University of Montana

ScholarWorks at University of Montana

Graduate Student Theses, Dissertations, & Professional Papers

Graduate School

1999

Abundance and population structure of some economically important trees of Piedras Blancas National Park, Costa Rica

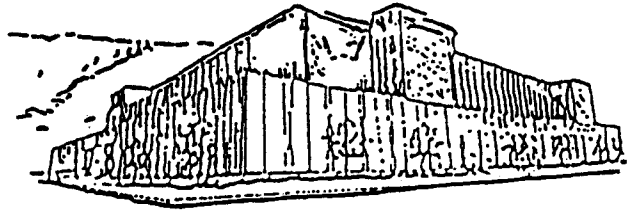Miguel Guevara Gonzalez
The University of Montana

Follow this and additional works at: https://scholarworks.umt.edu/etd

Let us know how access to this document benefits you.

THE ABUNDANCE AND POPULATION STRUCTURE OF SOME ECONOMICALLY

IMPORTANT TREES OF PIEDRAS BLANCAS NATIONAL PARK, COSTA RICA

By

Miguel Guevara González

B.S. The University of Montana, 1989

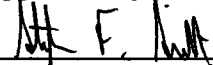Presented in partial fulfillment of the requirements

For the degree of

Master of Science

The University of Montana

1999

Approved by:

Chairman

Dean, Graduate School

6-15-99

Date

UMI Number: EP34498

UMI

Dissertation Publishing

UMI EP34498

ProQuest

Guevara, Miguel G. . M.S.. May 1999

The Abundance and Population Structure of Some Economically Important Trees in Piedras Blancas National Park, Costa Rica.

Director: Steve Siebert SFS

ABSTRACT

The abundance and population structure of <u>Brosimum utile</u>, <u>Calophyllum brasiliense</u>, <u>Carapa guianensis</u>, <u>Peltogyne purpurea</u>, <u>Qualea paraensis</u>, <u>Schizolobium parahyba</u>, <u>Symphonia globulifera</u>, <u>Tachigali versicolor</u>, <u>Terminalia amazonica</u>,<u>Vantanea barbourii</u> and <u>Vochysia hondurensis</u> were studied in primary well-drained wet forest of Piedras Blancas National Park, Costa Rica. Seventy five plots, each 0.04 ha were established along three transects between 50 and 400 m elevation. In each plot the abundance and population structure of each species were determined by recording the total number of individuals of all trees ≥2.5 cm dbh. Three types of diameter-size class distribution were recognized. Type 1, represented by five species (<u>Brosimum utile</u>, <u>Calophyllum brasiliense</u>, <u>Carapa guianensis</u>, <u>Symphonia globulifera</u>, and <u>Tachigali versicolor</u>), is typical of climax forest (shade tolerant species), showing a characteristic inverse J-shape. Type 2 represented by five species (<u>Qualea paraensis</u>, <u>Schizolobium parahyba</u>, <u>Terminalia amazonica</u>,<u>Vantanea barbourii</u> and <u>Vochysia hondurensis</u>), is typical of "gap" or "light demanding species". Type 3 represented by one species (<u>Peltogyne purpurea</u>) is intermediate between the more shade-tolerant and light demanding species. <u>Brosimum utile</u>, a Type 1 species, is the most abundant and dominant species in PBNP and displayed an average density of 27 individuals ≥ 2.5 cm dbh and basal area of 3.22m². In general, shade-tolerant species were more dominant and widespread in PBNP than light demanding species and the lattered tend to have a patchy distribution. <u>Tachigali versicolor</u>, another abundant and widlely distributed species, is a monocarpic wind-dispersed (large seeds) long-lived canopy species in which trees die within one year after producing a fruit crop. PBNP appears to be a dynamic site when compared to other areas in the Golfo Dulce-Osa Peninsula. Natural disturbances such as wind, lightning, floods, mudslides and tree fall in conjunction with steep topography open gaps for light-demanding species

ACHNOWLEDGEMENTS

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

INTRODUCTION

Forests fulfill vital functions such as the conservation of biological diversity; the protection of the soil and the hydrologic resources; and the regulation of CO_2 (responsible in part for the green house effect[1]) (Schipulle & Burger 1997). Tropical rainforests are the richest ecosystems on earth in terms of species diversity (Wilson 1992). Despite this, more than half of the world rainforests have been destroyed (Richards 1996; Whitmore 1997).

Costa Rica is a small country (51,000 square km^2), but is endowed with remarkable biological diversity due to its: 1) geological history which united North and South American flora and fauna thus acting as a natural bridge; 2) climatic diversity, specifically its geographic position, wide altitudinal range and varied topography; and 3) great variety of soils. However, much of the flora and fauna is threatened by the destruction and degradation of the country's natural resources (TSC 1982; UNED 1996). To counter deforestation, Costa Rica has set aside more than one forth of the national land area under some degree of protection and management, but many of these areas are little more than paper parks. With non-protected forests near exhaustion, lack of budget from the government to control logging, corruption from powerful business interests and a large population of landless campesinos, Costa Rica's remaining wildlands, are under increasing pressure (Tico Times 26 February 1999; La Extra 28 May 1999).

Due to a shortage of lumber, forest plantations, utilizing exotic species are increasing (Ramirez & Maldonado 1991). The use of exotic species can have an adverse ecological and hydrological effects (Rainforest Action Network 1993). One alternative to this situation could be reforesting with native species. However, basic knowledge about the biology and ecology of native species is lacking and such knowledge is essential for successful reforestation (Schipulle & Burger 1997).

---

[1] It is the heating phenomenom in which gases in the Earth's inner atmosphere trap rising heat. These gases act like the glass of a greenhouse by preventing the radiation back to space of infra-red radiation. The main gas is carbon dioxide (Stolzenburg 1998, 8).

Most of the studies done in the Golfo Dulce-Osa peninsula have focused on the structure and floristic composition of the forest (Sawyer 1966; Holdridge et al. 1971; Werner and Weissenhofer 1996; Thömsen 1997). Allen (1956) has published noteworthy ecological information about some forests in the Golfo Dulce region and Herwitz (1981) studied the regeneration of selected species in the Osa Peninsula. However, few studies have investigated the abundance and the population structure of ecologically and economically-important tree species in the Golfo Dulce. In this study I investigate the abundance and population structure of eleven economically-important tree species in primary, well-drained tropical wet forest of Piedras Blancas National Park (PBNP) in southwestern Costa Rica (Figure 1).

It is important to analyze the population structure of economically-important tree species in undisturbed forest since that can be employed to identify general succession and regeneration patterns. These processes are important for both conservation and forestry (Richards 1996). Because tropical forests are so heterogeneous, it is difficult to quantify species abundance, especially those with a wide distribution. However, a population structure's relative density (for each size class) can be used as an indicator of abundance (Knight 1975).

Most tropical rainforest communities are characterized by a high tree species diversity represented by low densities of most species (Pires & Prance 1977; Lieberman & Lieberman 1994; Richards 1996). The number of trees per hectare in more or less level, free-draining lowland primary forest with a dbh $\geq$ 10 cm averages about 300-700 (Richards 1996). In a study done in the primary wet forest of Rincón de Osa, Costa Rica, for example, Sawyer (1966) estimated tree density of 503 individuals ha^{-1}, with 102 different species. In another study, in the primary forest of La Selva, Costa Rica, 70% of the tree and liana species in 12.4 ha (three plots on different soils) had overall densities of less than 1 individual larger than 10 cm dbh ha^{-1} (Lieberman & Lieberman 1987). Tree species diversity is strongly correlated with annual precipitation and seasonality. In general, species diversity increases with decreasing seasonality and increases with the total annual precipitation. Usually, the number of tree species $\geq$ 10

cm dbh in a primary moist forest is between 60-150 per ha, but in species-rich areas in tropical wet forest such as the upper Amazon-basin in western South America and parts of Malaysia can exceed 200 or even 300 per hectare (Hartshorn 1983; Richards 1996). Table 1 compares the tree density with a dbh $\geq$ 10 cm, diversity and basal area (m^2) ha^{-1} in some Neotropical forests. Comiskey et al. (1994) for example, found a total of 498 trees ha^{-1} representing 72 species in a Guyanan moist forest. In comparison, one of the richest Neotropical wet forests is the Cuyabeno Reserve, Ecuador, where Korning & Balslev (1994) recorded 697 trees $\geq$ 10 cm dbh in 313 different species in a single hectare (i.e. about every other tree was a different species).

Table. 1. Tree density $\geq$10 cm dbh, diversity, basal area (sqm) per ha and area sampled of 10 different Neotropical forests

Locality	Forest type	# of stems ha^{-1}	# of species ha^{-1}	Basal area m^2 ha^{-1}	Plot size m^2	Source of data
Kwakwani region, Guyana	Moist forest	498	72	25.7	20,000	Comiskey et al. (1994)
Cuyabeno Reserve, Ecuador	Wet forest	697	313	not reported	10,000	Korning & Balsev (1994)
La Selva, Costa Rica	Wet forest	446	96	27.8	124,000	Lieberman & Lieberman (1987)
Alto Ivon, Bolivia	Moist forest	649	94	21.5	10,000	Boom (1986)
Monteverde, Costa Rica	L.m. wet forest*	555	111	62.0	40,000	Nalini et al. (1995)
Piedras Blancas, Costa Rica	Wet forest	527	140	35.5	10,000	Weissenhofer (1996)
Rincón de Osa, Costa Rica	Wet forest	503	102	40.4	7,500	Sawyer (1966)
Manaus, Brazil	Wet forest	346	165	24.7	10,000	Prance et al. (1976)
Rincón de Osa, Costa Rica	Wet forest	569	162	37.7	40,000	Thömsen (1997)
Corcovado N. P. Costa Rica	Wet forest	354	108	45.8	10,000	Hartshorn (1983)

*Lower montane wet forest

In some rainforests, a few relatively abundant species often represent a considerable proportion of the whole stand. More frequent species can be considered characteristic of an area because they have a greater effect on the forest (Schultz 1960; Prance et al. 1976; Richards 1996). Prance et al. (1976) found out that in any part of the Amazon rainforest five to fifteen tree species $\geq$ 30 cm dbh account for 50% of the individuals present. For example, in a hectare near Manaus, they documented that the most common eleven species accounted for 25.4% of the total number of trees $\geq$ 15 cm dbh. In another forest inventory done in Bolivian Amazon, Boom (1986) found that the forest is dominated by 10 species, representing 10.6% of the total species present.

