A botanical survey of Caño Palma Biological Station (Estación Biológica Caño Palma), Tortuguero, Costa Rica

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**ABSTRACT**. The Caribbean lowlands of Costa Rica are renowned for their botanical diversity. Despite previous work in Costa Rica’s lowland wet rainforests, remote areas are still ecologically poorly known. Botanical species lists for such areas are often incomplete. Here, a preliminary survey of a remote research station on the Atlantic coast near Tortuguero, Costa Rica is presented. The forest was surveyed, measured and divided into plant zones to investigate species composition. The more abundant species of vegetation were identified and species records for the site updated to compile the first published inventory for the station. One species identified was a rare *Vitex kuylenii* (Lamiaceae), which has previously only been known from lowland areas of southeastern Nicaragua. This presents a range extension for this species.

**RESUMEN**. Las tierras bajas del Caribe de Costa Rica son renombradas para su diversidad botánica. A pesar del trabajo previo en Costa Rica las selvas tropicales húmedas de tierras bajas, áreas remotas todavía permanecen ecológicamente desconocidas. Las listas de La flora para tales áreas son a menudo incompletas. En este trabajo se presenta , un diagnóstico preliminar de un centro de investigación alejado en la costa atlántica cerca de Tortuguero, Costa Rica . El bosque fue examinado, medido y dividido en zonas para investigar la composición de especies. Las especies más abundantes fueron identificadas y se confecciono el primer inventario florístico para la estación. espécie rara identificadas fue *Vitex kuylenii* (Lamiaceae), conocida previamente solamente de áreas de tierras bajas Del sureste de Nicaragua, lo cual representa una extensión de ámbito de distribución para la especie.

**KEY WORDS.** Flora, Zones, lowland forest, Caño Palma, Costa Rica

Despite triumphant contributions in history, large parts of tropical flora remain understudied (Prance *et al.* 2000). Historically and currently, natural tropical ecosystems worldwide are suffering alteration (Laurance & Bierregaard 1997) with 90 % of original habitats being reduced (Wright & Muller-Landau 2004). This rate of ecosystem change carries serious consequences for species (Whitmore & Sayer 1992, May *et al.* 1995, Reid 1997, Pitman & Jørgensen 2002). Extinction rates are estimating that large fractions of existing species may become extinct by the middle of this century (Wilson 1992, Bini *et al.* 2005). This also applies to Neotropical locations (Pitman *et al.* 2002) where synergistic impacts could affect organisms at all trophic levels (Schulze *et al.* 2004). The need for even basic botanical inventory work is great in the Neotropics (Goldsmith 1998, Sheil 2001, Laurance 2006) which holds six global biodiversity hotspots (Myers *et al.* 2000) and 35 % of all higher plant species (Gentry 1982). Numbers of plants documented to date are still rising fast. Re-classifications are continually springing new species in a rush to document and conserve tropical trees and plants (Whitmore 1998, Janzen 1986, Prance *et al.* 2000). This paper provides discussion and a crucial botanical inventory for a lowland tropical forest in Costa Rica.

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# MATERIAL AND METHODS

Tortuguero is a small coastal fishing village located near the juncture of the Rio Tortuguero, Laguna Penitencia, and Laguna Tortuguero in Limón province (Figure 1). Caño Palma Biological Station is found 8 km north of Tortuguero (N 103536.1/W 833139.4) (Figure 1). The Biological Station’s land is situated on the boundaries of Tortuguero National Park (18 947 ha) and the Barra del Colorado Refuge (92 000 ha). Combined these reserves connect with forests in Nicaragua to form the largest area of lowland Atlantic tropical wet forest in Central America. Caño Palma Biological Station has been owned and managed by the Canadian Organisation for Tropical Education and Rainforest Conservation (COTERC) since 1990. The station’s land comprises 40 ha of Atlantic lowland tropical wet rainforest (Holdridge 1967). It is bordered on three sides by rivers and by secondary forest on the remaining side. A distance of 200 m separates the station from the Caribbean Ocean. The nearest road is sixty miles southeast at Limón.



**Figure 1.** Map showing the approximate location of Caño Palma, the location of the Rio La Suerte and the Caño Palacio / Caño Palma confluence (Instituto Geográphico de Costa Rica (Servicio Geodesico InterAmericano. IGCR Mapa Edicion 1. Hoja 3447 I 1:50,000. N 104081/W 833081).

