

## Amazonian caatinga and related communities at La Esmeralda, Venezuela: forest structure, physiognomy and floristics, and control by soil factors

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### Abstract

Tall and short Amazonian caatinga at La Esmeralda (rainfall 2600 mm yr<sup>-1</sup>) are described and compared with those at San Carlos de Río Negro (3600 mm yr<sup>-1</sup>). The tall forests have much in common: thin-boled trees, many with scleromorphic mesophylls, lack of thick-stemmed climbers and of herbs, species paucity in all life-forms, domination by *Eperua*, and a high proportion of Bombacaceae, Clusiaceae and Euphorbiaceae. The short caatingas are also structurally and floristically similar but at La Esmeralda the notophyll scrubland species are lacking. At La Esmeralda, the common tree species are autochorous, but the majority of plants (particularly understorey species) are zoochorous. Relatively high transmission of light to the floor of the tall caatinga (1.5% PAR) may explain how trees with light-demanding architecture regenerate in the understorey. The presence of *Cecropia* and 'weedy' species in the caatinga only at San Carlos may be the result of greater human interference there. The soils at San Carlos and La Esmeralda are similar: thick humus overlying bleached sand, waterlogged most of the year. The water table at La Esmeralda drops to >1 m depth during the drier months, but tensiometers at 30 cm depth did not indicate significant water shortage. Soils are consistently wetter in the short caatinga than the tall. Shortage of nitrogen appears to determine the major structural and physiognomic features of the caatinga, and depth of aerated soil appears to determine its stature. Comparisons are made between tall caatinga, wallaba and swamp forest in the Guianas and heath forests of Malaysia.

*Abbreviations:* PRF – Palm-Rich Forest; SC – Short Caatinga; TC – Tall Caatinga

*Nomenclature:*

Gleason 1931; Eden 1974, unless in Table 6 or 7

### Introduction

Amazonian caatinga (henceforth caatinga) is a type of forest community which grows on seasonally waterlogged and extremely oligotrophic bleached white sand, drained by black waters; it is characterized by low stature, thin boles, dominance by a few tree species and a relatively high transmission of light to the understorey (Anderson 1981; Medina & Cuevas 1989). This kind of forest is very widespread in southern Venezuela (Huber & Alarcon 1988) and in Brazil (Takeuchi 1962; Klinge & Medina 1979; Anderson 1981; Prance 1989).

In structure and physiognomy it is closely similar to the wallaba forests of the Guianas, which occur on free-drained bleached white sands (Davis & Richards 1934; Richards 1952). Some of the campinas of the Amazon basin near Manaus, called 'caatinga woodlands' by Anderson (1981), appear to have been induced by human activity (Prance & Schubart 1978), but there is no evidence that caatinga and wallaba forests are other than natural vegetation-types.

For a site near San Carlos de Río Negro in southern Venezuela (henceforth San Carlos) Bongers, Engelen & Klinge (1985) have given a detailed account of

a transition from tall caatinga (TC) to a low scrub ('bana'), which occurs on domes of deeper sand – rising about 2 m in 200 m. Four communities were recognized along the continuum: TC 17–25 (–30) m in height, tall bana 6–12 (–18) m, low bana 3–5 (–10) m, and open bana 2 m with about 90% open ground in which herbs grow between the treelets. The low bana and open bana differ from the tall bana and TC in having a dominance of notophylls rather than of mesophylls *sensu stricto* (Medina 1984; Bongers *et al.* 1985). Medina & Cuevas (1989) referred to the tall bana and low bana collectively as 'low caatinga'; we shall use the term 'short caatinga' (SC) for the tall bana (as the name refers to stature and not position in the landscape), and reserve the term 'bana' for communities with notophylls dominant. The leaves in bana are highly scleromorphic and steeply inclined (Medina, Sobrado & Herrera 1978; Sobrado & Medina 1980; Medina, García & Cuevas 1990). It was found by Bongers *et al.* (1985) that the reduction in height of the community was related to a reduction in the depth of the layer of aerated soil above the water table. The reduction in leaf size and increase in mean inclination were related by Medina *et al.* (1978 & 1990) to the risk of short-lived dry spells taking the water table far below the roots in the shallow persistently aerated layer.

Published studies on the functioning of caatinga have almost all been made at San Carlos. These studies have covered biomass, girth increment, litterfall, nutrient cycling, water relations, leaf form and limitations to growth (all reviewed by Medina & Cuevas 1989 and Jordan 1989), penetration of light (Heuvel-dop 1978), mycorrhiza (Moyersoen 1993) and photosynthetic rates in relation to leaf longevity (Reich, Uhl, Walters & Ellsworth 1991; Reich, Walters, Ellsworth & Uhl 1994, Reich & Walters 1994).

The objectives of this paper are (i) to provide a description of tall and short caatingas in a part of southern Venezuela with a lower total rainfall and more marked dry season than is found at San Carlos, and (ii) to provide new evidence on the factors controlling their development. We provide a more detailed account of the physiognomy and floristics of the caatinga than has been published for San Carlos. We describe briefly the forest and savanna communities associated with the caatinga. These studies provide the background for experimental work on the importance of root competition in the TC, a topic not previously investigated.

## Climate

La Esmeralda (3°10' N, 65°33' W, 99 m above sea level), which had a mean annual rainfall of  $2633 \pm 86$  mm in 1970–86, lies on a gradient from  $>3600$  mm yr<sup>-1</sup> in the San Carlos area to  $<1600$  mm yr<sup>-1</sup> in central northern Amazonia (Fig. 1). Data on pan evaporation, sunshine hours, screen temperature and relative humidity are not available for La Esmeralda, and we have therefore used in Fig. 2 values recorded 40 km to the south-east at Ocamo where the total annual rainfall ( $2514 \pm 78$  in 1970–88) and seasonal distribution are much the same as at La Esmeralda. As shown in Fig. 2 rainfall exceeds pan evaporation from April to November (henceforth wet season) but not from December to March (dry season). In contrast, at San Carlos rainfall exceeds pan evaporation for all months of the year (Medina & Cuevas 1989). At La Esmeralda the mean number of dry days ( $<1$  mm) per month is strongly negatively dependent on mean total rainfall for the month ( $y = 21.4 - 0.052x$ ,  $n = 7$ ,  $r^2 = 0.896$ ). The probability of a given number of consecutive dry days in a month is much greater at La Esmeralda than at San Carlos (Fig. 3); dry spells of  $>9$  days are extremely rare at San Carlos but occur in virtually every dry season at La Esmeralda, at which time fires in the savannas are common. At Ocamo the mean number of sunshine hours per month over 13 years was  $240 - 0.3 \times$  mean rainfall for that month ( $r^2 = 0.92$ ). Veillon (1989) has classified the area as having only very soft winds ( $0-5$  km h<sup>-1</sup>) except in association with storms.

## Geology

Pre-cambrian igneous-metamorphic rock underlies the region and is exposed in several places, most notably the Serranía de Imataca, the Sierra Parima and the many inselbergs near Puerto Ayacucho (Colvee 1971). Sedimentary deposition of the Roraima Sandstone Formation in the Pre-cambrian was followed by regional uplift and intrusion to form dykes and sills (Cooper 1979). The immensely long period since the Cambrian until the present day, was apparently free of tectonic activity, and has permitted erosive elements to shape the landscape. An estimated 80% of the Roraima sandstone has been eroded, depositing 2–3 million km<sup>3</sup> of sediments at the mouths of the Orinoco, Río Negro and Berbice (Cooper 1979) and covering vast tracts of land with white sand. Remnants of the Roraima formation

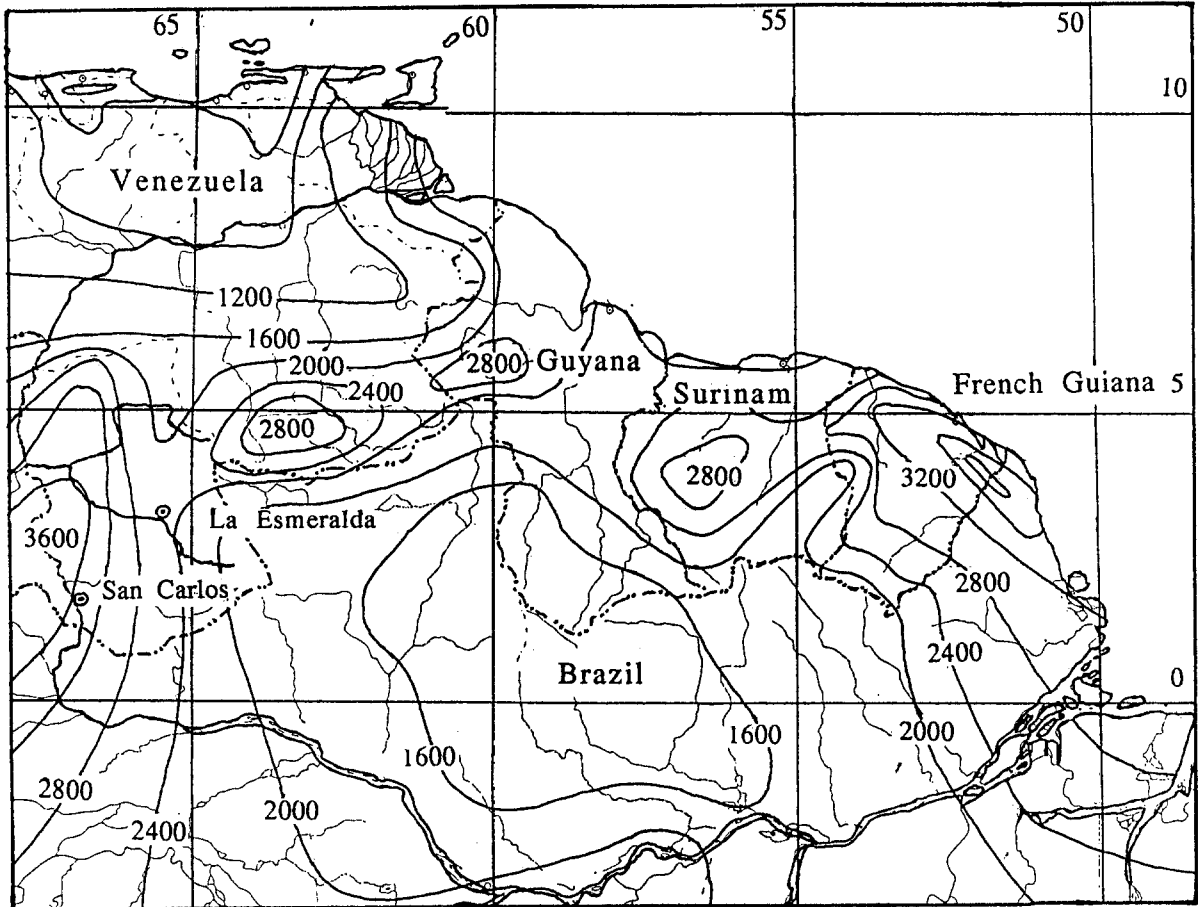


Figure 1. The distribution of total annual precipitation (mm) in north-eastern South America. Redrawn from MARNR (1982) and Schwerdtfeger (1976).

remain as impressive table-top mountains ('tepuis'), of which Mt Duida (2358 m), a few km north of La Esmeralda, is an example (Tate & Hitchcock 1930). On the north side of the village is the Esmeralda ridge (Gleason 1931), which is only 20–40 m high but runs discontinuously for tens of km in an approximately east-west direction; it is composed of strongly weathered schist, once intercalated with quartz veins which have weathered to leave quartz crystal deposits.

### Human disturbance

Pre-hispanic history remains obscure and controversial, although some research suggests that indigenous populations could have been much greater than at the

present day (Hecht & Cockburn 1989). La Esmeralda was briefly an important colonial centre in the 1770s, but was reduced to a village of 12–15 families in 1785 (Humboldt, 1818–1820). It seems that there were even fewer inhabitants between 1785 and 1958; during the 1920s the savannas were used for pasturage by cattle (Tate & Hitchcock 1930). In 1958 the Salesian order founded a mission, which was expanded in 1978 to include a multi-ethnic school. The village's population of Yek'wana and Baré Amerindians has steadily increased to around 500 in 1994. They rely on slash-and-burn agriculture to produce plantains, cassava and pineapples; much of the land near the village is unsuitable for agriculture because it is under savanna or seasonally waterlogged, and most farm plots are in the forests along the Orinoco and Iguapo rivers. The peo-

Table 1. A summary of the major vegetation-types around La Esmeralda; the dominant leaf-size class for dicotyledonous trees in forest-types 1.2 to 1.5 is mesophyll *sensu* Webb (1959). Widely distributed species in forest type 1.1 are marked with daggers.

