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Floristics and structure of the *Pterocarpus officinalis* swamp forest in Guadeloupe, Lesser Antilles

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ABSTRACT. Swamp forest covers *c*. 2600 ha of coastal wetlands in Guadeloupe. An inventory of all vascular plants was conducted together with a characterization of the main abiotic descriptors within seventeen 10-m × 40-m plots, systematically sampled throughout the forest. Girth at breast height (GBH) was measured for all trees $\geqslant$10 cm GBH. Four forest types were discriminated according to pH, clay content and redox potential of the soils. Among the 107 species recorded, lianas and epiphytes were as much represented as tree species (28%). However, no epiphytes were encountered at the canopy level where *Pterocarpus officinalis* (Papilionaceae) was the evenly dominant tree. Local hummock-hollow topography was responsible for an aggregated distribution of *P. officinalis*. This species exhibits several adaptative traits which may explain its dominance over all of the lowland swamp forests subjected to permanent waterlogging in the hurricane-prone Caribbean islands.

KEY WORDS: forest structure, Lesser Antilles, plant biodiversity, *Pterocarpus officinalis*, tropical swamp forest

INTRODUCTION

In the Caribbean islands, coastal forested wetlands belong to two main plant communities: mangroves, expanding over tidal areas, and swamp forests located landward on floodplains and along freshwater streams. Whereas much work has already been done on the ecology of mangroves in this region (e.g. Pool *et al*. 1977, Rodriguez 1987), lowland swamp forests have received little attention. Except for the study of Alvarez-Lopez (1990) in Puerto Rico, essentially only descriptive and sketchy information is available (Bacon 1990). Areas of lowland swamp forests substantially decreased in the last centuries due to land reclamation for agriculture and, more recently, to road infrastructure and

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urban or industrial development (Imbert *et al*. 1988). The small size of the remaining forest patches, widespread throughout the islands, makes them particularly vulnerable to mounting threats (Lugo & Brown 1988). Furthermore, in the context of the current global rise in sea-level, the expected changes within coastal wetland vegetation (Field 1995, Snedaker, 1995, Stumpf & Haines 1998) may have a strong impact on the structure and biodiversity of the coastal swamp forests.

This study focuses on the swamp forest of the Grand Cul-de-sac Marin Bay, in Guadeloupe, the largest known swamp forest area in the Caribbean islands. *Pterocarpus officinalis* (Papilionaceae) is the dominant tree species as in most of other freshwater, coastal forested wetlands of these islands (Bonhême *et al*. 1998). Enlarging upon the earlier work carried out by Portecop & Crisan (1978) and Lescure (1980) in a small area of this forest, the present paper aims to put forward the main floristic and structural characteristics of this swamp forest as compared with the surrounding vegetation types and the other Caribbean swamp forests.

STUDY SITE

Guadeloupe coastal wetlands occupy an area of 7000 ha which extends over most of the islands of the archipelago (Imbert *et al*. 1988). However, the major part of these wetlands are located around the large bay of the Grand Cul-de-sac Marin (Figure 1). The *Pterocarpus* swamp forest has an area of 2600 ha, beyond the salt-water zone which is covered by the mangrove and patches of brackish *Cladium* or *Acrostichum* marshes. In large floodplains, fresh-water herbaceous swamps or marshes and cattle-grazed water meadows surround the forest landward, up to the cultivated areas. When the swamp forest extends along narrow karstic valleys of Grande-Terre island or along the lower part of the streams of the volcanic island of Basse-Terre, the vegetation may abruptly change from swamp to moist or dry forest at the bottom of hill-slopes. Until the middle of the 20th century, the swamp forest contributed to the sugar cane industry, providing large amounts of fuelwood. Some areas have been reclaimed for pasture or sugar cane cultivation, whereas the dasheen *Colocasia esculenta* (Araceae) is still widely cultivated in the outer part of the swamp forest as an understorey crop (Braux 1981). *Pterocarpus officinalis* is the dominant tree species of the forest, forming a dense, almost evenly flat canopy.

The soil of the swamp forest has developed on terrigenous clay deposits. In the inner part of the forest, the organic clay is overlain by a peat layer that may reach 7 m depth (Feller *et al*. 1992). The contrasting pattern of rainfall (Imbert & Portecop 1986) results in seasonal variations of the water-table level that may fluctuate from 10 cm above, to 40 cm below, ground level (Febvay *et al*. 1981). The average annual rainfall for the study area ranges from 1200 to 2500 mm (Cabaussel 1982).

