ASPECTS OF RAIN FOREST NUTRIENT DYNAMICS AT LOS TUXTLAS, MEXICO

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A MIS PADRES PRIMO CONSTANTINO Y ENRIQUETA

DECLARATION

I hereby declare that this thesis has been composed by myself and except where otherwise stated the work contained herein is my own.

Jose Luis Martinez S.

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ACKNOWLEDGEMENTS

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ABSTRACT

Several aspects of nutrient cycling were studied in the Lowland Tropical Rain Forest at Los Tuxtlas. This is at (18° 34' - 18° 36' N, 95° 04' - 95° 09' W) and represents the northernmost extension of the rain forest Formation in the New World. The relationships among the forest structure, small litterfall production (22 months), small litterfall element concentrations, and soil nutrients were investigated. The degree of nutrient resorption between fresh and dehisced leaves was evaluated for several tree species.

The forest had a preponderance of mesophylls, a relatively low tree species diversity, basal area, and small litterfall production. An estimation of leaf litterfall contribution was provided for 119 woody species and the temporal variation of the leaf litterfall was described. Soil nutrient concentrations were high probably owing to the volcanic eruption of 1793. Nutrient-element concentrations were relatively high in the small litterfall and fresh leaves, and nutrient resorption was relatively low.

The soil nutrient concentrations in pastures of 12, 32, and 52 years of age were compared with the forest and were relatively high in spite of their maintaining a high density of cattle.

The soil under isolated trees in the pastures had higher nutrient concentrations than the open pastures. There was a higher diversity of seedling species under the isolated trees but a growth experiment in a tree nursery did not show differences among the soils from the undisturbed forest, open-pastures and under the isolated trees. It seems that soil nutrients are always high at Los Tuxtlas and override any effect of nutrient addition by the isolated trees.

Keywords: Tropical rain forest, pastures, litterfall, nutrients, soil, Mexico, isolated trees, seedlings experiment.

RESUMEN

Se analizaron diversos aspectos del ciclo de nutrientes del Bosque Tropical Lluvioso y sus pastizales derivados, de Los Tuxtlas, Ver. México. Este Bosque localizado a los 18° 34' - 18° 36' lat. Norte y 95° 04' - 95° 09' long. Oeste, posee particular importancia ya que representa el límite norte de distribución de esta formación vegetal en el continente Americano.

En el bosque se estudió la relación existente entre su estructura, la producción de hojarasca (22 meses), el contenido de nutrientes de la hojarasca, y el contenido de nutrientes del suelo. También se cuantificó la translocación de nutrientes de las hojas seniles en varias especies arboreas. Se encontró un suelo con una alta fertilidad probablemente debido a la última erupción volcánica en 1793. La estructura y fisonomía del bosque se caracteriza por una diversidad de especies leñosas, area basal y producción de hojarasca, relativamente bajas, y una dominancia de hojas mesófilas. Se estimó la producción de hojarasca foliar de 119 especies leñosas, y se describe la variación temporal de la hojarasca foliar de 34 de estas especies. La concentración de nutrientes fue relativamente alta en la hojarasca y hojas frescas, y la translocación de nutrientes de hojas seniles relativamente baja.

Se comparó el contenido de nutrientes en el suelo de potreros de 12, 32 y 52 años de uso con el del bosque natural, y se encontraron niveles relativamente altos en los potreros a pesar de un uso prolongado y alta densidad de ganado.

Se estudiaron también los árboles remanentes en los potreros, y se encontró una mayor diversidad de plántulas en comparación con los sitios abiertos del mismo potrero. Se analizó el contenido de nutrientes del suelo, y se encontró mayor fertilidad que en el suelo del sitio abierto, sin embargo un experimento de crecimiento de plántulas no mostró diferencias entre el suelo proveniente del bosque natural, árboles remanentes y sitios abiertos en los potreros. El suelo de Los Tuxtlas es lo suficientemente rico en nutrientes, que no se observaron los efectos del aporte de nutrientes de la deforestación y de los árboles remanentes en el crecimiento de plántulas.

Palabras clave: Bosque Tropical Lluvioso, Selva Alta Perennifolia, potreros, hojarasca, nutrientes, suelo, México, árboles remanentes, crecimiento de plántulas.

[illegible] nutrient dynamics of the undisturbed lowland evergreen tro [illegible] Richards 1996) and the surrounding pastures in Los Tuxtlas, Ve [illegible]

The first aim was to investigate the relationships among [illegible] concentrations, forest structure, forest production, leaf litter [illegible] and nutrient resorption. The relationship between the soil and t [illegible] a matter of debate (Richards 1996, Proctor 1987, Whitmore 19 [illegible] evergreen rain forests has shown both nutrient-poor and nutrie [illegible] of varying stature and diversity (Proctor *et al.* 1983a, S [illegible] & Proctor 1984), a range of litterfall mass and nutrient conce [illegible]) and a [illegible] in nutrient-element resorption in leaf li [illegible] [illegible]2).

The second aim was to investigate by soil analyses [illegible] experiment some effects of the conversion of forest to [illegible] longevity of pastures. There is much evidence to show that [illegible] are unable to maintain agriculture and livestock production [illegible] erosion and loss of the natural fertility [illegible] Much experience has been obtained from studies on [illegible] tropical soils [illegible] 1986, Sanchez [illegible] Tuxtlas which has had relatively recent volcanic [illegible] Studies of forest recovery on abandoned pastures [illegible] Kellman [illegible] McDonnell & [illegible] element [illegible] forest regeneration (Guevara [illegible]). Living [illegible] riparian co [illegible] may be [illegible]

Chapter 1. INTRODUCTION

The project was designed to analyse the physical environment, vegetation and aspects of nutrient dynamics of the undisturbed lowland evergreen tropical rain forest (*sensu* Richards 1996) and the surrounding pastures at Los Tuxtlas, Veracruz, México.

The first aim was to investigate the relationships among the forest soil nutrient concentrations, forest structure, forest production, leaf litter nutrient concentrations, and nutrient resorption. The relationship between the soil and the forest it bears is still a matter of debate (Richards 1996, Proctor 1987, Whitmore 1998). Work on lowland evergreen rain forests has shown both nutrient-poor and nutrient-rich soils bearing rain forests of varying stature and diversity (Proctor *et al.* 1983a, Scott *et al.* 1992, Swamy & Proctor 1994a), a range of litterfall mass and nutrient concentration values (Proctor 1984), and a variation in nutrient-element resorption in leaf litterfall (*e.g.* Scott *et al.* 1992).

The second aim was to investigate by soil analysis and a seedling growth experiment some effects of the conversion of forests to pastures and to ascertain the longevity of pasture use. There is much evidence to show that forest soils in the tropics are unable to maintain agriculture and livestock production indefinitely owing to the erosion and leaching of the mineral nutrients (Buschbacher 1987a,b; Jordan 1989). Such experiences have been obtained from studies on old leached and nutrient-poor tropical soils (Nye & Geenland 1960, Sanchez 1976) which are unlike to those at Los Tuxtlas which has had relatively recent volcanic activity (last eruption in 1793, Chapter 2). Studies of forest recovery on abandoned pastures have involved isolated trees (Kellman 1979, 1985; McDonnell & Stiles 1983) as sites for natural tree seedling establishment and as foci of forest regeneration (Guevara *et al.* 1986, Guevara *et al.* 1992). Living fences and riparian corridors may be also sites for natural seedling establishment but are less well studied and not dealt within in detail in this thesis. It is considered from work in savannas (Kellman 1979, Belsky *et al.* 1989) that isolated trees provide a better physical environment for seedling establishment. In this thesis the effect of the isolated trees on soil nutrients is explored by analysing the soils under them and comparing the results with those from the forests and open-pastures.

The conversion of the lowland evergreen rain forest to pastures is still occurring at a high rate in México. Major causes of deforestation are the expanding cattle industry (mostly supported by governments), agriculture, the careless use of fire, and logging. In the Neotropics, including México, pastures are the main reason for the loss of lowland rain forest (Whitmore 1998). Lowland evergreen rain forest represented 40.7% (715 million ha) (25% in Asia, 63% in America and 12% in Africa) of the world's tropical forest in 1990 (Whitmore 1998). Terborgh (1992) has predicted a sad scenario if no reduction in forest conversion is imposed by the governments. Estimated (1989) rates of deforestation based on satellite images, of tropical rain forest (which presently covers only about 7% of the Earth's surface), were 14.2 million ha yr^{-1} which was equivalent to 1.8% yr^{-1} of that remaining in the world. With this rate of deforestation tropical forest will disappear by 2045. However the estimated rate of deforestation is not likely to be constant since it moved from 0.9% in 1979 to 1.8% in 1989 as a result of increasing population pressure and tropical forest disappearance may take place before 2045 (Terborgh 1992).

In México the lowland rain forest is being lost at a rate of 2.0% yr^{-1} (Cairns *et al.* 1995), which is within the highest rates of deforestation for countries like the Philippines (2.5%), Costa Rica (2.3%), Brazil (1.5%) and Ghana (1.2%) (Whitmore 1998). Tropical rain forest in México has been reduced to 5% of its original area owing to deforestation for agriculture (Guevara & Laborde 1993). Thirty years ago tropical lowland evergreen rain forest had its northernmost distribution in the Neotropics in México at about 22° N (Dirzo & Miranda 1991) but currently the northernmost extension is at Los Tuxtlas, in the State of Veracruz, at about 19° N (Dirzo & Miranda 1991, Richards 1996, Whitmore 1998). Its northermost location in Africa is at *c.* 9° N (Richards 1996) and in Asia at 27° 31′ N (Proctor *et al.* 1998). Judging from the present climate, about 65% of Veracruz with an area of 7,281,500 ha was occupied by rain forests (Ordóñez & García-Oliva 1992) compared with only 9% presently (Barrera & Espejel 1992). More than 50% of the State's territory is devoted to livestock (Barrera & Rodríguez 1993). At Los Tuxtlas by 1986 an estimated 84% of the original forest area (850 km^2, 18° 25' - 18° 45' N, 95° 00' - 95° 18' W) had been converted to pastures (Dirzo & García 1992) with an annual rate of deforestation of 4.3%. The landscape is now a mosaic of forest fragments of different sizes and shapes surrounded by pastures and fields. A small portion of the remaining forest is protected at the forest reserve of the Biological Station (Chapter 2).

The history of cattle ranching in tropical México, particularly in the State of Veracruz has been documented by Barrera & Rodríguez (1993) and González (1996). Cattle (Bos taurus) first arrived on the American continent in Veracruz in 1525 having been brought there by Hernán Cortés (Barrera & Rodríguez 1993). According to Dusenberry (1963) this activity quickly expanded and by the middle of the 16th century many ranchers owned more than 100,000 head of cattle. After the Independence of México in 1810 cattle ranching experienced a decline. The Governor of Veracruz in 1831 reported 305,300 head of cattle in the State (Melgarejo Vivanco 1980). The main cattle race found in Veracruz from the colonial times to the beginning of this century was the Creole which gave low meat and milk yields. From 1903 several races were introduced of which the Swiss, and the species Bos indicus (Zebu), which first arrived in Tampico in the north of the State in 1923, were the most successful.

The industry has continued to grow and mixtures with Creole, Swiss and Zebu races and their hybrids are common. According to Feder (1980, 1982 in Toledo *et al.* 1993), between 1971 and 1977 the World Bank and the Interamerican Development Bank gave loans for cattle husbandry in México for a total of $U.S. 527.4 x 10^6, which represented 48.7% of the total amount given to Latin America for the same activity. The Mexican counterpart, the Bank of México, provided $U.S. 639 x 10^6.

In the world context, the meat and milk production from pastures in the tropics, represents an important component of tropical agriculture. About half of the world's permanent pastures and half of the cattle population are in the tropics (Sanchez 1976), but the lower productivity of tropical livestock means that only one-third of the world's meat and one sixth of its milk are from this region (Jones 1972). The low productivity of forage-consuming animals in the tropics has been attributed to several factors such as heat stress, animal diseases, and pasture production which is related to soil properties (Sanchez 1976).

Establishment of pastures for cattle grazing has often followed shifting cultivation, either after cutting the mature forest as in huge areas in Brazil, or after crop yields have fallen, which is a common case in México for maize. Pastures appear to be viable in the long term only on the fertile soils like andosols, clays over limestones and alluvial soils. Pastures on the less fertile soils appear to be productive for a few years, then the palatability, digestibility and nutritional value of their forage decreases and they are abandoned (Baillie 1996).

The first aim of the present study dealt with in Chapters 2 to 7, and the second aim is dealt with in Chapters 8 to 10. Chapter 2 describes the physical environment and the locations of the study sites and Chapter 3 the forest vegetation of the plots where the studies (soil analyses, litterfall production, and nutrient dynamics) were made. Chapter 4 describes the soil analyses from the forest and open pastures of three different ages. Chapter 5 describes the forest small litterfall production (total and by leaf litter species); Chapter 6, the small litterfall nutrient contents; and Chapter 7 the leaf nutrient resorption of the most productive species. Chapter 8 describes the pasture vegetation, Chapter 9 the soil analyses under the isolated trees in the pastures, Chapter 10 the seedling growth experiment on the soils of the different sites, and Chapter 11 discusses the two aims and gives the final conclusions.

Chapter 2. THE LOCATION AND PHYSICAL ENVIRONMENT OF THE STUDY PLOTS

The study was located in the State of Veracruz, México (Figure 2.1). The forest site was in the 640 ha grounds of the Biological Station 'Estación de Biología Los Tuxtlas' (18° 34' - 18° 36' N, 95° 04' - 95° 09' W) (henceforth referred as BS) which is a natural forest reserve belonging to the Universidad Nacional Autónoma de México. The BS has a surrounding mosaic of forest fragments and pastures with frequent isolated tall trees and tree lines, mainly of the freely sprouting Bursera simaruba, as pasture boundaries. Also trees are frequently left along stream sides which retain a relatively diverse riparian forest.

There were three 50 m x 50 m plots in the undisturbed forest and in each of the three pasture sites. The forest plots (1-3) were located within 2 km of the field station buildings at the altitudes: plot 1, 120 m; plot 2, 170 m; plot 3, 200 m (Figure 2.2). Details of forest plot locations and also the forest plot of Bongers *et al.* (1988) (BP) (used for comparisons) are also shown. The pasture sites were of a known history and of three ages after forest clearance: 12, *c*. 32 and *c*. 52 years. The 12-yr pasture (plots 4 - 6) was located between 1.5 and 2 km NE of the BS, the 32-yr pasture (plots 7 - 9) was around 3.5 km N of the BS, and the 52-yr pasture (plots 10 -12) was around 6 km SE of the BS (Figure 2.3). All the plots were placed in accessible representative areas in each of their vegetation types. Pasture site replication was impossible. The plots were treated as statistically independent samples relying on plot replicates within the same type of forest or pasture (pseudoreplicates, Hurlbert 1984). All the plots were divided into 25 subplots (10 m x 10 m) and the forest plots were marked with permanent red-painted plastic poles around each 10 m of the perimeters. The slope of the terrain was obtained at each intersection of the subplots (36 measures per plot).

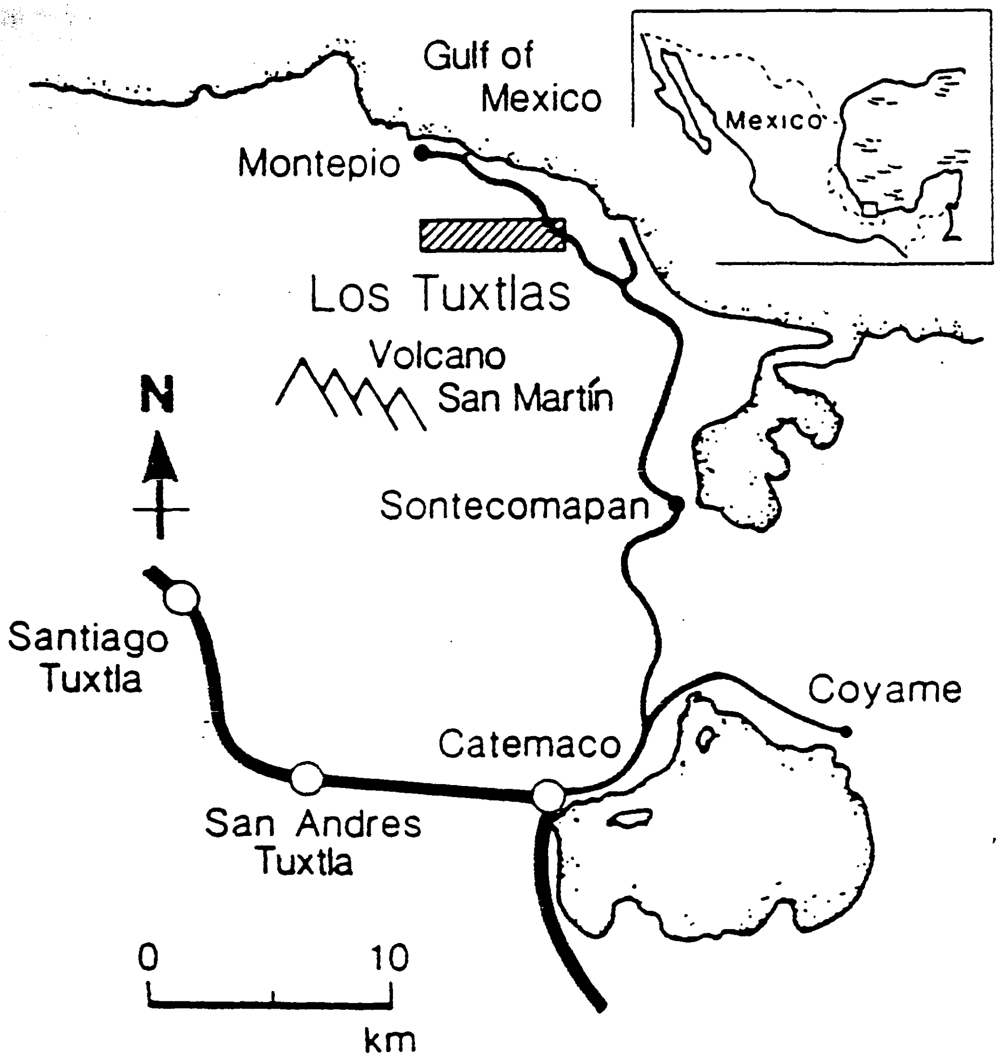


Figure 2.1. The mountain chain “Sierra de San Martin Tuxtla” and the BS (hatched) (18° 34' to 18° 36' N, 95° 04' to 95° 09' W) (Bongers *et al.* 1988).

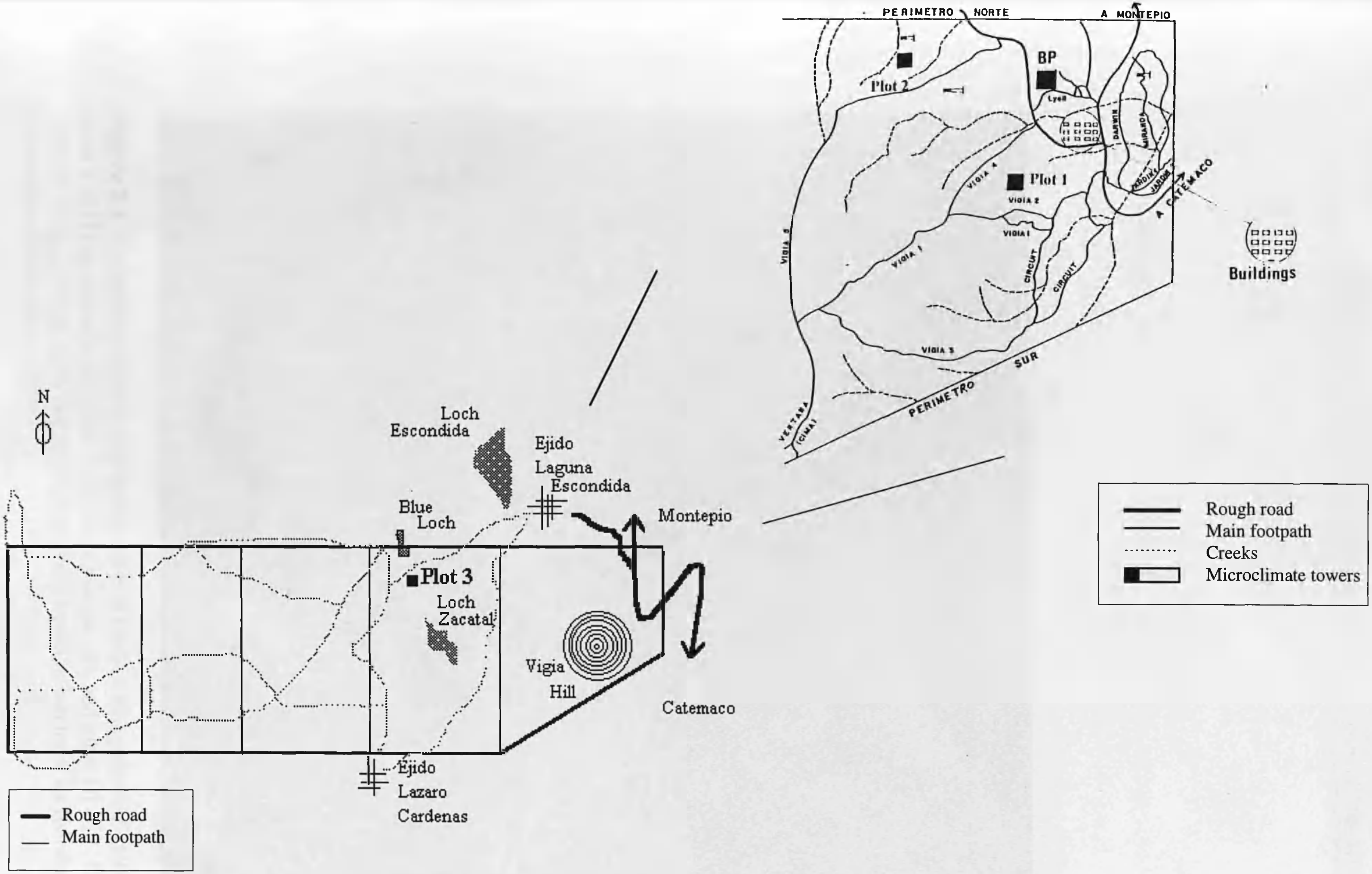


Figure 2.2. Map of the BS and location of plots 1- 3 and the Bongers *et al.* (1988) plot (BP).

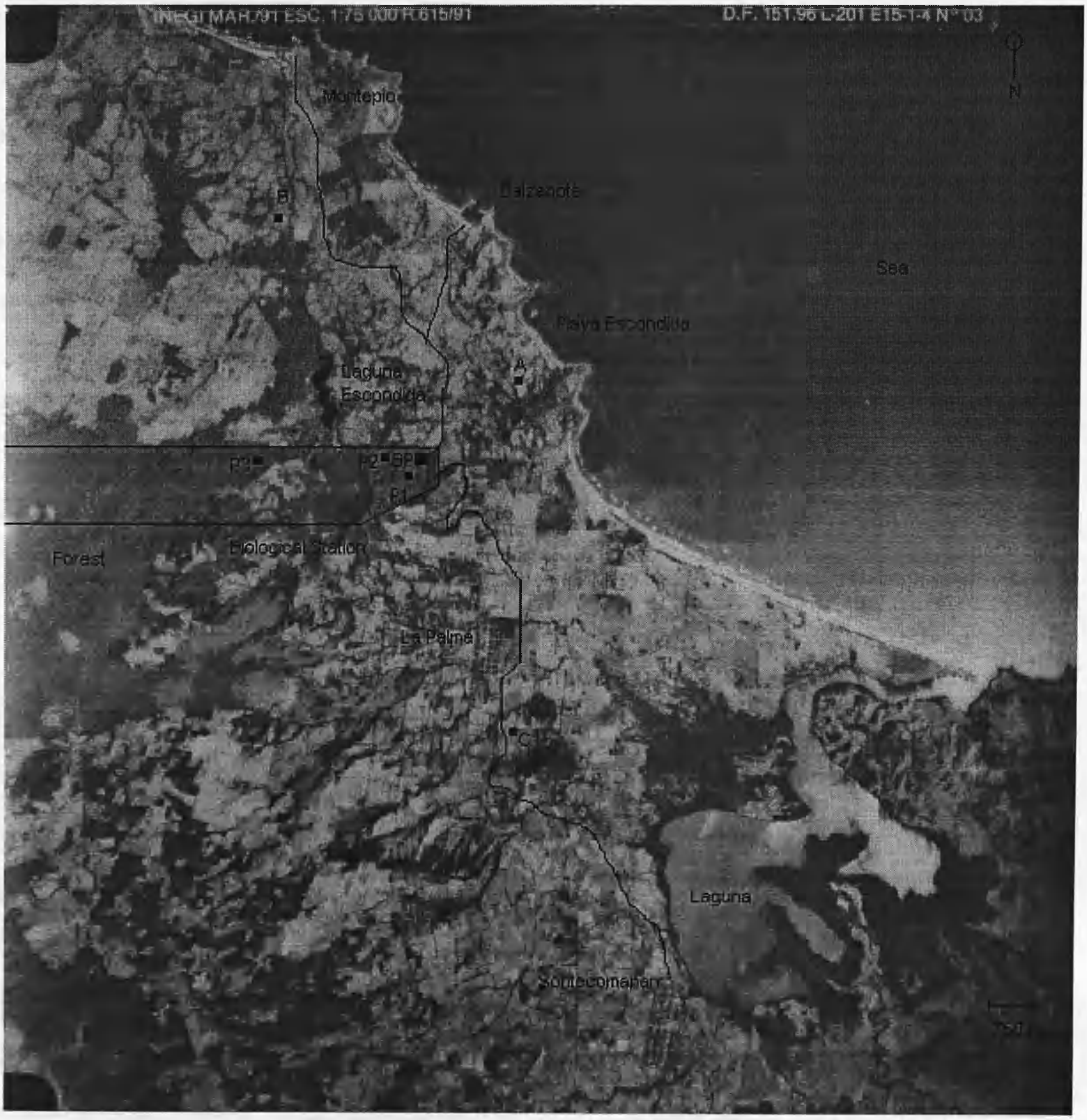


Figure 2.3. Location of plots 1- 3 (Forest), the plot (BP) of Bongers *et al.* (1988); and plots 4 -6 (12-yr pasture, A); plots 7 - 9 (32-yr pasture, B); and plots 10 - 12 (52-yr pasture, C). (__) rough road. Air photograph from Instituto Nacional de Estadística Geografía e Informática, 1991.

GEOLOGY

All the Los Tuxtlas volcanic field (18° 11' - 18° 41' N, 94° 38' - 95° 26' W) including the highest volcanoes of San Martin Tuxtla (1650 m) and Santa Marta (1460 m) lies over basaltic rocks erupted in two series. The older series dates from 1 and 3 million years ago, and the younger series from about 800,000 years ago (Nelson & Gonzalez-Caver 1992). The last eruptions of Volcán San Martin were in 1664 and 1793 (Friedlaender & Sander 1923 in Martin-Del Pozzo 1997). 'Eruptions have been mostly of the strombolian type, producing significant quantities of ash and a small volume of lava flows' (Nelson & Gonzalez-Caver 1992). The alkaline basaltic rocks from Los Tuxtlas have higher concentrations of K, Na and Ti than the calc-alkaline and andesitic basalts of the Mexican Volcanic Belt (Martin-Del Pozzo 1997).

Based on the geologic map of Nelson & Gonzalez-Caver (1992) most of the BS lies on the younger series, the 12-yr and 32-yr pastures on the older series, and the 52-yr pasture on a smaller area of quaternary alluvium substratum, at the northern limit of the Los Tuxtlas volcanic field.

CLIMATE

Temperature

Temperature data were available from the BS (110 m altitude) with some gaps in the records from 20 September 1988 to 25 May 1991 and from 10 April 1993 to 31 December 1997 (Table 2.1). The mean annual temperature is 25.1 °C, the hottest month is May with a mean temperature of 28.3 °C and a mean maximum of 32.2 °C; the coldest months are January and February with a mean of 21.5 °C and a mean minimum of 18.7 °C (Figure 2.4). The absolute highest and lowest temperatures recorded were 39.0 °C on 30 May 1990 and 12.0 °C on 16 December 1997.

Table 2.1. Number of daily records for minimum and maximum temperatures (°C) for the BS.

Year	Min.	Max.
1988	79	70
1989	299	287
1990	304	123
1991	108	43
1993	244	244
1994	343	343
1995	329	329
1996	355	355
1997	348	348
Total	2409	2142

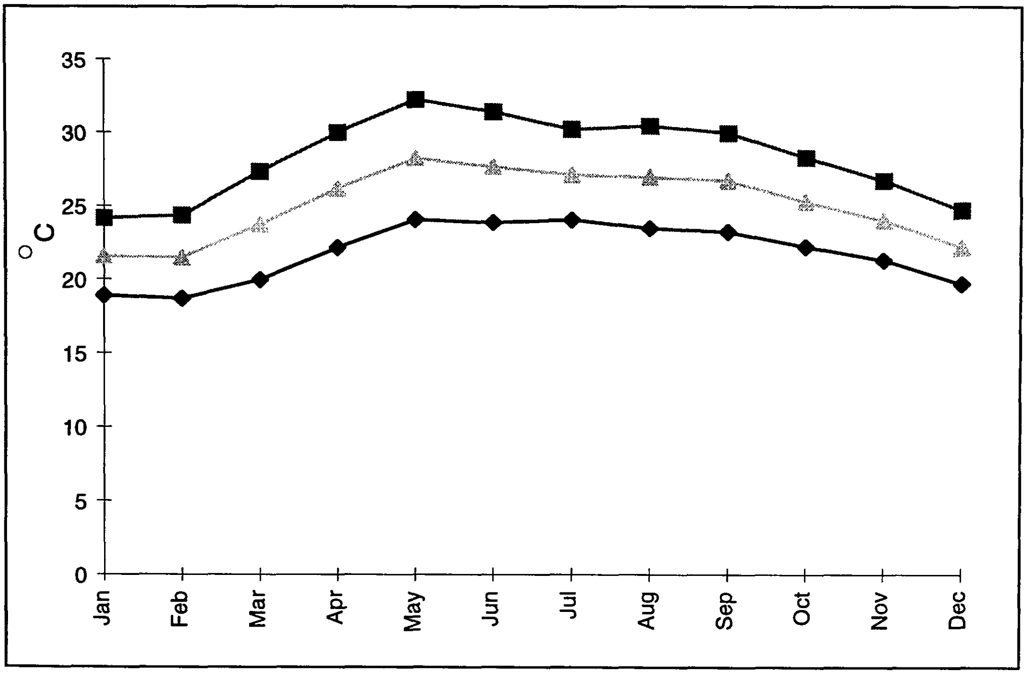


Figure 2.4. Mean monthly maximum, mean, and minimum temperatures at the BS from 1988-1997 (source: Data from the BS).

Rainfall

Mean annual rainfall at the BS from 1972 to 1997 (data missing for the complete years 1974, 1988 and 1989) was 4,487 mm. All the months June to January have a mean monthly rainfall of over 300 mm while February (261 mm), March (115 mm), April (97.5 mm), and May (105 mm) are drier (Figure 2.5). Of the annual total rainfall, 48% falls from August to November. Occasionally there have been months when the total rainfall exceeded 1,000 mm (July 1972, August 1973, October 1975, June 1978 and September 1991).

There are 157.4 rain (> 0 mm) days per year on average with a lowest mean of 5.7 rain days in May and a highest mean of 18.8 rain days in August (Figure 2.6). In the tropics the distribution of rainfall is as important as the total amount from the ecological point of view (Brinkmann 1985) and the number of rain days in drier spells can be crucial in preventing a shortage of water for plants (Davis & Richards 1933).

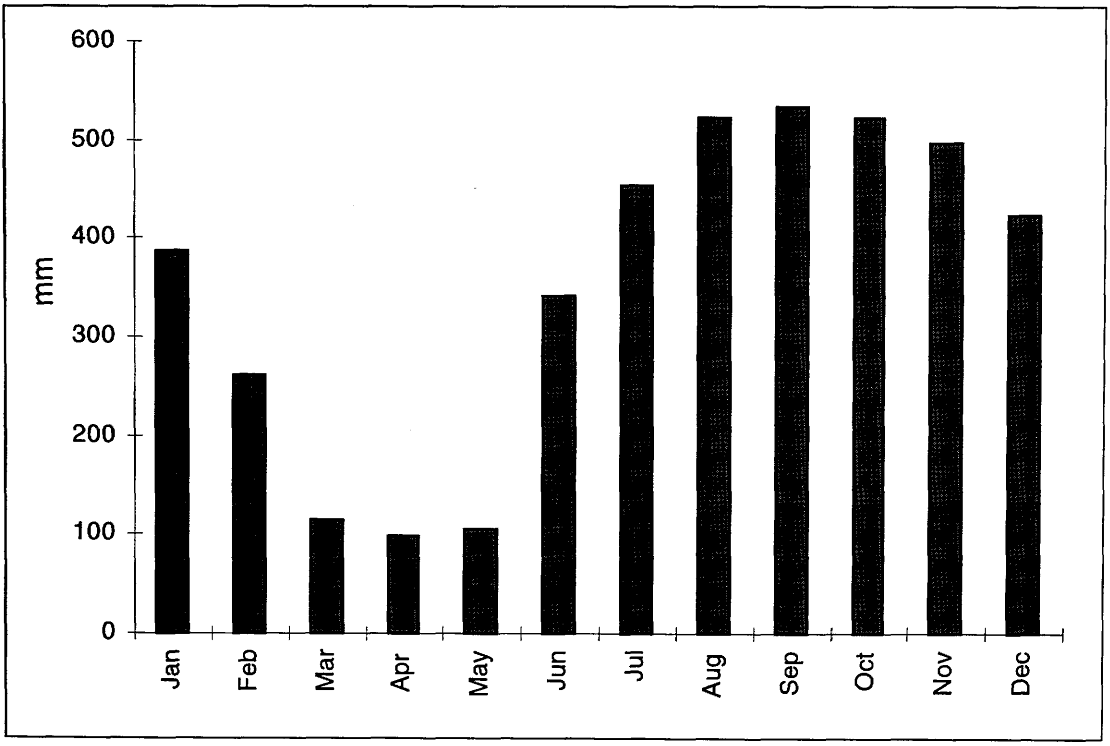


Figure 2.5. Mean monthly rainfall from 1972 to 1997 at the BS.

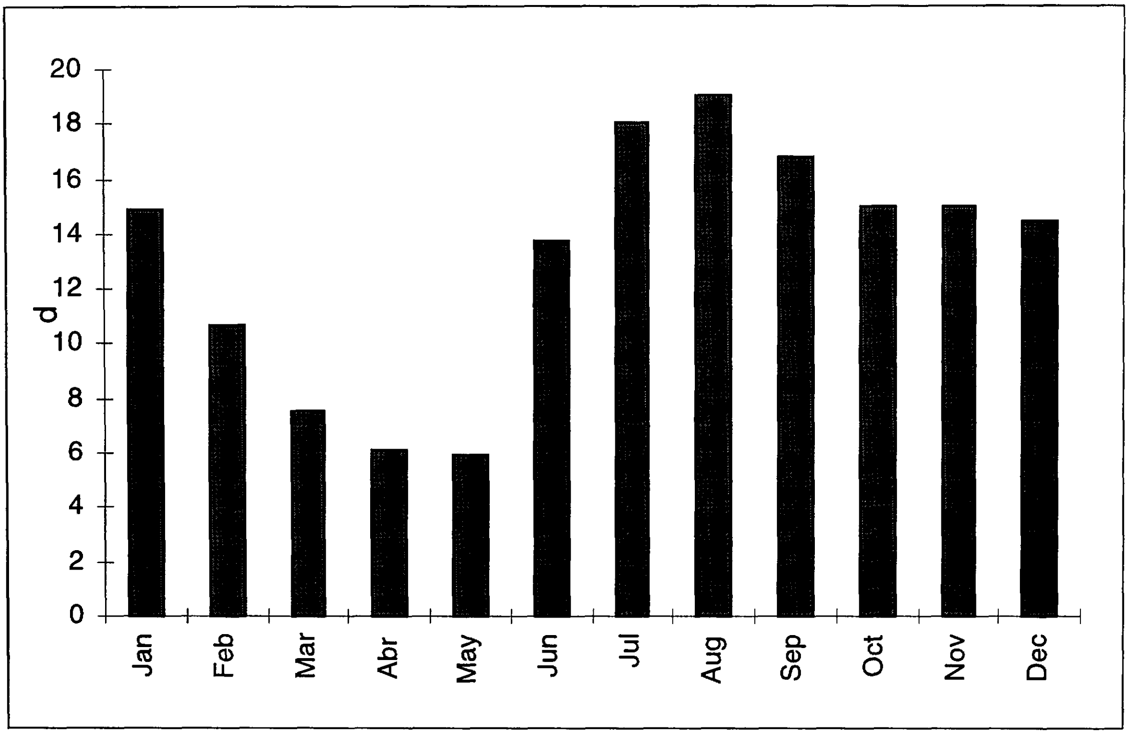


Figure 2.6. Mean monthly number of days with rain from 1983 to 1997 at the BS.

Wind

Wind speed and wind direction were estimated daily at 0800 hr at Sontecomapan (18° 31' N, 95° 02' W, and 86 m altitude) about 10 km SE from the BS from January 1976 to December 1997 by the Comisión Nacional del Agua, since no data were available for the BS. Wind speed was estimated using the Beaufort scale (Ahrens 1993).

For most of the time wind speed at outside the forest was between 2 and 11 km h^{-1}. July had the lowest wind speed (Figure 2.7). Dominant winds at Los Tuxtlas are chiefly from the SE (29.1%) and NE (27.3%), the former are distributed roughly evenly over the year and the latter prevail in summer (Figure 2.8). Summer NE-winds are responsible for the highest rainfall. The local opinion is that the strongest winds, called 'nortes', with speeds of up to 100 km h^{-1} (Bongers *et al.* 1988) are northerlies which occur from October to February. The 22-years data set at Sontecomapan shows a higher frequency of strong SE winds (measured at 0800 hr) during March, April and

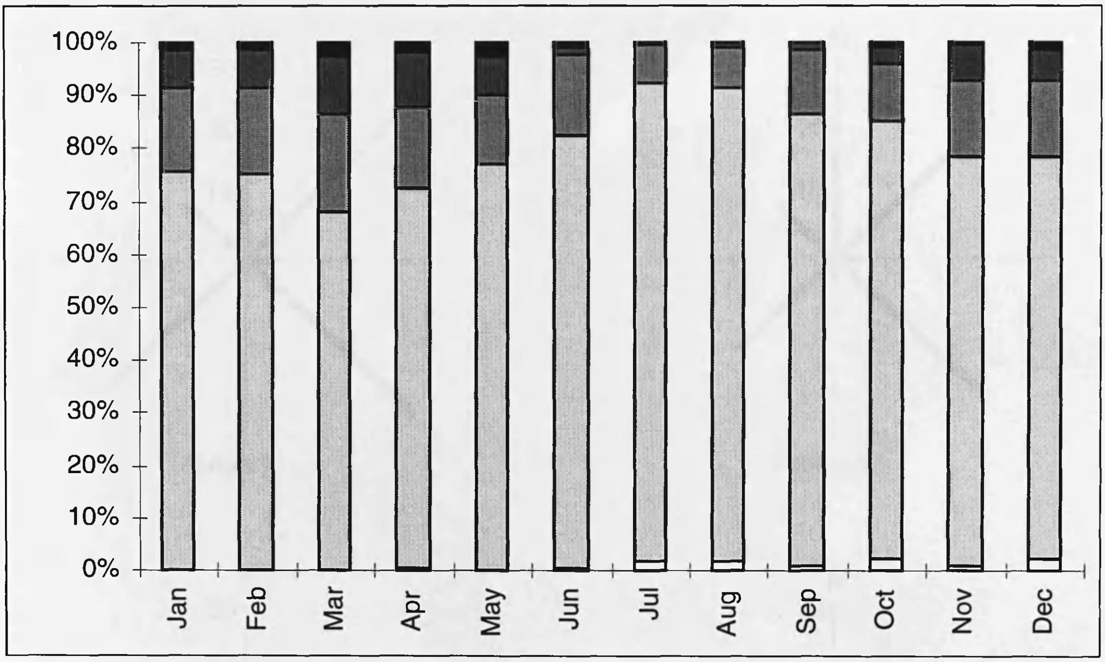
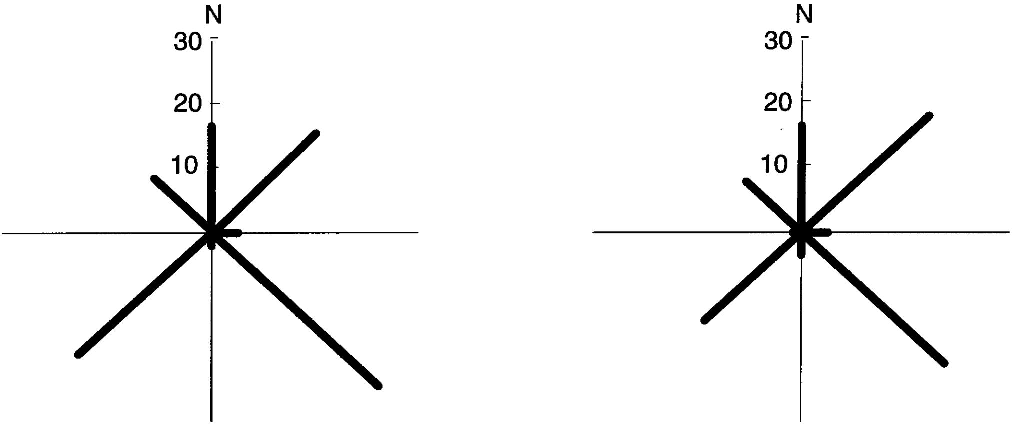


Figure 2.7. Mean monthly frequency of the wind speed at 0800 hr from 1976 to 1997 at Sontecomapan (10 km SE of the BS). □ = < 2 km h^{-1}, ▨ = 2-11 km h^{-1}, ▦ = 12-29 km h^{-1}, ▩ = 30-50 km h^{-1}, and ■ = 51-61 km h^{-1}.

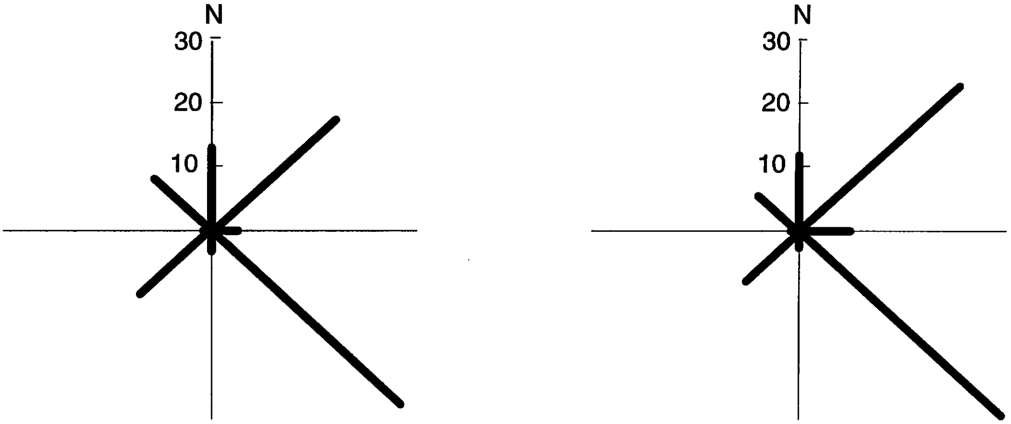
May, with speeds of 62-101 km h^{-1}. There are no records of hurricanes at this location, but at Veracruz City (*c*. 120 km NW) there was a storm in 1949 with winds of 128 km h^{-1}, and an hurricane in 1950 with winds of 175 km h^{-1} (Andrle 1964). However at the BS there are no patches of pioneer trees which might be expected to follow hurricane damage. Wind speeds have been measured in other lowland evergreen rain forests. Brinkmann (1985) measured a mean maximum speed of 2.4 km h^{-1} inside a forest in Amazonia at 1.2 m above the ground. Outside the forest at 12 m above sea level in Sabah, Malaysia, Proctor *et al.* (1988) measured a mean speed of 5.4 km h^{-1} with a maximum of 34.9 km h^{-1}. Between 1954 and 1975 the strongest wind recorded near sea level 100 km north was 76.3 km h^{-1} and the highest estimated once-in-fifty-years wind was 87.5 km h^{-1} (Proctor *et al.* 1988). Table 2.2 shows that the prevailing wind direction is different in the three localities around the BS.