The Tortuguero region receives 5 000 mm of rainfall annually. Average daily temperatures are 26 °C (23 min: 32 max.) and 70 % RH (60 min: 95 max). Caño Palma’s climate is unpredictable and annual rainfall may exceed 5 000 mm. This coastal fringe is seasonal but does not always conform to the customary wet and dry seasons of the Neotropics (March Sept: dry and Sept Feb: wet). Heavy rainfall and extensive flooding routinely occur in November-January and can be coupled with storms. Caño Palma’s drier months are between January and September (Myers 1990). Of Costa Rica’s 12 ecological life zones, tropical wet forests account for 5 % (2 352 km²) of the national territory (when including herbaceous marshes), most of which occur in the Caribbean lowlands (Janzen 1983, Myers 1990). Most lowland wet forests are characterised by a combination of palm swamps in saturated high canopy forest. There are many different palm swamps but essentially three types in the Neotropics monospecific, speciesrich and seasonal. The Tortuguero region boasts a large expanse of monospecific swamp that is seasonally or permanently flooded. Monospecific swamps contain intermediate, mixed dicotyledons and several species of palm. The palms are predominantly *Raphia* and *Manicaria* genus. *Raphia* palms are an old world African genus but one species exists in the Neotropics (*Raphia taedigera*). *Manicaria saccifera* however, is strictly Neotropical (Myers 1990). The regions surrounding Tortuguero and Laguna Penitencia (Figure 1) have several types of monospecific swamp; *Manicaria* rainfed and river-fed *Raphia* swamp. Caño Palma’s forests are *Manicaria* swamp bounded by the Caribbean coastal fringe, and Caño Penitencia, Cerros de Coronel, and Laguna Samay canals. The predominant vegetation type is *Manicaria* palm with *Raphia* groves in topographical depressions at the water level and mixed forest above the water table. The semi-permanent swamp nature of Caño Palma enables dry and wet soil species to co-exist, enhancing the diversity of flora and fauna. Servicio de Parques Nacionales listed 109 species of large trees and palms mainly of the Lauraceae, Fabaceae, Moraceae, Rubiaceae, Sapotaceae, Annonaceae and Arecaceae families. This incomplete list of tree species could reach over 300 (UICN/ORCA 1992). The *Manicaria* habitat at Caño Palma contains a mean plant species density of 7.0 per 0.1 ha (Myers 1990).

Caño Palma’s forest have a network of trails containing hummocky mounds with subtle depressions and channels that remain as permanent pools and adjoin during heavy rain and flooding. The *Raphia* trail proceeds alongside the Caño Palma through dicotyledon tree species and circumnavigates the property. The first 500 m parallel to the canal is noticeably drier, shaded and higher in elevation than other trails. Toward the northern part of the property the vegetation changes to *Manicaria* flora. This area contains scattered semi-permanent flood pools. The *Manicaria* swamp trails exhibit a climax community across the crown of the property with marsh/swamp flora. A few dicotyledon trees are among this area but many die young from intolerance to flooding or are shaded out by falling *Manicaria* fronds. When the larger palm trunks die they are generally replaced by young shoots or nearby clumps, maintaining shaded cover. Toward the south-western section the trail exhibits a drier, gladded territory that connects with the Colubri trail.

This study was conducted in an area of 5 000 m² within Caño Palma’s borders. The purpose of surveying the site was to identify and quantify key vegetation zones, provide an updated quantitative map for the trail networks, compile a list of the major types of vegetation, and locate zones relative to the trails. An accepted transect walking method by Phillips *et al.* (2003) was used. Simple map, compass, and measuring tapes were used to map the trails and measure zones of vegetation. Each zone was named and classified according to its vegetation type. Zones were investigated and abundant and rare species noted. Samples and uncertain identifications were collected verified by the Juvenal Valerio Rodríguez Herbarium (JVR) at Universidad Nacional in Heredia (UNA). The study was conducted around the network of trails within the forest.

**Figure 2.** Caño Palma Biological Station forest showing forest trails, transects (T1, T2 and T3 respectively), and the three vegetation zones (*Manicaria*, Edge and Transition).

# RESULTS

The network of trails within the forest isolated an area of 5 007 m². The *Raphia* trail is the largest. It was used to cross section compass points, access deeper parts of the forest, and led to the creation of a 2-D map (Figure 2). Transects 1, 2 and 3 were cut originally for separate study purposes but were included in its description as they provided good access for identifying zone change. Three essential types of vegetation were identified; Edge, *Manicaria* and Transitional. The Edge vegetation was the smallest zone described, covering 178.5 m² corresponding to 3.6 % of the surface area. It was bordered to the east by Caño Palma and to the south by the Biological Station grounds. Historically this area has been cleared of vegetation. Transect 1 began within Edge vegetation near the border of the Transitional zone and extended into *Manicaria* forest. It was the only transect to cross all three zones of vegetation. The Transitional vegetation zone was patchier across the area, giving rise to islands of vegetation surrounded by *Manicaria* palm. This zone was 1 410.3 m² or 28.6 % of the total area and was the most topographically diverse and species rich of the zones. Varied ground elevation and occasional flooding were its main characteristics. The Transitional zone boasted species that were more competitive on less saturated soils. All transects crossed through the Transitional zone. Transects 2 and 3 started within the zone and continued into the *Manicaria* zone. The *Manicaria* occupied 3 393.3 m² or 67.8 % of the total area and was the largest of the zones. *Manicaria* was less diverse than other zones and was characterised by an abundance of groundwater pools and lack of penetrable sunlight in the understory. Transect’s 1, 2 and 3 stopped within this zone of vegetation.

