



Floristic composition and diversity of three swamp forests in northwest Guyana

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Received 10 November 2000; accepted in revised form 11 April 2002

Key words: Conservation, Flooded forests, Forest structure, Guyana, Palms, Species dominance

Abstract

This paper reviews the floristic composition, vegetation structure, and diversity of three types of swamp forest that cover a considerable part of Guyana's North-West District. Trees, shrubs, lianas, herbs, and hemi-epiphytes were inventoried in three hectare plots: one in Mora forest, one in quackal swamp, and one in manicole swamp. The Mora forest, flooded annually by white water, was dominated by relatively few, large individuals of *Mora excelsa*. The very dense, thin-stemmed quackal forest, almost permanently flooded by black water, was characterized by *Tabebuia insignis* and *Symphonia globulifera* and contained few palms. The somewhat less dense manicole swamp, flooded regularly by brackish water, was distinguished by large numbers of *Euterpe oleracea*. Although the three swamps showed little overlap in floristic composition and densities of dominant species, they represent some of the lowest diversity forest in the Neotropics, with an α -diversity of 7.4 for the Mora forest, 8.2 for the quackal forest and 5.7 for the manicole swamp. When compared with similar vegetation types in the Guiana Shield, the swamp forests in this study show some interesting differences in species composition and density. The wetlands of the North-West District form the last stretch of natural coastline in Guyana and play an important role in the protection of riverine ecosystems. Furthermore, there is commercial potential for the extraction of non-timber forest products from these low-diversity forests. Nevertheless, in prolonged dry periods, large tracts of quackal forest are being burnt to give way to almost treeless, flooded savannas. For these reasons, adequate management and conservation strategies must be developed for the area.

Introduction

Amazonian flooded forests have been the focus of increasing interest in recent times, because of their importance for conserving biodiversity and protecting river quality (Rosales Godoy et al. 1999), their suitability for agriculture due to the annual soil enrichment caused by flooding (Prance 1979; Padoch and Pinedo-Vasquez 1999), and their significance to local fish ecosystems (Goulding et al. 1988; Henderson and Robertson 1999). Furthermore, the general low diversity of Amazonian swamp forests has been mentioned as a great advantage for the sustainable extraction of non-timber forest products (NTFP) (Peters et al. 1989; Johnston 1998). The management of forests dominated by economically important species could

be a viable enterprise if product value is high and the potential for conflicting land use is minimal (Anderson 1988).

Although the floodplain forests of Guyana cover extensive areas in the deltas of its magnificent rivers, they have not received much scientific attention. Forest inventories have mainly focused on the timber-producing region in central Guyana (Johnston and Gillman 1995; Ek 1997; Hout 1999; ter Steege et al. 2000). In fact, only the riparian Mora forest, dominated by the commercial timber species *Mora excelsa*, has been described in detail (Davis and Richards 1934; Polak 1992; ter Steege (1990, 1993); Johnston and Gillman 1995). Few surveys have been conducted in the coastal peat swamps of the country, because of the rather high costs of survey work and