The length of day from sunrise to sunset at 20° N has a maximum difference of 2.4 hr between summer and winter (Ahrens 1993).



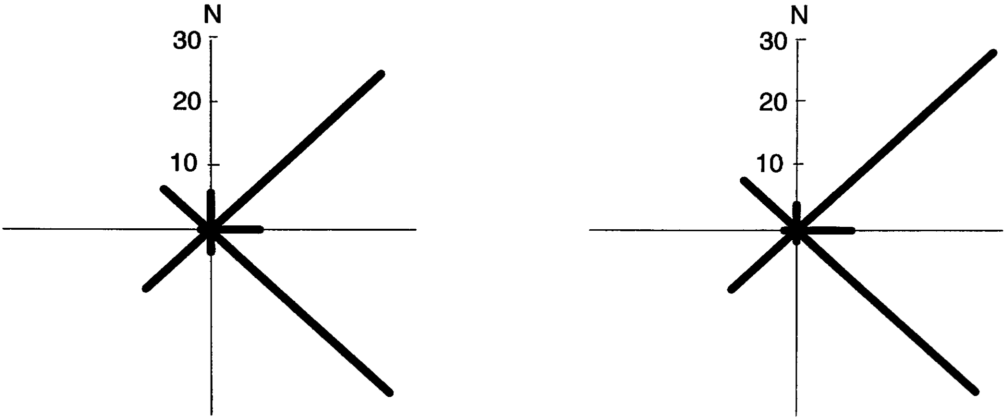
January

February



March

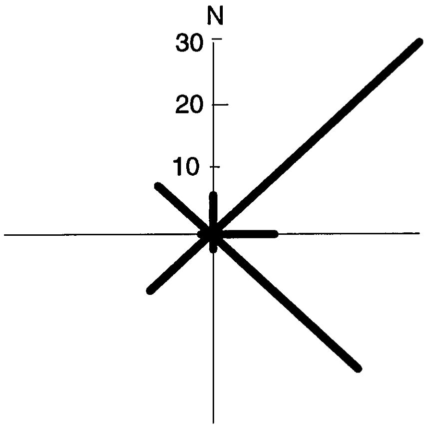
April



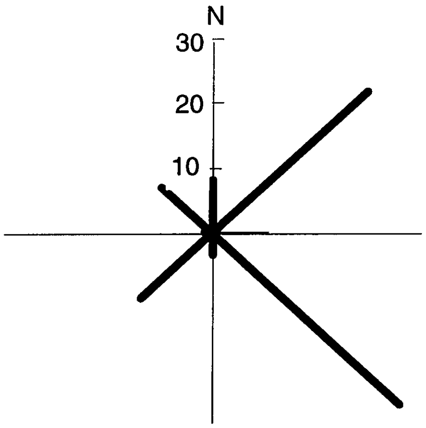
May

June

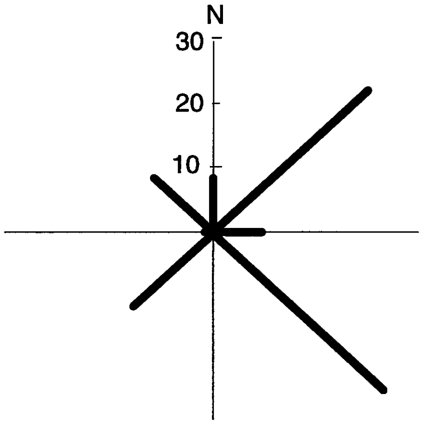
Figure 2.8. Annual percentage of wind direction at 0800 hr, from 1976 to 1997 at Sontecomapan (10 km SE from the BS).



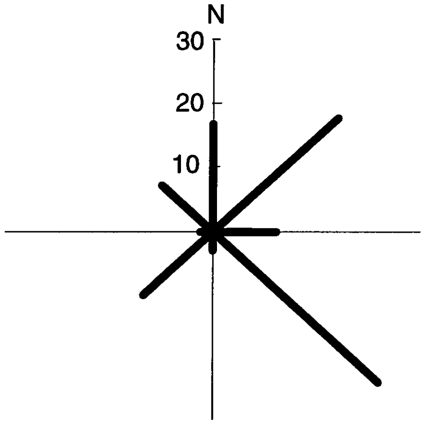
July



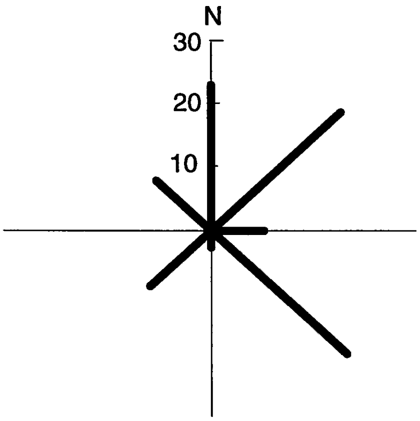
August



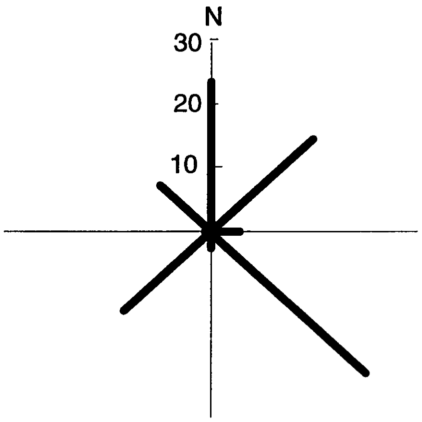
September



October



November



December

Table 2.2. Frequency of wind direction (%).

Station	N	S	E	O	NE	SE	NW	SW	Source
Catemaco	39	8	12	3	37	0.6	0.3	0	Soto & Gama (1997)
Coyame	34	15	36	0.5	13	0.5	0	1	Soto & Gama (1997)
Sontecomapan	12.4	2.4	6.3	0.7	27.3	29.0	8.4	13.4	Comisión Nacional del Agua

Chapter 3. THE FOREST PLOTS AT LOS TUXTLAS

INTRODUCTION

A description of the Los Tuxtlas forest has been provided by Bongers *et al.* (1988) from a 1-ha plot (BP in Figure 2.2). It was decided that this single sample should be supplemented and the forest structure and physiognomy described from a further three replicate plots from a wider area of the forest, which also formed part of the design of further work on the forest and pastures.

METHOD

For each of the plots 1 - 3 all trees, palms and lianas with a dbh ≥ 10 cm were numbered and tagged and the following data were collected for each individual: coordinates of positions within the plot, girth at breast height (1.3 m), maximum height of buttresses (≥ 1.3 m), species, leaf area calculated as maximum width x 2/3 length of blade to the base of the drip tip, and the presence of simple or compound leaf types. Multiple stems (≥ 10 cm dbh) from the same individual were considered altogether as a single individual. When there were buttresses (≥ 1.3 m height) present, the girth of the trunk was measured 10 cm above the top of the buttress. Leaf size was obtained from typical leaves taken from the bottom of the canopy (2 - 5 m) of the trees, except for those without low branches which were climbed to the lowest branch. When it was not possible to collect the leaf from a tree in the study plots, it was collected from another tree of the same species. Raunkiaer size classes as modified by Webb (1959) were used for classifying leaf size. Species determination was checked with the herbarium records of the BS. Species richness (S) was obtained as the number of species, and diversity calculated by three indices, Shannon - Wiener (H'), Simpson (C) and the Equitability (E):

1. $H' = - \Sigma (Pi) (\log_2 Pi)$

2. $C = \Sigma (Pi)^2$

where $Pi = n_i/N$; n_i = number of individuals of species i, and N = total number of individuals.

3. $E = H'/H_m$

where $H_m = \log_2 (S)$; S = number of species.

RESULTS

Plot 1 faced NE with a slope of 30 °, most of plot 2 faced NW with a slope 30 ° and the rest SE, and plot 3 faced NE with a slope 25 °. A total of 306 individuals $\geq$ 10 cm dbh were found with a total basal area of 24.9 m^2 for the three plots combined (0.75 ha). Mean basal area per individual ranged from 0.06 to 0.11 m^2 (Table 3.1). Only 2.0% of the individuals ($\geq$ 10 cm dbh) from the three plots were lianas, the rest were trees. Figure 3.1 shows that plots 2 and 3 had more individuals in the smallest diameter class than plot 1. There were 81 woody (75 trees and six lianas) species ($\geq$ 10 cm dbh) belonging to 38 families (Appendix 1). Species richness and diversity indices are shown in Table 3.2. Table 3.3 shows the family ranking by percent contribution to the basal area. Families having a relatively high proportion of compound leaves were the Meliaceae, Anacardiaceae and Fabaceae. Appendix 2 shows the corresponding species ranking.

Most of the leaves were mesophylls (58%). About 75% of the species and 82% of the individuals were simple-leaved and about 25% of the species and 18% of the individuals were compound-leaved (Table 3.4).

Table 3.1. Number of individuals (≥ 10 cm dbh) and basal area from three (0.25 ha) plots at Los Tuxtlas, México.

		Plot 1	Plot 2	Plot 3	Total
Total	Individuals	70	127	109	306
	BA (m^2)	8.0	8.1	8.8	24.9
Mean BA	individuals $^{-1}$	0.11	0.06	0.08	0.08
Trees	% Individuals	100	98.4	96.2	98
	% BA	100	99.6	99.3	99.7
Lianas	% Individuals	0	1.6	3.8	2.0
	% BA	0	0.4	0.6	0.3

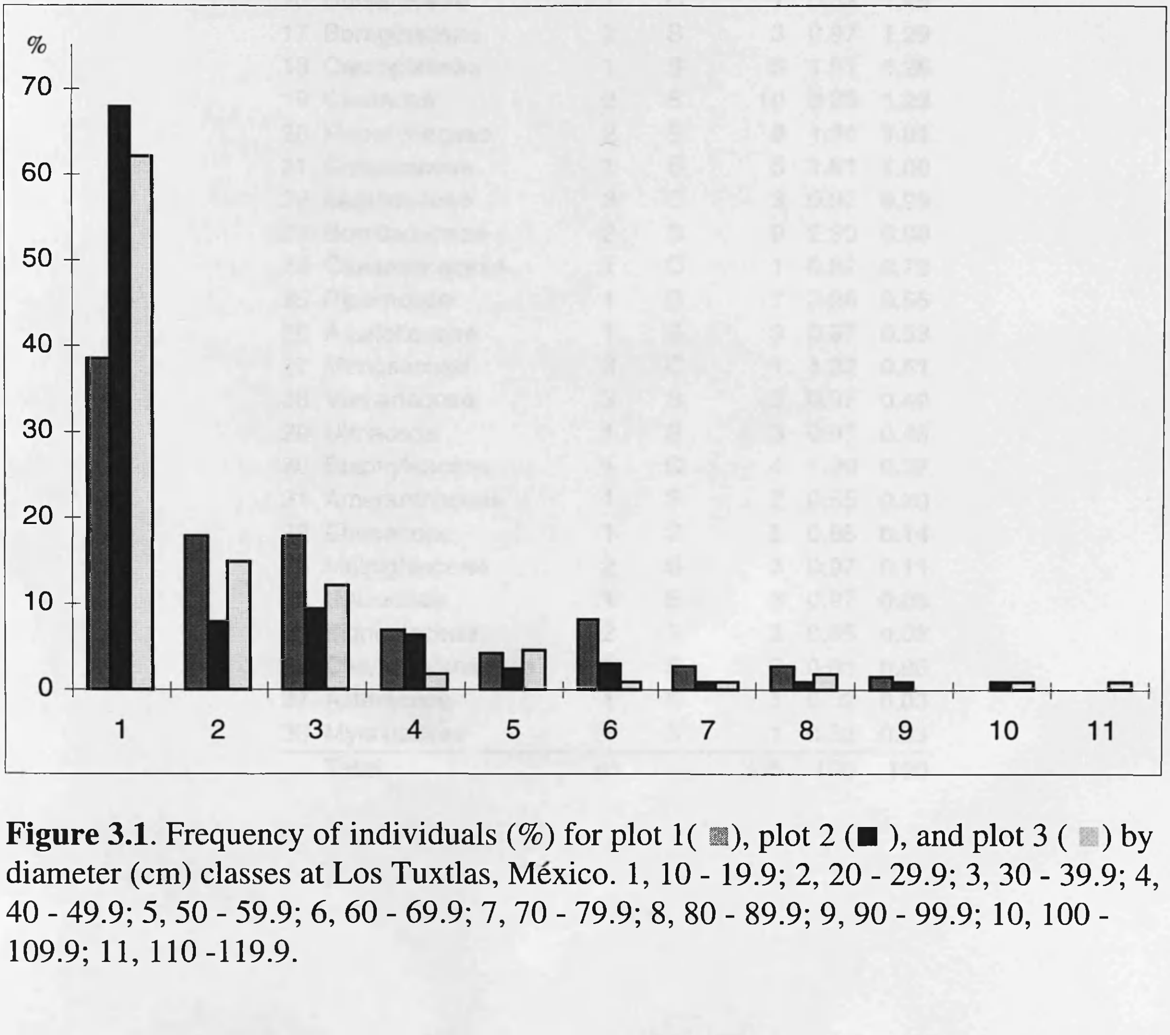


Figure 3.1. Frequency of individuals (%) for plot 1(▨), plot 2 (■), and plot 3 (▨) by diameter (cm) classes at Los Tuxtlas, México. 1, 10 - 19.9; 2, 20 - 29.9; 3, 30 - 39.9; 4, 40 - 49.9; 5, 50 - 59.9; 6, 60 - 69.9; 7, 70 - 79.9; 8, 80 - 89.9; 9, 90 - 99.9; 10, 100 - 109.9; 11, 110 -119.9.

Table 3.3. Family ranking for Los Tuxtlas based on percentage of basal area (BA). Number of species, trees (≥ 10 cm dbh), and percentage of trees from the total of the three plots (0.75 ha) for each family are also shown. T = leaf type of the species sampled: S, simple-leaved; C, compound-leaved.

	Family	Species	T	No. of trees	% of trees	% BA
1	Lauraceae	5	S	21	6.77	**19.62**
2	Moraceae	8	S	41	13.23	**13.27**
3	Fabaceae	4	C	7	2.26	**11.82**
4	Anacardiaceae	1	C	12	3.87	**11.08**
5	Euphorbiaceae	3	S	27	8.71	**5.83**
6	Meliaceae	3	C	14	4.92	**5.51**
7	Sapotaceae	6	S	12	3.87	**4.02**
8	Violaceae	2	S	20	6.45	**3.82**
9	Rubiaceae	3	S	43	13.87	**2.06**
10	Nyctaginaceae	2	S	3	0.97	**1.83**
11	Capparaceae	1	C	2	0.65	**1.77**
12	Annonaceae	3	S	11	3.55	**1.67**
13	Tiliaceae	2	S	4	1.29	**1.65**
14	Araliaceae	1	S	4	1.29	**1.61**
15	Apocynaceae	3	S	9	2.90	**1.47**
16	Burseraceae	1	C	1	0.32	**1.45**
17	Boraginaceae	2	S	3	0.97	**1.29**
18	Cecropiaceae	1	S	5	1.61	**1.26**
19	Clusiacae	2	S	10	3.23	**1.23**
20	Flacourtiaceae	2	S	6	1.94	**1.01**
21	Celastraceae	1	S	5	1.61	**1.00**
22	Sapindaceae	3	C	3	0.97	**0.99**
23	Bombacaceae	2	S	9	2.90	**0.98**
24	Caesalpinaceae	1	C	1	0.32	**0.72**
25	Piperaceae	1	S	7	2.26	**0.55**
26	Aquifoliaceae	1	S	3	0.97	**0.53**
27	Mimosaceae	3	C	1	1.32	**0.51**
28	Verbenaceae	3	S	3	0.97	**0.49**
29	Ulmaceae	1	S	3	0.97	**0.45**
30	Staphyleaceae	1	C	4	1.29	**0.27**
31	Amaranthaceae	1	S	2	0.65	**0.20**
32	Ebenaceae	1	S	2	0.65	**0.14**
33	Malpighiaceae	2	S	3	0.97	**0.11**
34	Urticaceae	1	S	3	0.97	**0.08**
35	Bignoniaceae	2	S	2	0.65	**0.08**
36	Chrysobalanaceae	1	S	2	0.65	**0.06**
37	Asteraceae	1	S	1	0.32	**0.03**
38	Myrsinaceae	1	S	1	0.32	**0.03**
	Total	81		306	100	**100**

Table 3.2. Diversity indices from three (0.25 ha) plots at Los Tuxtlas, México. A = the three plots together, B = for a 1-ha (BP) plot from Bongers *et al.* (1988).

	Plot 1	Plot 2	Plot 3	A	B
Individuals	70	127	109	306	359
Species richness	36	47	45	81	88
Shannon-Wiener index	5.0	4.68	5.04	5.48	5.31
Simpson index	0.14	0.08	0.04	0.04	0.05
Equitability index	0.97	0.84	0.92	0.86	0.82

Table 3.4. Percentage of individuals and species (≥ 10 cm dbh) in Raunkiaer leaf-size classes *; and simple and compound-leaves, from three (0.25 ha) plots at Los Tuxtlas, México. A, the three plots together; B, a 1-ha plot (BP) from Bongers *et al.* (1988).

		Plot 1	Plot 2	Plot 3	A	B
Leptophyll	Individuals	0	0	0	0	0
	Species	0	0	0	0	0
Nanophyll	Individuals	0	0	0	0	0
	Species	0	0	0	0.6	2.6
Microphyll	Individuals	4.3	4.0	2.7	3.3	5.0
	Species	4.3	4.0	2.8	3.6	9.0
Notophyll	Individuals	17.4	27.6	25.5	29.5	55.6
	Species	17.1	32.8	32.7	29.1	46.2
Mesophyll	Individuals	72.5	59.3	57.3	58.3	33.1
	Species	74.3	56.0	52.8	57.9	33.3
Macrophyll	Individuals	5.8	8.9	14.5	8.9	5.0
	Species	2.9	8.8	13	8.6	7.7
Megaphyll	Individuals	0	0	0	0	0.6
	Species	0	0	0	0	1.3
Simple	Individuals	74.3	87.4	80.7	82.1	81.4
	Species	74.3	77.3	75.6	74.4	73.1
Compound	Individuals	25.7	12.6	19.3	17.9	18.6
	Species	25.7	22.7	24.4	25.6	26.9

*) Leptophyll (< 0.25 cm^2), nanophyll (0.25 - 2.3 cm^2), microphyll (2.31 - 20 cm^2), notophyll (20.1 - 45 cm^2), mesophyll (45.1 - 180 cm^2), macrophyll (180.1 - 1,600 cm^2), megaphyll (> 1,600 cm^2).

DISCUSSION

The plots in this study were from a mature forest and similar to those described by Bongers *et al.* (1988). Plot 1 had no obligate gap and gap-dependent species, plot 2 had three individuals of Cecropia obtusifolia (obligate gap, *sensu* Popma *et al.* 1992) and one of Piper amalago (gap-dependent), and plot 3 had three individuals of C. obtusifolia, one Heliocarpus appendiculatus (obligate gap), one P. amalago and one Urera elata (obligate gap). Plot 1 can be considered as the most mature with the least stem density, highest basal area and absence of obligate gap species, and plots 2 and 3 less mature with a higher stem density, higher proportion of trees in the smallest diameter class, and the presence of obligate gap species.

The Los Tuxtlas forest is of relatively moderate stature (Table 3.5). It has a closed canopy at 30 - 35 m and few trees emerge above this, possibly owing to the frequent strong and cold northern winds during winter (Chapter 2, Bongers *et al.* 1988). Bongers *et al.* (1988) provided comparative values for rain forest structure elsewhere in the world (for trees ≥ 10 dbh): density ranged from 300 - 900 trees ha^{-1} and basal area from 24 - 58 m^2 ha^{-1}. Compared with these values the Los Tuxtlas forest has a low density (408, 359 trees ha^{-1}) and a low basal area (33.2, 34.9 m^2 ha^{-1}) (this study, Bongers *et al.* 1988).

Twenty one and a half percent of the trees had buttresses above 1.3 m which is similar to the value of 22.8% for a buttress height of > 0.5 and < 2.0 m reported by Pendry & Proctor (1997) in Brunei in a plot at 200 m altitude. For a plot at 100 m altitude on Volcán Barva, Costa Rica, Heaney & Proctor (1989) reported 23% of the trees with buttresses between 50 - 100 cm height and 6% above 1 m, whereas Lieberman *et al.* (1996) for the same altitude and location reported 32% of buttressing over 2 m height. Thompson *et al.* (1992) on Maracá Island, Brazil reported 11.9% of individuals with buttresses > 50 cm height.

Similar to other lowland evergreen rain forests elsewhere, Bongers *et al.* (1988) found that in plot BP for trees ≥ 10 cm dbh, 46.2% of the leaves (on a species basis) were in the notophyll class and 33.3% in the mesophyll class; whereas for my plots 1-3 the corresponding values were 29.1% notophyll and 57.9% mesophyll (Table 3.4). The higher proportion of larger leaves in my work may be due to sampling in the lower part of the canopy. Extreme sizes like leptophyll, nanophyll and megaphyll were less than 3% of the leaves (Bongers *et al.* 1988). The percentage of compound-leaf species at Los Tuxtlas (25.6% in this study and 29.2% in Bongers *et al.* 1988) is in the middle range (13 - 47.6%) of tropical rain forests around the world (Bongers *et al.* 1988). The percentage of deciduousness is in the middle range also (Table 3.7). Compound leaves and deciduousness are partly seen as adaptations to seasonal drought (Givnish 1978) but droughts are short at Los Tuxtlas where the majority of the species (69.7%) are simple-leaved and evergreen. Of the remaining species 19.7% are compound-evergreen, 4.9% are simple-deciduous, and 5.6% are compound-deciduous (Bongers *et al.* 1988). For trees dbh ≥ 30 cm the proportions of deciduous and compound-leaved species were 15% and 32.5% (Bongers *et al.* 1988).

For trees ≥ 10 cm dbh I (0.75 ha) found similar values to Bongers *et al.* (1988) (1-ha plot) for species richness (81 *vs.* 88) as well as diversity indices (H' = 5.48, C = 0.04 and E = 0.86; *vs.* H' = 5.31, C = 0.05 and E = 0.82) (Table 3.2). Compared with other lowland tropical forests in general H′ and E at Los Tuxtlas were lower, and C higher (Table 3.6). Forests from Asia and South America show the highest diversities (Richards 1996). Ibarra-Manríquez & Sinaca (1995, 1996a, 1996b) in a survey of over 640 ha at the BS have found around 380 species of trees (≥ 2 m height) and lianas (probably many below 10 cm dbh), whereas Lieberman *et al.* (1996) in a census of a 23.4 ha plot at 100 m altitude on Volcán Barva, Costa Rica found 561 species with stems ≥ 10 cm dbh.

The description in this study from three plot replicates on a wider area of the reserve matched the description of Bongers *et al.* (1988) from a single 1-ha plot. The forest at Los Tuxtlas is considered as a tropical lowland evergreen rain forest (*sensu* Richards 1996), from its general structure, physiognomy, and evergreen trees, and compared with tropical rain forests elsewhere the forest has: similar leaf physiognomy with a preponderance of mesophylls, a lower tree species diversity, a lower density, and a lower basal area.

Table 3.5. Comparison of canopy height in lowland evergreen tropical rain forests.

	Location	Canopy height (m)	Tallest trees (m)	Author
Africa	Nigeria	37 - 46	47.1- 62	Richards (1939)
America	Guyana	35	42	Davis & Richards (1933)
	Brazil	26-36	40	Thompson *et al.* (1992)
	Costa Rica	35 - 40	50	Grieve *et al.* (1990)
	México	30 - 35	40	Bongers *et al.* (1988)
	México	20 - 40	44 - 46	Meave (1990)
Asia	Malaysia	34	45.7, 61	Richards (1936)
	Malaysia	30 - 40	57.5	Proctor *et al.* (1983a)
	Malaysia	30 - 35	49	Proctor *et al.* (1988)
	New Guinea	26 - 35	46 - 67	Paijmans (1970)
	Borneo, East Kalimantan	30 - 55	70.7	Yamakura *et al.* (1986)
	Brunei	30 - 50	60	Pendry & Proctor (1997)

Table 3.6. Comparison of diversity components (for individuals dbh ≥ 10 cm) in several lowland rain forests.

Location	Prec. (mm)	Area (ha)	Number of species			Shannon-Wiener index			Equitability index			Simpson index			Author
				A	B		A	B		A	B		A	B	
Los Tuxtlas	4,487														
Brazil		1	108	79		6.23	5.17		0.92	0.82		0.03	0.06		Pires *et al.* (1953)
Brazil		1	87	79		5.37	5.17		0.83	0.82		0.04	0.06		Black *et al.* (1950)
Costa Rica		1	115	79		3.97	5.17								Lieberman *et al.* (1996)
Malaysia	4,100	0.75	168		81	4.15		5.48							Pendry & Proctor (1997)
Nigeria	2,080	1.5	34, 42, 70												Richards (1939)
Venezuela (means of two plots)		0.5	71	54.5	59	5.35	4.89	5.03	0.87	0.85	0.85	0.04	0.06	0.05	Uhl & Murphy (1981)
Venezuela (Plot C)		1	83	79		4.8	5.17		0.75	0.82		0.08	0.06		Uhl & Murphy (1981)

The column A (Bongers *et al.* 1988) and B (this study) compares the values of Los Tuxtlas with the other locations (previous column) for the same area. Areas from column A values are 0.5 and 1 ha, and from column B, 0.75 ha and 0.5 ha (considering plots 1 and plot 2 together).

Table 3.7. Percentage of deciduous species and individuals in several evergreen lowland tropical forests.

Location	Limit	Species (ind)	Author
México	≥ 10 cm dbh	16.7 (10.1)	Bongers *et al.* (1988)
	≥ 15 cm dbh	15	
Brazil	≥ 10 cm dbh	(5.7)	Thompson *et al.* (1992)
Costa Rica	upper storey	27	Frankie *et al.* (1974)
	total	17	
Panama	n.d.	20	Croat (1978)
Ghana	≥ 10 cm dbh	(19, 22)	Hall & Swaine (1976)

n.d. = no data.

Chapter 4. SOIL NUTRIENTS IN THE FOREST AND PASTURES

INTRODUCTION

SOIL NUTRIENTS

The soil chemical characteristics analysed in this study were: pH_{H2O}, pH_{KCl}, total nitrogen, exctractable phosphorus, exchangeable potassium, sodium, calcium, magnesium, aluminum, hydrogen ion and cation exchange capacity. The mineral-elements are absorbed by plants as cations and anions from the soil solution as: ammonium $(NH_4)^+$, nitrate $(NO_3)^-$, phosphate $(H_2PO_4)^-$, and the bases K^+, Na^+, Ca^{2+}, Mg^{2+}, and Al^{3+} (Tivy 1990). The hydrogen ion does not exist as a free proton (H^+) in solution but rather is combined with at least one molecule of water forming the oxonium or hydronium ion, H_3O^+. The cation exchange capacity (CEC) is the capacity of the soil colloids to retain cations (Tivy 1990).

Free elements in the soil solution have two major sources: rock weathering and organic matter. 'From 16 elements known to be essential for plant growth, 13 come from the soil, and all of them, except N, originate in the mineral reserve' (Weischet & Caviedes 1993). Unfortunately only total nitrogen could be measured in this study because of an equipment failure with the $(NO_3)^-$ and $(NH_4)^+$ autoanalyzer. This nitrogen would only be available over the long term but the measured extractable P, K^+, Ca^{2+} and Mg^{2+} reflects pools which plants may draw on immediately (Nye & Greenland 1960) and are required in relatively large quantities. K^+, Ca^{2+} and Mg^{2+} are essential elements but unlikely to be limiting growth, and Na^+ is generally not an essential element (Grubb & Edwards 1982).

Nutrient stocks of an ecosystem depend on the soil parent material and then on the nutrient cycling between the vegetation and soil (Nye & Greenland 1960). Nutrient cycling in an ecosystem involves inputs and outputs. Inputs include atmospheric depositions from rain and dust, mineral weathering, and microbial fixation; and outputs include harvesting, soil leaching, soil erosion, water run-off, and denitrification. There are two types of nutrient cycles in tropical rain forests. The 'closed' cycle operates in leached soils and is often associated with much nutrient storage in the aerial biomass and dense shallow root systems with much mycorrizal infection (Buschbacher 1987b, Buschbacher *et al.* 1988, Jordan 1987, Saldarriaga 1987, Scott 1987, Kellman 1989, Medina & Cuevas 1989, Baillie 1996). In such a forest type in Venezuela from the total ecosystem (vegetation plus soil), 44.0% of N, 75.7% of K, 86.9% of Ca, and 76.4% of Mg, are contained in the biomass (Jordan 1989). In Brazil, Klinge & Rodriguez (1973) and Klinge *et al.* (1975) estimated 91.4% of P, 90.5% of K, 88.8% of Ca, and 93.8% of Mg were in the biomass. More open nutrient cycles in forests on less nutrient-deficient soils such as andosols (Jordan & Herrera 1981, Golley 1986, Bruijnzeel 1990) are associated with less nutrient storage in the biomass (Whitmore 1984), little accumulation of litter, and deeper root systems possibly with less dependence on mycorrhizas particularly for P (Janos 1983).

From several lowland rain forests listed by Proctor (1987) mineral stocks in the biomass are in the following sequence: N and Ca > K > Mg > P. In a montane rain forest, stems accounted for the greater proportion (60 - 70%) of this nutrient pool, then roots and then leaves; and 61 - 82% was in the trees gbh > 30 cm, 4 - 12% in the trees gbh < 30 cm, shrubs, saplings, climbers and scramblers; 1 - 5% in the epiphytes and ephiphytic soil; and 4 - 22% in the floor litter, dead trunks and branches (Grubb & Edwards 1982).

A major cause of tropical rain forest loss has been shifting cultivation which may or may not be followed by conversion to grassland. When tropical forests are cut and burnt many nutrients stored in the biomass are added to the soil in the form of carbonates in the ash, thus increasing soil pools (Nye & Greenland 1960, Brinkmann & Nascimento 1973, Scott 1978, Ewel *et al.* 1981, Uhl *et al.* 1983, Werner 1984, Richards 1996). The carbonates cause the soil pH to rise (UNESCO 1978). Elements like N, C and S are released to the atmosphere by volatilisation (Nye & Greenland 1960). The newly added soil nutrients may be removed by erosion and leaching, thus causing nutrient loss and reaching the original nutrient levels of the pre-disturbed forest (Nye & Greenland 1960, Sanchez 1976, Richards 1996). Losses by erosion and leaching after burning a lower montane forest in Costa Rica accounted for 51% of the P, 45% of the Ca, and 40% of the Mg of the preburn forest including above ground biomass, soil and roots up to 3 cm deep. In the top 3 cm soil 20% of P, 41% of Ca and 45% of Mg, remained (Ewel *et al.* 1981). In many forest soils it seems that the availability of N, P and K^+ may soon limit crop growth (Nye & Greenland 1960, Uhl *et al.* 1983, Jordan 1989). In poor tropical soils repeated cropping is not possible unless the soil is fertilized or long fallows are permitted (Nye & Greenland 1960). Studies on tropical pasture development after forest conversion and the effect of time on the soil nutrient status were started in the neotropics by Daubenmire (1972), and Krebs (1975), and then followed by Falesi (1976), Sanchez (1976), Scott (1978) and Serrão *et al.* (1978).

Generalizations about the relative nutrient status of forests and pastures are difficult. Table 4.1 shows the main processes that contribute to higher soil nutrient concentrations in the forest than in the pastures, and those that contribute to higher soil nutrient concentrations in the pastures than in the forest.

There are considerable sampling problems associated with the selection of pastures for research. It is very difficult to get pastures which differ only in the age factor which is being studied. Observations will usually be confounded by different parent materials and perhaps fertiliser treatments. In the case of the Los Tuxtlas the geologic map of Nelson & Gonzalez-Caver (1992) was used to help select the study sites (Chapter 2). The forest plots lie over the younger volcanic series, the 12-yr pasture and the 32-yr pasture on the older volcanic series, while the 52-yr pasture lies on a quaternary alluvium stratum.

Table 4.1. Processes that contribute to higher soil nutrient concentrations in the forest than in the pastures, and those that contribute to higher soil nutrient concentrations in the pastures than in the forest.

Processes that contribute to a higher soil nutrient concentrations in the forest than in the pastures:

1. There is a higher atmospheric nutrient interception in the forest canopy (Richards 1996) than in the pastures (Kellman 1989).
2. In the forest a higher percent of rainfall returns to the atmosphere via interception and evapotranspiration minimizing water infiltration and nutrient leaching (Denslow 1987, Richards 1996).
3. The pumping water process of woody plants from the lower profiles reduces nutrient leaching (Grubb 1989).
4. Higher amounts of litter in the soil retain more water reducing nutrient leaching (Nye & Greenland 1960).
5. In the pastures there is a continuous nutrient output from cattle removal.

Processes that contribute to a higher soil nutrient concentrations in the pastures than in the forest:

1. Addition of ash from burning the forest.
2. Root density in the upper profile is higher in the pastures than in the forest.
3. Conversion from forest decreases soil mixing by fossorial arthropods, earthworms and small mammals (Clark 1990). Higher soil compaction may reduce infiltration and percolation rates (Reiners *et al.* 1994) and hence nutrient leaching.

THE STUDY PASTURES

Accurate information about the history of the pastures is more difficult to obtain with their increasing age and number of owners. However some reliable information was obtained for the sites by talking with the owners: Luis Juan Arguelles at Balzapote (the 12- and 32-yr pasture), and Homero Couvert at La Palma (the 52-yr pasture). Livestock on these pastures was mostly a mixture of Swiss and Zebu races used for milk and beef production. Flat sections of the pastures in the region are sometimes cultivated with crops depending on the wealth of the owner and when cultivation takes place in 'winter' (November to February) production is always lower. The location of the pastures was described in Figure 2.3 and their slopes and aspects are given in Table 4.2.

Table 4.2. Maximum slope of the terrain of the three pastures of different ages at Los Tuxtlas, México.

	12-yr			32-yr			52-yr		
Plot	4	5	6	7	8	9	10	11	12
Maximum slope (°)	30	44	23	3	4	24	2	5	3
Direction	SW	SE	SE	W	SW	SW	NE	NE	NE

12-yr old pasture. This pasture was on the SW side of a hill around 0.5 km from the sea at 80 m altitude, and 200 m below a forest fragment. The forest was cut and burned in 1985. During 1985 and 1986 maize was grown on the site and then left fallow from 1987 to 1990. In 1990 and 1991 more maize was obtained after burning the fallow and in 1992 the land was sown with the grass, Cynodon plectostachyus. Herbicides were used during the maize growing. No fertilizer was applied at any time. The pasture was 15 ha in total and was located in hilly terrain. Four hectares were used for setting up the three plots one each on a hill top, slope and depression. Cattle density in the pasture was between one (dry season) and three (wet season) cows ha^{-1}.

32-yr old pasture. This pasture was located at 30 m altitude at *c.* 750 m from the rough road to Montepio at about 2 km N from an intersection of a road to Balzapote village (Figure 2.3). The plots were located in a stratified random way within the 20-ha pasture. Plots 7 and 9 were on flattish ground, and plot 8 was located on a slope.

When the forest was cut and burned the plots were cultivated with maize for two (plot 8) and three (plots 7 and 9) years, and then left to pasture with the native species Paspalum conjugatum, and Cynodon plectostachyus which were sown. Plot 7 has been cultivated several times with three-month crops. One crop of peanuts (Arachis hypogaea) and another of chili (Capsicum annuum) were harvested at ten-year intervals each, and two of peanuts and maize in the last five years. On the wet season an average of 2 to 3 t ha^{-1} of maize was obtained and about 700 - 800 kg ha^{-1} during winter. No fertilisers were ever applied. The rest of the time the plots have been pasture without any fallow and burning.

The pasture now has around four cows ha^{-1} in the rainy season (June to October) and one cow ha^{-1} in the dry and 'winter' season (November to February) with Paspalum conjugatum grass, and around 5 cows ha^{-1} in the rainy season and 2 to 3 cows ha^{-1} in the dry and 'winter' season with Cynodon plectostachyus where present. The cattle need 3 years to reach the market weight of 380 - 600 kg depending on the race. Milk production is 3 - 4 l day^{-1} cow^{-1}.

52-yr old pasture. The pasture is located next to the road about 800 m from La Palma in the direction of Catemaco town at 20 m altitude (Figure 2.3). The pasture is 25 ha and the plots were set up in treeless areas. When first cut, a couple of maize crops were grown and the land left to pasture. At first there were native grasses and then Cynodon plectostachyus was sown. There are currently 3 cows ha^{-1} during winter and 4 cows ha^{-1} during summer. Cattle for beef production are reared in the pastures until they are 3 years old and most of them get to the pasture at the age of 10 months, thus in little more than 2 years they gain 400 kg in body weight. Cattle for milk production give an average of 6 l daily. Since this is a flat pasture some sections are usually cultivated. Maize production is about 3 t ha^{-1}. Old pastures like these are difficult to maintain without further human input. The pasture has never shown any evidence of nutrient limitation though it has been fertilised to improve production in the last three years with 120 kg ha^{-1} of P, N and K each, and 700 kg ha^{-1} of urea as nitrogen for chili (Capsicum annuum), maize (Zea mays) and melon (Cucumis melo) cultivation.

The aim of the work described in this chapter was to analyse some physical and chemical soil properties in the forest, and in the pastures as the time of use increases. It was expected to find the lowest soil nutrient concentrations in the oldest pastures.

METHODS

During May 1996 and October 1996 ten soil samples (0 - 10 cm deep) were collected in a stratified random way with a 8-cm diameter soil corer from each of the twelve plots. For soil nutrient analyses the samples were immediately air-dried, and then passed through a 1.2-mm mesh. Samples were kept in polythene bags at 20 °C until the laboratory analyses. For soil bulk density analyses, samples were oven-dried at about 95 °C to a constant weight and weighed to obtain the dry weight per unit volume (g cm^{-3}). Soil texture and bulk density were not analysed for all the samples owing to time limitation.

Soil analyses were made in the Instituto de Geologia of the Universidad Nacional Autonoma de México. Analyses were all made in duplicate and checked with international standards. pH was determined in H_20 and in a 1 M KCl solution. For total N analyses the samples were digested with sulphuric acid, distilled in boric acid and determined by titration with 0.1 M sulphuric acid (the Kjedahl method). P was extracted by 0.025 M HCl and 0.03 M NH_4F and determined by photocolorimetry at

660 mμ. Exchangeable cations were extracted by 1 M amonium acetate and by centrifugation for 5 min at 2500 rpm. Ca^{2+} and Mg^{2+} were determined by atomic absorption spectophotometry in 0.5% lanthanum chloride solution, and K^+ and Na^+ by flame photometry in a $CaCl_2$ solution. Exchangeable Al^{3+} and H^+ ions were determined by titration with 0.01 M NaOH in a solution of 1 M KCl. Cation exchange capacity (CEC) was assessed by the summation of exhangeable cations. Soil texture was determined by a hydrometry technique (Bouyoucos 1963) and the soils were not completely dried according to the method for andosols (Silvia Sanchez, personal communication).

Statistical analyses were made with Minitab release 11.12 and exclude the 52-yr open-pasture since it has been fertilised. Student's t-test for equal and unequal variance, one-way ANOVA and linear regression analyses were applied. A Tukey means comparison test was applied to the ANOVA results. $\log_e$ and χ^2 transformations were applied when necessary (Zar 1984). When data did not match the assumptions for a parametric test, a non-parametric Mann-Whitney test (for two samples) and a Kruskal-Wallis test for three or more samples were used. In the latter, a Tukey medians comparison test was applied (Zar 1984). A Student-t test was made for mineral concentrations in relation to the slope of the terrain. For this I selected two plots with a gentle slope and two on a steep terrain from the 12-yr and 32-yr open-pastures. The slope values were: 3° (32-yr pasture), 4° (32-yr pasture), 24° (32-yr pasture) and 44° (12-yr pasture).

RESULTS

PHYSICAL PROPERTIES

The forest soil had similar amounts of silt, clay and sand, the soil in the 12-yr pasture had a major proportion of silt, that in the 32-yr pasture had a major proportion of silt and clay, and that in the 52-yr pasture a major proportion of sand (Table 4.3). The forest had a clay clay-loamy soil, the 12-yr pasture mainly a clay loam with a lower proportion of clay and sandy silt loamy soil, the 32-yr pasture a clay clay-loamy soil with a lower proportion of silty clay soil, and the 52-yr pasture, a mainly clay loamy soil. The forest had a significantly lower (median 0.75 g cm^{-3}) soil bulk density than the open-pastures where there were no changes with the increasing age of the sites (Table 4.4).

Table 4.3. ANOVA for mean percentage of the soil textural analysis by the UK classification system. Different superscript letters indicate a significant difference within a row (Tukey test, $p \leq 0.05$).

	Forest	12-yr pasture	32-yr pasture	52-yr pasture	p =
Clay	33.8^{ab}	28.3^{a}	36.6^{b}	27.7^{a}	0.0001
Silt	31.9^{a}	40.1^{b}	37.2^{b}	30.9^{a}	0.0001
Sand	34.3^{a}	31.5^{ab}	26.2^{b}	41.4^{c}	0.0001
n	26	22	23	25	

Table 4.4. Kruskall-Wallis test for the soil bulk density (g cm^{-3}) of the forest and the pastures of different age ($p = 0.0001$). Different superscript letters indicate a significant difference (Tukey test, $p \leq 0.05$).