In terms of basal area, the species with the highest relative density are often the species with the highest values of relative dominance, (i.e. only a few large trees within the higher size-classes dominate the area). In La Selva lowland forest, Costa Rica, for example, the most abundant species ha^{-1} (including palms, lianas, tree-ferns and

strangler figs) was <u>Pentaclethra macroloba</u> (Mimosaceae) which accounted for 13.7% of all stems ≥ 10 cm dbh and 36% of the basal area ha⁻¹; <u>Welfia meiantha</u>, a palm with 9.6% of all stems and 3.3% of the basal area ha⁻¹; and <u>Carapa guianensis</u> (Meliacea) contributed with a large basal area (4.9% ha⁻¹) with only 1.4% of all the stems (Lieberman & Lieberman 1987). In another study in the primary wet forest of Piedras Blancas National Park, Costa Rica, Weissenhofer (1996) reported that two tree species: <u>Brosimum utile</u> and <u>Carapa guianensis</u> accounted approximately one fourth of the total basal area among 527 individual trees ≥ 10 cm dbh ha⁻¹ or 5.9 % of all stems. However, each species varies considerably in its abundance from place to place within its range of dispersion, due to the influence of the physical environment (soil, orography, etc), climate, and ecological, biological and evolutionary patterns (dispersal center and habitat ecological situation) (Pires & Prance 1977; Burger 1980; Liebermann & Lieberman 1987; Richards 1996).

The distribution of size-classes among individuals of the same tree species depend on two variables; growth and mortality. The normal pattern of size-class distribution of tree diameters in most species-rich tropical rainforests is a reverse J-shape or negative exponential distribution. The number of trees per unit area is always greater in the smaller than in the larger diameter-classes. In the La Selva study, for example, Lieberman & Lieberman (1987) documented a mean seedling density between 50,000 and 150,000 ha⁻¹ (although for short periods heavy germination increased the local density substantially); a mean density of 1992 saplings ≥ 2 ≤ 10 ha⁻¹ and a mean density of 446 trees ≥ 10cm dbh ha⁻¹. The results were similar in a montane wet forest at Monteverde Reserve, Costa Rica, where Nalini et al. (1995) documented an overall density of stems in all size classes of 2062 individuals ha⁻¹. Densities of small (2-10 cm), medium (>10 <30 cm) and large stems (> 30 cm) were 1507, 396 and 159, respectively. In terms of basal area the few large trees within the higher size classes account for most of the total basal area. In the same Monteverde study, Nalini et al. (1995) estimated that the largest trees (>90 cm dbh), which constituted only 1% of the total stems, accounted for 30% of the total basal area.

There are relatively few large trees in Neotropical rainforests, due primarily to the dynamics of the primary forest. High frequency of natural tree falls prevents most trees from attaining large size. For example, an average of 2.6 ± 1.7 trees or fewer than 1% of the stems ≥ 10 cm dbh ≥ 1 m ha⁻¹ occurs at La Selva forest, Costa Rica. Exceptions exist when tropical forests were subject to disturbance as well as where restrictive site factors exist, often resulting in species-poor or single species stands: e.g., Prioria copaifera (Caesalpinaceae) swamp forests or tropical montane Quercus spp. (Fagacea) (Holdridge 1967: Hartshorn 1978).

The importance of gaps in the process of regeneration of rainforest trees have been intensely studied by Shultz 1960; Hartshorn 1978, 1980; Whitemore 1980; Hubbell & Foster 1986; Denslow & Hartshorn 1994. Most trees which are regenerating continuously in the forest are relatively shade-tolerant. Other species regenerate in large gaps or clearings (often referred to as "pioneer") or cannot regenerate without a gap of moderate size (often referred to as "gap" "light-demanding" or "shade-intolerant" species). However, in a regeneration study done in the rainforests of Venezuela, Rollet (1974) argued that the 'normal' pattern of size-class distribution -shown by shade-tolerant tree species- and the more light-demanding species are only relative terms. He recognized seven types of diameter-class distribution ≥ 10 cm dbh, each representing different regeneration strategies. According to some observations, Hartshorn (1980) assumed that 320 tree species at La Selva are shade intolerant — dependent on light gaps for successful regeneration. Light gaps are not only necessary for the regeneration of the more light-demanding species, but also for relatively shade-tolerant species. In general, seedlings and saplings of relatively shade-tolerant species persist in a suppressed state for a long period of time until the canopy is opened by a tree fall. Seedlings and saplings already in place would be expected to dominate in new gaps. For example, Dipterix panamensis was classified as a gap species until Clark & Clark (1987) demonstrated that this species is regenerating in situ. Uhl et al. (1988) also found in a Venezuelan Amazonian forest that nearly all young trees were from advance regeneration, not from seedlings establishing after the gap formed. However, more field

research needs to be done with individual species to fully understand the regeneration processes.

PBNP contains many potentially valuable tree species which are endangered or threatened elsewhere in Costa Rica including Peltogyne purpurea, Tachigali versicolor, Vantanea barbourii and Qualea paraensis (Jimenez 1995). Logging is a common practice in the Golfo Dulce-Peninsula de Osa region and uncontrolled logging is reported in and around the park (Tico Times 7 November 1997, La Nacion 9 August 1998, La Republica 11August 1998, La Nación 28 February 1999). Agriculture (specifically cocoa plantations, fruit trees, Gmelina plantations and cattle ranches) is also widespread, especially on flat, fertile land and is a threat to the maintenance of forest cover. Approximately, half of PBNP is private land and many of the landowners are under economic pressure to clear the forest [ECOLAND, Web-site: (http://w.w.w.ji.org/usiji/ecoland.shtml) 1995; Rainforest of the Austrians, Web-site: (http://w.w.w.regenwald.at) 1998]. Hunting for game species is also widespread within PBNP. The Golfo Dulce-Osa Peninsula region and PBNP in particularly, is one of the most diverse and important centers of biodiversity in Costa Rica and in fact in all of Central America and is the only large remaining block of lowland wet forest on the Pacific side of Central America (Fundación Neotrópica 1989; Fallas 1994; Donovan 1994; Werner 1996; Weissenhofer 1996).

In PBNP primary well-drained tropical wet forest type are found from sea level to about 400 m of elevation, whereas the upland forest is found within the cool-transitional climate (Holdridge 1967; Personal observations 1998). The physiognomy of the wet forest, cool transition type or the upland forest differs from the well-drained wet forest mainly due to elevation, cloudiness, mist and wind, which create favorable conditions for some trees. Cloud forest trees combine with many of the trees that grow at lower elevation (Holdridge 1967). However, the well-drained tropical wet forest type maintains the greatest biodiversity due to the mixture of species of many other areas and the large number of tree associations that range from the lowlands to the hillsides, rugged rocky slopes with small plateaus on top, steeply dissected clay ridges and

narrow and deep valleys. None of the association of tree species is universally

dominant. The canopy trees form completely mixed stands unless there is specialized

situation (e.g. steep terrain, rocky walls, particular type of soil, etc). Some of the more

conspicuous tree associations in well-drained forests are: Brosimum utile/Vochysia

spp/Carapa guianensis , Brosimum utile/Vantanea barbourii and Peltogyne

purpurea/Brosimum utile/Carapa guianenesis (Allen 1956; Holdridge et al. 1971). It is

important to mention however, that superficially similar situations of soil, elevation,

drainage, slope, etc, may support different arrangements of species, so that it is

probable that local ecological conditions alone do not dictate the associations of species

in particular places but also reflect random disturbances and other factors (Allen 1956).

RESEARCH SITES AND METHODS

Study site

Field work was conducted in June and July 1998 in Piedras Blancas National

Park (8°42'N and 83°13' W), in the Golfo Dulce-Esquinas region of southern Costa Rica

(Figure 1). This region forms part of Puntarenas province and is located near the town

of Golfito —the most important port in southern Costa Rica. PBNP was created in

1991 as an extension of Corcovado National Park (Esquinas Forest Section). The

national park totals 14,000 ha, of which 80% is covered with primary forest. Due to the

exceptionally steep terrain and infertile soils, the Esquinas forest is suited only for

protection (La Gaceta 17 July 1991).

According to Holdridge et al. (1971), the entire Golfo Dulce region falls within the

Tropical (Basal) Wet Forest Life Zone. Most of the park (ca. 80%) is within the non-

transitional climate of this life zone. The remaining 20% is within the cool-transition of

this life zone (beginning at about 300-400 m of elevation) and extending up to Cerro

Nicuesa (579 m) —the highest point within the park. The well-drained lowland wet

forest is considered to be a climatic association[2] while the upland forest is considered to be an atmospheric association[3].

Formerly, the flatter areas of PBNP were covered with poorly-drained wet forests which are considered to be an edaphic[4] or hydric[5] association whereas the littoral woodland is considered to be within the edaphic association such as some of the forests by the Gallardo-Mansito coast (Figure 1).

Some ecological characteristics found by Holdridge et al. (1971) in areas of the well-drained wet forest type of Golfo Dulce include a tall, multistrata evergreen forest with gaps common, particularly in steep terrain. The crowns of the dominant trees form a nearly continuous cover, with only small amounts of direct sunlight reaching the forest floor. A few canopy species are briefly deciduous, but the overall forest is evergreen. Forest canopy height averages between 45-55 m. Epiphytes are common but not conspicuous. Some of the steep slopes are open with only a few scattered trees, trees that often form the subcanopy or understory layers on more gentle slopes. Soils in the study area are Udults, Ustults, Tropepts and are typically shallow to deep, well drained, reddish in color, heavy textured, strongly eroded, acidic and with low fertility. The terrain is steeply dissected to mountainous with slopes of 40-80% (Vasquez 1979).

The region of Esquinas receives 4,000 mm to 7,000 mm of annual precipitation from the plains to the ridge tops respectively, making it one of the wettest regions in Costa Rica (Tosi 1975; Fundación Neotrópica 1992).

---

[2] Climatic or zonal association is the area occupied by a plant community growing on a zonal climate (Holdridge 1967).

[3] Atmospheric association is occupied by a community in an azonal climate due to factors of elevation, cloudiness and wind (Ibid).

[4] Edaphic association is the area occupied by a community on an azonal or intrazonal soil (Ibid).