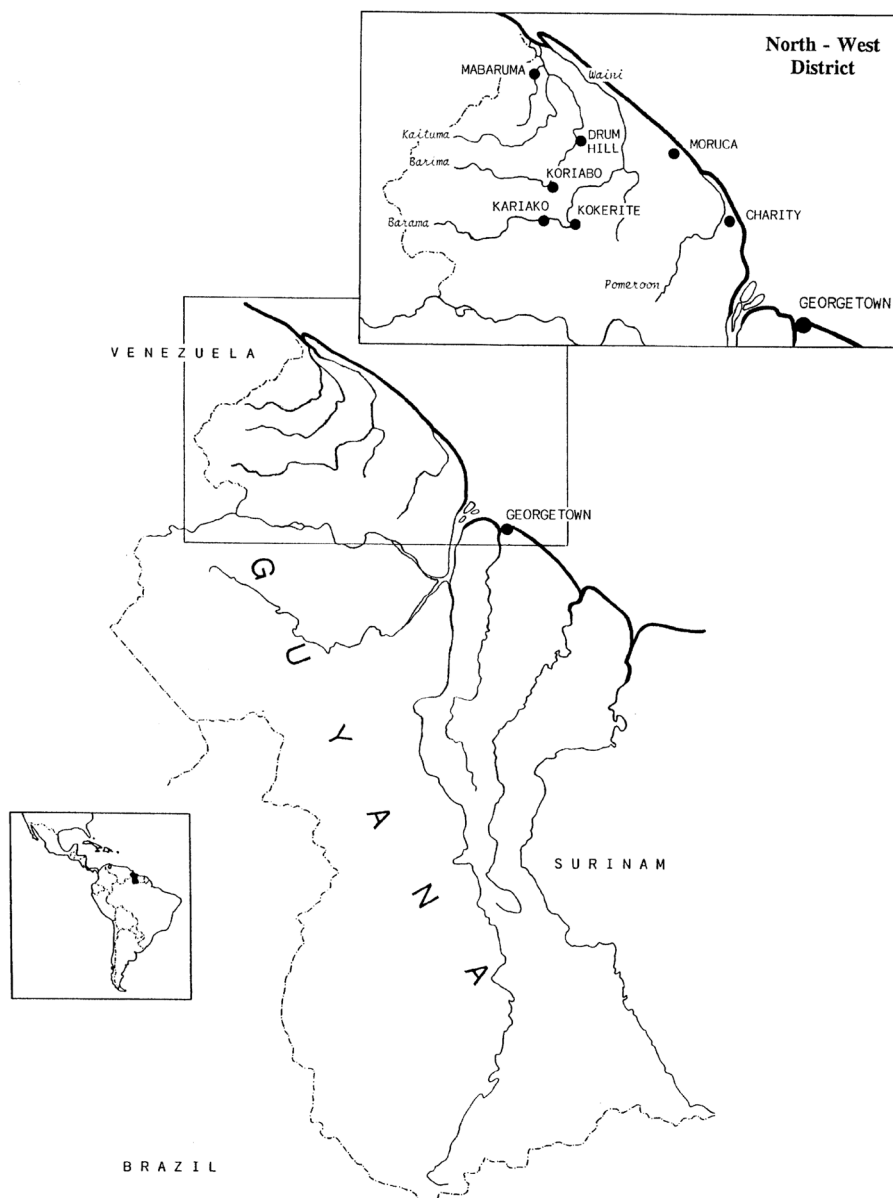


Figure 1. Map of Guyana. North-West District is located in upper box (see also Figure 2).

‘the forest being of little economic importance’ (Davis (1929): 159).

Although poor in plant species and commercial timber, the wetlands of the North-West District (Figure 1) form the last stretch of natural coastline in Guyana. While the swamp forests deeper inland protect some of the key watersheds in the country, the coastal wetlands play an important role in the protection against spring tides, rising seawater levels, and other natural hazards. Furthermore, these swamps are

subject to the commercial extraction of palm heart, one of the main NTFP of the country (van Andel et al. 1998; van Andel 2000). At the same time, large areas of swamp forests are being burnt during dry periods, and transformed into almost treeless, flooded savannas.

For the conservation of tropical forests and the establishment of protected areas, a good understanding of their biodiversity is needed (Ek and ter Steege 1998). Moreover, in order to design adequate man-

agement plans, quantitative information is needed on the diversity, population structure, and distribution patterns of useful (and non-useful) species in these vegetation types. This information should, however, not be limited to the canopy layer, but also include the forest understorey. Gentry and Dodson (1987) showed that, although neglected in most studies, the undergrowth generally contains between 25 and 46% of the total number of species found in wet tropical forests and may harbour various useful species as well.

Little has been published on the swamp forests of the North-West District, although some general accounts of dominant swamp species have been given (Anderson 1912; Davis 1929). The only detailed quantitative study of the coastal wetlands was provided by Fanshawe (1952, 1954), who described several different plant assemblages and communities based on species composition, soil type, seasonal flooding, and palm dominance. He based his classifications on a few study plots of 1.5 to 2.1 hectares, but stated that 'the formation is so complicated and obscure that only a complete study of the whole complex will bring out the dominant vegetation trends. Localised studies are of little value for the understanding of the whole' (Fanshawe (1952): 41). Nevertheless, the few existing vegetation maps of the North-West District (Forest Industries Development Survey (FIDS) 1970; Huber et al. 1995), are largely based on Fanshawe's forest classifications, provide few details on species composition and do not mention regional variation within the main forest types.