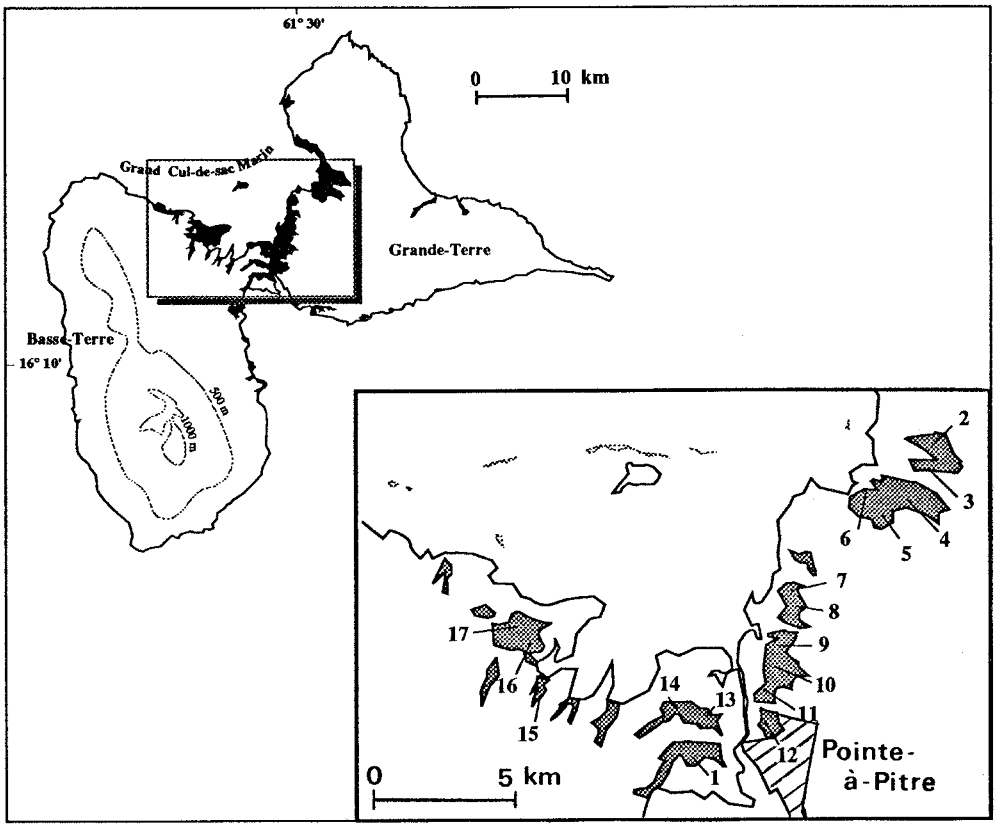

Figure 1. Coastal wetlands (black) around the two main islands of Guadeloupe Archipelago, with swamp forest patches (grey) within the study area and locations of the study sites (inset).

METHODS

Field sampling

Systematic sampling of inventory plots was performed by means of a grid of rectangular units (corresponding to 250-m × 500-m in the field) placed at random on the map of the vegetation of coastal wetlands drawn by Gabinaud *et al.* (1984). Such a method allowed sound probability inferences to be made subsequently from sample calculations (Thionet 1953, quoted by Daget & Godron 1982). Each node of the grid located within an area of the map referring to swamp forest was assumed to be the centre of a plot. In order to avoid heavy anthropogenic disturbance of the vegetation, only the plots that fell further than 100 m from the forest edge and into patches of forest greater than 10 ha were accepted.

Seventeen plots were sampled and located in the field using compass and Topochaix® distance measurer. Each one was 10 m wide and 40 m long, and subdivided into sixteen 5-m × 5-m subplots.

Vegetation survey and site characterization

Girth at breast height (GBH) was measured in each 25 m^2-subplot for all woody stems of $\geqslant$10 cm GBH. When girth was impossible to measure at breast height due to buttresses, measurement was made just above them or even assessed by eye when buttresses reached $\geqslant$ 2 m high. Measurements of each 400-m^2 plot were completed by identifying all vascular plants < 10 cm GBH. For each species, abundance and life-form as well as vertical position in the main forest ecotopes for epiphytes and lianas (i.e. ground-and-stump, tree-bole and canopy levels) were recorded using relevant codes. Furthermore, all species encountered while walking from the forest edge to the plot were listed separately. Floristic nomenclature follows the Flora of the Lesser Antilles (Howard 1979, 1988; 1989a, b).

A general characterization of each site was made by assessing the main biotic and abiotic environmental descriptors of the plots. For each vertical stratum of the forest stand the following structural parameters were taken into account: dominant species, vegetation height and cover. Epiphytes and liana communities were characterized by their overall abundance and dominant species in each vertical ecotope. Soil profile was described based on soil cores extracted from up to 1 m depth by means of a hand-auger. Soil consistency, colour and texture (clay, muck or peat) was assessed by direct observation. Hydrogen potential (pH), redox potential (Eh) and salinity of interstitial water were measured for the cores at 10 and 80 cm depth using a portable pH/Eh-meter and a hand refractometer. The water-table level was measured and microtopographic features noticed, as well as any evidence of anthropogenic disturbance.