[5] Hydric association is the area occupied by a plant community growing in shallow water where the soil is covered with water for all or nearly all of the year or periodic flooding (Ibid).
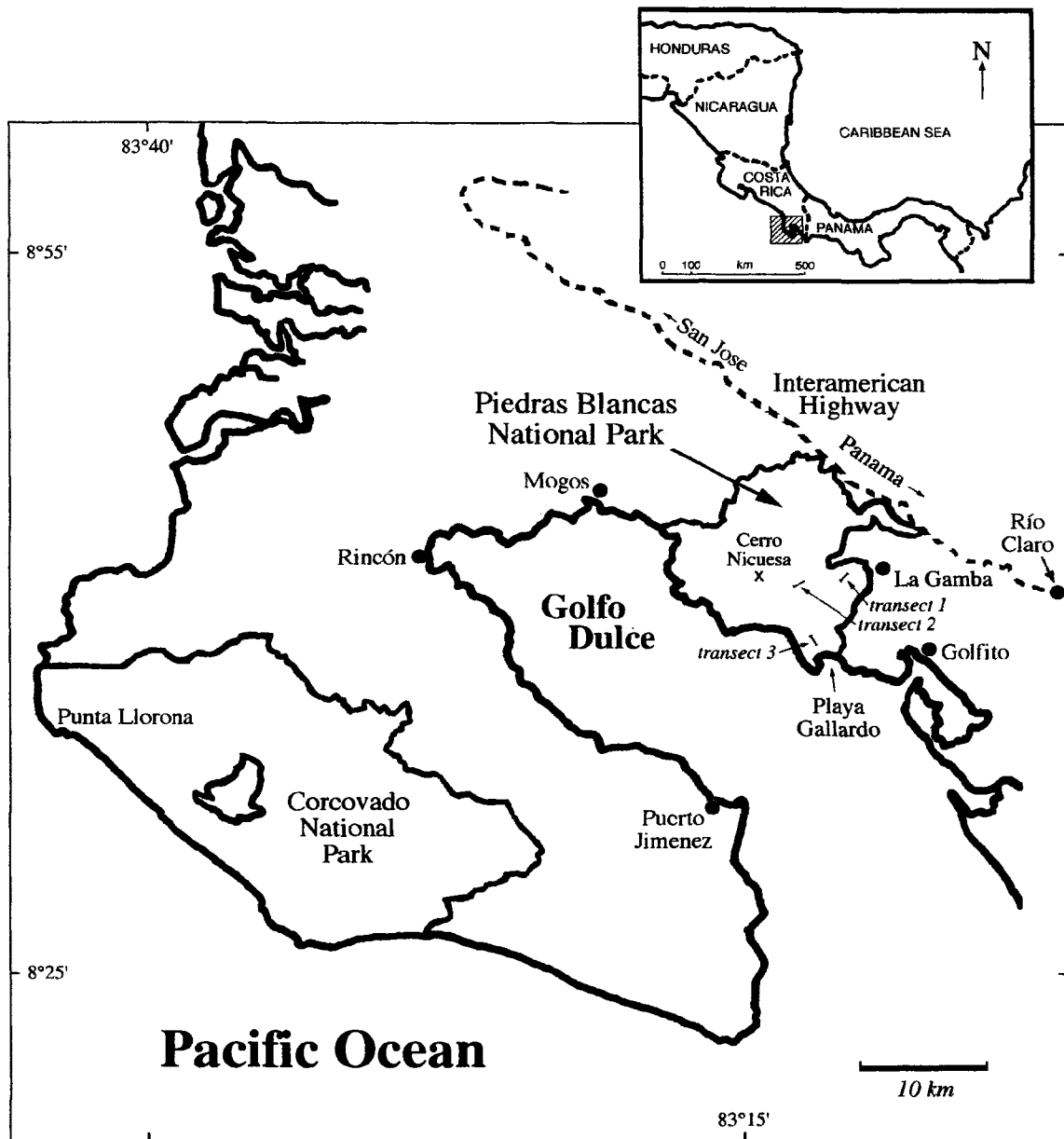
Figure 1. Map of Golfo Dulce-Osa Peninsula region showing the area of study.

The nearest meteorological station to PBNP (Río Claro, 8°41' N, 83°04' W,

elevation 56m above sea level) recorded an average of 4,811mm of rain per year over 15

years (Institute Meteorológico Nacional 1998) (Figure 2). Monthly precipitation was

greater than 400 mm in May-November with October averaging 698 mm per month.

The period with the least precipitation is from January-March with February receiving

on average 106 mm. Rainfall exceeds evapotranspiration all months resulting in

perhumid conditions (perhumidity index= 21.0) (Walsh 1992). The average monthly air temperature over 15 years was 26°C.

RIO CLARO (58 m) 26.81 °C 4831 mm
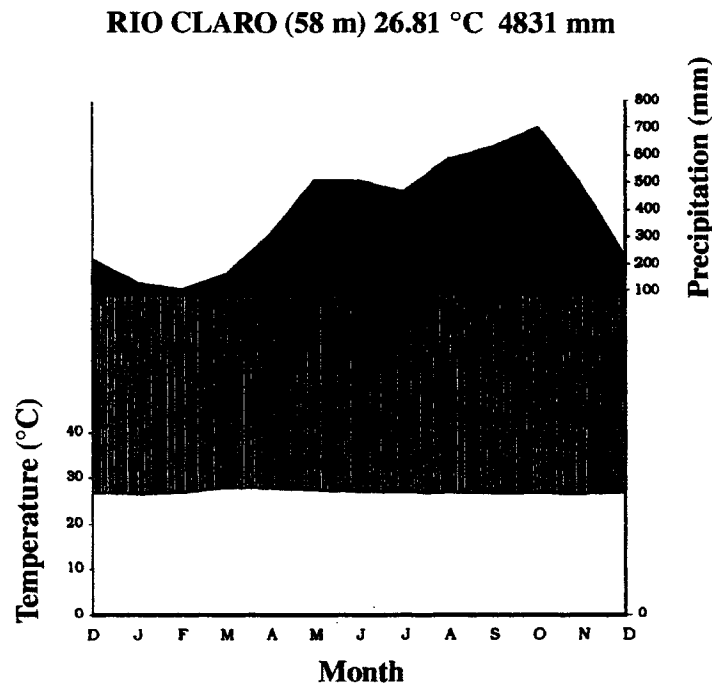
Figure 2. Mean Average monthly precipitation and temperature over 15 years in Río Claro, C. R. (Instituto Meteorológico Nacional).

Research methods

Three transects were established in three different locations in primary, well drained wet forest from 50 to 400 m elevation (Table 2). Due to the rugged topography and varying slope steepness, transects of varying length were employed to sample lowland and upland forest types. Sample plots (20 x 20 m) were selected along the transects (25 plots per transect) where it was possible to study the plot (Table 3) (along this was extremely rugged and steep). Transect #1 went up and down for about 1500 m with 5% to 70% slopes. Transect # 2 followed a ridge uphill for about 1500 m and ranged from 250 m to 400 m elevation. Fifteen plots were selected along this transect with 35% to 50% slopes, while the other 10 plots were selected within 1000 m going

down to the other side of the hill. Transect # 3 began 200 m north of Gallardo beach and run west uphill to ridge top at 390 m elevation (Table 3).

In species-rich forests it is recommended that sample areas should be greater than one hectare in size since species-area curve show little tendency to flatten until about of 4-5 ha (Richards 1996). Since the mature wet forests of Golfo Dulce are composed of more than 500 species of trees, a total of 75 0.04-ha or 3 ha of forest was sampled.

Table 2. Information about the three transects

	Location	Latitudes	Longitudes	Length (km)	Elevation range (m)	Slope range (%)
Transect 1	eastern border of Park	8°42'26"N	83°12'24"W	1.5	70-310	(5-70)
		8°41'44"N	83°12'56"W			
Transect 2	outskirts of Nicuesa Hill	8°41'46"N	83°14'11"W	2.4	100-400	(35-65)
		8°40'14"N	83°15'23"W			
Transect 3	Gallardo-Bajo Mansito	8°38'39"N	83°13'57"W	1.5	50-390	(25-45)
		8°38'58"N	83°14'38"W			

Table 3. Distance between the plots (meters) and slopes (%) in each transect

Plot #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Totals
Transect 1	0	80	70	60	70	90	105	95	60	15	70	50	65	90	85	70	20	50	10	90	20	50	30	70	90	1505
Slope (Trans.1)	35	5	35	40	45	40	60	30	35	70	35	40	40	45	50	45	45	45	45	70	50	50	40	30	45	
Transect 2	0	80	130	90	120	70	80	90	130	30	150	160	90	110	100	60	40	110	130	140	100	90	120	80	110	2410
Slope (Trans.2)	35	45	30	35	35	35	35	35	35	35	40	50	45	35	35	60	65	65	65	60	65	60	60	65	60	
Transect 3	0	70	20	60	50	50	60	90	40	50	60	80	110	40	5	105	80	70	60	100	70	10	70	100	60	1510
Slope (Trans.3)	25	45	40	40	45	45	40	45	45	45	40	40	45	40	40	40	40	40	45	45	45	40	40	45	40	

Economically-important trees were selected for study from a list of the most important commercial species in the Golfo Dulce-Osa Peninsula (Dirección General Forestal, MINAE 1996; Jimenez 1996; Maldonado 1997) (Table 4). The most common species from this list were selected based on forestry inventories (Allen 1956; Brealey 1972) and the advice of local expert; A. Rodriguez, pers. communication). Eleven tree species were selected: vaco (Brosimum utile), nazareno (Peltogyne purpurea), cedro maría (Callophyllum brasiliense), cerillo (Symphonia globulifera), reseco (Tachigalia versicolor), chancho blanco (Vochysia hondurensis), cedro macho (Carapa guianensis), masicarán (Qualea paraensis), caracolillo (Vantanea Barbourii), gallinazo (Schizolobium parahyba) and amarillón (Terminalia amazonica). Most of these trees are easily recognized from seedlings to adult trees by Augusto Rodriguez (an experienced dendrologist from the Osa Peninsula and research assistant in this project).