This zone comprised two layers; an understory and a sub-canopy or middle sized tree layer. The understory contained an abundance of Spiny Earth Bromeliads (*Aechmea magdalenae*) in some sections, as well as the small *Calathea micans* (Marantaceae). The most common genus’ were; *Calathea* (Marantaceae) with species such as *C. inocephala* and *C. leucostachys; Costus* (Costaceae) with *C. laevis* and *C. pulverulentus* and *Heliconia* (Heliconiaceae) species such as *H. pogonantha*, *H. irraza* and *H. latispatha*. The most common species of the understory were the Rubiaceae *Psychotria poeppigiana*, the very common shrub *Piper littorale* (Piperaceae) and the treelet *Potalia turbinata* (Gentianaceae)*.* A large number of species from the Melastomataceae such as *Miconia tomentosa*, *M. nervosa*, *M. impetiolaris*, *M. lateriflora*, *Clidemia japurensis*, and *C capitellata* were commonly found in the understory. Many species of vines such as *Doliocarpus multiflorus, Davilla nitida* (Dilleniaceae) and *Mansoa kerere* (Bignoniacea) were also abundant. The sub-canopy layer was filled with middle sized trees. In this layer aggressive, pioneer species *Hampea appendiculata, Apeiba membranacea* (both Malvaceae) and *Cecropia obtusifolia* (Urticaceae) occurred frequently. Small trees of the Melastomataceae and Annonaceae such as *Conostegia xalapensis, Miconia tomentosa* and *M. impetiolaris* and *Xilopia sericophylla* were also present. The trees *Psychotria grandis* (Rubiaceae)*, Simarouba amara* (Simaroubaceae)*, Symphonia globulifera* (Clusiaceae)*, Guatteria diospyroides* (Annonaceae) and an unusual find, a rare *Vitex kuylenii* (Lamiaceae) were present.

*V. kuylenii* is endangered and previously only known in lowland areas of southeastern Nicaragua (Nelson 1998). This presents a range extension for this species. *V. kuylenii* was found in this zone as a small tree, in addition to two big individuals growing in the *Manicaria* vegetation zone.

The transitional vegetation covered 28.6 % of the treated area and was characterised by multiple layers; understory, middle sized trees or sub-canopy and canopy. The understory was dominated by Rubiaceae herbaceous species such as *Psychotria glomerulata* and *P. chagrensis*, both also present in the *Manicaria* and Edge zone. Another species found along the canal in this, and the Edge, zone is *Piper littorale* (Piperaceae). Species such as the vine *Strychnos panamensis* and *S. peckii* (Loganiaceae) and *Potalia turbinata* (Gentianaceae) were also common. Other not so common vines were *Gurania makoyana* (Cucurbitaceae) and *Passiflora vitifolia* (Passifloraceae). The treelets *Palicourea guianensis* and *Isertia haenkeana* of the Rubiaceae and some species of the Melastomataceae family, such as *Miconia tomentosa* and *Conostegia xalapensis*, were dominant. Young saplings of *Xilopia sericophylla* (Annonaceae), *Grias cauliflora* (Lecythidaceae) and *Sterculia recordiana* (Malvaceae) fairly abundant in this area. In the sub-canopy, species such as *Dendropanax arboreus* (Araliaceae), *Apeiba membranacea* (Malvaceae) and *Vismia macrophylla* (Hipericaceae) were dominant. *Manicaria saccifera* palms were infrequently found. A few individual *Raphia taedigera* were present but not sufficient in number to classify the whole forest as strictly *Raphia*. Other species of tree present in the sub-canopy included; *Simarouba amara* (Simaroubaceae)*, Garcinia madruno* (Clusiaceae)*, Grias cauliflora* (Lecythidaceae)*, Brosimum guianense* (Moraceae), *Gymnantes riparia* (very uncommon), *Amanoa guianensis* (Euphorbiaceae) and *Byrsonima arthropoda* (Malpighiaceae). Species such as *Zygia inequalis* (Fabaceae) and *Pachira aquatica* (Malvaceae) were found sporadically, growing close to the canal, even though they tend to be very common in the greater area. Floral diversity appeared higher in this zone. The canopy was dominated by hardwood species. *Pentaclethra macroloba* (Fabaceae) and *Carapa nicaraguensis* (Meliaceae) were the more abundant trees with *Symphonia globulifera* (Clusiaceae)*, Xilopia sericophylla* (Annonaceae) and *Vochysia ferruginea* (Vochysiaceae) also prominent. *Pentaclethra macroloba* (Fabaceae) was a common tree in both Transitional and *Manicaria* zones. An uncommon hardwood species was also found *Sacoglottis trichogyna* (Humiriaceae)*,* which is highly prized for its timber*.* Other species included *Abarema* sp. (Malvaceae), *Hirtella triandra* (Chrysobalanaceae)*, H. tubiflora* (Chrysobalanaceae)*, Sterculia recordiana* (Malvaceae) and *Theobroma simiarum* (Malvaceae)*.*

Covering 67.8 % of the study area, *Manicaria* was the largest but least diverse zone. In the understory the most common species was *Psychotria chagrensis* (Rubiaceae). Large abundances of *Manicaria saccifera* (Arecaceae) blanketed the area creating a darker yet spatially open understory. Saplings of *Grias cauliflora* (Lecythidaceae), *Lacistema aggregatum* (Lacistemaceae) and *Vochysia ferruginea* (Vochysiaceae) were found growing in this zone. The sub-canopy mostly comprised *Malouettia guatemalensis* (Apocynaceae)*, Cassipourea elliptica* (Rhizophoraceae), *Garcinia madruno* (Clusiaceae) and the less common *Laetia thamnia* (Salicaceae). *Zygia latifolia* (Fabaceae) was found alongside *Pachira aquatica* (Malvaceae), close to the canal. The canopy comprised *Pentaclethra macroloba* (Fabaceae) interspersed with *Carapa nicaraguensis* (Meliaceae)*, Prioria copaifera* (Fabaceae)*, Symphonia globulifera* (Clusiaceae), *Calophyllum brasilense* (Clusiaceae), *Vochysia ferruginea* (Vochysiaceae), *Sacoglotis trichogyna* (Humiriaceae)*,* sporadic *Coumarouna oleifera* (Leguminosae), and along the canal *Pterocarpus officinalis* (Leguminoseae).

