing rivers

1.1.6.2. Riverine flood plain forest along slow flowing and meandering streams with waterlooged soils

1.1.6.3. Riverine forest along fast flowing rivers and streams with well drained soils and gravel banks

1.1.6.4. Vegetation on sandy soil and gravel banks with Gynerium sagittatum (Poaceae)

1.1.7. Natural forest gaps

1.2. Coastal and beach vegetation

1.2.1. Rocky shoreline

1.2.2. Beach vegetation

1.3. Mangroves and swamp forest

1.3.1. Mangroves

1.3.2. Swamp forest

1.4. Herbaceous swamp vegetation

2. Secondary vegetation

2.1. Secondary forests

2.1.1. Young secondary forest with canopy trees up to 15 m

2.1.2. Old secondary forest with canopy trees > 15 m

2.1.3. Forest edges

2.2. Fern-dominated vegetation

2.2.1. Vegetation dominated with *Dicranopteris pectinata* (Gleicheniaceae)

2.2.2. Vegetation dominated with *Nephrolepis multiflora* (Oleandraceae)

3. Anthropogenic ecosystems

3.1. Pasture

3.1.1. Regular pasture

3.1.2. Swampy pasture

3.1.3. Abandoned pasture (tacotal)

3.2. Plantations

3.2.1. Timber plantations (*Gmelina arborea* and *Tectona grandis*)

3.2.2. Oil palm plantation of *Elaeis guineensis*

3.2.3. Agricultural land with short-lived field crops

3.3. Preparation of land for cultivation

3.4. Settlements and gardens

(C) Ecosystem descriptions

1. Primary vegetation

1.1. Primary forests and riverine vegetation

1.1.1. Forest on plains

Characteristics: Well structured and tall forest (trees up to 50(-80) m), on well-drained alluvial flats and terraces with very wet soil conditions.
Coverage: 0.2% of the study area.
Size and location of the investigated sites: 1 ha. E 254443 m, N 967913 m. Altitude: 35 m.
Diversity/Density (d.b.h. ∅ 10 cm): no detailed data available, estimated 90-100 spp./250-300 ind./ha.
Characteristic plants:
Emergents: *Anacardium excelsum* (Anacardiaceae), *Ceiba pentandra* (Malvaceae).
Canopy: *Spondias mombin* (Anacardiaceae), *Sloanea ampla* (Elaeocarpaceae), *Carapa guianensis* (Meliaceae), *Virola koschnyi* (Myristicaceae), *Luehea seemannii* (Malvaceae).
Mid-subcanopy: *Bravaisia integerrima* (Acanthaceae), *Guatteria chiriquiensis* (Annonaceae), *Cryosophila guagara*, *Welfia regia*, *Socratea exorrhiza* (Arecaceae), *Ficus tonduzii* (Moraceae).
Understorey and ground layer: Relatively dense. *Dieffenbachia concinna* (Araceae), *Asterogyne martiana* (Arecaceae), *Chevaliera magdalenae* (Bromeliaceae), *Costus pulverulentus* (Costaceae), *Cyclanthus bipartitus*, *Carludovica drudei* (Cyclanthaceae), *Heliconia danielsiana*, *H. imbricata*, *H. lathispatha*, *H. nigripraefixa* (Heliconiaceae), *Calathea insignis* (Marantaceae). *Psychotria* spp. (Rubiaceae), *Myriocarpa longipes* (Urticaceae).
Palms: common in the in the understorey and mid-subcanopy layer.
Epiphytes: rare.
Hemiepiphytes: rare. *Blakea littoralis* (Melastomataceae).
Lianas: rare.

This forest type is found on well-drained alluvial flats and terraces. The forest comprises trees up to 50 m tall. Tree diversity and density is relatively low, with c. 100 species and 250-300 trees/ha (d.b.h. ≥ 10 cm) (HOLDRIDGE et al. 1971).

Giant emergent trees are *Anacardium excelsum* (Anacardiaceae) and the rare *Ceiba pentandra* (Malvaceae), which may grow up to 80 m tall (BOZA 1988). The canopy layer is relatively dense and consists of species which are often found also along rivers, e.g. *Luehea seemannii* (Malvaceae).

The mid-subcanopy is dominated by the rare fan palm *Cryosophila guagara*, which sometimes forms pure stands and is seldom found in other primary forests. The stilt-rooted tree *Bravaisia integerrima* (Acanthaceae) is also a very conspicuous constituent of the forest.

In the understorey, broad-leaved and succulent herbs – mostly monocotyledons – are abundant and very characteristic. The "suita" palm, *Asterogyne martiana*, which is used for roofs in the region is very common. Clumps of the spiny *Chevaliera magdalenae* (Bromeliaceae) are remarkable. Epiphytes and lianas are uncommon, but large-leaved araceous climbers are widespread.

Hemiepiphytes are rare: only *Blakea littoralis* (Melastomataceae) which grows in the lower sections of the tree trunks (5-10 m height) is abundant. Lianas are also uncommon, but interestingly, the trailing shrub *Warszewiczia coccinea* (Rubiaceae) was common.

Soils of flood plains are very suitable for banana and oil palm plantations. As a result, this forest type has become extremely rare and is almost extinct in the Esquinas forest. The only known forest of this type in the region is situated near Laguna Machaca, La Guaria (km 40) at c. 70 m above sea level. This is probably the last remnant of this ecosystem. This forest type is floristically related to riverine forests along slow flowing rivers and ravine forests.

1.1.2. Forest on hill-tops and ridges

Characteristics: well structured and tall forest (up to 50 m) on ridges (above 200 m altitude) with relatively dry climatic conditions.
Coverage: 2.0% of the study area.
Size and location of the investigated site: 1 ha. Fila trail near Esquinas Rainforest Lodge. E 256932 m, N 962246 m. Altitude: 230 m.
Diversity/Density (d.b.h. ∅ 10 cm): 179 spp./847 ind./ha.
Characteristic plants:
Emergents: -
Canopy: *Aspidosperma spruceanum* (Apocynaceae), *Calophyllum brasiliense*, *C. longifolium Symphonia globulifera* (Clusiaceae), *Macrolobium hartshornii* (Fabaceae-Caesalpinioideae), *Parkia pendula* (Fabaceae-Mimosoideae), *Peltogyne purpurea* (Fabaceae-Caesalpinioideae), *Humiriastrum diguense* (Humiriaceae), *Couratari guianensis* (Lecythidaceae), *Qualea polychroma* (Vochysiaceae), *Vochysia ferruginea* and *V. megalophylla* (Vochysiaceae).
Mid-subcanopy: *Welfia regia*, *Socratea exorrhiza* (Arecaceae), *Marila laxiflora* (Clusiaceae), *Pausandra trianae* (Euphorbiaceae), *Brosimum guianense* (Moraceae), *Compsoneura excelsa* (Myristicaceae).
Understorey and ground layer: relatively dense. *Geonoma congesta* (Arecaceae), *Diplasia karatifolia*, *Bequerelia cymosa* (Cyperaceae) *Euphorbia elata* (Euphorbiaceae), *Heliconia longiflora*, *H. irrasa* (Heliconiaceae), *Clidemia densiflora* (Melastomataceae), *Metaxya rostrata* (Metaxyaceae), *Faramea occidentalis*, *F. suerrensis*, *Psychotria elata*, *P. poeppigiana*, *P. solitudinum* (Rubiaceae), *Zamia fairchildiana* (Zamiaceae).
Palms: very common. *Welfia regia*, *Oenocarpus mapora*, *Socratea exorrhiza*.
Epiphytes: common. *Philodenron* spp., *Anthurium* spp., *A. lancifolium* (Araceae), *Guzmania lingulata*, *Werauhia viridiflora* (Bromeliaceae), *Codonanthe crassifolia* (Gesneriaceae), *Elleanthus* spp., *Trigonidium egertonianum*, *Lockhartia hercodonta*, *Scaphoglottis prolifera* (Orchidaceae).
Hemiepiphytes: common. *Clusia valerioi* (Clusiaceae).
Lianas: common *Doliocarpus hispidus* (Dilleniaceae).

Profile diagram 1: Forest on hill tops and ridges. Fila trail, near Esquinas Rainforest Lodge. E 256932 m, N 962246 m. Altitude: 230 m. The strip is 50 m long and 10 m wide. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Tapirira myriantha* (Anacardiaceae), **2**. *Aspidosperma spruceanum* (Apocynaceae), **3**. *Socratea exorrhiza* (Arecaceae), **4**. *Welfia regia* (Arecaceae), **5**. *Bombacopsis sessilis* (Malvaceae), **6**. *Protium costaricense* (Burseraceae), **7**. *Protium tenuifolium* (Burseraceae), **8**. *Licania sparsipilis* (Chrysobalanaceae), **9**. *Calophyllum brasiliense* (Clusiaceae), **10**. *Marila laxiflora* (Clusiaceae), **11**. *Symphonia globulifera* (Clusiaceae), **12**. *Sloanea brachytepala* (Elaeocarpaceae), **13**. *Sloanea guianensis* (Elaeocarpaceae), **14**. *Peltogyne purpurea* (Fabaceae-Caesalpinioideae), **15**. *Talauma gloriensis* (Magnoliaceae), **16**. *Henriettea succosa* (Melastomataceae), **17**. *Guarea grandifolia* (Meliaceae), **18**. *Brosimum guianense* (Moraceae), **19**. *Ficus bullenei* (Moraceae), **20**. *Virola guatemalensis* (Myristicaceae), **21**. *Calyptrantes pallens* (Myrtaceae), **22**. cf. *Heisteria scandens* (Olacaceae), **23**. *Panopsis suaveolens* (Proteaceae), **24**. *Elaeoluma glabrescens* (Sapotaceae), **25**. *Sterculia recordiana* (Malvaceae), **26**. *Qualea polychroma* (Vochysiaceae), **27**. *Vochysia ferruginea* (Vochysiaceae), **28**. *Vochysia megalophylla* (Vochysiaceae).

This is the most species-rich and individual-rich forest found in the region with around 179 different tree species and 847 ind./ha (d.b.h. > 10 cm) (HUBER 2005, WEISSENHOFER 2005). The profile diagram is therefore very densely covered with trees. This is mainly because light may penetrate into the forest due to its exposure on the hill tops.

Canopy trees grow up to 50 m tall and consist mainly of relatively thin individuals with thick and fissured bark (e.g. *Calophyllum* spp. – Clusiaceae), an unusual feature for rainforest trees. Some of the species drop their leaves during the dry season, e.g. *Couratari guianensis* (Lecythidaceae).

Fig. 2: A typical individual-rich forest on hill tops and ridges at the Fila Trail, La Gamba.

The mid-subcanopy is dense. Aside from tree species, palms are abundant with up to 10% of all individuals.

The heterogeneous understorey is often composed of clustered palms (*Geonoma congesta*) and treelets, mainly from the Melastomataceae and Rubiaceae. At more open sites, the fern *Metaxya rostrata* (Metaxyaceae) and Cyperaceae such as *Diplasia karatifolia* and *Bequerelia cymosa* may dominate the underground vegetation. A remarkable plant is the living fossil *Zamia fairchildiana* which is frequently observed in the understorey.

Epiphytes are common in the lower parts of the tree trunks and in the crown section. In the lower parts, Araceae and Orchidaceae are the most common epiphytes whereas in the crown region, *Codonanthe crassifolia* (Gesneriaceae) is abundant. Lianas and hemiepiphytes are common, making up 1% of the individuals. The strange climbing orchid *Vanilla planifolia* is frequently observed.

Due to the exposed position, wind and rain play an important role in determining forest composition on ridges. Tree-fall gaps caused by falling boles and crowns are common. Larger gaps are invaded by pioneer trees, treelets and tall shrubs. In young gaps, the scrambling vine *Scleria secans* (Cyperaceae) and the fern *Dicranopteris pectinata* (Gleicheniaceae) can form impenetrable thickets.

Forests on hill tops and ridges are floristically inhomogeneous and in transition with other forest types. At lower altitudes (up to 200 m), they are more humid and have a denser understorey layer than the upper and drier sections. Species composition at those sites are similar to inland slope forests. At the ridges near the coast they are probably affected by salty conditions and floristically related to the coastal slope forest.

On the highest mountain tops, e.g. Cerro Nicuesa (579 m), the ridge forest is widely open and gaps are abundant. Due to the exposure, strong winds and lightning affect the stand substantially. Tree species compositon is very similar to those stands at lower altitudes, except *Cojoba arborea* (Fabaceae-Mimosoideae) and *Ormosia* sp. (Fabaceae-Faboideae), which may dominate the vegetation. It is noticeable that epiphytes such as *Pitcairnia* sp., *Guzmania scherzeriana* (Bromeliaceae) are very abundant on the tree trunks, probably due to frequent condensation of humid air at higher sea level. *Vriesea monstrosa* (*Bromeliaceae*) is a new record for the Golfo Dulce area and has been found so far only on Cerro Nicuesa.

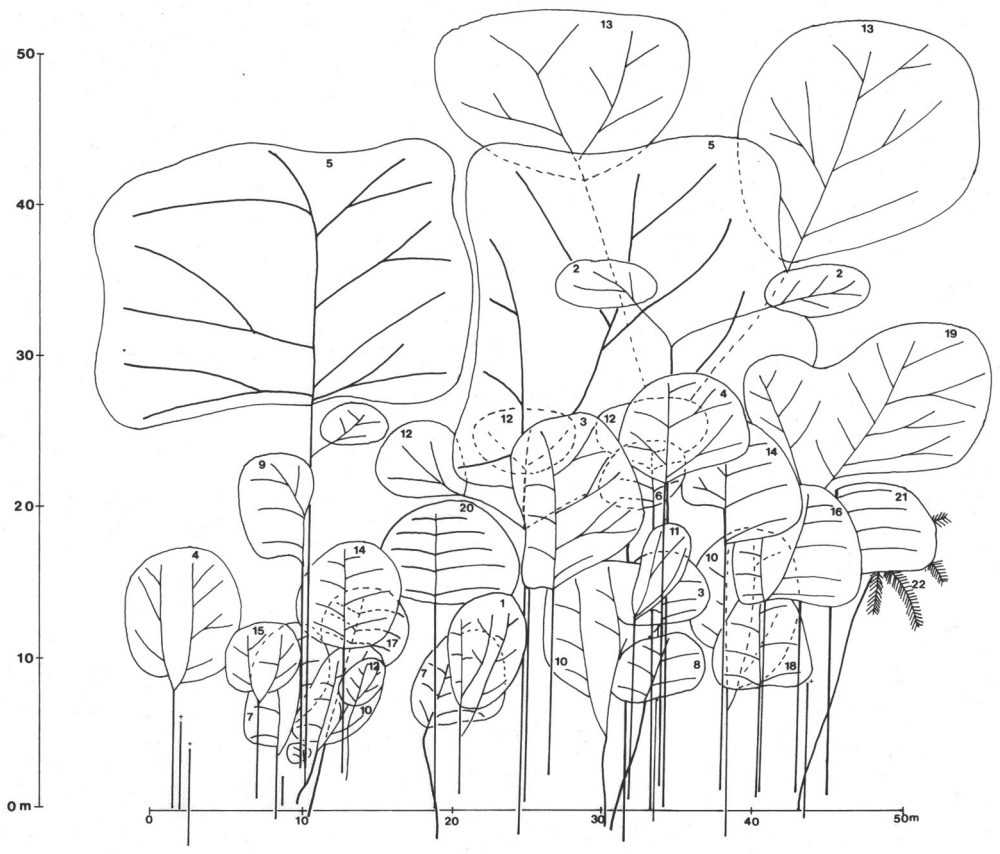
1.1.3. Forest on inland slopes

Characteristics: well structured and tall forest (up to 50 m) on steep slopes with many palms.
Coverage: 45.2% of the study area.
Size and location of the investigated site: 1 ha. Near Tropical Station La Gamba, Fila trail. E 257235 m, N 961337 m. Altitude: 266 m.
Diversity/Density (d.b.h. ∅ 10 cm)**:** 140 spp./527 ind./ha.
Characteristic plants:
Emergents: -
Canopy: *Aspidosperma spruceanum* (Apocynaceae), *Copaifera camibar* (Fabaceae-Caesalpinioideae), *Humiriastrum diguense* (Humiriaceae), *Ruptiliocarpon caracolito* (Lepidobotryaceae), *Carapa guianensis* (Meliaceae), *Brosimum utile* (Moraceae), *Otoba novogranatensis*, *Virola guatemalensis* (Myristicaceae) and *Vochysia megalophylla* (Vochysiacae).
Mid-subcanopy: *Guatteria amplifolia* (Annonaceae), *Dendropanax arboreus* (Araliaceae), *Iriartea deltoidea*, *Socratea exorrhiza*, *Welfia regia* (Arecaceae). *Protium tenuifolium* (Burseraceae), *Marila laxiflora*, *Symphonia globulifera* (Clusiaceae), *Mabea occidentalis* (Euphorbiaceae), *Brosimum lactescens* (Moraceae), *Compsoneura excelsa* (Myristicaceae), *Parathesis aeruginosa* (Myrsinaceae).
Understorey and ground layer: relatively bare. Arecaceae, *Mapania assimilis* (Cyperaceae), Cyclanthaceae, *Voyria* sp. (Gentianaceae), Marantaceae, *Amphydasia longicalycina* (Rubiaceae).
Palms: very common in the mid-subcanopy layer (*Iriartea deltoidea*, *Socratea exorrhiza*, *Welfia regia*) and in the understorey (*Asterogyne martiana*, *Calyptrogyne ghiesbreghtiana*, *Geonoma cuneata*).
Epiphytes: common. Bromeliaceae, Orchidaceae, Gesneriaceae.
Hemiepiphytes: common. *Clusia valerioi* (Clusiaceae), *Ficus* spp. (Moraceae).
Lianas: common *Doliocarpus hispidus*, *D. multiflorus* (Dilleniaceae).

This forest type occurs on the slopes of the Piedras Blancas National Park. Climatic conditions are intermediate between the more humid ravine and the more dry ridge forest.