Table 4. Ecnomically-important trees in Golfo Dulce-Osa
Peninsula region, Costa Rica (MINAE 1996)

Scintific name	Common name	Family	Total volume (m³)
Aspidosperma spruceanum	Manglillo	Apocynaceae	279.2
Astronium graveolens	Ron-ron	Anacardiaceae	7.0
Brosimum utile	Lechoso/baco	Moraceae	1973.2
Carapa guianensis	Cedro macho	Meliaceae	438.8
Calophyllum brasiliense	Cedro maría	Clusiaceae	364.7
Caryocar costaricensis	Ajillo	Caryocaraceae	781.5
Caryodaphnopsis burgueri	Quira	Lauracea	17.0
Dilodendron costaricensis	Iguano	Sapindaceae	139.2
Dussia spp.	Sangrillo blanco	Fabaceae/Pap.	106.9
Hyeronyma alchorneides	Pilón	Euphorbiaceae	339.0
Hymenaea courbaril	Guapinol	Fabaceae/Caes.	135.8
Manilkara staminodella	Níspero chicle	Sapotacea	134.8
Minquartia guianensis	Manú	Olacaceae	74.2
Ocotea spp.	Ira	Lauraceae	145.5
Poulsenia armata	Calugo	Moraceae	186.3
Peltogyne purpurea	Nazareno	Fabaceae/Caes.	810.3
Qualea paraensis	Masicarán	Vochysiaceae	231.2
Schizolobium parahybium	Gallinazo	Fabaceae/Caes.	200.2
Sloneaspp.	Abrojo	Elaeocarpaceae	143.4
Symphonia globulifera	Cerillo	Clusiaceae	140.0
Tachigalia versicolor	Reseco	Fabaceae/Caes.	141.6
Tapiria myriantha	Cedrillo	Anacardiaceae	105.0
Terminalia amazonica	Amarillón	Combretaceae	150.9
Vantanea barbourii	Chiricano/Caracolillo	Humiriaceae	355.0
Virola spp.	Fruta dorada	Myristicaceae	988.2
Vochysiaspp.	Mayo	Vochysiaceae	75.7

The chosen trees have an asterisk in front

In this study, population structure was determined by recording the total number of all individuals of the selected tree species ≥ 2.5 cm dbh, and noting their diameter size classes: 2.5< 10 cm; 10-20 cm; 20-40 cm; 40-60 cm; 60 ≤ 80 cm; > 80 cm. Individuals ≥ 2.5 cm dbh were selected assuming that they are more or less established in the community since seedling mortality in the tropical forest is quite high. Diameter above buttress or stilt roots was used where necessary, otherwise diameter was recorded at dbh (diameter at breast height). In addition, the number of seedlings of Brosimum utile, Calophyllum brasiliense, Carapa guianensis, Peltogyne purpurea, Qualea paraensis, Symphonia globulifera and Shizolobium parahyba were counted. Seedlings of Vochysia hondurensis and Terminalia amazonica were not recorded due to their morphological similarity to other species, seedlings of Tachigali versicolor were not recorded because they were either unrecognizable or not encountered, and no seedlings of Vantanea barbourii were encountered. Since there appeared to be some correlation, between diameter and height (Richards 1996), I

designated trees >20 cm dbh as adult trees, individuals ≥ 2.5 < 20 cm as subadults and those ≤ 2.5 cm as seedlings and saplings.

Population structure was estimated by dividing the class size totals for each species by the total number of individuals in all size classes of the selected species found in the transects. This provided a relative density of each size class for each species. The relative density data for each species' size class also provides an estimate of population structure. Relative densities serve not only as an indication of abundance but provide important successional information (Knight 1975).

Since there are several types of diameter-size class distributions representing different regeneration strategies (Rollet 1974), tree species with similar population structures were grouped together to facilitate the study.

RESULTS

Size class distribution

Three patterns or types of diameter-size class distribution were recognized in this study (Figure 3). These three patterns appear to be representative of species in primary well-drained wet forest of PBNP. The estimated average size distribution ha^{-1} for the eleven selected species is summarized in table 5.

Type 1 diameter-size class distribution is represented by five species (Brosimun utile, Calophyllum brasiliense, Carapa guianensis, Symphonia globulifera and Tachigali versicolor). Their size-class distribution was continuous except for Tachigali versicolor which is special case (Fig. 3; table 6). In general, these species show a regular decrease of the number of trees with increasing diameter.

Type 2 diameter-size class distribution is also represented by five species (Qualea paraensis, Schizolobium parahyba, Terminalia amazonica, Vantanea barbourii and Vochysia hondurensis). Their size-class distribution of individuals show a marked deficiency in the lower and/or middle size classes (Figure 3; table 5). In an extreme case, Schizolobium parahyba does not have any individuals in subadult classes (i.e.< 20 cm dbh) (Figure 3; table 5).

Type 3 diameter-size class distribution is represented by one species (Peltogyne purpurea). This type is characterized by having about the same number of small individuals as large ones. Many seedlings were counted for this species but this type of size-class distribution does not show a regular decrease in the number of trees with increasing diameter. The average size classes from 10 to > 80 cm are more or less evenly represented by the same number of individuals.

Table 5. Average size distribution for eleven selected species in 1 ha of PBNP (on three transects). Relative densities (%) are provided in parenthesis after the mean except for seedlings and saplings

	Seedlings and Saplings	Subadults	Adults	
	< 2.5	2.5 < 20	> 20	
Brosimum utile	399.0	15.3 (12.8%)	11.0	(9.2%)
Calophyllum brasiliense	80.3	9.3 (7.8%)	4.3	(3.6%)
Carapa guianensis	100.0	14.0 (11.7%)	8.0	(6.7%)
Peltogyne purpurea	115.0	3.6 (2.0%)	4.6	(3.9%)
Qualea paraensis	47.0	2.3 (2.0%)	5.3	(4.4%)
Shizolobium parahyba	3.3	0.0 (0.0%)	2.3	(2.0%)
Symphonia globulifera	44.3	12.3 (10.3%)	9.7	(8.1%)
Tachigalia versicolor	not recorded	3.0 (2.5%)	1.3	(1.1%)
Terminalia amazonica	not recorded	0.6 (0.5%)	1.3	(1.1%)
Vantanea barbourii	not recorded	0.6 (0.5%)	4.7	(3.9%)
Vochysia hondurensis	not recorded	3.0 (2.5%)	6.0	(5.0%)

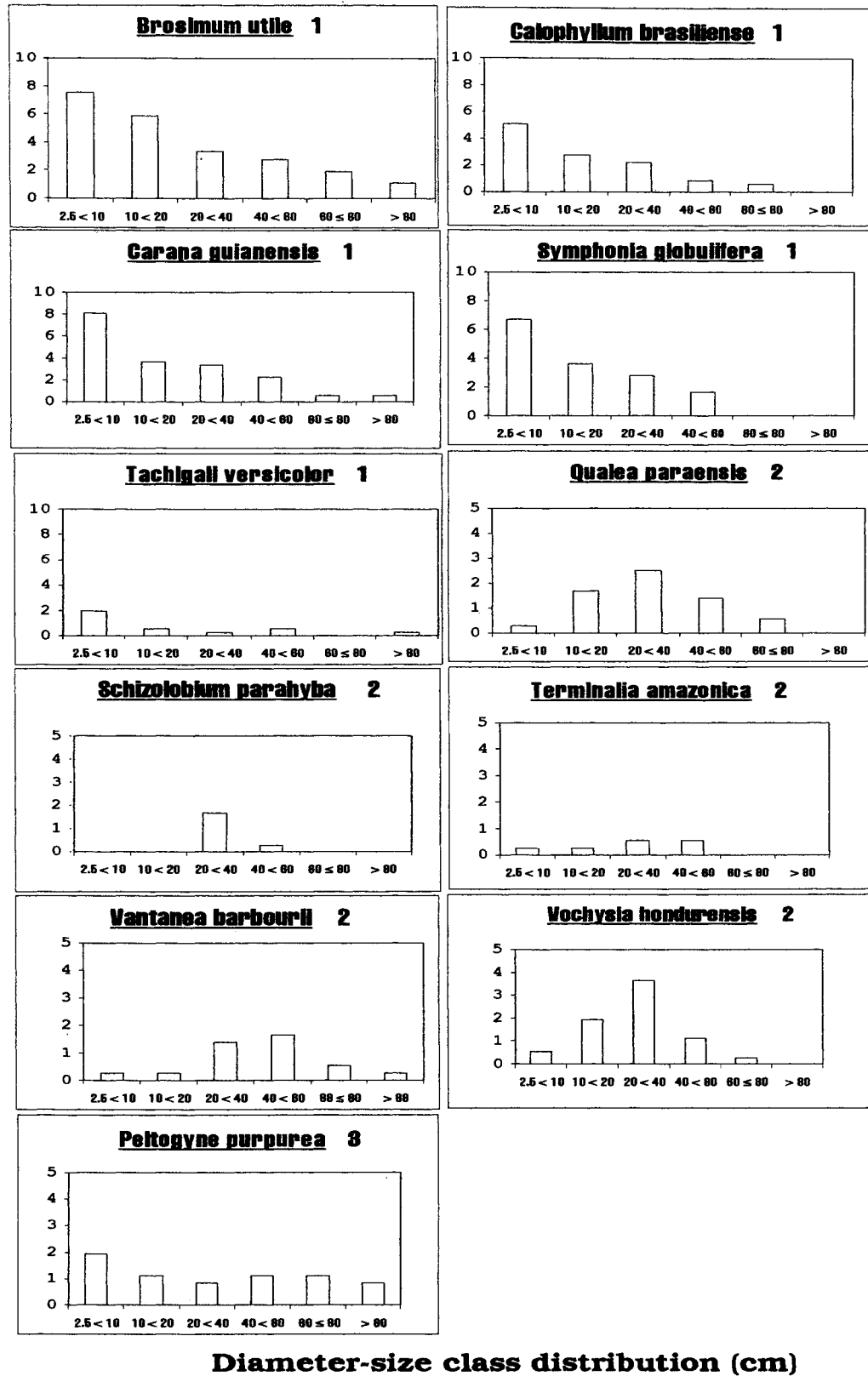**Diameter-size class distribution (cm)**

Fig. 3. The population structure of eleven selected tree species and their diameter-size distribution in PBNP, CR.

Density

The average density of the eleven selected species ≥ 2.5 DBH ha⁻¹ observed on the three transects in well-drained wet forests of PBNP was 119.3 trees (Table 6, Fig. 4).