This paper compares the floristic composition, structure, and diversity of three, previously poorly known swamp forest types in Guyana's North-West District. It also sheds a light on the origin of the flooded savannas in the region. These inventories formed part of a broader study on the abundance and diversity of NTFP in the major forest types of north-west Guyana (van Andel (2000, 2001)). The vegetation descriptions presented here will hopefully contribute to a better understanding of the structure and floristic diversity of the forests of the North-West District, and allow for a comparison with other swamp forest studies conducted in the Guiana Shield region. It is further hoped that the results of this research will provide baseline data for the future sustainable exploitation of NTFP.

Study sites

The study was conducted in the lowland rain forests of Guyana's North-West District. This area has a tropical climate with a mean annual temperature of 26.5 °C. The average precipitation is 2750 mm per year, with a distinct dry season from February to April and a less obvious dry period from August to November (Ramdass 1990). Rainfall is at its highest from May to July, with another small peak occurring in December and January. There is little indication of climate gradients within the district.

The first study site was located near the remote village of Kariako on the Barama River, a few day's journey by boat from the Atlantic coast (Figure 2). The settlement is inhabited by Carib Indians. The Barama is a strongly meandering white water river, with its origin in the Imataka Mountains near the Venezuelan border and its mouth in the Waini River. At Kariako, situated some 80 km from its mouth, the Barama has a width of ca. 50 m. Like many meandering rivers, the riverbank collapses in the convex bends, while sediments are deposited in the concave curves. In the dry season, the water level in the river drops significantly, so that the river is barely navigable due to fallen trees blocking the waterway. Although the forest adjacent to the river is flooded only during the rainy season, the heavy clay soils (distric Fluvisols) remain swampy for most of the year. This floodplain forest is dominated by *Mora excelsa* and is therefore known as Mora forest. This forest gradually gives way to mixed forest on the higher, well-drained soil behind the floodplain. Large Mora trees can, however, be found along creeks traversing the mixed forest.

The second study site was in the vicinity of the Santa Rosa Amerindian Reserve, located along the Moruca River in the coastal swamplands (Figure 2). Santa Rosa is a predominantly Arawak village. The Moruca is a small black water river, linked to the Waini by a network of smaller rivers and having its mouth in the Atlantic Ocean. The river is flanked on both sides by an open flooded savanna, in which many small sandy islands arise, remnants of ancient sand dunes (Anderson 1912). Individual homesteads, cultivated fields, and entire villages can be found on these islands. Moving inland, these sandy islands gradually merge into a mainland of well-drained secondary and primary forest. The soil of the savanna is largely organic, consisting of a thick layer of decayed vegetative matter, also known as 'pegasse' (Histosol).