The tallest trees reach 50 m and species diversity is high with up to 140 species per hectare (HUBER 2005, WEISSENHOFER 2005). In general, *Brosimum utile* (Moraceae) and *Carapa guianensis* (Meliaceae) are the most abundant tree species of the canopy. Slope forests are also the habitat of extremely rare timber species such as *Copaifera camibar* (Fabaceae-Caesalpinioideae). In the western part of the Piedras Blancas National Park, *Schizolobium parahyba* (Fabaceae-Caesalpinioideae) which is typical for Coastal slope forests can dominate the canopy (e.g. near Riyito).

The mid-canopy layer is often discontinuous and contains many species from different families. Some species are more common (*Symphonia globulifera*, *Marila laxiflora*) than others, but in general there is no dominance. A considerable portion of the trees are immature individuals of the canopy.



Profile diagram 2: Forest on inland slopes. Near Tropical Station La Gamba, Fila trail. E 257235 m, N 961337 m. Altitude: 266 m. The strip is 50 m long and 10 m wide. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Ardisia compressa* (Myrsinaceae), **2.** *Bombacopsis sessilis* (Malvaceae), **3.** *Brosimum alicastrum* (Moraceae), **4**. *Brosimum lactescens* (Moraceae), **5.** *Brosimum utile* (Moraceae), **6**. *Byrsonima crispa* (Malpighiaceae), **7**. *Compsoneura excelsa* (Myristicaceae), **8**. *Hirtella triandra* (Chrysobalanaceae), **9**. *Licania sp.* (Chrysobalanaceae), **10**. *Marila laxiflora* (Clusiaceae), **11**. *Micropholis melinoniana* (Sapotaceae), **12**. *Pithecelobium macradenium* (Fabaceae-Mimosoideae), **13**. *Pouteria sp.* (Sapotaceae), **14**. *Pouteria* sp.1 (Sapotaceae), **15**. *Protium* sp. (Burseraceae), **16**. *Protium tenuifolium* (Burseraceae), **17**. *Protium ravenii* (Burseraceae), **18**. *Rinorea dasyadena* (Violaceae), **19**. *Ruptiliocarpon caracolito* (Lepidobotryaceae), **20**. *Symphonia globulifera* (Clusiaceae), **21**. *Virola sebifera* (Myristicaceae), **22**. *Welfia regia* (Arecaceae).

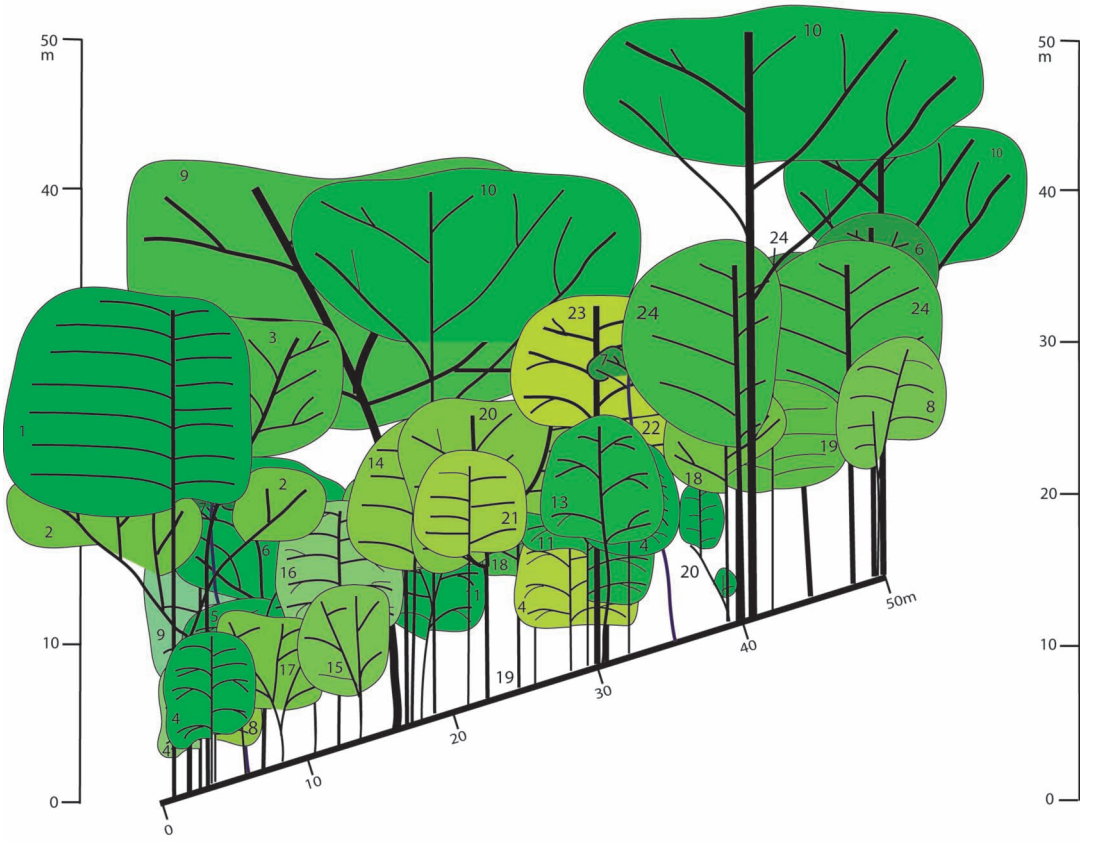
The sub-canopy layer contains fewer gaps than the upper storeys and the density of the foliage is probably higher than in any other level of the forest. The richest and most important structural elements with up to 25% of the individuals ∅ 10 cm d.b.h. are palms. The most important palms are the stilt-rooted *Iriartea deltoidea* and *Socratea exorrhiza* as well as the majestic *Welfia regia* which often occurs in or near canopy gaps.

The understorey and the forest floor is relatively bare and dominated by dwarf palms and the thick-leaved *Euphorbia elata* (Euphorbiaceae). This may be due to the steepness and the wash-out effects of seeds and seedlings. Interestingly, heliconias are not as common as in ravine forests, but are replaced by Cyclanthaceae and Marantaceae. A common parasitic plant is *Voyria* sp. (Gentianaceae), with yellow or pinkish flowers.

Large lianas are rare, while hemiepiphytes, mainly *Clusia* spp. (Clusiaceae), are common, but rarely reach more than 10 cm d.b.h.. The latter are found mainly on trees which drop their leaves during the dry season (e.g. *Brosimum utile*).

Epiphytes such as *Guzmania lingulata*, *G. scherzeriana* (Bromeliaceae) and *Gongora tricolor* (Orchidaceae) are commonly found on tree boles. Epiphytes in the tree crowns are adapted to canopy conditions and include orchid species (*Elleanthus poiformis*, *Elleanthus* spp., *Maxillaria* spp., *Scaphyglottis boliviensis*), bromeliads *Tillandsia* spp. and the very common gesneriad *Codonanthe crassifolia*.

Fig. 3: *Brosimum utile* (Moraceae) is a characteristic tree of the inland slope forest. Note the white latex at the buttresses. Piedras Blancas National Park.



Profile diagram 3: Forest on coastal slopes. Near Golfo Dulce Lodge. E 252183 m, N 958911 m. Altitude: 185 m. The strip is 50 m long and 10 m wide. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Symphonia globulifera* (Clusiaceae), **2.** *Caryocar costaricense* (Caryocaraceae), **3**. *Hirtella papillata* (Chrysobalanaceae), **4.** *Sorocea cufodontisii* (Moraceae), **5.** *Perebea hispidula* (Moraceae), **6**. *Guarea grandifolia* (Meliaceae), **7.** *Cecropia obtusifolia* (Urticaceae), **8.** *Compsoneura excelsa* (Myristicaceae), **9**. *Dussia macroprophyllata* (Fabaceae-Faboideae), **10**. *Schizolobium parahyba* (Fabaceae-Caesalpinioideae), **11**. *Heisteria concinna* (Olacaceae), **12**. *Ocotea leucoxylon* (Lauraceae), **13**. *Brosimum guianense* (Moraceae), **14**. *Garcinia madruno* (Clusiaceae), **15**. *Brosimum lactescens* (Moraceae), **16**. *Protium aracouchinii* (Burseraceae), **17**. *Chrysophyllum* cf. *argenteum* (Sapotaceae), **18**. *Tapirira myriantha* (Anacardiaceae), **19**. *Apeiba tibourbou* (Malvaceae), **20**. *Guarea pterorhachis* (Meliaceae), **21**. *Inga umbellifera* (Fabaceae-Mimosoideae), **22.** *Annona papilionella* (Annonaceae), **23**. *Ampelocera macrocarpa* (Ulmaceae), **24**. *Trichospermum grewiifolium* (Malvaceae).

Fig. 4: Coastal slope forest with the characterstic emergent *Schizolobium parahyba* (Fabaceae-Caesalpiniaceae). Coast near Playa San Josesito.

1.1.4. Forest on coastal slopes

Characteristics: well structured and tall forest (up to 55 m) on the steep hills near the coast.
Coverage: 12.8% of the study area.
Size and location of the investigated site: 1 ha. Near Golfo Dulce Lodge. E 252183 m, N 958911 m. Altitude: 185 m.
Diversity/Density (d.b.h. ∅ 10 cm): 108 spp./588 ind./ha.
Characteristic plants:
Emergents: frequent, *Schizolobium parahyba* (Fabaceae-Caesalpinioideae).
Canopy: *Caryocar costaricense* (Caryocaraceae), *Calophyllum longifolium* (Clusiaceae), *Manilkara staminodella* (Sapotaceae).
Mid-subcanopy: *Protium* spp. (Burseraceae), *Garcinia madruno*, *Symphonia globulifera* (Clusiaceae), *Guarea pterorhachis* (Meliaceae), *Brosimum costaricanum*, *Brosimum lactescens*, *Sorocea cufodontisii* (Moraceae), *Compsoneura excelsa* (Myristicaceae), *Heisteria concinna* (Olacaceae), *Elaeoluma glabrescens*, *Pouteria* spp. (Sapotaceae), *Ampelocera macrocarpa* (Ulmaceae), *Pourouma bicolor* (Urticaceae).
Understorey and ground layer: bare and species-poor. *Spathiphyllum silvicola* (Araceae), *Chamaedorea cuneata*, *Geonoma cuneata*, *Neonicholsonia watsonii* (Arecaceae), *Psychotria solitudinum* (Rubiaceae).
Palms: rare.
Epiphytes: extremely rare.
Hemiepiphytes: small hemiepiphytes are common, extremely rare are individuals ∅ 10 cm d.b.h..
Lianas: very common, 3% of the individuals ∅ 10 cm d.b.h.. *Doliocarpus multiflorus* (Dilleniaceae), *Aristolochia* sp. (Aristolochiaceae), *Bauhinia* sp. (Fabaceae-Caesalpinioideae), *Entada* sp. (Fabaceae-Mimosoideae).

This forest type covers the major part of the Piedras Blancas National Park along the coast. The forest is tall (up to 55 m) and with 588 individuals relatively dense, but with 105 spp./ha ∅ 10 cm d.b.h. not as diverse as other primary forest sites (HUBER 2005, WEISSENHOFER 2005). Forest structure and species composition change abruptly at the summits of the coastal hills, maybe due to salty conditions. We found the largest trees in this forest although the plot is very steep.

The most conspicuous emergent to canopy tree is *Schizolobium parahyba* (Fabaceae-Caesalpinioideae), a deciduous pioneer legume with wind-dispersed, winged fruits which has its flowering period during December and January. Typical canopy trees often have strongly fissured barks. The taller trees are arranged in a step-like fashion, and tend to be asymmetric and overlapping instead of forming a continuous level or undulating canopy (see profile diagram 3). This is typical of forests on steep slopes. In general, forests on slopes show a more irregular structure, and the heights given for the strata are approximate averages.

The understorey and ground layer are species-poor and extremely scarce. They consist mainly of seedlings and young trees that belong to the upper layers. Palms are extremely rare, which may be due to the salty conditions. Beside trees, hemiepiphytes and lianas are important structural elements of the forest, although large hemiepiphytes are rare.

The climbing fern *Lygodium radiatum* (Schizaeaceae) which grows on nearly all mid-canopy trees is ubiquitous.

On the boles of the trees, epiphytes are very scarce and small succulent orchids (e.g. *Elleanthus* spp., *Maxillaria* spp.), bromeliads (e.g. *Aechmea dactylina*, *Araeococcus pectinatus*) and *Sphyrospermum ellipticum* (Ericaceae) could only be found in the upper part of the boles and in the crown region. No tree ferns or cycads were found.

The steep and rocky hills along the coastline create frequent tree-fall gaps and landslides, making this forest particularly dynamic. In fact, the whole forest type can be seen as a mosaic at different stages of regeneration (i.e. gap, building, and mature phases). Large gaps are rapidly invaded by various herbaceous vines of the families Cucurbitaceae and Convolvulaceae.

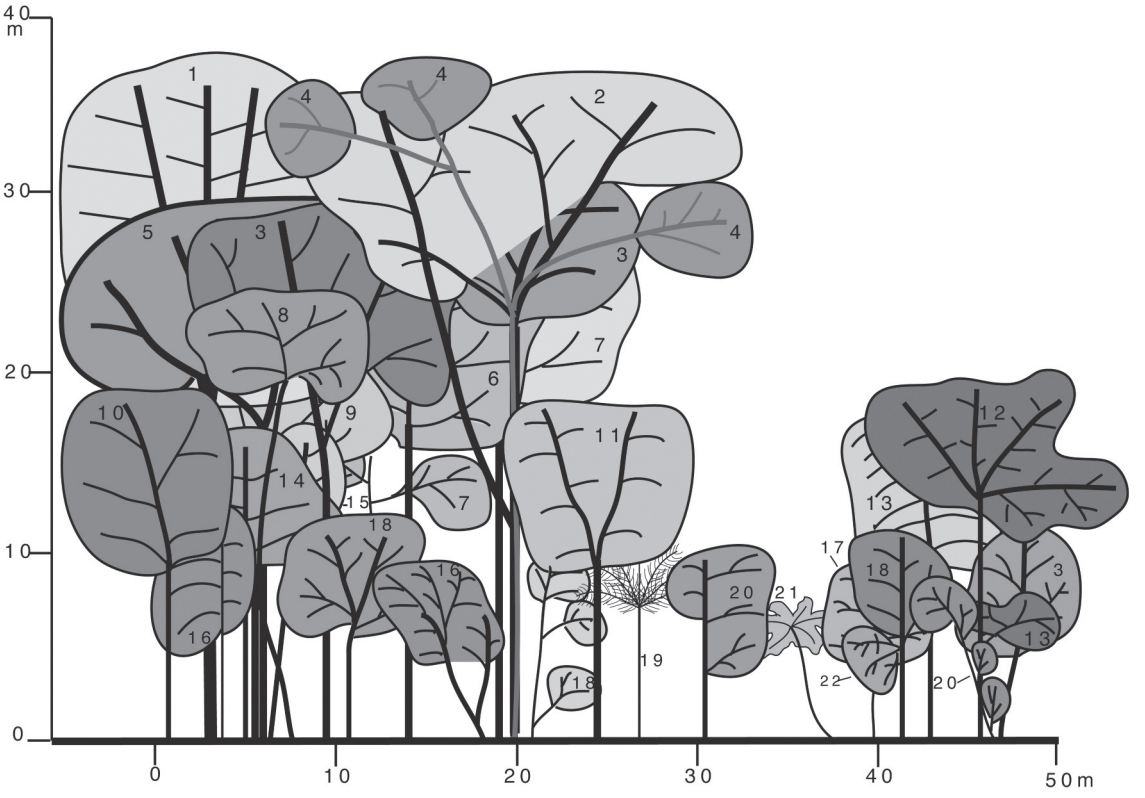
1.1.5. Forest in ravines

Characteristics: well structured forest of medium-sized to tall trees (up to 35-40 m) with very humid conditions throughout the year.
Coverage: 1.4% of the study area.
Size and location of the investigated site: 1 ha. Near Esquinas Rainforest Lodge, Ocelot trail. E 257176 m, N 962123 m. Altitude: 125 m.
Diversity/Density (d.b.h. ∅ 10 cm): 121 spp./482 ind./ha.
Characteristic plants:
Emergents: -
Canopy: *Terminalia bucidoides* (Combretaceae), *Sloanea medusula* (Elaeocarpaceae), *Dussia discolor*, *Lonchocarpus heptaphyllus* (Fabaceae-Faboideae), *Mortoniodendrum anisophyllum* (Malvaceae), *Carapa guianensis* (Meliaceae), *Virola guatemalensis* (Myristicaceae), *Billia colombiana* (Sapindaceae).
Mid-subcanopy: *Guatteria recurvisepala* (Annonaceae), *Dendropanax sessiliflorus* (Araliaceae), *Cryosophila guagara*, *Iriartea deltoidea*, *Welfia regia* (Arecaceae), *Cordia cymosa* (Boraginaceae), *Perrottetia sessiliflora* (Celastraceae), *Calatola costaricensis* (Icacinaceae), *Grias cauliflora* (Lecythidaceae), *Apeiba tibourbou*, *Trichospermum grewiifolium* (Malvaceae), *Rinorea dasyadena* (Violaceae), *Tetrathylacium macrophyllum* (Salicaceae), *Cecropia obtusifolia* (Urticaceae).
Understorey and ground layer: very dense, large-leaved giant herbs. *Dieffenbachia oerstedii*, *Dieffenbachia* spp., *Dracontium pittieri*, *Homalomena* spp., *Rhodospatha* spp. (Araceae), *Chamaedorea* spp., *Geonoma* spp. (Arecaceae), *Alsophila firma* (Cyatheacee), *Heliconia danielsiana*, *H. imbricata*, *H. nigripraefixa*, *H. trichocarpa* (Heliconiaceae), *Costus* spp. (Costaceae) and *Calathea* spp. (Marantaceae).
Palms: common in the mid-subcanopy layer and in the understorey, up to 6% of the individuals ∅ 10 cm d.b.h..
Epiphytes: very common. *Anthurium hoffmannii*, *A. pentaphyllum*, *A. ravenii*, *Stenospermation angustifolium* (Araceae), *Aechmea angustifolia*, *Guzmania lingulata*, *G. scherzeriana*, *Tillandsia anceps*, *T. monadelpha* (Bromeliaceae), *Asplundia* spp. (Cyclanthaceae), *Maxillaria neglecta*, *M. uncata*, *Pleurothallis* spp., *Scaphyglottis* spp., *Stanhopea cirrhata*, *Stelis* spp. (Orchidaceae), ferns (e.g. *Hymenophyllum* spp., *Elaphoglossum* spp., *Nephrolepis* spp.).
Hemiepiphytes: very common. *Blakea gracilis* (Melastomataceae).
Lianas: common *Bauhinia* spp. (Fabaceae-Caesalpinioideae). *Doliocarpus hispidus* (Dilleniaceae).