Data processing

Ordination of floristic data from the 17 sample plots was implemented using correspondence analysis (ANAMUL™ software; Febvay & Bonnot 1991). In this analysis, environmental variables were introduced as supplementary variables. Ecological significance of the axes was inferred from the correlation (Spearman's rank coefficient) between the component score of environmental variables and that of the plots or species. Grouping of plots and detection of natural clusters of species was investigated using average-linkage agglomerative, hierarchical classification with the Euclidean distance between component scores issued from the correspondence analysis (ECODATA™ software; Bouchon 1996).

Differences for structural characteristics such as canopy height, number of stems, basal area, species richness and equitability ($E = H'/H'_{max}$, from Shannon–Weiner index) were tested between forest types using the Mann–Whitney U-test. Detection of non-randomness in *Pterocarpus* distribution among the 272 subplots of 25 m^2 was investigated using χ^2-test to compare the terms of the Poisson series with the observed data, and Student's t-test to establish whether the observed variance:mean ratio significantly departed from the expected value of 1 (Kershaw & Looney 1985). To minimize spatial autocorrelation between subplots (Dale 1999), tests were applied on average subsets resulting from 10 repeated random sequences of 30% of the subplots. Statistics were run on STATVIEW™ software (Abacus Concept 1987).

RESULTS

Floristics

The number of species per plot (400 m^2) ranged from 13 to 37 (mean = 22; SD = 6), with a total number of 107 species. The species–area curve was obtained by incrementing randomly the sampling area from 400 to 6800 m^2 (Figure 2). Each of the last four plots adds to the inventory an average of four new species, meaning that a complete species inventory was far from being achieved. In fact, taking into account the observations made outside the sample plots brings 71 additional species, giving a total of 178 species of vascular plants for the whole inventory.

Tree species accounted only for 28% of the total number of species, followed by ground herbs (26%), lianas (17%), shrubs (13%), epiphytes (11%), hemi-epiphytes (2%), palms (1%) and parasites (1%). Sixty-six families were represented. Polypodiaceae (Pteridophyta) had the highest number of species (17), followed by Araceae (monocots) with 13 species and Rubiaceae (dicots) with 12 species.

Eight species were present at least in half of the plots. Only one of them is

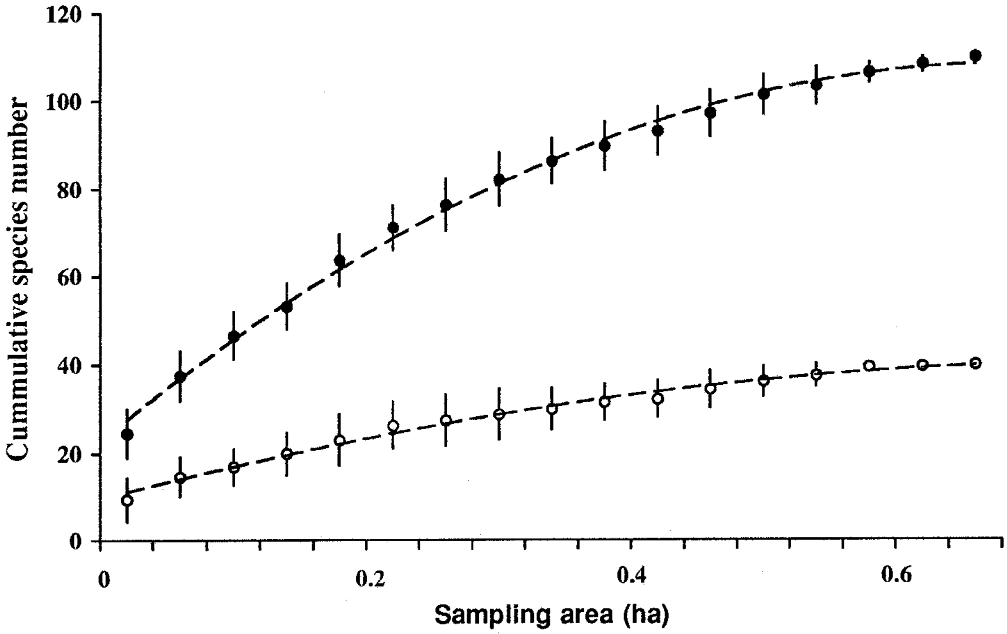

Figure 2. Species–area curves for vascular plant species of the *Pterocarpus* swamp forest in Guadeloupe. Mean values (± SD) have been calculated for all species (●) and for species ≥ 10 cm GBH (○), from 10 randomly combined sequences of 17 randomly permuted 400-m^2 plots.

a tree, *Pterocarpus officinalis*, present in all plots as well as the liana *Hippocratea volubilis*. Thirty-eight woody species ⩾10 cm GBH were recorded and ranked according to their abundance (Figure 3). The first species, *Pterocarpus officinalis*, contributed 76% to the total number of individuals, whereas the next two species, *Sterculia caribaea* and *Stilogyne lateriflora*, only contributed 6 and 2% respectively. The diversity index (H′) computed for the 17 plots altogether was 1.39, and the equitability (E) was 0.37.