Type 1 diameter-size class tree species (Brosimun utile, Calophyllum brasiliense, Carapa guianensis , Symphonia globulifera and Tachigali versicolor) accounted for an average of 71.5% of all the trees whereas type 2 and 3 diameter size class tree species accounted for an average of 21.4% and 7.1% respectively. Brosimum utile is the most abundant tree species, accounting for an average density of 27 ± 1.5 stems ha⁻¹ or 23% of the eleven selected tree species (figure 4; Table 6). The next most numerous tree species is Carapa guianensis with an average density of 22 ± 1.5 individuals ha⁻¹ or 18% of the eleven selected tree species. Symphonia globulifera is the third most common species with an average density of 17.7 ± 0.7 individuals ha⁻¹. Tachigali versicolor only have an average density of 4.3 ± 0.7 individuals ha⁻¹ or 4% of the total number of the eleven selected tree species.

Brosimum utlile showed greater relative basal area than relative values, while Calophyllum brasiliense, Carapa guianensis , Symphonia globulifera and Tachigali versicolor showed greater relative densities than relative basal area.

The most abundant tree species in the Type 2 diameter-size class was Vochysia hondurensis with an average density of 9 ± 5.5 individuals ha⁻¹ or 7% of the eleven selected tree species. This species has the most variable average density among the eleven tree species, while Terminalia amazonica had the least variability. T. amazonica was also the least abundant species in the study with an average density of 2 individuals ha⁻¹.

Vochysia hondurensis, Shizolobium parahyba and Terminalia amazonica showed slightly higher relative densities than relative basal areas, while Vantanea barbourii and Qualea paraensis showed higher relative basal area than relative density.

Table 6. Summary of the means and standard errors (Std.Errs) of tree density, average dbh (cm), basal area (sqm), relative density (%) relative dominance (%) and frequency (%) for 11 selected tree species ≥ 2.5 cm dbh three 1 ha transects

Species	Number of trees ha⁻¹	Average DBH (cm)	Basal area m² ha⁻¹	Relative density (%)	Relative dominance (%)	Frequency %
Brosimum utile	27.0 (1.5)	28.16 (1.8)	3.22 (0.3)	22.87 (2.3)	28.9 (1.5)	68.0
Calophyllum brasiliense	13.66 (2.2)	19.46 (2.0)	0.77 (0.1)	11.58 (2.2)	6.88 (1.2)	45.3
Carapa guianensis	22.0 (1.5)	22.24 (2.0)	1.79 (0.4)	18.48 (1.4)	15.65 (1.8)	60.0
Peltogyne purpurea	8.33 (0.6)	36.69 (1.2)	1.48 (0.2)	7.08 (0.6)	12.72 (0.7)	26.7
Qualea paraensis	7.66 (1.5)	34.30 (3.9)	0.80 (0.0)	6.35 (1.0)	7.52 (1.4)	14.7
Shizolobium parahyba	2.33 (1.5)	18.66 (9.4)	0.17 (0.1)	1.97 (1.3)	1.77 (1.4)	6.7
Symphonia globulifera	17.66 (0.7)	15.79 (0.7)	0.62 (0.0)	15.0 (0.3)	5.75 (0.9)	54.7
Tachigalia versicolor	4.33 (0.7)	21.44 (5.0)	0.38 (0.2)	3.61 (0.5)	3.05 (1.2)	10.7
Terminalia amazonica	2.0 (0.0)	27.41 (2.0)	0.15 (0.0)	1.67 (0.0)	1.56 (0.0)	8.0
Vantanea barbourii	5.33 (0.7)	46.91 (6.3)	1.13 (0.3)	4.49 (0.5)	9.65 (1.0)	17.3
Vochysia hondurensis	9.0 (5.5)	28.90 (2.5)	0.73 (0.5)	7.11 (4.0)	5.60 (2.8)	20.0
Totals	119.3		11.24			

Peltogyne purpurea is the sixth most abundant species (8.3 ± 0.7) among the eleven selected species. The relative density of this species was less than the relative basal area values.

Basal area

The average basal area observed on the three transects in the well-drained wet forests of PBNP was 11.2 m^2 ha^{-1} for the eleven selected species ≥ 2.5 DBH. (Table 6; Figure 5). Type 1 accounted for a relative dominance average of 57.3% while types 2 and 3 had an average relative dominance of 30% and 12.7% respectively. The two tree species with the highest densities were also the two most dominant in the transects. Brosimum utile accounted for a relative dominance average of 29% (Table 6). Basal area coverage averaged 0.1 m^2 per tree of B. utile (the equivalent of a 28.2 cm DBH) (Table 6). Carapa guianensis accounted for a relative dominance average of 15.7% (Table 6). Basal area coverage averages 0.1m^2 per tree of Carapa guianensis (the equivalent of a 22.2 cm DBH).

The next dominant species representing Type 3 is Peltogyne purpurea with a basal area of 1.5 m^2 ha^{-1}. Compared to more abundant species, P.purpurea averaged only 8.3 ± 0.7 trees ha^{-1} (7.1%) but had much larger average diameters (36.7 cm). The average basal area of this species was 0.2 m^2 (Table 6; Figure 4 & 5).

Vantanea barbourii is the other species that stands out in terms of dominance. Vantanea barbourii averaged only 5.3 trees ha^{-1} (4.5%) but had a large basal area and relative dominance (1.1 m^2 ha^{-1} or 9.7%), respectively. The tree's average diameters were very large (46.9 cm), and had an average basal area of 0.2m^2 (Table 6). Tachigali versicolor's basal area was the lowest of the trees in Type 1, only 0.4 ± 0.2 m^2 ha^{-1}, with an average basal area coverage of 0.1 m^2.

Vochysia hondurensis had the most variable dominance in the three transects, while Terminalia amazonica exhibited the least variability.
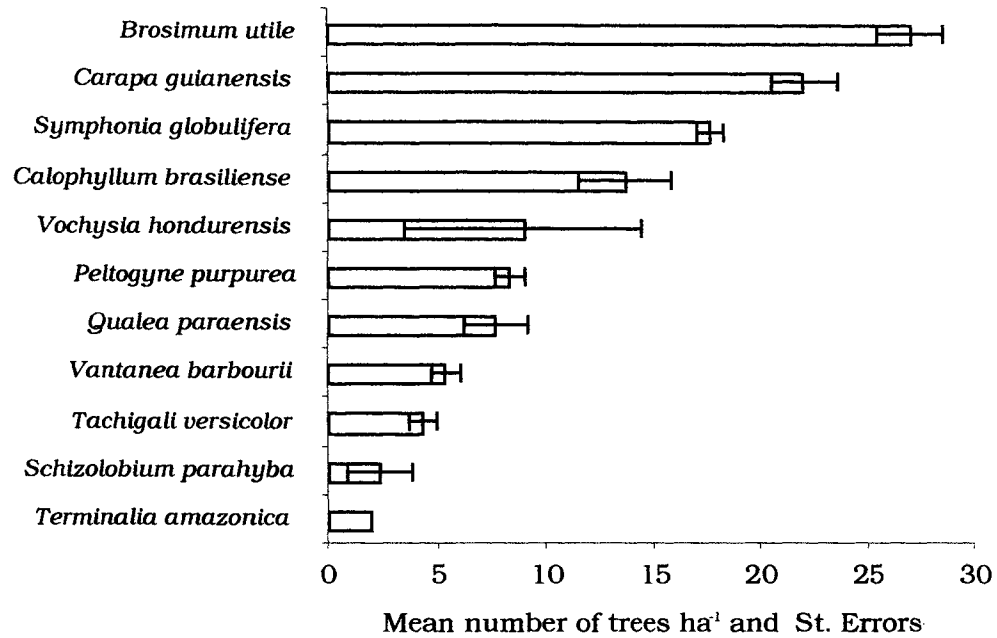
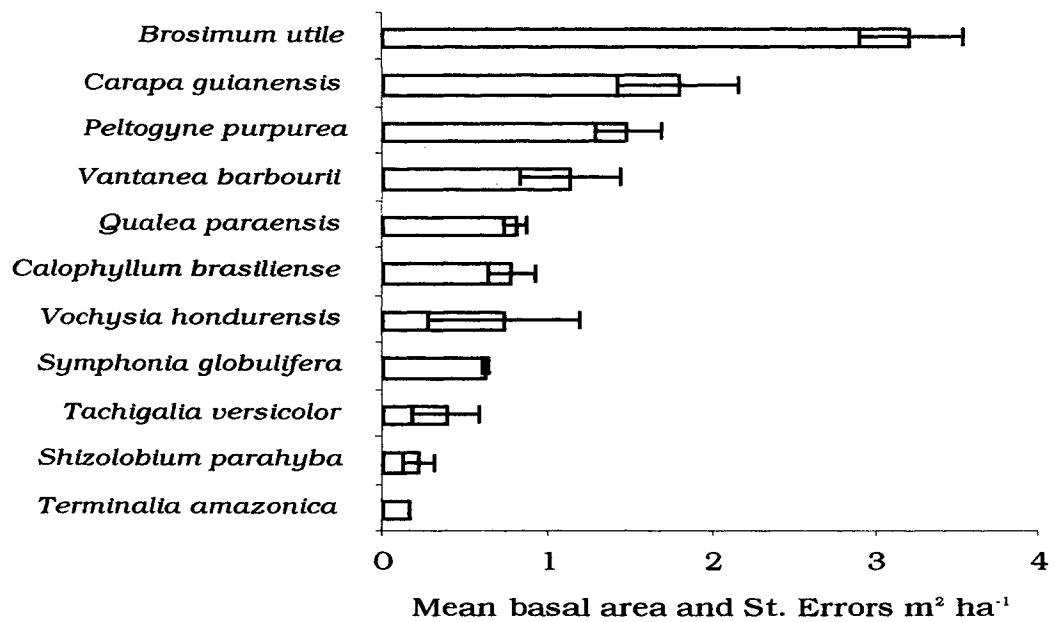Figure 4. Mean density of the eleven trees ha-1 in PBNP

Figure 5. Basal area of the eleven selected species in PBNP

Frequency

The four most frequently observed species were: <u>Brosimum utile</u> (68%), <u>Carapa guianensis</u> (60%), <u>Symphonia globulifera</u> (54.67%) and <u>Callophyllum brasiliense</u> (45.33%) (Table 6). <u>Shizolobium parahyba</u> was the least frequently observed (6.7%), followed by <u>Terminalia amazonica</u> (8%) (Table 6).