**DISCUSSION**

Caño Palma has received sparse botanical study since its establishment as a reserve. Previous work by Myers (1990) in the Tortuguero area identified Caño Palma as a monospecific swamp forest. The report also suggested that species diversity in lowland forests increases with improved drainage. Organic accumulation and leaching during high water table levels creates the characteristic blackwater canals that are a typical feature of this area (Myers 1990). Myers (1990) reported that regular changes in percolation, coupled with poor light levels in *Manicaria* forests could inhibit understory growth (Myers 1990). This report concurs with evidence from species presence and absence that support this hypothesis. Most of the hardwood trees occurred in the two largest zones, especially the Transitional zone which was more drained. This zone may also have encouraged more hardwood tree species through a combination of higher ground (although this is only slight; about 1.0 m max), increased light levels and different soil structure created by a well vegetated understory.

Zone preference was shown by several species. In the small Edge vegetation zone, with its high incidence of light and minimal amount of tall trees, an optimal environment was created that favoured colonisation of *Psychotria poeppigiana* and *Piper littorale* in the understory. The high incidence of these colonizing species and lack of tall trees is possibly a result of re-growth after the area was cleared approximately fifteen years previously. In the Transitional zone, *Psychotria poeppigiana* was replaced by *Psychotria glomerulata* while *Piper littorale* persisted. All of the colonizing species such as *Psychotria* spp. and *Piper* spp. found in the Edge and Transitional zone were scarce in the *Manicaria* zone. In the Edge zone *Hampea appendiculata* was dominant but then displaced by *Vismia macrophylla* and *Garcinia madruno* in Transitional and *Manicaria* zones respectively. The affect of edge dynamics is documented for lowland tropical forest (Gascon *et al.* 2000). Although distance of edge vegetation can be as wide as 300 m (Laurance *et al.* 1997, Laurance 2000), at Caño Palma it penetrated only 50 m into the forest from the Biological Station grounds. Arguably the Edge vegetation zone penetrated deeper into the forest and influenced the Transitional zone. However, this would be a complex theory to conclude without further investigation due to topographical and soil differences between the two zones. Many tropical tree species respond individually in soil-water relation and may structurally be affected in species assemblage by water availability (Enquist & Leffler 2001).

The Transitional zone had a greater range of species, possibly due to a blend of plant associations between it and the Edge and *Manicaria* zones. It’s hardwood species were composed mostly of *Carapa nicaraguensis*, although prized trees such as *Simarouba amara* (used medicinally by local people), *Garcinia madruno* (a source of food for wildlife), *Grias cauliflora, Brosimun guianense, Amanoa guianensis, Gymnantes riparia* (a toxic tree) and *Byrsonima arthropoda* also occurred. Species such as *Zygia inequalis* and *Pachira aquatica* were found closer to the canal and are commonly associated with gallery forest (Kricher 1999). The density of these species found in the Transitional zone was higher than in the other two zones. The Transitional canopy was further dominated by the hardwoods; *Pentaclethra macroloba, Carapa nicaraguensis, Symphonia globulifera, Xilopia sericophylla, Sacoglotis trochogyna* and *Vochysia ferruginea*. *Pentaclethra macroloba* nitrogen fixing capabilities, flowering, and fruiting at a very early life-stage may be a key function in ensuring its abundance in both Transitional and *Manicaria* zones (Flores-Vindas & Obando-Vargas 2003). Toxicity of *Pentaclethra macroloba’s* seeds, and that they can be dispersed by water, may also play a role in its success. *Abarema* sp.*, Hirtella triandra, H. tubiflora* and *Sacoglotis trichogyna* were less abundant but patchily established. Epiphytes were observed more frequently in this zone and were present in the mid to high canopy, a known humid micro-climate of such plants (Gentry & Dobson 1987, Küper *et al.* 2004).