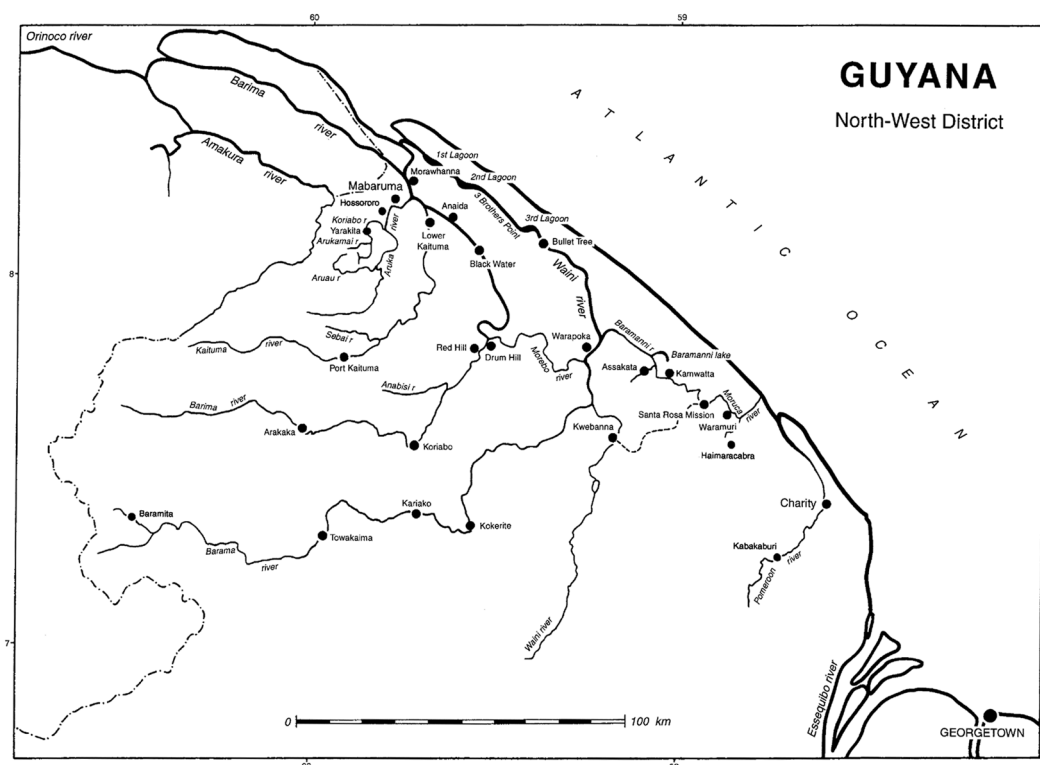


Figure 2. Map of North-West District.

The acid peat is underlain with alluvial and marine clay at a depth of sometimes more than 4 m. This clay layer impedes drainage and keeps the soil waterlogged most of the time. Only in the dry season can these soils be trod on. Moving towards the coast beyond the savanna, one encounters a dense swamp forest that has been given the name 'quackal swamp' because of the abundance of the small tree *Marlierea montana*, locally known as 'quackoo'. It was in such a forest that the second plot was laid out.

In the course of this study, it became clear that the savannas bordering the quackal forest were not natural, but man-made. They were once covered by quackal forest, but annual fires have transformed them into open plains. A small section was therefore dedicated to the degradation of quackal swamps and the species composition of these savannas.

Moving up the Moruca River towards the Baramanni River (Figure 2), the savannas change into dense swamp forest in which *Euterpe* palms (manicole) are dominant. The third study site was located in manicole swamp near the mouth of the Assakata Creek, which leads to a village by the same name inhabited by Arawak and Warao Indians. In the wet

season, both the quackal and manicole swamps are heavily flooded and must be entered by canoe.

Methods

Layout of hectare plots

The first plot was laid out in August-September 1996 in Mora forest near Kariako ($7^{\circ}23' \text{ N}$, $59^{\circ}43' \text{ W}$). The second plot was established in September 1997 in a quackal swamp near Santa Rosa ($7^{\circ}41' \text{ N}$, $58^{\circ}55' \text{ W}$), while the third plot was laid out in November 1997 in a manicole swamp near Assakata ($7^{\circ}44' \text{ N}$, $59^{\circ}04' \text{ W}$). All plots were located in areas accessible to Amerindians of nearby villages to be sure that these forests were subject to NTFP collection. A nested sampling method was used in the present study, including trees, shrubs, lianas, and herbs (Alder and Synott 1992; Hall and Bawa 1993; Ek 1997). Each plot was systematically surveyed by identifying, measuring, and tagging all trees with a diameter at breast height (DBH) $> 10 \text{ cm}$, and estimating their height. Every 100 m, species with a DBH $< 10 \text{ cm}$ and a height \geq

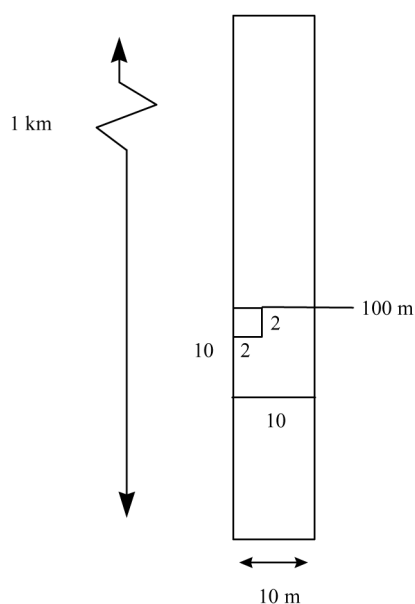


Figure 3. Layout of a hectare plot.