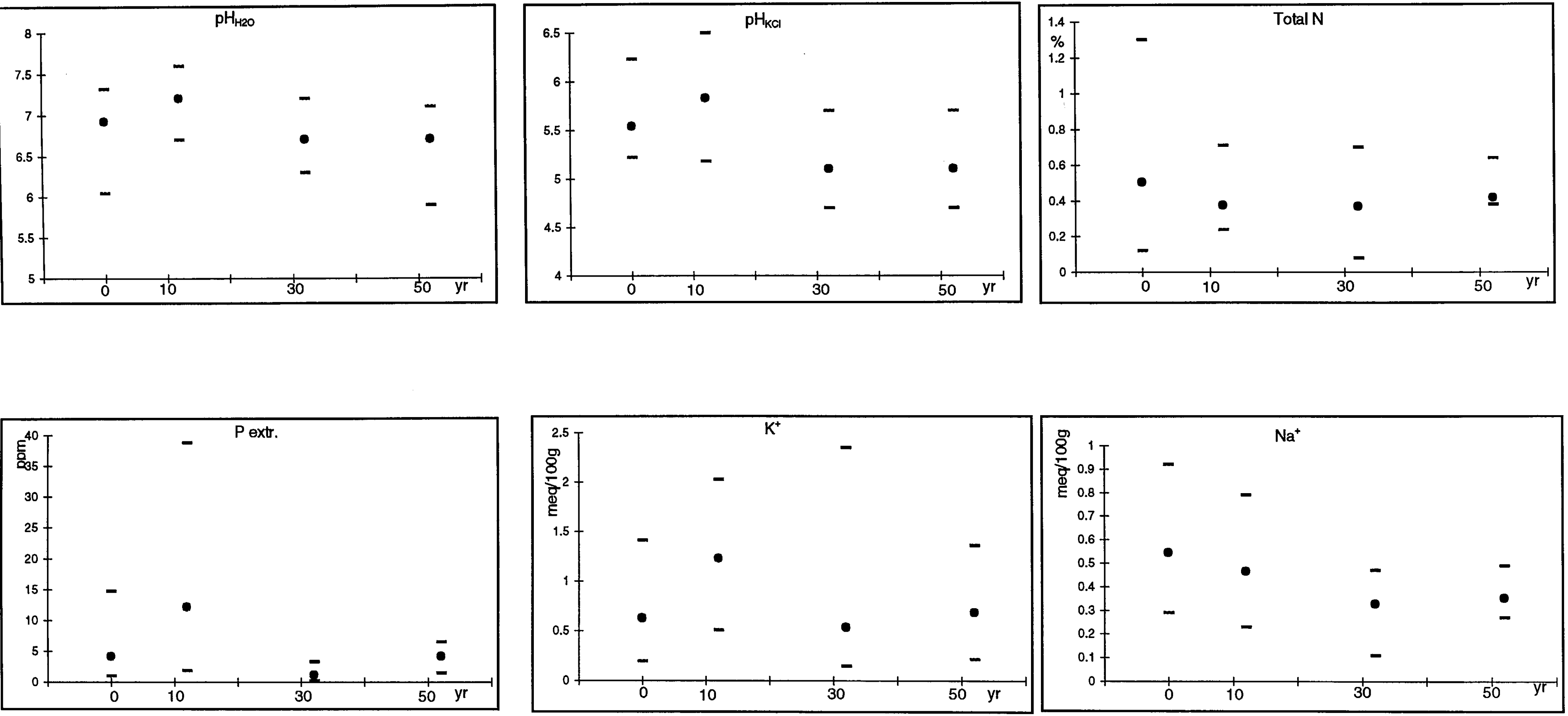
Groups	Sample	Median	Min	Max
Forest	30	$0{,}75^{a}$	0.357	1.091
12-yr pasture	25	$0{,}98^{b}$	0.794	1.112
32-yr pasture	30	1.00^{b}	0.741	1.144
52-yr pasture	30	1.00^{b}	0.844	1.321

CHEMICAL PROPERTIES

Table 4.5 shows the results of the soil chemical analyses. The lowest values of Mg^{2+}, H^+ and Al^{3+} were found in the forest and the 12-yr pasture, of pH in the 52-yr pasture, and for the rest of the elements in the 32-yr pasture. The highest values for N, Na^+, Ca^{2+}, H^+, Al^{3+} and CEC were found in the forest, for pH and P in the younger pasture, and for K^+ and Mg^{2+} in the 32-yr pasture. Mineral elements mostly had within-site coefficients of variation higher than 20%, with extractable P, K^+ and Al^{3+} around 90%. pH was the only factor with a low coefficient of variation (< 6%). Coefficients of variation by site were roughly similar for all the elements with the exception of K^+ which was more variable in the 32-yr pasture, and Al^{3+} in the forest and young pasture.

Table 4.5. Mean, minimum value, maximum value, and coefficient of variation (%) of the soil characteristics at Los Tuxtlas, México, from the forest and open-pastures of different ages. Overall minimum and maximum values are in bold. n = 30.

		pH H_20 (1:2.5)	pH KCl (1:2.5)	N total (%)	P Bray ($\mu g\ g^{-1}$)	K^+ (meq/ 100g)	Na^+ (meq/ 100g)	Ca^{2+} (meq/ 100g)	Mg^{2+} (meq/ 100g)	Al^{3+} (meq/ 100g)	H^+ (meq/ 100g)	CEC (meq/ 100g)
Forest	Mean	6,92	5,54	0,5	4,11	0,62	0,54	14,25	8,56	0,14	0,31	24.4
	Min	6,05	5,22	0,12	1.0	0,2	0,29	7,11	4,91	***0.0***	***0,04***	14.8
	Max	7,32	6,23	***1,3***	14,7	1,41	***0,92***	***24,2***	14,36	***0,75***	***0,71***	***39.4***
	% CV	4.0	4,6	40,8	76,2	58	23,5	29	29,4	91,3	38,5	23.9
12-yr pasture	Mean	7,16	5,83	0,37	12,1	1,23	0,47	13,8	7,1	0,05	0,18	22.8
	Min	6,71	5,17	0,24	1,9	0,5	0,23	6,9	***4,05***	***0.0***	***0,04***	12.4
	Max	***7,6***	***6,5***	0,71	***38,8***	2,03	0,79	21,6	13,8	0,15	0,34	34.8
	% CV	3,2	5,7	23,6	86,8	31,9	22,3	27,5	30,6	87	43,7	23.8
32-yr pasture	Mean	6,73	5,23	0,37	1,13	0,54	0,33	7,67	8,08	0,15	0,21	17.0
	Min	6,3	***4,7***	***0,08***	***0,2***	***0,15***	***0,11***	***4,6***	4,11	0,04	0,11	***10.3***
	Max	7,15	5,71	0,7	3,3	***2,35***	0,47	11,6	14,5	0,3	0,38	25.2
	% CV	3,5	5,2	25,7	66,1	91,1	20,7	28,9	31,8	48,5	30,6	26.3
52-yr pasture	Mean	6,65	5,07	0,42	4,09	0,68	0,35	8,58	9,22	0,1	0,16	19.1
	Min	***5,9***	***4,7***	0,38	1,5	0,22	0,27	5,73	6,15	***0.0***	***0,04***	14.5
	Max	7,09	5,7	0,64	6,5	1,36	0,49	11,4	***26,1***	0,22	0,3	38.0
	% CV	4,8	4,8	12,3	33,7	50,4	18,5	14,7	44	61,7	39,8	24.8



igure 4.1. Means and ranges of soil characteristics in the forest (0) and open-pastures of 12, 32 and 52-yr old at Los Tuxtlas, Mexico. The short horizontal lines indicate maximum and minimum values.

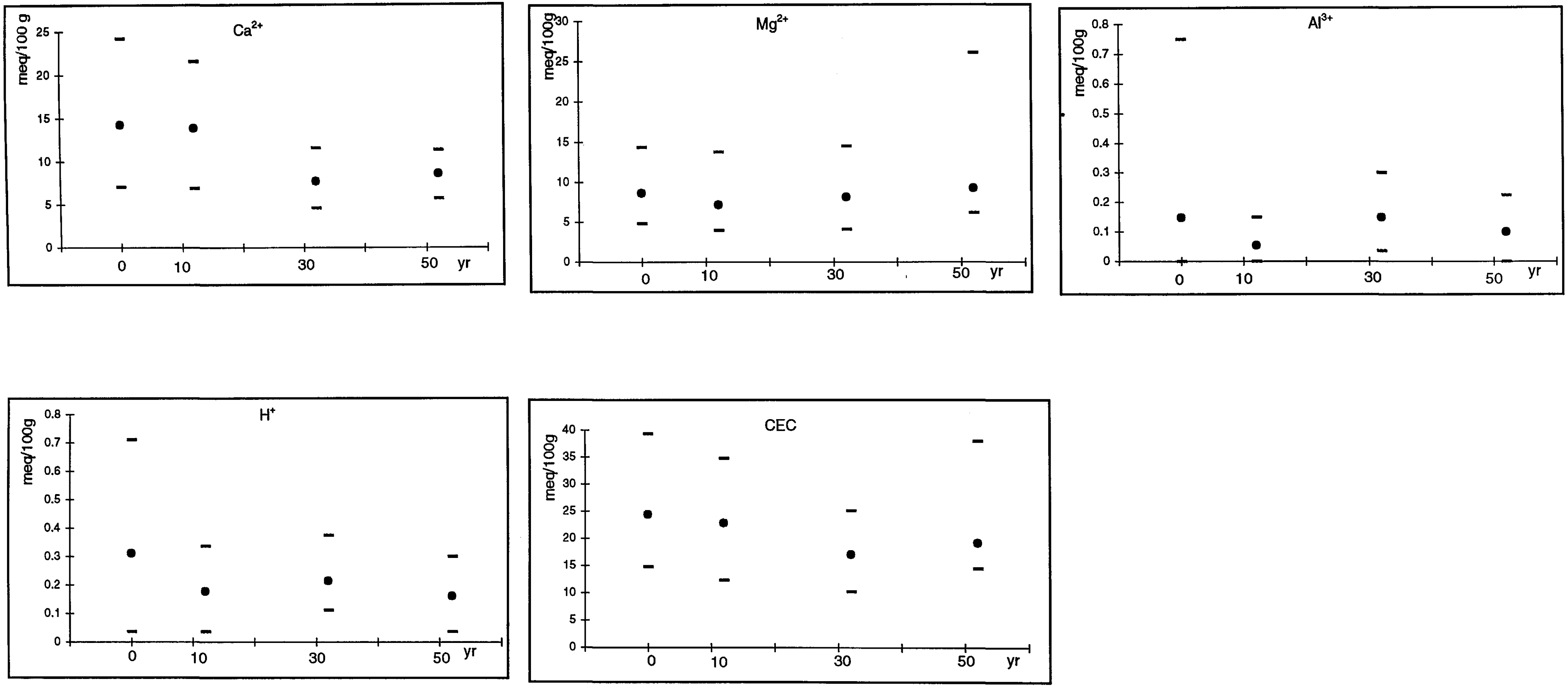


Fig. 4.1 continue

A) Comparison of the forest and pastures of different ages

Figure 4.1 shows the trends and within-site variation for all the elements. The 52-yr pasture was excluded from the following statistical analyses since it had been fertilised. Na^+, Ca^{2+} and CEC showed a significant, though not strong, decrease from the forest through the pastures of increasing age (Na^+, $r^2 = 0.44$; Ca^{2+}, $r^2 = 0.44$ and CEC, $r^2 = 0.27$; all $p < 0.0001$) (Figures 4.2 - 4.4). Table 4.6 shows that pH was highest in the 12-yr pasture and then decreased in the 32-yr pasture below the forest levels. Total N was higher in the forest than in the pastures. P was higher in the 12-yr pasture, than in the forest and the 32-yr pasture. Mg^{2+} did not show differences. K^+ was highest in the 12-yr open-pasture. H^+ was less in the pastures, and Al^{3+} was least in the 12-yr pasture.

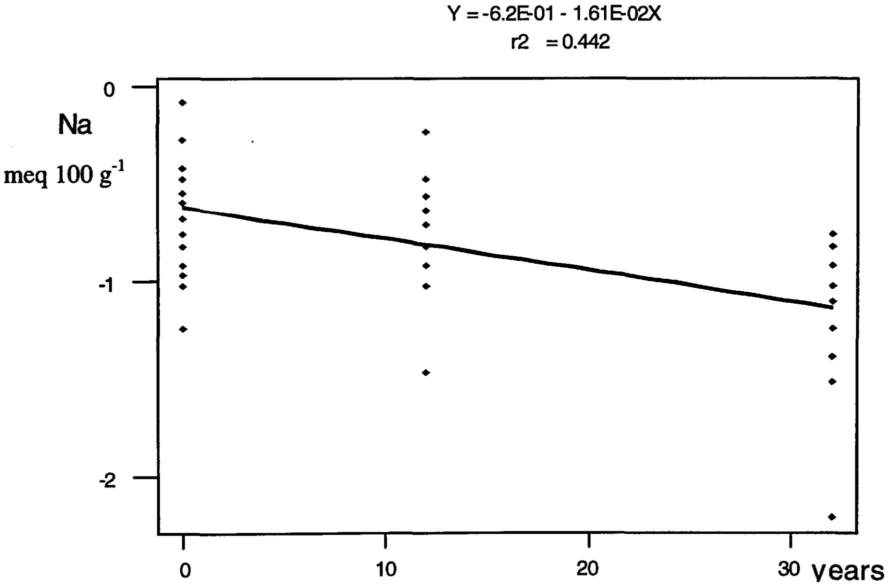


Figure 4.2. Regression of $\log_e$ transformed Na^+ on age from the forest to the 32-yr pasture. In this graph several Na^+ values were very similar and the dots overlap.

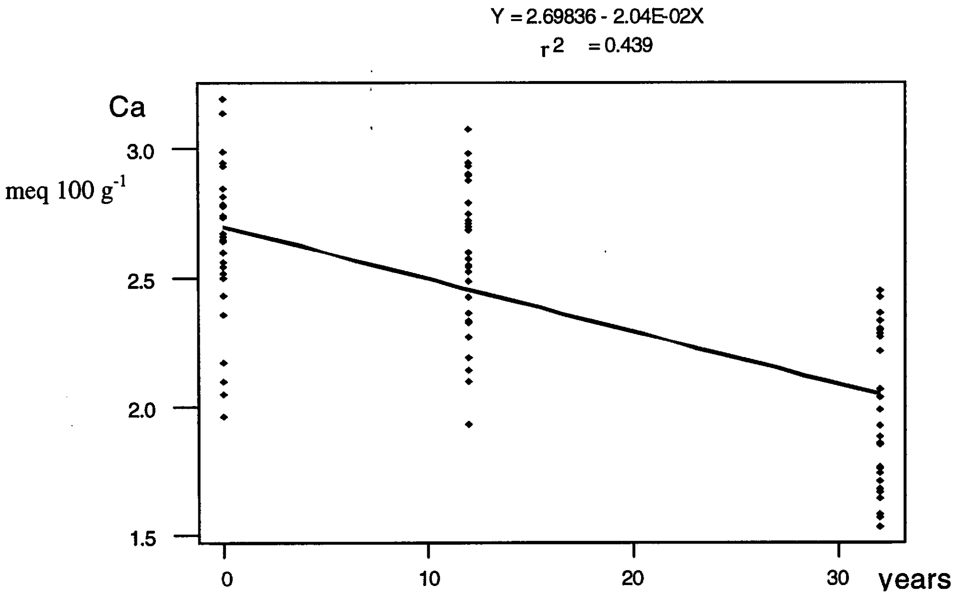


Figure 4.3. Regression of $\log_e$ transformed Ca^{2+} on age from the forest to the 32-yr pasture.

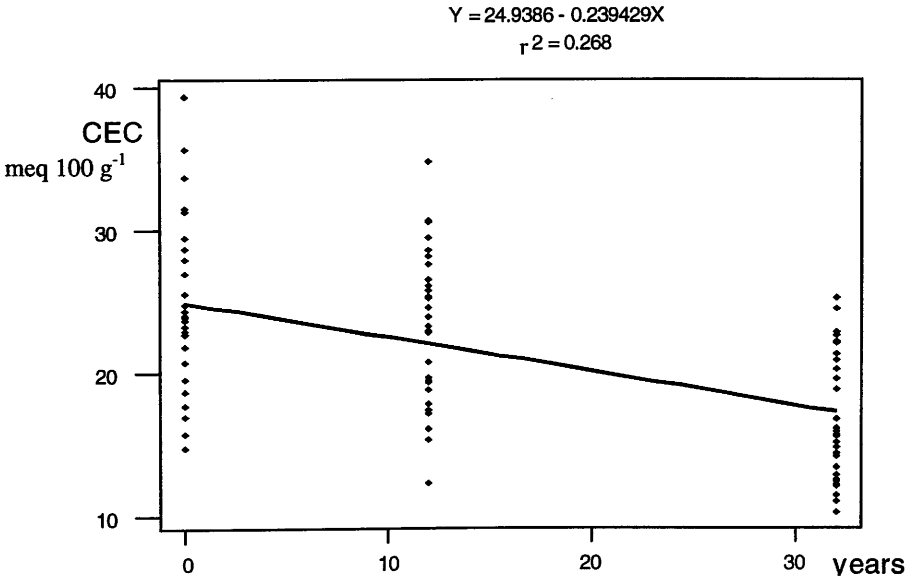


Figure 4.4. Regression of CEC on age from the forest to the 32-yr pasture.

Table 4.6. One-way Anova (mean ± S.D.) and Kruskal-Wallis test* (medians) for soil characteristics of the forest and pastures of different ages. n = 30. Different superscript letters indicate a significant difference within a row (Tukey test, $p \leq 0.05$).

	Forest	12-yr old	32-yr old	p
pH_{H2O}	6.9^{a} ± 0.27	7.2^{b} ± 0.23	6.7^{c} ± 0.23	<0.0001
pH_{KCl}	5.5^{a} ± 0.26	5.8^{b} ± 0.33	5.2^{c} ± 0.27	<0.0001
Total N (%)*	0.495^{a}	0.365^{b}	0.40^{b}	<0.0001
P (µg g^{-1})	4.1^{a} ± 3.1	12.1^{b} ± 10.5	1.12^{c} ± 0.74	<0.0001
K^+ (meq/100g)*	0.51^{a}	1.23^{b}	0.33^{a}	<0.0001
Na^+ (meq/100g)	0.54^{a} ± 0.4	0.46^{a} ± 0.4	0.31^{b} ± 0.29	<0.0001
Ca^{2+} (meq/100g)	14.2^{a} ± 4.1	13.8^{a} ± 3.1	7.6^{b} ± 2.2	<0.0001
Mg^{2+} (meq/100g)	8.6^{a} ± 2.52	7.1^{a} ± 2.18	8.1^{a} ± 2.6	= 0.07
H^+ (meq/100g)*	0.28^{a}	0.19^{b}	0.19^{b}	<0.0001
Al^{3+} (meq/100g)*	0.11^{a}	0.06^{b}	0.15^{a}	<0.0001
CEC (meq/100g)	24.3^{a} ± 6.8	22.8^{a} ± 5.9	17.2^{b} ± 4.3	<0.0001

B) Analysis of the effect of slope of the terrain

Only P and Na showed higher concentrations in the terrain with steep slopes than gentle slopes (Table 4.7).

Table 4.7. Students-t* (means ± S.D.) and Mann-Whitney (medians) tests for soil characteristics in two sites with a gentle slope (3° - 4°) and two with a steep slope (24° - 44°) at Los Tuxtlas. n = 20.

	Steep slope		Gentle slope		
	Mean /Med	S.D.	Mean/ Med	S.D.	p
pH_{H2O}*	6.8	0.34	6.8	0.22	n.s.
pH_{KCl}*	5.4	0.5	5.4	0.2	n.s.
N	0.36	-	0.4	-	n.s.
P	3.6	-	0.85	-	= 0.001
K^+	0.57	-	0.6	-	n.s.
Na^+	0.49	-	0.30	-	<0.0001
Ca^{2+}	10.0	-	7.6	-	n.s.
Mg^{2+}	7.3	-	7.52	-	n.s.
H^+	0.19	-	0.19	-	n.s.
Al^{3+}	0.13	-	0.13	-	n.s.
CEC*	19.7	6.3	17.7	4.1	n.s.

DISCUSSION

Although as previously described, the 12-yr pasture remained for six years in cultivation and fallow, and for six years as a pasture, it has been referred as a 12-yr pasture because it was considered that the time of deforestation was the dominant effect on soil nutrients.

Physical properties. The upper 10 cm of soils at Los Tuxtlas have a clay content sufficient to give good structural properties and high aggregate stability. Scott (1978) mentioned that in the long term, grassland soils are likely to have less sand, similar silt, and more clay with increasing depth as a result of erosion and eluviation, and that soil compaction can also produce textural differences. At Los Tuxtlas soil bulk density in the forest was lower than in the pastures and did not change with increasing age of pasture. It increased during the first years of pasture with no further increase after 50 years. Cattle compact the soil (Reiners *et al.* 1994). In a 20-36-yr old pasture, Reiners *et al.* (1994) found a higher soil density (0.837 g cm^{-3}) at 5 - 10 cm depth than in the primary forest (0.687 g cm^{-3}). Scott (1978) in a mature secondary forest in Peru recorded a bulk density as low as 0.25 g cm^{-3} at 3 cm depth, and 1 g cm^{-3} at 50 cm depth. In an Amazonian forest in Venezuela, Jordan (1989) found a much higher value of 1.17 g cm^{-3}. Values for Los Tuxtlas pastures (1 g cm^{-3}) were similar to those found by Scott (1978) in old grassland soils in Peru (0.75 to 1 g cm^{-3} at 0-12 cm depth). This author found also that pasture bulk density values increased as much as 25% in the dry season compared with the wet season.

Chemical properties. In this study it is difficult to know what is the effect of the age of the pasture on soil nutrients and what is the result of there being different soil types initially. However a broad idea can be obtained from Nelson & Gonzalez-Caver's (1992) geologic map in which the forest plots lie over the younger volcanic series, the

12-yr pasture and the 32-yr pasture on the older volcanic series, and the 52-yr pasture lies on a quaternary alluvial stratum.

Mineral elements in the top 10 cm of the soil were found to be variable in space, (Table 4.5). The forest soil showed the highest spatial variation whereas the oldest open-pasture had the least. Beckett & Webster (1971) and Grieve *et al.* (1990) found a similarly high spatial variation in the tropical forest soils investigated by them. Differences between individual trees in nutrient uptake and litterfall contribute to the spatial variability of soils under undisturbed forests (Baillie & Ashmad 1984), as do the harvesting activities of nest-building insects (Salick *et al.* 1983). Burghouts (1993) found mineral-elements highly spatially correlated among litterfall, litter layer and topsoil in Sabah, Malaysia. At Los Tuxtlas it is possible to find adjacent pastures with different parent materials and soil types (Chizón 1984). The 32-yr pasture had a higher spatial heterogeneity than the 12-yr open-pasture possibly because of its higher cattle density and clumping of excrement (Buschbacher 1987a) or because the 12-yr pasture is located on a slope where water movement might reduce nutrient spatial heterogeneity.

Only pH, P and K^+ had higher values in the 12-yr pasture than in the forest, probably an aftermath of burning (Table 4.6). Three soil characteristics (Na^+, Ca^{2+} and CEC) showed a linear decrease from the forest to the 32-yr pasture (Fig 4.2-4.4); and pH, total N, P and H^+ had lower values in the 32-yr pasture than in the forest (Table 4.6). The increment of element concentrations in the 52-yr pasture was probably due to the fertilisation. Compared with the intensive pasture fertilisation in oxisols and ultisols in Puerto Rico of up to 1,800, 80 and 670 kg ha^{-1} of N, P and K (Vicente-Chandler *et al.* 1974), the amounts (740, 40 and 40 kg ha^{-1} of N, P and K) applied to the 52-yr pasture can be considered as moderate. The decline of soluble P in the soil is probably the most important factor in declining pasture production in the Amazon (Serrão *et al.* 1978).

Analysis of soil nutrients in changes of land-use in the tropics, refer more to the cutting and burning of the forest (Nye & Greenland 1960, Ewel *et al.* 1981, Buschbacher 1987b, Uhl 1987), secondary succession after disturbance (Saldarriaga

1987), and to the years of cropping (Jordan 1987), than to pasture use. Few authors refer to the soil nutrient status in pastures through the time of use. Bruce (1965) reported a decrease in total N in the upper 15 cm from 0.37% to 0.27% during 22 years of pasture use in Australia, whereas at Los Tuxtlas total N declined from 0.50% to 0.37% in 32 years of pasture use. Conversion of forest to crop fields and pastures resulted in a decline in soil organic matter, pH, N, Ca^{2+}, and Mg^{2+} and an increase in Al^{3+} through time (Krebs 1975). In Brazil, after forest clearing, soil extractable P, K^{+}, Ca^{2+}, and Mg^{2+} were higher in a pasture of 0.5-yr and less in one of 4.5-yr, whereas N kept increasing (Buschbacher 1987b, Buschbacher *et al.* 1987). Later on, vegetation recovery restored soil nutrient stocks, and differences were observed only in vegetation biomass. In heavily disturbed pastures, seed availability, good soil structure and slash residues, are more important than soil nutrient stocks for vegetation recovery (Buschbacher *et al.* 1988). Krebs (1975) found in a volcanic soil in Costa Rica, a decline of pH, total N, K^{+} and Ca^{2+} in a 4-yr pasture compared with the original forest, and then an increase in a 15-yr pasture up to the concentrations in the forest. In a semi-evergreen seasonal forest in Brazil where rainfall was not as high as in a lowland forest, Falesi (1976) reported increments of pH, K^{+}, and divalent cations (Ca^{2+} and Mg^{2+}) from a forest to a 13-yr pasture of Panicum maximum, while extractable P, which had its highest value in a 3-yr pasture, subsequently decreased with age. Al^{3+} decreased consistently with age. Though Reiners *et al.* (1994) did not find differences in concentrations of Na^{+}, Ca^{2+}, and Mg^{2+} among the forest and two pastures of 20-31-yr old and one of 36-yr old, they found more K^{+} in the A horizon (0 - 15 cm depth) and a higher base saturation in the B horizon of the pastures than in the forest. They presented four hypotheses to explain this result, of which the most likely is that the original nutrient input into pastures by forest conversion had maintained a higher pH and nutrients even in relatively old pastures. The pastures had a higher soil density and less porosity than the forest (Reiners *et al.* 1994), thus reducing infiltration and percolation rates and hence probably nutrient leaching. On an old (several hundred years) fire-subclimax Andropogon grassland, Scott (1978) found that exchangeable Ca^{2+} and Mg^{2+} increased to 5.4 and 1 meq 100 g^{-1} compared with 0.4 and 0.3 meq 100

g^{-1} in the mature secondary forest. Between 6 - 18 cm depth, the forest had a higher pH, more organic matter, total N, K^+, Mn^{2+}, and Zn^{2+} than the grassland, and less Al^{3+} and a lower CEC. The old grassland had more exchangeable bases owing to the annual burning, which is not practised at Los Tuxtlas; and a higher CEC possibly owing to a higher clay content. Soil microorganism populations declined as conditions became more acidic. On a sandstone parent material some chemical properties differed from the previous soil type. Between 0 - 6 cm depth, the forest similarly had higher soil organic matter, total N, and P, but lower pH, K^+ and Al^{3+} than the old grassland (Scott 1978).

As for Falesi (1976) (13-yr pasture) in Brazil for pH and K^+, there was an increase in the Los Tuxtlas pastures 12 years after conversion from forest. As for Krebs (1975) (15-yr pasture) in Costa Rica, and Falesi (1976) (13-yr pasture), in the 12-yr pasture at Los Tuxtlas Ca^{2+} remained similar to the forest soil. Reiners *et al.* (1994) did not find lower pH, K^+, Na^+ and Ca^{2+} until 36 years after forest conversion in contrast to Los Tuxtlas for the 32-yr pasture. Similarly to Reiners *et al.* (1994) Mg^{2+} had similar values in the forest and the 32-yr pasture in Los Tuxtlas. Al^{3+} concentrations did not change with time in contrast to Krebs (1975) who found increasing Al^{3+} but otherwise a similar situation to Los Tuxtlas, with lower pH, total N and Ca^{2+} with increasing age.

An explanation for the decline at Los Tuxtlas of total N, P (after 12 years), and exchangeable cations is as follows. A partial depletion of N is accounted by the grasses. Grasses remove large quantities of N annually and cattle returned 80% via excrement and urine (Vicente-Chandler *et al.* 1964), but only 40% from the original amount is incorporated in the soil owing to volatilisation and leaching (Parsons 1976). Total N was higher in the forest than in the pastures and this may be a reflection of the higher humus contents. Humus has the following properties: 1) it breaks down readily to yield the plant-available forms of mineral N, P, and S, but not rapidly enough to allow excessive losses of nutrients; 2) it has a high cation-exchange capacity; 3) it improves the constitution of the soil, thereby improving its water relationships and the diffusibility of carbon dioxide and oxygen; and 4) it provides food for the soil micro-organisms (Nye & Greenland 1960).

Soil clay minerals and humic acids both have a specific number of permanent sites with negative charges which bond nutrient cations and avoid leaching from the soil (Weischet & Caviedes 1993). Organic matter is responsible for a high proportion of CEC by providing exchange sites (Werner 1984). P is tightly bonded with iron, Al^{3+} and hydroxides, making it largely unavailable for plants (Nye & Greenland 1960, León & Hammond 1985). Al^{3+} was low in the 12-yr open-pasture at Los Tuxtlas, thus giving a higher free P. Since pH in most volcanic soils is high the level of free Al^{3+} is low and it does not present a problem. This is the case for Los Tuxtlas even in the 52-yr pasture.

The uptake by cattle and leaching explain decreasing cations in the grasslands. There is a greater nutrient leaching in pastures than in the forest. In seasonal climates the main body of grass roots die back in the dry season, therefore reducing the absorption of percolating water. In the forest the amount of water entering the soil is reduced because it is intercepted by leaves or absorbed by the leaf litter (Nye & Greenland 1960). Because of their lower leaf area than forest, pastures have less evapotranspiration. When rainfall is higher than evapotranspiration a larger fraction of the soil solution may be leached from the pastures than from the forest (Weischet & Caviedes 1993).

In contrast to the expected movement downslope of mineral elements by water run-off and leaching in a humid climate and their accumulation in the depressions, no differences were found between steep and gentle slopes. This comparison deserves more analysis because the better pasture commonly observed in depressions, could be the effect of more water rather than more nutrients.

Comparison of the Los Tuxtlas forest soil with lowland evergreen rain forests elsewhere. Richards (1952), Nye & Greenland (1960) and Sanchez (1976) stated that most tropical forests around the world and particularly from South America have nutrient-poor soils. Proctor *et al.* (1983a) listed soil characteristics from different soil types from a range of tropical rain forests around the world (Malaysia, Australia, Ghana, Venezuela, Peru and Brazil) and concluded that no generalization could be made about tropical soil nutrients. Values ranged as follows: pH (3.0 - 6.6), % total N (0.02 - 1), K^+ (0.03 - 1.6 meq 100 g^{-1}), Na^+ (0 - 0.57 meq 100 g^{-1}), Ca^{2+} (0 - 29 meq 100 g^{-1}), Mg^{2+} (0 - 4.6 meq 100 g^{-1}), and CEC (2.5 - 43 meq 100 g^{-1}). From these ranges and Table 4.8 it is possible to see that the Los Tuxtlas values are in the mid and high ranges, especially for Mg^{2+}.

At Los Tuxtlas pH in particular is high and proximity to the sea does not seem to have a great influence on this, since surface pH and Na^+ concentrations from the nearest pastures to the sea (12-yr and 52-yr) were not higher than in the most distant pasture (32-yr), and pH did not decrease consistently down through the soil profiles up to 1 m. Bongers *et al.* (1988) had previously determined a pH_{H2O} of 6.3 at a 15 cm depth in their forest plot at Los Tuxtlas. Table 4.9 shows that the amounts of soil nutrients at Los Tuxtlas when expressed on a volume basis are also in the high range compared with those elsewhere.

Table 4.8. Soil pH and nutrient concentrations (on a mass basis) in some tropical undisturbed forests. -, are no data.

Location	Soil Type	Depth (cm)	pH *	Total N (%)	Ext. P (µg g^{-1})	K^+ (meq 100 g^{-1})	Na^+ (meq 100 g^{-1})	Ca^{2+} (meq 100 g^{-1})	Mg^{2+} (meq 100 g^{-1})	CEC (meq 100 g^{-1})	Author
Costa Rica	Alluvial	0-10	4.5	0.40	3.6	0.22	0.13	0.75	0.35	7.0	Werner (1984)
Costa Rica	Entisol	0-15	3.7	-	2.2	0.17	0.11	1.09	0.29	34.3	Grieve *et al.* (1990)
Ghana	Ochrosol	0-23	6.5	-	-	0.36	-	8.48	1.9	12.04	Charter (1955)
Ghana	Oxisols-Ochrosol	0-23	5.3	-	-	0.26	-	4.02	1.0	9.5	Charter (1955)
Malaysia	Alluvial	0-10	4.4	0.54	-	0.24	0.08	5.3	0.53	38.0	Proctor *et al.* (1983a)
Malaysia	Ultisol	0-10	4.1	0.51	-	0.25	0.06	0.04	0.18	37.0	Proctor *et al.* (1983a)
México	Eutropept	0-12	5.7	0.53	-	-	-	7.2	-	15.2	Chizón (1984)
México	Andosol	0-45	5.0	-	3.91	2.30	-	14.4	7.3	60.3	Sommers-Cervantes *et al.* (Unpublished data)
México	-	0-10	6.9	0.50	4.11	0.62	0.54	14.25	8.56	24.4	This study
Venezuela	Oxisol	-	-	0.27	-	3.5	-	1.8	-	-	Uhl *et al.* (1983)

* All values are for pH_{H2O} except for the Costa Rican entisol which is pH_{CaCl2}.

Table 4.9. Soil nutrient concentrations (on a volume basis) (kg ha^{-1}) in tropical mature forests. -, are no data.

Location	Soil Type	Depth (cm)	Total N	Ext. P	K^+	Na^+	Ca^{2+}	Mg^{2+}	Author
Brazil	Oxisol	-	1,300	50	100	-	600	200	Buschbacher *et al.* (1987)
Brazil	-	0-10	578	-	36	-	60	28	Thompson *et al.* (1992)
Malaysia	Alluvial	0-30	7,800	-	95	30	1,600	69	Proctor *et al.* (1983a)
Malaysia	Ultisol	0-30	6,000	-	95	24	4.6	22	Proctor *et al.* (1983a)
México	Andosol	0-10	3,750	3	18.2	9.3	427.5	156	This study
Peru	-	-	10,000	15	325	-	880	180	Scott (1987)
Venezuela	Ultisol	0-30	2,500	25	20	-	-	5	Buschbacher (1987b)
Venezuela	Oxisol	0-30	1,450	3	35	-	30	-	Saldarriaga (1987)
Venezuela	Oxisol	-	1,951	-	22.7	-	6.9	5.2	Jordan (1989)

Chapter 5. SMALL LITTERFALL

INTRODUCTION

The net primary production of an ecosystem is distributed in four ways. Some is stored as biomass, some secreted as soluble organic matter, some consumed by animals, and some is shed as plant litter including roots. The root litter is very difficult to quantify. Above-ground litterfall undoubtedly constitutes a big component of forest production and is an important part of nutrient cycling and its quantification (at least of its smaller fractions) provides a relatively easy way of comparing some ecosystem processes among forests. Large quantities of annual small litterfall are characteristic of lowland evergreen tropical rain forests and comprise leaves, flowers, fruits, branches, trash and all kinds of plant or animal material (Proctor 1983). In particular, leaf-litter quantity, quality and time of falling affect heterogeneity of the litter layer, litter decomposition, humus formation, and hence nutrient cycling (Burghouts 1993). Seedling establishment is also affected (Sydes & Grime 1981).

In the present Chapter the small litterfall production for the Los Tuxtlas rain forest, the species composition of the leaf litter (the main fraction of the litterfall), and the temporal patterns of the main leaf litterfall species are examined.

METHODS

On 8 December 1995, 44 litter traps each of 0.159 m^2 were randomly placed in each forest plot (0.25 ha) to give a litterfall sample area of 7.15 m^2 per plot. The traps were cone-shaped, 45 cm diameter at the rim and they were made with a nylon open cloth with *c.* 0.5 mm holes and were well drained. A circular wire for holding the trap was attached by folding the edges to the top of a plastic pole buried in the ground (Figure

5.1). The traps were level and never observed to be disturbed by the weight of the litter. Trap height was between 50 cm and 100 cm from the ground.

The sampling period was from 8 December 1995 to 19 November 1997, however the collection for May 1997 was lost. From 4 January 1996 to 4 May 1996 collections were made monthly, and then every 15 days until November 1997. A 5-day experiment was made putting peanuts (Arachis hypogaea) in five traps to test for fruit and seed removal by animals. No removal was observed but as a precaution a plastic plate was placed on the poles to prevent terrestrial frugivores reaching the litterfall (Figure 5.1).

Litter from the 44 traps of each plot was bulked before sorting. Material was dried for 15 days (20 - 40 °C) and a sub-sample was oven-dried at 105 °C to obtain a moisture correction factor. The litterfall was sorted into five categories: small wood (≤ 2 cm diameter); leaves including petioles; fruits and seeds; miscellaneous (3 - 20 mm diameter), material too small to sort, which contained plant and invertebrate remains; and trash (debris under 3 mm). Flowers were all small and were included with the miscellaneous fraction. Proctor (1983) defined the trash fraction as all material passing through a sieve of 2-mm or 5-mm mesh, which contains frass, unrecognizable remains and fine particles. However in my study there was too much material between this limit and 2 cm (longest diameter) containing pieces of reproductive parts, leaves, wood, bark, moss, invertebrate remains and faeces which were difficult to sort (miscellaneous fraction). Herbohn & Congdon (1993) had similar problems sorting the miscellaneous fraction and had floral fragments in the trash fraction also. Leaf litterfall taxa with a dry weight of over 1 g in any month in any plot were identified to species level. A period of three consecutive collections was considered enough to obtain the confidence limits of the sample mean from the three plots, with the total small litterfall dry weight from each single trap. This was made during January 1997. A one-way ANOVA and a Tukey test for means differences (Zar 1984) were used to compare the total small litterfall among these three plots for the three collections.

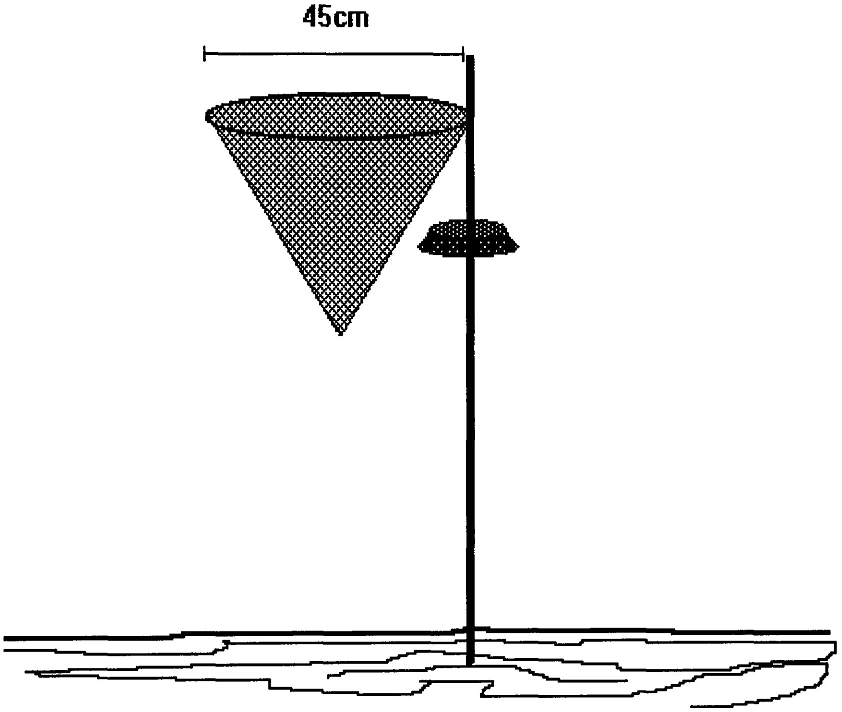


Figure 5.1. Design of the trap used for a litterfall study at Los Tuxtlas, México.

RESULTS

A) Total small litterfall

For all litterfall fractions the dry weight (g) was divided by the trap area (7.15 m^2) for each plot and then by 710 days of sampling to obtain a value of g m^{-2} d^{-1}, which was extrapolated to t ha^{-1} yr^{-1}. A total of 10.6 t ha^{-1} yr^{-1} of litterfall dry weight was obtained (Table 5.1). A one-way ANOVA showed that plot 1 had a higher total small litterfall production than plots 2 and 3 ($p = 0.003$, $n = 132$) (Table 5.1). Leaves were the preponderant fraction (around 60%) while small wood was only 12.7%. Miscellaneous plus trash was about 20.4% whereas fruits were only 7.5% (Table 5.2). The C.L.'s for the total small litterfall for the three consecutive collections (n = 44) for plot 1 ranged between 12 and 20%; for plot 2, 15 and 26%; and for plot 3, 14 and 19%, depending on the collection.

Total and leaf litterfall trends over the 22 months of sampling were similar (Figure 5.2). There was a peak in the dry season, and a smaller peak in the 'norte' season (September-November), though there were stronger winds in the dry season (Chapter 2). In the second year there was a large peak owing to a wind storm in October 1997 resulting in a significantly higher production (13.2 t ha^{-1} yr^{-1}) compared with the previous year (7.9 t ha^{-1} yr^{-1}). Small wood was very variable and did not show any pattern with the exception of the high value after the wind storm. Almost half of the monthly means of small wood litterfall had a large range and only a few had very small ranges (Figure 5.3). In the fruit litter there were two peaks in both years: April to June (dry season), and August to November (rainy and windy season) (Figure 5.4). Miscellaneous and trash (Figure 5.5) had two peaks in the year at the same time as the leaves. Miscellaneous (3 - 20 mm diameter) production was significantly higher than trash (< 3 mm diameter) during the wind storm in the second year. No flowers bigger than 2 cm were found in the samples. Figure 5.6 shows the relationship between leaf litterfall and rainfall, days without rain, maximum temperature and mean wind speed.

Table 5.1. Production (t ha^{-1} yr^{-1}) of the small litterfall fractions (with the 95% C.L.'s (n = 44) for the total production) from three collections, in sample traps from three (0.25 ha) plots during 710 days at Los Tuxtlas, México. Different superscript letters indicate a significant difference among the plots (Tukey test, $p \leq 0.05$).

	Plot 1	Plot 2	Plot 3	Mean
Leaves	6.39	6.19	6.3	6.29
Small wood	1.28	1.35	1.37	1.33
Fruits	1.02	0.91	0.44	0.79
Miscellaneous	1.41	1.02	1.36	1.26
Trash	0.97	0.78	0.95	0.90
Total	11.07^{a} ± 1.75	10.25^{b} ± 1.93	10.42^{b} ± 1.64	10.58 ± 1.77

Table 5.2. Percentage of each fraction and the total small litterfall in several lowland evergreen tropical rain forests. n.d. = no data.