*Manicaria’*s canopy comprised mostly *Pentaclethra macroloba* interspersed with *Carapa nicaraguensis, Prioria copaifera, Symphonia globulifera, Calophyllum brasilense* and *Vochysia ferruginea*. This was similar in composition between the Transitional and *Manicaria* canopies. Despite this composition the *Manicaria* zone lacked the same species diversity as the other zones. Instead, it was heavily dominated by *Manicaria saccifera* palm, a typical feature of swamp (Hartshorn 1983, Webb 1997). The palm’s huge fronds inhibited sunlight penetration and coupled with constant high groundwater, possibly affected understory sapling development. This low light, low nutrient swamp environment favours palms (Myers 1990). *Raphia* and *Manicaria* palms are considered a pioneer species of poorly drained soils (Anderson & Mori 1967, Myers 1990) and although not always found in, they are often associated with blackwater canals. The mechanisms of blackwater canals that operate in low nutrient systems such as Caño Palma may help maintain the stability of palms in the habitat. Periodic flooding chokes the understory species and possibly allowed *Manicaria* to establish itself as the dominant sub-canopy palm. Despite this dominance, saplings of *Grias cauliflora* and *Lacistema aggregatum* continued to colonise in the smallest of sunlit gaps but with limited success. These sunlit gaps would, in other lowland wet forests, lead to seedling establishment (Hartshorn 1978, Brokaw 1982, Denslow 1987, Shashar *et al.* 1998, Clark & Clark 1992, Ellison *et al.* 1993). However, *Manicaria saccifera* canopy remains closed during early development, preventing pockets of dicotyledon trees from succeeding. This clump forming habit, longevity, competitiveness and aseasonal reproduction enhance the palm’s survival by closing pockets of light on saturate soils (Myers 1984). In circumstances of heavy abundance such as the *Manicaria* zone at Caño Palma, *Raphia* and *Manicaria* could even be justified as a climax community species (Devall & Kiester 1987). Competitive filtering by shading that ultimately alters the distribution and abundance of seedlings is also a feature of other palms and palmlike cyclanths (Denslow *et al.* 1991, Mongommery 2004), but little is known about the mechanisms behind this competitive strategy.

Numerous studies of tropical forests worldwide have demonstrated that plant species distribution is influenced by variations of the substratum, particularly geologically influenced ground water regimes and soil chemical properties (Newbery *et al.* 1986, ter Steege *et al.* 1993, Clark *et al.* 1998, Stevenson 1999, Botrel *et al.* 2002). Primary geological and demographical factors could also influence the development of the zonal preference of flora exhibited at Caño Palma (Condit *et al.* 2006). Costa Rica’s varied geology (Castillo-Muñoz 1983) becomes more constant in the Tortuguero region. The region has quaternary sedimentary rocks made up of alluvial materials (Vásquez Morera 1983). Data on classification of soils in this region has been gathered since 1954 (Vásquez Morera 1983) and show that the hydromorphic soils of Caño Palma are of variable alluvial origin, being derived from deposition during delta formation and coastal regosols. These poorly drained soils have no morphogenetic development and slopes of < 1 % (Aquents). The result is heavy accumulation of organic matter that readily leaches from one canal system to another. Source nutrients are therefore at premium. Sufficient physiological knowledge not available for each and every species of plant in this area to know what level of soil nutrients could optimise species abundance. Without further study of the soil attributes, plant nutrients and environmental requirements, it is not quantitatively certain what mechanisms drive local preferences. Observationally however, it was clear that some species flourished in areas with slightly higher ground elevation and faster percolation. The species composition blended gradually over zones with the highest levels of change occurring in the sub-canopy. It was easy to observe the complexity of the inter-relationships among the plant species within the three zones, Edge, Transitional and *Manicaria*, at Caño Palma, but further study of the plant-soil associations and relations within zones could reveal the fascinating mechanisms behind its functional ecology.

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# LITERATURE CITED

Anderson, R. & S. Mori. 1967. A preliminary investigation of *Raphia* palm swamps, Puerto Viejo, Costa Rica. Turrialba 17: 221-224.

Bini, L. M., J. A. F. Diniz, P. Carvalho, M. P. Pinto. & L. V. Rancel. 2005. Lomborg and the Litany of biodiversity crisis: what the peer-reviewed literature says. Conservation Biology 19: 1301-1305.

Botrel, R. T., A. T. Oliveira Filho, L. A. Rodrigues & N. Curi. 2002. Influência do solo e topografia sobre as variações da composição florística e estrutura da comunidade arbóreo-arbustiva de uma floresta estacional semidecidual em Ingaí, MG. Revista Brasileira de Botanica 25: 195-213.

Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. Biotropica 14: 158-160.

Castillo-Muñoz, R. 1983. Geology. *In:* D. H. Janzen (ed.). Costa Rican Natural History. University of Chicago Press, Chicago. pp. 47-62.

Clark, D. A. & D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a Neotropical rain forest. Ecological Monographs 62: 315-344.

Clark, D. B., D. A. Clark & J. M. Read. 1998. Edaphic variation and the mesoscale distribution of tree species in a Neotropical rain forest. Journal of Ecology 86: 101-112.

Condit, R., P. Ashton, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, C. Ewango, R. Foster, I. A. Gunatilleke, C. V. Gunatilleke, P. Hall, K. E. Harms, T. Hart, C. Hernandez, S. Hubbell, A. Itoh, S. Kiratiprayoon, J. Lafrankie, S. L. de Lao, J. R. Makana, M. N. Noor, A. R. Kassim, S. Russo, R. Sukumar, C. Samper, H. S. Suresh, S. Tan, S. Thomas, R. Valencia, M. Vallejo, G. Villa & T. Zillio. 2006. The importance of demographic niches to tree diversity. Science 313: 98-101.

Denslow, J. S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431-451.

Denslow, J. S., E. Newell & A. M. Ellison. 1991. The effect of understory Palms and Cyclaths on the growth and survival of *Inga* seedlings. Biotropica 23: 225-234.

Devall, M. & R. Kiester. 1987. Notes on *Raphia* at Corcovado. Brenesia 28: 89-96.