Name	Topography and soil	Height (m), structure & physiognomy	Major species
1. Evergreen forests			
1.1 Ridge forest	Esmeralda Ridge boulders with lithosol	4; trees with relatively small thick leaves, lacking drip tips; few thin-stemmed climbers; very few epiphytes	Trees: <i>Bysonima crassifolia</i> †, <i>Clusia columnaris</i> , <i>Ficus oblanceolata</i> †, <i>Humiria floribunda</i> †, <i>Ouratea spruceana</i> , <i>Pagamea coriacea</i> , <i>Qualea esmeraldae</i> , <i>Remija hispida</i> and <i>Tratinnickia burseraefolia</i> † Shrubs and treelets: <i>Acanthella conferta</i> , <i>Elsonia diversifolia</i> †, <i>Ernestia tenella</i> , <i>Eupatorium tylerti</i> , <i>Gouateria sessilis</i> and <i>Gouateria</i> sp., <i>Ladenbergia lucens</i> , <i>Mandevilla sub-carnosa</i> , <i>Miconia albicans</i> , <i>Polymnia stenocarpa</i> and <i>Retiniphyllum schomburgkii</i> Herbs: (a) on rocks <i>Anthurium hookeri</i> , <i>Pitcairnia nuda</i> , <i>Smilax benthamiana</i> , <i>Tillandsia aloifolia</i> and 3 orchids (commonest <i>Sobralia liliistrum</i> ), (b) under overhanging rocks <i>Anemia buntifolia</i> , <i>Oleandra hirta</i> , <i>Paepalanthus fasciculatus</i> and <i>Selaginella radiata</i>
1.2 Palm-rich forest on loamy sand	Terra firme. Deep hollows c. 1 m wide every c. 10 m are seasonally waterlogged	18-28; most of tallest trees with spreading crowns; few trees > 60 cm dbh; few buttress roots; few herbs, climbers or epiphytes	Characteristic palms: <i>Jessenia bataua</i> (to 20 m), <i>Bacris</i> cf. <i>simplicifrons</i> and unidentified fish-tail palm (understorey). Tallest trees: <i>Caryocar glabrum</i> , <i>Humiria balsamifera</i> Trees reaching 15-22 m: <i>Aldina</i> sp., <i>Emmotium acuminatum</i> , <i>Eschweilera parviflora</i> , <i>Licania octandra</i> , <i>Licania</i> sp., <i>Micropholis guyanensis</i> , <i>Ouratea</i> sp., and <i>Protium crassipetalum</i> Understorey trees: <i>Duguetia</i> (2 spp.) and <i>Eschweilera</i> sp.
1.3 Palm-rich forest on sandy loam	Terra firme. Deep hollows c. 1 m wide every c. 10 m are seasonally waterlogged	35; most of tallest trees with spreading crowns; many trees > 60 cm dbh (some > 100 cm); some with buttresses to 1.5 m; frequent broad-leaved herbs and small palms; thick-stemmed climbers	Characteristic palms: <i>Jessenia bataua</i> (commonest, to 20 m), <i>Manicaria saccifera</i> (occasional, 10 m), <i>Iriarteia</i> sp. and <i>Leopoldina piassaba</i> (both rare, 10 m) Dicot trees to 15-35 m: <i>Apeiba</i> cf. <i>echinata</i> , <i>Couma</i> sp., <i>Enterolobium</i> sp., <i>Hevea</i> sp., <i>Parkia</i> sp., <i>Pouteria</i> sp., <i>Protium crassipetalum</i> , <i>Swarizia</i> sp. and <i>Theobroma</i> sp. Small palms: species of <i>Bactris</i> , <i>Chamaedorea</i> Giant herb: <i>Phenakospermum</i> Other herbs: <i>Heliconia</i> sp., <i>Marantaceae</i> (2 spp.), <i>Parietaria</i> sp. <i>Poaceae</i> ); <i>Spathiphyllum</i> sp. ( <i>Araceae</i> ) on the river-bank
1.4 Tall caatinga	Seasonally waterlogged white sand with thick superficial humus. Hummocks and hollows c. 2 m across	18-23; very few spreading crowns; few trees > 30 cm dbh; buttresses very rare; stilt roots, knee roots and pneumatophores common; shrubs common and broad-leaved herbs very rare; climbers thin-stemmed; vascular epiphytes few, on boles	Characteristic palms: <i>Mauritia carana</i> (scattered, not abundant as a juvenile, 23 m), <i>Euterpe</i> sp. 378 and <i>Mauritia aculeata</i> (rare, 18 m) Other palms: <i>Jessenia bataua</i> (scattered, only immatures to 1 m) and rare individuals of small palms from forest-type 1.3 Dicot trees to 20-23 m: <i>Bombacopsis</i> cf. <i>amazonica</i> , <i>Caraipa longipedicellata</i> , <i>Iryanthera</i> cf. <i>elliptica</i> , <i>Micrandra siphonoides</i> Dominant tree to 20 m: <i>Eperua obusata</i> Other common trees to 8-20 m: <i>Dendropanax arboreus</i> , <i>Hevea pauciflora</i> , <i>Neocouma ternstroemiacea</i> , <i>Protium aracouchini</i> and <i>P. carolense</i> Shrubs: <i>Myrmidone macroperma</i> , <i>Psychotria egenis</i> , <i>P. humboldtiana</i> , <i>Tococa macrophysca</i> Herb: <i>Trichomanes</i> sp. 432

Table 1. Continued.

Name	Topography and soil	Height (m), structure & physiognomy	Major species
1.5 Short caatinga	Like 1.4 but water table persistently nearer surface	3-8; no spreading crowns; few trees >20 cm dbh; no buttresses; stilt roots, knee roots and pneumatophores common; shrubs very common; no broad-leaved herbs; small climbers and epiphytes quite common	Characteristic palms: <i>Mauritia carana</i> (scattered, not abundant as a juvenile, 8 m), <i>Euterpe</i> sp. 378 (rare, 6 m) Dicot trees to 6-8 m: <i>Bombacopsis</i> cf. <i>amazonica</i> , <i>Byrsonima wurdackii</i> , <i>Caraipa longipedicellata</i> , <i>Iryanthera</i> cf. <i>elliptica</i> Dominant tree to 6 m: <i>Eperua obtusata</i> (less dominating than in 1.4) Other common trees to 4-6 m: <i>Clusia spathulafolia</i> , <i>Hevea pauciflora</i> , <i>Macrobolium gracile</i> , <i>Neea</i> cf. <i>mapouritoides</i> , <i>Pagamea plicata</i> , <i>Protium carolense</i> and <i>Protium</i> sp. Shrubs: <i>Clidemia heteroneura</i> , <i>Myrmidone macroperma</i> , <i>Psychotria hoffmanseggiana</i> & <i>P. humboldtiana</i> , <i>Tococa macrophysca</i> Herbs: Cyperaceae 406, <i>Trichomanes</i> spp. Common climbing epiphyte: <i>Codonanthe crassifolia</i>
2. Savannas			
2.1 Trachypogon plains savanna	Plains; various soils, not purest sands	0.3; codominated by grasses with tall pseudostems; forbs sparse; trees, treelets and shrubs absent or scattered	Grasses: <i>Trachypogon plumosus</i> agg., <i>Axonopus pulcher</i> , <i>Leptocoryphium lanatum</i> , <i>Mesosetum rotibollioides</i> and <i>Paspalum pulchellum</i> Sedge: <i>Bulbostylis paradoxa</i> Dicot herbs: <i>Eriosema simplicifolia</i> , <i>Irlbachia alata</i> , <i>Perama galioides</i> and <i>Rhynchanthera grandiflora</i> . Shrubs and trees: <i>Byrsonima crassifolia</i> , <i>Casearia sylvestris</i> , <i>Qualea esmeraldae</i> , <i>Xylopia aromatica</i> . The palm <i>Mauritia flexuosa</i> follows depressions and watercourses
2.2 Sedge plains savanna	Plains, sandy soils varying in organic matter; more persistently waterlogged than for 2.1	0.2; dominated by sedges with short pseudostems and erect leaves; ericocaulids & xyrids common	Grasses: <i>Panicum</i> spp. Sedges: <i>Cabypitrocarya fragifera</i> , <i>Rhynchospora</i> spp. Other monocot herbs: <i>Abolboda macrostachya</i> , <i>Burmammia bicolor</i> , <i>Duckeella</i> sp., <i>Eriocaulon</i> spp., <i>Monotrema</i> sp., <i>Syngonanthus setifolius</i> , and <i>Xyris</i> spp. Dicot herbs: <i>Curatia tenuifolia</i> , <i>Cynanchum strictum</i> , <i>Irlbachia caerulea</i> Shrubs and treelets: <i>Humiria balsamifera</i> , <i>Ocotea</i> sp., <i>Sauvagesia ramosa</i> , <i>Vochysia</i> sp.
2.3 Smooth (boulder-free) hill savannas	Gravel soil with clayey matrix	0.1-0.2; sedges common with relatively distant tussocks and stiff erect leaves.	Grass: <i>Trachypogon plumosus</i> agg. Sedges: <i>Bulbostylis capillaris</i> , <i>B. junciformis</i> , <i>Rhynchospora globosa</i> and <i>R. lanata</i> Dicot herbs: <i>Irlbachia alata</i> , <i>Buchneria</i> cf. <i>palustris</i> , <i>Orthopappus augustifolius</i> , <i>Perama galioides</i>

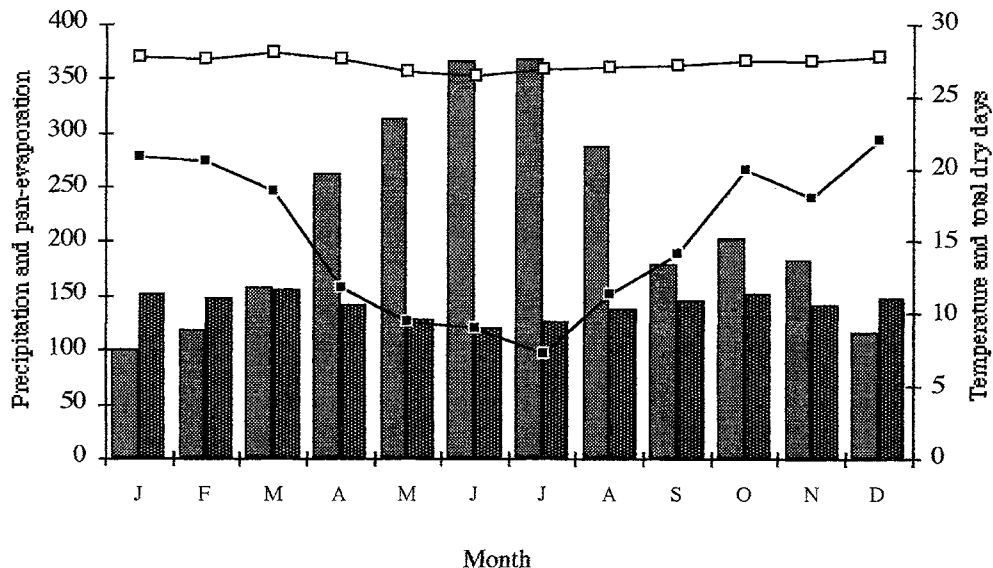


Figure 2. Mean monthly rainfall (lightly-shaded bars, mm) and dry days (lines with filled squares) from La Esmeralda 1970–86, evapotranspiration (heavily-shaded bars, mm) and temperature (line with open squares, °C) from Ocamo 1970–88, 40 km SE. All data from MARNR, Caracas.

ple augment their diet with tinned and maize-based foods, with forest fruits (especially from the palms *Jessenia bataua* and *Mauritia flexuosa*), and with fish and game, which is locally depleted. The missionaries and Yek'wanas graze cattle on the extensive savannas. In recent years the Venezuelan government has taken many steps to conserve the region, prohibiting logging in 1978, mining in 1989, and establishing the Humboldt Research Station at La Esmeralda in 1990–1994. The perceived threat of Brazilian gold mining on the border has led to a marked increase in military activity, including the enlargement of the airstrip in 1994 and the establishment of a large long-term army post.

In summary, it appears that the population of La Esmeralda over most of the last 100–200 years has been very small, and that human impact on the local vegetation has been much less than, for example, at San Carlos, where there has been a large settlement at least since 1880 (cf. Spruce 1908; Saldarriaga 1987). Sanford *et al.* (1985) have documented the widespread occurrence of charcoal in the soils around San Carlos, and suggested that fires are a natural force in the forests. We suggest that their incidence has been greatly increased by human activity, and that the forests around San Carlos may have been substantially more

affected by humans than those around La Esmeralda (see Discussion).