DISCUSSION

Size class distribution

General population structure patterns or types were identified by examining size class data without information on growth and mortality (Knight 1975). The five species (<u>Brosimum utile</u>, <u>Calophyllum brasiliense</u>, <u>Carapa guianensis</u>, <u>Symphonia globulifera</u> and <u>Tachigali versicolor</u>) representing Type 1 size class distribution are typical of climax forest (Jones 1956; Schultz 1960; Budowski 1970; Knight 1975; Barros & de Sausa 1989; Oppelt 1997). These trees show a characteristic inverse J-shape which decreases logarithmically as dbh increases. These type of curves are typical of shade tolerant species suggesting that even without growth and mortality data they are capable of regenerating continuously in the forest understory. These species are shade tolerant, but only in relative terms because light requirements change in later stages and light may become vital for their survival in the forest.

In general Type 1 species produce large quantities of fruits and seeds (Hartshorn 1983; Nichols & González 1992) and their large seeds are disseminated by gravity, mammals (especially rodents, monkeys and bats) and birds (Budowski 1970; Hartshorn 1980) . Thus, Type 1 seeds have a greater chance to widespread dissemination and possibly of reaching a gap. Germination of Type 1 seeds in the primary forest is good, although those that germinate in dense shade are less likely to survive (Jimenez 1995; Oppelt 1997). Most of the Type 1 species have many small individuals that survive in a suppressed state for years in the understory, however if light conditions do not improve they will not recruit. However, dead seedlings are replaced by new waves of

regeneration, thus there are always seedlings present to take advantage of light gaps, especially in the case of Brosimum utile (Oppelt 1997). Regeneration of Brosimum utile is excellent which explains why this species is particularly common in PBNP.

The case of Tachigali versicolor is a special one. This species is a monocarpic wind-dispersed, long-lived canopy species in which trees die within one year after producing a fruit crop (Foster 1977; Gentry 1993). Kitajima & Augspurger (1989) documented that juvenile survival of Tachigali versicolor at Barro Colorado Island was high due to a combination of characteristics such as: large seeds, dispersal capability, photosynthetic flexibility to contrasting light conditions, and probability of seedling survival in the shaded understorey in the first year. Foster (1977) postulated that mature Tachigali versicolor die so as to leave gaps in the canopy for the development of their own seedlings. If this is the case, the large trees observed in PBNP were probably maturing trees that had yet to produce fruit (i.e. only a low density of saplings were observed found surviving in the understory).

The five species (Qualea paraensis, Shizolobium parahyba, Terminalia amazonica, Vantanea barbourii and Vochysia hondurensis) representing Type 2 size-class distribution are "gap" or "light-demanding" species. These species show little or no replacement in the stand. They lack individuals in the smaller size classes apparently because they can not survive in the understory environment of PBNP. These species are represented almost entirely by larger trees. Since gaps are common in PBNP particularly in steep terrain, it may be possible that all Type 2 species will persist in the forest through the regeneration of an occasional individual. Steep terrain may also benefit light-demanding species since it results in variable light penetration below the canopy. Seedlings of Q. paraensis, S. parahyba and V. hondurensis were observed, but these species will probably become less common over time (unless a gap occurs) since very few individuals between 2.5 and < 20 cm dbh were encountered.

Most light-demanding species are associated with secondary-growth forests; although they also occur in primary forests (Flores 1993). In primary forests, they often show a patchy or clumped distribution linked to light gaps (Jones 1956). Schyzolobium

parahyba, Vochysia hondurensis, Qualea paraensis, and Terminalia amazonica are anemochrous (wind-dispersed) (Gentry 1993; Flores 1993, 1994b). Most wind-dispersed seeds do not travel far and survive in the surrounding light gaps near the parent tree (Augspurger 1986; Kitajima & Augspurger 1989).

The establishment of individuals of Schizolobium parahyba in the lower classes is triggered by favourable conditions, specifically disturbances. Schizolobium parahyba is a fast-growing, late successional species (Gentry 1993) that occurs in secondary forests or forms local colonies in steep slopes or in large gaps in primary forest, since they are strong light-demanding species (Allen 1956; Budowski 1970; Brealey 1972). This species is very common in PBNP and grows in an almost pure stands (i.e. consociation) along the hills that face Golfo Dulce (Allen 1956). These hills are steep and have been disturbed through natural mass wasting and clearing. In fact, most of the individuals within the plots were found in the Gallardo-Bajo Mansito transect near to Playa Gallardo beach (Figure 2).

The case of V. barbourii is somewhat different. Vantanea barbourii is an emergent tree that is only known in Nicaragua, Costa Rica and Panamá. The fruit is an ovoid, smooth drupe, about 3 cm long (Hartshorn 1983; Jimenez 1995). Many seeds were observed under parent trees but no seedlings were found in this study. It seems that subadult trees have high mortality, probably because they do not receive light adequate for optimal growth. However, if they find a gap they appear capable of growing to adult trees. Hartshorn (1983) found practically no regeneration of V. barbourii in Corcovado National Park. According to Jimenez (1995) the seedlings tolerate shade but regeneration is poor and there are no individuals in the middle storeys. Thus, light-demanding species may be maintained at low population density in the primary forest largely in saplings and subadults stages.

Peltogyne purpurea is the only species representing Type 3 size-class distribution. Peltogyne purpurea shows a population pattern that is difficult to interpret without additional information on growth and mortality data. Peltogyne purpurea is a canopy species (sometimes emergent) that produces large quantities of

fruits and seeds (Jimenez 1995). Peltogyne purpurea is only native of Panamá and Costa Rica and characteristic of the primary forest of Golfo Dulce-Osa Peninsula region (Jimenez 1995; Maráz 1997). Peltogyne purpurea is perhaps intermediate between the more shade-tolerant and light-demanding species. This species shows several shade tolerant traits including a tendency to germinate under the mother tree (Jimenez 1995). Thus, gaps are not required for germination and young individuals possess some degree of tolerance in the understory (Fig.3). On the other hand, P.purpurea does not flower every year (Allen 1956), thus there will not be always seedlings present to take advantage of light gaps. The critical period for this species occurs during sapling and subadult stages where abundant light (i.e. gaps) becomes essential for recruitment to larger size-classes. It seems that once the trees have sufficient light in the canopy they are able to thrive since about half of the trees recorded were present in the larger size classes.

Comparison with other studies

Density and basal area

I compared the density of trees ≥ 10 cm dbh and basal areas of my site with four other studies conducted in the wet forest of Golfo Dulce-Osa Peninsula region (Table 7).

Table 7. Environmental characteristics about five tropical wet forests

Location	Forest type	Elevation range (m)	Annual rainfall (mm)	Plot size m^2	Source
Rincón de Osa	well-drained Wet forest	130-150	3749[a]	7500	Sawyer 1966
Llorona, Corcovado N.P.	undulating plateau Wet forest	< 50	3500	10000	Hartshorn 1983
Piedras Blancas N.P.	well-drained Wet forest	300-350	> 4000	10000	Weissenhofer 1996
Rincón de Osa	non-inundated wet forest	285-392	4400[b]	40000	Thömsen 1997
Piedras Blancas N.P.	well-drained Wet forest	50-390	4831	30000	this study

[a]Period—1962 thru 1965

[b]Period of 1990

These other studies focused on the structure and floristic composition of trees > 10 cm dbh. Hartshorn (1978) and Thömsen (1997) established sample plots in the best stands in the region and only the ten most important tree species were reported. Sample areas in the studies ranged from 7,500m^2 (Sawyer 1966) to 40,000 m^2 (Thömsen 1997).

Table 8. Number of trees ≥ 10 cm dbh and basal area (sqm) of the eleven tree species in different studies

Source	Brosimum utile		Calophyllum brasiliense		Carapa guianensis	
	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹
Sawyer 1966	9	1.61	5	0.87	8	0.23
Hartshorn 1983*	23	3.53	not[1]	not[1]	9	1.34
Weissenhofer 1996	15	not[1]	0	0	15	not[1]
Thömsen 1997*	8.5	2.26	not[1]	not[1]	17.5	2.46
This study	18	3.19	9	0.76	12	1.77

Source	Peltogyne purpurea		Qualea paraensis		Shizolobium parahyba	
	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹
Sawyer 1966	17	1.26	1	0.98	0	0
Hartshorn 1983*	not[1]	not[1]	21	5.89	not[1]	not[1]
Weissenhofer 1996	2	not[1]	2	not[1]	0	0
Thömsen 1997*	not[1]	not[1]	11	3.07	not[1]	not[1]
This study	6.66	1.28	6.33	0.79	2.66	0.21

Source	Symphonia globulifera		Tachigalia versicolor		Terminalia amazonica	
	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹
Sawyer 1966	27	2.74	12	0.4	4 [2]	0.09
Hartshorn 1983*	20	1.34	not[1]	not[1]	not[1]	not[1]
Weissenhofer 1996	18	not[1]	0	0	0	0
Thömsen 1997*	23	1.9	not[1]	not[1]	not[1]	not[1]
This study	12.33	0.61	2	0.36	1.66	0.14

Source	Vantanea barbourii		Vochysia hondurensis	
	# of trees ha⁻¹	Basal area m² ha⁻¹	# of trees ha⁻¹	Basal area m² ha⁻¹
Sawyer 1966	7	1.71	5	3.2
Hartshorn 1983*	10	9.23	not[1]	not[1]
Weissenhofer 1996	0	0	0	0
Thömsen 1997*	4	1.21	not[1]	not[1]
This study	5	1.12	8.33	0.73

*Reported only the ten most important tree species
[1]not available

[2] Reported as Terminalia spp.

This comparison among the different sites is interesting due to their geographical proximity and similar elevation and rainfall. Llorona (Hartshorn 1983) is about 50 km from this study area and Rincón (Sawyer 1966; Thömsen 1997) is about 30 km from PBNP (about half way between Corcovado N. P. and PBNP). Brosimum utile, Carapa guianensis, Qualea paraensis and Symphonia globulifera are present in the five inventories, suggesting that they are common species in the Golfo Dulce-Osa Peninsula region, even though Q.paraensis is a gap species (Table 8).