This forest type is located in ravines and creeks where microclimatic conditions are extremely humid throughout the year. Compared to slope and ridge forests, ravine forests are not as tall, with canopy trees around 30-35(40) m tall. Species diversity is high with c. 120 species/ha (d.b.h. ≥ 10 cm) and up to 450-500 individuals/ha (HUBER 2005, WEISSENHOFER 2005).

The crowns of the canopy are generally in contact, but many gaps are found. Crowns are mostly wider than high and tend to be umbrella-shaped.

The mid-subcanopy is more continuous than the canopy, but also has many gaps. A considerable portion (c. 20%) of the trees are immature individuals of the



Profile diagram 4: Forest in ravines. Near Esquinas Rainforest Lodge, Ocelot trail. E 257176, N 962123. Altitude: 125 m. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Virola guatemalensis* (Myristicaceae), **2**. *Dussia discolor* (Fabaceae-Faboideae), **3**. *Guarea grandifolia* (Meliaceae), **4**. *Bursera standleyana* (Burseraceae), **5**. *Tapirira myriantha* (Anacardiaceae), **6**. *Billia colombiana* (Sapindaceae), **7**. *Pterocarpus* cf. *officinalis* (Fabaceae-Faboideae), **8**. *Cordia collococca* (Boraginaceae), **9**. *Cordia cymosa* (Boraginaceae), **10**. *Carapa guianensis* (Meliaceae), **11**. *Pterocarpus hayesii* (Fabaceae-Faboideae), **12**. *Coccoloba standleyana* (Polygonaceae), **13**. *Casearia arborea* (Salicaceae), **14**. *Coussarea hondensis* (Rubiaceae), **15**. *Sapium laurifolium* (Euphorbiaceae), **16**. *Tetrathylacium macrophyllum* (Salicaceae), **17**. *Rinorea dasyadena* (Violaceae), **18**. *Grias cauliflora* (Lecythidaceae), **19**. *Welfia regia* (Arecaceae), **20**. *Perrottetia sessiliflora* (Celastraceae), **21**. *Cyathea delgadii* (Cyatheaceae), **22**. *Blakea gracilis* (Melastomataceae).

canopy. *Tetrathylacium macrophyllum* (Salicaceae) is the most prominent species in this layer.

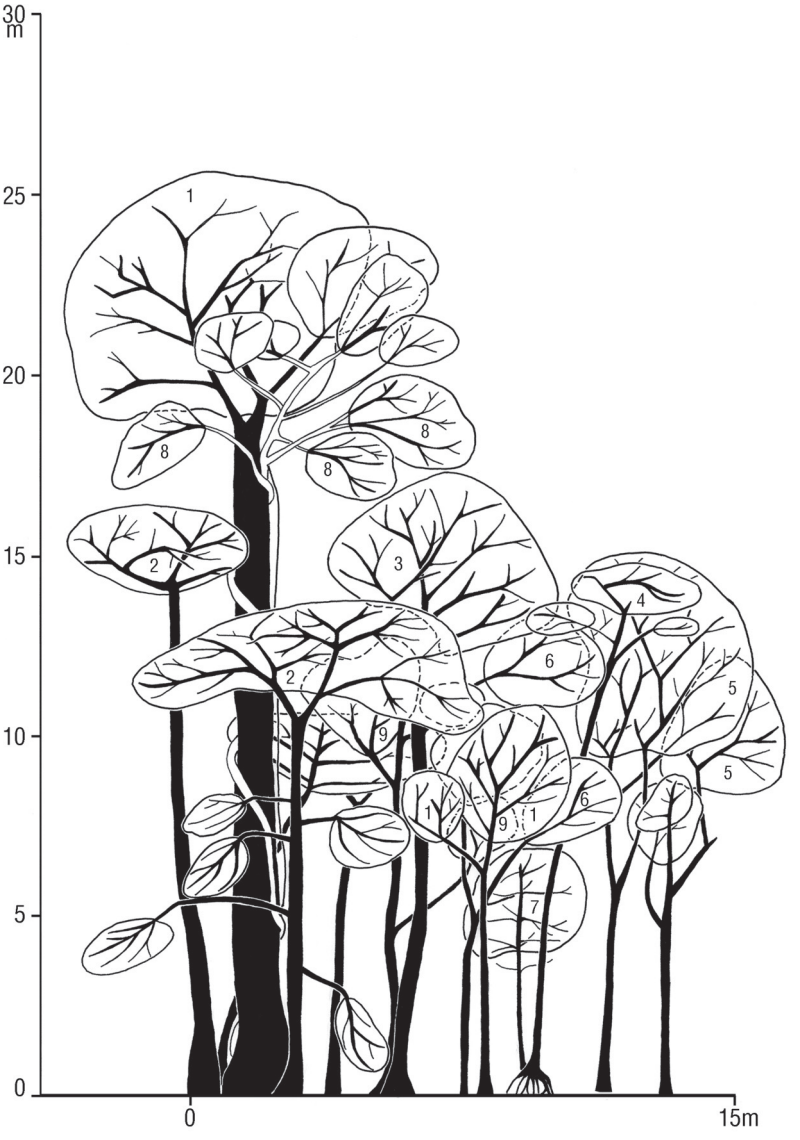
The understorey is very dense and comprises a wide range of species. Broad-leaved and succulent herbs in the Araceae, giant heliconias and members of Cyclanthaceae are impressive and give this forest a special character. Noteworthy plants are the ubiquitous tree fern *Cyathea delgadii* and the litter-trapping treelet *Clavija costaricana* (Theophrastaceae), which is rare in adjacent areas. A significant portion of the layer consists of ferns and *Selaginella* species.

Fig. 5: Characteristic forest in deep valleys and ravines. Near La Gamba.

Epiphytes are very common and the trees are densely covered with mosses, particularly those along the river. Lianas are common, especially *Bauhinia guianensis* and the recently discovered *B. bahiachalensis* (Fabaceae-Faboideae).

It is worth noting that many trees harbour hemiepiphytes, especially in the mid canopy. They seldom they reach more then 10 cm d.b.h.. A common species at about 5-10 m height of the phorophytes is *Blakea gracilis* (Melastomataceae), and another, *Clusia valerioi* (Clusiaceae), is found in the upper storeys at about 20-30 m. Secondary hemiepiphytes are common, many of them belonging to the aroid family (*Philodendron* spp., *Monstera* spp.).

Profile diagram 5: Lowland riverine forest along slow to medium flowing rivers (Río Bonito). E 256303 m, N 963833 m. Altitude: 80 m. The strip is 25 m long and 10 m width. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Spondias mombin* (Anacardiaceae), **2**. *Guatteria chiriquensis* (Annonaceae), **3**. *Unonopsis* cf. *pittieri* (Annonaceae), **4**. *Cecropia peltata* (Urticaceae), **5**. *Croton schiedeanus* (Euphorbiaceae), **6**. *Casearia comersoniana* (Salicaceae), **7**. *Ocotea rivularis* (Lauraceae), **8.** *Ficus* sp. (Moraceae), **9**. *Apeiba tibourbou* (Malvaceae).



Ravine forests are very dynamic and the most common causes of tree death are uprooting due to the waterlogged soil conditions, and snapping. Smaller gaps are invaded by *Cecropia* spp. (Urticaceae) and *Myriocarpa longipes* (Urticaceae) and the remarkable tree ferns *Alsophila firme* and *Cyathea delgadii* (Cyatheaceae). Larger gaps are invaded by giant herbs like *Heliconia* spp. (Heliconiaceae), *Costus* spp. (Costaceae) and Marantaceae. The ravine forest is related to riverine forests along slow to medium flowing rivers, e.g. along the the Quebrada Gamba.

1.1.6. Riverine vegetation

General: Vegetation types of this category are seldom listed as a distinct formation, but species found in such locations are either not duplicated in the adjacent forest, or occur in such concentrations as to give them an entirely different aspect. On the strength of the different river systems in the region, lowland riverine forests could not be treated as one forest type or ecosystem. One may find small streams to large rivers, slow-flowing and meandering streams up to fast-flowing rivers. Each river type causes different ecological situations and conditions, e.g. soil types and microclimate, so that they differ conspicuously in forest structure and species composition. Three different forest types are described in the following as independent ecosystems (1.1.6.1 to 1.1.6.3). In the vegetation map we combined these forest types to one category as "lowland riverine forest", because the minimum area for a specific category is often too small. In addition to the types of riverine forest, another type of riverine vegetation, i.e. vegetation on gravel banks dominated by *Gynerium sagittatum*, is described and mapped (1.1.6.4).

Riverine vegetation covers 0.7% of the study area (1.1.6.1. to 1.1.6.3.: 0.3%, 1.1.6.4.: 0.4%).

Fig. 6: Riverine forest along the Río Bonito with the conspicuous *Bursera simaruba* (Burseraceae).

1.1.6.1. Riverine forest along slow to medium flowing rivers (Río Bonito and Río Gamba)

Characteristics: well structured and tall forest (up to 40 m) along slow to medium flowing lowland rivers and adjacent flat terraces with ± well drained soils. Very humid, trees often with buttresses.
Size and location of the investigated site: a) 0,1 ha along Río Bonito: E 256303 m, N 963833 m. Altitude: 80 m) 0.1 ha at Quebrada Gamba: E 257983 m, N 960049 m. Altitude: 127 m.
Diversity/Density (d.b.h. ∅ 10 cm): 28 spp./81 ind/0,1 ha (Río Bonito) to 42 spp./81 ind. (Río Gamba).
Characteristic plants:
Emergents: *Ceiba pentandra* (Malvaceae), rare.
Canopy: *Anacardium excelsum*, *Spondias mombin* (Anacardiaceae), *Bursera simaruba* (Burseraceae), *Sloanea medusula* (Elaeocarpaceae), *Hyeronima alchorneoides* (Euphorbiaceae), *Ocotea rivularis* (Lauraceae), *Luehea seemannii*, *Pachira aquatica*, *Mortoniodendron anisophyllum* (Malvaceae), *Carapa guianensis* (Meliaceae), *Castilla tunu* (Moraceae), *Otoba novogranatensis*, *Virola* spp. (Myristicaceae).
Mid-subcanopy: *Guatteria chiriquensis* (Annonaceae), *Tetragastris panamensis* (Burseraceae), *Inga oerstediana* (Fabaceae-Mimosoideae), *Ocotea mollifolia*, *O. rivularis* (Lauraceae), *Apeiba membranacea*, *A. tibourbou* (Malvaceae), *Siparuna andina* (Monimiaceae), *Otoba novogranatensis* (Myristicaceae).
Understorey and ground layer: dense. *Dieffenbachia concinna*, *D. oerstedii* (Araceae), *Bactris guianensis* (Arecaceae), Costaceae, *Carludovica drudei* (Cyclanthaceae), *Zapoteca portoricensis* (Fabaceae-Mimosoideae), *Heliconia* spp. (Heliconiaceae), *Calathea lutea* (Marantaceae), *Clavija costaricana* (Theophrastaceae), *Thelypteris angustifolia* (Thelypteridaceae).
Palms: canopy palms are rare (*Iriartea deltoidea*, *Cryosophila guagara*), the understorey palm *Bactris guianensis* is common.
Epiphytes: very common. *Werauhia gladioliflora*, *Tillandsia anceps* (Bromeliaceae), *Columnea flaccida*, *Codonathe crassifolia* (Gesneriaceae), *Sobralia* sp., *Vanilla* cf. *planifolia* (Orchidaceae) *Polypodium fallax*, *Niphidium crassifolium* (Polypodiaceae).
Araceae, Orchidaceae, Bromeliaceae, Ericaceae, Gesneriaceae, ferns.
Hemiepiphytes: abundant, large individuals are rare.
Lianas: abundant, large lianas are rare.

This forest type is found along slow to medium flowing rivers with adjacent flat terraces. Species diversity is generally high with 28 spp./81 ind/0.1 ha (Río Bonito) to 42 spp./81 ind. (Río Gamba), but varies depending on the grade of natural disturbance.

The kapok tree *Ceiba pentandra* (Malvaceae) is an impressive but rare emergent tree which may grow very tall and is found in the region mainly along rivers.

Trees of the canopy layer reach 35-40 m and often have massive trunks with large spreading buttresses. Very conspicuous is the "indio desnudo" *Bursera simaruba* (Burseraceae) with its conspicuous red-brown peeling bark. This tree usually grows at drier sites (e.g. Province Guanacaste), but in the Golfo Dulce region, it is found only in ravines or along rivers. *Mortoniodendron anisophyllum* (Malvaceae) is another common species.

The mid-subcanopy layer is relatively open. Malvaceae, Lauraceae and Tiliaceae are the most important families regarding individual richness.

The understorey is dense and lush and composed of various giant herb species from monocotyledonous families. Interestingly, *Dimerocostus strobilaceus* (Costaceae) has been found so far only in the Río Bonito valley and is an conspicuous understorey species at the forest edge.

The ground layer is bare due to regular flooding except for *Selaginella* spp. (Selaginellaceae) and *Leersia* sp. (Poaceae).

Epiphytes are very common and conspicuous on exposed branches. Most prominent and is *Columnea flaccida* (Gesneriaceae) with its large red flowers and white fruits, often hanging down several metres from branches.

Hemiepihytes are important structural elements, but rarely reach more than 10 cm d.b.h.. Lianas are common along the riverside e.g. *Doliocarpus multiflorus* (Dilleniaceae), but inside the forest they are rare.

Heavy rains, inundations and waterlogged soils frequently cause tree fall and makes the forest very dynamic. Typical pioneer species invading disturbed areas are *Ochroma pyramidale* (Malvaceae), *Trichospermum grewiifolium* (Malvaceae), and *Cecropia* spp. (Urticaceae).

1.1.6.2. Riverine flood plain forest along slow-flowing and meandering streams with waterlooged soils (e.g. the confluence of the Río Bonito and the Río Oro)

Characteristics: very dynamic and poorly structured forest with low diversity. Trees up to 26(30) m tall. Very humid, dominated by pioneer trees.
Size and location of the investigated site: 0.1 ha at the confluence of the Río Bonito and Río Oro. E 261447 m, N 964693 m. Altitude: 70 m.
Diversity/Density (d.b.h. ∅ 10 cm): 9 sp./26 ind/0,1ha.
Characteristic plants:
Emergents: rare, maybe *Ceiba pentandra* (Malvaceae).
Canopy: *Spondias mombin* (Anacardiaceae), *Ochroma pyramidale* (*Malvaceae*), *Luehea seemannii* (Malvaceae).
Mid-subcanopy: *Bravaisia integerrima* (Acanthaceae), *Hernandia stenura* (Hernandiaceae), *Nectandra reticulata*, *Ocotea laetivirens* (Lauraceae), *Inga ruiziana* (Fabaceae-Mimosoideae).
Understorey and ground layer: dominated by *Dieffenbachia concinna* (Araceae), *Carludovica drudei* (Cyclanthaceae), *Heliconia lathispatha* (Heliconiaceae), *Calathea lutea* (Marantaceae), *Gynerium sagittatum* (Poaceae), *Geophila* cf. *repens* (Rubiaceae).
Palms: -
Epiphytes: rare, due to ephemerality of the trees.
Hemiepiphytes: not found.
Lianas: rare.

This forest type is found along waterlogged and swampy soils along slow-flowing rivers. The flattest parts are poorly drained and already small differences in the ground level have a noticeable effect mainly on the ground vegetation.

The canopy layer is very open and dominated by pioneer species. The tallest trees grow up to 30 m and are confined to the somewhat elevated and drier parts, because of a minor effect of flooding and washout.

The mid-subcanopy layer consist mainly of younger trees of the canopy layer. Even small differences in the ground level (10 cm) result in a complete change of the ground cover.

The ground layer is dominated by typical species of poorly drained soils. The woody grass *Gynerium sagittatum* (Poaceae) dominates the wettest areas. At somewhat drier sites, the creeping Rubiaceae *Geophila* cf. *repens*, can be dominant.

Epiphytes are rare and hemiepiphytes were not found, maybe due to the short lifespan of the pioneer trees. Only small liana individuals of *Doliocarpus hispidus* (Dilleniaceae) were recorded.

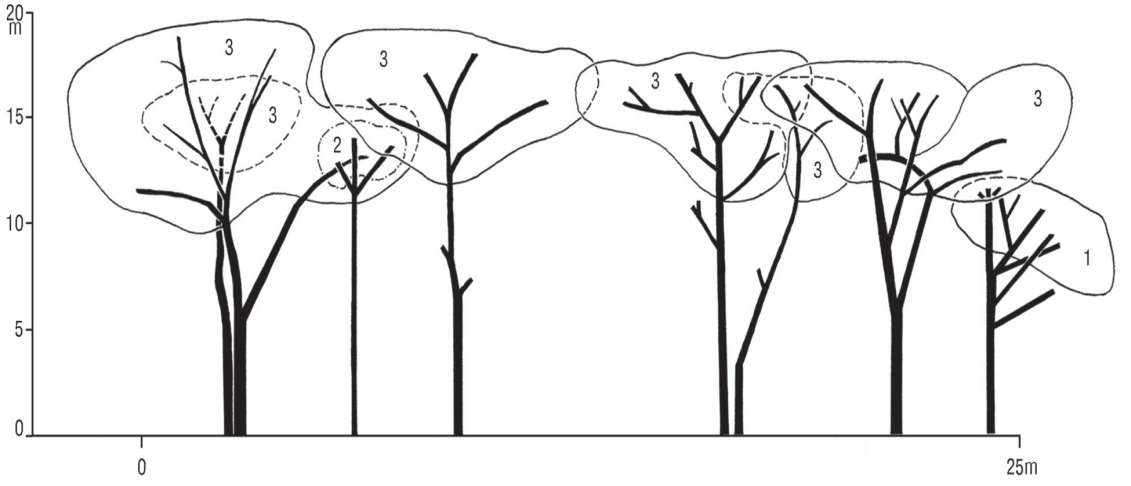
Interestingly, palms are totally missing, which is unusual for the region.