	Leaves	Small wood	Flower and fruits	Trash and miscellaneous	Total ($t\ ha^{-1}\ yr^{-1}$)	Reference
Brazil [1]	64.4	17.4	5.5	12.3	7.80	Luizão (1989)
Brazil	67.9	14.4	13.0	4.5	9.28	Scott *et al.* (1992)
Malaysia [2]	57.4	20.9	3.5	16.4	11.5	Proctor *et al.* (1983b)
Malaysia [3]	61.4	23.9	2.9	12.5	8.8	Proctor *et al.* (1983b)
Malaysia	59.3	22.6	3.2	14.9	6.51	Proctor *et al.* (1989)
México	67.9	21.6 [4]	3.7	6.8	7.26	Alvarez & Guevara (1985, 1993)
México	54.0	18.0	5.0	21.0	6.44	Sanchez & Alvarez (1995)
México	59.5	12.6	7.5	20.4	10.58	This study
Venezuela	73.9	22.4	3.9	n.d.	10.25	Cuevas & Medina (1986)

1) = Mean from two sites
2) = Alluvial forest
3) = Dipterocarp forest
4) = No upper size limit was established

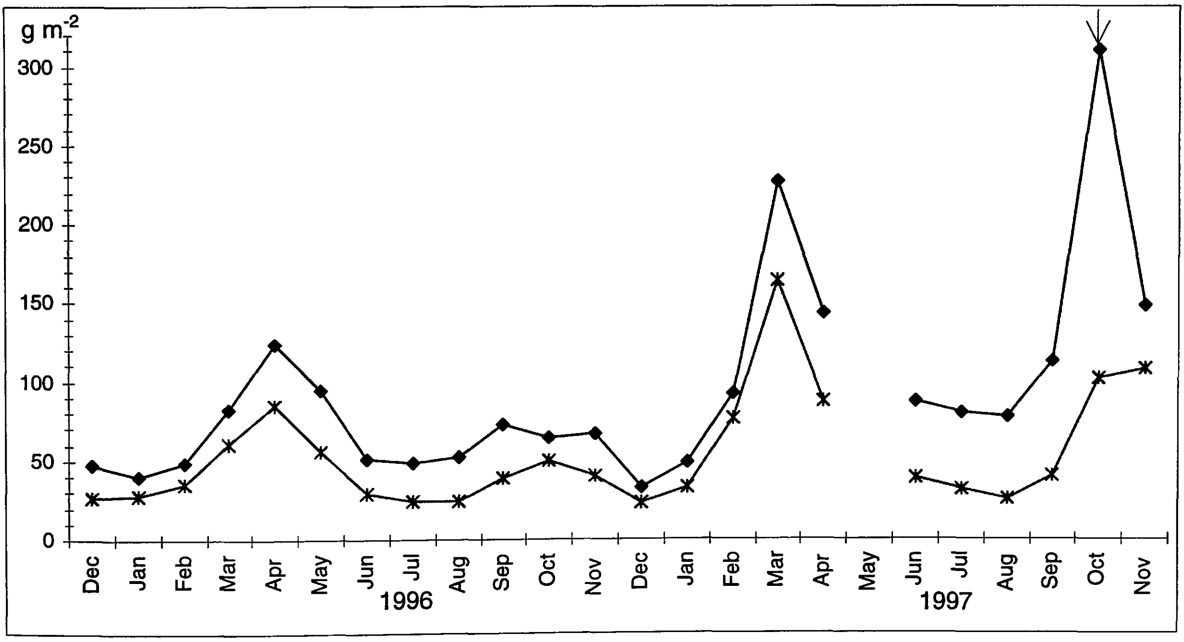


Figure 5.2. Mean total small (upper line) and leaf (lower line) litterfall from three (0.25 ha) plots at Los Tuxtlas, México. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

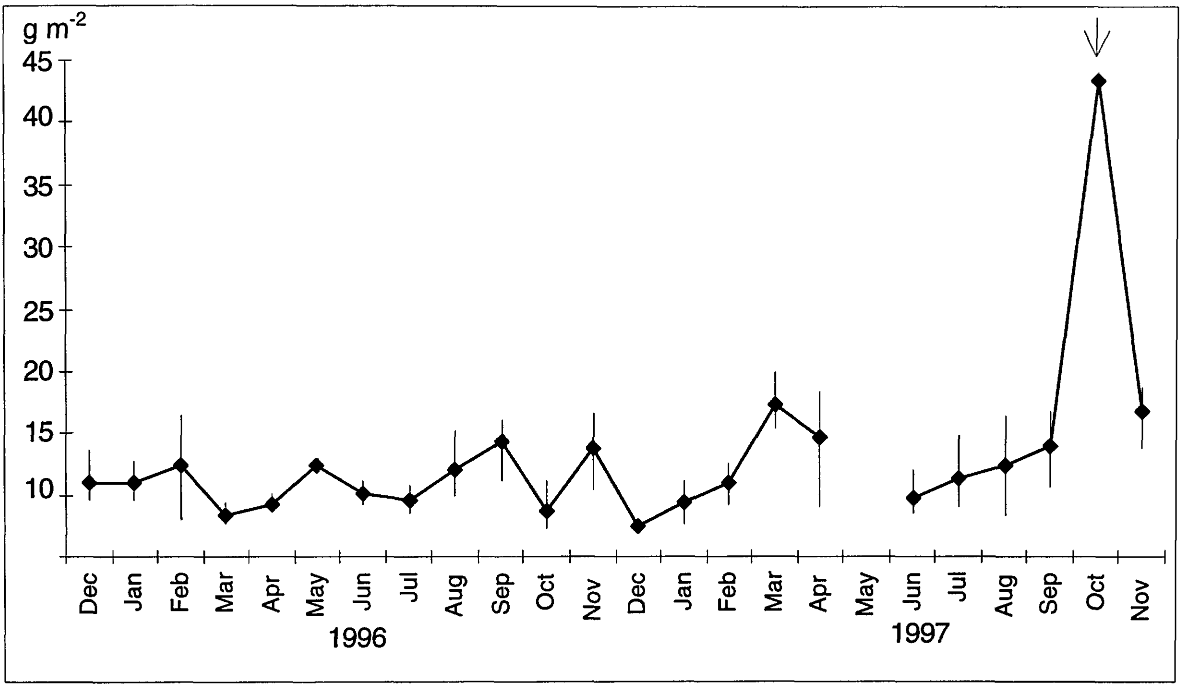


Figure 5.3. Mean small wood litterfall from three (0.25 ha) plots (range) in the forest at Los Tuxtlas, México. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

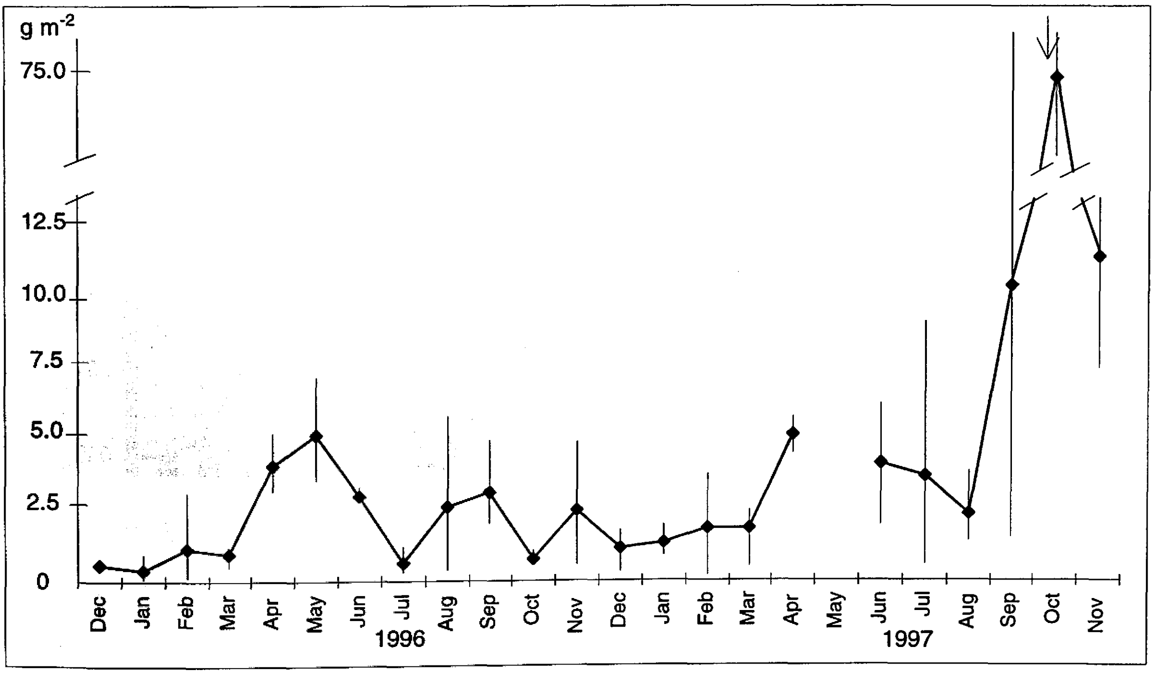


Figure 5.4. Mean fruit litterfall from three (0.25 ha) plots (range) in the forest of Los Tuxtlas, México. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

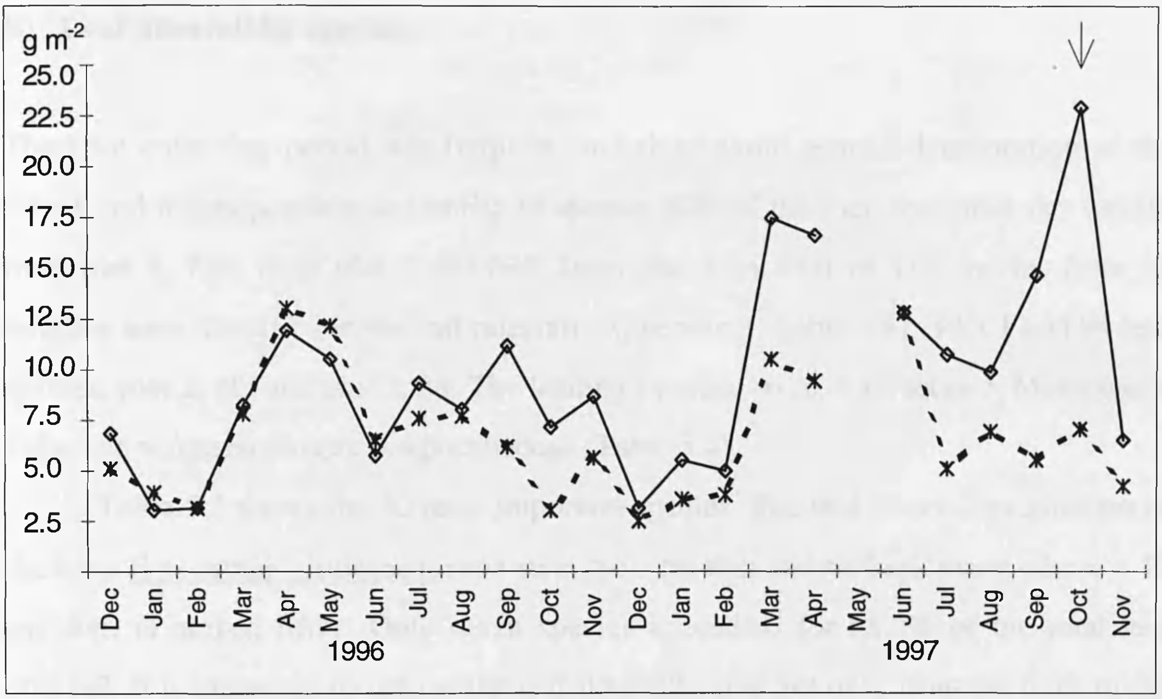


Figure 5.5. Mean miscellaneous (continuous line) and trash (dashed line) litterfall from three (0.25 ha) plots in the forest of Los Tuxtlas, México. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

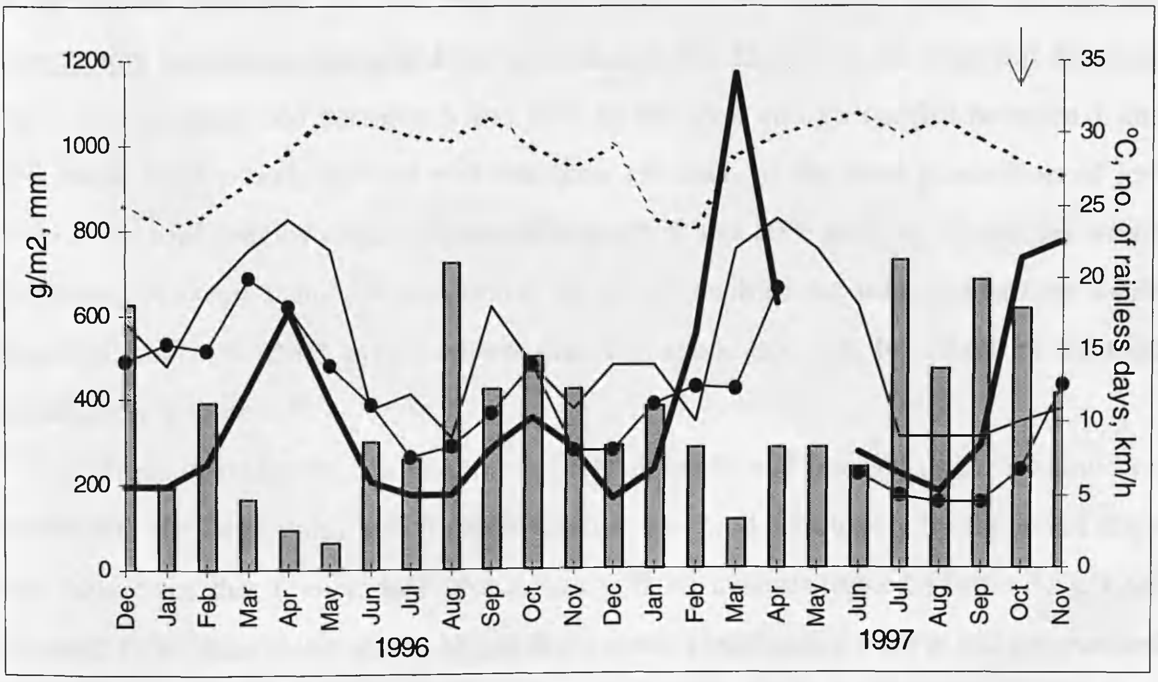


Figure 5.6. Leaf litterfall (▬, g m^{-2}), rainfall (▨, mm), monthly mean maximum temperature (---, °C), number of rainless days (—), and mean wind speed (●, km h^{-1}). Leaf litterfall data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

B) Leaf litterfall by species

The 15-d collecting period was frequent enough to avoid serious deterioration of the leaves and it was possible to identify to species 80% of the total leaf litter dry weight from plot 1, 75% from plot 2 and 69% from plot 3. A total of 119 species from 51 families were identified in the leaf litterfall (Appendix 3, Table 5.4). Plot 1 had 94 leaf species; plot 2, 80; and plot 3, 88. The leading families were: Lauraceae > Moraceae > Fabaceae > Anacardiaceae > Apocynaceae (Table 5.4).

Table 5.3 shows the 20 most important species. The leaf litterfall production of the liana Forsteronia viridescens (one stem ≥ 10 cm dbh and perhaps many others < 10 cm dbh) is ranked fifth. Only seven species accounted for 58.2% of the total leaf litterfall. It is important to notice that leaf litterfall came not only from the trees in the plots (Chapter 3), but also from trees < 10 cm dbh and from those outside the plots. Figure 5.7 shows the relative contribution of each of the 119 species to the total leaf litterfall dry weight and compares the proportion of the species grouped by classes of contribution (percent) to the total leaf litterfall dry weight. Only one species (Nectandra ambigens) accounted for more than 10% (22.6%) of the total leaf litterfall. Four species produced between 5 and 10% of the total and 16 species between 1 and 5% each. Ninety-eight species had less than 1% each of the total production of leaf litter. The four species which produced between 5 and 10% and the 16 species which produced between 1 and 5% accounted for 28.9% each of the total production, while the 82.4% species which produced less than 1%, accounted only for 19.6% of the total production (Figure 5.7).

Trees provided 86.3% of the total leaf litterfall and lianas 11.4%. It should be noted that the large palm leaf fraction was not sampled adequately by the small traps and hence for this family, leaf production will be underestimated (Table 5.5). Leaf litterfall from individuals of any height from species potentially > 20 m tall represented 74.9%; from species potentially 10 - 20 m tall, 19.6%; and from species potentially 0 - 10 m tall, 5.4% (Table 5.6). Leaf litterfall at family and species level was more correlated to tree basal area (r = 0.94, r = 0.89) than to tree density (r = 0.5, r = 0.34).

Table 5.3. Percent of the 20 species with most leaf litterfall dry weight from the total of 119 found in three (0.25 ha) plots at Los Tuxtlas, México during 22 months. n = number of individuals (≥ 10 cm dbh) present in the plots.

Species	%	n	Species	%	n
1 *Nectandra ambigens*	22,58	15	11 *Clarisia biflora*	1,84	1
2 *Spondias radlkoferi*	8,48	13	12 *Guarea glabra*	1,59	10
3 *Vatairea lundellii*	8,39	2	13 *Omphalea oleifera*	1,57	10
4 *Pseudolmedia oxyphyllaria*	6,28	29	14 *Ficus petenensis*	1,51	1
5 *Forsteronia viridescens*	5,80	1	15 *Tuxtla pittieri*	1,46	0
6 *Ficus tecolutensis*	3,74	1	16 *Pouteria sapota*	1,41	1
7 *Poulsenia armata*	2,93	4	17 *Ampelocera hottlei*	1,38	2
8 *Pteropcarpus rohrii*	2,71	2	18 *Bursera simaruba*	1,26	2
9 *Ficus yoponensis*	2,16	2	19 *Oeropanax obtusifolius*	1,17	0
10 *Neea psychotroides*	2,07	2	20 *Pouteria reticulata*	1,06	1

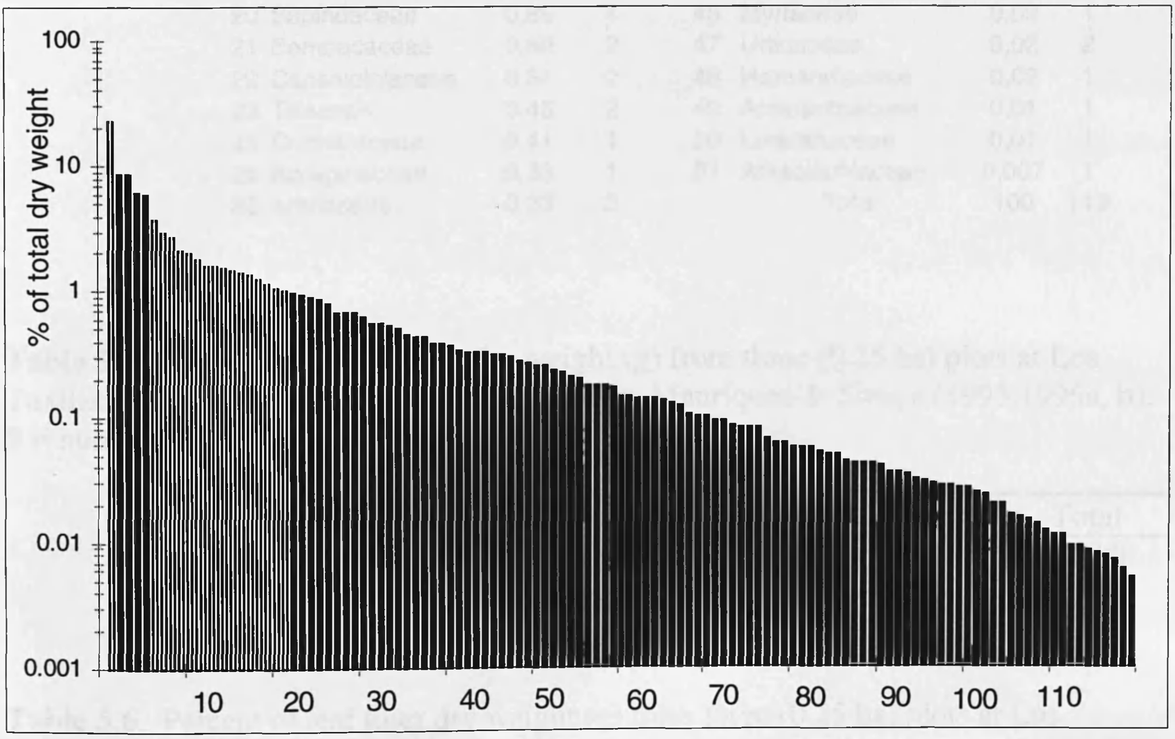


Figure 5.7. The proportion of leaf litterfall production contributed by each species at Los Tuxtlas, México during 710 days in three (0.25 ha) plots. Y-axis = % of total dry weight on a logarithmic scale. X-axis = species code number from Appendix 3. White and black columns represent the number of species in each dry-weight category (Y-axis, see text).

Table 5.4. Percentage of leaf litter (LL) contributed by families in three (0.25 ha) plots at Los Tuxtlas, México. S = number of species.

	Family	LL	S		Family	LL	S
1	Lauraceae	24,41	5	27	Flacourtiaceae	0,29	2
2	Moraceae	18,51	10	28	Capparaceae	0,29	1
3	Fabaceae	12,01	5	29	Dilleniaceae	0,23	1
4	Anacardiaceae	7,75	2	30	Cecropiaceae	0,21	1
5	Apocynaceae	5,97	3	31	Malvaceae	0,18	1
6	Sapotaceae	3,75	7	32	Verbenaceae	0,17	2
7	Meliaceae	2,45	3	33	Mimosaceae	0,16	1
8	Euphorbiaceae	2,18	3	34	Staphylaceae	0,15	1
9	Nyctaginaceae	2,17	2	35	Aquifoliaceae	0,15	1
10	Araceae	1,98	6	36	Malphigiaceae	0,10	2
11	Araliaceae	1,74	2	37	Menispermaceae	0,10	1
12	Asteraceae	1,56	3	38	Hippocrateaceae	0,09	2
13	Ulmaceae	1,49	2	39	Convolvulaceae	0,08	1
14	Bignoniaceae	1,44	7	40	Chrysobalanaceae	0,06	1
15	Rubiaceae	1,39	4	41	Polygonaceae	0,04	1
16	Clusiaceae	1,30	5	42	Solanaceae	0,04	1
17	Burseraceae	1,16	1	43	Rhamnaceae	0,03	1
18	Violaceae	1,04	2	44	Piperaceae	0,03	1
19	Annonaceae	0,97	2	45	Celastraceae	0,03	1
20	Sapindaceae	0,88	4	46	Myrtaceae	0,02	1
21	Bombacaceae	0,80	2	47	Urticaceae	0,02	2
22	Caesalpiniaceae	0,54	2	48	Hernandiaceae	0,02	1
23	Tiliaceae	0,45	2	49	Amaranthaceae	0,01	1
24	Connaraceae	0,41	1	50	Loranthaceae	0,01	1
25	Boraginaceae	0,33	1	51	Aristolochiaceae	0,007	1
26	Arecaceae	0,33	2		Total	100	119

Table 5.5. Percentage of leaf litter dry weight (g) from three (0.25 ha) plots at Los Tuxtlas, México. Species life forms from Ibarra-Manríquez & Sinaca (1995,1996a, b). S = number of species.

	Trees	Lianas	Epiphytes	Hemi-epiphytes	Palms	Total
%	86.3	11.4	1.2	0.7	0.3	100
S	83	27	4	3	2	119

Table 5.6. Percent of leaf litter dry weight (g) from three (0.25 ha) plots at Los Tuxtlas, México. HCS = high canopy species, MCS = medium canopy species, LCS = low canopy species. S = Number of species. Species height classes from Ibarra-Manríquez & Sinaca (1995, 1996a,b).

Category	HCS	MCS	LCS	Total
%	74.9	19.6	5.4	100
S	27	32	18	77

c) Temporal patterns of leaf litterfall by species

Most species tend to follow the general leaf fall pattern with a peak in the dry season (Figure 5.2) but others peak at different times of the year. Few species had a steady leaf litterfall over the year, most had one or two peaks. The most productive species (34) were graphed to analyze the general leaf litterfall of the forest and six patterns of leaf fall were identified:

1. Species with a peak in the dry season (March - April): *e.g.* Ficus tecolutensis, Nectandra ambigens and Vatairea lundellii (Figure 5.8); Ampelocera hottlei, Clarisia biflora, Omphalea oleifera, Pouteria reticulata, Quararibea funebris, Sideroxilon portorisence (Figure 5.9); and Clusia flava, Dendropanax arboreus, Orthion oblanceolatum, Psychotria simiarum and Q.yunckeri (Figure 5.10).
2. Species with a peak in the dry season and a second peak in the beginning of the 'norte' season (August - November): *e.g.* Pseudolmedia oxyphyllaria and Spondias radlkoferi (Figure 5.11); and Guarea glabra, G. grandifolia, Ficus yoponensis and Machaerium floribundum (liana) (Figure 5.12).
3. Species with a peak at the beginning of the rainy season (June and July): *e.g.* Faramea occidentalis and Philodendron guttiferum (Figure 5.13).
4. Species with a main peak half way through the 'norte' season (September-December) : *e.g.* Bursera simaruba, Neea psychotroides, Poulsenia armata, Pterocarpus rohrii and Tuxtla pittieri (Figure 5.14).
5. Species which drop their leaves through out the year: *e.g.* Connarus shultesii, Cymbopetalum baillonii, Oreopanax obtusifolius, Rheedia edulis, Serjania goniocarpa and Tetracera volubilis (Figure 5.15).
6. The liana Forsteronia viridescens which ranked fifth in the total production had a maximum leaf fall in the wet season with a minimum in the dry season (Figure 5.16).

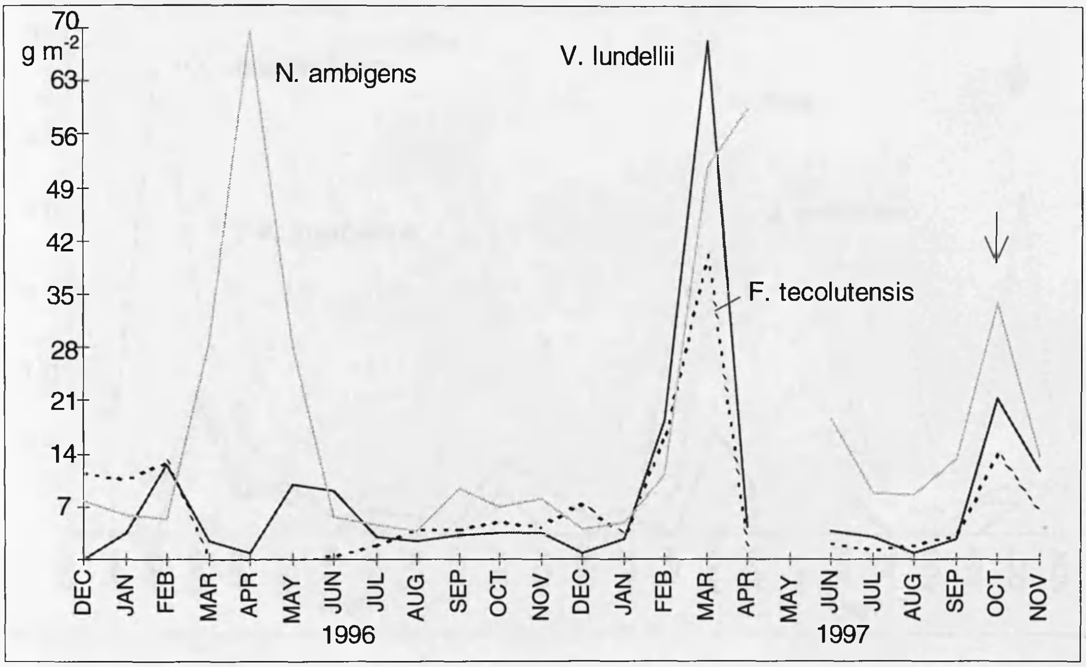


Figure 5.8. Leaf litterfall of species with a peak in the dry season (March - April) in three (0.25 ha) plots. Ficus tecolutensis (n=1), Nectandra ambigens (n=16), and Vatairea lundellii (n=2). n = number of individuals of ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

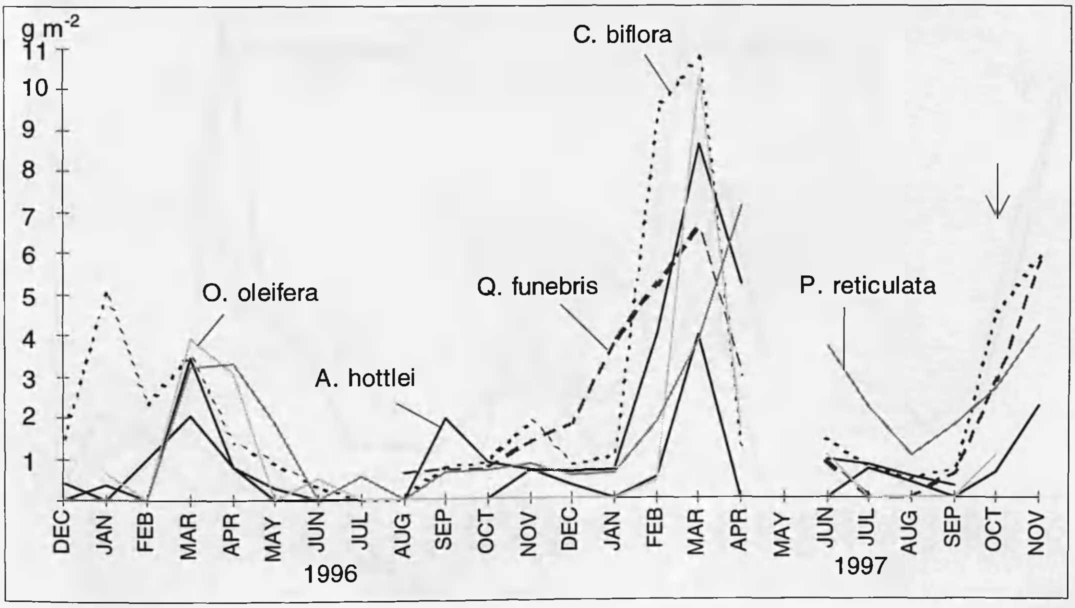


Figure 5.9. Leaf litterfall of species with a peak in the dry season (March - April) in three (0.25 ha) plots. Ampelocera hottlei (n=2), Clarisia biflora (n=1), Omphalea oleifera, Pouteria reticulata (n=1), Quararibea funebris (n=3) and Sideroxilon portorisence. n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

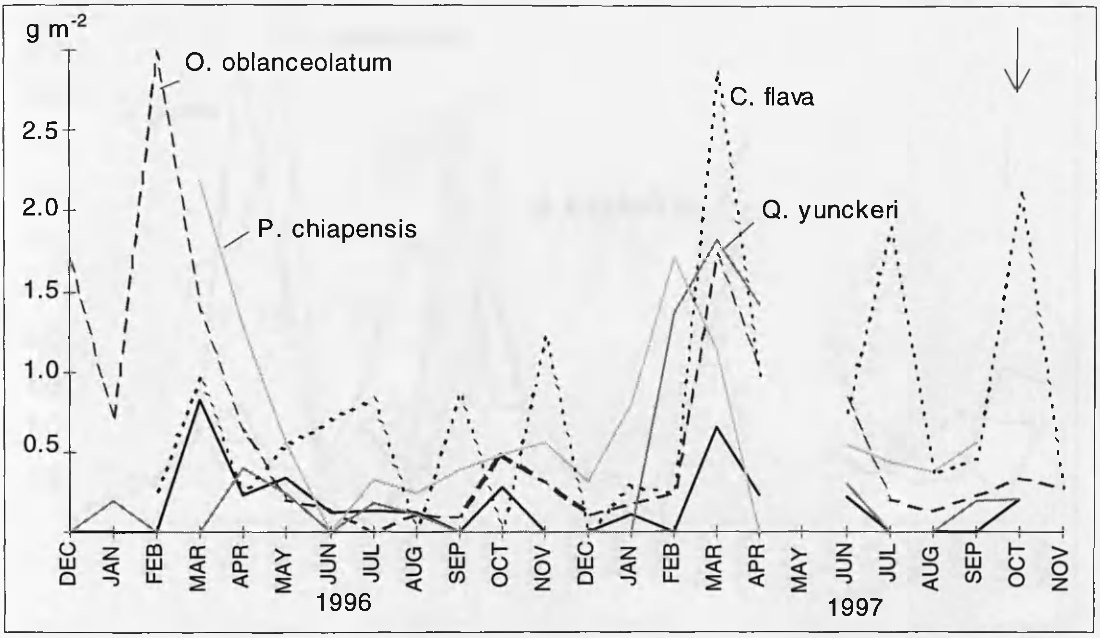


Figure 5.10. Leaf litterfall of species with a peak in the dry season (March - April) in three (0.25 ha) plots. Clusia flava, Dendropanax aroboreus, Orthion oblanceolatum (n=17), Psychotria simiarum (n=9) and Q. yunckeri (n=6). n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a ‘norte’ wind.

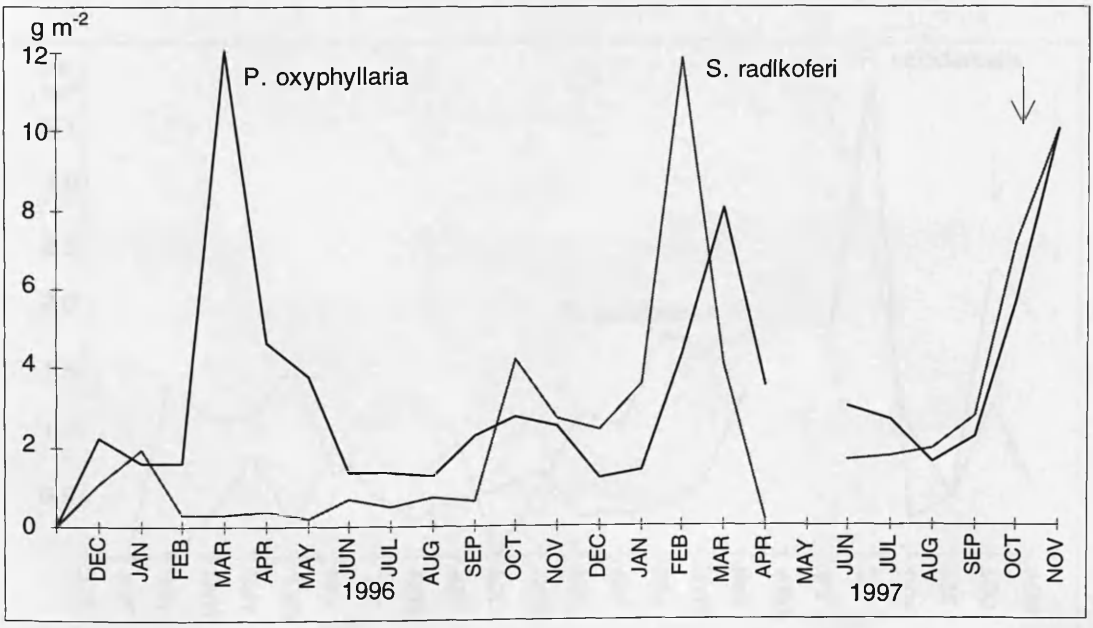


Figure 5.11. Leaf litterfall of species with a peak in the dry season and a second peak at the beginning of the ‘norte’ season (August - November) in three (0.25 ha) plots. Pseudolmedia oxyphyllaria (n = 29) and Spondias radlkoferi (n=13). n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a ‘norte’ wind.

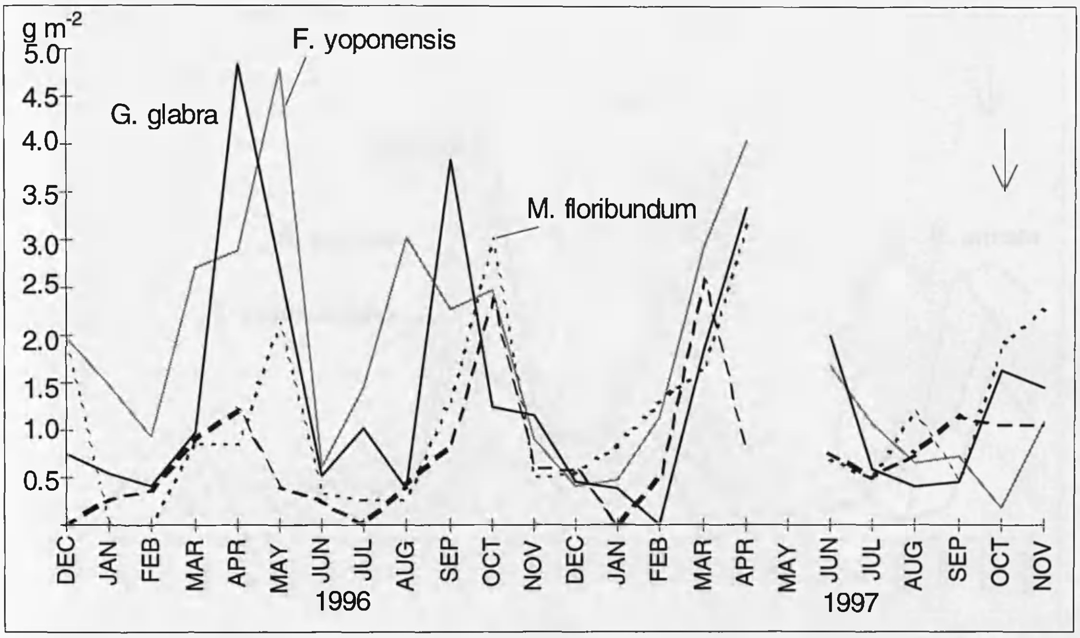


Figure 5.12. Leaf litterfall of species with a peak in the dry season and a second peak in the beginning of the 'norte' season (August - November) in three (0.25 ha) plots. Guarea glabra (n=10), G. grandifolia, Ficus yoponensis and Machaerium floribundum (n=1). n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

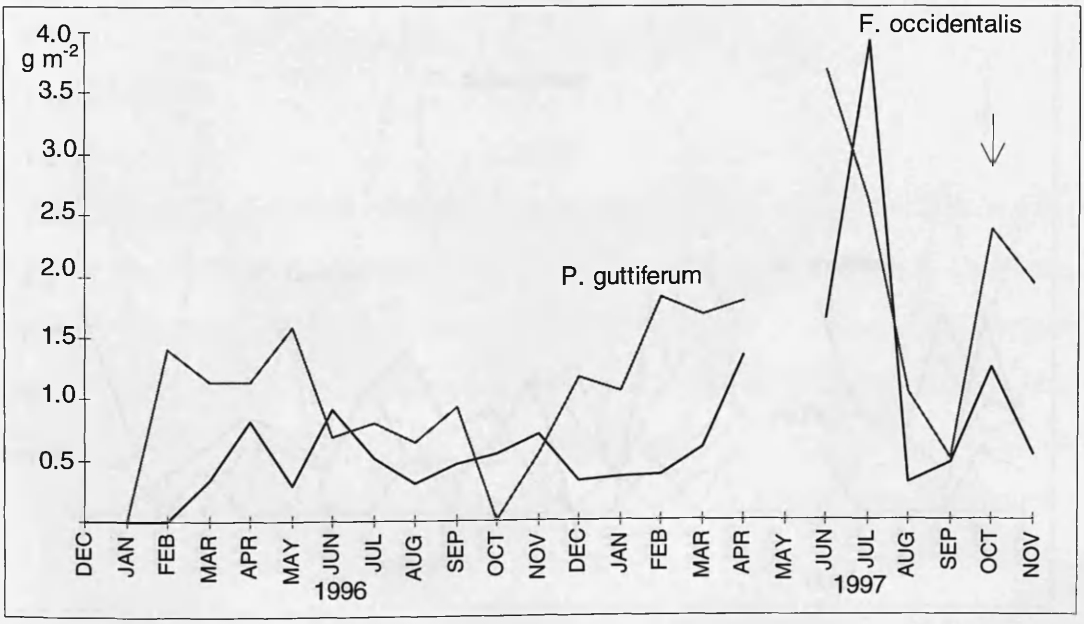


Figure 5.13. Leaf litterfall of species with a peak at the beginning of the rainy season (June and July) in three (0.25 ha) plots. Faramea occidentalis (n=31) and Philodendron guttiferum. n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

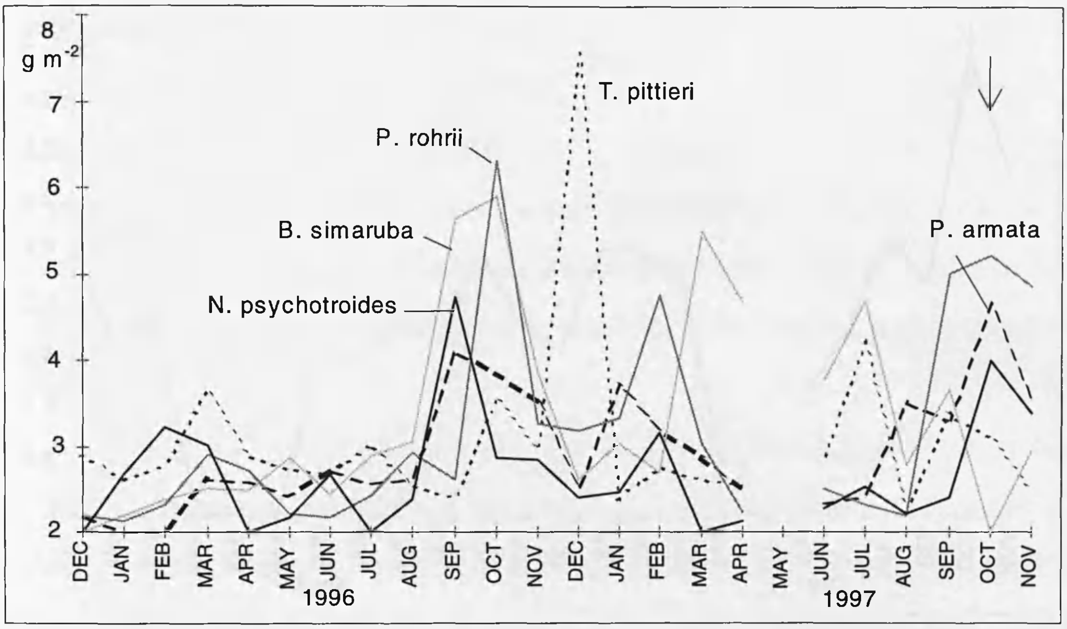


Figure 5.14. Leaf litterfall of species with a main peak half way through the 'norte' season (September-December) in three (0.25 ha) plots. Bursera simaruba, Neea psychotroides (n=2), Poulsenia armata (n=8), Pterocarpus rohrii (n=3) and Tuxtla pittieri. n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

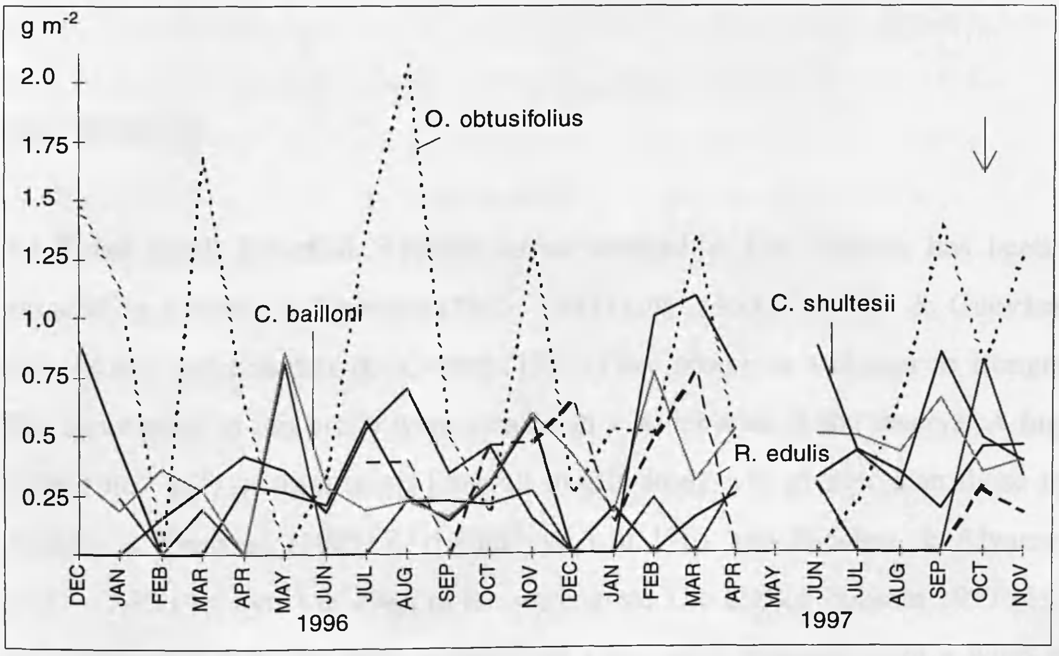


Figure 5.15. Leaf litterfall of species which drop their leaves throughout the year in three (0.25 ha) plots. Connarus shultesii, Cymbopetalum baillonii (n=4), Oreopanax obtusifolius, Rheedia edulis (n=9), Serjania goniocarpa and Tetracera volubilis. n = number of trees ≥ 10 cm dbh present in the plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

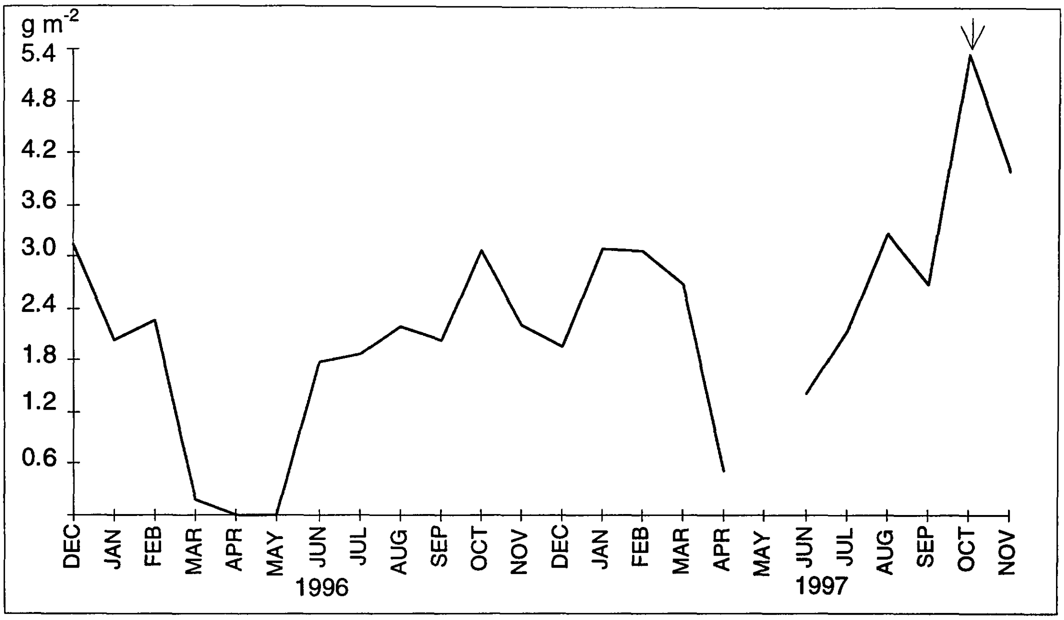


Figure 5.16. Leaf litterfall of the liana Forsteronia viridescens with a peak in the wet season with a minimum in the dry season in three (0.25 ha) plots. Data for May 1997 are missing. The arrow indicates the occurrence of a 'norte' wind.