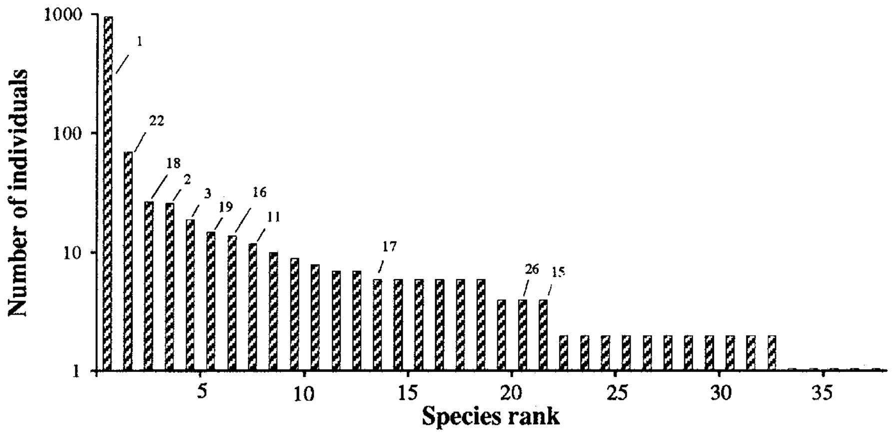

Figure 3. Dominance-diversity relationship for species ≥ 10 cm GBH for the *Pterocarpus* swamp forest in Guadeloupe. Codes refer to most frequent species listed in Table 1. Total area censused = 0.68 ha.

Forest structure

Species of trees and woody lianas ⩾10 cm GBH occurred with a mean of six species per plot (maximum 16). Stem density varied from 15 to 123 individuals per plot (mean = 73), some plots comprising mainly some large, old *Pterocarpus* stumps whereas others comprised a lot of trees with low GBH. Basal area was more evenly distributed, ranging from 1.4 to 3.5 m^2 per plot (mean = 2.3 m^2 with 92% *Pterocarpus*). Canopy height ranged from 11 to 23 m. Shrubs and small trees often constituted an intermediate stratum while an herbaceous layer up to 2 m high, mainly composed of ferns and/or *Montrichardia arborescens* (Araceae), was present in all plots. Multivariate analysis of lianas and epiphytes occurrence led to the identification of five species assemblages (G1, $G2_{A,B,C}$, G3) based on three forest ecotopes, i.e. canopy, trunk and stump/ground levels (Figure 4). The woody lianas *Hippocratea volubilis*, *Dalbergia monetaria*, *Cydista aequinoctalis*, *Heteropterys purpurea* and *Omphalea diandra* were characteristic of the open canopy environment (G1), while the epiphytes *Asplenium serratum* and *Peperomia nigropunctata* were found only in the shady environment, at stump/buttress level (G3). The third assemblage of species comprised three subgroups of species occuring most often at the intermediate level. One subgroup ($G2_B$) was exclusively composed of species never found in the canopy nor on stumps (understorey lianas and light demanding epiphytes), another was composed of