### Outline of vegetation and soil-types

We recognise 5 major forest-types and 3 major savanna-types occurring within 5 km of the centre of La Esmeralda (Table 1). The ridge forest is markedly different in many respects from the non-ridge forests, which were studied in detail only within the area shown in the lower inset of Fig. 4. No attempt was made to map areas of secondary vegetation accurately.

Sections of a 4 m wide transect from the PRF on brown loamy sand through TC to SC, is shown in Fig. 5. The tall and short caatingas are described in detail in the following section. The PRF on brown sandy loam at La Esmeralda resembles the terra firma forest on oxisol at San Carlos in its abundance of the palm *Jessenia bataua*, and development of a root mat which quickly penetrates freshly fallen litter. However, the tallest trees have relatively wide crowns and the palm seems much more abundant in the La Esmeralda forest, commonly causing deep shade in the understorey (0.7% PAR at breast height) and a major reduc-

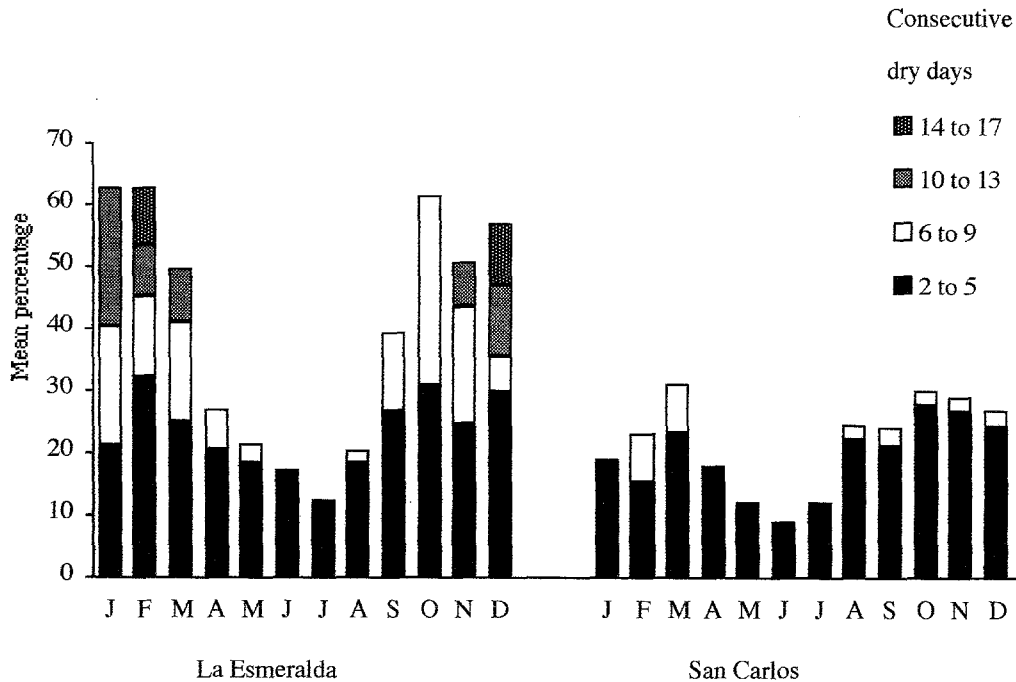


Figure 3. The percentage of each month taken up by a given number of consecutive dry days, using means from rainfall data at La Esmeralda (1970–88) and data from Heuvelodop (1980) for San Carlos de Río Negro, with 2–5 consecutive dry days as black bars, 6–9 unfilled bars, 10–13 lightly shaded bars, 14–17 densely shaded bars.

tion in the development of the sapling and shrub layer, much as happens with *Eugeissonia tristis* in hill dipterocarp forest in western Malaysia (Whitmore 1984). The abundance of small palms and broad-leaved herbs in the PRF on yellow loamy sand which forms a narrow belt between the caatinga we studied and the nearest small river, makes a link with the forests of the Amazon basin which are very rich in species of herb and climber, e.g. that on shale and limestone in Ecuador described in detail by Grubb, Lloyd, Pennington & Whitmore (1963). This forest resembles in some ways the forests of yevaro (*Eperua purpurea*) and guaco (*Monopteryx* cf. *uacu*) on ultisols at San Carlos with their tall (35 m), wide crowns and well developed buttresses or stilt roots, but apparently with few broad-leaved herbs (R. Herrera, private communication).

The relationships between soil-types and floristics in the savannas around La Esmeralda are complex. Here we recognize three reference types: two on the plains and one on the hills north of the Esmeralda Ridge. Savannas 2.1 and 2.3 are grouped as llanos-type savannas by Huber (1982) and have been studied by

Eden (1974). The palm *Mauritia flexuosa* occurs along water courses in the llanos-type savanna, as single rows in regularly burned areas, but forming thick stands in association with tall aroids and dicot trees in marshes. Class 2.2 is probably Amazonian-type savanna (*sensu* Huber 1982), though the virtual absence of dwarf shrubs, and the absence of Araceae, Bromeliaceae and Haemodoraceae makes it somewhat distinct.

### Detailed description of the tall and short caatingas

#### Methods

Samples were taken with a 20 mm corer from the surface soils (0–10 cm) of the TC, SC and PRF on loamy sand. At each locality 24 cores were taken randomly from 1 ha, and combined to make 3 samples, each of 8 cores. Samples were air-dried in the field and pH measured electronically in a 1:2.5 soil to deionized water mixture and 1 M KCl. Texture was measured using hydrometers (Anderson & Ingram 1987) at the Institu-

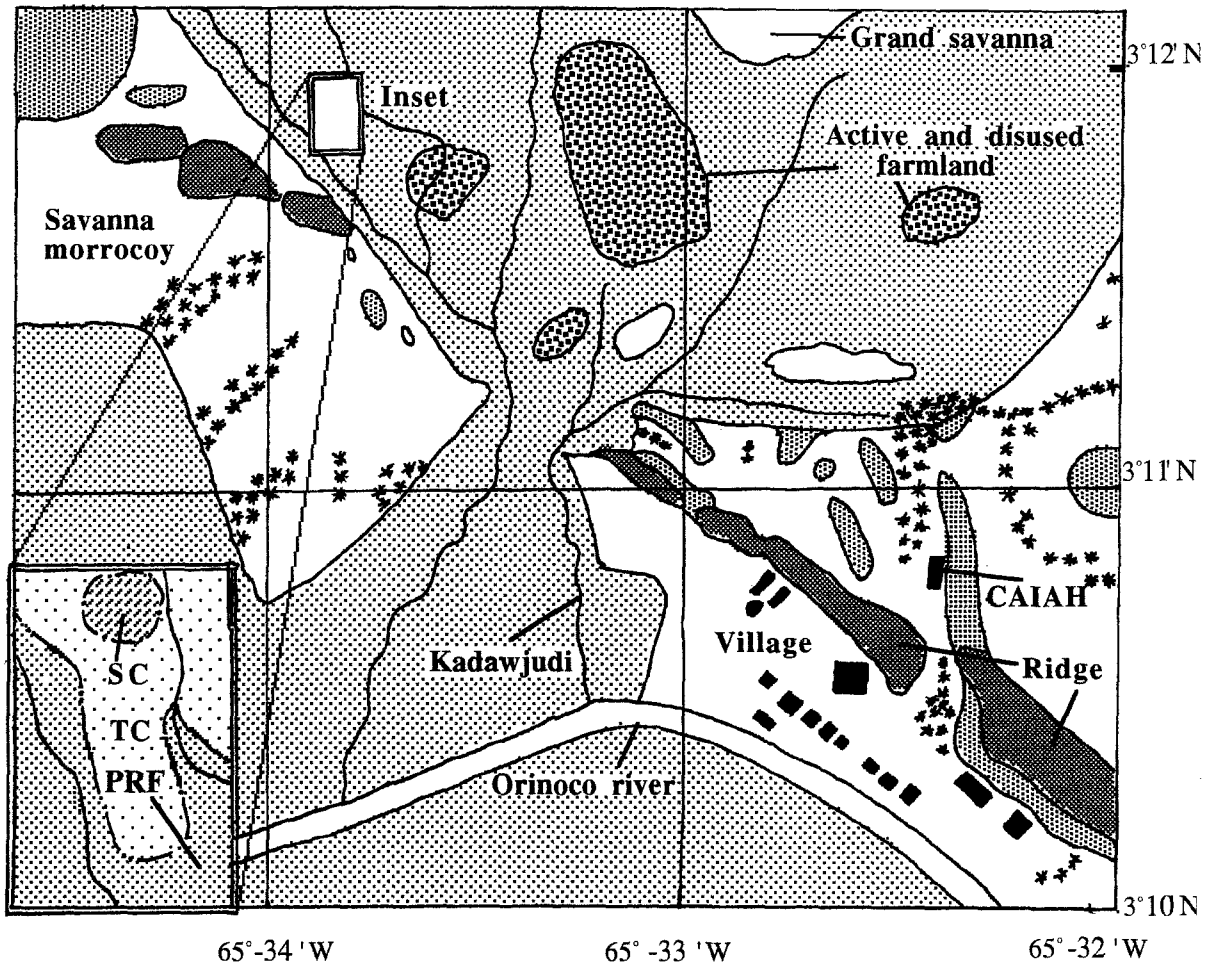


Figure 4. Vegetation map of La Esmeralda, based on coordinates from a portable Garmin GPS system (accurate to  $\approx 30 \text{ m}^2$ ). Buildings (black boxes), farmland active and disused (pattern of small squares), plains savanna (unshaded), hill savanna (densely shaded), *Mauritia flexuosa* stands (black stars), lowland forest (lightly shaded), ridge forest (very densely shaded), and streams (black lines). Inset in bottom left-hand corner is the study site, with SC, TC and PRF labelled.

to Venezolano de Investigaciones Científicas (IVIC), Caracas. Smaller samples were oven-dried, and taken to Cambridge for measurement of loss on ignition, and total N, P and K using standard methods (Allen, Grimshaw, Parkinson & Quarmby 1974) documented in Grubb, Turner & Burslem (1994). Macro-porosity of the top 10 cm of soil at field capacity was determined on cores taken 24 hours after heavy rain; water was poured into each core until all the air was displaced and the weight of added water was measured.

Water table fluctuations were monitored approximately weekly for 6 months spanning the dry and wet seasons at 12 points along an 800 m transect; 3 in each of the PRF on loamy sand, TC, SC and in the zone between the TC and SC. Holes were dug to 1 m (or to the gravel layer) with a corer, and a PVC pipe (drilled with 2 mm holes) was inserted. Mercury column tensiometers were inserted to a depth of 30 cm at 5 random locations in each of these forests, and measurements taken for six weeks in the dry season.



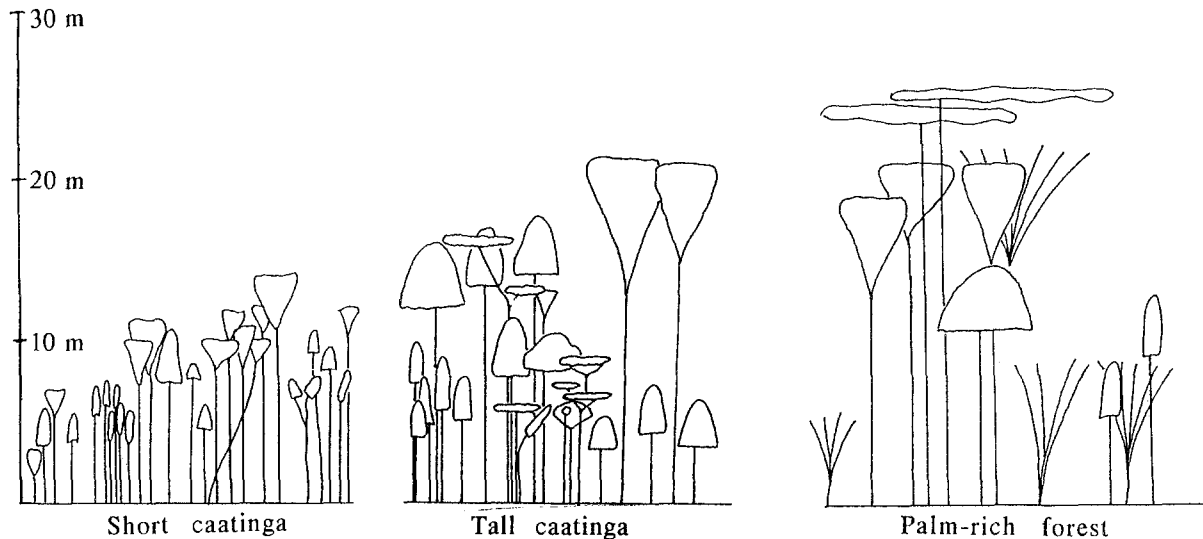


Figure 5. Three sections of a line transect (4 m wide) through palm-rich forest on loamy sand, tall caatinga and short caatinga.