DISCUSSION

A) Total small litterfall. Mature forest litterfall at Los Tuxtlas has been studied already by Alvarez & Guevara (1985, 1993) (one plot), Carabias & Guevara (1985) (two plots), and Sanchez & Alvarez (1995) (two plots), in and near to Bongers' plot. The three plots in this study were located in a wider area of the reserve. A high value (10.6 t ha^{-1} yr^{-1}) of total small litterfall in this study was greater than those found by Alvarez & Guevara (1985) (7.6 t ha^{-1} yr^{-1}) in 1982 and Sanchez & Alvarez (1995) (5.77 - 7.33 t ha^{-1} yr^{-1}) in 1986 in the same area. The higher value in 1997 (13.2 t ha^{-1} yr^{-1}) compared with the 1996 value (7.93 t ha^{-1} yr^{-1}), resulted from a wind storm in October 1997 (Figure 5.2) which dislodged much small wood and fruits (Figure 5.3 and Figure 5.4). Proctor *et al.* (1983b), Herbohn & Congdon (1993) and Brouwer (1996) observed a similar effect owing to strong winds and heavy rains. Herbohn &

Congdon (1993) claimed that the causes of this bimodal pattern of litterfall may be related to the washing down of litter retained in the canopy. A range of small litterfall production of 5.7 t ha^{-1} yr^{-1} in a heath forest in Venezuela to 12.4 t ha^{-1} yr^{-1} in Zaïre can be found for lowland evergreen tropical rain forests (Proctor 1984). It can be seen that the mean values for the Los Tuxtlas forest are in the mid-range of values of total small litter production, but this involves a low value in 1996 combined with a high value of 1997.

As Proctor (1983) pointed out, few papers on litterfall production have been concerned about the precision of the estimates. He recommended that the use of 20 litter traps or more to give 95% confidence limits which are less than 10% of the means for all fractions and total litterfall. In this study, confidence limits for the total small litterfall were wide (16 - 19% depending on the plot) considering the high number of replicates (44 traps). Confidence limits for each litterfall fraction separately could not be obtained from my data but they may be wider (Villela 1995). Carabias (1979) estimated that the understorey (0 - 5.5 m) represented 33.3% of the leaf cover of the Los Tuxtlas forest, and the palm Astrocaryum mexicanum, which has the highest dominance value in this stratum, is a species which retains leaf litterfall from the upper canopy owing to the inverted cone shape of the branches with thorns. Alvarez & Guevara (1985) collected leaf litter retained in 10 palms during one year and found that they retained about 3.7% of the total leaf litterfall. The density of this palm was not measured in my work but in the Bongers' plot was 2,324 individuals ha^{-1} (> 0.5 m height) (Bongers *et al.* 1988).

The largest component of the forest litterfall is leaves which were 60% of the total litter (6.3 t ha^{-1} yr^{-1}). Lower values of 5.5 t ha^{-1} yr^{-1} and 3 - 4 t ha^{-1} yr^{-1} were found by Alvarez & Guevara (1985) and Sanchez & Alvarez (1995). The result of Alvarez & Guevara (1985) might be an underestimate since there were long intervals (31-52 days) between collections in the wet season when leaves might be partly decomposed. Other workers have reported that between 54% and 74% of tropical forest small litterfall is leaves (Table 5.2). At Los Tuxtlas leaf production had its maximum value in the dry season which was 43.1% of the annual production. Luizão

(1989) recorded between 45.0% and 50.2% of the annual leaf fall in the dry season in a forest near Manaus, Brazil. High dry season leaf litterfall was observed in many tropical rain forests (Hopkins 1966, John 1973, and Birk & Simpson 1980) and it can be interpreted as a strategy for avoiding or reducing water loss (Longman & Jenik 1987). Van Schaik *et al.* (1993) suggested that higher irradiance associated with the flushing of new leaves might be more important than water stress. Other causes that may favour leaf abscission in the tropics are: shortening of day length, low light intensities, leaf age, mineral deficiency, and physical damage (Longman & Jenik 1987). Several litterfall peaks had been reported in the wet season (Lugo *et al.* 1979, Brasell *et al.* 1980, Proctor *et al.* 1983b, and Spain 1984), but they are likely to be associated with wind and species seasonal pattern of leaf shedding (Proctor *et al.* 1983b). Hopkins (1966) and John (1973) associated litterfall also with wind activity. There is a strong relation between leaf fall and the growing of new leaves (Njoku 1963, Medway 1972, Frankie *et al.* 1974 and Carabias & Guevara 1985). Monk (1966) suggested that perennial species reduce mineral loss from the ecosystem by continuous leaf fall and decomposition and slow mineral-nutrient release rates to the soil.

Although there seems to be a relationship between litterfall and the yearly weather pattern (Figure 5.6) and several authors (Gong & Ong 1983, Carabias & Guevara 1985, Luizão 1989 and Sanchez & Alvarez 1995) have related litterfall with rainfall at particular sites, it is difficult to show it statistically owing to the non-independent nature of the litterfall samples. Brinkmann (1985) and Carabias & Guevara (1985) have stressed the importance of short periods without rain rather than seasonal or annual patterns of rainfall. On a world scale Spain (1984) has shown weak relationships of leaf litterfall with latitude, altitude and precipitation. Vitousek (1984) considering tropical forests up to 20° N found small litterfall inversely correlated with latitude ($r^2 = 0.67$).

Comparing litter fractions with some studies from Brazil, Venezuela and Malaysia, the Los Tuxtlas proportions for leaves and fruits are in the middle, small wood in the low, and trash in the high range (Table 5.2). The smallest components are fruits and flowers, and trash. Fruits were only 7.5% of the forest litterfall at Los

Tuxtlas. Alvarez & Guevara (1993) found 3.1% and Sanchez & Alvarez (1995) 3 - 7% in the same area. Spain (1984) from an analysis of 22 studies around the world found a mean of 8.2%. Fruit litterfall was not consistent in my study but a marked difference in seasonal pattern was observed by Alvarez & Guevara (1985). In my study the lowest value was during December - March, and the highest peak in May in 1996, and in September and October in 1997. The October 1997 peak followed the storm at that time. In Alvarez & Guevara (1985) and Sanchez & Alvarez (1995) the lowest fruit fall was observed in June and the highest in August and November. Flower and fruit litterfall fractions are the most seasonal since they are highly dependent on species natural history and influenced by a changing climate (Carabias & Guevara 1985). Most fruit falling during the wet season might be related to a tree strategy for ensuring seed germination and seedling establishment (Alvarez & Guevara 1985). Alvarez & Guevara (1993) and Sanchez & Alvarez (1995) found for Los Tuxtlas between 0.6% and 2% of flowers as a proportion of the total litter biomass with the highest production during the dry season.

B) Leaf litterfall by species. One hundred and nineteen species (75% of the leaf litterfall dry weight) which contributed at least 1 g month^{-1} were identified. Alvarez & Guevara (1993) identified 114 species in the leaf litterfall and Sanchez & Alvarez (1995) 120 species. Ten tree species from the sampling plots (Appendix 1) were not found in the litterfall. This was mainly because no litter traps were near the trees, and for the case of the Mimosaceae species, Acacia hayesii and Albizia purpusii, leaflets of compound leaves were too small (< 2 cm long) to be sorted and were hence included in the miscellaneous fraction. There were 49 species found in the leaf litterfall which were not censused in the forest plots (Appendix 3). These species came from stems (< 10 cm dbh) of trees, palms, and lianas; epiphytes; and from stems adjacent to the plots, and contributed with 9.8% of the total leaf litterfall. There were 34 species of lianas, epiphytes and hemi-epiphytes in the litterfall which suggests that litterfall analysis could be a method of sampling species richness in these life forms.

Table 5.4 shows that the species with the highest basal area, Nectandra ambigens, contributed 22.6% to the total leaf litterfall, and was followed by Spondias radlkoferi (8.5%) and so on down to 2% with a contribution from only 10 species. Ninety-eight species contributed to 19.5% (Figure 5.7). Depending on the year, Alvarez & Guevara (1993) reported 12.3 and 28.6% for N. ambigens, 3.4 and 10.3% for Pseudolmedia oxyphyllaria, and 4.0 and 5.9% for Poulsenia armata with the five most important species providing between 26 and 55%. In Sanchez & Alvarez (1995) seven species provided 60% of leaf litterfall in one site and six species 47% in another site. In Sabah, Malaysia the six and 16 most productive species in two plots contributed 36% and 58% respectively from the total leaf litterfall (Burghouts 1993). Comparing Tables 5.3 and 5.4 with Appendix 2 and Table 3.3, most dominant tree families and species accounted for the dominant leaf litterfall production with the exception of the liana F. viridescens which had a disproportionately high litterfall contribution but was not abundant as stems ≥ 10 cm dbh in the plots. Small litterfall production appeared better correlated with tree basal area than with the tree density. Similarly Burghouts (1993) found in Malaysia a correlation of 0.8 with basal area and 0.71 with tree density at a family level. However within forest type and between forest types the relationship of litterfall and basal area was not clear. In Brazil, Villela (1995) did not find a significant difference in leaf litterfall among three forest types with different basal areas, although Luizão (1995) did find such a relationship but with more contrasting forest types (Table 5.7). Tanner (1980) based on montane rain forests emphasized that small litterfall is an unreliable estimate of above-ground production.

At Los Tuxtlas 75% of the leaf litter fell from the canopy species, 19.6% from the mid-canopy and 5.4% from the understorey species (Table 5.6); and in Sabah, Malaysia, 39% from the emergent trees, 37% from the canopy species, 10% from the understorey and 13% from climbers (Burghouts 1993).

Table 5.7. Basal area (BA, $m^2 ha^{-1}$) and litterfall production ($t ha^{-1} yr^{-1}$) for three plots in Los Tuxtlas, Brazil and Malaysia.

	Author	Lowland rain forest	BA	Litterfall
	This study	Plot 1	32.0	11.07
Within forest type		Plot 2	32.4	10.25
		Plot 3	35.2	10.42
	Villela (1995)	Forest without *Peltogyne*	27.2	8.60
		Peltogyne-rich forest	32.8	7.90
		Peltogyne-poor forest	33.1	9.07
	Luizão (1995)	Small heath forest	9.5	3.80
Among forest types		Tall heath forest	16.6	6.26
		Lowland evergreen forest	31.0	7.76
	Proctor *et al.* (1983b)	Alluvial forest	28.0	11.5
		Dipterocarp forest	57.0	8.80

C) Temporal patterns of leaf litterfall by species. Even in seasonal tropical forests, where the dry season is long enough to result in a generally large peak in leaf fall, tree species differed in their temporal pattern of leaf fall (Frankie *et al.* 1974, Kunkel-Westphal & Kunkel 1979). In a seasonal tropical forest these differences are more pronounced (Medway 1972, Addicott 1978) and are expected to cause a heterogeneous mosaic of leaf fall and litter mass on the forest floor (Heatwole 1961, Medway 1972). This mosaic pattern may reflect differences among individual trees, species or families, and on a large scale, among phases of the forest canopy (Burghouts 1993).

At Los Tuxtlas from the 34 most productive species (28.6% of the total identified), most drop their leaves in the dry season and during strong winds. Most species as shown in Figure 5.7 have too small a leaf fall to detect a seasonal pattern. Although not clearly shown by my own data (Figure 5.6, Chapter 2) and as discussed previously, higher wind speeds and lower temperatures may be an important factor in the leaf fall, and the peak of many species from October to December might be related to this. Sanchez & Alvarez (1995) from a fraction of a total of 120 leaf litter species defined three groups with respect to their peak litterfall: dry season, wet season and windy season. Between 40% and 52% of the species were in the dry-season group depending on the site, around 5% in the wet-season, and less than 10% in the windy-season. Some species in my study fitted Sanchez & Alvarez's (1995) groups: Guarea glabra, Ficus yoponensis, Nectandra ambigens, Pseudomedia oxyphyllaria, and Pterocarpus rohrii. Others did not: Bursera simaruba, Cymbopetalum bailloni, Forsteronia viridescens, Rheedia edulis and Spondias radlkoferi. I also found species with a continuous leaf fall, including understorey tree species; and two species with a leaf loss at the beginning of the rainy season. Shrubs tend to have more regular patterns from year to year than trees (Carabias & Guevara 1985). Villela (1995) found very small variation in palm leaf litterfall over the year and among different forest types in Brazil. Surprisingly Sanchez & Alvarez (1993) showed for the same species, different seasonal patterns in different study sites during the same study period, which exemplifies the high variation at the individual level (Carabias & Guevara 1985). Cycles of leaf renewal can be of variable length and are not necessarily synchronized among individuals (Chabot & Hicks 1982, Burghouts 1993). Burghouts *et al.* (1992) emphazised the importance of litterfall spatial variation and found a high variation in a 4 ha plot as a result of the variable composition and structure of the vegetation. In my work a spatial effect on total small litterfall at a scale of 0.25 ha plots was found.

Carabias & Guevara (1985) in a five-year study at Los Tuxtlas showed that flowering is in the dry season, and fruiting takes place in October when a second leaf fall peak is produced. Rathcke & Lacey (1985), Frankie *et al.* (1974) and Janzen (1967) provided an explanation of this asynchrony in phenology and proposed that leaf fall exposed the reproductive parts to pollinators and dispersal events.

The length of this study (22 months) as in many others was too short to ensure that the litterfall pattern was consistent, although Carabias & Guevara (1985) found a consistency in seasonal patterns of leaf and flower shedding during five years of study in Los Tuxtlas.

Chapter 6. LITTERFALL NUTRIENTS

INTRODUCTION

In forest ecosystems litterfall plays a fundamental role in the cycling of nutrients and in the transfer of energy between plants and soil (Bray & Gorham 1964, Herrera *et al.* 1978, Cuevas & Medina 1986). On weathered, nutrient-poor soils the vegetation may depend on the recycling of the nutrients contained in the litterfall (Singh 1969, Proctor *et al.* 1983b). Nutrients are also returned in throughfall and rainfall and added to the forest in atmospheric depositions (Brasell & Sinclair 1983). In a Mixed forest in Guyana, from the total mineral input of N, P, K, Ca and Mg, 1.8% was returned in atmospheric depositions, 4.8% in throughfall, 33.8% in small litterfall, 7.3% in coarse litterfall and 52.3% in the root-mat (Brouwer 1996).

METHODS

The sampling of litterfall and the estimation of its mass were described in Chapter 5. Leaf litterfall element analysis was made on the 16 tree species with most leaf litterfall and which accounted for 68% of the total mass of leaf litterfall (Table 5.3). Five g of freshly (< 3 days) fallen leaves were collected during September 1997 (rainy season) from the forest floor under each of three trees (≥ 10 cm dbh) for each species and dried at 40 °C. For Forsteronia viridescens (liana) leaves were collected in one site only.

Small wood, fruits and seeds, and trash for nutrient-element analyses were obtained from the dried material collected for the litterfall mass study (Chapter 5). In each case a sample of 5 g dry weight was obtained from each of the three undisturbed forest plots from the bulked collection of the 44 litter-traps. Samples from six months, two from the dry season (April and May) and four from the wet season (June, August, October and December) were analyzed. For a comparison between dry and wet season, April and May (dry) and August and October (the wettest) were used.

N was analyzed by microkjeldahl digestion with sulphuric acid and distillation with boric acid, indicators (0.01 g of bromocrosol and 0.07 g of methyl red in 95% of ethanol), and sodium hydroxide. This was followed by titration with sulphuric acid (0.01 N) using methyl orange as an indicator. P, K, Ca and Mg were analyzed by digestion with nitric acid (HNO_3) and perchloric acid ($HClO_4$) (2:1) for a minimum of 12 h. The determination of P was done in a 7.5 ml of vanadomolybdenum-phosphorus complex by photometry at 470 nm, and by atomic absorption spectophotometry for the rest of the elements.

I used a Student's t-test for equal and unequal variance and a one-way ANOVA. A Tukey means comparison test was applied to the ANOVA results. When data did not match the assumptions for a parametric test, a $\log_e$ transformation was applied, and if still did not match, a non-parametric Mann-Whitney test for two samples and à Kruskal-Wallis test for three or more samples were used. In the latter case a Tukey medians comparison test was applied (Zar 1984). In all cases analyses were on balanced designs (number of replicates were equal).

RESULTS

Table 6.1 shows the mean element concentrations for the four small litterfall fractions for each element. Leaf fraction concentrations were calculated using a weighted mean to reflect the contribution from each of the 16 species from Table 6.2. The weighting was made by multiplying the mass of each species of leaf litter by its element concentration and then the total was divided by the total mass of litterfall of the 16 species. Table 6.2 shows the mean element concentrations for the freshly fallen leaves from the 16 tree species which have the highest representation in the litterfall. Table

6.3 shows the estimated rate of addition of each element for the total small litterfall and for each fraction.

Because it was only possible to analyse a limited number of samples, leaf litterfall nutrient concentrations could only be analysed for one collection date and hence there is no information on their temporal variations. Analyses for more than one collection date were possible for the other fractions however. There were no significant variations during the year in N with the exception of fruit litterfall which had a peak in June (Figure 6.1). P seemed to change only in the trash litter and decreased towards the end of the year (Figure 6.2). K concentrations in fruit and trash litter showed several indistinct peaks, and small wood did not show any significant change (Figure 6.3). Ca had higher concentrations in small wood in the dry season, the fruits had a peak concentration in June, and the trash litter did not show any significant change (Figure 6.4). Mg showed a peak in March for small wood and fruit litter, and only trash litter seemed to decrease consistently with the advance of the year (Figure 6.5). In the total small litterfall P and K concentrations were higher during the dry than the wet season (Table 6.4).

Table 6.1. One-way ANOVA[1] (means) and Kruskal-Wallis[2] (medians) tests for the weighted mean mineral concentrations (mg g^{-1}) of small-litter fractions. n = 18. Different superscript letters indicate a significant difference between means within a column (Tukey test, $p \leq 0.05$).

	N	P	K	Ca	Mg
Leaf	11.0^{ab}	1.14^{a}	10.1^{a}	24.6^{a}	4.8^{a}
Small wood	9.1^{a}	1.08^{a}	2.5^{b}	20.0^{ab}	3.0^{bc}
Fruits and seeds	13.2^{bc}	1.59^{b}	12.4^{a}	11.0^{c}	3.0^{bc}
Trash	22.9^{c}	1.87^{b}	4.5^{b}	16.5^{bc}	4.0^{ac}
p	$< 0.0001^{2}$	$<0.0001^{1}$	$= 0.0001^{2}$	$<0.0001^{2}$	$<0.0001^{2}$

Note: The leaf fraction comes from 16 leaf species with three replicates each (Table 6.2) and was estimated by multiplying the mass of each species leaf litter by its element concentration and then the total was divided by the total litterfall mass of the 16 species.

Table 6.2. Mean mineral element concentrations (mg g^{-1}) with the range (for three replicates) in parenthesis in leaf litterfall from 16 species collected during September 1997. The percentage contribution to the mass of the total leaf litterfall is given in the first column. Maximum and minimum mean values for each element are in bold.

	%	N	P	K	Ca	Mg
Nectandra ambigens	22.6	10.1	1.6	11.6	28.7	3.3
		(9.1-11.9)	(1.2-2.0)	(7.3-16.3)	(25-35)	(2-5)
Spondias radlkoferi	8.5	10.4	0.9	***4.8***	26.7	5.3
		(9.3-11.1)	(0.8-1.0)	(4.0-6.0)	(25-30)	(4.0-6.0)
Vatairea lundelli	8.4	11.8	0.9	7.5	14.0	5.7
		(11-12.7)	(0.8-1.0)	(6.7-8.0)	(9-17)	(4.0-7.0)
Pseudolmedia oxyphyllaria	6.3	12.8	0.8	11.0	15.3	5.7
		(12-13.3)	(0.7-0.85)	(8.3-12.7)	(14-40)	(5.0-6.0)
Forsteronia viridescens	5.8	12.6	0.8	***18.7***	19.3	4.3
		(10.1-15.2)	(0.7-0.9)	(17.7-20.7)	(18-21)	(4.0-5.0)
Ficus tecolutensis	3.7	8.6	0.8	8.0	18.7	4.3
		(7.1-10.2)	(0.7-0.9)	(7.7-8.7)	(18-19)	(4.0-5.0)
Poulsenia armata	2.9	9.5	1.2	13.8	31.7	6.3
		(8.4-10.1)	(1-1.3)	(10-16.3)	(30-35)	(6.0-7.0)
Pterocarpus rohrii	2.7	13.9	1.5	8.0	25.3	6.7
		(12.2-16)	(0.8-2.0)	(4.0-10.0)	(25-26)	(5.0-8.0)
Ficus yoponensis	2.2	9.9	0.5	9.4	***51.7***	***13.7***
		(7.9-11.2)	(0.1-0.8)	(6.0-11.3)	(35-80)	(12-15)
F. petenensis	1.5	7.7	0.6	5.0	38.3	2.2
		(7.2-8.3)	(0.5-0.7)	(3-8)	(30-45)	(1.9-2.5)
Orthion oblanceolatum	1.0	***22.7***	1.9	12.7	23.3	7.0
		(22.1-23.2)	(1.6-2.3)	(12-13.3)	(18-30)	(6-8)
Faramea occidentalis	0.9	12.4	0.8	4.9	24.0	***3.0***
		(11.3-13.6)	(0.7-0.9)	(2.7-7.3)	(21-26)	(1.0-4.0)
Rheedia edulis	0.5	7.9	0.5	5.0	***11.7***	1.7
		(7.6-8.3)	(0.4-0.6)	(4.3-6.0)	(11-13)	(1.0-2.0)
Cecropia obtusifolia	0.3	11.9	1.7	9.6	21.0	5.0
		(10.3-13.3)	(1-2.3.0)	(7.7-11.3)	(20-23)	(3.0-7.0)
Trichospermum mexicanum	> 0.1	***7.1***	***0.4***	6.4	19.7	8.3
		(6-8.9)	(0.3-0.6)	(4.3-8.7)	(19-21)	(7.0-11)
Heliocarpus appendiculatus	0.1	10.3	***2.3***	16.7	23.7	9.0
		(9.2-11.7)	(1.6-3.0)	(12.7-22.3)	(19-27)	(5.0-12)

Table 6.3. Estimated rate of addition (kg ha^{-1} yr^{-1}) of mineral elements for total and small litterfall fractions Los Tuxtlas, México. Since the miscellaneous fraction was not chemically analysed, it was calculated using the mean mineral concentrations of the trash fraction.

	N	P	K	Ca	Mg
Total small litterfall	144.5	13.9	88.2	225.8	52.0
Leaf	70.6	7.2	63.5	154.0	35.9
Branches	12,6	1,4	4,7	27,8	4,5
Fruits	11,6	1,2	9.0	8,5	2,5
Miscellaneous	28.9	2.4	5.7	20.8	5.05
Trash	20,8	1,6	5,3	14,5	4,1

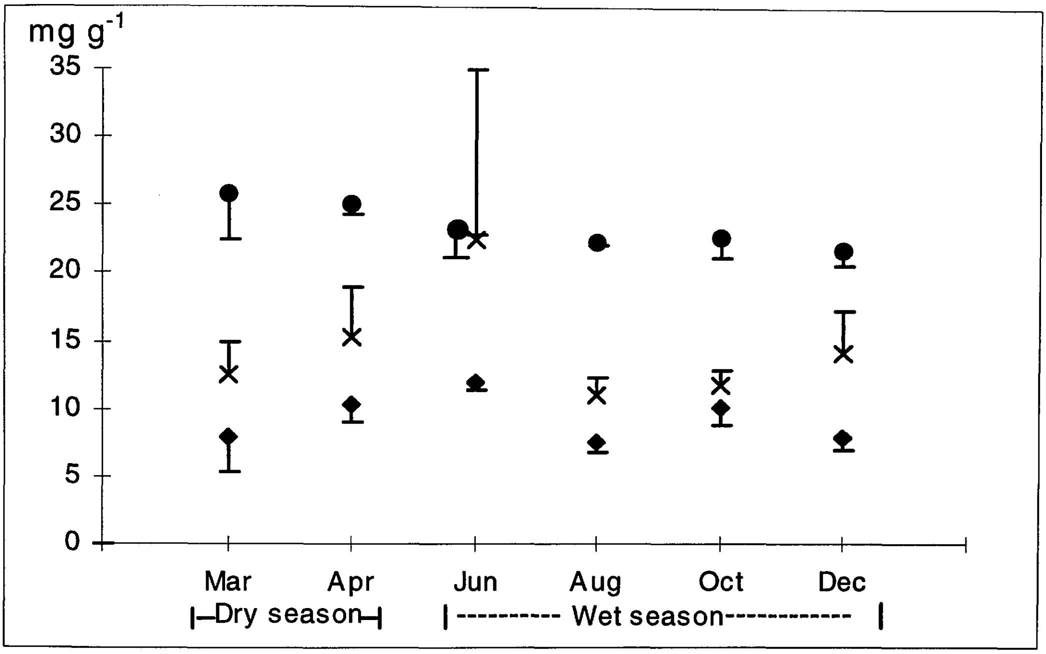


Figure 6.1. Mean ± S.D. concentrations of N in small wood (◆), fruits and seeds (x), and trash (●) from the three forest plots.

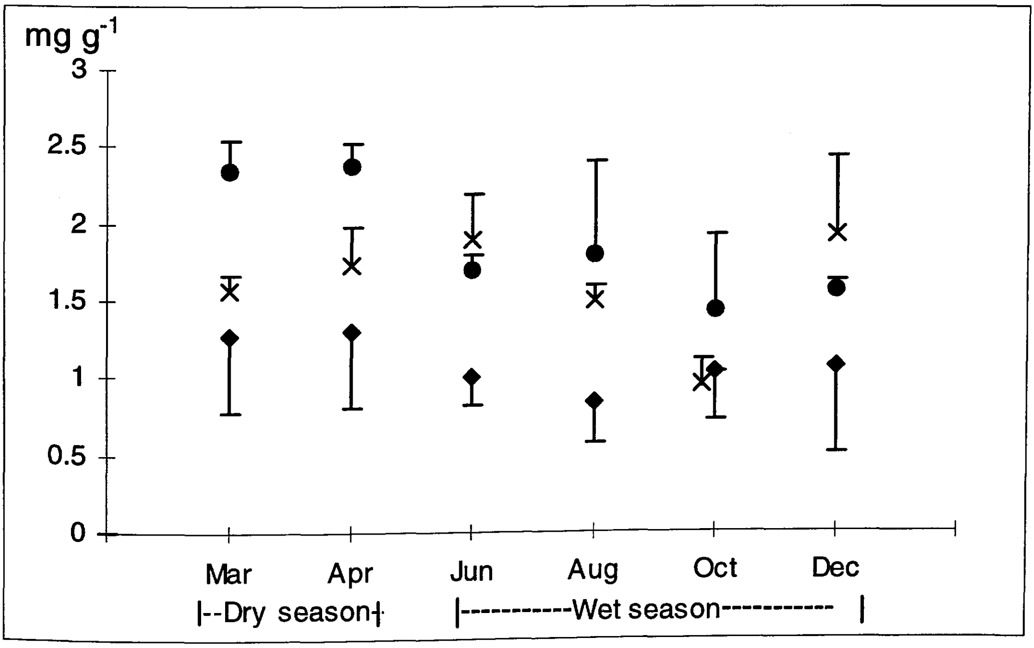


Figure 6.2. Mean ± S.D. concentrations of P in small wood (◆), fruits and seeds (x), and trash (●) from the three forest plots.

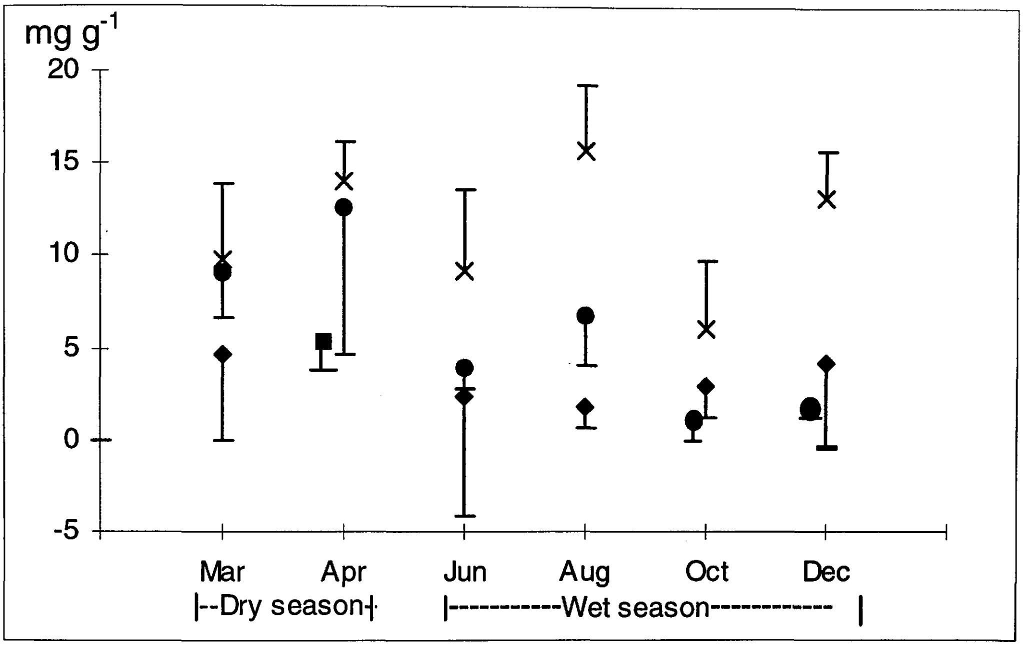


Figure 6.3. Mean ± S.D. concentrations of K in small wood (◆), fruits and seeds (x) and trash (●) from the three forest plots.

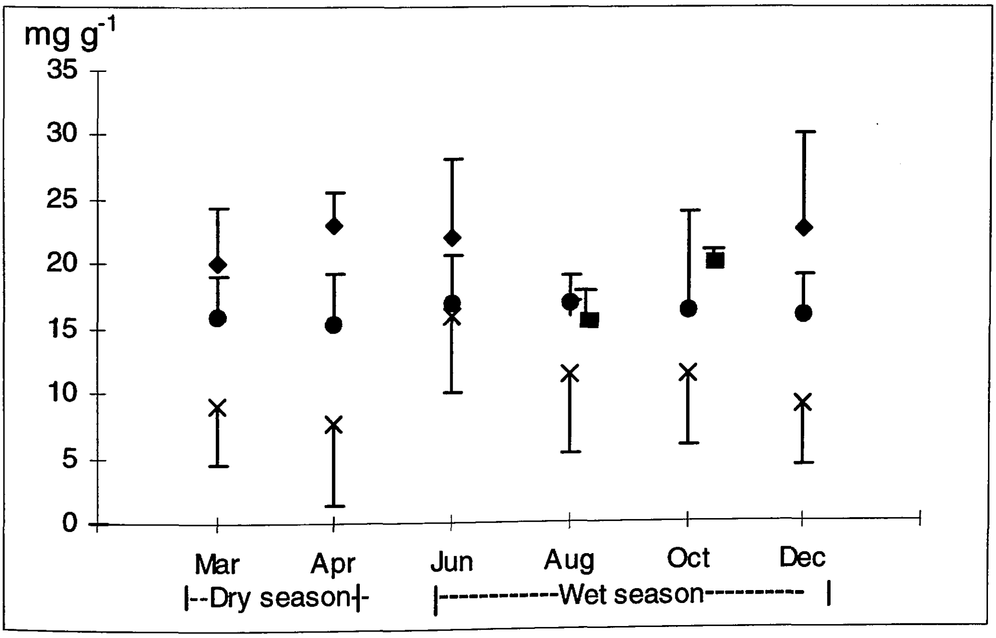


Figure 6.4. Mean ± S.D. concentrations of Ca in small wood (◆), fruits and seeds (x) and trash (●) from the three forest plots.

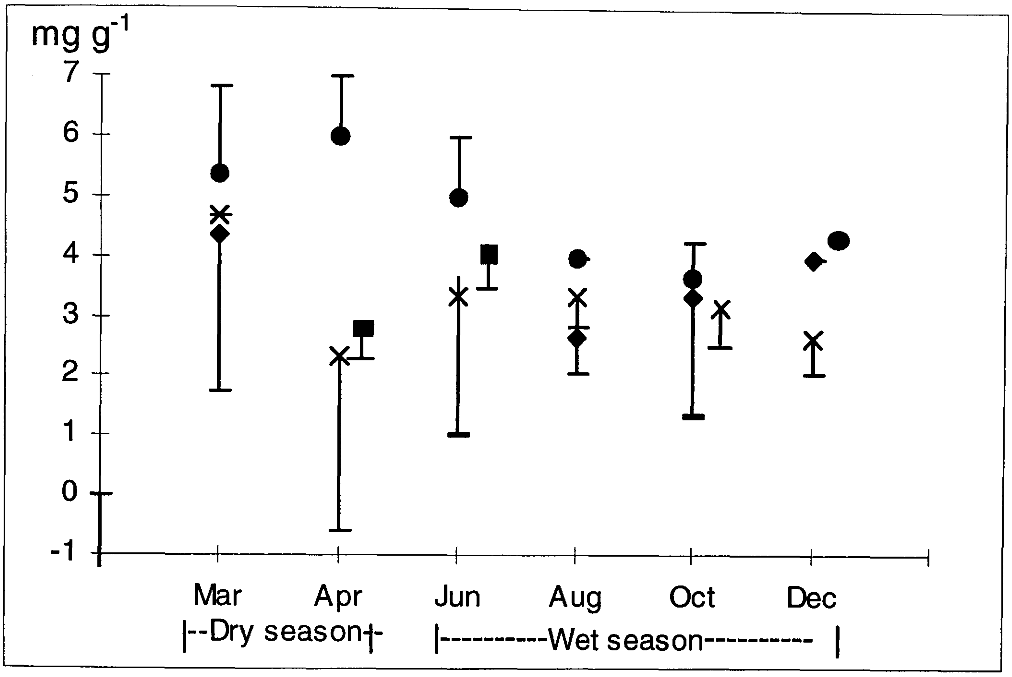


Figure 6.5. Mean ± S.D. concentrations of Mg in small wood (◆), fruits and seeds (x), and trash (●) from the three forest plots.

Table 6.4. Student-t test[1] (means) and Mann-Whitney[2] test (medians) for mineral element concentrations (mg g^{-1}) of total small litter (n = 18) and small litter fractions (n = 6) between dry (March and April) and wet (August and October) seasons.

		N	P	K	Ca	Mg
Total	Dry	11.1	1.76	9.18	15.16	3.5
	Wet	13.2	1.25	5.86	15.3	3.0
	p	n.s.[2]	<0.005[1]	<0.05[1]	n.s.[1]	n.s.[2]
Small wood	Dry	9.16	1.28	4.83	21.5	3.0
	Wet	8.86	0.93	2.43	18.0	3.0
	p	n.s.[1]	n.s.[1]	n.s.[1]	<0.05[1]	n.s.[2]
Fruits & seeds	Dry	13.9	1.65	11.9	8.33	3.0
	Wet	11.4	1.21	10.8	11.3	3.0
	p	n.s.[1]	<0.02[1]	n.s.[1]	n.s.[1]	n.s.[2]
Trash	Dry	25.4	2.35	10.7	15.6	5.5
	Wet	22.4	1.61	4.28	16.6	4.0
	p	<0.01[1]	<0.003[1]	<0.02[1]	n.s.[1]	<0.01[2]

DISCUSSION

During the study there was a maximum of 15 days between litterfall collections. Swift *et al.* (1981) found a quick release of K (by leaching) and a slow release of Ca during leaf litterfall decomposition. Since trash is small fragmented material it is more prone to leaching and may be one reason for showing more seasonal differences in mineral concentrations. N and P concentrations (mg g^{-1}) were higher in trash and lower in small wood, K was higher in fruits and seeds and lower in small wood, and Ca and Mg were higher in leaf and trash litter, and lower in fruit litterfall (Table 6.1). Ca was particularly high in small wood. The estimated rate of addition (kg ha^{-1} yr^{-1}) to the soil for all the elements was highest in leaf litterfall and lowest in fruit litterfall with the exception of K. Leaf litterfall provided a high input to the soil of all the mineral elements. Litterfall mineral-element addition was chiefly of N and Ca, then of K and Mg, and to a less extent of P (Table 6.3). The mineral addition from the miscellaneous fraction itself may be overestimated since it was calculated with the trash mineral concentrations which are high.

In my study K was higher in the dry season and had its highest concentration in trash litterfall. P was also highest in the dry season and was concentrated in the fruits. Scott *et al.* (1992) noticed a dry-season peak for K concentrations and to a lesser extent for leaf N. Leaf litterfall P seemed to peak in the wet season and early dry season. González-Iturbe (1988) in Los Tuxtlas for the same five elements analyzed with eight species, found only higher K concentrations in the leaf litterfall in the dry season. Bernhard (1970), Cornforth (1970), Cuevas & Medina (1986), Brasell *et al.* (1980) and Luizão (1989) did not find seasonal differences of litterfall elements. The higher nutrient concentrations in the dry season than in the wet season could be partly owing to leaching of the nutrients during the wet season by rain water (Larcher 1977, Brasell & Sinclair 1983). K particularly is a highly mobile element since it is not strictly fixed to any molecules (Medina 1984).

Mineral-element concentrations (mg g^{-1}) for small litterfall fractions at Los Tuxtlas, are all in the higher parts of the ranges of those elsewhere and Mg is the highest (Table 6.5). Leaf litterfall concentrations (mg g^{-1}) of P, K, Ca and Mg in Los Tuxtlas are also higher than the values collated by Scott *et al.* (1992) for a range of several Amazonian forests (N, 6 - 18; P, 0.20 - 0.71; K, 1.3 - 6.6; Ca, 1.5 - 7.7; Mg, 0.7 - 3.5). From several lowland evergreen rain forests around the world (Table 6.5), concentrations in the litterfall fractions can be ranked in the following manner: N, trash > flowers and fruits (FF) > leaves > small wood; P, trash and FF > leaves and small wood; K, FF > trash and leaves > small wood; Ca, small wood > trash and leaves > FF; and Mg, trash, FF and leaves > small wood. From Grubb & Edwards (1982) working in a montane forest it is possible to see that the distribution of mineral-elements in litterfall fractions reflects in a great extent the distribution in the living mass. Estimated rates of small litterfall production in Los Tuxtlas are relatively low compared with other lowland tropical forests but mineral-element concentrations are higher giving relatively high nutrient additions to the soil (Table 6.6). Dantas & Phillipson (1989) gave wider ranges (kg ha^{-1}) for other tropical rain forests in Africa, Asia, Central and South America: N (28 - 224), P (0.8 - 14), K (8 - 130), Ca (8 - 290), Mg (1 - 64).

Table 6.5. Mean element concentrations (mg g^{-1}) for small litterfall fractions in lowland tropical forests around the world.

	Forest type	N	P	K	Ca	Mg	Reference
Leaf	Alluvial forest	9.0	0.27	2.62	24.4	1.96	Proctor *et al.* (1983b),
	Dipterocarp forest	9.5	0.10	4.47	1.51	1.07	Sarawak, Malysia
Branches	Alluvial forest	7.1	0.17	1.30	28.8	1.22	
	Dipterocarp forest	6.2	0.04	1.82	1.32	0.66	
Flowers and Fruits	Alluvial forest	11.9	0.72	4.00	13.8	1.60	
	Dipterocarp forest	11.6	0.50	4.82	1.33	1.12	
Trash	Alluvial forest	14.2	0.75	2.10	23.8	1.61	
	Dipterocarp forest	13.1	0.41	3.43	2.07	1.27	
Total	Alluvial forest	10.5	0.48	2.50	22.7	1.59	
	Dipterocarp forest	10.1	0.26	3.63	1.55	1.03	
Leaf	Plateau	13.7	0.2	1.5	3.8	1.8	Luizão (1989),
	Valley	17.8	0.3	3.3	7.7	2.1	Brazil
Branches	Plateau	12.5	0.3	1.9	6.5	1.4	
	Valley	16.7	0.4	2.2	10.1	1.6	
Flowers and Fruits	Plateau	16.7	0.9	3.7	3.3	1.7	
	Valley	18.5	- -	4.2	4.6	2.0	
Trash	Plateau	20.0	0.7	2.2	4.5	1.6	
	Valley	22.9	0.8	3.0	7.2	1.7	
Total	Plateau	15.7	0.5	2.3	4.5	1.6	
	Valley	18.9	0.5	3.1	7.4	1.8	
Leaf	Lowland rain forest	12.6	0.57	4.67	7.36	2.66	Scott *et al.* (1992),
Branches	“ “	9.74	0.71	2.71	9.31	2.05	Brazil
Flowers and Fruits	“ “	14.6	1.30	10.7	4.81	2.63	
Trash	“ “	19.3	1.12	6.13	8.03	2.55	
Total	“ “	12.4	0.64	5.05	7.21	2.46	
Leaf	Lowland rain forest	11.4	0.33	6.1	5.9	3.0	Pendry & Proctor (1996)
Branches	“ “	7.9	0.22	3.7	7.0	2.7	Brunei
Flowers and Fruits	“ “	17.8	1.02	7.3	4.7	2.7	
Trash	“ “	20.8	0.85	3.7	5.5	2.2	
Total	“ “	14.5	0.60	5.2	5.7	2.6	
Leaf	Lowland tropical forest	14.2	1.33	10.9	20.9	4.5	Songwe *et al.* (1997),
Branches	“ “	0.9	1.22	5.8	23.8	1.9	Cameroon
Fruits	“ “	15.0	2.50	19.7	9.8	2.7	
Total	“ “	10.0	1.68	12.1	18.2	3.0	
Leaf *	Lowland rain forest	23.8	1.05	4.35	20.9	4.8	González-Iturbe (1988)
Leaf	Lowland rain forest	11,2	1,08	9,6	24,6	6,9	This study, Mexico
Branches	“ “	9,3	1,08	3,5	20,6	3,4	
Fruits	“ “	14,6	1,60	11,3	10,7	3,2	
Trash	“ “	23,4	1,90	6,0	16,3	4,7	
Total	“ “	14.6	1.40	7.6	18.1	4.5	

*) Mean of two years, México.