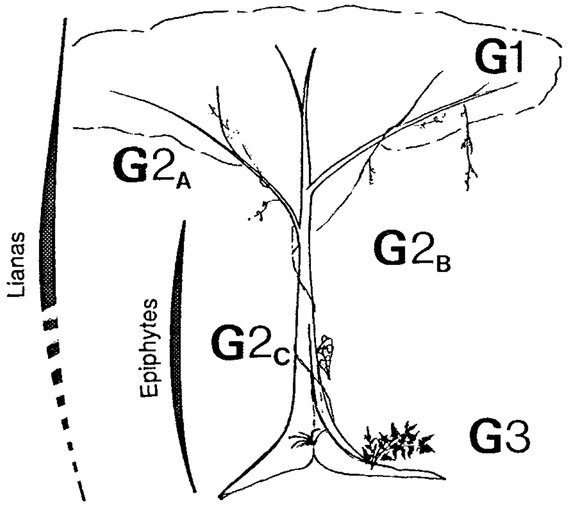

Figure 4. Identification of five species assemblages of lianas and epiphytes from ground to canopy levels. Light-demanding lianas (G1): *Hippocratea volubilis*, *Dalbergia monetaria*, *Cydista aequinoctalis*, *Heteropteris purpurea* and *Omphalea diandra*; shade-tolerant lianas ($G2_A$): *Philodendron scandens*, *Marcgravia umbellata*, *Dioscorea alata*, *Ipomœa* sp.; understorey lianas and light-demanding epiphytes ($G2_B$): *Aristolochia trilobata*, *Coccoloba ascendens*, *Hylocereus trigonus*, *Monstera adansonii*; lower levels epiphytes ($G2_C$): *Philodendron giganteum*, *Anthurium* spp., *Polypodium latum*, *Nephrolepis biserrata*; Exclusively stump/buttress-level epiphytes (G3): *Asplenium serratum*, *Peperomia nigropunctata*.

shade tolerant lianas occurring above as well as below the forest canopy ($G2_A$), and a third subgroup was composed of epiphytes non-exclusively located on stumps ($G2_C$). No epiphyte was found in the canopy. No species of lianas was exclusively located at stump level.

Correspondence analysis (CA) and hierarchical classification (HC) of presence/absence data were conducted alternatively for all species and for non-epiphytic (ground germinating) species only. Both sets of data evidenced that five plots were strongly and positively linked to the first CA axis (respectively 18 and 20% of the variance), this axis being significantly correlated with soil pH values at low and higher depth (respectively: $r_s = -0.694$, $P < 0.01$; $r_s = -0.762$, $P < 0.01$). These five plots, correlated with acid soils, were all located in the northern part of Basse-Terre island and were referred to as forest type A (Figure 5). The other plots have been separated into three subgroups by analysing the occurrence of non-epiphytic species. On the bottom of the first axis, four plots appeared to be more or less strongly related to higher pH. They were all located in the north of Grande-Terre island, and were referred to as forest type B1. The second axis, which contributed to 11% of the variance, was significantly correlated with Eh values at 0.8 m, soil texture (peat/muck/clay) and consistency (respectively: $r_s = 0.429$, $P < 0.05$; $r_s = 0.488$, $P < 0.05$; $r_s = 0.495$, $P < 0.05$). Along this axis, three plots were strongly associated with highly reduced peat soils (forest type B2), plot 1 being added to this subgroup on the basis of the results of the HC analysis, in spite of its poor contribution

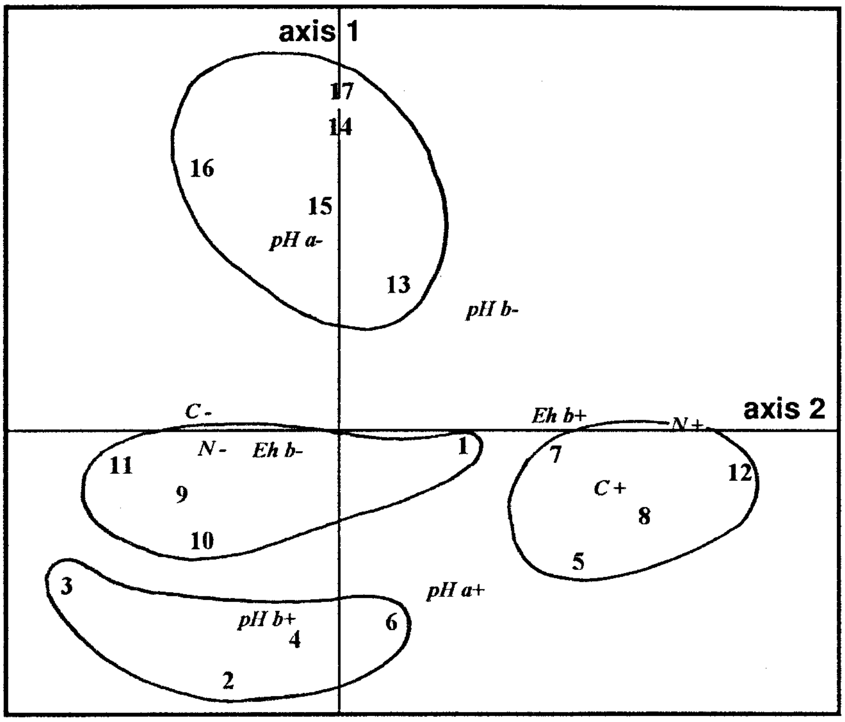

Figure 5. Correspondence analysis biplot of sample plots (S1 to S17). Soil parameters were added as supplementary variables; only those that exhibited a significant correlation with sample scores ($P < 0.05$) have been plotted. Axes 1 and 2 accounted for 18.3 and 11.5% of the variation, respectively. Grouping of sample plots is from an hierarchical classification analysis. Key to soil parameters: C = consistency; N = amount of clay vs. organic material; Eh = redox potential; pH = hydrogen potential; a = 10 cm depth ; b = 80 cm depth; + = higher values; − = lower values.

to the second axis of the CA. The last four plots, which were associated with less anoxic, firm, clayey soils, were referred to as forest type B3. This type seemed to be more related to inland location compared with type B2.