The forest is very dynamic and tree fall is caused by frequent inundations and the resulting swampy soils, which causes instability of the trees. Gaps are invaded by pioneer tree species of the upper storey, so that woody seedlings in the understorey consit of the same species. Regeneration of the forest is a shortened cycle in the sense of succession, that never reaches "stable conditions" with climax species.

Profile diagram 6: Riverine flood plain forest along slow-flowing and meandering streams with waterlogged soils. Confluence Río Bonito and Río Oro. E 261447 m, N 964693 m. Altitude: 70 m. The strip is 25 m long and 10 m width. **1**. *Ochroma pyramidale* (Malvaceae), **2**. *Inga ruiziana* (Fabaceae-Mimosoideae), **3**. *Luehea seemannii* (Malvaceae).

Due to logging for cattle breeding and banana plantations during the last decades this forest type is nearly extinct. Only small areas remain along the Río Oro, Río Bonito and Río Esquinas.

Fig. 7: Pioneer species such as *Ochroma pyramidale* and *Trichospermum grewiifolium* (Malvaceae) are characteritstic trees for floodplain forest along slow-flowing rivers.



Profile diagram 7: Lowland riverine forest along fast flowing rivers and streams with well drained soils and gravel bank. Río Esquinas (km 40). E 260524 m, N 967136 m. Altitude: 82 m. **1**. *Ochroma pyramidale* (Malvaceae), **2**. *Cecropia peltata* (Urticaceae), **3**. *Albizia carbonaria* (Fabaceae-Mimosoideae).

Fig. 8: *Albizia carbonaria* (Fabaceae-Mimosoideae) is the dominant species in the dynamic riverine forest along fast flowing rivers. Río Esquinas, km 40.

Fig. 9: *Gynerium sagittatum* (Poaceae) grows in pure stands at gravel banks and sandy soils. Río Esquinas near Riyito.

1.1.6.3. Riverine forest along fast flowing rivers and streams with well drained soils and gravel banks (e.g. mountain section of Río Esquinas)

Characteristics: very dynamic and unstable, poorly structured forest with low diversity on gravel banks. Dominated by pioneer species. Dry soil conditions (gravel).
Size and location of the investigated site: 0.1 ha. Río Esquinas (km 40). E 260524 m, N 967136 m. Altitude: 82 m.
Diversity/Density (d.b.h. ∅ 10 cm): 5 spp./26 ind/0,1 ha.
Characteristic plants:
Emergents: -
Canopy: *Lonchocarpus heptaphyllus* (Fabaceae-Faboideae), *Albizia carbonaria* (Fabaceae-Mimosoideae), *Ochroma pyramidale* (Malvaceae), *Hasseltia floribunda* (Salicaceae), *Cecropia peltata* (Urticaceae),
Mid-subcanopy: young trees of the canopy layer. *Senna reticulata* (Fabaceae-Caesalpinioideae), *Dicraspidia donnel-smithii* (Malvaceae), *Siparuna thecaphora* (Monimiaceae), *Psidium guajava* (Myrtaceae), *Myriocarpa longipes* (Urticaceae).
Understorey and ground layer: relatively dense. *Clibadium anceps* (Asteraceae), *Begonia multinervia* (Begoniaceae), *Costus pulverulentus* (Costaceae), *Desmodium adscendens* (Fabaceae-Faboideae), *Heliconia latispatha*, *H. wagneriana* (Heliconiaceae), *Calathea lutea*, *C. crotalifera* (Marantaceae), *Ossaea robusta* (Melastomataceae), *Nephrolepis multiflora* (Oleandraceae), *Piper aduncum* (Piperaceae), *Gynerium sagittatum*, *Lasiacis standleyi*, *Paspalum distichum* (Poaceae), *Hamelia patens* (Rubiaceae).
Palms: -
Epiphytes: rare, due to the short lifespan of the trees.
Hemiepiphytes: not found.
Lianas: rare, only small lianas.

This forest type is found on the banks of fast-flowing rivers with montane characteristics (e.g. Río Esquinas). The site conditions are dry and meagre, since gravel has quite a small water capacity and the organic layer is relatively thin.

The open canopy layer is dominated by several pioneer species. Trees grow up to 23 m tall. The most important tree is *Albizia carbonaria* (Fabaceae-Mimoso-

ideae) which dominates the vegetation and gives this ecosystem its special character.

The mid-subcanopy layer is open and consists mainly of younger trees of the canopy layer and several subcanopy pioneer species. The underground is often dominated by the woody grass *Gynerium sagittatum* (Poaceae). Seedlings of typical riverine forests species such as *Anacardium excelsum* and *Spondias mombin* (Anacardiaceae) are abundant in the ground cover. Since they are not found in the canopy, they are presumably washed away by the frequent flooding. It is noticeable that several species which are typical for mountain rainforests are common, e.g. *Rolandra* sp., *Vernonia brachiata* (Asteraceae) and not found along more slowly flowing rivers (e.g. Río Bonito).

Palms, epiphytes and hemiepiphytes are not found. Lianas are rare and only one species *Micania guaco* (Astereaceae) was collected.

The forest is very dynamic due to frequent flooding. Stronger floods may drastically change the underground vegetation when it is washed away, and they can destroy the taller and already established tree vegetation as well. Gaps are invaded by pioneer tree species of the upper storey. The forest type is abundant in the confluence of Río Esquinas with Río Bonito.

1.1.6.4. Vegetation on sandy soil and gravel banks with Gynerium sagittatum (Poaceae)

Characteristics: very dynamic and poorly structured vegetation on gravel banks with low diversity. Dominated by *Gynerium sagittatum* (Poaceae). Dry soil conditions (gravel).
Size and location of the investigated site: 0.1 ha at Río Bonito. E 255880 m, N 962493 m and E 255838 m, N 962455 m. Altitude 80 m.
Diversity/Density (d.b.h. ∅ 10 cm): 3 spp./5 ind/0,1 ha.
Characteristic plants:
Emergents: -
Canopy: *Hyeronima alchorneoides* (Euphorbiaceae), *Ormosia coccinea* (Fabaceae-Faboideae), *Luehea seemannii* (Malvaceae), *Cecropia peltata* (Urticaceae).
Mid-subcanopy: seedlings of the canopy layer. Pioneer species such as *Vismia baccifera* (Clusiaceae), *Senna reticulata* (Fabaceae-Caesalpinioideae), *Ochroma pyramidale* (Malvaceae), *Hedychium coronarium* (Zingiberaceae).
Understorey and ground layer: dense. *Vernonia brachiata* (Asteraceae), *Costus lima*, *Dimerocostus strobilaceus* (Costaceae), *Carludovica drudei* (Cyclanthaceae), *Senna alata* (Fabaceae-Caesalpinioideae), *Mimosa pudica* (Fabaceae-Faboideae), *Heliconia wagneriana* (Heliconiaceae), *Gynerium sagittatum* (Poaceae), *Hedychium coronarium* (Zingiberaceae).
Palms: -
Epiphytes: rare, due to the short lifespan of the trees.
Hemiepiphytes: rare.
Lianas: rare, herbaceous vines are abundant.

This open and unstable vegetation type is found on the gravel banks of medium to fast flowing rivers (e.g. Río Bonito). The site conditions are dry and meagre, since gravel has low water storage capacity and the organic layer is marginal. A similar vegetation with the dominating *Gynerium sagittatum* (Poaceae) is found on mud banks along meandering streams, e.g. Río Esquinas.

The canopy layer is very open and consists of several pionier species which may invade the dense underground vegetation. Most of them are bird-dispersed. The tallest trees grow up to 15 m.

The mid-subcanopy layer is also open and contains seedlings of the canopy species and subcanopy pioneer species.

The understorey and ground layer is dense and dominated by *Gynerium sagittatum* (Poaceae) and *Senna alata* (Fabaceae-Caesalpinioideae). The naturalised *Hedychium coronarium* (Zingiberaceae) grows along the bank.

Hemiepiphytes are rare, with only *Philodendron tripartitum* (Araceae) collected. Also only one liana *Davilla nitida* (Dilleniaceae) was found, but in contrast herbaceous vines such as *Calopogonium caeruleum*, *Desmodium adscendens* (Fabaceae-Faboideae), *Vanilla* sp. (Orchidaceae) and *Cissus biformifolia* (Vitaceae) are abundant as well as species out of Apocynaceae, Asteraceae and Convolvulaceae. No epiphytes were found.

A remarkable association on gravel banks on fast-flowing rivers is an association with *Tessaria integrifolia* (Asteraceae), which is found mainly at the Río Esquinas and Río Piedras Blancas somewhat outside the study area.

1.1.7. Natural forest gaps

General. Changes in vegetation result in a forest cycle consisting of distinguishable phases, a process which was first described by AUBREVILLE (1938). Later, WHITMORE (1978, 1984) recognised three distinct phases, which he called gap, building and mature phase. The phases are arbitrarily divided stages in the development cycle found in all tropical rainforests. They have ill defined boundaries and can be distinguished in structure and floristic composition. The mature phase is recognised by a closed canopy formed by A and B storey trees. When these die or fall down, they form gaps and damage smaller trees and other plants around them. The gaps are quickly filled with light-preferring herbs, climbers and young trees. As the tree seedlings grow taller, the gap passes into the building phase. Many years later (50 or more?) the mature phase is re-established.

The size and shape of gaps caused by fallen trees depends on the weight of their crowns, the branching pattern and the density of the surrounding canopy. Small

Fig. 10: Typical forest gap due to tree snapping (c. 150 m²). Ocelot trail, La Gamba.

trees cause small gaps and increased light may stimulate one-sided growth of the neighbouring crowns. Such a gap closes very quickly. Tall trees cause larger gaps and the opening in the crown layer is accompanied by a significant change in the microclimate.

If the gap is large enough, sunlight can reach the ground level and temperature and humidity regimes approach those of open clearings. This change allows the germination and establishment of shade-intolerant tree species (light-demanding species). They often include rapidly growing pioneer species which are characteristic of young secondary forests. Later in the succession these short-lived species are replaced by slow growing, shade-tolerant species characteristic for each mature forest type.

The most common natural causes of forest gaps is the falling of large trees and snapping. The removal of a single tree creates a gap of several hundred square metres, and a single falling branch may make a sizeable gap. Dead or dying trees, both standing and fallen, can be seen everywhere in undisturbed forests. Natural openings of a hectare or more in size are usually the result of catastrophic winds, and occasionally very extensive areas are destroyed by wind. In May 1997, a powerful thunderstorm occurred in the area around Golfito and many gaps of various sizes were created.

Another important cause of gaps in the area is landslips, mainly on steep slopes. They can be frequently seen in Piedras Blancas along the coastline. Gaps are also frequent in the inland parts, for example in deep valleys.

We studied several gaps of the different primary forest types and give an overview of the most important gap species in the region. Species diversity and abundance may distinguish one site from another, depending on the degree of disturbance, age, size and site (forest type) of the gap.

Characteristics: poorly structured open habit with dense underground vegetation and remaining trees of the primary forest with relatively light and dry climatic conditions.
Coverage: not considered in the vegetation map due to the specified minimum mapping unit of 0.5 ha
Size and location of the investigated site: 0.2 ha. Coordinates: a) gap at the ridge forest: E 256740 m, N 961446 m. Altitude: 318 m. b) gap at the ravine forest: E 257265 m, N 961891 m. Altitude: 124 m.
Diversity/Density (d.b.h. ∅ 10 cm): depending on age and grade of disturbance.
Characteristic plants:
Emergents: -
Canopy and mid-subcanopy: *Aspidosperma spruceanum* (Apocynaceae), *Dendropanax arboreus*, *D. sessiliflorus* (Araliaceae), *Socratea exorrhiza* and *Welfia regia* (Arecaceae), *Croton schiedeanus*, *Mabea occidentalis* (Euphorbiaceae), *Carapa guianensis*, *Apeiba tibourbou*, *Trichospermum grewiifolium* (Malvaceae), *Trichilia septentrionalis* (Meliaceae), *Otoba novogranatensis*, *Virola* spp. (Myristicaceae), *Cecropia* spp. (Urticaceae), *Qualea polychroma* and *Vochysia* spp. (Vochysiaceae).
Understorey and ground layer: relatively dense and diverse. *Asterogyne martiana*, *Calyptrogyne ghiesbreghtiana* (Arecaceae), *Hedyosmum* sp. (Chloranthaceae), *Costus pulverulentus* (Costaceae), *Bequerelia cymosa*, *Scleria secans* (Cyperaceae), *Euphorbia elata* (Euphorbiaceae), *Vachellia allenii* (Fabaceae-Mimosoideae), *Heliconia* spp. (Heliconiaceae), *Ischnosiphon inflatus* (Marantaceae), *Clidemia densiflora*, *Leandra* cf. *granatensis* (Melastomataceae), *Piper* spp. (Piperaceae), *Psychotria elata*, *Psychotria poeppigiana*, *Psychotria solitudinum*, *Duroia costaricensis* (Rubiaceae) and *Renealmia cernua* (Zingiberaceae).
Palms: remnants of the primary forest and seedlings.
Epiphytes, hemiepiphytes: rare.
Lianas: big lianas are rare, small lianas are abundant. *Doliocarpus hispidus* (Dilleniaceae).

Gaps are poorly structured ecotones depending on the grade of disturbance and the size and age of the gap.

One of the most common plants found in gaps are *Cecropia* species (Urticaceae). Interestingly, primary forest palms of the mid-subcanopy germinate rapidly and are also abundant, e.g. *Socratea exorrhiza* and *Welfia regia* (Arecaceae). Longer-living pioneer species (e.g. *Aspidosperma spruceanum* – Apocynaceae), may survive several stages of succession and may still be extant in the mature forest.

The diverse understorey is dominated by fast-growing giant herbs, palms, treelets and ferns mainly of monocotyledonous families. Ferns are abundant and specialised to the different forest sites where gaps are developed. At forest gaps on ridges, *Metaxya rostrata* (Metaxyaceae), *Nephrolepis pectinata* (Oleandraceae) and *Polybotrya cervina* (Polybotryaceae) are abundant.

Epiphytes, hemi-epiphytes are generally rare, depending on the age of the gap or trees.

Large lianas are scarce, but gaps are often filled with shoots of different liana species and may form thickets.

1.2. Coastal and beach vegetation

Along the coastline of the Golfo Dulce, especially in the Esquinas area, there is significant alternation of steep and rocky hills and sandy beaches. The typical plant formations probably never exceeds several metres in width, but vegetation structure and species composition is extremely different compared to the natural vegetation behind the coastline, into which it merges imperceptibly. In general, the vegetation is influenced by salt water and spindrift as well as dry soil conditions. Most of the species are evergreeen and have leathery leaves. We can distinguish between a) rocky shoreline and b) sandy beach vegetation.

1.2.1. Rocky shoreline

Characteristics: extremely dynamic forest vegetation dominated by fast growing trees up to 15(20) m tall with many gaps, affected by spindrift and relatively dry soil conditions.
Length: 21.4 km.
Size and location of the investigated site: 0.01 ha (100 m²). E 253918 m, N 954537 m. Altitude: 5 m.
Diversity/Density (d.b.h. ∅ 10 cm): 6 spp./8 ind./0.01 ha (100 m²).
Characteristic plants:
Emergents: -
Canopy: *Bursera simarouba*, *Spondias purpurea* (Anacardiaceae), *Ochroma pyramidale*, *Trichospermum grewifolium* (Malvaceae), *Inga punctata* (Fabaceae-Mimosoideae).
Mid-subcanopy: *Nectandra martinicensis* (Lauraceae), *Calyptranthes chytraculia*, *Myrcia* sp. nov. (Myrtaceae).
Understorey and ground layer: relatively dense. *Begonia* sp. (Begoniaceae), *Costus comosus*, *C. pulverulentus* (Costaceae), *Carludovica drudei* (Cyclanthaceae), *Xiphidium coeruleum* (Haemodoraceae), *Heliconia latispata* (Heliconiaceae), *Pleiostachya pruinosa* (Marantaceae), *Russelia sarmentosa* (Scrophulariaceae), *Zamia fairchildiana* (Zamiaceae).
Palms: -
Epiphytes: rare. *Catopsis* sp. (Bromeliaceae), *Brassavola nodosa* (Orchidaceae).
Hemiepiphytes: rare.
Lianas: common, *Entada polystachya* (Fabaceae-Mimosoideae), *Serjania racemosa* (Sapindaceae), *Lygodium radiatum* (Schizaeaceae) and the trailing shrub *Warszewiczia coccinea* (Rubiaceae).

This forest type is found along the rocky coastline of the Piedras Blancas National Park, which is only metres wide and merges inland with the coastal slope forest. Spindrift and dry soil conditons influence the vegetation heavily. Species of the dry forest such as *Bursera simarouba* (Burseraceae) and *Byrsonima crassifolia* (Malpighiaceae) may be abundant and are important trees of the canopy.

Due to the steepness, emergents are not found and the forest height is relatively low at 15-20 m. The canopy is formed by relatively fast growing (pioneer) trees. The mid-subcanopy layer is scarce.

Fig. 11: The steep and rocky coast on the southern border of the Piedras Blancas National Park.

The relatively dense and heterogenous understorey and ground layer is composed of various families. Several species are adapted to the specific climatic conditions and are seldom found at other sites (e.g. *Russelia sarmentosa* – Scrophulariaceae). Palms are not found, probably due to the salty conditions. Epiphytes and hemiepiphytes are rare for the same reasons.

Lianas and climbers are very common and conspicuous along the whole coastline.

Warszewiczia coccinea (Rubiaceae) a trailing shrub with scarlet bracts is frequent and eye-catching, even from far away when following the coastline by boat.

Fig. 12: Exposed rock with its typical vegetation adapted to dry soil conditions.

Fig. 13: Sandy beach vegetation with coconut palms and *Hibiscus pernambucensis* (Malvaeae).

The forest is extremely dynamic due to the steepness and exposition of the terrain. Tree-fall gaps caused by fallen trees and landslides are characteristic.