Table 6.6. Total small litterfall estimated rates of addition (kg ha^{-1} yr^{-1}) of mineral elements in lowland tropical forests around the world.

Forest type	N	P	K	Ca	Mg	Reference
Secondary tropical rain forest [1]	92.0	6.0	30.0	140.0	27.0	Swift *et al.* (1981)
Site 1 [2]	126.6	10.8	55.8	171.4	28.7	Brasell & Sinclair (1983
Site 2 [2]	130.2	11.3	64.3	211.2	30.6	Brasell & Sinclair (1983
Alluvial forest [3]	111.0	4.1	26.1	286.0	20.1	Proctor *et al.* (1983b)
Dipterocarp forest [3]	81.0	1.2	33.0	13.0	8.9	Proctor *et al.* (1983b)
Terra-firme rain forest [4]	- - -	2.2	12.7	18.4	12.6	Luizão & Schubart (1987)
Terra-firme rain forest [4]	115.0	3.6	28.5	114.2	15.9	Dantas & Phillipson (1989
Plateau [4]	109.0	3.1	15.0	36.7	13.8	Luizão (1989)
Valley [4]	151.0	3.7	22.2	58.2	14.0	Luizão (1989)
Lowland rain forest [4]	118.0	6.7	48.5	63.7	23.8	Scott *et al.* (1992)
Lowland rain forest [5]	122.0	3.9	60.0	64.0	31.0	Pendry & Proctor (1996)
Lowland rain forest *, [6]	137.2	5.7	19.9	120.7	33.9	González-Iturbe (1988)
Lowland rain forest [6]	144.5	13.9	88.2	225.8	52.0	This study

*) Mean of two years. Location:[1] = Nigeria , [2] = Australia, [3] = Sarawak, [4] = Brazil, [5] = Brunei, [6] = Mexico.

Table 6.7. Estimated rates of addition (kg ha^{-1} yr^{-1}) of elements of the litterfall fractions in lowland tropical forests around the world.

	Forest type	N	P	K	Ca	Mg	Reference
Leaf	Alluvial forest	59.0	1.8	17.0	160.0	13.0	Proctor *et al.* (1983b), Sarawak
	Dipterocarp forerst	51.0	0.56	24.0	8.1	5.8	
Branches	Alluvial forest	17.0	0.42	3.1	70.0	3.0	
	Dipterocarp forerst	13.0	0.08	3.7	2.7	1.4	
Flowers and Fruits	Alluvial forest	4.8	0.30	1.6	5.6	0.6	
	Dipterocarp forerst	3.1	0.13	1.3	0.3	0.3	
Trash	Alluvial forest	30.0	1.6	4.4	50.0	3.4	
	Dipterocarp forerst	14.0	0.45	3.7	2.3	1.4	
Leaf	Lowland rain forest	79.1	3.6	29.4	46.4	16.8	Scott *et al.* (1992), Brazil
Branches	" "	13.1	1.0	3.6	12.5	2.7	
Flowers and Fruits	" "	17.6	1.6	12.9	5.8	3.2	
Trash	" "	8.1	0.5	2.6	2.6	1.1	
Leaf	Lowland rain forest	90.0	2.6	48.4	46.1	23.5	Pendry & Proctor (1996), Brunei
Branches	" "	14.4	0.4	6.7	13.0	4.9	
Flowers and Fruits	" "	8.5	0.5	3.5	2.3	1.3	
Trash	" "	9.2	0.4	1.7	2.4	1.0	
Leaf	Lowland rain forest	71,5	6,8	61.0	156,7	44,2	This study, Mexico
Branches	" "	12,6	1,4	4,7	27,8	4,5	
Fruits	" "	11,6	1,2	9.0	8,5	2,5	
Trash	" "	20,8	1,6	5,3	14,5	4,1	

Chapter 7. NUTRIENT RESORPTION

INTRODUCTION

'At the ecosystem level nutrient resorption from senescing leaves has important implications for element cycling. The nutrients which are resorbed during senescence are directly available for further plant growth, which makes a species less dependent on current nutrient uptake. Nutrients which are not resorbed, however, will be circulated through litterfall' (Aerts 1996).

In lowland tropical rain forests mineral-element concentrations in leaf litterfall are in general lower than in fresh leaves which may reflect a possible mechanism of nutrient conservation of a limiting nutrient in plants (Edwards & Grubb 1982, Vitousek & Sanford 1986, Proctor *et al.* 1989, Thompson *et al.* 1992, Songwe *et al.* 1997).

METHODS

During September 1997 the fresh leaves of 12 tree species from the 16 species which had leaf litterfall nutrient-element analysis (Chapter 6) were selected for mineral-element analysis. Twelve species were used in order to have three species from each of species-life-history group (*sensu* Popma *et al.* 1992) and three species (regardless of their life history) to compare nutrient concentrations from sun and shade leaves. The 12 species were: obligate gap species (Cecropia obtusifolia, Heliocarpus appendiculatus and Trichospermum mexicanum); gap-dependent species (Nectandra ambigens, Spondias radlkoferi and Ficus tecolutensis); gap-independent species (Faramea occidentalis, Orthion oblanceolatum and Rheedia edulis); and Ficus yoponensis, Forsteronia viridescens and Pseudolmedia oxyphyllaria. From each of the same three trees per species used for the leaf litterfall collection (Chapter 6), 5-g dry-weight samples of fresh mature shade leaves were collected from the tree crown (not exposed to direct light) at a height of 5 -15 m. For Forsteronia viridescens (liana) fresh leaves were obtained from one stem only. For F. yoponensis, F. tecolutensis, N. ambigens and S. radlkoferi, shade and sun leaves from the light-exposed part of the canopy (about 15 m height) were collected. All leaves were dried at *c.* 40 °C for three days.

It has been shown that variable amounts of organic matter and nutrient-elements are withdrawn prior to abscission. Edwards (1977) found that about 10% of leaf dry weight is resorbed before abscission. To overcome this problem and reduce variation of the quotients, Vitousek & Sanford (1986) estimated resorption by comparing fresh and litter leaf nutrient/calcium quotients on the assumption that Ca is immobile once it reaches the leaves. In my study element resorption was calculated by the quotient leaf litter/fresh leaf concentration on a Ca basis, and then on a mass basis. K has been considered a readily leachable mineral-element in fresh leaves and leaf litter because it is not attached to any molecule (Medina 1984, Scott *et al.* 1992), and hence it is not considered in this study since leaching losses would be confounded by those of resorption.

Mineral element and statistical analyses were as described for Chapter 6.

RESULTS

Table 7.1 shows the mean concentrations in fresh leaves and leaf litterfall from the 12 species analysed. For N, P and Ca, mineral concentrations were significantly different among fresh leaves and litterfall leaves. Concentrations of N and P were higher, and Ca lower, in fresh leaves. Accepting that the per-unit-calcium values are more meaningful, as leaves senesced, N decreased 52.2%; P, 42.8%; and Mg, 23.6%. On a mass basis N decreased 36.3%; P, 23.8%; Ca increased 33.3% and Mg 1.9%.

Table 7.2 shows the mineral-element concentrations of fresh leaves for each species. Rheedia edulis a gap-independent species, had the least fresh-leaf mean element concentrations, and Cecropia obtusifolia had the highest Mg/Ca quotient (1.0). Table 7.3 shows the fresh leaves mineral-element concentrations on a leaf-area basis for nine species. Table 7.4 gives the significant differences between fresh leaves and leaf-litter element concentrations for each species. S. radlkoferi and P. oxyphyllaria had different mean concentrations (fresh *vs.* leaf litter) for three elements, Faramea occidentalis and Forsteronia viridescens for one element, and the rest of the species for two elements (Table 7.4). Considering only the significant differences from Table 7.4, Table 7.5 shows the mineral-element concentration quotients and resorption on a Ca basis and mass basis for each species. The elements showed a wide range of resorption and N was the element retranslocated in most species. Nectandra ambigens, Ficus yoponensis and the obligate gap species Cecropia obtusifolia, Heliocarpus appendiculatus and Trichospermum mexicanum were the species with the highest N resorption on a Ca basis. Ca increase on a mass basis was significant only for four species and Mg (on a Ca basis) increased in Pseudolmedia oxyphyllaria, Spondias radlkoferi and F. yoponensis.

Mineral concentrations in fresh leaves were significantly different among the species' life-history groups for all the elements with the exception of Ca (Table 7.6). Obligate gap species had higher fresh leaf concentrations of N than gap-dependent and gap-independent species. Regarding leaf litterfall, only N and Mg concentrations differed among the life-history groups. Obligate gap species had the highest leaf litterfall concentrations of Mg (Table 7.6). Analyzing the percentage of leaf litter/fresh leaf mineral concentrations among the life history groups, only N was resorbed in different amounts (Table 7.7). Obligate gap species had higher reductions in N concentrations from fresh leaves to leaf litterfall than gap-dependent, and gap-independent species. When analyzing within-group differences (with three species each) only in the gap-dependent and obligate gap groups did species differ in the element concentrations between fresh leaves and leaf litterfall. In the gap-dependent group, Nectandra ambigens had a higher increase in Ca (95.5%) in the leaf litterfall than Spondias radlkoferi (8.1%) and Ficus tecolutensis (0%), while in Mg there was a reduction (41.7%) in the leaf litterfall of Nectandra ambigens. In Ficus tecolutensis it increased 8.3% and almost 78% in Spondias radlkoferi. In the obligate gap group Leaf litterfall Mg concentrations increased more in Heliocarpus appendiculatus (125%) than in Trichospermum mexicanum (56.2%), while in Cecropia obtusifolia decreased (50.2%). None of the other species had significantly different fresh leaf to leaf litterfall mineral-element concentrations. Table 7.8 shows element mean concentrations for sun and shade leaves which were not significantly different for this study.

Table 7.1. Student's-t test for mineral-element concentrations (mg g^{-1}) between fresh leaves and leaf litter. The percentage of litterfall/fresh leaf concentrations calculated for: element concentration per unit calcium (a), and element concentration per unit mass (b). The percentages of nutrient resorption in a calcium basis (c); and in a mass basis (d) are shown. n = 36 individuals from twelve tree species with three individuals each.

	N	P	Ca	Mg
Fresh	17.9	1.43	17.67	5.78
Litter	11.4	1.09	23.64	5.89
p	< 0.0001	=0.009	=0.002	n.s.
a	47.8%	57.2%	100.0%	76.4%
b	63.7%	76.2%	133.3%	101.9%
c	52.2%	42.8%	0	23.6%
d	36.3%	23.8%	+ 33.3%	+ 1.9%

Table 7.2. Means with ranges in parenthesis of mineral element concentrations (mg g^{-1}) in fresh leaves from 12 species collected during September 1997. The highest and the least values are shown in bold.

	N	P	K	Ca	Mg
Cecropia obtusifolia	19.9	1.8	10.1	12.7	**12.7**
	(17.7-22.3)	(1.5-2.4)	(9.3-11)	(12-13)	(6-25)
Faramea occidentalis	14.0	1.1	8.3	15.7	4.0
	(12.3-15.2)	(0.5-1.9)	(1.3-17.7)	(13-20)	(1-9)
Ficus tecolutensis	13.8	1.1	11.1	18.7	4.0
	(12.4-15.7)	(1-1.2)	(8.7-12.7)	(16-21)	(3-5)
F. yoponensis	20.8	1.5	12.9	23.3	9.7
	(19.1-23.1)	(1.5-1.6)	(11.3-15.3)	(18-26)	(7-12)
Forsteronia viridescens	17.9	1.4	20.2	21.3	7.7
	(15.6-20.2)	(1-1.9)	(10-26.3)	(19-26)	(5-11)
Heliocarpus appendiculatus	22.6	**2.9**	**22.1**	15.0	4.0
	(21.4-24.3)	(2.4-3.3)	(19.3-24)	(12-18)	(3-5)
Nectandra ambigens	16.8	1.3	10.6	14.7	6.0
	(15.5-18)	(1.1-1.6)	(9.3-11.7)	(13-21)	(4-7)
Orthion oblanceolatum	**31.8**	1.7	19.9	19.7	4.7
	(27.9-35.4)	(1.3-1.9)	(17.3-23)	(14-25)	(3-8)
Pseudolmedia oxyphyllaria	15.4	1.1	17.0	15.7	7.3
	(14.9-16.2)	(0.9-1.3)	(12.7-19.7)	(15-17)	(7-8)
Rheedia edulis	**10.8**	**0.7**	**5.4**	**11.0**	**1.0**
	(10-11.4)	(0.6-0.8)	(3-8.3)	(8-13)	0
Spondias radlkoferi	12.5	1.3	**5.4**	**24.7**	3.0
	(11.7-13.1)	(1.2-1.4)	(4.3-6.7)	(22-27)	0
Trichospermum mexicanum	18.5	1.2	19.0	19.7	5.3
	(17.3-20.4)	(1.1-1.4)	(12.7-29)	(12-25)	(4-6)

Table 7.3. Fresh leaves mineral-element concentrations on a leaf-area basis (g m^{-2}) with the mean specific leaf weights values taken from Bongers & Popma (1990). The highest and the least values are shown in bold.

	N	P	K	Ca	Mg
Cecropia obtusifolia	1.56	0.14	0.79	0.99	**0.99**
Faramea occidentalis	1.21	0.09	0.72	1.36	0.35
Heliocarpus appendiculatus	1.17	0.15	1.14	**0.77**	0.20
Nectandra ambigens	**2.3**	**0.18**	1.45	**2.01**	0.82
Orthion oblanceolatum	2.22	0.12	1.39	1.37	0.33
Pseudolmedia oxyphyllaria	1.33	0.09	1.47	1.35	0.63
Rheedia edulis	1.44	0.09	0.72	1.47	**0.13**
Spondias radlkoferi	**0.9**	0.09	**0.39**	1.77	0.22
Trichospermum mexicanum	1.79	0.11	**1.84**	1.91	0.51

Table 7.4. Student-t test for fresh leaves and leaf litter mineral-element concentrations (mg g^{-1}). n = 3.

	N			P		
Species	Fresh	Litter	p <	Fresh	Litter	p <
Cecropia obtusifolia	19.9	11.9	0.01	1.9	1.7	n.s.
Faramea occidentalis	13.9	12.5	n.s.	1.1	0.8	n.s.
Ficus tecolutensis	13.7	8.6	0.05	1.1	0.8	0.05
F. yoponensis	20.8	9.9	0.001	1.53	0.8	n.s.
Forsteronia viridescens	17.9	12.6	0.05	1.4	0.8	n.s.
Heliocarpus appendiculatus	22.6	10.3	0.0005	2.9	2.3	n.s.
Nectandra ambigens	16.8	10.1	0.005	1.6	1.35	n.s.
Orthion oblanceolatum	31.7	22.6	0.05	1.9	1.65	n.s.
Pseudolmedia oxyphyllaria	15.4	12.8	0.005	1.1	0.8	0.05
Rheedia edulis	10.8	7.9	0.005	0.7	0.5	0.05
Spondias radlkoferi	12.5	10.4	0.05	1.3	0.9	0.01
Trichospermum mexicanum	18.5	7.1	0.0005	1.2	0.4	0.005

	Ca			Mg		
Species	Fresh	Litter	p <	Fresh	Litter	p <
C. obtusifolia	12.7	21.0	0.01	7.2	4.0	n.s.
F. occidentalis	15.7	24.0	0.05	4.0	2.5	n.s.
F. tecolutensis	18.6	18.7	n.s.	4.0	4.3	n.s.
F. yoponensis	23.0	45.0	n.s.	9.7	13.7	0.05
F. viridescens	19.5	22.5	n.s.	7.6	4.3	n.s.
H. appendiculatus	15.0	23.7	0.05	4.0	9.5	n.s.
N. ambigens	14.7	28.7	0.05	6.0	3.5	n.s.
O. oblanceolatum	20.0	23.2	n.s.	5.0	7.0	n.s.
P. oxyphyllaria	15.5	14.8	n.s.	7.3	5.7	0.05
R. edulis	10.8	11.7	n.s.	1.0	1.7	n.s.
S. radlkoferi	24.0	27.0	n.s.	3.0	5.3	0.05
T. mexicanum	19.8	19.5	n.s.	5.5	8.5	n.s.

ble 7.5. The percentage of leaf litter/fresh leaf element concentration as calculated per unit calcium (a), and per unit mass (b); and the percentage of ement resorption on a calcium basis (c) and on a mass basis (d). -, are species with no significant differences between fresh leaves and leaf litter mineral ncentrations from Table 7.4.

	N				P				Ca				Mg			
ecies	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
ecropia obtusifolia	36.2	59.6	63.8	40.4	-	-	-	-	100	165.3	-	+65.3	-	-	-	-
ramea occidentalis	-	-	-	-	-	-	-	-	100	152.9	-	+52.9	-	-	-	-
cus tecolutensis	62.8	62.5	37.2	37.5	72.7	75.5	27.3	24.5	-	-	-	-	-	-	-	-
yoponensis	24.3	47.5	75.7	52.5	-	-	-	-	-	-	-	-	72.2	141.2	27.8	+41.4
rsteronia viridescens	61.0	70.3	39.0	29.7	-	-	-	-	-	-	-	-	-	-	-	-
eliocarpus appendiculatus	28.9	45.6	71.1	54.4	-	-	-	-	100	158.0	-	+58.0	-	-	-	-
ectandra ambigens	30.8	60.1	69.2	39.9	-	-	-	-	100	195.2	-	+95.2	-	-	-	-
rthion oblanceolatum	61.5	71.3	38.5	28.7	-	-	-	-	-	-	-	-	-	-	-	-
seudolmedia oxyphyllaria	87.0	83.1	13.0	16.9	76.1	72.7	23.9	27.3	-	-	-	-	81.8	78.1	18.2	21.9
heedia edulis	67.5	73.1	32.5	26.9	65.9	71.4	34.1	28.6	-	-	-	-	-	-	-	-
ondias radlkoferi	73.9	83.0	26.1	17.0	61.5	69.2	38.5	30.8					157.1	176.7	+57.2	+76.7
ichospermum mexicanum	38.9	38.1	61.1	61.9	33.8	35.0	66.2	65.0	-	-	-	-	-	-	-	-

Table 7.6. One-way ANOVA[1] (means) and Kruskal-Wallis[2] tests (medians) for mineral-element concentrations (mg g^{-1}) between gap-dependent species (D), gap-independent species (I) and obligate gap species (O). n = 9 for each treatment from three tree species with three individuals each. Different superscript letters indicate significantly different means within a column (Tukey test, $p < 0.05$).

	N		P		Ca		Mg	
	Fresh leaf	Litterfall	Fresh leaf	Litterfall	Fresh leaf	Litterfall	Fresh leaf	Litterfall
D	13.2^{a}	9.71	1.2^{a}	1.12	19.3	24.6	4.0^{ab}	4.3^{a}
I	14.6^{a}	14.3	1.0^{b}	1.07	15.4	19.6	2.0^{a}	3.8^{a}
O	20.4^{b}	9.74	1.5^{a}	1.45	15.7	21.4	6.0^{b}	7.4^{b}
p	$= 0.03^{2}$	n.s.[1]	$= 0.04^{2}$	n.s.[1]	n.s.[1]	n.s.[1]	$= 0.05^{2}$	$< 0.01^{1}$

Table 7.7. One-way ANOVA for the percentage of leaf litter/fresh leaf mineral-element concentrations (a), and the percentage of nutrient resorption (b) on a Ca basis among gap-dependent species (D), gap-independent species (I), and obligate gap species (O). n = 9 for each treatment from three tree species with three individuals each. Different superscript letters indicate significantly different means within a column (Tukey test, $p < 0.05$).

		N	P	Ca	Mg
		Mean	Mean	Mean	Mean
a)	D	57.6^{a}	73.2	100	83.9
a)	I	76.9^{a}	84.0	100	149.2
a)	O	35.0^{b}	70.8	100	90.3
	p	= 0.0001	n.s.	n.s.	n.s.
b)	D	42.4	26.8	0	16.1
b)	I	23.1	16.0	0	+49.2
b)	O	65.0	29.2	0	9.7

Table 7.8. Means (mg g^{-1}) of sun- and shade-leaf nutrient concentrations in Los Tuxtlas, México. Bongers & Popma (1988) comparisons were significantly different ($p < 0.001$, $n = 61$ species with one individual each) with the exception of the N/P ratio. In This study means were not significantly different ($n = 12$ from four tree species with three individuals each for each treatment). -, indicates no data.

	Bongers & Popma (1988)		This Study	
	Sun-leaves	Shade-leaves	Sun-leaves	Shade-leaves
N	16.63	17.88	15.93	15.9
P	1.28	1.43	1.30	1.32
N/P	14.06	13.67	12.25	12.1
Ca	-	-	18.9	20.3
Mg	-	-	5.4	5.6

DISCUSSION

Methods. The fresh mature leaves were collected in September at a time when the phenological stage of the species used was different (Figures 5.8, 5.10, 5.11, 5.13). Faramea occidentalis was at an immature stage, Ficus tecolutensis, Nectandra ambigens, Orthion oblanceolatum and Rheedia edulis were at a mature stage, Ficus yoponensis, Pseudolmedia oxyphyllaria and Spondias radlkoferi were at a senescent stage and for the rest of the species, the stage was unknown. Since the flushing of new leaves takes several days giving a cohort of different stages of leaf development, it was possible to find mature leaves from all species at the time of sampling, and the effect of mature leaves of different ages in the nutrient-element analysis was ignored. Since leaf litter was collected within a few rainless days after shedding, the leaching effect was considered negligible also. Leaf litterfall belonged to the whole tree canopy, while fresh leaves were collected from the bottom part of the canopy. However Thompson *et al.* (1992) did not find mineral-element concentration differences among the low, medium and top crown level in five species in Brazil.

Overall nutrient resorption. Significant differences were found among fresh leaves and leaf litter mineral-element concentrations for N, P and Ca. N and P showed a reduction from fresh leaves to leaf litterfall concentrations, while Ca increased. Similar results have been found in lowland tropical forests elsewhere (Proctor *et al.* 1989, Scott *et al.* 1992). Nutrient resorption was variable depending on the species but important for N and P.

Quotients of fresh leaf/leaf litter element concentrations lower than 1 meant a possible mechanism of element excretion into senescing leaves in soils with a relative high element concentrations (Proctor *et al.* 1989). Scott *et al.* (1992) found a retranslocation of N and P in senescing leaves. Mg and Ca are less mobile elements and its concentrations tend to increase in senescing leaves (Scott *et al.* 1992). At Los Tuxtlas Mg was retranslocated in almost 50% of the species analysed (Table 7.4). Studying just one tree of Terminalia superba, Songwe *et al.* (1997) found that with increasing leaf age over 10 months the concentration of nutrient-elements in the leaves decreased. After one month, there were large reductions of 53%, N; 83%, P; and 12%, Mg, in the leaf concentrations. Then just before leaf abscission the concentrations of N (44%), and P (53%) declined, while Ca (40%) and Mg (29%) increased. In one tree of Pycnanthus angolensis there was a reduction of 32%, 23% and 11% of N, P and Mg, while Ca increased. Guha & Mitchell (1965), and Evans (1979) in Gmelina arborea also found decreases in N, P and K before abscission. McHargue & Roy (1932), Guha & Mitchell (1966), and Evans (1979) also found Ca and Mg increases as the leaves age. Attiwill (1968) reported for Eucalyptus obliqua that 70% of the P and K, 50% of the Na and 35% of the Mg in plant parts were withdrawn before litterfall, and 33% of the Ca was immobilized in the litter.

N, P and K are vital elements in the functioning of the leaf. P and especially N are important for photosynthesis (Mooney *et al.* 1978, Field & Mooney 1987, Hirose & Werner 1987). Ca tends to accumulate in leaves and bark (Mengel & Kirkby 1982) because it is immobile in the phloem (Larcher 1977). Mg is important in the chlorophyll molecule and in the fitting of some enzymes to their substrate. Concentrations of N per leaf area and per leaf weight show a good correlation with maximum photosynthetic rates over a wide range of species (Field & Mooney 1987). N and P showed a correlation on both an area and weight basis (Ovington & Olson 1970, and Grubb & Edward 1982 for montane forests; and Medina 1984, and Bongers & Popma 1990 for lowland forests). Körner *et al.* (1986) found that specific leaf weight (SLW) (g m^{-2}) was strongly negatively correlated with N concentrations on a leaf mass basis. Bongers & Popma (1990) found negative correlations of SLW with P and K.

Although Vitousek & Sanford (1986) proposed to calculate litterfall/fresh leaf nutrient quotients on a Ca basis in order to reduce variation of the quotient, the N/Ca quotient at Los Tuxtlas, and most quotients at Maracá (Scott *et al.* 1992) were more variable than those expressed on a mass basis (Table 7.9).

As Grubb & Edwards (1982) found for a montane rain forest, mineral element concentrations in fresh leaves for lowland forests were in the following sequence: N > Ca > K > Mg > P. Nutrient concentrations of fresh leaves from Los Tuxtlas were N = 17.4, P = 1.3 and K = 10.5 mg g^{-1} (Bongers & Popma 1990 for 68 species), and N = 17.9, P = 1.4, K = 13.5, Ca = 17.7 and Mg = 5.8 mg g^{-1} (this study). N and P concentrations in fresh leaves from nine tree species in Los Tuxtlas, were similar to those of Bongers & Popma (1990) with the exception of N in Orthion oblanceolatum and P in Heliocarpus appendiculatus and Pseudolmedia oxyphyllaria which were almost twice as high in my study (Table 7.10). K was higher in my study in almost all species. Proctor *et al.* (1989) and Bongers & Popma (1990) listed fresh foliar concentrations in a range of lowland tropical forests (mean mg g^{-1}): N (11.6 - 25.2), P (0.54 - 1.8), K (3.3 - 16.7), Ca (3 - 20.4), Mg (2.6 - 4.5), and N/P ratio (9.3 - 21.7). Compared with these, foliar nutrient concentrations of fresh leaves from Los Tuxtlas are in the mid-range for N, in the mid-high range for P, and in the high range for K and Ca. Mg in this study appears as the highest value for lowland tropical forests including the ultramafic forests studied by Proctor *et al.* (1989). Los Tuxtlas N and P concentrations are higher than those of montane forests and sclerophyllous tropical rain forests. With the exception of one forest in Panama, N/P and K/P quotients from Los Tuxtlas are in the lower part of the range for tropical rain forests (Bongers &

Popma 1990), which means that P supply is higher than in those forests. Compared with forests from Malaysia and Brazil (Table 7.11), Los Tuxtlas has higher quotients of fresh leaf/leaf litterfall concentrations for N, and lower ones for P, K and Ca, and intermediate for Mg. This means that in Los Tuxtlas higher amounts of N are retranslocated from the senescing leaves, but lower amounts of P and K compared with the other forests.

Nutrient resorption by species life-history groups. From a total of 42 and 38 species analyzed, Proctor *et al.* (1989) and Thompson *et al.* (1992) found big interspecific differences and substantial intraspecific variation in fresh-leaf element concentrations. Singh (1969) found much variation in the concentration of nutrients in the leaf litterfall of different species. There is a notable variation among species in mineral retranslocation from senescing leaves. As more species are analysed for nutrient resorption higher ranges are found (Table 7.9). Aerts (1996) found also that nutrient resorption varied widely both within and among species, and suggested that this variation might have a biochemical basis like the control of the ratio of soluble and insoluble compounds in senescing leaves. In my study N appeared as the element most strongly retranslocated possibly because it plays a role in many plant functions and its supply might be limiting. There were species which translocated three elements while other species translocated only one (Table 7.4). Aerts (1996) found that about 47% of N was retranslocated in the senescent leaves of evergreen species in general and about 54% in deciduous species. Scott *et al.* (1992) emphasized in their conclusions the lack of knowledge of plant nutrition in the tropical forest based on the high variation found on nutrient resorption by species. I tried to resolve some of the problems by analyzing resorption strategy by life-history group: of obligate gap species, gap-dependent species, and gap-independent species (Popma *et al.* 1992). Obligate gap species (pioneer species; Hartshorn 1980, Whitmore 1984) start and complete their entire life cycle in large gaps. Gap-dependent species are usually canopy species which require small gaps to pass one or several stages in their life cycle, but which are able to survive prolonged periods in the shade. The third group consists of gap-independent species which are able to complete their entire life cycle in the shade. These are small-sized tree species and are also known as shade tolerant species (Hartshorn 1980, Martínez-Ramos 1985). Although as Popma *et al.* (1992; p. 207) pointed out, 'most species can easily be classified into one of these groups, boundaries between groups are diffuse rather than discrete, so intermediate species do exist'. On a Ca basis, N was the only mineral element that was retranslocated in different amounts among the species groups. All the rest of the elements were retranslocated in a similar fashion (Table 7.7). Obligate gap species have a higher N retranslocation, than both gap-dependent and gap-independent species. Since obligate gap species have higher growth rates than the other groups N may be a limiting nutrient element. Regarding leaf litterfall, gap-independent species had higher N concentrations than gap-dependent and obligate gap species, suggesting that N is less needed and retranslocated in slow growing gap-independent species. Obligate gap species had higher concentrations of Mg than the other two groups. González-Iturbe (1988) in Los Tuxtlas analyzed leaf litterfall mineral concentrations of several species and found that species like Ficus insipida had higher contents of Ca and Mg, and Dussia mexicana of N and P. Nectandra ambigens and Heliocarpus appendiculatus in particular excreted high amounts of Ca and Mg (Table 7.4). In the case of fresh leaves only P concentrations were higher in the obligate gap species than in the other two groups, and K in the obligate gap than in the gap-dependent species only. Once again, it seems that obligate gap species need more P for fast growth, but its small retranslocation suggests it is not limiting. Regarding fresh leaves, Popma *et al.* (1992) found that gap-dependent species had more N, P and K per unit leaf area than obligate gap and gap-independent species. Los Tuxtlas surprisingly has higher proportions of leaf N retranslocated in comparison to other lowland rain forests. The fact that the soil nutrient concentrations are high (Chapter 4) does not mean that nutrient resorption should not exist, since perhaps this could be an easier way of nutrient access than from the soil in a high density and competitive environment.

Finally, sun-leaves had lower concentrations of N, P and K on a weight basis than shade-leaves, but higher concentrations on an area basis (Bongers & Popma 1988). These authors proved that the reduction of K concentration on a weight basis is probably an adaptation to a sunny environment, while a reduction in N concentration on an area basis is probably an adaptation to a shade environment. N/P ratios did not vary with different environments (Bongers & Popma 1988). In contrast to Bongers & Popma (1988) I did not find differences between sun- and shade-leaves in any element concentrations in a weight basis. The leaves selected in my study were from the light exposed part of the canopy at 15 m and perhaps not fully sun-exposed since the means did not differ greatly from shade-leaf means (Table 7.8).

Table 7.9. Means range of the percentage of leaf litter/fresh leaf mineral-element concentration as calculated for a) element concentration per unit Ca, b) element concentrations per unit mass.

	N	P	K	Ca	Mg	No. of Species	Reference
a	20 - 85	22 - 98	31 - 138	1	27 - 164	12	
b	38 - 89	36 - 129	37 - 218	92 - 244	5 - 233	12	This study
a	27 - 83	18 - 59	15 - 48	1	58 - 182	6	
b	58 - 68	39 - 56	28 - 49	78 - 219	6 - 174	6	Scott *et al.* (1992)

Table 7.10. Nutrient concentrations (mg g^{-1}) of fresh leaves of nine tree species: A) Bongers & Popma (1990) and B) this study. 1) *Cecropia obtusifolia*, 2) *Faramea occidentalis*, 3) *Heliocarpus appendiculatus*, 4) *Nectandra ambigens*, 5) *Orthion oblanceolatum*, 6) *Pseudolmedia oxyphyllaria*, 7) *Rheedia edulis*, 8) *Spondias radlkoferi*, 9) *Trichospermum mexicanum*.

		1	2	3	4	5	6	7	8	9
A	N	22.08	12.35	21.16	16.9	15.91	10.36	7.54	14.18	18.06
	P	1.22	0.83	1.69	1.04	2.59	0.68	0.79	1.12	1.11
	K	6.88	5.11	6.95	3.49	11.03	10.4	6.65	6.38	9.65
	N/P	18.15	14.93	12.51	16.29	6.18	15.23	9.6	12.62	16.4
B	N	19.9	14.03	22.63	16.8	31.7	15.37	10.8	12.53	18.53
	P	1.8	1.07	2.87	1.3	1.67	1.13	0.7	1.33	1.23
	K	10.1	8.33	22.1	10.57	19.87	17.03	5.43	5.43	19
	N/P	11.05	13.11	7.88	12.92	18.98	13.6	15.42	9.42	15.06

Table 7.11. Mean fresh leaves/leaf litter quotients of mineral concentrations from Malaysia, Brazil and México.

N	P	K	Ca	Mg	Authority
1.42	2.78	2.71	1.22	1.36	Proctor *et al.* (1989)
1.57	2.16	2.67	0.87	0.88	Scott *et al.* (1992)
1.66	1.86	1.57	0.82	1.08	This study

Chapter 8. PASTURE VEGETATION

INTRODUCTION

Pastures at Los Tuxtlas are dominated by the neotropical native grasses Axonopus compressus, Paspalum conjugatum, Panicum spp., and the African grass Cynodon plectostachyus, introduced in 1970 (Guevara *et al.* 1992). Trees occur in the pastures as isolated individuals (which are dealt with in detail in this study) and also as living fences and in riparian vegetation.

The aim of this Chapter was to compare the vegetation under the isolated trees with that from the open-pasture and to relate it later with the soil nutrient status from Chapters 4 and 9.

METHODS

The locations and descriptions of the pastures are given in Chapters 2 and 4. For vegetation analysis I used a subjective method of plant cover-abundance estimation, the Domin scale (Kershaw & Looney 1985), on 4-m^2 subplots located in a stratified random way in the open-pasture plots and under the tree crowns. From the 12-yr open-pasture plot 6 was not sampled. Ten subplots were sampled in both situations in the 12-yr pasture, 15 (open-pasture) and 12 (under trees) in the 32-yr pasture, and 15 (open-pasture) and 9 (under trees) in the 52-yr pasture (Figure 8.1 for the open-pastures). The difference in sample numbers were caused by a lack of time since it was originally proposed to sample 15 subplots from each vegetation type. Appendix 4 lists the species which were found.

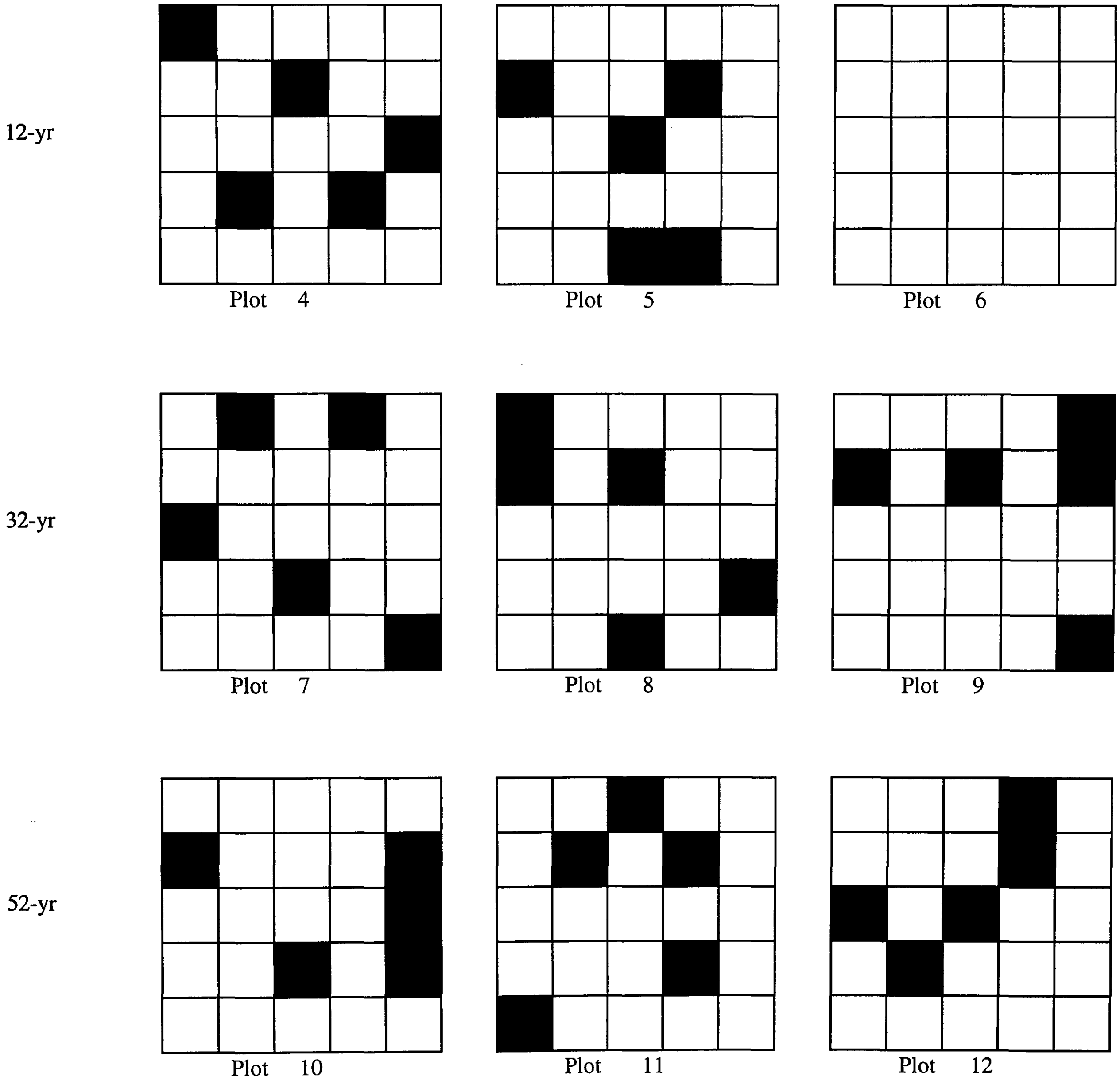


Figure 8.1. Location of the sampling subplots in the three open-pastures.

RESULTS

Frequency (percentage of occurrence from the total number of subplots) of the herb species was 100% in the open-pastures and under the trees, while the frequency of seedling trees and climbers (non-woody stems) were lower in the open-pasture (30%, 50%) than under the trees (80.6%, 90.3%) (Table 8.1). The frequency of seedlings in the open-pastures and under the trees were: for lianas, 2.5% and 9.7%; palms 0% and 9.7%; and unidentified taxa 42.5% and 9.7%.

There were 44 plant species in the open-pasture subplots (160 m^2) against 61 under the isolated trees (124 m^2) including six unidentified taxa (four from the 52-yr open-pasture). There were seedlings of only seven forest trees species in the open-pastures but 21 under the isolated trees (Table 8.1). The 52-yr open-pasture had no tree seedlings. The oldest pasture had the least seedling tree species and the youngest the most, with an opposite trend for the herbs.

Table 8.2 shows the main species ranked by their cover-abundance in the open-pastures and under the isolated trees. The 12-yr open-pasture was dominated by Cynodon plectostachyus, Paspalum conjugatum and Hiptis atrorubens; the 32-yr pasture by P. conjugatum, Mimosa pudica and H. atrorubens; and the 52-yr pasture by P. conjugatum, C. plectostachyus and C. dactilum. The under-crown vegetation of the trees in the 12-yr pasture was dominated by C. plectostachyus and P. conjugatum; in the 32-yr pasture by Drimaria cortata, Hiptis atrorubens, P. conjugatum, Selaginella sp. and Syngonium chiapensis; and in the 52-yr pasture by Pavonia shiediana.

Table 8.1. Number of seedling species by life-form found in the subplots of each of the three pastures of different ages and from the three pastures (Total A) in two different conditions (open-pastures, P; under tree crowns, T). Total B is the number of seedling species of all life forms sampled in each pasture age-class.

	Herbs		Trees		Non-woody climbers		Lianas		Palms		Unknown		Total B	
	P	T	P	T	P	T	P	T	P	T	P	T	P	T
12-yr	16	8	4	10	2	2	0	0	0	0	2	1	24	21
32-yr	15	22	3	17	2	3	0	0	0	0	0	3	20	45
52-yr	19	10	0	10	2	4	1	1	0	1	4	2	26	28
Total A	30	30	7	21	2	4	1	1	0	1	4	4	44	61

Table 8.2. Percentage of cover of the main species estimated with the Domin scale in the open-pastures (P) and under the isolated trees (T). Only species with ≥ 75% cover in at least one subplot are considered.

	P 12-yr	T 12-yr	P 32-yr	T 32-yr	P 52-yr	T 52-yr
Cynodon dactilon					5 - 100	
C. plectostachyus	34 - 100	26 - 100			1 - 100	
Drimaria cortata				<1 - 75		
Hiptis atrorubens			<1 - 75			
Mimosa pudica			1 - 75			
Paspalum conjugatum	11 - 90	<1 - 100	51 - 100	11 - 100	5 - 100	
Pavonia schiedeana						11 - 75
Selaginella sp.				<1 - 75		
Syngonium chiapensis				5 - 75		

DISCUSSION

The greater tree-seedling species richness under the Ficus trees of the 32-yr pasture may be because the figs are highly attractive to dispersers. Herbs showed a similar frequency and number of species under the isolated trees and in the open-pastures, but the vegetation under the isolated trees had more plant species and three times more forest plant species, than the open-pasture (Table 8.1). Guevara *et al.* (1992) found at Los Tuxtlas 191 plant species beneath the tree canopies of 50 trees sampled in 13 pastures (5- 30-yr old) in contrast to 106 species in the open-pastures with the same sample area (200 m^2) in both conditions. They also reported that the site under the canopy near the trunk had higher plant diversity than under the canopy perimeter. Under the isolated trees there were 109 woody species against 42 in the open-pastures, and 97 were zoochorous against 40 zoochorous species in the open-pastures. This can be explained either by a higher propagule availability beneath the canopy or by a more favourable environment or both (Guevara *et al.* 1992). Plant diversity is increased under the isolated trees since they are visited by birds and bats as sites for perching and feeding, and since seed dispersal by birds is mainly during perching and after take-off but not during flying (McDonnel & Stiles 1983, Stiles & White 1986, Charles-Dominique 1986). For neotropical rain forest species, seed dispersal by animals is critical, since 75% or more depend on frugivorous vertebrates (Howe & Smallwood 1982). The higher species number found by Guevara *et al.* (1992) with a slightly higher sample area (200 m^2) than in the present study (160 m^2) was due to the higher number of trees sampled (50 against 10) and to their exclusion of sampling sites with recent cow disturbance.