1.5 m ('shrubs') were sampled in a subplot of 10 × 10 m (Figure 3). Herbs and seedlings smaller than 1.5 m were sampled in quadrates of 2 × 2 m. Hemi-epiphytes were counted only if they occurred within reach on lower trunks or on the forest floor, or when their aerial roots had a DBH ≥ 10 cm. Care was taken that the hectare plots covered a homogeneous forest area and did not include transitions in vegetation. If the vegetation did change along the kilometre line, the shape of the plot was altered in such a way (smaller plots were laid out next to each other) that a total surface area of one hectare could still be achieved. Natural gaps were included in the plots.

Plant collection

Plant collections, fertile ones where possible, were made of all species growing in the plots. In addition, flowering and fruiting material was collected outside the plots to match the sterile specimens in the plots. Although this procedure required a great deal of time, it definitely decreased the number of unidentified plants. This 'additional collection' method was also successfully implemented in biodiversity studies conducted in the Mabura Hill area (Ek 1997). Flowering and fruiting material is particularly important in the study of useful plants, as correct identifications are essential. Duplicates were deposited at the Herbarium of the University of Guyana (BRG) and the Utrecht

branch of the National Herbarium of the Netherlands (U). A complete list of all identifiable species found in the three hectare plots is given with full authority in the Appendix.

Data analysis

The Importance Value index (I.V.) of Cottam and Curtis (1956) was used to describe and compare the species composition of the plots. This method has been employed in various other quantitative studies on vegetation structure and NTFP (Balée 1994; Valkenburg 1997; Dallmeijer and Comiskey 1998). The I.V. of a species is defined as the sum of its relative dominance (Rdom), its relative density (Rden) and its relative frequency (Rfreq): $I.V. = Rdom + Rden + Rfreq$. The last three indices are calculated using the following equations:

Relative dominance ($Rdom$) = total basal area for a species/total basal area for all species × 100%
(basal area = $\pi \cdot (DBH/2)^2$)

Relative density ($Rden$) = number of individuals of a species/total number of individuals × 100%

Relative frequency ($Rfreq$) = frequency of a species/sum frequencies of all species × 100%

The frequency of a species is defined as the number of subplots (100 × 10 m) in which it is present. The theoretical range for $Rdom$, $Rden$ and $Rfreq$ is 0–100%. Thus, the I.V. of a species may vary between 0 and 300%.

According to the definitions of Johnston and Gillman (1995), a dominant species in the vegetation is a single species accounting for over 20% of the total number of individuals. Co-dominance is characterized as one or more taxa each representing 10–20% of the trees. To see whether one hectare was sufficient to cover the major variety of species in a particular forest type, I drew a species-area curves for trees with a DBH ≥ 10 cm in each of the three plots. To compare the results of the study plots with other forest types, I quantified species richness using the Fisher's α diversity index (Fisher et al. 1943). Fisher's α is relatively insensitive to sample size and is calculated with the formula: $\alpha - (\alpha + N) e^{-S/\alpha} = 0$, where N is the number of individuals in the sample, S the number of species in the sample, and α = Fisher's α .

Table 1. Summary of the floristic composition of three hectare plots in swamp forests in Barama, Moruca and Assakata. The second number in the range of species and families includes the number of unidentified species, regarded as a previously unrecorded species or family. Liana species include hemi-epiphytes and climbing ferns.