Five randomly located plots of  $50 \times 5$  m were enumerated in the TC and 4 plots of  $25 \times 2.5$  m in the SC. In the TC, the girth, species and coordinates of every stem  $>5$  cm dbh were recorded; in the short caatinga trees  $>3$  cm dbh were enumerated. In the first three transects of the TC counts were made of shrubs and treelets  $<5$  m tall, climbers, bole-epiphytes and herbs. In the fifth plot all trees  $>1.50$  m tall and  $>1$  cm dbh were recorded. Finally, 3 randomly chosen plots of  $4 \times 4$  m in the TC, and 3 of  $1 \times 16$  m in the SC, were used to enumerate all woody plants, i.e. including seedlings; the numbers of plants in the height classes  $<50$  cm, 50–200 cm, 2–5 m and  $>5$  m were recorded. In the TC, which has a hummock and hollow topography, the quadrats were split into 64 sub-quadrats of  $50 \times 50$  cm, and the topography was recorded in terms of the depth of the centre point of each of the sub-quadrats below the highest hummock in the whole quadrat; where necessary the sub-quadrats were further subdivided.

During two years of study we collected around 130 vouchers which are deposited at the Botanical Institute of Venezuela, Caracas (VEN); the Royal Botanic Garden, Kew (K), and the regional herbarium of the Ministry of the Environment, Puerto Ayacucho (TFAV). The collection numbers quoted are those of D.A. Coomes. Phenological data were derived from the dates of vouchers and from field notes and seed collections.

Mean specific leaf area (SLA) was calculated using leaves from the top of the canopy of 7 TC and 10 SC species; three trees were sampled for each species. For each tree, disks from 20 leaves were cut with a 9-mm borer, and weighed after drying. The concentrations of N, P and K were determined in Cambridge using the same methods as for soils.

The diffuse site factor (*sensu* Anderson M.C. 1964) was measured on overcast days using paired quantum sensors (SKYE, Llandrindod Wells, Powys, LD1 6DF). Instantaneous readings were taken simultaneously on an open hilltop and in the forest, the quotient giving the transmission of indirect irradiance to the understorey. Readings were taken at 0.4, 1.35 and 2.1 m height along 10 transects, 5 each in the tall and short caatingas. In the PRF on loamy sand readings were taken only at 1.35 m height along 5 transects. Readings were taken at 10 random points along each transect.

#### *Soils of the tall and short caatingas*

The soils are characterised by a mor humus layer overlying a bleached white-sand E horizon in which there are very few fine roots (Table 2). There is no spodic horizon above the compact gravel layer, which is composed of Roraima sandstone and which is found at a depth varying from 1–1.7 m in the TC to 0.4–1.1 m

Table 2. Brief descriptions of soil profiles in three contrasted forest-types.

Palm-rich forests on loamy sand	Tall caatinga	Short caatinga
<b>5–0 cm</b> Rusty brown litter, 4–5 leaves deep; roots invading and adhering to freshly fallen litter	<b>2–0 cm</b> Rusty brown litter, 3–4 leaves deep; adhering roots few, especially in hollows	<b>2–0 cm</b> Rusty brown and black litter, 0–2 leaves deep; adhering roots few
<b>0–25 cm</b> Very dark brown humus layer with many fine roots. Sharp lower boundary	<b>0–40 cm</b> Dark chocolate brown humus, spongy with fine and coarse roots, highly porous and bulk density low. A little blackened sand. Diffuse lower boundary	<b>0–20 cm</b> Dark chocolate brown humus, spongy with fine and coarse roots, highly porous and bulk density low. A little blackened sand. Diffuse lower boundary
<b>25–70 cm</b> Brown sand, massive, with occasional thick roots.	<b>40–45 cm</b> Sand, blackened by humus, structureless with few large pores or roots. Diffuse lower boundary.	<b>20–30 cm</b> Sand, blackened by humus, structureless with few large pores or roots. Diffuse lower boundary.
<b>70 cm+</b> Blocks composed chiefly of pale yellow clay with bands of organic matter. Few fine roots.	<b>55–100 cm</b> Bleached fine white/pink sand; structure massive. Few roots, mainly of <i>Mauritia carana</i>	<b>30–50 cm</b> Bleached fine white/pink sand; structure massive.
	<b>100–140 cm</b> Sand becomes progressively more compact and contains traces of clay	<b>60 cm+</b> Compacted horizon of sandstone gravel (1–5 cm diameter) and fine sand.
	<b>140 cm+</b> Compacted horizon of sandstone gravel (1–5 cm diameter) and fine sand.	

Table 3. Chemical properties of soils (0–10 cm) from palm-rich forest on loamy sand, tall caatinga and short caatinga at La Esmeralda

Forest	pH <sub>H20</sub>	pH <sub>KCl</sub>	Porosity (%)	LOI (%)	N (mg g <sup>-1</sup> )	P (mg g <sup>-1</sup> )	K (mg g <sup>-1</sup> )
PRF	4.1 ± 0.4	3.4 ± 0.1	73 ± 10.1	23.9	4.1	0.08	0.35
TC	4.0 ± 0.5	3.2 ± 0.5	53 ± 8.8	27.4	4.4	0.12	0.31
SC	4.8 ± 0.9	3.6 ± 0.6	61 ± 6.8	23.3	4.7	0.16	0.22

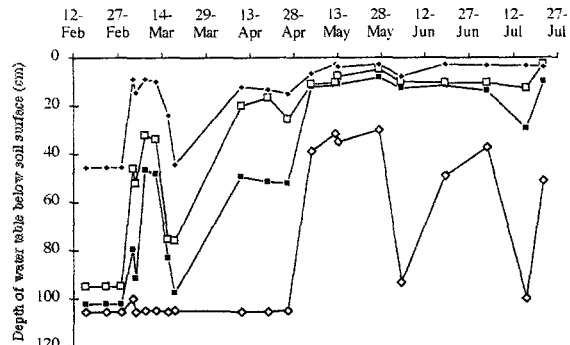


Figure 6. The depth of the water table (cm) below the soil surface in the palm-rich forest on loamy sand (open diamond), tall caatinga (closed square), intermediate zone (open square) and short caatinga (closed diamond) of La Esmeralda, from February to July 1993 i.e. from the middle of the dry season to the wet season. Each value is the mean of 3 tubes, each 1.0 m long, except for in the short caatinga where they were inserted only as far as the gravel layer at 45, 50 and 70 cm.

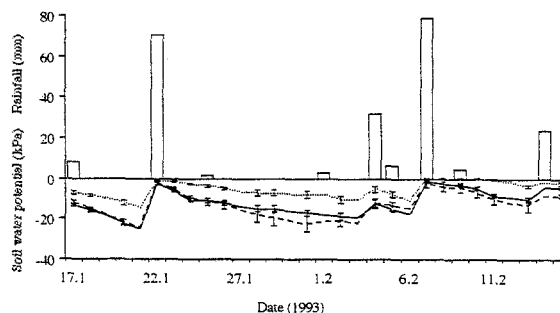


Figure 7. Mean soil-water tension (kPa) in the PRF (dashed), TC (continuous) and SC (dotted) with standard errors; 5 tensiometers in each forest type. Precipitation (mm) is shown as bars. Tensions plotted without error bars are estimates.

in the SC. The soils are all strongly acidic (not significantly different) and highly porous in the humus horizon (Table 3).

Table 4. The mean basal areas and densities ( $\pm$  SEM) of all trees greater than a certain dbh in the tall and short caatingas at La Esmeralda and San Carlos; the minimum dbh used in each set of observations is given in column 2. Number and size ( $m^2$ ) of plots: A = 5 of 250, B = 3 of 125, C = 11 of 100, D = 3 of 100, E = 4 of 62.5, F = 2 of 75, G = 6 of 25.

Forest	Min. dbh (cm)	Basal area ( $m^2/ha$ )	Density (/100 $m^2$ )	Max. height (m)	Max. dbh (cm)	Author
Tall caatinga						
La Esmeralda A	5	46 $\pm$ 6	37.6 $\pm$ 4.5	c. 25	36 $\pm$ 8	Present study
La Esmeralda B	1		159 $\pm$ 20			Present study
San Carlos C	1	37 $\pm$ 4.4	114 $\pm$ 8.4	21 $\pm$ 1.1	32 $\pm$ 3.5	Klinge and Herrera 1978
San Carlos D	1		171 $\pm$ 31	26 $\pm$ 1.7	35 $\pm$ 4.5	Moyersoen 1993
	3		13.5			
Short caatinga						
La Esmeralda E	1		c.340	c. 10	19 $\pm$ 4.0	Present study
	3	38 $\pm$ 5	98 $\pm$ 6.2			
San Carlos F	1	32	258 $\pm$ 82.6	18	29	Bongers <i>et al.</i> 1985
San Carlos G	1	23 $\pm$ 3	168 $\pm$ 19.5	9.5 $\pm$ 1.5	14 $\pm$ 0.5	Moyersoen 1993
	3		41 $\pm$ 15.2			

Table 5. Mean values with ranges or  $\pm$ SEM for specific leaf area (SLA) and foliar nutrient concentrations in tall caatinga ( $n=7$ ) and short caatinga ( $n=10$ ) at La Esmeralda (this study) compared with values reported for San Carlos (Medina *et al.* 1990) and values in a range of lowland moist tropical forests on infertile oxisols/ultisols and spodosols/psamments reported by Vitousek and Sanford (1986).

	SLA ( $cm^2g^{-1}$ )	Nutrient concentration ( $mg g^{-1}$ )		
		N	P	K
Tall caatinga				
La Esmeralda	66 $\pm$ 5.1	12.4 (11.1–15.6)	0.85 (0.6–1.1)	6.9 (3.7–11.5)
San Carlos	76 $\pm$ 4.9	11.6 $\pm$ 4.7	0.73 $\pm$ 0.08	6.2 $\pm$ 0.4
Short (low) caatinga				
La Esmeralda	69 $\pm$ 10.2	14.3 (8.3–41.2)	0.84 (0.4–2.2)	7.3 (3.4–16.4)
San Carlos	47 $\pm$ 3.2	7.4 $\pm$ 0.64	0.50 $\pm$ 0.05	6.4 $\pm$ 0.8
Forests over:				
Spodosols and psamments		10.2 (7.4–12.9)	0.6 (0.2–1.2)	6.0 (3.5–7.2)
Oxisols and ultisols		17.1 (13–19)	0.6 (0.5–0.7)	4.7 (3.8–5.4)

The depth of the water table responded to single rainfall events; heavy rain brought the water table within 1 cm of the soil surface in the SC and within 20 cm in the TC (Fig. 6). In dry periods the water table fell more quickly in the TC than in the SC (10 vs 6 cm  $day^{-1}$ ). During the driest months of the year, the soil water tension rarely exceeded 30 kPa; at a depth of 30 cm the PRF on loamy sand and the TC had a similar tension, whereas the SC was consistently less dry (Fig. 7).

#### Structure, physiognomy and floristics of the tall caatinga

The 5 transects of 50  $\times$  5 m (henceforth large plots) had on average 37.6  $\pm$  4.5 stems  $>$ 5 cm dbh per 100  $m^2$ , and these stems had a basal area of 46  $\pm$  6  $m^2 ha^{-1}$  (Table 4). On the three 4  $\times$  4 m transects (henceforth small plots) there were 17 seedlings  $m^{-2}$  (0–50 cm tall) and 6 saplings  $m^{-2}$  (50–200 cm tall) and these were found mostly on the hummocks (Fig.

8). On these three small plots 28–85% of the surface (based on water table data in Fig. 6) was under water during the wet season, and seedlings of only a few species were found to survive the long-term anoxia of the hollows, notably *Bombacopsis amazonica*, *Eperua obtusata*, *Hevea pauciflora*. Most trees die on their feet, or make only small canopy gaps when blown over. Large tip-ups are rare; only the broad-crowned *Micrandra siphonioides* and the heavy-crowned strangling hemi-epiphyte *Clusia* sp. 320 make relatively large gaps when they fall. Even in these gaps there is an almost total lack of distinctive species requiring large gaps – only rarely *Ischnosiphon* sp. 465 (Marantaceae) was found.