Analysis of species projection onto the plane determined by the first two CA axes allowed a list of characteristic species for each forest type (Table 1). The lianas *Dioscorea altissima*, *Heteropterys platyptera* and *Omphalea diandra* were found only in type A, with a frequency over 0.5. Mean values of structural characteristics for each forest type are shown in Table 2 with comparative statistics. Stands from type A had significantly lower tree densities than those from types B1 and B2, and stands from type B3 exhibited the lowest equitability values (Mann–Whitney U-test, $P < 0.05$ for both).

Distribution of Pterocarpus officinalis

At the scale of 25 m^2 (subplot area), the distribution of *Pterocarpus officinalis* trees was found to be significantly contagious in the stands from forest type A ($\chi^2 = 3.91$, df = 1, $P < 0.05$; t = 3.32, df = 23, P = < 0.01) and forest type B2

Table 1. Most frequent species (frequency ≥ 15%) recorded in the 17 sampled plots in swamp forest in Guadeloupe.

Code	Species	Life form[1]
Common species		
1	*Pterocarpus officinalis* Jacq. (Papilionaceae)	tree
2	*Dalbergia monetaria* L. f. (Papilionaceae)	liana
3	*Hippocratea volubilis* L. (Hypocrateaceae)	liana
4	*Polypodium latum* T. Moore ex Sodiro (Polypodiaceae)	epi.
5	*Anthurium grandifolium* (Jacq.) Kunth. (Araceae)	epi.
6	*Anthurium palmatum* (L.) Schott (Araceae)	epi.
7	*Thelypteris reticulata* (L.) Proctor (Polypodiaceae)	herb.
Characteristic species		
	Type A	
8	*Palicourea crocea* (Sw.) Roemer & Schultes (Rubiaceae)	shrub
9	*Dioscorea altissima* Lam. (Dioscoreaceae)	liana
10	*Heteropterys platyptera* DC (Malpighiaceae)	liana
11	*Omphalea diandra* L. (Euphorbiaceae)	liana
12	*Clidemia hirta* (L.) D. Don (Melastomaceae)	herb.
13	*Dieffenbachia seguine* (Jacq.) Schott (Araceae)	herb.
14	*Struchium sparganophorum* (L.) Kuntze (Asteraceae)	herb.
	Type B1	
15	*Pisonia fragrans* Dum.-Cours. (Nyctagynaceae)	tree
16	*Chrysophyllum argenteum* Jacq. (Sapotaceae)	s. tree
17	*Ixora ferrea* (Jacq.) Bentham. (Rubiaceae)	s. tree
18	*Stylogyne lateriflora* (Sw.) Mez (Myrsinaceae)	s. tree
19	*Tabernaemontana citrifolia* L. (Apocynaceae)	s. tree
20	*Marcgravia umbellata* L. (Marcgraviaceae)	liana
21	*Thelypteris interrupta* (Willd.) Iwastsuki (Polypodiaceae)	herb.
	Type B2	
22	*Sterculia caribaea* R. Br. (Sterculiaceae)	tree
23	*Symphonia globulifera* L. f. (Clusiaceae)	tree
24	*Aristolochia trilobata* L. (Aristolochiaceae)	liana
25	*Acrostichum danaefolium* Langsd. et Fisher (Polypodiaceae)	herb.
	Type B3	
26	*Cassipourea guianensis* Aublet (Rhizophoraceae)	s. tree
27	*Piper dilatatum* Rich. (Piperaceae)	shrub
28	*Cydista aequinoctialis* (L.) Miers. (Bignoniaceae)	liana
29	*Tectaria incisa* Cav. (Polypodiaceae)	herb.
30	*Thelypteris dentata* (Forssk.) E. St John (Polypodiaceae)	herb.
31	*Peperomia nigropunctata* Miq. (Piperaceae)	epi.

[1] tree: ≥ 8 m high; s. tree: small tree (4–8 m); shrub: < 4 m high; epi.: epiphyte; herb.: ground herbaceous species.

($\chi^2 = 8.35$, df = 2, $P < 0.02$; $t = 6.58$, df = 19, $P < 0.001$). In the field, this pattern of distribution was often associated with a typical hummock-hollow topography: most of the trees were clumped on the hummocks, forming large stumps surrounded by hollows of several metres wide, up to 30 cm depth, inundated during the rainy season. In the other stands, the topography was more uniform and the distribution of trees did not significantly depart from random.