At Los Tuxtlas the vegetation under the canopy of isolated trees is structurally and floristically different from the open-pasture, resulting from a higher deposition of rain forest species seeds by zoochorous animals (bats and birds) (Guevara & Laborde 1993). There is a higher density and richness of woody seedlings under isolated trees than in the open-pastures and these trees may play an important role in forest regeneration (Kellman 1985, Guevara *et al.* 1992). The isolated trees in the pastures may provide better conditions than the open-pastures for seedling establishment. Solar irradiance, and fluctuations in temperature and humidity are reduced beneath the canopy (Belsky *et al.* 1989) and soil water capacity is increased (Joffre & Rambal 1988). Soil bulk density was lower under the trees than in the open-pasture (Chapter 4), while microbial activity may be higher (Mordelet *et al.* 1993). According to Knoop & Walker (1985) the southern African savanna grasses take up water at a rate sufficient to affect germination and establishment of woody seedlings. Where the ratio of topsoil to subsoil water is high as under remnant trees, woody plants may become dominant. At Los Tuxtlas, González (1996) found that remnant trees had important local effects on the microclimate in pastures. In the open-pastures, soil moisture seemed to depend on grass cover (González 1996).

Chapter 9. SOIL ANALYSIS UNDER THE ISOLATED TREES IN THE PASTURES

INTRODUCTION

The landscape at Los Tuxtlas is characterized by the presence of isolated remnants of forest trees, riparian corridors and living fences. Isolated trees are left alive for shade for cattle and people and for their timber when it is of economic value. Considering only natural forest elements, Guevara *et al.* (1992) censused 265 isolated trees from 14 to 39 m height, belonging to 57 species, in 81.4 ha of pastures. Tree density in the pastures was usually from three to eight per hectare.

Higher soil nutrient concentrations are expected under the trees than in the open-pastures since the tree crowns protect the soil from leaching, and higher nutrient amounts are provided by litterfall. In the grasslands of Wisconsin, soil moisture and nutrients were observed to decrease as distance from the trunks of oak trees into the open grassland increased, and plant composition under their canopies was found to differ from that outside the canopy, indicating a clear effect of the oaks on seedling establishment (Ko & Reich 1993). Many investigations on isolated trees in the tropics have been made in savannas which have similarities with grasslands at Los Tuxtlas. Soils under isolated tree canopies have less light, lower temperatures in mid-afternoon and higher fertility compared with the open savanna (Belsky 1994, Mordelet *et al.* 1993, Isichei & Moughalu 1992). Kellman (1979) reported the enrichment of soils around trees, which serve as perching and nesting sites for birds. Hoffman (1996) found forest tree seedlings in the savanna more susceptible to nutrient, temperature or water stress than seedlings in the forest.

Analyses were made to test if there were differences in soil nutrient concentrations under the trees compared with the open-pastures at Los Tuxtlas. As the age of the pasture increased, higher differences were expected between the soil nutrient concentration under the isolated and the open-pastures.

METHODS

The nearest isolated trees to the study plots in the open-pastures were selected for soil analyses. Three trees were selected in the 12-yr and 52-yr pastures, and four in the 32-yr pasture (ten trees in total) (Table 9.1). In the 52-yr pasture the trees belonged to the species Mangifera indica which were planted immediately after forest conversion and hence have been used for shade by cattle for about 40 yr. In the 12-yr and 32-yr pastures the trees were in or between the study plots, and in the 52-yr pasture between 15 and 150 m from the study plots which had been fertilised.

During May 1996 and in October 1996 ten soil samples in each pasture from the isolated trees (30 for the three sites) were randomly collected on each date for soil nutrient and bulk density analyses. Samples were collected from the top 10 cm of the ground with a 100-ml soil core for soil bulk density. Sample drying, textural and nutrient analyses were as described in Chapter 4. Soil texture was not analysed in all samples. In contrast to Chapter 4, the soil samples of the isolated trees from the 52-yr pasture were included in the statistical analyses since they were not on fertilised soils but were 15 m and 150 m away from the fertilised study plots.

Statistical analyses were made with Minitab release 11.12. One-way ANOVA and linear regression analyses were applied. A Tukey means-comparison test was applied to the ANOVA results. $\log_e$ and χ^2 transformations were applied when necessary (Zar 1984). When data did not match the assumptions for a parametric test, a Kruskal-Wallis test for three or more samples was used. In the latter, a Tukey medians comparison test was applied (Zar 1984).

Table 9.1. Species and size of the isolated trees selected in the open pastures.

Pasture age (yr)	Species	Family	Height (m)	DBH (cm)
12	*Brosimum alicastrum*	Moraceae	27.0	102
	Pouteria sapota	Sapotaceae	30.0	59
	Spondias radlkoferi	Anacardiaceae	25.0	69
32	*Bursera simaruba*	Burseraceae	22.6	52
	Ceiba pentandra	Bombacaceae	30.1	113
	Ficus sp. 1, *Ficus* sp. 2 (stranglers)*	Moraceae	12.7	98
	Platymiscium pinnatum	Fabaceae	21.3	50
52	*Mangifera indica*	Anacardiaceae	8.4	86
	M. indica	Anacardiaceae	13.8	102
	M. indica	Anacardiaceae	16.2	104

*) The *Ficus* stranglers were of the same height and on the same tree their trunks overlapped so that separate diameters could not be obtained.

RESULTS

Comparing Table 9.2 with Table 4.2 it is possible to see that soil texture under the trees did not differ much in the open-pasture. Table 9.2 shows that the soil under the isolated trees in the 12-yr pasture had the highest proportion of silt while those in the 32-yr pasture had most clay and those in the 52-yr pasture most sand. The soils under the isolated trees in the 12-yr pasture had the highest bulk density and were mostly clay clay-loamy soils, the trees in the 32-yr pasture had mostly clay soils with some clay loam, while those in the 52-yr pasture had mostly clay loams.

pH and total N appeared as the soil characteristics with a relatively low coefficient of variation (2 - 14%). Other coefficients of variation were higher. The 52-yr pasture trees had a lower coefficient of variation (Table 9.3).

Table 9.2. ANOVA for mean percentage of the textural analysis by the UK classification system and bulk density (g cm^{-3}) for the soil under the isolated trees in the pastures of Los Tuxtlas, México. Different superscript letters indicate significant differences within rows (Tukey test, $p < 0.05$). [1] = sample size for textural analysis, [2] = sample size for bulk density.

	Forest	12-yr pasture	32-yr pasture	52-yr pasture	p
Clay	30.9^{ab}	28.2^{a}	39.6^{b}	25.1^{a}	= 0.006
Silt	32.2^{a}	38.9^{a}	35.2^{a}	32.0^{a}	n.s.
Sand	36.9^{a}	32.9^{a}	25.2^{b}	42.8^{a}	< 0.0001
Soil bulk density	0.76^{a}	0.96^{b}	0.84^{ab}	0.8^{a}	= 0.007
n	$10^{1},10^{2}$	$8^{1},9^{2}$	$12^{1},10^{2}$	$7^{1},9^{2}$	

Table 9.3. Mean, minimum, maximum, and % of coefficient of variation of the soil characteristics at Los Tuxtlas, México, under isolated trees in the pastures of different ages. Overall minimum and maximum values are in bold.

		pH H_20 (1:2.5)	pH KCl (1:2.5)	N Total (%)	P Bray (μg/g)	K^+ (meq/ 100g)	Na^+ (meq/ 100g)	Ca^{2+} (meq/ 100g)	Mg^{2+} (meq/ 100g)	H^+ (meq/ 100g)	Al^{3+} (meq/ 100g)	CEC (meq/ 100g)
12-yr	Mean	7,26	5,92	0,42	4,8	1,12	0,59	10,9	5,8	0,20	0,05	18.7
pasture	Min	6,96	5,46	***0,3***	1,2	0,89	0,44	6,5	***3,3***	0,11	0,04	***12.0***
trees	Max	***7,52***	***6,37***	0,47	11,6	1,36	0,75	***20,9***	8,32	0,3	0,07	30.5
n = 9	% CV	2,1	4,4	12,3	67.0	15,2	19,9	40,2	30,7	36,8	75.0	31.5
32-yr	Mean	6,47	5,14	0,45	1,3	0,51	0,53	9,5	9,9	0,32	0,21	21.0
pasture	Min	***5,19***	***4,09***	0,4	***0,6***	***0,23***	0,36	***5,1***	5,3	***0,19***	***0.0***	13.6
trees	Max	6,89	5,82	0,5	2,4	1,33	***0,76***	13,2	***20,1***	***0,94***	***0,97***	31.0
n = 12	% CV	9.0	12,3	11,4	44,6	69,1	25,8	26,6	47,5	61,6	130,6	28.9
52-yr	Mean	7,05	5,92	0,48	5,5	1,62	0,38	11,9	12,6	0,22	0,03	26.7
pasture	Min	6,72	5,67	0,4	3.0	0,79	***0,29***	7,5	10,4	0,11	***0.0***	19.3
trees	Max	7,34	6,32	***0,6***	***11,9***	***3,46***	0,47	15,3	14,5	0,34	0,11	***31.7***
n = 9	% CV	3.0	4,3	13,9	49,3	49,5	16.0	24,3	10,7	32,3	131.2	13.6

A) Comparison of the soil characteristics under the isolated trees in the pastures

With a weak coefficient of determination only Na^+ decreased ($r^2 = 0.26$, $p<0.001$) (Figure 9.1). Table 9.4 shows that pH, Ca^{2+} and notably K^+ are lower under the isolated trees of the 32-yr pasture, H^+ is lower under the isolated trees of the 12-yr pasture than in the forest, Mg^{2+} is higher under the isolated trees of the 52-yr pasture than the 12-yr pasture, Al^{3+} is lower under the isolated trees of the 12-yr and 52-yr pasture, and CEC and P are highest under the isolated trees of the oldest site. Total N did not change.

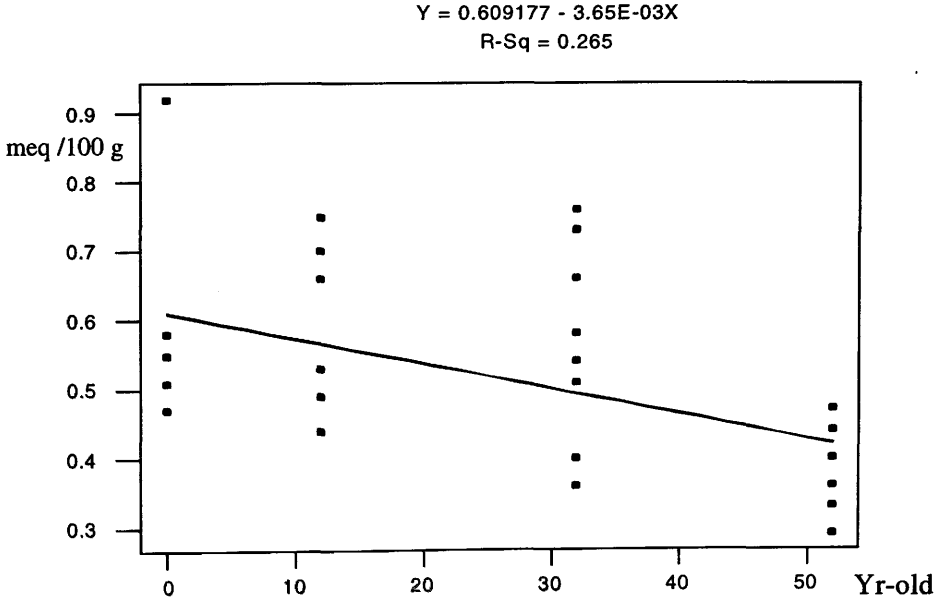


Figure 9.1. Regression of Na^+ on age from the forest to the isolated trees in the 52-yr pasture.

Table 9.4. Kruskal-Wallis test (medians), except Na^+ (Anova, means ± S.D.), for the soil characteristics of the isolated trees in the pastures of different ages. Different superscript letters indicate a significant difference within a row (Tukey test, $p < 0.05$).

	12-yr	32-yr	52-yr	p<
	n = 9	n = 9	n = 12	
pH_{H2O}	7.3^{a}	6.7^{b}	7.0^{ab}	0.0001
pH_{KCl}	5.88^{b}	5.35^{a}	5.87^{b}	0.0001
Total N (%)	0.42^{a}	0.45^{a}	0.46^{a}	n.s.
Ext. P (μg g^{-1})	4.42^{a}	1.57^{a}	6.1^{b}	0.003
K^+ (meq 100 g^{-1})	1.07^{a}	0.31^{b}	1.5^{a}	0.0001
Na^+ (meq 100 g^{-1})	$0.59^{a} \pm 0.4$	$0.53^{a} \pm 0.4$	$0.38^{b} \pm 0.35$	0.001
Ca^{2+} (meq 100 g^{-1})	10.9^{a}	9.5^{b}	11.9^{a}	0.02
Mg^{2+} (meq 100 g^{-1})	5.54^{b}	8.44^{ab}	12.6^{a}	0.0001
H^+ (meq 100 g^{-1})	0.19^{b}	0.26^{ab}	0.23^{ab}	0.01
Al^{3+} (meq 100 g^{-1})	0.08^{b}	0.13^{a}	0.0^{b}	0.002
CEC (meq 100 g^{-1})	18.7^{a}	21.0^{a}	26.7^{b}	0.01

B) Comparison of the soil characteristics among the forest, the isolated trees and the open-pastures.

Soil bulk density was lower (0.86 g cm^{-3}, $t = 3.27$, $p = 0.005$) under the isolated trees than in the open-pastures (0.97 g cm^{-3}). Figure 9.2 compares the nutrient concentrations for the open-pasture and the isolated trees. Differences in nutrient concentrations between the isolated trees in the pasture and the open-pastures did not increase clearly with pasture age with the exception of K^+ (Figure 9.2). Table 9.5 shows that pH did not change substantially in the three situations. P was least in the open-pastures than under the isolated trees and the forest. Ca^{2+} was lower under the isolated trees and the open-pastures than in the forest. K^+ was higher and Al^{3+} lower under the isolated trees than in the forest and open-pastures. CEC was higher in the forest than the open-pastures. Table 9.6 shows that most of the changes in mean element concentrations from forest-trees, forest-pastures, and trees-pastures, were reductions. Table 9.7 gives the element

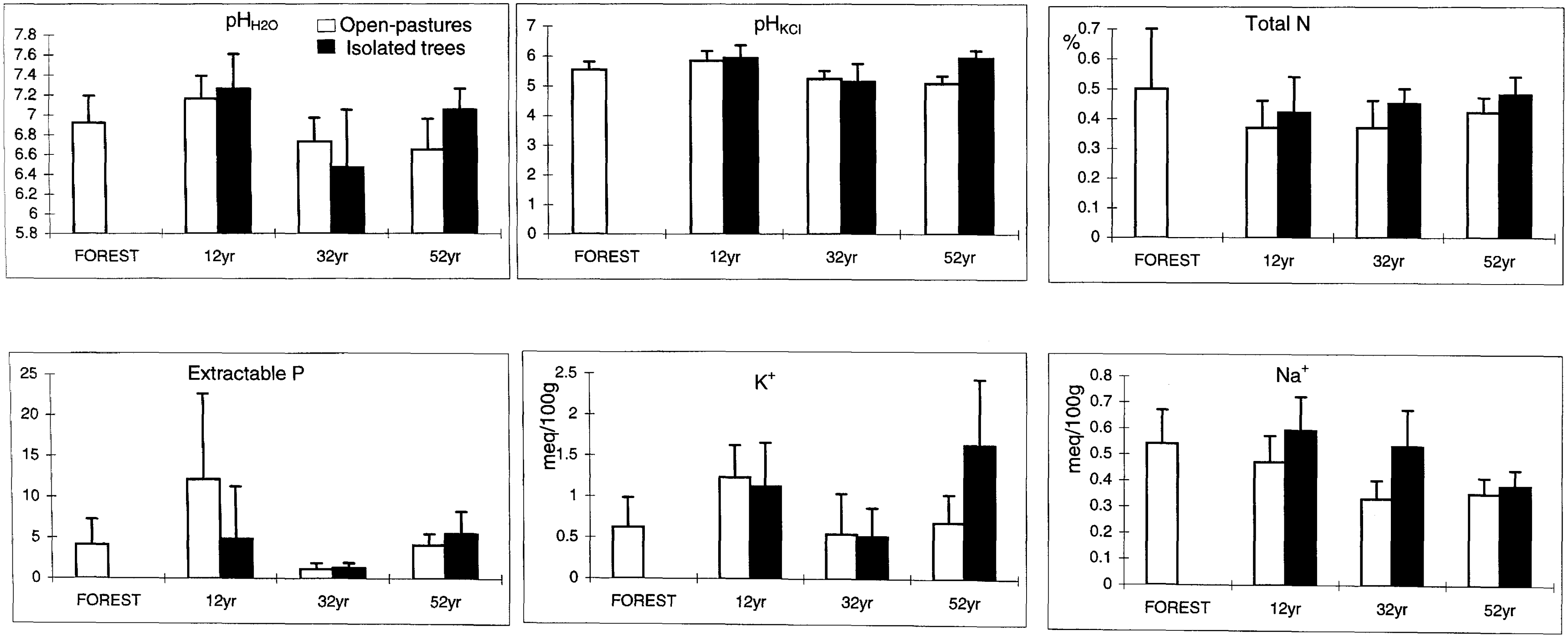


Figure 9.2. Means + S.D. of pH, mineral element concentrations and CEC in the forest, the open-pastures of different ages and the isolated trees of the pastures at Los Tuxtlas, Mexico.

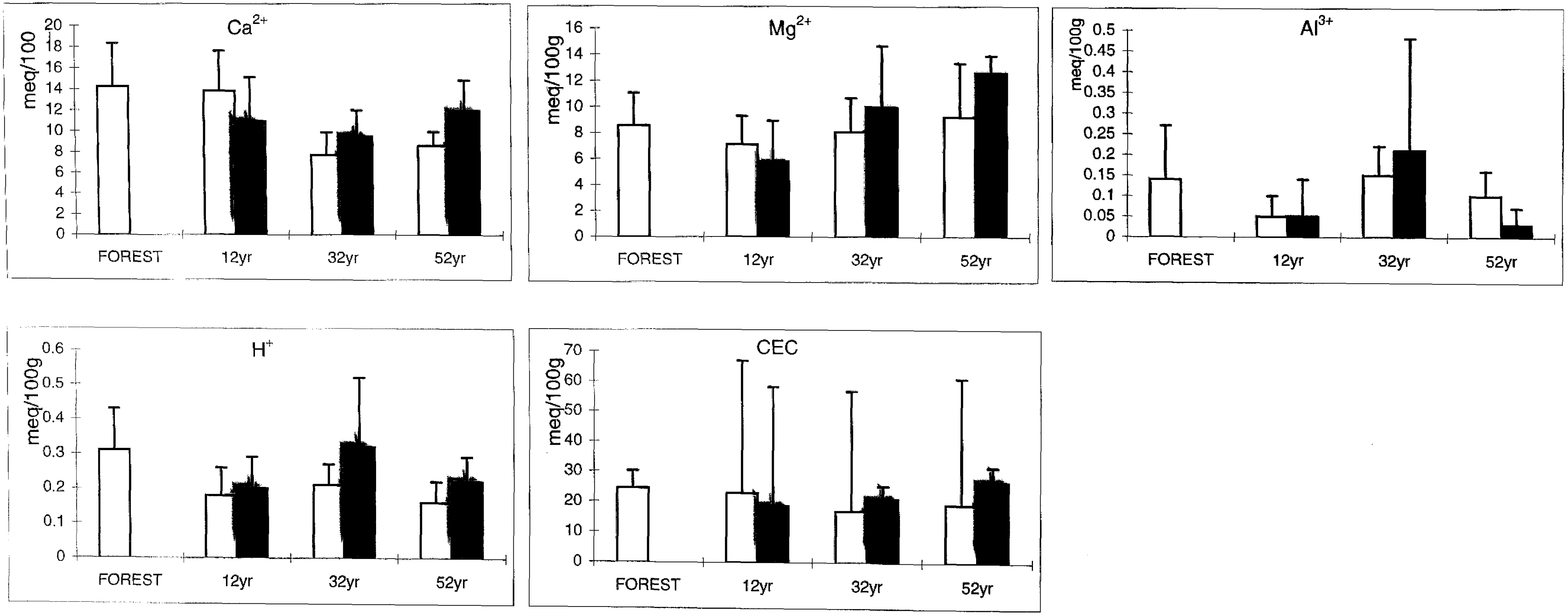


Fig. 9.2 continued

concentration on a volume basis of the forest, the isolated trees in the three sites, and the 12- and 32-yr open-pastures.

Table 9.5. One-way Anova* (means ± S.D.) and Kruskal-Wallis (medians) tests for the soil characteristics of the forest, the isolated trees in the three sites, and the 12- and 32-yr open-pastures. Different superscript letters indicate a significant difference within a row (Tukey test, $p < 0.05$). n = 30. For the pastures 15 samples were randomly obtained from the 30 samples analised for each pasture.

	Forest	Trees	Pastures	p
pH_{H2O}	6.9	6.9	6.8	n.s
pH_{KCl}	5.5^{a}	5.7^{b}	5.4^{a}	= 0.025
Total N (%)	0.49^{a}	0.44^{a}	0.36^{b}	<0.0001
Ext. P* ($\mu g\ g^{-1}$)	4.1 ± 3.1	3.6 ± 2.9	5.3 ± 8.9	n.s.
K^{+}(meq 100 g^{-1})	0.51^{a}	1.0^{b}	0.64^{a}	<0.05
Na^{+} *(meq 100 g^{-1})	$0.54^{a} \pm 0.24$	$0.5^{a} \pm 0.27$	$0.38^{b} \pm 0.26$	<0.0001
Ca^{2+} *(meq 100 g^{-1})	$14.2^{a} \pm 4.1$	$10.6^{b} \pm 3.3$	$10.1^{b} \pm 3.4$	<0.0001
Mg^{2+} (meq 100 g^{-1})	7.9	8.6	7.6	n.s.
H^{+} (meq 100 g^{-1})	0.28^{a}	0.26^{ab}	0.21^{b}	<0.0001
Al^{3+} (meq 100 g^{-1})	0.11^{a}	0.08^{b}	0.1^{a}	= 0.02
CEC* (meq 100 g^{-1})	$24.3^{a} \pm 6.8$	$22.0^{ab} \pm 6.2$	$19.2^{b} \pm 4.5$	= 0.002

Table 9.6. Percentage of average change in soil characteristics among the three conditions.

	PH_{H2O}	pH_{KCl}	Total N	P ext.	K^{+}	Na^{+}	Ca^{2+}	Mg^{2+}	H^{+}	Al^{3+}	CEC
Forest-Trees	0	+3.6	+10.2	-8.2	+96.0	-74.0	-13.5	+8.9	-7.1	-27.3	-9.8
Forest-pastures	-1.4	-1.8	-26.5	+29.3	+25.5	-29.6	-28.9	-3.8	-0.25	-9.0	-21.3
Trees-pastures	-1.4	-5.3	-18.2	+47.2	-36.0	-24.0	-4.7	-11.6	-19.2	+2.5	-12.7

Table 9.7. ANOVA (means ± S.D.) and Kruskal-wallis* (medians) tests for element concentration on a volume basis of the forest, the isolated trees in the three sites, and the 12- and 32-yr open-pastures. Different superscript letters indicate a significant difference within a row (Tukey test, $p < 0.05$). For the pastures 15 samples were randomly obtained from the 30 samples analised for each pasture.

	Forest (n=30)	Trees (n=28)	Pastures (n=30)	p
Soil bulk density (g cm^{-3})	0.75^{a}	0.86^{b}	0.96^{c}	< 0.0001
Total N (% cm^{-3})*	0.34	0.38	0.34	n.s.
Ext. P (μg cm^{-3})*	2.00	2.52	1.92	n.s.
K^{+}(meq cm^{-3})	$0.27^{a} \pm 0.11$	$0.35^{b} \pm 0.10$	$0.35^{b} \pm 0.11$	< 0.01
Na^{+} (meq cm^{-3})	0.41 ± 0.12	0.44 ± 0.15	0.39 ± 0.12	n.s.
Ca^{2+} (meq cm^{-3})	10.79 ± 3.79	9.37 ±3.44	9.91 ± 4.54	n.s.
Mg^{2+} (meq cm^{-3})	6.43 ± 2.48	8.15 ±3.57	7.08 ± 2.52	n.s.

DISCUSSION

Different amounts of nutrients can be added to the soil by the litterfall from different tree species (Chapter 7). Since the soils analysed came from different tree species, this could be a significant part of the variation in the comparisons among the pastures. However the 52-yr pasture with planted trees of Mangifera indica did not show a lower coefficient of variation in nutrient concentrations than the pastures with different tree species.

Although trampling is high under the isolated trees, the soils had a lower bulk density than those of the open pastures, possibly because of the effect of cattle droppings or a higher surface soil moisture or both. Soil bulk density has been reported to be lower under tree clumps (Mordelet *et al.* 1993). Also there is a common practice among the land owners of cutting the under-crown vegetation (mainly composed of forest tree seedlings and saplings) at least once a year and leaving it in place, to keep the sites accessible for cattle to the shade (Guevara *et al.* 1992).

In grazed pastures the nutrient cycle is faster than in the forests since the young grass leaves are eaten before nutrient resorption takes place and generally have a higher nutrient concentration than the tree litter (Chapin *et al.* 1986). There are some data on the input and concentration of mineral nutrients added to the soil by the cattle. High concentrations of readily available nutrients are excreted in the faeces and urine (Dean *et al.* 1975, McNaughton *et al.* 1983). "More than 80% of the N, P, and K consumed by the animals is excreted in their urine and faeces and is fairly well distributed if the animals are allowed to move freely around the pasture" (Vicente-Chandler *et al.* 1974, Mott 1974). Vicente-Chandler *et al.* (1974) calculated that in oxisols and ultisols in Puerto Rico, intensively (5 animals ha^{-1}) managed grazing return annually 176 kg ha^{-1} of N, 20 kg ha^{-1} of P, and 115 kg ha^{-1} of K, to the soil as excrements. In Puerto Rico the fertilizer requirements of cut forages are twice those of grazed pastures (Sanchez 1976). However Parsons (1976) claimed that there was an uneven distribution of the excrement and only 40% of the total could be used by the grass owing to losses by volatilisation and leaching.

The soil nutrients under isolated trees in pastures can be affected by the cattle density and mining effects of the deep roots of the trees (Baillie 1989). Comparisons of soil nutrient trends in Figure 9.2 shows the addition of cations (K^+, Ca^{2+}, Mg^{2+}), and extractable P from burning to the 12-yr open-pasture, which is not the case for the isolated trees. After then (32-yr, 52-yr pastures) all elements showed slightly higher values under isolated trees than in the open-pasture, particularly for K^+ in the 52-yr site which is strikingly higher under isolated trees where there is a high density of cows. Mg^{2+} showed an increase from the 12-yr to the 52-yr site in the open-pasture and under the trees which seems more likely to be due to the soil parent material, since the cows under the isolated trees did not change the trend. Trends for P, K^+ and Ca^{2+} are similar in both conditions (a decrease in the 32-yr site and then an increase in the 52-yr site) indicating the effect of deforestation at the 12-yr site and the effect of the parent soil material at the old site. Na^+ decreased in both sites progressively. Under the isolated trees CEC seemed to be determined by Mg^{2+} while in the open-pasture by the other cations. pH to a large extent reflects P, K^+ and Ca^{2+} concentrations. The soil under the trees from the 52-yr pasture was not fertilised. The isolated trees can absorb nutrients from the open-pasture by means of their extensive lateral roots, however one tree was about 150 m and two were about 15 m from the fertilised plots.

pH_{KCl}, total N, K^+, Na^+ and Mg^{2+} had higher concentrations under isolated trees than in open-pastures, whereas Al^{3+} was in lower concentrations ($p < 0.05$). However since soil density under the isolated trees was lower than in the open-pastures, nutrient amounts on a volume basis are similar (Table 9.7). The forest soil had higher concentrations of total N than the isolated trees even though it had no cattle excrement (Table 9.5).

The data from Los Tuxtlas fit the view that the soils under isolated trees in the pastures tend to have greater concentrations of nutrients (except P) than in the surrounding areas (Radwanski & Wickens 1967, Kellman 1979, Puerto & Rico 1988, Belsky *et al.* 1989, Weltzin & Coughenour 1990, Isichei & Moughalu 1992, Ko & Reich 1993, Mordelet *et al.* 1993, Belsky 1994).

Chapter 10. EXPERIMENTS GROWING SEEDLINGS WITH THE SOILS FROM THE FOREST AND PASTURES

INTRODUCTION

Soil fertility declined with increasing age of pasture (Chapter 4, Figures 4.2 - 4.4, Table 4.5), and it was decided to make an experiment in which native and crop plants were grown in soils from the forest, 12-yr, 32-yr and 52-yr pastures, and isolated trees from these pastures in order to know if the lowest nutrient concentrations were limiting plant production. It was expected to find the least seedling growth in the soil from the oldest pastures.

MATERIALS AND METHODS

During July 1996 seeds of six native tree species were collected: Cecropia obtusifolia (obligate gap, *sensu* Popma *et al.* 1992), Cojoba arborea, Cordia megalantha (gap-dependent), Erythrina folkersii (obligate gap), Inga sinacae (gap-dependent), and Pouteria campechana (gap-dependent). These species were selected as fast growing common species, with small seeds which would depend more on the soil nutrients than the seed reserves. The seeds' longest dimensions were: Cecropia obtusifolia (*c.* 1 mm), Cojoba arborea (*c.* 2 cm), Cordia megalantha (*c.* 1 cm), Erythrina folkersii (*c.* 0.5 cm), Inga sinacae (*c.* 2 cm), and Pouteria campechana (*c.* 3 cm). Additionally seeds of two crop species (maize, Zea mays and beans, Phaseolus vulgaris) were used twice in subsequent experiments. Seeds were checked for damage, fungus and insect predation and unhealthy seeds were discarded. Soils from the top 10 cm from the forest, 12-yr, 32-yr and 52-yr open-pastures and under isolated trees in all the pastures were collected randomly within the plots and bulked for each plot. Between 20 and 22 July 1996, seeds were allowed to germinate in a shade house which was made with a green mesh (1.2 mm) nylon net which allowed in rain water and was open to fresh air. The shade house was outside the forest. Pots with large holes in their bases were filled with soil and each placed in a separate tray and watered with previously collected rain water when required. Five replicates (pots) with five seeds each were used for each treatment. After 30-90 days the seedlings were thinned to one per pot.

All trays with the seedlings were randomly relocated every 20-30 days. A pesticide (Carbofuran) at a concentration of 1 ml l^{-1} of water was applied three times to the seedlings to control herbivory observed in some species from October 1996 onwards.

All seedlings of the same species were harvested at the same time, and the seedlings were dried in a drying room for 7 to 30 days depending on their size and a correction factor from a sample oven dried at 95 ^{o}C to constant weight was applied. The dry weight was obtained for total leaves, stems and roots for each seedling. A student-t test and one-way ANOVA were used. Results were checked for normality and homogeneity of variance, and a $\log_e$ transformation was applied when required. A Tukey means comparison test was applied to the ANOVA results.

RESULTS

Germination took 15 - 56 d depending on the species. Maize, beans and obligate gap species like Cecropia obtusifolia and Erythrina folkersii were harvested after two and five months. Gap-dependent species like Cojoba arborea, Cordia megalantha, Inga sinacae and Pouteria campechana took up to eight months to be big enough for growth comparisons. Several seeds and seedlings were lost owing to mice, insects, and overheating by the black plastic pots.

Shoots (leaves and stems), roots and total plant (roots and shoots) showed good growth only in the 32-yr pasture soil (Tables 10.1, 10.2 and 10.3). C. obtusifolia (shoot and total), C. arborea (root, shoot and total), E. folkersii (root, shoot and total), I. sinacae (total), P. campechana (total) and maize (root and shoot) had higher growth in the 32-yr pasture soil than in the other sites, and beans (root, shoot and total) lower growth. Comparisons among the soil under the trees in the pastures of different ages showed higher shoot and total growth only for C. megalantha under the trees of the 32- and 52-yr pasture, higher root growth under the trees of the 52-yr pasture and under the trees of the 12-yr pasture for beans (Tables 10.4, 10.5 and 10.6). Comparisons between the soil of the open-pasture (12-yr, 32-yr and 52-yr) and that under the isolated trees in the pasture (considering the three sites together) showed differences only in maize (shoot) with the soil from the isolated trees producing the better growth (Tables 10.7, 10.8 and 10.9).

Higher root growth compared with the shoot and leaf growth was observed in the soil from the 32-yr open-pasture and the forest for beans, the 12-yr open-pasture for C. obtusifolia, and the 52-yr open-pasture for E. folkersii and I. sinacae (Table 10.10). Comparisons among the soils under the isolated trees did not show any significant differences (Table 10.11). The comparisons between the soils from the isolated trees in the pastures and the open-pastures (considering the three sites together) showed higher root/shoot ratio in the open-pasture only for I. sinacae. For the rest of the species there were no significant differences (Table 10.12). A high negative correlation ($r = -0.86$, $p = 0.0001$) was found between root/shoot ratios and total biomass, from 127 samples of different species, sites and conditions.

Table 10.1. Student-t test (*) and one-way ANOVA for shoot dry weight (g) of seedlings growing in soil of undisturbed forest and open-pastures (12-yr, 32-yr and 52-yr). Different superscript letters indicate significantly different means (Tukey test, $p < 0.05$) (n = number of seedlings; -, are no data because of seed or seedling mortality).

Pasture age	Forest		12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	n	mean	p =
C. obtusifolia	4	0.82^{a}	5	0.33^{a}	5	1.88^{b}		-	0.001
C. arborea	4	1.76^{a}	5	1.89^{a}	3	8.26^{b}	5	1.71^{a}	0.004
E. folkersii	5	2.50^{a}	5	3.84^{a}	4	8.35^{b}	5	2.56^{a}	0.009
I. sinacae		-	3	5.04	3	5.3	3	2.0	n.s.
I. sinacae	5	2.67		-	5	3.84	3	3.31	n.s.
*P. campechana**		-		-	5	3.06	4	1.57	n.s.
Beans	5	2.07^{ab}	5	3.06^{a}	5	0.99^{b}	5	2.99^{a}	0.03
Beans	3	1.42	5	1.93	5	0.74	4	1.99	n.s.
Maize	5	0.77^{a}	5	1.03^{ab}	5	1.47^{b}	5	1.38^{b}	0.007
Maize	5	0.79	5	0.66	4	0.56	4	0.58	n.s.

Table 10.2. Student-t test (*) and one-way ANOVA for root dry weight (g) of seedlings growing in soil of undisturbed forest and open-pastures (12-yr, 32-yr and 52-yr). Different superscript letters indicate significantly different means (Tukey test, $p < 0.05$) (n = number of seedlings; -, are no data because of seed or seedling mortality).

Pasture age	Forest		12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	n	mean	p =
C. obtusifolia	4	0.56	5	0.21	5	0.47		-	n.s.
C. arborea	4	0.59^{a}	5	0.44^{a}	3	1.67^{b}	5	0.31^{a}	0.002
E. folkersii	5	0.46^{ab}	5	0.42^{ab}	4	1.05^{a}	5	0.31^{b}	0.04
I. sinacae		-	3	1.46	3	1.07	3	0.71	n.s.
I. sinacae	5	0.46		-	5	0.77	3	0.56	n.s.
*P. campechana**		-		-	5	1.08	4	0.56	n.s.
Beans	5	0.27	5	0.29	5	0.18	5	0.22	n.s.
Beans	3	0.24^{a}	5	0.22^{a}	5	0.09^{b}	4	0.23^{a}	0.006
Maize	5	0.06^{a}	5	0.08^{a}	5	0.23^{b}	5	0.17^{b}	0.0001
Maize	5	0.21	5	0.17	4	0.15	4	0.15	n.s.

Table 10.3. Student-t test (*) and one-way ANOVA for total dry weight (g) of seedlings growing in soil of undisturbed forest and open-pastures (12-yr, 32-yr and 52-yr). Different superscript letters indicate significantly different means (Tukey test, $p < 0.05$) (n = number of seedlings; -, are no data because of seed or seedling mortality).

Pasture age	Forest		12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	n	mean	p =
C. obtusifolia	4	1.38^{a}	5	0.54^{a}	5	2.35^{b}		-	0.02
C. arborea	4	2.36^{a}	5	2.33^{a}	3	9.93^{b}	5	2.02^{a}	0.01
E. folkersii	5	2.96^{a}	5	4.25^{a}	4	9.39^{b}	5	2.94^{a}	0.006
I. sinacae		-	3	6.5^{a}	3	6.37^{a}	3	2.71^{b}	0.01
I. sinacae	5	3.13		-	5	4.56	3	3.87	n.s.
*P. campechana**		-		-	5	4.13	4	2.13	0.02
Beans	5	2.39^{a}	5	3.5^{a}	5	1.16^{b}	5	3.20^{a}	0.003
Beans	3	1.66^{ab}	5	2.13^{ab}	5	0.83^{a}	4	2.22^{b}	0.025
Maize	5	0.89	5	1.07	5	1.62	5	1.52	n.s.
Maize	5	1.0	5	0.78	4	0.70	4	0.83	n.s.

Table 10.4. Student-t test (*) and one-way ANOVA for shoot dry weight (g) of seedlings growing in soil under the trees in pastures of three different ages (n = number of seedlings; -, is no data because of seed or seedling mortality).

Pasture age	12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	p =
C. megalantha	5	2.49^{a}	4	11.02^{b}	5	15.02^{b}	0.01
I. sinacae *		-	3	3.16	4	2.57	n.s.
I. sinacae	3	1.38	3	4.66	3	4.51	n.s.
Beans	4	3.72	5	0.99	5	2.32	n.s.
Maize	5	1.97	5	1.46	5	1.43	n.s.
Maize	5	0.74	5	0.90	5	1.12	n.s.

Table 10.5. Student-t test (*) and one-way ANOVA for root dry weight (g) of seedlings growing in soil under the trees in pastures of three different ages (n = number of seedlings; -, is no data because of seed or seedling mortality).

Pasture age	12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	p =
C. megalantha	5	0.35^{a}	4	0.13^{a}	5	0.61^{b}	0.007
*I. sinacae**		-	3	0.95	4	0.63	n.s.
I. sinacae	3	0.9	3	1.26	3	1.07	n.s.
Beans	4	0.29^{a}	5	0.15^{b}	5	0.19^{ab}	0.04
Maize	5	0.26	5	0.22	5	0.14	n.s.
Maize	5	0.15	5	0.26	5	0.19	n.s.

Table 10.6. Student-t test (*) and one-way ANOVA for total dry weight (g) of seedlings growing in soil under the trees in pastures of three different ages (n = number of seedlings; -, is no data because of seed or seedling mortality).

Pasture age	12-yr		32-yr		52-yr		
	n	mean	n	mean	n	mean	p =
C. megalantha	5	2.64^{a}	4	11.13^{b}	5	15.67^{b}	n.s.
I. sinacae *		-	3	4.10	4	3.20	n.s.
I. sinacae	3	2.28	3	5.90	3	5.58	n.s.
Beans	4	4.98	5	1.18	5	2.63	n.s.
Maize	5	2.22	5	1.67	5	1.56	n.s.
Maize	5	0.90	5	1.16	5	1.38	n.s.

Table 10.7. Student-t test for shoot dry weight (g) seedlings from soil under isolated trees in the pastures all together and the three open-pastures (n = number of seedlings).

	Trees		Pasture		
	n	mean	n	mean	p =
I. sinacae	9	3.52	8	3.64	n.s.
Beans	14	2.25	15	2.35	n.s.
Maize	15	1.53	15	1.29	n.s
Maize	15	0.92	13	0.61	0.05

Table 10.8. Student-t test for root dry weight (g) seedlings from soil under isolated trees in the pastures all together and the three open-pastures (n = number of seedlings).

	Trees		Pasture		
	n	mean	n	mean	p =
I. sinacae	9	0.77	8	1.08	n.s
Beans	14	0.21	15	0.23	n.s
Maize	15	0.21	15	0.16	n.s
Maize	15	0.20	13	0.15	n.s

Table 10.9. Student-t test for total dry weight (g) of seedlings from soil under isolated trees in the pastures all together and the three open-pastures (n = number of seedlings).

	Trees		Pasture		
	n	mean	n	mean	p =
I. sinacae	9	4.28	8	4.73	n.s
Beans	14	2.52	15	2.54	n.s
Maize	15	1.72	15	1.49	n.s
Maize	15	1.13	13	0.75	n.s

Table 10.10. Student-t test (*) and one-way ANOVA for quotients of root/shoots dry weight (g) of seedlings grown in soil of undisturbed forest, 12-yr, 32-yr and 52-yr open-pastures. Different superscript letters indicate significantly different means (Tukey test, p < 0.05) (n = number of seedlings; -, are no data owing to seed or seedling mortality).

	Forest		12-yr P		32-yr P		52-yr P		
	n	mean	n	mean	n	mean	n	mean	p =
C. obtusifolia	4	0.668^{a}	5	0.712^{a}	5	0.25^{b}		-	0.05
C. arborea	4	0.369	5	0.256	3	0.213	5	0.176	n.s.
E. folkersii	5	0.193^{a}	5	0.131^{a}	4	0.144^{a}	5	0.380^{b}	0.03
I. sinacae		-	3	0.260^{a}	3	0.200^{a}	3	0.363^{b}	0.02
I. sinacae	5	0.174		-	5	0.203	3	0.175	n.s.
*P. campechana**		-		-	5	0.358	4	0.372	n.s.
Beans	5	0.130^{a}	5	0.100^{a}	5	0.200^{b}	5	0.076^{a}	0.007
Beans	3	0.162^{a}	5	0.111^{b}	5	0.125^{b}	4	0.116^{b}	0.006
Maize	5	0.071	5	0.076	5	0.156	5	0.123	n.s.
Maize	5	0.258	5	0.260	4	0.267	4	0.258	n.s.

Table 10.11. Student-t test (*) and one-way ANOVA for quotients of root/shoot dry weight (g) of seedlings grown in soil under the trees in pastures of three different ages. (n = number of seedlings; -, is no data owing to seed or seedling mortality).

	12-yr P		32-yr P		52-yr P		
	n	mean	n	mean	n	mean	p =
C. megalantha	5	0.145	4	0.01	5	0.047	n.s.
I. sinacae *		-	3	0.30	4	0.256	n.s.
I. sinacae	3	0.07	3	0.27	3	0.237	n.s.
Beans	4	0.07	5	0.15	5	0.08	n.s.
Maize	5	0.132	5	0.102	5	0.097	n.s.
Maize	5	0.202	5	0.288	5	0.169	n.s.

Table 10.12. Student's-t test for quotients of root/shoot dry weight (g) of seedlings growing in soil from under isolated trees in the pasture all together and three open-pastures (n = number of seedlings).