On **exposed rocks**, where micro-climatic conditions are extremely dry, a characterisitc vegetation is developed which differs from that on rocky coastline. It consists of several species which are characteristic for drier sites, e.g. dry forest in the north of Costa Rica. The most important trees are *Bombacopsis sessilis* (Malvaceae), *Bursera simaruba* (Burseraceae), *Hirtella americana* (Chrysobalanaceae), *Swartzia ochnaceae* (Fabaceae-Faboideae), *Cojoba rufescens* (Fabaceae-Mimosoideae), *Byrsonima crassifolia* (Malpighiaceae), *Myrcianthes fragrans* (Myrtaceae), *Alibertia edulis* (Rubiaceae) and *Trema micrantha* (Ulmaceae). The bare understorey and ground vegetation must be salt resistant and consists of epiphytes which grow directly on the rocks. The most abundant species are *Anthurium* cf. *ravenii* (Araceae), *Catopsis* sp., *Pitcairnia halophila*, *Werauhia viridiflora* (Bromeliaceae) and *Brassavola nodosa* (Orchidaceae). In addition hemi-epiphytes which root directly on the rocks are characterisitic, e.g. *Clusia rosea* and *C. peninsula* (Clusiaceae).

1.2.2. Beach vegetation

Characteristics: sandy beach vegetation, dominated by coconut palms and *Terminalia catappa* (Combretaceae). Simply structured and species-poor, trees up to 30 m.
Length: 12.9 km.
Size and location of the investigated sites: 0.05 ha (500 m²). E 252130 m, N 957204 m. Altitude: 2 m.
Diversity/Density (d.b.h. ∅ 10 cm): 6 spp./8 ind./0.05 ha (500 m²).
Characteristic plants:
Emergents: -
Canopy: open canopy. *Cocos nucifera* (Areacaceae), *Terminalia catappa* (Combretaceae), *Lonchocarpus heptaphyllus* (Fabaceae-Faboideae).
Mid-subcanopy: *Chrysobalanus icaco* (Chrysobalanaceae), *Dalbergia brownei* (Fabaceae-Faboideae), *Hibiscus pernambucensis* (Malvaceae), *Amphitcecna latifolia* (Rubiaceae).
Understorey and ground layer: poorly developed. *Ipomoea pescaprae* (Convolvulaceae), *Canavalia rosea* (Fabaceae-Faboideae).
Palms: only coconut palm.
Epiphytes: rare. *Werauhia gladioliflora* (Bromeliaceae), *Codonanthe crassifolia* (Gesneriaceae), *Brassavola nodosa* (Orchidaceae).
Hemiepiphytes: rare, *Ficus* spp. (Moraceae) are seldom found.
Lianas: rare. *Entada gigas*, *Entada polystachya* (Fabaceae-Mimosoideae), *Smilax* sp. (Smilacaceae). Herbaceous vines are common: *Dalbergia brownei* (Fabaceae-Faboideae), *Philodendron tripartitum* (Araceae), *Martinella obovata* (Bignoniaceae), *Stigmaphyllon ellipticum* (Malpighiaceae).

On sandy beaches, the coconut palm (*Cocos nucifera*) is the most widespread species forming typical palm beach vegetation. In general the vegetation is species-poor and partially inhomogeneous, depending to soil conditions. Epiphytes and hemi-epiphytes are scarce due to salty conditions. The ground layer is poorly developed and mainly contains seedlings of the canopy and mid-subcanopy layer. The creeping herbaceous vines *Ipomoea pescaprae* (Convolvulaceae) and *Canavalia rosea* (Fabaceae-Faboideae) are common sand-dwelling herbs. On shingle beaches, *Hibiscus pernambucensis* (Malvaceae) may dominate the vegetation.

Natural vegetation on coastal plains is highly disturbed due to human interference.

1.3. Mangrove and swamp forest

1.3.1. Mangrove

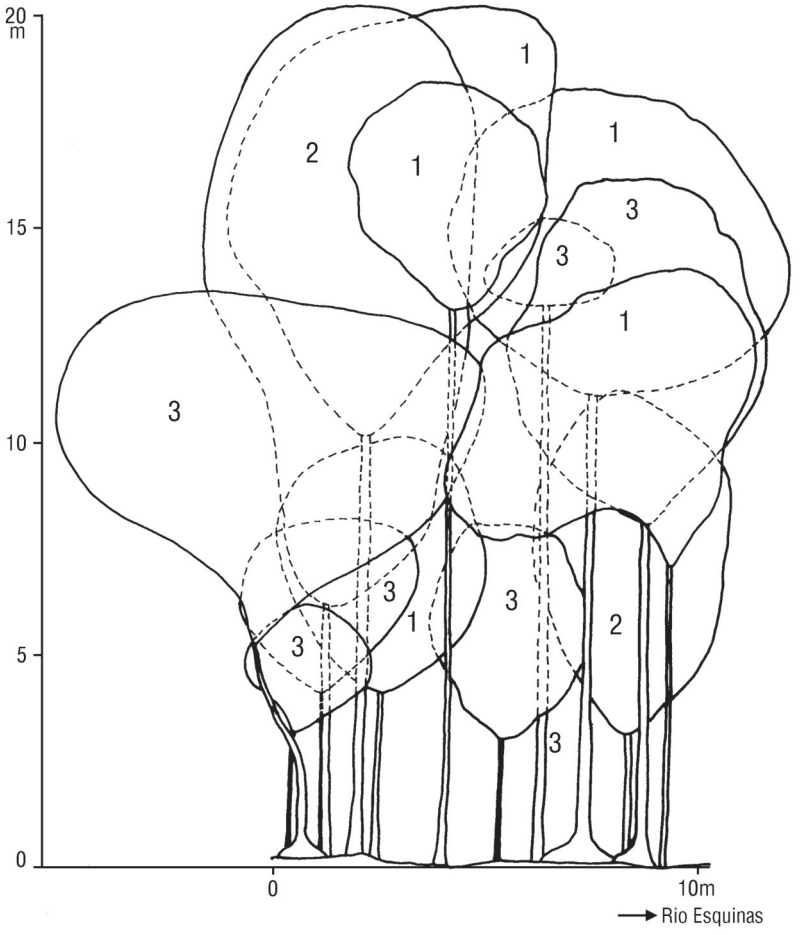
Characteristics: species-poor forest in the estuaries of rivers, trees up to 20(25) m.
Size and location of the investigated site: 0.03 ha. Río Esquinas, 300 m inland from the mouth: E 244815 m, N 965599 m. Altitude: 7 m.
Coverage: 1.8% of the study area (together with 1.3.2. Swamp forest).
Diversity/Density (d.b.h. ∅ 10 cm): low diversity, 20 ind./2 spp./0.03 ha (3.000 m²).
Characteristic plants:
Emergents: -
Canopy: *Rhizophora mangle*, *R. racemosa* (Rhizophoraceae), *Avicennia germinans* (Acanthaceae), *Laguncularia racemosa*, *Conocarpus erectus* (Combretaceae), *Pelliciera rhizophorae* (Theaceae).
Understorey and ground layer: poorly developed. *Crinum erubescens* (Amaryllidaceae), *Tabebuia palustris* (Bignoniaceae), *Acrostichum aureum* (Pteridaceae).
Epiphytes: rare. *Anthurium* sp. (Araceae), *Werauhia gladioliflora* (Bromeliaceae), *Codonanthe crassifolia* (Gesneriaceae), *Brassavola nodosa*, *Trigonidium* sp. (Orchidaceae).
Hemiepiphytes: rare. *Clusia valerioi* (Clusiaceae).
Lianas: rare. *Machaerium lunatum* (Fabaceae-Faboideae).

Mangrove and swamp forest formations occur in the salt-water and brackish tidal zone of river estuaries and bays along the coast of the Golfo Dulce. The largest mangrove forests occur in the the mouth of the Río Coto, Río Esquinas, Río Sierpe, Río Sirena, Río Llorona, Río Corcovado, and around the shores in the town of Golfito. Mangrove forests are floristically poor, thus representing the opposite extreme of tropical forests with their rich species diversity.

The distribution is determined by the inherently high salt tolerance. Only a few species, mostly from unrelated families, are sufficiently salt-tolerant to be able to grow in such an adverse habitat. The most important species which protects against erosion is the red mangrove *Rhizophora mangle* (Rhizophoraceae) with its characteristic stilt roots. This species is found in the mouths of the rivers and inland along the shoreline to a certain point, depending on the influence of the tides. The black mangrove *Avicennia germinans* (Verbenaceae) and other species occupy higher ground deeper inside the forest.

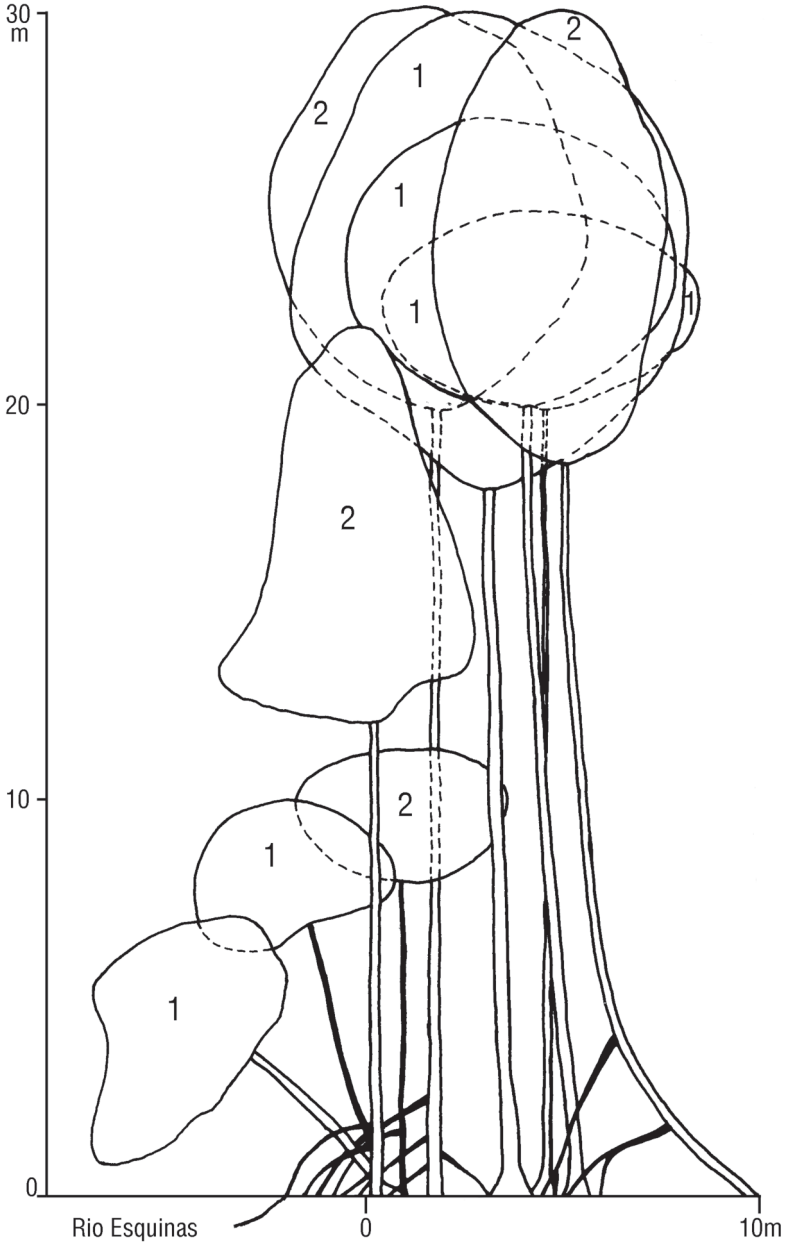
The understorey and the ground layer are species-poor and consist mainly of *Crinum erubescens* (Amaryllidaceae) and the fern *Acrostichum aureum* (Pteridaceae).

In the past, *Rhizophora* trees were extensively harvested for their bark used in leather tanning and charcoal production and for shrimp farming. Nowadays, law prohibits the cutting of mangroves.



Profile diagram 8: Mangroves at the Río Esquinas, 300 m inland from the mouth. E 244815 m, N 965599 m. Altitude: 7 m. The strip is 10 × 10 m. Only trees ∅ 10 cm d.b.h. are shown. **1**. *Pelliciera officinalis* (Pellicieraceae); **2**. *Rhizophora mangle* (Rhizophoraceae). Profile diagram drawn by Gaafar & Prader during field course 1999.

Fig. 14: Typical mangrove with *Rhizophora mangle* (Rhizophoraceae) and *Pelliciera rhizophorae* (Theaceae). Río Esquinas.



Profile diagram 9: Swamp forest at the Río Esquinas, 1 km inland from the mouth. E 246332 m, N 965413 m. Altitude: 10 m. The strip is 10 × 10 m. Only trees ∅ 10 cm d.b.h. are shown. **1**. *Mora oleifera* (Fabaceae-Caesalpinioideae); **2**. *Pelliciera officinalis* (Pellicieraceae); **3**. *Pterocarpus officinalis* (Fabaceae-Faboideae). Profile diagram drawn by Gaafar & Prader during a field course in 1999.

1.3.2. Swamp forest

Characteristics: species-poor forest near mangroves, characterised by its low relief and poor draingage, trees up to 25(30) m.
Coverage: see 1.3.1. Mangrove
Size and location of the investigated site: 0.03 ha. 1 km inland from the mouth of the Río Esquinas: E 246332 m, N 965413 m. Altitude: 10 m.
Diversity/Density (d.b.h. ∅ 10 cm): low diversity, 29 ind./4 spp./0.03 ha (3.000 m²).
Characteristic plants:
Emergents: -
Canopy: *Mora oleifera* (Fabaceae-Caesalpinioideae), *Andira inermis*, *Pterocarpus officinalis* (Fabaceae-Faboideae), *Pelliciera rhizophorae* (Theaceae).
Understorey and ground layer: poorly developed. *Crinum erubescens* (Amaryllidaceae), *Tabebuia palustris* (Bignoniaceae), *Acrostichum aureum* (Pteridaceae).
Epiphytes: rare. *Anthurium* sp. (Araceae), *Werauhia gladioliflora* (Bromeliaceae), *Codonanthe crassifolia* (Gesneriaceae), *Brassavola nodosa*, *Trigonidium* sp. (Orchidaceae).
Hemiepiphytes: rare. *Clusia valerioi* (Clusiaceae).
Lianas: rare. *Machaerium lunatum* (Fabaceae-Faboideae)

From the true mangroves landwards, swamp forests dominate the vegetation. The sites are characterised by their low relief and poorly drained soils. Several species grow in this habitat, and many of them have large buttresses (e.g. *Pterocarpus officinalis*). The floristic cover may vary conspicuously from site to site and probably reflects soil differences and degrees of relative salinity. The understorey and the ground layer are species-poor and consist mainly of the same species found in mangroves. Epiphytes, hemiepiphytes and lianas are scarce due to salty conditions.

Allen (1956) recognised three associations: 1. *Pterocarpus officinalis-Carapa guinensis*, 2. *Pterocarpus officinalis-Mora oleifera* and 3. *Symphonia globulifera*. In the region, we found only association 2 near the mouth of the Esquinas river, but somewhat outside the study area extensive swamp forests are found in the lower part of the Río Coto, at the mouth of the Río Rincón, and on the periphery of the palm swamps of the Corcovado lagoon.

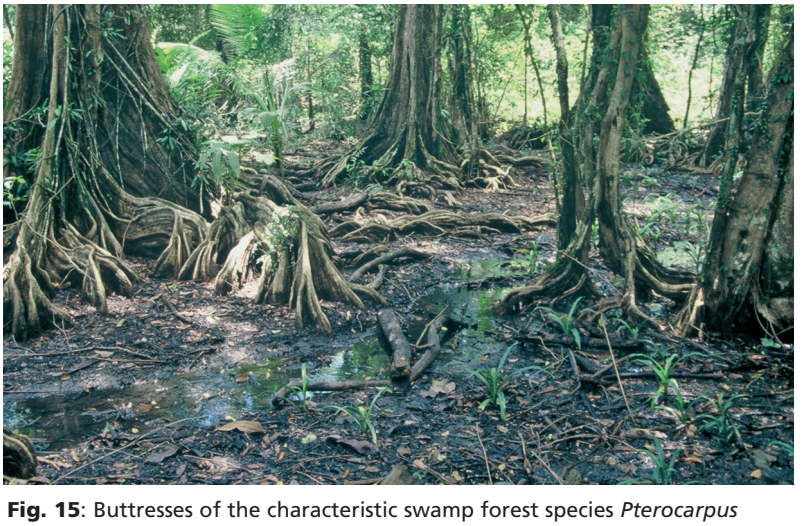


Fig. 15: Buttresses of the characteristic swamp forest species *Pterocarpus officinalis* (Fabaceae-Faboideae).

1.4. Herbaceous swamp vegetation

Characteristics: old lagoons which are invaded by specialised plant species (e.g. Poaceae).
Coverage: 0.2% of the study area.
Size and location of the investigated site: 0.01 ha (100 m²). E 254889 m, N 967614 m. Altitude: 30 m.
Characteristic plants:
Emergents: -
Canopy and mid-subcanopy: not developed.
Understorey and ground layer: dense vegetation mainly formed by grasses. *Cyperus* spp. (Cyperaceae), *Aeschynomene* sp. (Fabaceae-Faboideae), *Heliconia lathispatha*, *H. imbricata* (Heliconiaceae), *Calathea insignis*, *C. lutea* (Marantaceae), *Ludwigia hyssopifolia*, *L. latifolia*, *L. ocotvalis* (Onagraceae), *Echonochloa polystachya*, *Paspalum paniculatum*, *Hymenachne amplexicaulis* and *Panicum parviflorum* (Poaceae), *Polygonum* sp. (Polygonaceae).
Palms, epiphytes, hemiepiphytes, lianas: not found.

Large areas of herbaceous marshes can be found in the Laguna Machaca near the village of Piedras Blancas. This vegetation type is in sharp contrast to the surrounding arborescent flora. It appears that many of these open tracts represent old lagoons that have been filled by the encroaching vegetation, particularly grasses and sedges. Small shrubs and herbs adapted to the wet conditions may be abundant. Giant herbs of monocotyledonous families may form thickets. At the edge of the swamps, some tree species, e.g. *Symphonia globulifera* (Clusiaceae) and *Pachira aquatica* (Malvaceae) are abundant and may form colonies.

In somewhat brackish water, the fern *Acrostichum cf. daneiflorum* (Pteridaceae) dominates the vegetation (see also the chapter on mangroves).