DISCUSSION

The strong dominance of a few tree species is a common feature in swamp forests throughout the world (Bacon 1990, Longman & Jenik 1987, Richards

Table 2. Ranges of the structural characteristics of the four swamp forest types, Guadeloupe. The Mann–Whitney U-test was used to compare types: differences were significant at $P < 0.05$.

Forest type	Number of plots	Number of species		Tree density (400 m^2)	
		All sizes	GBH > 10 cm	*Pterocarpus*	All trees
A	5	19–28	2–9	350–1500	375–1700
B1	4	20–25	7–16	550–1750	1525–2700
B2	4	13–37	2–12	1150–2500	1775–3075
B3	4	13–23	3–4	950–2300	1050–2375
Statistics		NS	A/B1, B1/B3	A/B2	A/B1, A/B2

	Basal area (m^2 ha^{-2})		Canopy height	Equitability
	Pterocarpus	All trees		
A	33–57	35–57	13–23	0.21–0.68
B1	41–75	42–87	13–15	0.41–0.86
B2	31–64	34–79	11–17	0.25–0.67
B3	56–77	56–79	13–15	0.15–0.30
Statistics	A/B3	A/B1, A/B3	NS	B3/A, B3/B1, B3/B2

1952). It is assumed to be a consequence of harsh edaphic conditions resulting from poorly aerated or saturated waterlogged soils, as only plants developing metabolic and morphologic adaptations to flooding may grow in such an environment (Lugo *et al.* 1990). Among them are the Palmae–Lepidocaryoidae (Lot & Novelo 1990, Myers 1990) and species from various families such as Leguminosae. Plants belonging to this family are well known for their ability to develop symbiotic nitrogen fixation. Barrios & Herrera (1994) reported that Leguminosae was the most prevalent family in a Venezuelan flooded forest and found several species of this family nodulated. The predominant Caribbean swamp forest tree *Pterocarpus officinalis* also is known as a nodulating species (De Souza 1966). Recently, Saur *et al.* (1998) established that such symbiotic fixation constitutes a significant contribution to nitrogen uptake for this species and assumed that this adaptative trait is probably conducive to its outstanding success in growing in the flooded areas of the neotropics. In addition, the large buttresses of *Pterocarpus officinalis* trees provide for them a broad platform that appears to minimize toppling (Lewis 1988). Furthermore, *Pterocarpus* may be regarded as a strikingly fast-recovering species with regard to hurricane damage (Bouchon *et al.* 1991) whereas the other typical swamp forest species *Symphonia globulifera* was prone to high mortality following windstorms (D. Imbert, unpubl. data).

However, species richness of the swamp forest was amazingly higher than that of the nearby mangrove forest and even higher than that of the semi-evergreen dry forest: no more than 11 non-epiphytic vascular species had been recorded over a 3.5-ha area of the mangrove forest (Imbert 1985), and only 56 species of all sizes on 0.24 ha in the semi-evergreen dry forest (D. Imbert &

J. Portecop, unpubl. data) as compared to 70 species on a same area in the swamp forest (cf. Figure 2). From these results it may be assumed that, in a tropical environment, among those three major environmental stressors i.e. salt groundwater, ground-water deficit and waterlogged soils, the latter has less detrimental effects on species richness. This higher richness is partly due to the correlative blooming of the epiphytic life form, which is scarcely represented in the salt-spray or air-drought environment of the other two forests. The relatively high species richness vs. low diversity is a striking feature of the swamp forest as compared with other lowland forests, in Guadeloupe. This has also been mentioned for montane rain forests as compared with lower montane rain forests in Guadeloupe (Rousteau 1996) and elsewhere (Schnell 1950). No exhaustive inventories of vascular plants are available from the literature on other lowland swamp forests of the Caribbean. In Puerto Rico, however, Alvarez-Lopez (1990) recorded one to seven species $\geqslant$ 8 cm GBH within 0.1-ha plots in coastal *Pterocarpus* swamp forests, and 13 species in a montane *Pterocarpus* stand. The latter number is closer to the mean value of 12 species $\geqslant$10 cm GBH in 0.12-ha given by the species-area curve (Figure 2), considering that such a number was reached for two plots of only 0.04 ha each. In their study of a montane floodplain palm forest (Luquillo Mountains, Puerto Rico), Frangi & Lugo (1985) reported 27 tree species $\geqslant$ 3 cm GBH in 2525 m^2, but owing to the use of such different protocols, there is no direct comparison possible with our results.