	Trees		Pasture		
	n	mean	n	mean	p =
I. sinacae	9	0.218	8	0.296	0.038
Beans	14	0.09	15	0.097	n.s.
Maize	15	0.137	15	0.124	n.s.
Maize	15	0.217	13	0.245	n.s.

DISCUSSION

The forest soil was high in total N, Na^+, Ca^{2+}, H^+ and CEC; the soil from the 12-yr pasture was high in pH, P and K^+; the soil from the 32-yr pasture was low in P (1.12 μg g^{-1}) and K (0.54 meq 100 g^{-1}); and the soil from the 52-yr pasture had intermediate values in general (Chapter 4). Soil under isolated trees in the pastures had significantly higher total N, K^+, Na^+ and less Al^{3+} than the open-pasture soils (Chapter 9).

There were many not significant differences in these experiments, partly because the sample size was low owing to the limitation of space in the shade house. Only total growth of seedlings is referred now since it combine the root and shoot growth results. Contrary to expectations owing to it being an old pasture and never fertilised, the native tree species had the highest growth in the soil from the 32-yr pasture while beans the least. Although as mentioned above, the forest and 12-yr open-pasture soils had higher concentrations of some nutrients than the older pastures, the plants did not grow better in them. No nutrient-element was in higher concentration in the 32-yr open-pasture. Growth means from under the trees were not higher than those from the open-pastures. Both unexpected results may be explained since the nutrient concentrations are not strikingly different and even in the older pastures concentrations are high (including P and K) enough to avoid growth limitation in all species tested with exception of beans.

As mentioned earlier, soil from the 32-yr open-pasture had the least P and K, and crops, particularly beans are known to demand high amounts of these nutrients. This difference might be related to the species life-history since pioneer species may have different nutrient requirements and responses than gap-dependent species, and crops like maize and beans might be expected to respond faster to nutrient addition (Luizão 1995). Tanner *et al.* (1990) in Jamaica found that the trees response to nitrogen addition was species-dependent. Pioneer species are fast growing and respond to the addition of nutrients while non-pioneer species are slow growing and do not respond to nutrients (Chapin 1980). However in this experiment C. obtusifolia and E. folkersii (pioneer species) grew better in the low concentration site (32-yr pasture).

Only maize showed a higher shoot mass in the soil from the isolated trees than from the open-pasture. As discussed in Chapter 9, soil from the isolated trees appeared richer than the open-pasture soils as a consequence of the concentration of cattle excretions. Harper (1977) reported a higher soil moisture and fertility in abandoned livestock corrals, which resulted in accelerated seedling emergence and enhanced survivorship and growth of Acacia tortilis seedlings compared with those grasses in the adjacent open savanna.

Plants tend to have a higher root/shoot ratio at low soil nutrient concentrations as a response to acquire more nutrients (Marschner 1995). High root/shoot ratios would be associated with soil nutrient deficiencies and low ratios with ample nutrient supply. Comparisons of the root/shoot ratios amongst the soils of the different open-pastures and forest showed significant results only for three species out of eleven, though not in a consistent way. Similarly no effect was observed in the comparisons among the soils under the trees of the three different pastures, as well as those between the soil from the trees and the open-pastures.

In conclusion though there were some growth differences among sites in their capacity to support seedling growth, these differences did not show any consistency, probably because in no case are the nutrients in short supply and limiting growth.

Chapter 11. GENERAL DISCUSSION AND CONCLUSIONS

A) Relationship among soil nutrients, small litterfall nutrients, and the forest structure at Los Tuxtlas

The Los Tuxtlas forest is on a nutrient-rich soil and almost certainly belongs to a type of forest with a relatively open nutrient cycle associated with little accumulation of litter on the ground where nutrients may be lost by leaching and erosion (Baillie 1996). It has a lower basal area, canopy height, tree density, species richness and litterfall production than most other evergreen lowland tropical rain forests on nutrient-poor soils.

Whitmore (1998) showed that the amount of nutrients contained in the soil is not directly related to biomass since open-nutrient cycling systems tend to have high soil nutrient amounts and 'closed' nutrient cycling systems to conserve nutrients in the biomass. There are several possible strategies of conserving nutrients such as sclerophyllous leaves, quick nutrient absorption by root mats (Jordan 1989), nutrient resorption from abscised leaves (Scott *et al.* 1992), and high concentrations of lignins, and tannins which are probably primarily a defense against herbivores and pathogens, but which also reduce rates of mineralisation (Anderson *et al.* 1983). However these mechanisms are unlikely to be necessary in forests in nutrient-rich soils where nutrient conservation is less important. It is expected that nutrient resorption and nutrient-use-efficiencies are lower in forests on nutrient-rich soils than in those on nutrient-poor soils. Nutrient resorption at Los Tuxtlas was lower than in some 'closed' nutrient-cycle forests like in Malaysia and Brazil (Table 7.11). This confirms that nutrient conservation by this means is not a necessary feature in the Los Tuxtlas forest. Leaf nutrient dynamics can be partly related to the life strategy of the tree species, since N and P were more resorbed in the obligate gap species than in the gap-dependent and gap-independent species (Chapter 7).

A positive relationship between soil and leaf nutrient levels is sometimes present (Grubb 1977, Vitousek & Sanford 1986) and foliar nutrient concentrations at Los Tuxtlas were in line with the concentrations found on fertile soils (Vitousek & Sanford 1986). High nutrient concentrations in fresh leaves and small litterfall at Los Tuxtlas reflect a high availability of soil nutrients and no nutrient limitation for standing crop biomass, and a high nutrient accession to the forest floor. The Los Tuxtlas forest has the highest concentration of Mg (in soil, fresh leaves and litterfall) reported from lowland evergreen rain forests excluding the ultramafic forests which are particularly rich in this element (Proctor *et al.* 1988). This must be a consequence of the volcanic parent material at Los Tuxtlas which has a high concentration of Mg (Nelson & Gonzalez-Caver 1992).

Quotients of total annual inputs by litterfall to the mineral pool in the soil, show which elements cycle rapidly by decomposition. High values are for those elements which are in limited amounts in the soil *e.g.* K and Ca in the Maracá forest in Brazil (Scott *et al.* 1992). Table 11.1 shows that quotients for Los Tuxtlas are in general low compared with other lowland rain forests suggesting a slow mineral-element recycling. Swift *et al.* (1981) found no nutrient concentration differences in the litterfall of three sites though there were differences in soil nutrient concentrations, and Scott *et al.* (1992) found higher concentrations of Mg in the litterfall in a nutrient-poor forest in Brazil than in Costa Rica with higher soil nutrient availability.

Table 11.1. Quotients of litterfall/soil mineral-element assession for several lowland rain forests.

N	P/Tot P	K	Ca	Mg	Location	Reference
-	-	0.9	0.02	0.03	Australia	Brasell & Sinclair (1983) [1]
0.20	0.08	1.35	1.06	0.85	Brazil	Scott *et al.* (1992) [2]
0.03	0.005	0.27	0.36	0.47	Costa Rica	Heaney & Proctor (1989) [3]
0.038	-	0.48	0.053	0.03	Mexico	This study [2]

Soil depths: [1] = 30 cm, [2] = 10 cm, and [3] = 15 cm.

Foliar nutrient concentrations provide an alternative means of characterizing nutrient availability in tropical forests (Grubb 1977). A high nutrient-use-efficiency (NUE) may indicate more carbon is fixed per unit of nutrient (Vitousek 1982) and a large fraction of nutrients is resorbed from senescing plant parts (Grubb 1977). Inefficient nutrient economy indicates that the supply of nutrient to the trees is adequate (Grubb 1977, Vitousek 1982). Several authors (Cuevas & Medina 1983, Vitousek 1984, Villela 1995) have used the concept nutrient-use-efficiency (NUE) in tropical forests and compared it among forest communities on a range of soils. Grubb (1989) discussed the limitations of the use of NUE because of its incomplete estimation (restricted to the few fractions of the biomass considered), and also because there are unquantified nutrient losses such as herbivory, pollen, nectar, and root exudation. When comparing Los Tuxtlas with forest communities on nutrient-poor soils, the NUE appeared lower. However this is due to the inadequate criterion of dry weight of above-ground material per unit of nutrient, a trend that has been confirmed as more comparisons of NUE have been made between nutrient-rich and nutrient-poor forests (Grubb 1989).

Phosphorus has been suggested as the most likely limiting nutrient-element in lowland evergreen tropical forests. Associations of species with soil extractable P have been found by Gartlan *et al.* (1986) and Newbery *et al.* (1986). Newbery *et al.* (1986) in Cameroun in a census of 66.5 ha found 33 out of 96 tree species had a significant response of basal area to concentration of available soil P but in six different ways: U-shape response, Gaussian-shape, a gradually decreasing basal area and another a gradually increasing at the lower extreme of the P gradient, one model having a high basal area at the lower extreme of the gradient and another at the upper extreme. Vitousek (1984) found small litterfall P to be likely limiting small litterfall production but only under a concentration of 0.04% dry weight, and particularly in a subset of tropical forests in Amazonia. Some evidence of a possible relationship between P and production of small litterfall can be obtained from Proctor *et al.* (1983a,b) where estimations of small litterfall were directly related with soil P concentration in four contrasting forests in Malaysia. Other workers showed that P was not limiting for plant growth (Grubb 1989), and this may apply at Los Tuxtlas, since high amounts of P are returned in litterfall, thus the relatively low litterfall production in this forest may be limited by some other factors which may interact.

Hall & Swaine (1976) found for a number of Ghanaian forests with low rainfalls that species richness was inversely related to total exchangeable bases. Ashton (1977) in northwest Borneo, and Huston (1980) in Costa Rica found that the highest species diversity was associated with low or intermediate soil nutrient availability, and the lowest species diversity occurred on rich soils which favour fewer but strongly competitive species. Richards (1952) and Whitmore (1984) found a positive correlation between species diversity and soil fertility. Proctor *et al.* (1983a) found no clear relationship between species richness and nutrient concentrations in Malaysia: the nutrient-rich limestone forest was relatively poor in species, while both the nutrient-rich forest on alluvial gleys and the nutrient-poor dipterocarp forest were very rich in species. Species richness partly depends on many factors which may interact so that simple interpretations involving single factors are difficult (Proctor *et al.* 1983a). The evidence about the relationship between soil nutrients and species diversity is not conclusive (Richards 1996).

The relationship among soil nutrients, forest structure and productivity varies (Burnham 1989). 'Accepting the imperfections in our knowledge of soil nutrient supply, the existing data suggest that there is little correlation between soil chemistry, and forest structure and production' (Proctor 1992). 'A proportional relationship between soil nutrient concentration and forest biomass would be more likely in young secondary forests (as long as other factors are not limiting) than in undisturbed primary forests with efficient nutrient cycling and long-term nutrient accumulation in living matter from the soil and rain-water' (Proctor *et al.* 1983a). Brasell *et al.* (1980), for instance did not find differences in litterfall production with differences in soil fertility. In Table 11.2 I compared several forests which have a high concentration of soil nutrients and hence may have open nutrient cycles. This comparison shows that not all forests on rich soils show similar structural characteristics to the Los Tuxtlas forest, so there is no generalisation and easy explanation of the particular structural features of the Los Tuxtlas forest.

Table 11.2. Soil chemical and structural features of evergreen rain forests on nutrient-rich soils (-, are no data).

	Australia	Australia	India	India	Mexico
Soil type	Krasnozems	Krasnozems	Inceptisols	Inceptisols	Andosol
Sample depth (cm)	0-10	0-10	5-10	5-10	0-10
pH_{H2O}	5.1	6.6	5.3	5.9	6.9
Total N (%)	0.49	0.59	0.51	0.77	0.5
Extractable P ($\mu g\ g^{-1}$)	-	-	28	21	4.11
K^+ (meq $100g^{-1}$)	0.32	1.09	0.52	0.58	0.62
Na^+ (meq $100g^{-1}$)	0.11	0.06	0.93	0.42	0.54
Ca^{2+} (meq $100g^{-1}$)	5.2	28.5	8.42	14.6	14.2
Mg^{2+} (meq $100g^{-1}$)	2.9	4.6	1.9	2.7	8.6
CEC	27.6	43.1	17.7	21.3	24.4
No. Species (> 10 cm dbh ha^{-1})	59	39	-	-	88
Basal area ($m^2\ ha^{-1}$)	60	61	42.3	40.2	35
Height of emergent tree (m)	35	35	-	-	40
Litterfall (t $ha^{-1}\ yr^{-1}$)	9.9	9.1	13.3	12.0	10.6, 7.6 [1], 5.8 [2], 7.3 [2]
Author	Brasell *et al.* (1980)	Brasell *et al.* (1980)	Swamy & Proctor (1994a,b)	Swamy & Proctor (1994a,b)	This study

[1] = Alvarez & Guevara (1985), and [2] = Alvarez & Sanchez (1995) obtained from nearly plots.

The Los Tuxtlas forest does not seem nutrient limited since nutrient amounts are high in the soil, high in the fresh leaves and high in the litterfall, and leaf nutrient resorption is not high (except for N). Other factors such as low minimum temperatures, and day length may play a more important causal role in the Los Tuxtlas forest than nutrients. Primack *et al.* (1987) evaluating 15-yr of data of plant growth in Sarawak did not find a relationship between soil fertility and growth rate, and other factors such as local weather patterns, elevation, tree competition, pests and pathogens, seemed more important.

A more reliable explanation of the forest structure and diversity at Los Tuxtlas could be related to the northerly latitude where there is increasingly more variation in day length, lower winter temperatures and a seasonal climate. Temperature, for instance, has a great influence on plant growth and may be a partial explanation of the lower stature of the Los Tuxtlas forest. Diurnal fluctuation of temperature in the tropical forest can sometimes be considerable, particularly in the upper canopy (Longman & Jenik 1987). Many tropical tree species are particularly sensitive to small temperature differences. Minimum temperatures in the range 6 - 10 °C in most tropical plants cause chilling injury and death (Crawford 1989), and Guarea trichilioides and Avicennia marina appear to have a minimum temperature of 21 °C for shoot growth (Altman & Dittmer 1973). However Proctor *et al.* (1998) have described a lowland tropical rain forest in northeast India at 530 m with night-time winter temperatures as low as 5 °C.

Of the total leaf litterfall, 86.3% was produced by trees and 75% by canopy layer species. An estimation of the leaf litterfall production for 119 species at Los Tuxtlas is provided (Figure 5.7, Appendix 3). Specific timber exploitation in the tropics should take into account the possible impact on litter production and hence nutrient cycling because of the harvesting of species with a high proportion of the litterfall production.

B) Soil nutrients in the pastures

Although 12 yr later, it was still possible to see the effect of forest conversion in the young pasture. As expected, soil nutrients in the 12-yr pastures were in higher amounts than in the forest as a result of the land-use change, and then decreased in the other pastures as the time of use increased, though not in a striking way. Main soil-nutrient changes with increased age of pasture, were for P and K^+ which showed an increase after 12-yr of deforestation and then decreased up to 52-yr, and pH decrease which still had high values in the 32-yr and 52-yr pastures. H^+ and Al^{3+} concentrations showed opposite trends to P, K^+, and Ca^{2+}. It seems that the local volcanic eruptions (Chapter 2), the higher soil compaction in pastures and their high root density, are the main features maintaining high nutrient concentrations. Also, a low CEC favours nutrient leaching (Bouwman 1990), and soil CEC at Los Tuxtlas is not low (Table 4.7). Los Tuxtlas forest and pastures have nutrient-rich soils for the lowland wet tropics. As Baillie (1996) mentioned, pastures appear to be viable in the long term only on the fertile soils like andosols, clays over limestones and alluvial soils. It is necessary to analyse more pastures of different ages to predict how long the nutrients in the pastures will remain high under the present management at Los Tuxtlas, but the 52-yr pasture shows that with moderate fertilisation it can be kept at a high level of production for a simple farming system.

There was a higher soil nutrient concentration under the isolated trees in the pasture than in the open-pastures possibly as a consequence of nutrient concentration from cattle excrement (Vicente-Chandler 1974, Parsons 1976) and root pumping from the isolated trees (Grubb 1989). Several authors (Radwanski & Wickens 1967, Kellman 1979, Puerto & Rico 1988, Belsky *et al.* 1989, Weltzin & Coughenour 1990, Isichei & Moughalu 1992, Ko & Reich 1993, Mordelet *et al.* 1993, Belsky 1994) have claimed that these higher soil nutrient concentrations under the isolated trees may favour the higher seedling diversity and density in these sites. However as has been discussed there is a lack of conclusive evidence that soil nutrients influence species diversity in forest communities and it is likely that the high seedling density and diversity may be due to the seed rain and the physical conditions in these sites such as soil moisture, temperature or grass competition.

The effect of soil nutrient concentrations from the different sites on seedling growth was tested. Seedling density and diversity in the open-pasture and under tree canopies must depend in a large extent on the seed rain (Guevara *et al.* 1993), seed germination, and seedling establishment, which should be tested with different kinds of experiments. Experiments on seedlings growth in the soils of the different sites did not show significant differences. Only maize showed better growth in the richer soil from the isolated trees compared with the open-pastures. It seems that the nutrient status of the soils generally at Los Tuxtlas is so good that it is unlikely to be a limiting resource in enhancing higher seedling growth under the isolated trees in the pasture.

Although information on cattle productivity of the pastures is based solely on personal communications from the owners, the Los Tuxtlas pastures seem very productive. In South America animal production is low; one animal requires 5 to 25 ha of grassland, and 4 to 5 years to attain a market-size weight of 400 to 450 kg (Sanchez 1976). In a few regions *e.g.* in Peru with acid ultisols a carrying capacity of one animal ha^{-1} is possible. At Los Tuxtlas, the average holding capacity is 2 to 4 cows ha^{-1}, and 2 years are required on average to attain 400 kg of body weight. Barrera *et al.* (1993) indicate a stocking rate of 2.8 ha^{-1} for the Los Tuxtlas region. Most Amazon pastures are only productive for 4 to 8 years (Serrão & Homma 1982), whereas at Los Tuxtlas it is possible to have 3 to 4 cows ha^{-1} over 50 years in a flat terrain. On native savannas in Brazil, annual live weight gains are of the order of 20 to 50 kg ha^{-1}; 100 to 300 kg ha^{-1}, on improved grass-legume mixtures with minimum fertilizer inputs, and 500 to over 1000 kg ha^{-1}, on intensively fertilised grass pastures (Sanchez 1976). At Los Tuxtlas considering an average weight of 400 kg animal^{-1}, cattle production is of the order of 400 to 800 kg ha^{-1} yr^{-1} with no fertilisation.

A plan for optimum land-use at Los Tuxtlas is beyond the scope of this thesis, since it would involve a detailed analysis of the socioeconomics of the region. The use of the native forest flora has been proposed as an alternative sustainable use of the tropical forest. In Kalimantan, Borneo, Leaman *et al.* (1992) found 213 forest plant species that the local people use for medical purposes. In México there are 1,330 useful plant species, 1,052 from primary forest yield 3,173 products from which 780 are medicinal and 102 timber products (Toledo *et al.* 1995). However Whitmore (1998) claims that the fact that rain forests contain enormous numbers of drugs awaiting for exploitation is far from reality, since drug companies should consider whether screening jungle plants will yield better drugs than computer modeling of molecules and their synthesis.

Collecting, screening, purifying and testing takes a long time and has high costs. Many drugs have already been developed from 25,000 species used worldwide in traditional medicine such that future discoveries from native plants are likely to be less (Whitmore 1998). In México, for instance the tuber of the yam (Dioscorea) is a major non-timber forest product since it provides diosgenin, the steroid used as a precursor molecule from which oral contraceptives and cortisona are made, but soyabean oil has recently become an important alternative source and total synthesis is common (Whitmore 1998). Whitmore (1998) from an analysis of 24 studies in tropical lowland rain forest, gives a general value of \$50 year^{-1} for non-timber products, and \$100 to \$200 for timber products. A particular case in Peru is given by Peters *et al.* (1989) who calculated that one hectare of species-rich rain forest, with a clear-cutting of timber would give an immediate profit of \$1,000. A long-term use with cattle ranching would give \$2,960, but a plantation of timber and pulpwood \$3,184. However a selective presumably sustainable logging also in Peru, might yield \$490 ha^{-1} which added to a value of \$6,330 ha^{-1} obtained by the fruits and rubber latex production a value of \$ 6,820 ha^{-1} could be obtained. Lowland tropical rain forests, might have a higher value for research, for example, than for any other activity. Tobias & Mendelson (1991) suggested a value of \$1,250 ha^{-1} for a research tropical rain forest reserve in Costa Rica.

CONCLUSIONS

1. The relationship of the soil nutrients and the forest structure of lowland evergreen rain forests is compared at several locations in the world and it is proposed that the climate conditions and the photoperiod at the northerly latitude are more likely to account for the physiognomy of the Los Tuxtlas forest than any nutrient element.

2. Nutrient resorption from senescing leaves did not appear as an important feature at Los Tuxtlas supporting the idea that the forest is not nutrient limited.

3. The study confirmed that pastures appear to be viable in the long term on andosols (Baillie 1996), and showed that even in old pastures, soil nutrients would support forest regeneration or continued cattle grazing.

4. At Los Tuxtlas, the volcanic replenishment, soil compaction and the high root density in the pastures are further factors which account for the nutrient-rich soil even after 50 years of use.

5. Soils from the isolated trees in the pastures did not appear to promote higher seedlings growth. The higher seedlings diversity and density is more likely to be due to seed rain and microclimate conditions.

6. The fact that at Los Tuxtlas, pastures without fallowing are viable for a relatively long time does not mean that this is the best use of the soil and forest resource or that forest conversion to very long-term cattle ranching will not seriously damage the ecosystem (*i.e.* biodiversity).

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pendix 1. Families and species found in the three (0.25 ha) plots in the forest of Los Tuxtlas, Mexico. Nomeclature follows Ibarra-Manriquez & Sinaca (1995, 1996a, 1996b).

aranthaceae

Iresine arbuscula Uline et W.L. Bray

acardiaceae

Spondias radlkoferi Donn. Sm.

nonaceae

Cymbopetalum baillonii R. E. Fr.
Guamia sp.
Tridimeris hahniana Baill. +

ocynaceae

Aspidosperma megalocarpon Müll. Arg.
Forsteronia viridescens S.F. Blake
Stemmadenia donnell-smithii (Rose) Woodson

uifoliaceae

Ilex valeri Standl.

aliaceae

Dendropanax arboreus (L.) Ecne. te Planch.

steraceae

Eupatorium galeottii B.L. Rob.

gnoniaceae

Amphitecna tuxtlensis A.H. Gentry
Mansoa verrucifera (Schltdl.) A.H. Gentry

ombacaceae

Quararibea funebris (La Llave) Vischer
Quararibea yunckeri Standl. subsp. sessiliflora Miranda ex W.S. Alverson

Boraginaceae

Cordia megalantha S.F. Blake
Cordia stellifera I.M. Johnston +

Burseraceae

Bursera simaruba (L.) Sarg.

Caesalpiniaceae

Dialium guianense (Aubl.) Sandwith.

Capparaceae

Crataeva tapia L.

Cecropiaceae

Cecropia obtusifolia Bertol.

Celastraceae

Maytenus schippii Lundell

Chrysobalanaceae

Couepia polyandra (Kunth) Rose

Clusiaceae

Calophyllum brasiliense Cambess.
Rheedia edulis (Seem.) Triana et Planch.

Ebenaceae

Diospyros digyna Jacq. +

Euphorbiaceae

Adelia barbinervis Schltdl. et Cham. +
Croton schiedeanus Schltdl.
Omphalea oleifera Hemsl.

Fabaceae

Machaerium floribundum Benth.
Platymiscium pinnatum (Jacq.) Dugand +
Pterocarpus rohrii Vahl
Vatairea lundellii (Standl.) Killip ex Record

Flacourtiaceae

Lunania mexicana Brandegee
Pleuranthodendron lindenii (Turez.) Sleumer

Lauraceae

Licaria velutina van der Werff
Nectandra ambigens (S.F. Blake) C.K. Allen
Nectandra globosa (Aubl.) Mez
Nectandra salicifolia (Kunth) Mez
Ocotea dendrodaphne Mez

Malpighiaceae

Bunchosia lindeniana A. Juss. +
Mascagnia rivularis C.V. Morton et Standl.

Meliaceae

Guarea glabra Vahl ('raza' bijuga (DC.) T.D. Penn., *sensu* Pennington 1981)
Guarea grandifolia A. DC.
Trichilia havanensis Jacq.

Mimosaceae

Acacia hayesii Benth. +
Albizia purpusii Britton et Rose +
Inga acrocephala Steud.

Moraceae

Brosimum alicastrum Sw.
Clarisia biflora Ruiz et Pav. subsp. mexicana (Liebm.) W.C. Burger
Ficus petenensis Lundell
Ficus tecolutensis (Liebm.) Miq.
Ficus yoponensis Desv.
Poulsenia armata (Miq.) Standl.
Pseudolmedia oxyphyllaria Donn. Sm.
Trophis mexicana (Liebm.) Bureau

sinaceae

Parathesis lenticellata Lundell +

taginaceae

Neea psychotrioides Donn. Sm.
Pisonia aculeata L. var. aculeata

eraceae

Piper amalago L.

biaceae

Faramea occidentalis (L.) A. Rich.
Psychotria faxlucens Lorence et Dwyer
Psychotria simiarum Standl.

pindaceae

Allophylus campstostachys S.F. Blake +
Sapindus saponaria L.
Serjania goniocarpa Radlk.

potaceae

Chrysophyllum mexicanum Brandegee ex Standl.
Pouteria campechiana (Kunth) Baehni
Pouteria durlandii (Standl.) Baehni subsp. durlandii
Pouteria aff. *reticulata* (Engl.) Eyma subsp. reticulata
Pouteria rhynchocarpa T.D. Penn.
Pouteria sapota (Jacq.) H. Moore et Stearn

aphyleaceae

Turpinia occidentalis (Sw.) G. Don. subsp. breviflora Croat

liaceae

Heliocarpus appendiculatus Turcz.
Mortoniodendron guatemalense Standl. et Steyerm.

lmaceae

Ampelocera hottlei (Standl.) Standl.

Urticaceae

Urera elata (Sw.) Griseb.

Verbenaceae

Aegiphila costaricensis Moldenke
Citharexylum affine D. Don

Violaceae

Orthion oblanceolatum Lundell
Rinorea guatemalensis (S. Watson) Barlett

+ = species not present in Appendix 4.

Appendix 2. Species ranking on percent of basal area for Los Tuxtlas, México. Species density (no. of individuals 0.75 ha^{-1}) is also shown.

	Species	Family	Density	% BA
1	*Nectandra ambigens*	Lauraceae	15	**18.85**
2	*Spondias radlkoferi*	Anacardiaceae	13	**11.17**
3	*Pterocarpus rohrii*	Fabaceae	2	**7.09**
4	*Omphalea oleifera*	Euphorbiaceae	11	**4.53**
5	*Pseudolmedia oxyphyllaria*	Moraceae	28	**4.51**
6	*Orthion oblanceolatum*	Violaceae	13	**3.59**
7	*Guarea grandifolia*	Meliaceae	3	**3.43**
8	*Vatairea lundellii*	Fabaceae	2	**3.39**
9	*Ficus tecolutensis*	Moraceae	1	**2.97**
10	*Ficus yoponensis*	Moraceae	2	**2.18**
11	*Poulsenia armata*	Moraceae	4	**1.95**
12	*Pouteria reticulata*	Sapotaceae	1	**1.92**
13	*Guarea glabra*	Meliaceae	9	**1.92**
14	*Crataeva tapia*	Capparaceae	2	**1.79**
15	*Neea psychotroiedes*	Nyctaginaceae	2	**1.78**
16	*Dendropanax arboreus*	Araliaceae	4	**1.62**
17	*Faramea occidentalis*	Rubiaceae	31	**1.51**
18	*Cymbopetalum baillonii*	Annonaceae	4	**1.49**
19	*Bursera simaruba*	Burseraseae	2	**1.47**
20	*Cecropia obtusifolia*	Cecropiaceae	5	**1.28**
21	*Albizia purpusii*	Mimosaceae	1	**1.26**
22	*Croton shiedeanus*	Euphorbiaceae	11	**1.22**
23	*Mytenus schippii*	Celastraceae	5	**1.01**
24	*Heliocarpus appendiculatus*	Tiliaceae	1	**0.98**
25	*Sapindus saponaria*	Sapindaceae	1	**0.82**
26	*Dialium guianense*	Moraceae	1	**0.74**
27	*Pouteria sapota*	Sapotaceae	1	**0.71**
28	*Mortoniodendron guatemalense*	Tiliaceae	3	**0.69**
29	*Pouteria durlandii*	Sapotaceae	4	**0.68**
30	*Calophyllum brasiliense*	Clusiaceae	1	**0.68**
31	*Cordia megalantha*	Boraginaceae	2	**0.66**
32	*Lunania mexicana*	Flacourtiaceae	3	**0.65**
33	*Cordia stellifera*	Boraginaceae	1	**0.65**
34	*Stemmadenia donnell-smithii*	Apocynaceae	7	**0.62**
35	*Rheedia edulis*	Clusiaceae	9	**0.57**
36	*Piper amalago*	Piperaceae	7	**0.56**
37	*Ilex valeri*	Aquifoliaceae	3	**0.54**
38	*Quararibea funebris*	Bombacaceae	3	**0.53**
39	*Inga acrocephala*	Mimosaceae	1	**0.52**
40	*Nectandra globosa*	Lauraceae	1	**0.49**
41	*Quararibea yunckeri*	Bombacaceae	6	**0.47**
42	*Ampelocera hottlei*	Ulmaceae	3	**0.46**
43	*Ficus petenensis*	Moraceae	1	**0.46**
44	*Clarisia biflora*	Moraceae	1	**0.45**
45	*Citharexylum affine*	Verbenaceae	1	**0.42**
46	*Psychotria simiarum*	Rubiaceae	2	**0.41**
47	*Chrysophyllum mexicanum*	Sapotaceae	1	**0.38**

48	*Pleuranthodendron lindenii*	Flacourtiaceae	3	**0.37**
49	*Pouteria rhynchocarpa*	Sapotaceae	4	**0.29**
50	*Rinorea guatemalensis*	Violaceae	7	**0.28**
51	*Turpinia occidentalis*	Staphyleaceae	4	**0.27**
52	*Licaria velutina*	Lauraceae	3	**0.25**
53	*Iresine arbuscula*	Amaranthaceae	2	**0.21**
54	*Guamia sp.*	Annonaceae	6	**0.20**
55	*Trichilia moschata*	Meliaceae	2	**0.20**
56	*Diospyros digyna*	Ebenaceae	2	**0.15**
57	*Allophylus campstostachys*	Sapindaceae	1	**0.13**
58	*Aspidosperma megalocarpon*	Apocynaceae	1	**0.12**
59	*Nectandra salicifolia*	Lauraceae	1	**0.11**
60	*Psychotria faxluscens*	Rubiaceae	10	**0.11**
61	*Rinorea guatemalensis*	Euphorbiaceae	4	**0.09**
62	*Machaerium floribundum*	Fabaceae	1	**0.09**
63	*Pouteria campechiana*	Sapotaceae	1	**0.08**
64	*Ocotea dendrodaphne*	Lauraceae	1	**0.08**
65	*Aegiphilla costaricensis*	Verbenaceae	2	**0.08**
66	*Bunchosia lindeniana*	Malpighiaceae	2	**0.08**
67	*Pisonia aculeata*	Nyctaginaceae	1	**0.07**
68	*Brosimum alicastrum*	Moraceae	2	**0.07**
69	*Couepia polyandra*	Chrysobalanaceae	2	**0.06**
70	*Amphitecna tuxtlensis*	Bignoniaceae	1	**0.06**
71	*Serjania goniocarpa*	Sapindaceae	1	**0.05**
72	*Forsteronia viridescens*	Apocynaceae	1	**0.05**
73	*Adelia barbinervis*	Euphorbiaceae	1	**0.05**
74	*Tridimeris sp.*	Annonaceae	1	**0.05**
75	*Acacia hayesii*	Mimosaceae	1	**0.05**
76	*Mascagnia rivularis*	Malphigiaceae	1	**0.04**
77	*Eupatorium galeottii*	Asteraceae	1	**0.04**
78	*Dialium guianense*	Caesalpinaceae	2	**0.04**
79	*Trophis mexicana*	Moraceae	1	**0.04**
80	*Parathesis lenticellata*	Myrsinaceae	1	**0.03**
81	*Mansoa verrucifera*	Bignoniaceae	1	**0.03**
Total			306	**100**

Appendix 3. List of species and their code numbers on Figure 5.7 from 22 months of study of leaf litter in three sites of Los Tuxtlas, Mexico. Nomeclature follows Ibarra-Manriquez & Sinaca (1995, 1996a, 1996b).

Amaranthaceae

110 *Iresine arbuscula* Uline et W.L. Bray

Anacardiaceae

2 *Spondias radlkoferi* Donn. Sm.
85 *Tapirira mexicana* Marchand +

Annonaceae

24 *Cymbopetalum baillonii* R.E.Fr.
81 *Guamia* sp.

Apocynaceae

113 *Aspidosperma megalocarpon* Mull. Arg.
5 *Forsteronia viridescens* S.F. Blake
76 *Stemmadenia donnell-smithii* (Rose) Woodson

Aquifoliaceae

61 *Ilex valeri* Standl.

Araceae

30 *Philodendron guttiferum* Kunth +
114 *Philodendron sagittifolium* Liebm. +
21 *Philodendron scandens* K. Koch et Sell +
59 *Rhodospatha* aff. *wendlandii* Schott +
77 *Syngonium* +
74 *Syngonium podophyllum* Schott +

Araliaceae

31 *Dendropanax arboreus* (L.) Ecne. te Planch.
19 *Oeropanax obtusifolius* L. O. Williams +

Arecaceae

48 *Astrocaryum mexicanum* Liebm. ex Mart. +
100 *Chamaedorea alternans* H. Wendl. +

Aristolochiaceae

104 *Aristolochia ovalifolia* Duch. +

Asteraceae

108 *Eupatorium galeottii* B.L. Rob.
117 *Mikania* +
15 *Tuxtla pittieri* (Greenm.) Villaseñor et Strother +

Bignoniaceae

105 *Amphitecna tuxtlensis* A.H. Gentry
69 *Anemopaegma chrysanthum* Dugand +
54 *Arrabidaea verrucosa* (Standl.) A. H. Gentry +
97 *Callichlamys latifolia* (Rich.) Schum. +
36 *Mansoa hymenaea* (DC.) A.H. Gentry +
27 *Mansoa verrucifera* (Schltdl.) A.H. Gentry
64 *Paragonia pyramidata* (Rich.) Bur. +

Bombacaceae

34 *Quararibea funebris* (La Llave) Vischer
40 *Quararibea yunckeri* Standl. subsp. sessiliflora Miranda ex W.S. Alverson

Boraginaceae

44 *Cordia megalantha* S.F. Blake

Burseraceae

18 *Bursera simaruba* (L.) Sarg.

Caesalpiniaceae

92 *Cynometra retusa* Britton et Rose +
32 *Dialium guianense* (Aubl.) Sandwith.

Capparaceae

49 *Crataeva tapia* L.

Cecropiaceae

47 *Cecropia obtusifolia* Bertol.

Celastraceae

98 *Maytenus schippii* Lundell

Chrysobalanaceae

78 *Couepia polyandra* (Kunth) Rose

Clusiaceae

43 *Calophyllum brasiliense* Cambess.
38 *Clusia flava* Jacq. +
101 *Clusia lundellii* Standl. +
109 *Clusia minor* L. +
33 *Rheedia edulis* (Seem.) Triana et Planch.

Connaraceae

37 *Connarus schultesii* Standl. ex R.W. Schult. +

Convolvulaceae

75 *Ipomoea phillomega* (Vell.) House +

Dilleniaceae

51 *Tetracera volubilis* L. +

Euphorbiaceae

83 *Alchornea latifolia* Sw. +
29 *Croton schiedeanus* Schltds.
13 *Omphalea oleifera* Hemsl.

Fabaceae

25 *Dussia mexicana* (Standl.) +
63 *Lonchocarpus cruentus* Lundell +
28 *Machaerium floribundum* Benth.
8 *Pterocarpus rohrii* Vahl
3 *Vatairea lundellii* (Standl.)

Flacourtiacaea

80 *Lunania mexicana* Brandegee
53 *Pleuranthodendron lindenii* (Turez.) Sleumer

Hernandiaceae

103 *Sparattanthelium amazonum* Mart. +

Hippocrateaceae

107 *Hippocratea* +
68 *Salacia megistophylla* Standl. +

Lauraceae

70 *Licaria velutina* van der Werff
1 *Nectandra ambigens* (S.F. Blake) C.K. Allen
65 *Nectandra globosa* (Aubl.) Mez
115 *Nectandra salicifolia* (Kunth) Mez
112 *Ocotea dendrodaphne* Mez

Loranthaceae

111 *Phoradendron piperoides* (Kunth) +

Malphigiaceae

50 *Hiraea fagifolia* (DC.) A. Juss. +
82 *Mascagnia rivularis* C.V. Morton et Standl.

Malvaeae

58 *Robinsonella mirandae* Gómez Pompa +

Meliaceae

12 *Guarea glabra* Vahl ('raza' bijuga (DC.) T.D. Penn., sensu Pennington 1981)
26 *Guarea grandifolia* A. DC.
84 *Trichilia moschata* Sw.

Menispermaceae

71 *Abuta panamensis* (Standl.) Krukoff et Barneby +

Mimosaceae

56 *Inga acrocephala* Steud.

Moraceae

46 *Brosimum alicastrum* Sw.
11 *Clarisia biflora* Ruiz et Pav. subsp. mexicana (Liebm.) W.C. Burger
90 *Ficus cotinifolia* aff. cotinifolia +
93 *Ficus lundellii* Standl. +
102 *Ficus pertusa* L. f. +
14 *Ficus petenensis* Lundell
6 *Ficus tecolutensis* (Liebm.) Miq.
9 *Ficus yoponensis* Desv.
7 *Poulsenia armata* (Miq.) Standl.
4 *Pseudolmedia oxyphyllaria* Donn. Sm.

Myrtaceae

99 *Eugenia mexicana* Steud. +

Nyctaginaceae

10 *Neea psychotrioides* Donn. Sm.
95 *Pisonia aculeata* L. var. aculeata

Piperaceae

96 *Piper amalago* L.

Polygonaceae

87 *Coccoloba* +

Rhamnaceae

94 *Gouania lupuloides* (L.) Urb. +

Rubiaceae

86 *Genipa americana* L. +
22 *Faramea occidentalis* (L.) A. Rich.
115 *Psychotria chiapensis* Standl. +
79 *Psychotria faxlucens* Lorence et Dwyer
41 *Psychotria simiarum* Standl.

Sapindaceae

67 *Paullinia fuscescens* Radlk. +
39 *Sapindus saponaria* L.
52 *Serjania goniocarpa* Radlk.
66 *Thinouia myriantha* Triana et Planchón +

Sapotaceae

45 *Crysophyllum mexicanum* Brandegee ex Standl.
57 *Pouteria campechiana* (Kunth) Baehni
55 *Pouteria durlandii* (Standl.) Baehni subsp. durlandii
20 *Pouteria* aff. *reticulata* (Engl.) eyma subsp. reticulata
88 *Pouteria rhynchocarpa* T.D. Penn.
16 *Pouteria sapota* (Jacq.) H. Moore et Stearn
35 *Sideroxylon portoricense* Urb. subsp. *minutiflorum* (Pittier) T.D. Penn. +

Solanaceae

91 *Juanulloa mexicana* (Schltdl.) Miers +

Staphylaceae

60 *Turpinia occidentalis* (Sw.) G. Don. Subsp. breviflora Croat

Tiliaceae

62 *Heliocarpus appendiculatus* Turcz.
42 *Mortoniodendron guatemalense* Standl. et Steyerm.

Ulmaceae

17 *Ampelocera hottlei* (Standl.) Standl.
89 *Celtis iguanaea* (Jacq.) Sarg. +

Urticaceae

106 *Urera caracasana* (Jacq.) Griseb. +
118 *Urera elata* (Sw.) Griseb.

Verbenaceae

73 *Aegiphila costaricensis* Moldenke
72 *Citharexylum affine* D. Don

Violaceae

22 *Orthion oblanceolatum* Lundell
119 *Rinorea guatemalensis* (S. Watson) Barlett

+ = species not present as individual > 10 cm dbh in the forest plots.

endix 4. Families and species found in the pastures of three ages and their isolated trees sampled, in Los Tuxtlas, Mexico.

nthaceae
Blechum brownei (L.) Ant. Juss.

ranthaceae
Achyranthes sp. +

cynaceae
Stemmadenia donnell-smithii (Rose) Woodson
Tabernaemontana alba Mill.
Thevetia ahouai (L.) DC

ceae
Syngonium chiapense Standl.
Xanthosoma robustum Schott

clepiadiaceae
Asclepias curassavica L.

teraceae
Chaptalia nutans (L.) Pol.
Pseudelephantopus spicatus (Aubl.) Rohr
Synedrella nodiflora (L.) Gaertn.

raginaceae
Cordia spinescens L.

rseraceae
Bursera simaruba (L.) Sarg.

esalpinaceae
Cassia covanense +

ryophyllaceae
Drymaria cordata (L.) Willd. ex Roem. et Shult.

usiaceae
Calophyllum brasiliense Cambess.

mmelinaceae
Commelina diffusa Burm. f.

nvolvulaceae
Ipomoea batatas (L.) Poir.

curbitaceae
Momordica charantia L.

yperaceae
Cyperus laxus Lam.
Scleria sp. +

ioscoraceae
Dioscoria sp. +

Euphorbiaceae
Acalypha sp. +
Acalypha arvensis Poepp. et Endl.
Caperonia sp. +
Chamaesyce sp. +
Euphorbia caperonia +
Phyllanthus niruri L.
Sapium laterifolium +

Fabaceae
Desmodium incanum DC.

Heliconiaceae
Heliconia sp. +

Lamiaceae
Hyptis atrorubens Poit.

Leguminosae
Leguminosae +

Malvaceae
Pavonia schiedeana Steud.
Sida rhombifolia L.

Meliaceae
Cedrela odorata L.

Mimosaceae
Acacia cornigera (L.) Willd.
Mimosa pudica L.

Moraceae
Brosimum alicastrum Sw.

Myrtaceae
Eugenia capuli (Schltdl. et Cham.) O. Berg

Myrsinaceae
Parathesis lenticellata Lundell
Parathesis psychotrioides Lundell

Passifloraceae
Passiflora sp. +

Piperaceae
Piper amalago L.
Piper hispidum Sw.
Piper umbellatum L.

Poaceae
Andropogon bicornis L.
Cynodon dactylon (L.) Pers.
Cynodon plectostachyus Pilger
Paspalum conjugatum Bergius

ypodiaceae

Polypodium sp. +

iaceae

Rubiaceae sp. +

aceae

Citrus (Lemon)
Citrus (Mandarine)
Citrus (Orange)
Zanthoxylum kellermanii P.G. Wilson

indaceae

Cupania glabra Sw.

izaeaceae

Lygodium venustum Sw.

aginellaceae

Selaginella sp. +

lanaceae

Cestrum grandiferum +
Solanum acerifolium +
Solanum ochraceo-ferrugineum +
Solanum schlechtendalianum Walp.

aceae

Cissus gossypifolia Standl.

= taxa not checked with herbarium records.

Appendix 5. Authorities for the plants and animals of common use mentioned throughout the thesis.

Arachis hypogaea L.
Bos indicus
Bos taurus
Capsicum annuum L.
Cucumis Melo L.
Mangifera indica L.
Phaseolus vulgaris L.
Zea mays L.