In the study area, one may find the greatest swamp vegetation at the Laguna Machaca, but somewhat outside the study area, this vegetation type borders the Corcovado lagoon (c. 10 km²) and the Laguna de Sierpe. The latter was recently discovered for tourism possibilites, since lagoons harbour a high diversity in bird species. Fortunately, explotation of the Laguna de Sierpe remains illegal.

2. Secondary vegetation

2.1. Secondary forest

General. When primary forest is logged or partially felled, micro-climatic conditions change depending on the grade of disturbance. Today, clear-cutting of the forest is prohibited by the forest law of Costa Rica.

When primary forest is cleared, robust herbs are the first plants to invade the bare land. The next step in recolonisation is the arborescent flora, consisting of species that are either rare or absent in primary forest. These species with high light requirements belong to different families and genera. Some are from river bank and gravel bank communities such as *Ochroma pyramidale* (Malvaceae) and *Senna reticulata* (Fabaceae-Caesalpinioideae), while others are rare elements of primary forest, e.g. *Trema micrantha* (Ulmaceae) and *Cecropia* spp. (Urticaceae).

The clearing of land initiates a long process, usually involving a succession of distinct associations which depend on the size of the disturbed area, and culminating in the reestablishment of the quasi-original forest structure. A typical succession may start with rapidly developing herbaceous cover composed of ferns and various heliconias (e.g. *H. lathispatha*) and *Calathea* spp. (Marantaceae), followed for a few years by *Cecropia* spp. (Urticaceae), *Ochroma pyramidale* (Malvaceae), *Psidium guajava*, *P. friedrichsthalianum* (Myrtaceae), *Trema micrantha* (Ulmaceae), and *Vismia ferruginea* (Clusiaceae). Species of *Vochysia* (Vochysiaceae) may invade this second successional stage, creating a microclimate more suitable for shade-tolerant climax species such as *Brosimum utile* (Moraceae) and *Carapa guianensis* (Meliaceae). The latter often reaches canopy height and persists for many years, thus completing the process of succession.

If timber trees are cut selectively from primary forest, succession starts at an advanced stage. In that case, secondary forest consists of remaining primary forest trees and of secondary and pioneer species, depending on the disturbance. However, the canopy and crown layer is interrupted and not uniform and closed as in primary forest. Palms, epiphytes, hemiepiphytes and large lianas in general are rare in secondary forests.

Secondary forests are not easy to classify, because their structure and species composition depends on the grade of disturbance, availability of the flora, microclimatic conditions and soil types, erosion and other ecological factors. Different sites, even if they are close together, may distinguish substantially in species composition and structure. Data were summarised from various research plots in the region during the last 15 years. What we present here, are two categorised forest types: a) young secondary forest with canopy trees up to 15 m and b) old secondary forest with trees more than 15 m tall and c) forest edges.

Profile diagram 10: Young secondary forest at the Fila trail. E 257634 m, N 962037 m. Altitude: 130 m. The strip is 25 × 10 m. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Trattinickia aspera* (Burseraceae), **2**. *Cecropia peltata* (Urticaceae), **3**. *Andira inermis* (Fabaceae-Faboideae), **4**. *Guettarda crispiflora* (Rubiaceae), **5**. *Trichospermum grewiifolium* (Malvaceae), **6**. *Vochysia ferruginea* (Vochysiaceae).

2.1.1. Young secondary forest with canopy trees up to 15 m

Characteristics: poorly structured forest with thin-stemmed trees up to 15 m tall and dense ground layer.
Coverage: 8.4% of the study area.
Size and location of the investigated site: 0.1 ha. Fila trail. E 257634 m, N 962037 m. Altitude: 130 m.
Diversity/Density (d.b.h. ∅ 10 cm): 24 spp./41 ind./0,1 ha.
Characteristic plants:

Emergents: -

Canopy: *Guatteria amplifolia* (Annonaceae), *Trattinickia aspera* (Burseraceae), *Vismia baccifera* (Clusiaceae), *Hampea appendiculata* (Malvaceae), *Guettarda crispiflora*, *Isertia laevis* (Rubiaceae), *Cecropia* spp. (Urticaceae), *Vochysia allenii*, and *V. ferruginea* (Vochysiaceae).

Mid-subcanopy: not existent.

Understorey and ground layer: relatively dense. *Salpichlaena volubilis* (Blechnaceae), *Costus laevis* (Costaceae), *Becquerelia cymosa* (Cyperaceae), *Dicranopteris pectinata* (Gleicheniaceae), *Heliconia irrasa*, *H. stilesii* (Heliconiaceae), *Aciotis caulialata*, *Clidemia densiflora*, *Miconia schlimii* (Melastomataceae), *Metaxya rostrata* (Metaxyaceae), *Nephrolepis multiflora* (Oleandraceae), *Piper* spp. (Piperaceae), *Psychotria elata*, *P. poeppigiana*, *P. solitudinum*, *Rudgea cornifolia* (Rubiaceae).

Palms: only seedlings of mid-canopy palms of primary forest (*Socratea exorrhiza*)

Epiphytes: rare. Araceae, *Tillandsia anceps* (Bromeliaceae), Orchidaceae.

Hemiepiphytes: rare. *Souroubea sympetala* (Marcgraviaceae), *Topobea maurofernandeziana* (Melastomataceae).

Lianas: common. *Davilla nitida*, *Doliocarpus multiflorus*, *D. hispidus* (Dilleniaceae), *Plukenetia penninervia* (Euphorbiaceae), *Banisteriopsis cornifolia* (Malpighiaceae), *Serjania racemosa* (Sapindaceae), *Smilax* spp. (Smilacaceae).

Young secondary forests are simply structured with trees up to 15 m tall and dense ground cover. The canopy is relatively closed and comprises several fast-growing pioneer species.

The mid-subcanopy is inconspicuous or not present, but the understorey and ground layer is dense, consisting of various growth forms (treelets, shrubs, lianas, herbaceous vines, ferns and herbs). Ferns may dominate the ground cover and seedlings of tree species of advanced successional stages are abundant, such as *Pausandra trianae* (Euphorbiaceae), *Laetia procera* (Salicaceae), *Ruptiliocarpon caracolito* (Lepidobotryaceae) and *Virola koschnyi* (Myristicaceae). Palm seedlings of *Socratea exorrhiza* are obvious, whereas no palms are found in the canopy.

Fig. 16: About 10-year old secondary forest with canopy heigth of c. 20 m. This area was formerly used as a road for logging.

Epiphytes are rare and found only on older trees and branches. Interestingly, hemi-parasitic Loranthaceae are very common. Hemiepiphytes are scarce and only small individuals were recorded. Small lianas and herbaceous vines are abundant, but large lianas are rare.

Young secondary forests are mainly found near settlements or fincas (farmhouses), when agricultural land, mainly pasture, is abandoned. This forest type ist found Profile diagram 10.

2.1.2. Old secondary forest with canopy trees > 15 m

Characteristics: relatively dense, but poorly structured forest on lateritic soil on slopes and ridges, with canopy trees often dominated by *Vochysia* sp. (Vochysiaceae), up to 30 m tall, dense ground layer.
Coverage: 11.1% of the study area.
Size and location of the investigated site: 0.1 ha. Way from Tropical Station La Gamba to Río Bonito. E 256486 m, N 962640 m. Altitude: 108 m.
Diversity/Density (d.b.h. ∅ 10 cm): 26 spp./65 ind./0,1 ha.
Characteristic plants:
Emergents: -
Canopy: *Jacaranda copaia* (Bignoniaceae), *Trattinickia aspera* (Burseraceae), *Carapa guianensis*, *Guarea grandifolia* (Meliaceae), *Vochysia ferruginea*, *V. guatemalensis* (Vochysiaceae).
Mid-subcanopy: species-poor. *Saurauia yasicae* (Actinidiaceae), *Guatteria amplifolia* (Annonaceae), *Euterpe precatoria*, *Welfia regia* (Arecaceae), *Mabea occidentalis* (Euphorbiaceae), *Miconia trinervia* (Melastomataceae), *Isertia laevis*, *Simira maxonii* (Rubiaceae), *Simarouba amara* (Simaroubaceae).
Understorey and ground layer: relatively dense. *Salpichlaena volubilis* (Blechnaceae), *Hedyosmum scaberrimum* (Chloranthaceae), *Costus laevis* (Costaceae), *Cyclanthus bipartidus* (Cyclanthaceae), *Becquerelia cymosa*, *Diplasia karatifolia*, *Mapania assimilis* (*Cyperaceae*), *Dicranopteris pectinata* (Gleicheniaceae), *Heliconia irrasa* (Heliconiaceae), *Clidemia densiflora*, *Clidemia capitellata*, *Leandra mexicana* (Melastomataceae), *Metaxya rostrata* (Metaxyaceae), *Piper fimbriulatum* (Piperaceae), *Psychotria capitata*, *P. elata*, *P. mortoniana*, *P. poeppigiana* (Rubiaceae).
Palms: rare. *Asterogyne martiana* in the ground cover, seedlings of midcanopy palms of primary forest (*Welfia regia*).
Epiphytes: rare. Araceae, Bromeliaceae, *Codonanthe crassifolia* (Gesneriaceae), Orchidaceae.
Hemiepiphytes: rare. *Ficus nymphaeifolia*-Moraceae.
Lianas: rare. *Davilla nitida*, *Doliocarpus multiflorus*, *D. hispidus* (Dilleniaceae), *Strychnos* sp. (Loganiaceae).

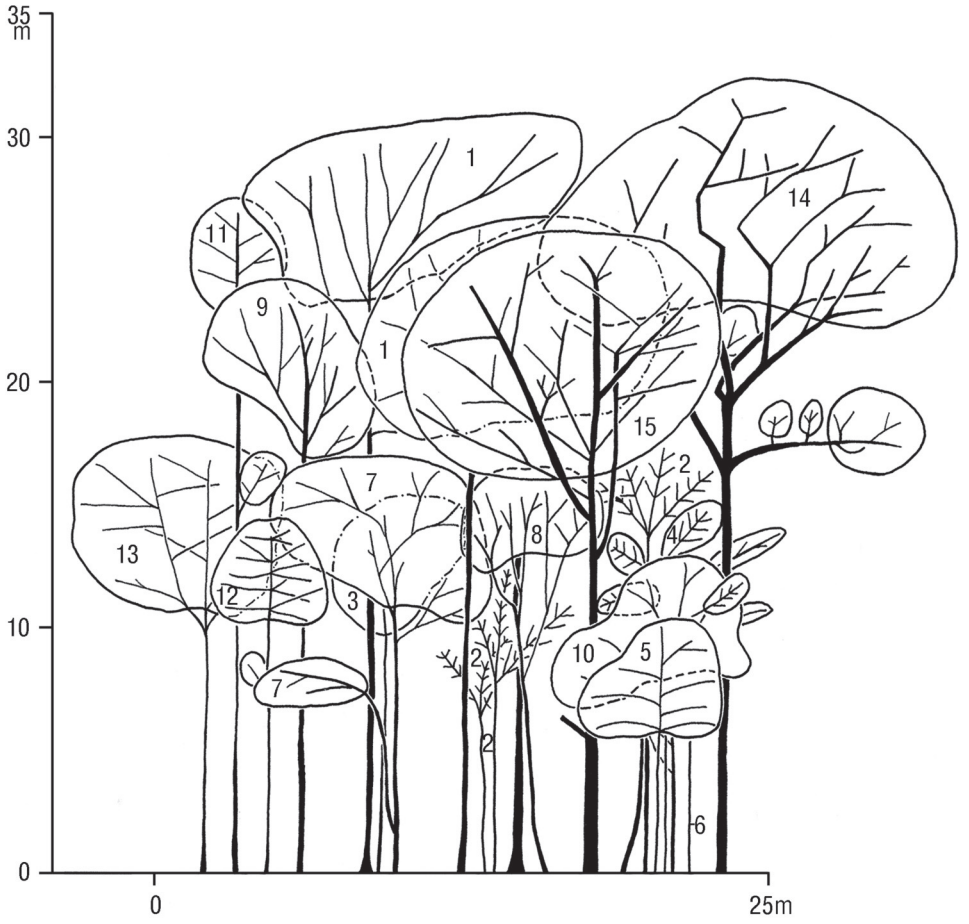
This vegetation type is a typical secondary forest on lateritic soils along ridges and steep slopes. It is a relatively simply structured forest with the canopy up to 30 m tall, often dominated by *Vochysia* spp. (Vochysiaceae).

The mid-subcanopy is species-poor and mainly dominated by younger individuals of canopy and other fast-growing pioneer species. The understorey and ground layer is dense and rich in species and growth forms such as treelets, shrubs, lianas, herbaceous vines, ferns and giant herbs. Tree seedlings of advanced successional stages (shade-tolerant species) are common such as *Aspidosperma spruceanum* (Apocynaceae), *Calophyllum longifolia*, *Symphonia globulifera* (Clusiaceae), *Ruptiliocarpon caracolito* (Lepidobotryaceae), *Carapa guianensis*, *Guarea grandifolia* (Meliaceae) and *Virola* spp. (Myristicaceae). Epiphytes are rare, because of the young age of the trees. Furthermore the oldest tree species, mainly *Vochysia* spp., older branches drop. Hemiepiphytes are scarce and only two bigger individuals were found. Small lianas and herbaceous vines are abundant, but large lianas are absent.

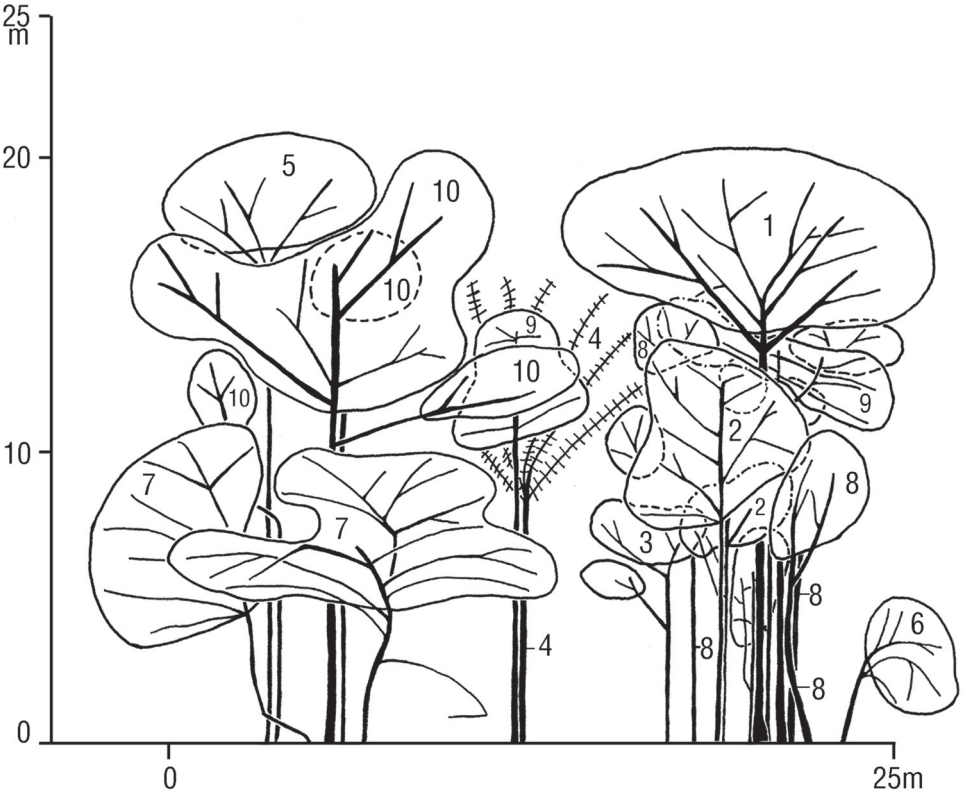
At several sites *Vochysia* spp. (Vochysiaceae) were found to dominate the vegetation and is then called "mayal", after the spanish name "mayo" for *Vochysia* sp., because of its flowering time during May. The "mayal" is a very typical secondary foreset vegetation on lateritic soil when bigger areas (e.g. more than one hectare) of primary forest are cleared. Within 10 years, a secondary forest with a closed and uniform canopy consisting of *Vochysia* sp. will develop. During flowering time in May, this forest is very conspicuous because of the yellow flowers.

Old secondary forests are prevalently found at more inaccessible sites near settlements or abandoned fincas (farmhouses).

Profile diagram 11: Old secondary forest with canopy trees > 15 m. Way from Tropical Station La Gamba to Río Bonito. E 256486 m, N 962640 m. Altitude: 108 m. The strip is 25 × 10 m. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Xylopia sericophylla* (Annonaceae), **2**. *Euterpe precatoria* (Arecaceae), **3**. *Symphonia globulifera* (Clusiaceae), **4**. *Croton tenuicaudatus* (Euphorbiaceae), **5**. cf. Flacourtiaceae, **6**. *Vachellia allenii* (Fabaceae-Mimosoideae), **7**. *Inga alba* (Fabaceae-Mimosoideae), **8**. *Inga thibaudiana* (Fabaceae-Mimosoideae), **9**. *Trichilia septentrionalis* (Meliaceae), **10**. *Brosimum costaricanum* (Moraceae), **11**. *Ficus* cf. *maxima* (Moraceae), **12**. *Virola guatemalensis* (Myristicaceae), **13**. *Virola sebifera* (Myristicaceae), **14**. *Simarouba amara* (Simaroubaceae), **15**. *Vochysia ferruginea* (Vochysiaceae).



Profile diagram 12: Forest edge near the Tropical Station La Gamba, Fila trail. E 257595 m, N 962034 m. Altitude: 130. The strip is 25 × 10 m. Only trees ≥ 10 cm d.b.h. are shown. **1**. *Anaxagorea* sp. (Annonaceae), **2**. *Guatteria amplifolia* (Annonaceae), **3**. *Dendropanax arboreus* (Araliaceae), **4**. *Euterpe precatoria* (Arecaceae), **5**. *Quararibea platyphylla* (Malvaceae), **6**. *Protium aracouchini* (Burseraceae), **7**. *Vismia grandifolia* (Clusiaceae), **8**. *Trichilia septentrionalis* (Meliaceae), **9**. *Virola sebifera* (Myristicaceae), **10**. *Trichospermum grewiifolium* (Malvaceae).