Beyond the overall flooding regime which prevails over the whole swamp forest and which is responsible for the selection of the best-adapted species, we have been able to correlate variations in soil characteristics such as pH, clay content or redox potential with floristic composition and even with stand richness. It is thus clear that despite the waterlogged soils, a great number of species may occur in response to local variations of the environment which have to be more fully understood. From our study, highly reduced peaty soils (forest type B2) exhibit higher species diversity than less reduced clayey soils (forest type B3). Thus, more than hydroperiod (Lugo *et al*. 1990), rate of water movement over and through the soil may be a key factor in explaining spatial variations of species richness (Heinselman 1970). Among the numerous scarcely represented species, very few may be regarded as peculiar to swamp forests (*Annona glabra*, *Chrysobalanus icaco*, *Symphonia globulifera*), several are dry forest species (*Bursera simaruba*, *Cytharexylum spinosum*, *Guettarda scabra*, *Randia aculeata*, *Tabebuia heterophylla*) but most of them are typically found in moist or rain forests. The occurrence of dry forest species in the swamp forest may be explained both by the proximity of these two forests in several places, and by local variations of topography and/or hydrology favourable to such species. Three centuries ago, agriculture development caused the loss of most of the lowland wet forests in the island of Basse-Terre and of all of them in the island of Grande Terre. The occurrence at the present time of scattered individuals of species from upland, wet forests deep inside the swamp forest raises questions about the perpetuation of such species in the coastal swamp forest. For some of them, seed dispersal from the uplands and across large, non-forested areas may be possible by wind (*Ceiba pentandra*), bats or birds (*Cecropia schreberiana*), or streams as for the riverine species *Hernandia sonora* and *Syzygium jambos*. Other species like *Maytenus guyanensis*, *Ixora ferrea* or *Sloanea* sp. which have short-range seed dispersal were recorded on the north-east part of the lagoon of the Grand Cul-de-sac Marin, 30 km away from Basse-Terre island. Such species may thus be considered as relict species of the primary seasonal wet forest of the island of Grande-Terre acknowledged by Pagney (1986) and Rousteau (1995).

Swamp forests have often been regarded as an edaphic climax of the so-called tropical rain forest (Richards 1952, Whitmore 1990). In the Caribbean islands, the riverine *Pterocarpus* stand of the Luquillo Forest (Alvarez-Lopez 1990) seems to be the only example of a *Pterocarpus* swamp forest within the rain forest climatic zone. In Guadeloupe, the *Pterocarpus* swamp forest has stronger floristic affinities with remnants of the moist seasonal forest than with other forest formations, including the lower montane rain forest. However, on a structural point of view, even though seasonal forests host far less vascular epiphytes in their canopy than rain forests do, the swamp forest completely lacks canopy epiphytes. The absence of such epiphytes is surprising insofar as air moisture and annual rainfall are quite equivalent for most of both forest environments. This may be explained by the high susceptibility of tree-crowns of *Pterocarpus* to hurricane damage (Bouchon *et al*. 1991). In the island of Grande-Terre, however, small patches of *Pterocarpus* forest are located in a drier environment (< 1300 mm annual rainfall) and Alvarez-Lopez (1990) mentioned that in Puerto Rico *Pterocarpus* was present in an area where the annual rainfall is less than 800 mm. Furthermore, swampy areas dominated by the dry forest species *Hœmatoxylon campechianum* have been reported for Martinique (Brossard *et al*. 1991) and for Guadeloupe (Gabinaud *et al*. 1984). Such swampy woodlands cover extensive areas of southeastern Mexico (Lot & Novelo 1990). The soils are shallow and/or clayey and the period of flooding is restricted to the rainy season. Especially during the dry season, soil moisture in the first 20 cm is much lower (*c*. 40% d.w.; Cuny 1990) than in the *Pterocarpus* forest (370% d.w.; Imbert 1985). It seems therefore that, in the Caribbean islands, *Pterocarpus* swamp forests may thrive in nearly each life zone as long as soil waterlogging is pronounced all year long.

The clumped distribution of *Pterocarpus* which was evidenced in nearly half of the studied stands may result from several interacting factors. Windstorms that cause tree uprooting on particularly unsteady soils as well as periodic strong run-offs contribute to create or maintain a local hummock-hollow topography. As the buoyant *Pterocarpus* seeds can germinate when afloat but do not root when water depth exceeds 3 or 4 cm (Alvarez-Lopez 1990, Bacon 1990), microtopography controls seed stranding and seedling establishment. Standing trees, themselves, help to raise ground level by trapping litter between buttresses (Lescure 1980). Such a pattern of seed establishment generates clumps of trees with some individuals growing so close to each other that trunk anastomosis may occur, the coalescent basis of stems appearing thus like a resprouting stump and making difficult the numeration of tree individuals. We believe therefore that reports about *Pterocarpus* resprouting from stumps or even from buttresses (Lescure 1980) did not take into account such a phenomena.

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