The trees >5 m tall have leaves of a wide range of sizes; mesophylls *sensu* Webb (1959) are dominant when equal weight is given to each species, and overwhelmingly so when the results are weighted by basal area on the five large plots (Fig. 9). Compound leaves on trees >5 m are abundant: 33% of species, 59% weighted by basal area. Of the tree species >5 m tall, 61% have drip-tips in the understorey (82% weighted by basal area), and 11% acuminate; leaves in the upper part of the canopy generally lack drip-tips. The mean SLA of well-lit leaves of 7 common tree species (accounting for 74% of the basal area on the large plots) was  $63 \pm 5 \text{ cm}^2 \text{ g}^{-1}$  (Table 5). The diffuse site factor was  $1.1 \pm 0.2\%$  at 0.4 m,  $1.7 \pm 0.3\%$  at 1.35 m and  $1.6 \pm 0.1\%$  at 2.1 m; our value of 1.7% at 1.35 m is close to the single value of  $\approx 1.5\%$  recorded by Heuvelink (1980) in TC at San Carlos. Much lower values were recorded by us at this height in the PRF on loamy sand ( $0.7 \pm 0.4\%$ ).

There are several notable adaptations of roots to soil anoxia (waterlogging): prop-roots and knee-roots are common, there are seasonally swelling lenticels near the bases of trunks and on knee-roots of several species (*Caraipa longipedicellata*, *Eperua obtusata*, *Micrandra siphonioides*) and *Mauritia carana* has pneumatophores which protrude from the water in hollows. Another possible adaptation is seen in the anastomosing stilt roots of *Clusia spathulaefolia* and also of species of *Duguetia* and *Virola* in the transition forest to PRF on loamy sand. Buttress roots are uncommon, and <1 m tall.

We characterised 46 species of tree >5 m tall, 14 shrubs and treelets <5 m tall, 9 herbs, 9 climbers and 8 epiphytes and 1 hemi-epiphyte, *Clusia* sp. 320 (Tables 6 & 7). Almost all of the collected climbers, epiphytes, herbs and shrubs were present in our sample of three large plots, whereas only 31 of the 46 known

tree species were recorded in these three plots, and 40 in the total of five plots (Fig. 10), partly because our threshold of 5.0 cm dbh for enumeration was larger than the dbh normally attained by the trees reaching a height of <10 m. Only two species of tree in the large plots remain unidentified to family level. Overall Leguminosae-Caesalpinioideae was the most important family in our sample (45% of basal area), followed by Euphorbiaceae, Clusiaceae, Burseraceae and Myristicaceae, although there was considerable variability among plots (Table 8).

*Eperua obtusata* accounted for 57% of the stems >5 cm dbh and 44% of the basal area (Fig. 11) in the five large plots. It was most strikingly dominant in the 10–20 cm dbh class, which corresponded to trees of 15–20 m height, and was far less important in the >20 cm dbh class in which the five canopy emergents *Bombacopsis amazonica*, *Caraipa longipedicellata*, *Iryanthera* aff. *elliptica*, *Micrandra siphonioides* and *Mauritia caraná* had a greater relative abundance (Table 6). Understorey species, most notably *Dendropanax arboreus*, were responsible for lowering the relative abundance of *Eperua* in the 5–10 cm dbh class.

The four most common shrubs by far were the melastomes, *Myrmidone macrosperma* ( $700 \text{ ha}^{-1}$ ) and *Tococa macrophysca* ( $100 \text{ ha}^{-1}$ ) and the rubiates *Psychotria egensis* ( $500 \text{ ha}^{-1}$ ) and *P. humboldtiana* ( $500 \text{ ha}^{-1}$ ). The total shrub density was moderate ( $2000 \text{ ha}^{-1}$ ) but much higher than the density of herbs ( $700 \text{ ha}^{-1}$ ), and almost all the herbs were very small. The only common herb was the fern *Trichomanes* sp. 432 (Table 7), the erect fronds of which can reach  $15 \times 3 \text{ cm}$ .

Only two species of climber were common: the aroid *Heteropsis melinonii* ( $1000 \text{ stems ha}^{-1}$ ) and a dicotyledon with alternate serrate leaves ( $1000 \text{ ha}^{-1}$ ); the former reaches a girth of <1 cm, and the latter rarely 5 cm. Vascular epiphytes were few ( $400 \text{ ha}^{-1}$ ) and were apparently restricted to the lower 3 m of the trunks; the most common were the succulent gesneriad *Codonanthe crassifolia* ( $200 \text{ ha}^{-1}$ ), the orchid *Pleurothallis* cf. *decipiens* ( $100 \text{ ha}^{-1}$ ) and *Anthurium gracile* ( $60 \text{ ha}^{-1}$ ).

#### *Structure, physiognomy and floristics of short caatinga*

Among our samples there were far more individuals >5 cm dbh per unit area in the SC than in the TC (Table 4). The  $1 \times 10 \text{ m}$  plots (henceforth small plots) had a higher density of seedlings than the TC, but a

Table 6. Species of trees and shrubs in (a) tall caatinga and (b) short caatinga separated into size classes. Column 2 indicates whether the species is present in the SC; if a species is present, its height class in the short caatinga is given. Basal areas for trees >5 cm dbh are given in column 3 for tall caatinga and column 4 for short caatinga and are printed in bold if >1 m<sup>2</sup>/ha. Fruit type (information for genera from van Roosmalen, 1985): (1) dry fruit including 1.1 legume, 1.2 capsule with rounded seeds, 1.3 capsule with kapok and 1.4 capsule with flattened and/or winged seeds; (2) fleshy fruit including 2.1 berry, 2.2 drupe, 2.3 dehiscent drupe with arilloid mesocarp, 2.4 capsule or legume with arillate seeds or with other flesh around seeds, 2.5 fig. Period of fruit fall: A, December to February; B, March to April; C, May to September; D, most months of the year. Leaf apex: N, no drip-tip; A, acuminate, D, drip-tip.

(a) TALL CAATINGA	Height in SC (m)	Basal area TC (m <sup>2</sup> /ha)	Basal area SC (m <sup>2</sup> /ha)	Fruit type	Fruit fall period	Leaf apex type
<b>Emergent trees to 25 m</b>						
<i>Bombacopsis</i> cf. <i>amazonica</i> Robyns (Bombacaceae)	6–10	0.9	0.6 ± 0.2	1.3	A	D
<i>Caraipa longipedicellata</i> Steyererm. ssp. <i>cordata</i> Kubitzky (Clusiaceae)	6–10	<b>5.3 ± 2.4</b>	0.5 ± 0.1	1.4	B	N
<i>Iryanthera</i> sp. aff. <i>elliptica</i> Ducke (Myristicaceae)	6–10	<b>3.6 ± 2.1</b>	<b>2.0 ± 1.0</b>	2.4	A	D
<i>Mauritia carana</i> Wallace (Arecaceae)	6–10	0.4 ± 0.3		2.2	B	N
<i>Micrandra siphonioides</i> Benth. (Euphorbiaceae)	Absent	<b>4.7 ± 4.2</b>		1.2	A	D
<b>Trees to 20 m</b>						
<i>Aldina trifoliolata</i> Ducke (Leguminosae-Caesalpinioideae)	Absent	0.2		2.2		D
<i>Couma catingae</i> Ducke (Apocynaceae)	Absent	0.1		2.1	C	D
<i>Eperua obtusata</i> Cowan (Leguminosae-Caesalpinioideae)	3–6	<b>19.3 ± 2.1</b>	<b>8.7 ± 0.9</b>	1.1	A	D
<i>Euterpe</i> sp. 378 (VEN) (Arecaceae)	3–6		0.1 ± 0.1	2.2	A-B	N
<i>Ficus</i> sp. s.n. A (Moraceae)	Absent			2.5		D
<i>Ficus</i> sp. s.n. B (Moraceae)	Absent			2.5		D
<i>Hevea pauciflora</i> Muell. Arg. var. <i>coriacea</i> Ducke (Euphorbiaceae)	3–6	0.7 ± 0.4	<b>2.1 ± 0.5</b>	1.2	A	D
<i>Hirtella ulei</i> Pilg. (Chrysobalanaceae)	Absent	0.02		2.2		D
<i>Macrolobium angustifolium</i> (Benth.) Cowan (Leguminosae- Caesalpinioideae)	Absent			1.1	A	D
Malpighiaceae sp. s.n.		0.1		1.4?	A	D
<i>Mauritia aculeata</i> H.B. & K. (Arecaceae)	Absent			2.2		N
<i>Micropholis</i> aff. <i>suborbicularis</i> Aubr. (Sapotaceae)	3–6	0.07 ± 0.1	0.2	2.1	B	N
<i>Mouriri</i> sp. s.n. (Melastomaceae)	Absent			2.1		N
<i>Pagamea plicata</i> Spruce ex Benth. (Rubiaceae)	3–6	0.1	<b>1.1 ± 0.6</b>	2.2	B	D
<i>Parkia igneiflora</i> Ducke (Leguminosae-Mimosoideae)	>6	0.2		1.1	A?	N
<i>Pourouma</i> sp. s.n. (Moraceae)	Absent			2.2		D
<i>Protium carolense</i> Daly (Burseraceae)	3–6	<b>1.8 ± 0.7</b>	<b>1.5 ± 0.3</b>	2.3	B	D
<i>Protium</i> s.n. (Burseraceae)	3–6	0.9 ± 0.4	0.5	2.3	A	D
<i>Pouteria cuspidata</i> (A.DC.) Baehni ssp. <i>cuspidata</i> (Sapotaceae)	Absent	0.2		2.1	B	N
<i>Qualea cassiquiarensis</i> Spruce ex Warm. (Vochysiaceae)	Absent	0.3		1.4	B	D
Unknown genus 483 (Clusiaceae)	Absent	0.01		2.2	B	D
Unknown genus 372 (Humiriaceae?)	Absent			2.2	A-B	N
Unknown genus s.n. (Euphorbiaceae)	Absent	0.1				D
<b>Trees to 15–20 m</b>						
<i>Caraipa punctulata</i> Ducke (Clusiaceae)	3–6	0.1		1.2	B	D
<i>Clusia spathulaefolia</i> Engler (Clusiaceae)	>6	0.03	<b>2.2 ± 0.1</b>	2.4	B	N
<i>Inga</i> sp. s.n. (Leguminosae-Mimosoideae)	Absent			2.4		A
<i>Macrolobium gracile</i> Spruce ex Benth. (Leguminosae- Caesalpinioideae)	3–6	<b>1.0 ± 0.5</b>	<b>2.6 ± 0.1</b>	1.1	A	N

Table 6. Continued.

(a) TALL CAATINGA	Height in SC (m)	Basal area TC (m <sup>2</sup> /ha)	Basal area SC (m <sup>2</sup> /ha)	Fruit type	Fruit fall period	Leaf apex type
<i>Nectandra</i> sp. 415 (Lauraceae)	3-6	0.3 ± 0.2	0.1	2.1		D
<i>Nectandra</i> sp. s.n. (Lauraceae)	Absent	0.1		2.1		D
<i>Neocouma ternstroemiacea</i> (Muell. Arg.) Pierre (Apocynaceae)	Absent	0.7 ± 0.4		2.1	D?	D
<b>Trees 10-15 m</b>						
<i>Casearia</i> sp. s.n. (Flacourtiaceae)	3-6					A
<i>Dendropanax arboreus</i> (L.) Decne. & Planch. (Araliaceae)	3-6	0.63 ± 0.2	0.2	2.2	A	D
<i>Ferdinandusa boomii</i> Steyererm. (Rubiaceae)	3-6	0.21 ± 0.1		1.2?		A
<i>Mabea</i> sp. s.n. (Euphorbiaceae)	3-6	0.11				D
<i>Schefflera japurensis</i> (Mart. et Zucc. ex E. March) Harms. (Araliaceae)	3-6	0.02	0.1	2.2	B	A
<b>Trees to 10 m</b>						
<i>Cybianthus</i> cf. <i>venezuelanus</i> Mez. (Myrsinaceae)	3-6			2.2		D
<i>Protium aracouchini</i> (Aublet) Marchand (Burseraceae)	3-6		0.2 ± 0.1	2.3	B	D
<i>Bombacopsis</i> sp. 205 (Bombacaceae)	3-6		0.1 ± 0.1	1.3		A
<i>Xylopia</i> sp. s.n. (Annonaceae)	3-6			2.2		N
Undetermined sp. s.n. (Rubiaceae)	Absent			1.1		A
<i>Ormosia</i> cf. <i>macrophyllum</i> Benth. (Leguminosae- Papilionoideae)	Absent			1.1		N
<b>Treelets and shrubs to 5 m</b>						
<i>Myrmidone macrosperma</i> (Mart.) Mart. (Melastomataceae)	<3			2.1	D	D
<i>Tococa macrophysca</i> Spruce (Melastomataceae)	<3			2.1	D	D
<i>Clidemia epibaterium</i> DC. (Melastomataceae)	Absent			2.1	D	D
<i>Miconia holosericea</i> (L.) DC. (Melastomataceae)	Absent			2.1	D	D
<i>Miconia radulaefolia</i> (Benth.) Naudin (Melastomataceae)	Absent			2.1	D	D
<i>Miconia rugosa</i> Triana (Melastomataceae)	<3			2.1	D	D
Leguminosae-Mimosoideae s.n. (sensitive-leaved)	Absent			1.1		N
<i>Palicourea longistipulata</i> (Muell. Arg.) Standl. (Rubiaceae)	Absent			2.2	D	D
<i>Piper</i> sp. 477 (Piperaceae)	Absent			2.2	D	D
<i>Psychotria deflexa</i> DC. (Rubiaceae)	Absent			2.2	D	D
<i>P. egenesis</i> Muell. Arg. (Rubiaceae)	<3			2.2	D	D
<i>P. hoffmannseggiana</i> (Roem. & Schult.) Muell. Arg.	<3			2.2	D	A
<i>P. humboldtiana</i> (Chom.) Muell. Arg. (Rubiaceae)	<3			2.2	D	D
<i>Retiniphyllum concolor</i> (Spruce ex Benth.) Muell. Arg. (Rubiaceae)	<3			2.2	B	N
Clusiaceae	Absent					D
<b>Hemi-parasite</b>						
<i>Clusia</i> sp. 320 (Clusiaceae)	Absent			2.4	B	A
<b>(b) SHORT CAATINGA SPECIALISTS</b>						
<b>Trees &amp; shrubs</b>						
<i>Byrsonima wurdackii</i> Rizz. (Malpighiaceae)	>6		4.0 ± 0.3	2.2	A	N
<i>Clidemia heteroneura</i> (DC.) Cogn. (Melastomataceae)	<3			2.1	D	D
<i>Neea</i> cf. <i>mapourioides</i> Steyererm. (Nyctaginaceae)	3-6		1.7 ± 1.2	2.1	B	D
<i>Pradosia schomburgkiana</i> (A.DC.) Cronq. (Sapotaceae)	>6		0.1 ± 0.1	2.1		N
<i>Retiniphyllum truncatum</i> Muell. Arg. (Rubiaceae)	<3			2.2		A
Unidentified species	>6		1.3 ± 1.3			