Ellison A. M., J. S. Denslow, B. A. Loiselle & D. M. Brenés. 1993. Seed and seedling ecology of Neotropical Melastomataceae. Ecology 74: 1733-1749.

Enquist B. J. & A. J. Leffler. 2001. Long-term tree ring chronologies from sympatric tropical dryforest trees: individualistic responses to climatic variation. Journal of Tropical Ecology 17: 41-60.

Flores-Vindas, E. & G. Obando-Vargas. 2003. Árboles del Trópico Húmedo, Importancia Socioeconómica. Editorial Tecnologica de Costa Rica. Cartago. Costa Rica. 920 p.

Gascon, C. G., G. B. Williamson & G. A. B. da Fonseca. 2000. Receding forest edges and vanishing reserves. Science 288: 1356-1358.

Gentry, A. H. 1982. Patterns of neotropical plant species diversity. Evolutionary Biology 15: 1-84. Gentry, A. H. 1993. Field Guide to the woody plants of Northwest South America. University of Chicago Press, Washington. 920 p.

Gentry, A. H. & C. Dodson. 1987. Diversity and phytogeography of Neotropical vascular epiphytes. Annals of the Missouri Botanical Garden 74: 205-233.

Goldsmith, F. B. 1998. Tropical Rainforests: A Wider Perspective. Kluwer Academic Publishers, Netherlands. 440 p.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. *In:* P. B. Tomlinson & M.

H. Zimmermann (ed.). Tropical Trees as Living Systems. Cambridge University Press, Cambridge. pp. 617-638.

Hartshorn, G. S. 1983. Plants: Introduction. *In:* D.

H. Janzen (ed.). Costa Rican Natural History. University of Chicago Press, Chicago. pp. 118157.

Holdridge, L. R. 1967. Lifezone Ecology (revised edition). San José Tropical Science Centre, San José. 206 p.

Holdridge, L. R. & L. J. Poveda. 1975. Arboles de Costa Rica: Vol. 2*.* Centre Cientifico Tropical, San José. 646 p.

Janzen, D. H. 1983. Costa Rican Natural History. University of Chicago Press, Chicago. 823 p.

Janzen, D. H. 1986. The future of tropical ecology. Annual Review of Ecology and Systematics 17: 305-324.

Küper, W., H. Kreft, J. Nieder, N. Köster & W. Barthlott. 2004. Large-scale diversity patterns of vascular epiphytes in Neotropical montane rain forests. Journal of Biogeography 31: 1477-1487. Laurance, W. F. & R. O. Bierregaard. 1997. Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities. University of Chicago Press, Chicago. 632 p.

Laurance, W. F. 2000. Do edge effects occur over large spatial scales? Trends in Ecology and Evolution 15: 134–135.

Laurance, W. F. & C. A. Peres. 2006. Emerging Threats to Tropical Forests. University of Chicago Press, Chicago. 520 p.

May, R. M., J. H. Lawton & N. E. Stork. 1995. Assessing extinction rates. *In:* J. H. Lawton & R. M. May (ed.), Extinction Rates. Oxford Press, New York. pp. 1-24.

Montgomerry, A. 2004. Effects of understory vegetation on patterns of light attenuation near the forest floor. Biotropica 36: 33-39.

Myers, R. L. 1984. Growth form, growth characteristics, and phenology of *Raphia taedigera* in Costa Rican palm swamps. Principes 28: 64-72.

Myers, R. L. 1990. Ecosystem of the World 15; Forested Wetlands. Elsevier, Amsterdam. 527 p.

Myers, N., R. A. Mittermeier, C. Mittermeier, G. Da Fonseca & J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853-858.

Nelson, C. 1998. *Vitex kuylenii*. *In:* IUCN 2009. IUCN Red List of Threatened Species. Version 2009.1. [<www.iucnredlist.or](http://www.iucnredlist.org/)g>. [September 2009].

Newbery, D. M., J. S. Gartlan, D. B. McKey & P. G. Waterman. 1986. The influence of drainage and soil phosphorus on the vegetation of Douala– Edea Forest reserve, Cameroon. Vegetatio 65: 149-162.

Phillips, O. L., R. Vásquez Martínez, P. Núñez Vargas, A. Lorenzo Monteagudo, M. E. Chuspe Zans, W. Galiano Sánchez, A. Peña Cruz, M. Timaná, M. Yli-Halla & S. Rose. 2003. Efficient plot-based floristic assessment of tropical forests. Journal of Tropical Ecology 19: 629-645.

Pitman, N. C. A. & P. M. Jørgensen. 2002. Estimating the size of the world’s threatened flora. Science 298: 989.

Pitman, N. & P. M. Jørgensen, R. Williams, S. LeónYánez & R. Valencia. 2002. Extinction rates for a modern Neotropical flora. Conservation Biology 16: 1427-1431.

Prance, G. T., H. Beentje, J. Dransfield & R. Johns. 2000. The tropical flora remains undercollected. Annals of the Missouri Botanical Garden 87: 6771.

Reid, W. V. 1997. Strategies for conserving biodiversity. Environment 39: 16-43.

Sánchez-Vindas, P. E. 2001. Flórula Arborescente del Parque Nacional Cahuita. 2nd. Ed. Universidad Estatal a Distancia, San José. 340 p.