Forest type Floristic composition	Barama Mora	Moruca quackal	Assakata manicole
TREE LAYER ≥ 10 cm DBH			
Number of individuals in 1 ha	321	946	664
Number of species in 1 ha	31	41	30
Number of families in 1 ha	21	24	18
Mean diameter trees ≥ 10 cm DBH [cm]	29.0	17.2	20.8
Canopy height [m]	30–45	12–15	15–25
α -diversity	7.4	8.0	5.7
SHRUB LAYER < 10 cm DBH and ≥ 1.5 m			
Number of individuals in 0.1 ha	1594	720	1603
Number of species in 0.1 ha	63	49	82
Number of families in 0.1 ha	34	29	37
HERB LAYER < 1.50 m			
Number of individuals in 4×10^{-3} ha	407	481	548
Number of species in 4×10^{-3} ha	47	34	47–48
Number of families in 4×10^{-3} ha	29	21	27–28
Total nr. of tree species ≥ 10 cm DBH	28	38	27
Total nr. of liana species ≥ 10 cm DBH	3	2	3
Total nr. of shrub /small tree species < 10 cm DBH	31	13	24
Total nr. of liana species < 10 cm DBH	22	15	37
Total nr. of species only found in herb layer	18	7	7
True herb species	9	2	4
Total nr. of species found in 1 ha plot	102	75	98
Total nr. of families found in 1 ha plot	49	36	43

Results

General forest composition

A total of 228 species (including three unidentified specimens) was found in the three hectare plots (see Appendix) and a summary of these findings is presented in Table 1. One remarkable aspect was that the Mora forest contained an unusually small number of trees. Mean diameter and canopy height, however, were the highest of all plots, indicating that the Mora forest was composed of few, large trees. In contrast, the other two swamp forests consisted of many small-stemmed trees. The α -diversity was generally very low. The manicole plot had the lowest number of tree species, but a richer understorey than the other two plots. The shrub layer of the quackal swamp was less dense than that of the Mora and manicole forests. Lianas and hemi-epiphytes were relatively common in all three plots. It can be deduced from Table 1 that the understorey harboured 45.3% (quackal) to 69.6% (Mora) of the total number of species in the plots.

These figures illustrate the importance of nested sampling when studying vegetation structure and species richness of tropical rain forests.

The three swamp forest plots clearly differed in family composition (Table 2). The only common aspect in the three plots seemed to be the abundance of Mimosaceae. The Mora forest was obviously dominated by Caesalpiniaceae (*Mora excelsa*). Fabaceae and Lecythidaceae were also more important in the Mora forest than in the two pegasse swamps. In contrast, Clusiaceae, Bignoniaceae, Ebenaceae, and Myristicaceae were typical aspects of the pegasse swamps, although somewhat more in the quackal than in the manicole swamp. The quackal forest was further characterized by the high presence of Humiriaceae and Myrtaceae, an aspect not shared with the others. The manicole swamp was the only forest dominated by Arecaceae. Mimosaceae and Caesalpiniaceae were the second and third most important families in that plot.

Table 2. Family dominance by tree density (percentage of individuals ≥ 10 cm DBH) for the 15 most common families in the three swamp forest plots.

Percentage of trees ≥ 10 cm DBH per plant family	Barama Mora	Moruca quackal	Assakata manicole
Leguminosae-Caesalp.	57.9	0.3	13.1
Leguminosae-Mimos.	10.0	13.5	20.0
Arecaceae	–	0.6	30.4
Clusiaceae	0.9	17.0	9.8
Bignoniaceae	–	12.9	6.0
Leguminosae-Fabac.	11.5	2.4	3.8
Ebenaceae	–	8.9	5.4
Humiriaceae	–	11.3	–
Myristicaceae	0.3	7.4	3.5
Sapotaceae	1.6	4.8	0.8
Myrtaceae	–	6.6	–
Lecythidaceae	6.5	–	–
Anacardiaceae	0.6	1.6	3.5
Sapindaceae	0.3	2.6	0.6
Lauraceae	0.3	2.4	0.3
Unidentified	–	–	0.2
Total of other families	10.0	7.6	2.7