2.1.3. Forest edges

Characteristics: poorly to well structured forest up to 20(25-30) m tall with influence of primary and secondary forest elements.
Coverage: not considered in the vegetation map.
Size and location of the investigated site: 0.1 ha. Near Tropical Station La Gamba, Fila trail. E 257595 m, N 962034 m. Altitude: 130 m.
Diversity/Density (d.b.h. ∅ 10 cm): 39 spp./86 ind./0.1 ha.
Characteristic plants:

Emergents: remnants of the primary forest are possible emergents.

Canopy: fast-growing trees such as *Dendropanax arboreus* (Araliaceae), *Ruptiliocarpon caracolito* (Lepidobotryaceae), *Trichospermum grewiifolium* (Malvaceae), *Carapa guianensis* (Meliaceae), *Virola sebifera* (Myristicaceae), *Simira maxonii* (Rubiaceae), *Simarouba amara* (Simaroubaceae), *Cecropia peltata* (Urticaceae).

Mid-subcanopy: dense. *Saurauia yasicae* (Actinidiaceae), *Guatteria amplifolia* (Annonaceae), *P. aracouchinii*, *Protium glabrum*, *P. ravenii*, *Tetragastris panamensis* (Burseraceae), *Marila laxiflora*, *Vismia grandifolia* (Clusiaceae), *Croton schiedeanus*, *Mabea occidentalis*, *Pausandra trianae* (Euphorbiaceae), *Vachellia allenii*, *Inga* spp. (Fabaceae-Mimosoideae), *Talauma gloriensis* (Magnoliaceae), *Trichilia septentrionalis* (Meliaceae), *Perebea hispidula* (Moraceae), *Compsoneura excelsa* (Myristicaceae), *Guettarda crispiflora* (Rubiaceae), *Casearia arborea* (Salicaceae).

Understorey and ground layer: relatively dense. *Spathiphyllum silvicola* (Araceae), *Asterogyne martiana*, *Chamaedorea allenii*, *Geonoma congesta*, *G. cuenata* (Arecaceae), *Costus laevis* (Costaceae), *Asplundia pittieri*, *Carludovica drudei*, *Cyclanthus bipartidus* (Cyclanthaceae), *Mapania assimilis* (Cyperaceae), *Besleria hirsuta*, *Episcia lilacina* (Gesneriaceae), *Heliconia* spp. (Heliconiaceae), *Calathea crotalifera*, *Hylaenthe allenii* (Marantaceae), *Clidemia densiflora*, *C. dentata*, *Leandra mexicana*, *Miconia gracilis*, *M. trinervia* (Melastomataceae), *Piper* spp. (Piperaceae), *Coccocypselum hirsutum*, *Faramea* spp., *Psychotria* spp. (Rubiaceae).

Palms: many seedlings of mid-canopy and understorey palms of primary forest.

Epiphytes: rare. Araceae, Orchidaceae, Bromeliaceae.

Hemiepiphytes: large remnants of primary forest and young and small individuals.

Lianas: common. *Davilla nitida*, *Doliocarpus hispidus* (Dilleniaceae), *Bauhinia* sp. (Fabaceae-Faboideae) and *Smilax* sp. (Smilacaceae).

Forest edges are ecotones at the intersection of primary forest and anthropogenic ecosystems. The vegetation consists of a mixture of primary and secondary forest species, which varies from site to site depending on soil, successional stage and microclimatic conditions. Primary forest species may be found aside fast-growing pioneer trees, which gives this ecotone its special character.

Emergents are rare, but if present, they are remnants of the primary forest. The canopy is relatively open and low in diversity. The mid-subcanopy layer is diverse and consists mainly of faster growing trees and young trees of primary forest species.

Fig. 17: Typical landscape at the border of the Piedras Blancas National Park with *Dicranopteris pectinata* (Gleicheniaceae) in the foreground and different stages of secondary forest in the background.

The understorey and ground layer is also relatively dense and diverse. Tree ferns are characteristic elements, e.g. *Cnemidaria choricarpa* (Cyatheaceae). Ferns such as *Salpichlaena volubilis* (Blechnaceae), *Metaxya rostrata* (Metaxyaceae) and *Nephrolepis multiflora* (Oleandraceae) dominate the ground cover. Many seedlings of different primary forest trees are conspicuous. Large palms are rare, but seedlings and understorey palms are abundant in the ground cover.

Epiphytes and larger hemi-epiphytes are rare, but interestingly, secondary hemi-epiphytes (Aracaeae) are common. Small lianas are abundant, but large lianas are absent or survive as remnants of former primary forest.

The data presented here were taken on a forest edge of primary and secondary forest to give an overview and a basic information of the heterogenous vegetation cover. Further studies are needed to understand the different floristic composition from site to site.

Fig. 18: At very wet sites which were influenced by humans the fern *Nephrolepis multiflora* (Oleandraceae) is the dominant species. Near the ranger station at Río Bonito.

2.2. Fern-dominated vegetation

2.2.1. Fern-dominated vegetation with *Dicranopteris pectinata* (Gleicheniaceae)

Characteristics: secondary vegetation on lateritic soils on steep slopes or ridges.
Coverage: 0.3% of the study area (together with 2.2.2.).
Size and location of the investigated site: 0.035 ha (350 m²). Close to Tropical Station La Gamba. E 257619 m, N 962511 m. Altitude: 80 m.
Diversity/Density (d.b.h. ∅ 10 cm): 1 sp./1 ind./0.035 ha.
Characteristic plants:
Emergents, canopy and mid-subcanopy lacking or scarcely present: *Vismia baccifera* (Clusiaceae), *Isertia haenkeana*, *Psychotria mortoniana* (Rubiaceae), *Tetrathylacium macrophyllum* (Salicaceae), *Cecropia peltata* (Urticaceae).
Understorey and ground layer: extemely dense. *Dicranopteris pectinata* (Gleicheniaceae), *Clidemia capitellata*, *C. dentata* (Melastomataceae), *Lantana camara* (Verbenaceae).
Palms, epiphytes, hemi-epiphytes: -
Lianas: only small lianas or climbers. *Mikania* sp. (Asteraceae), *Scleria secans* (Cyperaceae), *Davilla nitida*, *Doliocarpus hispidus* (Dilleniaceae), *Machaerium kegelii* (Fabaceae-Faboideae), *Coccocypselum hirsutum*, *Sabicea villosa* (Rubiaceae), *Lycopodiella cernua* (Sellaginellaceae).

This vegetation type is found on steep slopes and ridges with lateritic soils where large areas of primary forest (< 1 ha) were clear-cut. The first plant that invades such areas is the invasive fern *Dicranopteris pectinata* (Gleicheniaceae), which forms inpenetrable thickets. Few species can colonise the thicket, most of which are bird- or wind-dispersed. The highest diversity of invaders is found in climbing species (small lianas and herbaceous vines). Herbs and grasses are rare, e.g. *Leersia* cf. *hexandra*, *Paspalum virgatum* (Poaceae).

This vegetation type is very important for erosion control and protection after clear cutting.

The vegetation type is relatively stable, because the plant cover is nearly unpenetrable for seeds and seedlings as well, so that it can take several years (maybe up to 15-20 years) until other species may invade and colonise such areas and initialise succession. The fern neeeds full sunlight and dies rapidly when it is shaded. At a later stage, *Vochysia* spp. (Vochysiaceae) may invade such stands and form the so called "mayal", a *Vochysia* sp. dominated secondary forest.

2.2.2. Fern-dominated vegetation with *Nephrolepis multiflora* (Oleandraceae)

Characteristics: secondary vegetation on flat and swampy areas.
Coverage: see 2.2.1.
Size and location of the investigated site: 0.02 ha (200 m²). Near ranger station at Río Bonito. E 257654 m, N 962583 m. Altitude: 76 m.
Diversity/Density (d.b.h. ∅ 10 cm)**:** no individuum found.
Characteristic plants:
Emergents, canopy and mid-subcanopy lacking or scarcely present: *Psidium guajava* (Myrtaceae).
Understorey and ground layer: extemely dense. *Cyperus* sp. (Cyperaceae), *Phyllanthus amarus* (Euphorbiaceae), *Desmodium adscendens*, *Teramnus uncinatus* (Fabaceae-Faboideae), *Mimosa pudica* (Fabaceae-Mimosoideae), *Hyptis obtusiflora* (Lamiaceae), *Clidemia dentata* (Melastomataceae), *Nephrolepis multiflora* (Oleandraceae), *Ludwigia octovalis* (Onagraceae), *Leersia* sp. (Poaceae). The only vine species found was *Sabicea villosa* (Rubiaceae).
Palms, epiphytes, hemi-epiphytes: -
Lianas: not found, herbaceous vines rare.

This vegetation type is found on flat and very wet and swampy sites where wet soils inhibit forest vegetation or where large areas of primary forest (<1 ha) were clear-cut.

The fern *Nephrolepis multiflora* (Oleandraceae) may invade those areas and form poor, almost inpenetrable stands, similar to those with *Dicranopteris pectinata* (see above). Only a few, specialised species may colonise the ecosystem, most of them bird-dispersed or epizoochorous (e.g. *Desmodium*). In a 0.02 ha plot, only 12 different species were found, among them only one tree species.

The vegetation type is relatively stable and lasts for several years (maybe more than 15-20 years), because the plant cover is nearly unpenetrable for seeds and seedlings as well. We suppose that a late successional stage of this vegetation unit is a forest on plains with giant trees such as *Ceiba pentandra* (Malvaceae) and *Luehea seemannii* (Malvaceae) among others. Detailed data are still missing.

3. Anthropogenic ecosystems

3.1. Pasture

Pastures in the area are located mainly on flat land and used for cattle-breeding. They are man-made and lone trees still persist and demonstrate that it used to be lowland forest.

Remnants of the original forest cover may still be found. Common tree species are *Cedrela odorata* (Meliaceae), *Ficus insipida* (Moraceae) and *Ceiba pentandra* (Malvaceae). These trees were apparently common on flat ground, but were, and remain, scarce on hillsides. It is notable that some of these remnants are extremely rare species and some have been recently recognised as new to the flora of Costa Rica or to be new for science, e.g. *Pradosia* sp. ined. (Sapotaceae). Today, much pasture land is converted into plantations with the African oil palm.

Different soil conditions and levels of utilisation affect the floristic composition of pasture land, so that we distinguish between a) pasture land in use, b) swampy pasture land and c) abandoned pasture land.

3.1.1. Regular pasture

Characteristics: pasture land with grasses, Cyperaceae and weeds.
Coverage: 4.2% of the study area.
Size and location of the investigated site: 0.0325 ha (325 m²). Near Tropical Station La Gamba, Finca Ronald Moya Díaz. E 257759 m, N 962563 m. Altitude: 74 m.
Diversity/Density (d.b.h. ∅ 10 cm): -.
Characteristic plants:
Emergents, canopy, mid-subcanopy: not existent.
Understorey and ground layer: *Vismia baccifera* (Clusiaceae), *Cyperus* spp., *Eleocharis elegans* (Cyperaceae), *Phyllanthus amarus* (Euphorbiaceae), *Senna reticulata* (Fabaceae-Caesalpinioideae), *Desmodium adscendens* (Fabaceae-Faboideae), *Hyptis capitata*, *H. obtusiflora* (Lamiaceae), *Calathea* sp. (Marantaceae), *Clidemia dentata*, *Conostegia subcrustulata*, *Miconia argentea*, *M. schlimii* (Melastomataceae), *Piper aduncum*, *P. auritum*, *P. peltatum* (Piperaceae), *Panicum maximum*, *Panicum* sp., *Paspalum* sp. (Poaceae), *Pityrogramma calomelanos* (Pteridaceae), *Isertia haenkeana* (Rubiaceae).
Palms, epiphytes, hemi-epiphytes, lianas: not found, only herbaceous vines. *Mikania guaco* (Asteraceae), *Ipomoea* spp. (Convolvulaceae), *Mucuna mutisiana* and *Vigna* spp. (Fabaceae-Faboideae).

Pasture land is dominated by several grass species and fast-growing weeds and small shrubs that may survive the application of pesticides. Ornamental plants such as *Lagerstroemia speciosa* (Lythraceae) and fruit trees such as *Citrus aurantifolia* (Rutaceae) are also found. Remarkable are species of the hemi-parasitic family Loranthaceae (*Oryctanthus alveolatus*, *O. occidentalis*, *Struthanthus leptostachyus*) which may overgrow trees and treelets. Lianas are not present, but herbaceous vines are common.

Fig. 19: Landscape with different pasture types and soil conditions. In the background Fila Costeña. Near Tropical Station La Gamba.

3.1.2. Swampy pasture

Characteristics: pasture land with grasses at flat and swampy areas, with waterlogged soils.
Coverage: 0.7% of the study area.
Size and location of the investigated sites: 0.325 ha (325 m²). Near Tropical Station La Gamba, Finca Ronald Moya Díaz. E 257815 m, N 962840 m. Altitude: 70 m.
Diversity/Density (d.b.h. ∅ 10 cm): -.
Characteristic plants:
Emergents, canopy, mid-subcanopy: not existent.
Understorey and ground layer: grassland. *Dieffenbachia* sp. (Araceae), *Limnocharis flava* (Limnocharitaceae), *Calathea insignis* (Marantaceae), *Nephrolepis multiflora* (Oleandraceae), *Panicum maximum*, *Panicum* sp., *Paspalum* sp. (Poaceae), *Eichhornia crassipes* (Ponteteriaceae).
Palms, epiphytes, hemi-epiphytes, lianas: not found.

At very wet pasture sites (e.g. depressions), soils are waterlogged for most of the year. Plants adapted to this conditions may dominate the vegetation. The most important species beside the typical pasture grasses (see pasture land in use) are giant herbs from different monocotyledonous families, and ferns. Interestingly, the

Fig. 20: A typical swampy pasture with *Ludwigia hyssopifolia* and *L. octovalis* (Onagraceae).

Fig 21. Species that invade abandoned pasture land grow very quickly. In Spanish this vegetation type is called "tacotal".

floating invasive herb *Eichhornia crassipes* (Pontederiaceae) is common as well.

Swampy pasture land is often drained nowadays and converted into regular pasture land or oil palm plantation. This ecosystem harbours many animal species (e.g. amphibians, birds) and is therefore an important food source and breeding site.

3.1.3. Abandoned pasture (tacotal)

Characteristics: abandoned pasture land with grasses, weeds, shrubs and small treelets.
Coverage: 2.9% of the study area.
Size and location of the investigated sites: 0.0325 ha (325 m²). Near Tropical Station La Gamba, Finca Ronald Moya Díaz. E 257767 m, N 962608 m. Altitude: 70 m.
Diversity/Density (d.b.h. ∅ 10 cm): -
Characteristic plants:
Emergents, canopy, mid-subcanopy: not existent.
Understorey and ground layer: *Vernonia patens* (Asteraceae), *Vismia baccifera* (Clusiaceae), *Aeschynomene sensitiva* (Fabaceae-Faboideae), *Mimosa pudica* (Fabaceae-Mimosoideae), *Clidemia dentata*, *Conostegia subcrustulata* (Melastomataceae), *Psidium guajava* (Myrtaceae), *Ludwigia hyssopifolia*, *L. octovalis* (Onagraceae), *Lantana camara* and *L. trifolia* (Verbenaceae).
Palms, epiphytes, hemi-epiphytes, lianas: not found, only herbaceous vines. Hemi-parasites are abundant on treelets and trees.

If pasture land is abandoned for several months, natural succession begins and vegetation converts into the so called "tacotal", a shrubby version of cultivated pasture. In general, the vegetation is similar to that of cultivated pasture (see above), but there are typical and abundant tacotal species consisting of weeds, fast-growing treelets and trees. Epiphytes, hemi-epiphytes and lianas were not present, but herbaceous vines are abundant, as are hemiparasitic Loranthaceae (see above: pasture land in use).

Abandoned pasture land may convert within a relatively short time of several years into young secondary forest.

3.2. Plantations

3.2.1. Timber Plantations

In the last 20 years, introduced species from South-East Asia and some timber species native to other parts of Costa Rica have been cultivated in the vicinity of the Piedras Blancas National Park. The most important plantations are of grey teak *Gmelina arborea* (Verbenaceae), a fast growing lightwood tree which is used for furniture, pencils and in the paper industry. More valuable is the wood from teak *Tectona grandis* (Verbenaceae), which is used for construction and furniture. Plantations of the native *Terminalia amazonica* (Combretaceae) are quite new and show the increasing trend of cultivating local species instead of introduced tree species. Outside the study area, plantations with the native *Bombacopsis sessilis* (Malvaceae) can be found. Projects which promote mixed native timber plantations are undertaken from the Tropical Station La Gamba on a small scale in the region.

Timber plantations are usually simply structured and low in biodiversity. Species composition of the sub-canopy to the ground vegetation is tied to maintainance of the plantantion. The canopy is dominated by the cultivated trees and only a few wind-dispersed or bird-dispersed pioneer tree species invade the plantations. The ground layer is dominated by small trees and tall herbs. Palms are rare and herbaceous vines are occasionally found, but epiphytes, lianas and hemi-epiphytes are rare or missing.

Timber plantations took the pressure of logging of primary forests in the 1990s, when the first plantations were mature for cutting and substituted primary forest wood.

Fig. 22: Eight year old plantation of *Terminalia amazonica* (Combretaceae). La Gamba.

The coverage of all types of timber plantations is 0.2% of the study area.

Plantation of Gmelina arborea (Verbenaceae), Melina

Characteristics: simply structured and low in plant diversity with *Gmelina arborea* (Verbenaceae).
Size and location of the investigated site: 0.1 ha. Plantation on the Finca of Ronald Moya Díaz. E 258010 m, N 962794 m. Altitude: 116 m.
Diversity/Density (d.b.h. ∅ 10 cm): 3 spp./84 ind./0.1 ha.
Characteristic plants:
Emergents: -
Canopy: *Gmelina arborea* (Verbenaceae),
Mid-subcanopy: *Jacaranda copaia*, *Tabebuia* sp. (Bignoniaceae), *Tetragastris panamensis* (Burseraceae), *Calophyllum brasiliense*, *Symphonia globulifera* (Clusiaceae), *Inga densiflora* (Fabaceae-Mimosoideae), *Miconia* sp. (Melastomataceae), *Psidium guajava*, *Syzygium jambos* (Myrtaceae).
Understorey and ground layer: relatively open. *Cyperus luzulae*, *Eleocharis elegans*, *Rhynchospora tuerkheimii* (Cyperaceae), *Desmodium adsendens*, *D. axillare* (Fabaceae-Faboideae), *Heliconia latispatha* (Heliconiaceae), Marantaceae, *Miconia argentea* (Melastomataceae), *Alibertia edulis*, *Palicourea guianensis* (Rubiaceae).
Palms: -
Epiphytes: rare.
Hemi-epiphytes: -
Lianas: rare. *Mikania guaco* (Asteraceae), *Doliocarpus hispidus* (Dilleniaceae), herbaceous vines, *Paullinia serjaniifolia* (Sapindaceae).