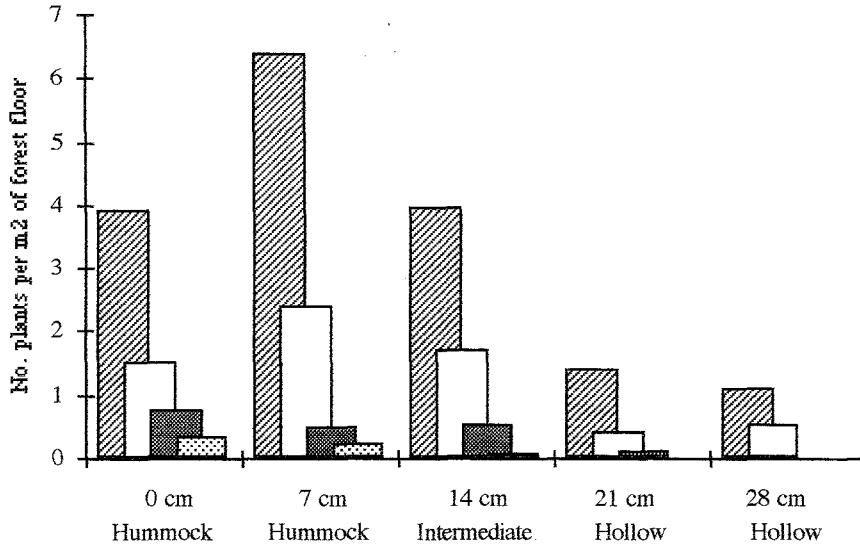


Figure 8. Mean densities of all woody plants ('seedlings' <50 cm, diagonally lined; 'saplings' 0.5-2 m, unshaded; 'poles' 2-5 m, densely shaded; 'trees' >5 m, dotted) at different microsite-types in 3 plots from the tall caatinga. The microsites are defined by depth below the highest hummock in the plot.

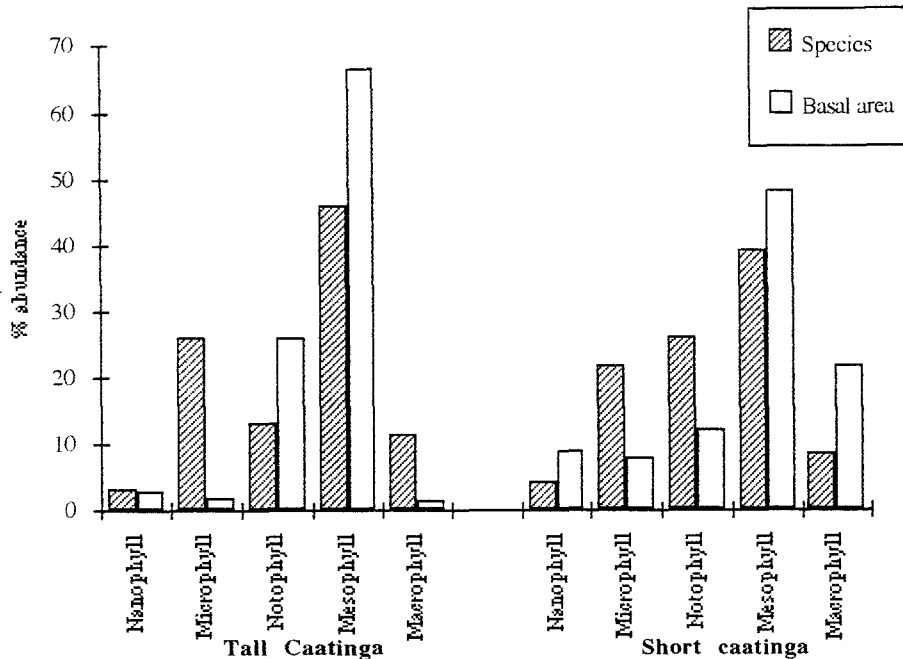


Figure 9. The size-class distributions (*sensu* Webb 1959) of leaves of trees >5 m tall in the tall and short caatinga with each species given equal weight (diagonal lines) and weighted by basal area (unshaded).

Table 7. Herbs, climbers and epiphytes of the tall and short caatingas.

Tall caatinga (* also in short caatinga)	Short caatinga only
Herbs	
Commelinaceae sp. s.n.	Cyperaceae sp. 406
<i>Ischnosiphon</i> sp. 465 (Marantaceae)	<i>Elaphoglossum</i> sp. 405 (Lomariopsidaceae)
<i>Lindsaea</i> spp. 404, 424 and s.n. (Lindsaeaceae)*	Fern sp. s.n.
<i>Schizaea</i> sp. 450 (Schizaeaceae)*	<i>Rapatea</i> sp. 412 (Rapateaceae)
<i>Trichomanes</i> sp. 432 (Hymenophyllaceae)*	
<i>Voyria aphylla</i> (Jacq.) Pers. (Gentianaceae)*	
<i>Wulfschlaegelia calcarata</i> Benth. (Orchidaceae)*	
Climbers	
<i>Heteropsis melinonii</i> (Engl.) Jonker & Jonker (Araceae)*	<i>Smilax</i> sp. (Smilacaceae)
<i>Philodendron pedatum</i> (Hook.) Kunth. (Araceae)*	<i>Vanilla</i> sp. (Orchidaceae)
7 unidentified species	1 undetermined sp. (Apocynaceae)
Epiphytes	
<i>Anthurium gracile</i> (Rudge) Lindl. (Araceae)*	<i>Aechmea</i> sp. s.n. (Bromeliaceae)
<i>Codonanthe crassifolia</i> (Focke) Morton (Gesneriaceae)*	2 unidentified orchids
<i>Philodendron hylaeae</i> Bunting (Araceae)*	1 unidentified bromeliad
<i>Pleurothallis</i> cf. <i>decipiens</i> (Ames) Schweinf. (Orchidaceae)*	
<i>P. migueliana</i> (Focke) Lindl. (Orchidaceae)*	
1 unidentified orchid*	
2 unidentified ferns	

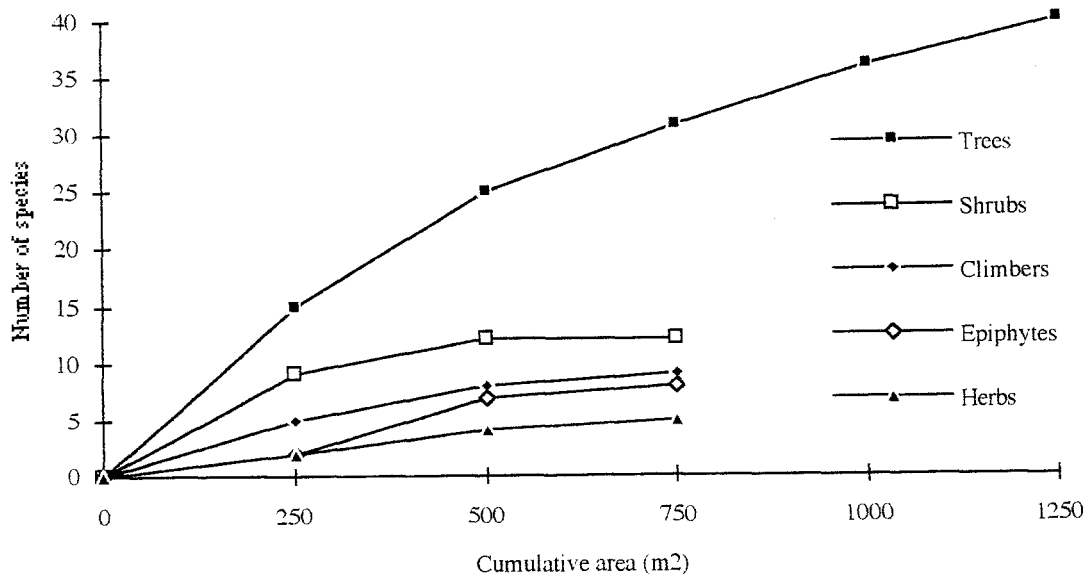


Figure 10. Species-area curves for trees, shrubs, climbers, epiphytes and herbs in the tall caatinga. Data from 5 randomly positioned plots of  $50 \times 5 \text{ m}^2$  for trees (3 for other life forms) and plotted in random order.



similar density of saplings (Fig. 11). We found 29 tree species >3 m tall, substantially fewer than in the TC (51); four were unique to the SC. There were 8 species of shrubs and treelets <5 m tall, 9 herbs, 10 climbers and 12 epiphytes.

The leaf size-class spectrum for the trees is similar to that for the trees of the TC, but there is a less marked dominance by mesophylls, especially when the spectrum is weighted by basal area (Fig. 9). The percentage of species with compound leaves (32% by species, 54% by basal area) is similar to that in the TC, while there are fewer drip tips (52% by species, 65% weighted by basal area). The mean SLA of well-lit leaves of 10 common species (accounting for 80% of the basal area) was slightly but not significantly greater than that found for the commonest TC species (Table 5). Diffuse site factor was  $1.6 \pm 0.1\%$  at 0.4 m height,  $3.0 \pm 1.2\%$  at 1.35 m and  $6.9 \pm 1.3$  at 2.1 m. The quotient of the mean diffuse site factor for the SC over that for the TC increases appreciably with height: 1.5, 1.8 and 4.3.

*Eperua obtusata* was much less dominant, accounting for 38% of the stems and 26% of the basal area of the large plots; it was rarely >5 m tall or >10 cm dbh (Fig. 11). The largest trees were of *Byrsonima wurdackii* and *Pradosia schomburgkiana*, which were not found in the TC, and of *Bombacopsis amazonica*, *Caraipa longipedicellata*, *Iryanthera* sp. aff. *elliptica*, *Macrobium gracile* and *Pagamea plicata*. *Neea* cf. *mapourioides*, which rarely attained a dbh >10 cm, accounted for 11% of the basal area, and was confined to the SC.

No quantitative study was made of shrubs, herbs, climbers or epiphytes. However, it was clear that the melastomes reached a higher density, with the balance of abundance shifted toward *Tococa macrophysca*, but neither was as common as *Clidemia heteroneura* (absent from TC) which covered about a third of the ground. Rubiataes also increased in abundance; *Psychotria humboldtiana* was common, but *P. egensis* was replaced by *P. hoffmannseggiana*, which appeared only rarely in the TC. Climbers were more abundant than in the TC; they included a succulent *Vanilla* sp., a *Smilax* sp. and two unidentified dicots which were absent from the TC. All species of epiphytes in the TC were also present in the SC, and the *Codonanthe crassifolia* in particular was very much more common. A yellow-flowered orchid, which was common (about  $1000 \text{ ha}^{-1}$ ) and facultatively terrestrial (*sensu* Poulsen *et al.* 1991), and an *Aechmea* bromeliad were unique to the SC. Among the herbs, the *Trichomanes* appeared

to be more common than in the TC, and a Cyperaceae (406) was widespread.