Sánchez P. E & L. J. Poveda. 1997. Claves Dendrológicas para la Identificación de los Principales Arboles y Palmas de la Región Norte y Atlántica de Costa Rica. Overseas Development Administration, San José. 144 p.

Schulze, C. H., M. Waltert, P. J. A. Kessler, R. Pitopang, A. Shahabuddin, D. Veddeler, M. Muhlenberg, S. R. Gradstein, C. Leuschner, I. Steffan-Dewenter & T. Tscharntke. 2004. Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. Ecological Applications 14: 1321-1333.

Shasha, N. P., T. P. Cronin, L. B. Wolff & M. A. Condon. 1998. The Polarization of light in a tropical rain forest. Biotropica 30: 275-285.

Sheil, D. 2001. Conservation and biodiversity monitoring in the tropics: realities, priorities and distractions. Conservation Biology 15: 1179-1182.

Stevenson, P. R., M. C. Castellanos & P. M. A. Del. 1999. Tree communities in the floodplains of the Tinigua National Park, Colombia. Caldasia 21: 38-49.

ter Steege, H., V. G. Jetten, A. M. Polak & M. J. A. Werger. 1993. Tropical rain forest factors in a watershed area in Guyana. Journal of Vegetation Science 4: 705-716.

UICN/ORCA. 1992. Estrategia de conservacion para el desarrollo sostenible de llanuras de Tortuguero, II Version. Borrador 29 Febrero 1992.

Vásquez Morera, A. 1983. Soils. *In:* D. H. Janzen (ed.). Costa Rican Natural History. University of Chicago Press, Chicago. pp. 63-65.

Webb, E. L. 1997. Canopy removal and residual stand damage during controlled selective logging in lowland swamp forest of northeast Costa Rica. Forest Ecology and Management 95: 117-129.

Whitmore, T. C. & J. Sayer. 1992. Tropical Deforestation and Species Extinction. Chapman and Hall, London. 156 p.

Whitmore, T. C. 1998. An Introduction to Tropical Rainforests. Oxford University Press, Oxford. 296 p.

Wilson, E. O. 1992. The Diversity of Life. Harvard University Press, Cambridge. 424 p.

Wright, S. J. & H. C. M-Landau. 2004. The future of tropical forests. Tropinet 36: 1-2.

Zamora, N. 1993. Flora Arborescente de Costa Rica. Cartago: Editorial Tecnológica de Costa Rica, 262 p.

**Table 1**. List of the observed common plants of the Edge vegetation zone (EVZ), Transitional vegetation zone (TVZ) and *Manicaria* vegetation zone (MVZ).

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Family** | **Species** | **EVZ** | **MVZ** | **TVZ** |
| Anacardiaceae | *Spondias mombin* L. | X |  | X |
| Annonaceae | *Guatteria diospyroides* Baill. | X |  | X |
|  | *Xylopia sericophylla* Standl & L.O. Williams | X |  | X |
| Apocynaceae | *Allamanda cathartica* L. | X |  |  |
|  | *Malouetia guatemalensis* (Müll. Arg.) Standl. |  | X | X |
| Araliaceae | *Dendropanax arboreus* (L.) Decne. & Planch. |  |  | X |
| Arecaceae | *Manicaria saccifera* Gaertn. |  | X | X |
|  | *Raphia taedigera* (Mart.) Mart. |  |  | X |
| Bignoniaceae | *Mansoa kerere* (Aubl.) A.H.Gentry | X |  |  |
| Bromeliaceae | *Aechmea magdalenae* (André) André ex. Baker | X |  |  |
| Burseraceae | *Protium glabrum* (Rose) Engl. | X |  | X |
| Chrysobalanaceae | *Hirtella triandra* Sw. |  |  | X |
|  | *Hirtella tubiflora* Cuatrec. |  |  | X |
| Clusiaceae | *Calophyllum brasiliense* Camb. |  | X |  |
|  | *Garcinia madruno* (Kunth) Hammel | X | X | X |
|  | *Symphonia globulifera* L. f. | X | X | X |
| Costaceae | *Costus laevis* Ruiz & Pav. | X |  |  |
|  | *Costus pulverulentus* C.Presl | X |  |  |
| Cucurbitaceae | *Gurania makoyana* (Lem.) Cogn. |  |  | X |
| Dilleniaceae | *Davilla nitida* (Vahl.) Kubitzki | X |  |  |
|  | *Doliocarpus multiflorus* Standl. | X |  |  |
| Elaeocarpaceae | *Sloanea medusula* K. Schum. & Pittier |  |  | X |
| Euphorbiaceae | *Amanoa guianensis* Aubl. |  |  | X |
|  | *Gymnanthes riparia* (Schltdl.) Klotzsch |  |  | X |
| Fabaceae/Caes. | *Abarema* sp. |  |  | X |
|  | *Crudia glaberrima* (Steud.) J.F.Macbr. |  |  | X |
|  | *Inga* sp. |  |  | X |
|  | *Pentaclethra macroloba* (Willd.) Kuntze |  |  | X |
|  | *Prioria copaifera* Griseb. |  | X |  |
|  | *Senna papillosa* (Britton & Rose)Irwin & Barneby | X |  |  |
|  | *Zygia inaequalis* (Willd.) Pittier |  |  | X |
| Fabaceae/Mim. | *Abarema adenophora* (Ducke) Barneby & J.W.Grimes |  | X |  |
|  | *Abarema macradenia* (Pittier) Barneby & J.W.Grimes |  | X |  |
|  | *Inga* sp. |  | X |  |