Brosimum utile, Carapa guianensis and Symphonia globulifera have similar densities in the five inventories suggesting that they are maintaining a steady

population in the region. The two most abundant tree species in this study (Brosimum utile and Carapa guianensis) had a very similar stem density to the other study done at PBNP (Weissenhofer 1996) (Table 8). Among the five inventories, the highest density of Brosimum utile was observed at Llorona, Corcovado N.P. and the lowest density at Rincón (Figure 2). Brosimum utile showed greater relative basal area than relative density values in the five inventories indicating that this species is dominant in the region. Carapa guianensis showed greater relative basal area than relative density values in Hartshorn's (1978) and Thömsen's (1997) studies but in this study the situation was reversal. I observed greater relative density than basal area values, although the difference was minimal. Carapa guianensis is a dominant species in PBNP but they are not as large here as in the other sites in the region. Although C. guianensis trees are distributed throughout all the diameter size-classes in this study, a few individuals are in the larger size-classes. According to Flores (1994c), most of the seeds of this species are dispersed by rodents especially pacas (Agouti paca) and agouties (Dasyprocta punctata) and collared peccaries (Tayassu tajacu) and white-lipped peccaries (Tayassu pecari). However, the dispersion patterns of Carapa guianensis could have changed in PBNP because hunting has significantly reduced rodent populations in the area. Pacas and agouties are now very uncommon, while spider monkeys and white-lipped peccaries are practically extinct in PBNP (Juan Silva, personal communication).

Although Symphonia globulifera is common in all the five studies; it is a unique case. This species has much greater relative density (15%) than relative basal area (5.9%) indicating that they are relatively small trees (perhaps understory species). Compared to the other studies, S. globulifera showed lower density and basal area values in this study. There are no trees greater than 60 cm dbh. This suggests that the S. globulifera in this study are probably younger and subject to some disturbance. According to Herwitz (1981) S. globulifera is adapted to regenerate in situ in undisturbed primary forest in close proximity to parent trees. If this is the case, other

species more partial to light have a better chance of growing in gaps in the forest. Perhaps, C. brasiliense regeneration take advantage of this gaps.

Calophyllum brasiliense is the fourth most common species in my study, but was not present in the other inventory done at PBNP (Weissenhofer 1996). It was also not one of the top-ten species in either the Hartshorn (1983) site or the Thömsen (1997) site. Sawyer (1966) reported only five individuals with greater relative basal area than relative density values (Table 8). According to Quezada et al. (1997) C. brasiliense is one of the most dominant species on the ridges that surround Rancho Quemado (near Rincón) between 350-500 m of elevation. Seedlings of C. brasiliense are tolerant of shade but grow very well under full sunlight (Flores 1994a). Saplings that were dispersed by bats, monkeys or rodents have a better chance of survival, since seedlings have little chance to survive directly under the mother trees. In the Osa Peninsula, regeneration of C.brasiliense was observed only found a few meters from the crown of mother trees (Stein 1997). This coincides with the observations of Janzen (1979) and Connell (1971) who hypothesized that seedling survival is enhanced with increasing distance from the parent tree. In addition, dispersion of the fruits increases the chance of reaching a gap, which is optimal for their development (Auspurger 1984). In this study C. brasiliense showed greater relative density than basal area values indicating that most of the trees were in the lower size classes and there were no trees greater than 80 cm diameter. However, it must be remembered that some individuals in lower classes can grow to large diameter size classes.

Tachigali versicolor is only present in this study and Sawyer's study (1966) (Table 8). In both, relative densities were greater than relative basal area values indicating that most individuals were in the smaller size classes.

Shade intolerant species are usually clumped and are only present on certain studies with the exception of Qualea paraensis. Looking at the densities and basal areas of the studies, Qualea paraensis seems to be a common canopy or sometimes emergent species in the region. This species showed greater relative basal area than relative density values in the five inventories, indicating that the species is represented

with large trees. However, in my study Q.paraensis had slightly greater relative basal area than relative density values thus most of the individuals concentrated in the middle diameter size classes. Qualea paraensis is not even represented in the diameter size-class greater than 80 cm. This suggest that most of the individuals in my study are adult but relatively young and can grow to bigger diameter size-classes. Also, when comparing the five inventories the large difference among the densities suggests that this species has a patchy ditribution in the Golfo Dulce-Osa Peninsula.

Terminalia amazonica is an uncommon tree species in the region. It was present only in this study and perhaps in Sawyer's study (1966), since he represented the genus Terminalia as a whole (this genus includes three native species in the region). In both studies T. amazonica showed greater relative densitiy than relative basal area values indicating that the majority of individuals were distributed in the smaller diameter size classes. According to Flores (1994b) T.amazonica is an emergent tree. No individuals greater than 60 cm were found in my plots indicating that the trees can attain greater diameter size-classes.

Vochysia hondurensis was only represented in Sawyer's study and my study. In Sawyer's study, V.hondurensis had much greater relative basal area than relative density indicating that few trees were represented in higher diameter size classes. In this study, V. hondurensis populations exhibited greater relative densities than basal area values, indicating that this species is mainly represented in the low and middle diameter size classes; no trees greater than 80 cm dbh were found. Based on these results, it seems that the Vochysia hondurensis trees are younger in my site and capable of growing to greater diameter size-classes. On the other hand, in Sawyer's study (1966) most if not all the trees were large and mature. Vochysia hondurensis in this study is the species with the highest standard error with respect to mean density and basal area. This indicates that the species' distribution throughout PBNP is patchy and only those places with gaps within the forest offer potential regeneration.

Vantanea barbourii is present in all the studies except for Weissenhofer's inventory (Table 8). The relative basal area showed greater than relative density values

in all inventories. The most impressive stand of V. barbourii is in Hartshorn'study with a much greater relative basal area than relative density values. Although the results of my study showed that V.barbourii trees are relatively large, if compared to the other studies, the V.barbourii trees in my study showed the lowest basal area in proportion to density.

The third type of diameter-size class represented by Peltogyne purpurea is present only in three studies. In this study P. purpurea showed greater basal area than relative density values indicating that a large percentage of the individuals are distributed in the larger diameter size classes. In Sawyer's study (1966) it is the other way around, P. purpurea showed greater relative density than relative basal area values indicating that most of the individuals are in the lower size classes. Based on the population structure, it seems that disturbance and thus gaps occur quite often in PBNP which help subadult individuals of P. purpurea reach the canopy. Peltogyne purpurea is rare in the Osa Peninsula but is becoming more common in the northern region, especially around Mogos (Figure 2) (Fundación Neotrópica 1992; Jimenez 1995). PNPB probably preserves one of the largest populations of P. purpurea in the country.

Even at short distances, forest in the Golfo Dulce-Osa Peninsula region seem to be composed of particular combinations of tree species linked to particular environmental factors. The region of PBNP seems to undergo more forest disturbance. According to Weissenhoffer (1996), more than 10% of his research plot at PBNP was in light gaps thus, classic climax stages are rare and mainly continue to flat areas where there is less disturbance.

CONCLUSION

In general, shade-tolerant species are more dominant and widespread in PBNP than light-demanding species and the latter tend to have a patchy distribution. Brosimum utile is the most abundant tree in PBNP with numerous young recruits in the population. Vochysia hondurensis is the most abundant species among "light-demanding" species in the primary forest of PBNP.

PBNP appears to be a dynamic site when compared to the other areas in the Golfo Dulce-Osa Peninsula. Natural disturbances such as wind, lightning, floods, mudslides, and tree fall in conjunction with the steep topography open gaps for light-demanding species. This contributes to the overall species diversity of the forest. All species benefit with gaps, especially "light-demanding" species. Apparently, most of the gap species at PBNP except Vantanea barbourii are trying to attain greater diameter size classes while in the other inventories in the region these species seem to be larger and more mature. Peltogyne purpurea which is an intermediate shade-tolerant to light-demanding species also seems to thrive in PBNP due to the frequency of natural disturbances.

The absence or low numbers of some animals that disperse seeds may adversely affect the abundance and dynamics of seedlings and understory plants. However, population of some important seed dispersing rodent species appear to be recovering since the park was created (Agustín Zúñiga, personal communication).

To fully understand the population dynamics of these and other important tree species a larger study should be undertaken so as to provide more information regarding of the size-class distribution of species such as Tachigali versicolor and Peltogyne purpurea. The regeneration pattern of Vantanea barbourii also warrants further investigation.

Past information about environmental factors and long-term studies are needed to clarify and understand the types of disturbance and regeneration that are characteristics of different sites in the Golfo Dulce-Osa Peninsula region and to develop forest and protected area management regimes for these important forest remnats.

REFERENCES

Allen, P.H. 1956. *The rain forest of Golfo Dulce*. The University of Florida Press.

Augspurger, C. 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *Amer. J. Bot.* 73(3): 353-363.

Barros, R.P. & E. Girnos de Sousa. 1989. Population structure, dispersion and microhabitat regeneration of Carapa guianensis in Northeastern Brazil. *Biotropica* 21 (3): 204-209.

Boom, B. 1986. A forest inventory in Amazonia Bolivia. *Biotropica* 18 (4): 287-294.

Brealey, O. 1972. *Manual de dendrología para las especies arbóreas de la Península de Osa, Costa Rica*. Organization for Tropical Studies, San José, Costa Rica.

Budowski, G. 1970. The distinction between old secondary and climax species in tropical Central American lowland forests. *Trop. Ecology* 11, 44-8.

Burger, W. C. 1980. Why are there so many kinds of flowering plants in Costa Rica. *Brenesia* 17:371-388.

Clark, D. & D.A. Clark. 1987. Population Ecology and Microhabitat distribution of *Dipterix panamensis*, a neotropical rain forest emergent tree. *Biotropica* (19): 236-244.

Clark, D.A. 1994. Plant demography. In *La Selva: ecology and natural history of a neotropical rain forest*. ed. Lucinda A. McDade, Kamaljit S. Bawa, Henry A. Hespenheide, and Gary S. Hartshorn, 90-105. The University of Chicago Press.

Cominskey, J. A., G. Aymard, & F. Dallmeier. 1994. Structure and composition of lowland mixed forest in the Kwakwani region of Guyana. *Biollania* 10: 13-28.

Connell, Hj.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302-1310.

Denslow, J.D. & G.S. Hartshorn. 1994. Tree-fall gap environments and forest dynamic processes. In *La Selva: ecology and natural history of a neotropical rain forest*. ed. Lucinda A. McDade, Kamaljit S. Bawa, Henry A. Hespenheide, and Gary S. Hartshorn, 120-127. The University of Chicago Press.

Dirección General Forestal, MINAE 1996. Expedientes de Planes de Manejo.

Donovan, R. 1994. BOSCOSA: Forest Conservation and Management through local institutions (Costa Rica). In *Natural Connections: Perspectives in Community-based conservation*. ed. D. Western, Michael R. Wright, and Shirley C. Strum, 215-223. Island Press, Washington, D.C

ECOLAND:Esquinas National park. 1995. U.S. INITIATIVE OF JOINT IMPLEMENTATION. Web site: (http://w.w.w.ji.org/usiji/ecoland.shtml).