This is a poorly structured tree plantation of the South-East Asian timber species *Gmelina arborea* (Verbenaceae), which forms the canopy and mid-subcanopy. In the 1980s, the timber company Ston Forestal entered the Golfo Dule region and grew plantations of *Gemlina arborea* for paper production, furniture, pencils and pallets, but many of the plantations were abandoned and are now changing into secondary forest where individuals of *G. arborea* gradually disappear. Thus far, this species has not been seen to invade primary forest. Plantantion of *G. arborea* are mainly found along the Interamerican Highway, where the plantation distance is 3 × 3 m (1.111 ind./ha).

Plantation of Tectona grandis (Verbenaceae), Teak

Characteristics: simply structured and and low in plant diversity with with *Tectona grandis* (Verbenaceae).
Size and location of the investigated site: 0.1 ha. Plantation in Río Bonito. E 255641, N 962474. Altitude: 90 m.
Diversity/Density (d.b.h. ∅ 10 cm): 6 spp./132 ind./0.1 ha.
Characteristic plants:
Emergents: -
Canopy: *Tectona grandis* (Verbenaceae).
Mid-subcanopy: *Jacaranda copaia* (Bignonicaceae), *Vismia baccifera* (Clusiaceae), *Schizolobium parahayba* (Fabaceae-Caesalpinioideae), *Luehea seemannii* (Malvaceae), *Conostegia subcrustulata* (Melastomataceae), *Psidium guajava* (Myrtaceae), *Cecropia peltata* (Urticaceae).
Understorey and ground layer: relatively dense. *Neurolaena lobata* (Asteraceae), *Costus laevis* (Costaceae), *Carludovica drudei* (Cyclantaceae), *Desmodium adscendens* (Fabaceae-Faboideae), *Mimosa pudica* (Fabaceae-Mimosoideae), *Heliconia latispatha* (Heliconiaceae), *Hyptis obhexiflora* (Lamiaceae), *Calathea insignis* (Marantaceae), *Aciotis caulialata*, *Clidemia densiflora*, *C. dentata*, *Conostegia subcrustulata*, (Melastomataceae), *Nephrolepis multiflora* (Oleandraceae), *Piper auritum*, *P. hirsutum*, *P. peltatum* (Piperaceae), *Lantana camara* (Verbenaceae).
Palms: -
Epiphytes: rare.
Hemi-epiphytes: -
Lianas: rare. *Mikania guaco* (Asteraceae), *Doliocarpus hispidus* (Dilleniaceae), *Mucuna mutisiana* (Fabaceae-Faboideae), *Smilax vanilliodora* (Smilacaceae). Herbaceous vines *Vigna luteola* (Fabaceae-Faboideae), *Passiflora costaricensis* (Passifloraceae), *Sabicea villosa* (Rubiaceae).

The plantation of *Tectona grandis* (Verbenaceae) is poorly structured. The canopy and mid-subcanopy is formed by *T. grandis* (Verbenaceae). *Tectona grandis* was introduced into the region in the 1980s together with *Gemlina arborea* for commercial use as timber. The climatic conditions with no dry season and high precipita-

Fig. 23: Six-year old plantation of the African oil palm. La Gamba.

Fig. 24: Rice field near La Gamba.

tion are not suitable for the species, which grows in its natural habitat in more dry forests in northern Malaysia. Many plantations have therefore been abandoned. In the drier regions e.g. Cental Pacific and northern Costa Rica, extensive plantations are found. Plantation distance is 3 × 3m (1111 ind./ha).

3.2.2. African oil palm plantation (*Elaeis guineensis* – Arecaceae)

Characteristics: simply structured and low in plant diversity with *Elaeis guineensis* (Arecaceae).
Coverage: 3.3% of the study area.
Size and location of the investigated site: 0.05 ha (500 m²). Finca de Braulio Moya. E 258252 m, N 961716 m. Altitude: 74 m.
Diversity/Density (d.b.h. ∅ 10 cm): 1 sp. /9 ind./0.05 ha.
Characteristic plants:
Emergents: -
Canopy: *Elaeis guineensis* (Arecaceae).
Mid-subcanopy: -
Understorey and ground layer: very open, only ground layer present. *Cyperus luzulae*, *Fimbristylis* sp. (Cyperaceae), *Leersia hexandra* (Poaceae), *Phyllantus amarus* (Euphorbiaceae), *Aciotis caulialata* (Melastomataceae), *Piper* spp. (Piperaceae).
Palms: native palms not present.
Epiphytes: epiphytic ferns are common in the crown region of *Elaeis guineensis*. *Anthurium* species (Araceae), *Asplenium serratum* (Aspleniaceae), *Nephrolepis biserrata*, *N. pectinata*, *Oleandra articulata* (Oleandraceae), *Peperomia pellucida* (Piperaceae), *Campyloneurum phyllitidis*, *Polypodium triseriale* (Polypodiaceae), *Adianthum latifolium* (Pteridaceae), *Vittaria lineata*, *Anetium citrifolium* (Vittariaceae).
Hemi-epiphytes: common. *Ficus colubrinae*, *Ficus costaricana*, *Ficus citrifolia*, *Ficus brevibracteata* (Moraceae).
Lianas: -

Plantations of the African oil palm are poorly structured and species-poor. The mid-subcanopy layer is not existent if the plantation is well maintained and the understorey cut, and the ground layer is also scant. The rotten leaf bases of the oil palm provide good substrates for epiphytes and hemi-epiphytes. The invasive ferns *Nephrolepis biserrata* and *N. pectinata* (Oleandraceae) are almost omnipresent. Small hemi-epiphytic stranglers are common as well.

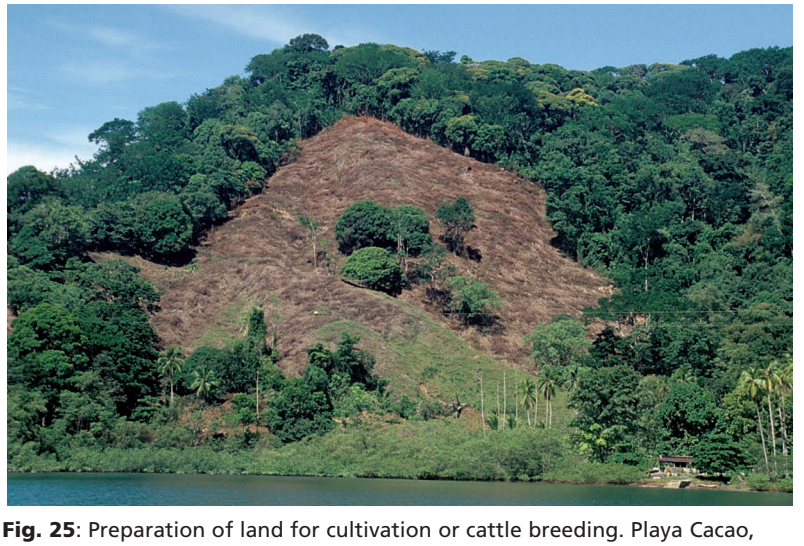


Fig. 25: Preparation of land for cultivation or cattle breeding. Playa Cacao, Golfito.

The African oil palm has been cultivated in the region since the end of the 1980s, when the United Fruit company left the region in 1986 and banana plantations were closed or abandoned. Then the former banana plantations were replaced with the African oil palm. Since then plantations have been extended and the enlargement still continues. The edible oil which is extracted from the seeds is used for cooking, in the cosmetics industry, as a detergent products and more recently as biofuel. The plantation distance is 9 × 9 m (143 ind/ha).

3.2.3. Agricultural land with short-lived field crops

Only a few field crops are suitable for the very humid tropical climate and are cultivated in the region. Traditionally, rice is the most common crop in the area, and this is one of the staple foods for the people of Costa Rica. In recent years, rice plantations have gradually been replaced by the African oil palm. In 2001, a large finca between La Gamba and Río Claro, where *Cucurbita pepo* (Cucurbitaceae) and yucca, *Manihot esculenta* (Euphorbiaceae) were produced for the export to the U.S., was also converted into oil palm plantation.

Overall, these plantations are low in diversity due to the application of pesticides. We investigated one rice plantation near the village of La Gamba.

Rice plantation (*Oryza sativa* – Poaceae)

Characteristics: rice field at wet and flat sites, low in diversity and interspersed with weeds.
Coverage: 1.2% of the study area.
Size and location of the investigated site: 0.1 ha. La Gamba. E 259018 m, N 962976 m. Altitude: 70 m.
Diversity/Density (d.b.h. ∅ 10 cm): no trees present.
Characteristic plants:
Emergents, canopy, mid-subcanopy, understorey: not present.
Ground layer: *Eleocharis elegans*, *Fimbristylis odorata* (Cyperaceae), *Phyllanthus skutchii* (Euphorbiaceae), *Hyptis obtusiflora* (Lamiaceae), *Mimosa pudica* (Fabaceae-Mimosoideae), *Limnocharis flava* (Limnocharitaceae), *Aciotis caulialata* (Melastomataceae), *Ludwigia hyssopifolia*, *L. octovalis* (Onagraceae). *Oryza sativa*, *Leersia hexandra*, *Paspalum distichum* (Poaceae), *Oldenlandia corymbosa* (Rubiaceae).
Palms, epiphytes, hemi-epiphytes, lianas: not present.

Rice fields are species-poor plantations on flat and wet sites in the region. Only a few species of various

families may invade the plantation and survive the application of pesticides. Interestingly, one fern species *Pityrogramma calomelanos* (Pteridaceae) and the tree *Luehea seemannii* (Malvaceae) were also found.

Rice is one of the most important staple foods in Costa Rica. Traditionally, rice is cultivated in the region on the nutrient-rich flood plains along the larger rivers (e.g. Esquinas, Bonito, Gamba). Many rice plantations are currently being replaced by plantations of the African oil palm.

3.3. Preparation of land for cultivation

If abandoned farmland, e.g. pasture, young secondary forest or fern-dominated vegetation is prepared for agriculture or timber production, the secondary growth is cut and often burned down. These areas are very conspicuous on the aerial photographs so that we decided to create a new category, which we called "preparation of land for cultivation". Coverage: 0.2% of the study area.

3.4. Settlements and gardens

Settlements in the region are mostly small villages and dispersed settlements. The biggest cities are Golfito, Río Claro and Ciudad Neilly. Nearly every house and farm (finca) has its own small domestic garden, where ornamentals, spices, herbs and fruit trees are cultivated for domestic use. Normally the gardens do not exceed more than a few hundred square metres and are therefore excluded from the vegetation map and are integrated in one category. A detailed study about house gardens in the region was made by PEKAREK 2004.

Coverage: 1.6% of the study area.

Conclusions

The present study is the result of 15 years' field experience in the Golfo Dulce region coupled with intensive collections and field trips during 2004-2008 with the assistance of various scientists and volunteers. The focus was to produce a detailed vegetation map of the Piedras Blancas National Park, the Golfito Forest Reserve and adjacent areas covering a total area of 255 km². The map will serve as a basis for further studies on vegetation diversity, conservation efforts and sustainable development in one of the most interesting areas in Costa Rica.

As described above, we have distinguished 28 ecosystems so far. Further ecosystems and ecotones will be discovered when the scale of investigation is refined.

The vegetation comprises a number of very distinctive plant associations whose composition and distribution depend on rainfall, slope, drainage, soil type, and other factors. Species found in one place are often completely lacking in another, even though the distance separating them may be minimal. Thus, superficially identical situations may support entirely different plant associations, and may sometimes be the result of fortuitous circumstances rather than of ecological conditions. Climatic formations are limited by rainfall distribution, and edaphic formations are determined by soil conditions or topography. Transitional formations, however, have been often shaped by human impact. Due to forest clearings for banana and oil palm plantations, as well as for pastures or timber exploitation, flat forest types are no longer preserved in the Golfo Dulce region, except for those in the Corcovado National Park.

The hillsides with their clay ridges and rocky slopes support a rich tree flora. The local conditions of the soil, slope, drainage, exposure to wind, and past history are reflected in the type of vegetation and its floristic composition. For example, the nearly pure stands of *Vochysia ferruginea* (Vochysiaceae) are very conspicuous during the flowering season in May, when the forest canopy is dotted with yellow patches. Large colonies of this species (e.g. Fila Gamba, Fila Cruces) probably originate from older clearings, as in Central America all species of the genus invade cleared forest.

The Piedras Blancas National Park and the adjacent Golfito Forest Reserve are covered almost completely with untouched primary vegetation. Remnants of primary rainforest between the settlements, pastures and plantations still connect those forests with the montane forests of the Fila Costeña. They serve as biological corridors and contribute essentially to the floristic and faunistic enrichment of both areas. Their conservation and extension is of utmost significance for the maintenance of the biological diversity in the area and we hope to contribute with this study in conservation decisions for these unique ecosystems.

Acknowledgements

Thanks go to INBio and the Museo Nacional de Costa Rica for identification of various plant species. Esther Greter is thanked for allowing us to include her private forest reserve in the investigations (coastal slope forest) and for the use of the Golfo Dulce Lodge during this time. Ing. Javier Guevara (MINAE) helped us to acquire collecting permits in Costa Rica. Thanks are due to the Costa Rican staff at the Tropenstation La Gamba who always offered help in the scientific and practical work, to Tamara Zhuber for various line drawings and last but not least to all trainees and students who helped with enthusiasm. CENAT (Centro de Alta Tecnología) provided logistic support with the aerial photographs and CENIGA (Centro Nacional de Infor-

mación Geoambiental) helped with aerial photographs TERRA 97/98. Many thanks go to OMV (Austria), the Federal Ministry of Agriculture, Forestry, Environment and Water Management (Austria) for the financial support and the Biology Centre Linz (Austria) for printing the vegetation map and the paper.

References

Allen P.H. (1956): The rainforests of Golfo Dulce. — Stanford: Univ. Press.

APG II. (2003): An update of the angiosperm phylogeny group classification for the orders and families of flowering plants: APG II. — Bot. J. Linn. Soc: 399-436.

Boza M.A. & R. Mendoza (1981): Costa Rica National Parks. — Madrid: Incafo.

Gómez L.D. (1986): Vegetación de Costa Rica: apuntes para una biogeografía costarricense. — San José: Universidad Estatal a Distancia.

Hammel B.E., Grayum M.H., Herrera C. & N.V. Zamora (2004): Manual de plantas de Costa Rica. — St. Louis: Missouri Bot. Gard.

Hartshorn G.S. (1983): Plants: introduction. — In: Janzen D.H. (ed.), Costa Rican natural history. Univ. Chicago Press: 118-157.

Holdridge L.R., Grenke W.C., Hatheway W.H., Liang T. & J.A. Tosi (1971): Forest environments in tropical life zones – A pilot study. — Oxford: Pergamon Press Ltd.

Huber W. (2005): Tree diversity and biogeography of four-one hectare plots in the lowland rainforest of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica. — PhD. Univ. Vienna.

Kappelle M., Castro M., Acevedo H., González L. & H. Monge (2003): Ecosistemas del Àrea de Conservación Osa (ACOSA). Instituto Nacional de Biodiversidad. — Santo Domingo de Heredia, Costa Rica.

Lobo Segura J. & F. Bolaños Vives (2005): Historia Natural de Golfito. Instituto Nacional de Biodiversidad. — Santo Domingo de Heredia, Costa Rica.

Madrigal M. (2007): Proceso compra tierras Parque Nacional Piedras Blancas. — MINAE.

Pekarek B. (2004): Die Heilpflanzen in den Hausgärten von La Gamba (Costa Rica): Ethnobotanische Untersuchungen zu Anwendung und Verarbeitung. — Diploma thesis: University of Natural Resources and Applied Life Sciences. Vienna.

Tosi J.A. Jr. (1975): The Corcovado Basin on the Osa Península. — In: Tosi J.A. Jr. (ed.), Potential national parks, nature reserves, and wildlife sanctuary areas in Costa Rica: a survey of priorities. San José: Centro Científico Tropical. Separate.

Vaughan C.S. (1981): Parque Nacional Corcovado: plan de manejo y desarrollo. — Heredia: Universidad Nacional.

Weber A., Huber W., Weissenhofer A., Zamora N. & G. Zimmermann (2001): An introductory field guide to the flowering plants of the Golfo Dulce rain forests, Costa Rica. — Stapfia **78**.

Wilson E.O. (1988): The current state of biological diversity. — In: Wilson E.O. (ed.), Biodiversity. Washington: National Academy Press.

Weissenhofer A. (2005): Structure and vegetation dynamics of four selected one hectare forest plots in the lowland rain forests of the Piedras Blancas National Park ("Regenwald der Österreicher"), Costa Rica, with notes on the vegetation diversity of the Golfo Dulce region. — Unpubl. doctoral thesis, University of Vienna, Vienna.

Addresses of authors:

Anton Weissenhofer
Werner Huber
Eva Schembera
Susanne Sontag
Anton Weber
Department of Palynology and Structural Botany
Faculty Centre of Botany
University of Vienna
Rennweg 14
A-1030 Vienna, Austria
E-mail: anton.weissenhofer@univie.ac.at
werner.huber@univie.ac.at
eva.schembera@univie.ac.at
susanne.sontag@univie.ac.at
anton.weber@univie.ac.at

Tatjana Koukal
Markus Immitzer
Institute of Surveying,
Remote Sensing and Land Information
University of Natural Resources
and Applied Life Science
Peter Jordan-Straße 82
A-1190 Vienna, Austria
E-mail: tatjana.koukal@boku.ac.at
markus.immitzer@boku.ac.at

Nelson Zamora
INBio, Instituto Nacional de Biodiversidad
Santo Domingo de Heredia, Costa Rica
E-mail: nzamora@inbio.ac.cr