Table 1. continued

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Family** | **Species** | **EVZ** | **MVZ** | **TVZ** |
|  | *Pentaclethra macroloba* (Willd.) Kuntze |  | X |  |
|  | *Zygia inaequalis* (Willd.) Pittier |  | X |  |
|  | *Zygia latifolia* (L.) Fawcett & Rendle |  | X |  |
| Fabaceae/Pap. | *Dipteryx oleifera* Benth. |  | X |  |
|  | *Machaerium falciforme* Rudd. |  |  | X |
|  | *Ormosia coccinea* (Aubl.) Jacks. |  | X |  |
|  | *Pterocarpus officinalis* (Jacq.) |  | X |  |
| Flacourtiaceae | *Homalium guianense* (Aubl.) Oken. | X |  | X |
| Gentianaceae | *Potalia turbinata* Struwe & V.A.Albert | X |  | X |
| Heliconaceae | *Heliconia irrasa* Lane ex R.R.Sm. | X |  |  |
|  | *Heliconia latispatha* Benth | X |  |  |
|  | *Heliconia pogonantha* Cufod. | X |  |  |
| Humiriaceae | *Sacoglottis trichogyna* Cuatrec. |  | X | X |
| Hypericaceae | *Vismia macrophylla* Kunth | X |  | X |
| Lacistemaceae | *Lacistema aggregatum* (P. J. Bergius) Rusby |  | X |  |
| Lamiaceae | *Vitex kuylenii* Standl. | X | X |  |
| Lecythidaceae | *Grias cauliflora* L. |  | X | X |
| Loganiaceae | *Strychnos panamensis* Seem. |  |  | X |
|  | *Strychnos peckii* B.L. Rob. |  |  | X |
| Malpighiaceae | *Byrsonima* sp. |  |  | X |
| Malvaceae | *Apeiba membranacea* Spruce ex. Benth. | X |  | X |
|  | *Hampea appendiculata* (Donn. Sm.) Standl. | X |  |  |
|  | *Pachira aquatica* Aubl. |  | X | X |
|  | *Sterculia recordiana* Standl. |  |  | X |
|  | *Theobroma simiarum* Donn. Sm. |  |  | X |
| Marantaceae | *Calathea inocephala* (Kuntze) H. Kenn & Nicolson | X |  |  |
|  | *Calathea leucostachys* Hook. F. | X |  |  |
|  | *Calathea micans* (L.Mathieu) Körn. | X |  |  |
| Marcgraviaceae | *Souroubea sympetala* Gilg. |  | X |  |
| Melastomataceae | *Clidemia capitellata* (Bonpl.)D.Don | X |  |  |
|  | *Clidemia dentata* D. Don | X |  |  |
|  | *Clidemia epiphytica* (Triana) Cogn. | X |  |  |
|  | *Clidemia japurensis* DC. | X |  |  |
|  | *Conostegia xalapensis* (Bonpl.) D.Don | X |  | X |
|  | *Miconia impetiolaris* (Sw.) D.Don | X |  | X |

Table 1. continued

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Family** | **Species** | **EVZ** | **MVZ** | **TVZ** |
|  | *Miconia lateriflora* Cogn. | X |  | X |
|  | *Miconia nervosa* (Sm.) | X |  |  |
|  | *Miconia tomentosa* (Rich) D.Don ex DC. | X |  | X |
|  | *Tococa guianensis* Aubl. |  |  | X |
| Meliaceae | *Carapa nicaraguensis* C. DC. |  | X | X |
| Moraceae | *Brosimun guianense* (Aubl.) Huber |  |  | X |
|  | *Ficus* spp. |  |  | X |
| Myristicaceae | *Compsoneura sprucei* (A. DC.) Warb. |  |  | X |
| Nyctaginaceae | *Neea* sp. |  | X |  |
| Piperaceae | *Piper littorale* C.DC. | X |  | X |
| Rhizophoraceae | *Cassipourea elliptica* (Sw.) Poir. |  | X | X |
| Rubiaceae | *Isertia haenkeana* DC. |  |  | X |
|  | *Palicourea guianensis* Aubl. |  |  | X |
|  | *Psychotria chagrensis* Standl. | X | X | X |
|  | *Psychotria glomerulata* (Donn. Sm.) Steyerm. | X |  | X |
|  | *Psychotria grandis* Sw . | X | X | X |
|  | *Psychotria poeppigiana* Müll. Arg. | X |  | X |
| Sabiaceae | *Meliosma donnel-smithii* Urb. |  |  | X |
| Salicaceae | *Laetia thamnia* L. |  | X | X |
| Sapindaceae | *Cupania largifolia* Radlk. |  |  | X |
| Simaroubaceae | *Simarouba amara* Aubl. | X |  | X |
| Urticaceae | *Cecropia obtusifolia* Bertol. | X |  |  |
|  | *Coussapoa villosa* Poepp. & Endl. |  |  | X |
| Vochysiaceae | *Vochysia ferruginea* Mart. |  | X | X |