Fallas, O. 1994. *Lucha contra la Ston*. Costa Rican Ecological Association (AECO). San José, Costa Rica.

Flores, E. 1993. *Vochysia guatemalensis. In Trees and seeds from the Neotropics*. ed. Museo Nacional de Costa Rica, 1-27, vol. 2, nº 1,: Impreso por Imprenta Nacional, San José, Costa Rica.

_____. 1994a. *Calophyllum brasiliense. In Trees and seeds from the Neotropics*. ed. Museo Nacional de Costa Rica, 55-86, vol. 3, nº 1,: Impreso por Imprenta Nacional, San José, Costa Rica.

_____. 1994b. *Terminalia amazonica. In Trees and seeds from the Neotropics*. ed. Museo Nacional de Costa Rica, .27-54, vol. 3, nº 1,: Impreso por Imprenta Nacional, San José, Costa Rica.

_____. 1994c. *Carapa guianensis. In Trees and seeds from the Neotropics*. ed. Museo Nacional de Costa Rica, .1-27, vol. 3, nº 2,: Impreso por Imprenta Nacional, San José, Costa Rica.

Foster, R.B. 1977. *Tachigali versicolor* is a suicidal neotropical tree. *Nature* 268: 624-626.

Fundación Neotrópica. 1989. *Osa 2000: Biological conservation & community development for Corcovado National Park and buffer zone on the Osa peninsula, Costa Rica.* San José, Costa Rica.

Fundación Neotrópica – Fondo Mundial para la Vida Silvestre. 1992. *Programa Boscosa: Evaluación ecológica rápida, Peninsula de Osa, Costa Rica.* San José, Costa Rica.

Gentry, A.H. 1993. *A field guide to the families and genera of woody plants of northeast South America.* Published in Association with Conservation International-University of Chicago Press.

Hartshorn, G.S. 1978. Tree falls and tropical forest dynamics. In *Tropical trees as living systems.* ed. P.B. Tomlinson, & M.H. Zimmermann, 617-638. Cambridge University Press.

_____. 1980. Neotropical forest dynamics. *Biotropica* 12 (suppl.): 23-30.

_____. 1983. Plants -- introduction. *In Costa Rican Natural History.* ed. Daniel H. Janzen, 118-157. The University of Chicago Press.

Herwitz, S.R. 1981. Regeneration of selected tropical tree species in Corcovado National Park, Costa Rica. *University of California Publications in Geography.* 24: vii—xii, 1-109.

Holdridge, L.R. 1967. *Life zone ecology.* San José, Costa Rica.

Holdridge, L.R., W. Grenke, W. Hatheway, T.Liang, & J. Tosi. 1971. *Forest environments in tropical life zones: A pilot study.* Pergamon Press, Oxford.

Hubbell, S. & R.B. Foster. 1986. Canopy gaps and the dynamics of a neotropical forest. In *Plant ecology,* 77-96. ed. M.J. Crawley. Blackwell Scientific Publications, Oxford.

Janzen, D.H. 1979. How to be a fig. *Ann. Rev. Ecol. Syst.* 10: 13-51.

Jimenez, J.J. 1996. *Diagnóstico del mercado de maderas de la Península de Osa.* Informe de consultoria elaborado por la Fundación Netrópica. Agua Buena de Osa, Costa Rica.

Jimenez, Q. 1995. *Arboles maderables en peligro de extinción.* 1ra . edición corregida. San José, C.R., INCAFO.

Jones, E.W. 1956. Ecological studies on the rain forest of southern Nigeria. IV. The plateau forest of the Okomu Forest Reserve, Part II, The reproduction and history of the forest. *J. Ecol.* 44, 63-117.

Kitajima, K. & C.K. Augspurger. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigali versicolor. Ecology,* 70 (4), 1102-1114.

Knight, D. 1975. A phytosociological analysis of species-rich tropical forest in Barro Colorado Island, Panamá. *Ecological Monographs,* 45: 259-284.

Korning, J. & H. Balslev. 1994. Growth and mortality of trees in amazonian tropical rain forest in Ecuador. *J. Veg. Sci.* 4, 77-86.

Lieberman, D. & M. Lieberman. 1987. Forest tree growth and dynamics at La Selva, Costa Rica. *J. Trop. Ecol.* 3: 347-58.

Lieberman, M. & D. Lieberman. 1994. Patterns of density and dispersion of forest trees. In *La Selva: ecology and natural history of a neotropical rain forest.* ed. Lucinda A. McDade, Kamaljit S. Bawa, Henry A. Hespenheide, and Gary S. Hartshorn, 106-119. The University of Chicago Press.

Maldonado, T. 1997. Uso de la tierra y fragmentación de Bosques. Algunas áreas críticas en el Area de Conservación Osa, Costa Rica. Fundación Neotrópica: Unidad Técnica. Centro de Estudios Ambientales. San José, Costa Rica.

Marás, L. 1997. *Peltogyne purpurea.* In Tropenökologisches Begleitprogramm (TÖB). ed. P. Splitter, 55-61. Deutsche Gesellschaft für Tehnische Zusammenarbeit (GTZ). República Federal de Alemania.

Nalini, M. N., T.J. Matelson, & W.A. Haber. 1995. Structural characteristics and floristic composition of a neotropical cloud forest, Monteverde, Costa Rica. *J. Trop. Ecol.* 11: 481-495.

Nichols, D. & E. González. 1992. *Especies nativas y exóticas para la reforestación en la zona sur de Costa Rica.* Memoria del II encuentro sobre especies forestales. Organizado por: Organización para los Estudios Tropicales (OET), Dirección General Forestal (DGF) & Universidad Estatal a Distancia (UNED).

Oppelt, A. 1997. *Brosimum utile.* In Tropenökologisches Begleitprogramm (TÖB). ed. P. Splitter, 16-25. Deutsche Gesellschaft für Tehnische Zusammenarbeit (GTZ). República Federal de Alemania.

Pires, J.M. & , G.T. Prance. 1977. The Amazon forest: a natural heritage to be preserved. In *Extinction is forever.* Ed. New York Botanical Garden, New York.

Prance, G. T., W.A. Rodriguez, & M.F. da Silva. 1976. Inventario florestal de um hectare de mata de terra firme km 30 da estrada Manaus – Itacoatiaria. *Acta Amazonica* 6, 9-35.

Quesada, F., Q. Jiménez, N. Zamora, R. Aguilar & J. González. 1997. *Arboles de la Peninsula de Osa,* 1ra edición. Intituto Nacional de Biodiversidad.

Rain Forest Action Network . 1993. *Alert #84: Stone Plans Massive Chip Mill in Costa Rica.* San Francisco, California.

Rainforest of the Austrians. 1999. La Gamba Biological Station. Web site: (http://w.w.w. regenwald.at).

Ramirez, A. & T. Maldonado. 1991. *Desarrollo socioeconómico y el ambiente natural de Costa Rica.* 2d ed. Fundación Neotrópica. Editorial Heliconia. San José, Costa Rica.

Richards, P.W. 1996. *The tropical rain forest.* 2d ed. Cambridge University Press.

Rollet, B. 1974. *L'architecture des Forest Denses Humides Sempervirentes de Plaine.* Centre Technique Forestier Tropical, Nogent-sur-Marne, France.

Sawyer, J. O. 1966. Selected vegetation types in diverse tropical environments in Costa Rica. Ph.D. diss., Purdue University.

Schipulle, H. P. & D. Burger. 1997. Preface. In Tropenökologisches Begleitprogramm (TÖB). ed. P. Splitter, 26-35. Deutsche Gesellschaft für Tehnische Zusammenarbeit (GTZ). República Federal de Alemania

Schultz, J.P. 1960. Ecological studies on rain forest in northern Suriname. In The vegetation of Suriname vol.2. ed. A.de Hulster, and J. Lanjouw. Published by Van Eedenfonds, Amsterdam, Netherlands.

Staein, R. 1997. Calophyllum brasiliense. In Tropenökologisches Begleitprogramm (TÖB). ed. P. Splitter, 26-35. Deutsche Gesellschaft für Tehnische Zusammenarbeit (GTZ). República Federal de Alemania.

Stolzenburg, W. 1998. Tree-venting the greenhouse. Nature Conservancy, November/December, 8-9.

Thömsen, K. 1997. Potential of non-timber forest products in tropical rain forest in Costa Rica. Ph.D. diss., University of Copenhagen.

Tosi, J.A. 1975. "The Corcovado basin on the Península de Osa". In potential National Parks, Nature Reserves, and Wildlife Sanctuary Areas in Costa Rica: A survey of priorities, 12. Photocopied from The Tropical Science Center.

Tropical Science Center. 1982. Costa Rica: Environmental Profile. Editorial Trejos, San José, Costa Rica.

Uhl, C., K. Clark, N. Dezzeo, and Maquirino. 1988. Vegetation dynamics in Amazonian treefall gaps. Ecology 69: 751-63.

Universidad Estatal a Distancia. 1996. ORO NO ES: Zonas de Vida en Costa Rica. Oficina Audiovisuales. San José, Costa Rica.

Vazquez, M. 1979. Soils of Costa Rica. In Costa Rican Natural History. ed. Daniel H. Janzen, 63-65. The University of Chicago Press.

Walsh, R.P.D. 1992. Representation and classification of tropical climates for ecological purposes using the perhumidity index. Suansea Geogr. 24, 109-29.

Weissenhofer, A. 1996. Ökologie und sruktur eines tieflandregenwaldes in der Pazifikregion von Costa Rica. Diplomarbeit an der Univ. Wien.

Werner, H. 1996. Floristische und biogeographische untersuchungen in einen tieflandregenwald in der Pazifischen region von Costa Rica. Diplomarbeit an der Univ. Wien.

Whitmore, T.C. 1980. Gaps in the forest canopy. In Tropical trees as living systems. ed. P.B. Tomlinson, & M.H. Zimmermann, 639-655. Cambridge University Press.

_____. 1997. Tropical forest disturbance, disappearance and species loss. In Tropical forest remnants: ecology, management, and conservation of fragmented communities. ed. William F. Laurance & R.O. Bierregaard, Jr. The University of Chicago Press.

Wilson, E.O. 1992. The diversity of life. Harvard University Press.