#### *Fruit characteristics & phenology in tall caatinga*

There are no cauliflorous trees and most species (72%) have berries, drupes or capsules with arillate seeds (endozoochorous); 19% are dispersed by the explosive shattering of their woody capsules. Of these species three (*Hevea pauciflora* and the two *Macrobium* spp.) have floating seeds which are possibly water-dispersed. Only 5% of species are synzoochorous and 2% anemochorous. There is a clear trend from autochory in taller trees to endozoochory in shorter ones. Three of the five emergent tree species and 7 common trees in the 10–20 m size-class are autochorous. The dehiscent fruits shatter during dry afternoons between January and April. All but 3 of the 21 woody species growing to <10 m have berries or drupes (Table 6).

There is a strong seasonality in flowering and fruiting (Table 6), seeds from 21 of the 46 species of tree being collected during March 1994. Some species (most notably *Eperua obtusata*) had one main flush of flowers and several smaller flushes in 1994, and most trees species bore many more flowers and fruit in the dry season of 1993–1994 than in the previous year. A few species of shrubs and understory trees had flowers and fruits simultaneously. The time taken for maturation of fruits by the taller tree species was 6–8 months; some understory trees took 10 months.

#### *Foliar nutrient concentrations*

The mean foliar concentrations of nitrogen, phosphorus and potassium of 7 common TC species (74% of basal area) and 10 SC species (80%) are given in Table 5. There was no significant intraspecific difference in the concentration of N, P or K between the TC and SC samples. The overall mean N, P and K concentrations of the dominant species *Eperua obtusata* in the TC and SC were 15.7, 0.83 and 7.1 mg g<sup>-1</sup> respectively, in all cases higher than the means across all species. The leaves of *Neea* cf. *mapourioides* (found only in the SC) had outstandingly high concentrations (41.2, 2.17 and 16.4 mg g<sup>-1</sup> respectively); they are succulent (mean water content at saturation 3.5 g g<sup>-1</sup> dry mass, compared with 3.2 in *Clusia spathulaefolia* and 1.0–2.3 in 14 other tree species; PJG & DAC, unpublished) and were found by Reich *et al.* (1994) at San Carlos to have an outstandingly high concentration of N. The mean values for N, P and K in the SC sam-

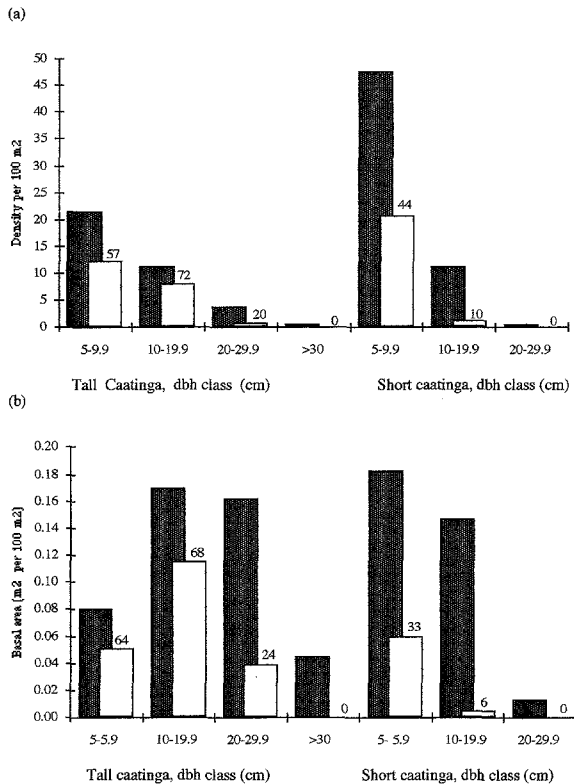


Figure 11. The (a) densities and (b) basal areas of all species (shaded) and of *Eperua obtusata* (unshaded) in different size classes in tall and short caatinga. For each size class, the percentage of the total density or total basal area accounted for by *Eperua* is given above each unshaded column.

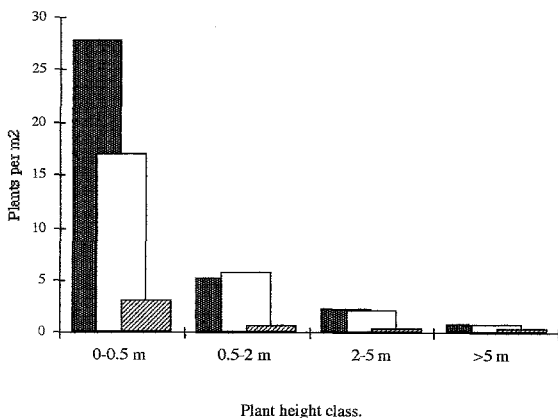


Figure 12. The total densities of woody plants in different height classes in palm-rich forest (diagonally lined), tall caatinga (unshaded) and short caatinga (densely shaded).

ples excluding *Neea* were 11.3, 0.69 and 6.24 mg g<sup>-1</sup> respectively.

## Discussion

### Structure and floristics of tall caatingas at La Esmeralda and San Carlos

The two are essentially similar in height, rarity of boles >30 cm dbh and of buttresses, dominance by mesophylls *sensu stricto*, and lack of thick-stemmed climbers. In contrast, the density of trees of dbh >10 cm is much higher in the La Esmeralda sample than in that reported for San Carlos (1480 vs 999 ha<sup>-1</sup>; cf. Klinge & Herrera 1983); the density at both sites is much higher than in most forests studied in the Amazon Basin (205–858 ha<sup>-1</sup>; cf. Campbell *et al.* 1986; Gentry 1988). The basal area recorded by us is also higher (37.6 vs 28.3 m<sup>2</sup> ha<sup>-1</sup>; cf. Moyersoen 1993) but is within the range quoted by Lamprecht (1972) for lowland forests in northern South America (30–40 m<sup>2</sup> ha<sup>-1</sup>). The two TCs have similar mean SLA values in the upper canopy, and in both cases about 1.5% day-light penetrates to about 1 m above the ground. There is no precise information published for the San Carlos caatinga concerning incidence of compound leaves, drip tips, thin-stemmed climbers, shrubs or herbs or on fruit and seed types.

The two sites are floristically similar, notably in the dominance of large areas (in terms of stems and biomass though not tree height) by a species of *Eperua*, and in the abundance of *Hevea*, *Iryanthera* and *Micrandra* (cf. Medina & Cuevas 1989). There are many species in common including *Caraipa longipedicellata*, *Couma catingae*, *Macrolobium gracile*, *Mauritia carana*, *Myrmidone macrosperma*, *Neocouma ternstroemiacea*, *Pagamea plicata*, *Psychotria humboldtiana*, *Retiniphyllum concolor* and *Tococa macrophysca* (cf. Clark & Liesner 1989). Many of the genera involved are widely distributed across the caatingas of the upper Río Negro (Ducke & Black 1953). A major difference between the two areas seems to be the comparative lack of Sapotaceae in the caatinga at La Esmeralda (Prof. E. Medina, private communication). *Pradosia schomburgkiana* ('*Glycoxylon inophyllum*') and *Manilkara* sp. are abundant at San Carlos (Medina & Cuevas 1989), but at La Esmeralda we found only occasional trees of the first (in the SC only), and of *Micropholis* sp. aff. *suborbicularis* and *Pouteria cuspidata*. The dominance

of Leguminosae-Caesalpinioideae would appear common to all South American forests on white sands. More generally Leguminosae as a whole commonly dominate forests in Amazonia (Gentry 1990), although Euphorbiaceae, Lecythidaceae, Moraceae and Myristicaceae may become locally dominant (cf. Thompson *et al.* 1992).

Anderson (1981) suggested that isolated caatinga patches should be species-poor relative to larger areas, following the island biogeographic arguments of MacArthur & Wilson (1967). Our finding only 62 woody species >1 cm dbh on 1.25 ha at La Esmeralda, compared with 130 on 1.3 ha recorded by Klinge & Herrera (1983) in the extensive area of TC at San Carlos supports this hypothesis.

Certain differences in floristics suggest to us that the caatinga at San Carlos may have been subjected to appreciable human disturbance, while that at La Esmeralda is still in a near-virgin state. First, at least one of the sites studied intensively at San Carlos has an abundance in the understorey of a low-growing small-leaved Marantaceae (possibly a *Monotagma* sp.) and a *Selaginella*; these elements are quite absent from the La Esmeralda caatinga, though a species of *Selaginella* is common in the secondary forests which develop after agriculture. Both species were seen by one of us (P.J.G.) in 1982 to flourish in gaps at San Carlos that had been made a few years previously by Dr. H. Klinge when harvesting biomass. It is tempting to suggest that they are 'late tolerants' *sensu* Oldeman (1990), needing substantial disturbance of the canopy to become established but persisting a long time in shade. They could have been let into the stand by a substantial disturbance – perhaps by the spread of fires into the caatinga from neighbouring cut-over areas in rare dry years (cf. Sanford *et al.* 1985). There is absolutely no doubt that the landscape around San Carlos generally has been grossly disturbed for more than a century (cf. Saldarriaga 1987), and one consequence is an abundance there of two *Cecropia* species, especially along the dirt road from San Carlos to Solano. Nowadays, *Cecropia* is even present in the seedbank of the caatinga at San Carlos (Uhl & Clark 1983), and occasionally trees of it are found in gaps (P.J.G., photos 1982). In contrast, *Cecropia* is quite absent from the caatinga at La Esmeralda, where it is found only in secondary forest.

#### *Comparison of short caatingas at La Esmeralda and San Carlos*

The SC at La Esmeralda is like that at San Carlos described by Bongers *et al.* (1985), with an uneven height of 2–10 m, though the density and basal area are considerably higher at La Esmeralda (Table 4). In both there are few trees >20 cm dbh, but more climbers, epiphytes and herbs than in TC.

What is strikingly different about the two is the presence at San Carlos, but not La Esmeralda, of many species with highly scleromorphic and steeply inclined leaves, whether of trees (such as Annonaceae) or herbs (such as the large almost woody-leaved aroid *Philodendron* sp. – probably *P. callosum* K. Krause or *P. pтарinum* Steyererm.). The presence of this feature in the SC at San Carlos reflects the fact the community there merges into bana scrubland, which is very strongly dominated by notophylls (Bongers *et al.* 1985) which are steeply inclined (Medina *et al.* 1978) and scleromorphic (Sobrado & Medina 1980). Some of the bana genera are present in the SC at La Esmeralda (*Byrsonima*, *Clusia*, *Pagamea*, *Retiniphyllum*) but many of the characteristic genera, cited by Sobrado & Medina (1980) or Medina & Cuevas (1989) are quite absent: *Aspidosperma* (Apocynaceae), *Catostemma* and *Rhodognapholopsis* (Bombacaceae), *Calycophyllum* and *Remijia* (Rubiaceae), *Heteropteris* (Malpighiaceae), and *Macairea* and *Mouriri* (Melastomataceae). The caatinga at our study site at La Esmeralda does not grade into bana, although there is Amazonian-type savanna nearby and this savanna is floristically linked to the vegetation of open bana, tepuis and shrub-patch white-sand savannas of the Guianas (cf. Cooper 1979; Duivenvoorden & Cleef 1994).

The difference between the SC at La Esmeralda and bana at San Carlos is highlighted by foliar nutrient analysis. The SC and TC at La Esmeralda have similar concentrations of N, P and K, whereas the bana has much lower values (Table 5). The difference between bana and caatinga in N concentration parallels the global trend of decreasing leaf N with increasing leaf mass per unit area (Turner 1994).

#### *Soil water status and nutrient supply as controls on forest development*

There are two issues to be considered: the development of the features peculiar to the caatinga when compared to most lowland rain forests, and the dwarfing of the low caatinga.

The soils of the TCs at La Esmeralda and San Carlos are essentially similar, having a deep highly organic layer in which the roots proliferate, no 'root mat' in the litter, a bleached sand horizon in which there are few fine roots, in draining black water and in becoming inundated briefly and only after exceptionally heavy storms whilst being waterlogged for several months each year. The soils are strongly acidic throughout ( $\text{pH}_{\text{H}_2\text{O}} \approx 4$ ). However, there are differences. At La Esmeralda, where there is a pronounced dry season, the perched water table sinks then to a depth of around 150 cm; the water potential at 30 cm depth is then similar to that in the surrounding *terra firme* sandy soils (Figs 6 & 7). The organic layer is dark brown rather than black and merges with the white sand below rather than showing a sharp junction. Also the bleached sand is underlain by sandstone gravel and boulders at a depth of 1.0–1.7 m, and no spodic horizon was found, whereas at San Carlos one is found at 0.6–1.0 m (Jordan 1989). Despite the presence of features tentatively related to regular seasonal drying (brown organic layer, diffuse boundary), it is the caatinga at La Esmeralda which has the more pronounced hummock-and-hollow topography of the type generally associated with water-logging of forest.

At San Carlos tensiometer measurements over a whole year in TC (Franco & Dezzio 1982) never showed a water potential at a depth of 20 cm in TC lower than  $-10$  kPa, the potential commonly regarded as field capacity (Milthorpe & Moorby 1982). At La Esmeralda tensiometers did show a fall in water potential to  $-35$  kPa at the end of the dry season when there was a 10-day spell without rain, but the values were still far above conventional wilting point ( $-150$  kPa). At that time the only midday wilting seen by us in the TC was in the soft-leaved melastome shrubs (notably in *Myrmidone macrosperma*) and saplings of *Macrolobium gracile*. In all these cases, only leaves in direct sunlight wilted, and the wilting was transient, being reversed by 1700 hours. Measurements with a porometer (Mark IV; Delta-T Devices, Burwell, Cambridge UK CB5 OEJ) showed relatively high conductances for shaded leaves at midday in a wide range of species at this time (to be published elsewhere). Thus, even though the soil of the TC at La Esmeralda dries out more than is expected or recorded for that at San Carlos, there is no reason to suppose that shortage of water rather than shortage of nutrients is the chief cause of the characteristic structure and physiognomy. Emphasis on shortage of nutrients rather than of water is consistent with the close parallel in structure and

physiognomy between the TCs and the wallaba forests on well drained sands in the Guianas.

The nitrogen concentrations in leaves taken from near the top of the canopy in the TCs at both La Esmeralda and San Carlos are within the range quoted by Vitousek and Sanford (1986) for forests on spodosols and psamments (Table 5). Although the absolute values are slightly higher at La Esmeralda than at San Carlos, the N:P quotients are similar (14.6 and 15.9) and are considerably lower than the mean value of 27 recorded for forests on oxisols and ultisols by Vitousek and Sanford (1986). As argued by Cuevas & Medina (1991), these data suggest nitrogen to be the major limiting nutrient. Cuevas & Medina (1988) found that nitrogen was indeed the primary limiting nutrient for fine root growth in TC, and we have found comparable evidence (to be published elsewhere) for the growth of whole saplings. Nitrogen limitation is thought to be uncommon in tropical lowland rain forests, but becomes important where the litter decomposition is slow, notably in montane forests (Tanner 1980; Edwards & Grubb 1982; Vitousek, Matson & Turner 1988). Marrs *et al.* (1988) demonstrated that it was principally waterlogging that led to low rates of nitrogen mineralization in montane forests in Costa Rica, and it would appear that this is the most likely explanation of our observations (cf. Cuevas 1983). Black water draining from caatinga contains very little dissolved oxygen (cf. Janzen 1974) and the lack of oxygen in all but the surface layer of soil causes strong reducing conditions (Turner and Patrick 1968) and restricted microbial activity (Medina *et al.* 1990).

The only tree of the caatinga with a very high foliar N concentration, *Neea*, was the only tree of the caatinga at San Carlos found by Moyersoen (1993) to have ectotrophic mycorrhiza. This finding is consistent with the fact that for at least some temperate plants ectotrophic mycorrhizas are able to utilize the N in soil organic matter directly (Francis & Read 1994).

The low foliar N concentrations of most caatinga species imply relatively slow rates of assimilation (cf. Field & Mooney 1983; Reich *et al.* 1994). Tanner (1985) showed that in unproductive tropical montane forest, much more carbon was allocated to leaves than to stems, and the relatively short stature and thin trunks of caatingas may be explained in an analogous way.

The further reduction in stature in the SC as opposed to TC appears to be a result of a shallower aerobic layer in the soil. Bongers *et al.* (1985) reported that at San Carlos the depth of the water table after heavy rain was similar to the lower limits of the rooting zone:

Table 8. The mean percentage contributions of tree families to basal area ( $\pm$  standard error). Based on trees  $>10$  cm dbh in 5 plots of  $5 \times 50$  m in TC at La Esmeralda

Family	Mean percentage
Leguminosae-	$45.4 \pm 6.3$
Caesalpinioideae	
Euphorbiaceae	$15.9 \pm 13.1$
Clusiaceae	$15.6 \pm 7.5$
Burseraceae	$7.6 \pm 2.5$
Myristicaceae	$7.5 \pm 4.1$
Bombacaceae	$2.7 \pm 2.7$
Apocynaceae	$1.9 \pm 1.0$
Arecaceae	$1.2 \pm 0.9$
Vochysiaceae	$0.9 \pm 0.9$
Sapotaceae	$0.6 \pm 0.6$
Lauraceae	$0.5 \pm 0.3$
Chrysobalanaceae	$0.1 \pm 0.0$

26 cm in the TC, 20 cm in the SC ('tall bana'), 13 cm in the low bana and 4 cm in the open bana. Our recordings during the rainy season of 20 cm in TC and 5 cm in SC clearly parallel their observations. In both cases the water table only very rarely rises above the surface. Other examples of dwarfed vegetation growing on waterlogged soils include some Brazilian campinas (Ducke and Black 1953), some Queensland heathlands (Specht 1981) and kerapah (Whitmore 1984). The simplest explanation of the lowered stature of the SC is that the amount of nitrogen becoming available per unit area of soil is reduced even further than in the TC. However the restriction of fine roots to a smaller depth (c. 40 cm vs c. 20 cm) may also be important.

The shallow root systems of low and open bana are suited to long-term waterlogging, but may be susceptible to water-shortage in dry weather, especially as the soil has only a modest accumulation of surface humus overlying bleached sand. The observation of Herrera (1977) that the water table of soil under bana can drop to about 1 m below the surface during a brief dry spell is therefore a possible explanation for the presence of the highly xeromorphic vegetation at San Carlos but not at La Esmeralda. Alternatively, the reduction in leaf size from caatinga to bana, and the increase in scleromorphy, could be related to extreme oligotrophy. These trends are seen in montane rain forest on mor humus compared with that on mull in Jamaica (Tanner 1977; Kapos & Tanner 1985); also Whitmore (1984) records a dominance of leaves smaller than mesophylls in wet soil heath forest (kerapah) in Borneo. On the other

hand the extremely stiff, vertically inclined leaves of a variety of bana species are hard to explain in terms of extreme oligotrophy on permanently waterlogged soil. Further research is needed on the behaviour of the water table in bana.

#### *Comparison of caatinga, swamp and wallaba forests*

As noted by Davis & Richards (1934), there are striking structural and physiognomic similarities between the caatingas on waterlogged soil in the Venezuelan Amazon and the wallaba on well-drained white sands in Guyana, notably low stature, small crowns, thin trunks, lack of buttresses, large number of trunks per unit area, relatively great penetration of light to the understorey and lack of thick-stemmed climbers. *Eperua* spp. dominate both forest-types; the genus is found only in the lowlands of northern south America and most commonly on very sandy soils (Cowan 1973, Klinge, Medina & Herrera 1977; Ter Steege 1993). A striking difference is that *Hevea*, *Iryanthera*, *Mauritia*, *Macrobium* and *Pradosia schomburgkiana* are found in the caatinga and not in the wallaba; these are commonly found growing in swamp-forests and along streams in Guyana (Polak 1992; van Roosmalen 1985). The mixture in the caatinga of species from swamp and well-drained forest provides a parallel with the forests of the far East. The kerapah of Sarawak, found on more or less permanently waterlogged podzols, is structurally and physiognomically a heath forest (Whitmore 1984), but differs in sharing many species with swamp forest (Brünig 1974; Corner 1978). Also interesting in this connection are the Malaysian peat swamps, which have on the periphery tall stands of swamp forest species that grade into a pole forest dominated by heath forest species at the centre (Anderson, J.A.R. 1964; Whitmore 1984).

Trees are the most species-rich life form in the TC; broad-leaved herbs are few, in contrast to many other neotropical lowland rain forests (Gentry 1990), and the understorey is dominated by shrubs, seedlings and saplings. Such herbs as are present are (a) small ferns, either filmy (*Trichomanes*) or xeromorphic (*Lindsaea*, *Schizaea*) or (b) 'saprophytic' (hyperparasitic?) angiosperms – *Voyria* and *Wulfschlaegelia*. Minimal herb cover, noted in the wallaba (Davis & Richards 1934) and caatinga, is a general feature of forests on infertile soils, both in the tropics (Gentry & Emmons 1987) and in the northern temperate zone (Grubb 1987).

*Penetration of the caatinga canopy by light, and regeneration of caatinga plants*

The simplest explanation of the greater penetration of light through the caatinga canopy than through that of most rain forests is that the leaf area index is lower (cf. Medina & Cuevas 1989). At both San Carlos and La Esmeralda we have reliable values for the SLA of leaves of common species in the upper canopy, but for neither site do we have information on the degree of variation through the canopy. Kira (1975) recorded an increase by a factor of  $>2$  down through the canopy of the evergreen oak *Castanopsis cuspidata* in warm temperate rain forest in Japan, although Bongers & Popma (1988) found that on average SLA was only 1.5 times higher in 'shade' leaves than in 'sun' leaves in tropical lowland rain forest in Mexico. All published values for LAI of rain forests must be subject to doubt until more information on the degree of variation in SLA is available, and stratified samples of canopy are linked with the studies of SLA. The failure of tree species to maintain leaves in as deep shade on nutrient-poor soil as on nutrient-rich soil was reported by Hesselman (cf. Ashby 1931) but still no mechanistic explanation is available.

Although the proportion of daylight intercepted by TC may seem trivially different from that in normal lowland rain forests (say 0.983 vs  $>0.993$  at 1.35 m), the relative increase in the amount of light reaching the saplings is great (say 0.017 vs 0.007) and could be critically important in reducing the degree of inhibition of subordinates by tall trees (cf. Osunkoya *et al.* 1993). We hypothesize that at the same time the many fine roots of established plants utilise almost all of the very slender nutrient supply available (cf. Grubb 1994). As a consequence, competition for nutrients may be as important as competition for light. We shall show elsewhere that root-trenching of saplings and seedlings of caatinga species leads to considerable increases in their growth. The relative importance of root competition, compared with limitation by shading, may be expected to increase as any given plant grows taller, especially since the absolute requirement for nutrients increases greatly with plant size (cf. Ingestad 1982). It is notable that the palm *Jessenia* and at least six other species of palm-rich forest trees establish commonly in the caatinga, but cannot grow taller than c. 1.5 m. This phenomenon awaits experimental investigation.

We do not mean to imply that different degrees of shade are of no consequence to the regeneration of caatinga plants. Observations by DAC on the growth

of seedlings and saplings (to be published elsewhere) have provided evidence of a range of responsiveness to canopy gaps. For example, *Parkia igneiflora* proved very sensitive while *Eperua obtusata* did not. There is no distinctive set of species requiring canopy gaps for establishment, aside from a few stragglers like *Ischnosiphon* from forest-savanna edges. However, there are several species with a type of architecture commonly found in strongly light-demanding species: compound leaves or simple leaves with long petioles and saplings with unbranched stems bearing their leaves apically (*Bombacopsis*, *Didymopanax*, *Hevea*, *Micrandra*, *Parkia*). Perhaps they can function effectively in the understory of caatinga because of the relatively high irradiance. *Couma* and *Micrandra* are the most light-demanding species in the TC; saplings of both are found very seldom outside large gaps, and seedlings of *Micrandra* in the understory were found to have a half life of c. 1 year.

Among the four commonest shrubs of the TC two have the 'optimist' design of Kohyama (1987), i.e. relatively low ratio of crown area to height, and two are 'pessimists'; the optimists are suited to early gap formation and the pessimists to late gap formation. The optimists are *Psychotria humboldtiana* and *Tococa macrophysca*; the pessimists are *P. egensis* and *Myrmidone macrosperma*. It is especially interesting in the SC where more light penetrates to 1 m above the ground, *Tococa* is relatively more abundant, and *Psychotria humboldtiana* maintains its abundance, while *P. egensis* seems to be absent. In the SC we find a new combination – species which appear to need a high level of PAR but have 'pessimist' morphology, being obligately low-growing and wide-crowned: *Psychotria hoffmannseggiana* and *Clidemia heteroneura*. Of these the *P. hoffmannseggiana* is very rare in the TC, and the *Clidemia heteroneura* apparently absent.

Our observations thus suggest that in caatinga both above- and below-ground competition are important in controlling regeneration. Future papers will deal with experimental evidence on this point.

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