Mora forest

The Mora forest in Barama was a tall, riparian forest with an average height of 30–45 m. Table 3 shows the I.V. scores of the 20 most common tree species. The forest was heavily dominated by *Mora excelsa*, accounting for more than 56% of the trees. All individuals with a DBH > 65 cm belonged to this species as well. The towering Mora trees had large buttresses, but were not deeply rooted. They were often felled by rainstorms or by the force of the meandering river. Apart from these natural gaps, the canopy was more or less closed. Several creeks traversed the plot. The clay soil remained swampy for months after the annual flooding in June–July. Mora fruited massively in December, evident by a carpet of seeds on the forest floor. Other common trees were *Pterocarpus officinalis* ssp. *officinalis*, *Pentaclethra maculosa*, and *Eschweilera wachenheimii*: the latter was also a characteristic species of the mixed forest further inland. Species like *Zygia latifolia* var. *communis*, *Spachea elegans*, *Ficus* spp., *Inga* spp., and *Spondias mombin* were common directly on the waterfront, but their importance gradually decreased further from the river. Likewise, curtains of lianas covered the riverbanks, while they were less abundant more inland. *Uncaria guianensis* was the most common woody liana in Mora forest.

Mora excelsa regenerated abundantly in the understorey. The thin saplings occupied most of the shrub layer (Table 4), leaving little space for other small trees like *Duguetia* spp. and *Tovomita* sp. TVA 1020. True shrubs were represented by *Gustavia augusta* and *Psychotria bahiensis* var. *cornigera*. *Geonoma baculifera* is frequently present in large quantities in Mora forest, but only two individuals were found in the plot. This may have two explanations. This clustered palm has a rather patchy distribution and, because its leaves are used as roof thatch, the species tends to be scarce around Amerindian settlements (van Andel 2000). The same applies to *Euterpe oleracea*, which also has an irregular distribution in Mora forests: it was only found in juvenile stage along small streams outside the plot. Hemi-epiphytes, such as *Philodendron rudgeanum* and the climbing fern *Cyclodium meniscioides* var. *meniscioides*, were common. The most frequent liana was *Dioclea scabra*, followed by *Paullinia caloptera*. The broad crowns of the Mora trees were covered with epiphytes (mostly bromeliads and orchids); however, these fell outside the scope of this inventory.

The lowest stratum contained several true herb species, such as *Hymenocallis tubiflora*, *Hypolytrum longifolium* ssp. *longifolium*, and *Calathea* cf. *micans*. The fern *Adiantum latifolium* was the most numerous plant in the herb layer, followed by recently germinated Mora seedlings (Table 5).

Table 3. Density, basal area and importance value of the 20 most common species of trees ≥ 10 cm DBH in one hectare of Mora forest, Barama. Species are ranked in order of decreasing importance value. * Liana.

Mora swamp forest Tree layer	Absolute density	Basal area	Importance value	Relative density	Relative dominance	Relative frequency
Species	[# ind./ha]	[m ² /ha]	[%]	[%]	[%]	[%]
<i>Mora excelsa</i>	182	28.44	152.81	56.70	84.49	11.63
<i>Pterocarpus officinalis</i> ssp. <i>officinalis</i>	27	1.41	20.75	8.41	4.20	8.14
<i>Eschweilera wachenheimii</i>	21	1.25	17.23	6.54	3.72	6.98
<i>Pentaclethra macroloba</i>	15	0.96	16.82	4.67	2.85	9.30
<i>Zygia latifolia</i> var. <i>communis</i>	16	0.27	13.93	4.98	0.80	8.14
<i>Licania persaudii</i>	5	0.14	7.79	1.56	0.42	5.81
<i>Spachea elegans</i>	4	0.17	6.40	1.25	0.51	4.65
<i>Brownea latifolia</i>	4	0.05	6.05	1.25	0.15	4.65
<i>Alexa imperatricis</i>	7	0.24	5.23	2.18	0.73	2.33
<i>Uncaria guianensis</i> *	5	0.05	5.20	1.56	0.15	3.49
<i>Chrysophyllum argenteum</i> ssp. <i>auratum</i>	4	0.06	4.91	1.25	0.18	3.49
<i>Vitex compressa</i>	3	0.11	4.76	0.93	0.34	3.49
<i>Trichilia rubra</i>	3	0.05	4.58	0.93	0.16	3.49
<i>Tovomita</i> sp. TVA 1020	3	0.03	3.36	0.93	0.09	2.33
<i>Duguetia pycnastera</i>	3	0.03	3.35	0.93	0.09	2.33
<i>Spondias mombin</i>	2	0.09	3.21	0.62	0.26	2.33
<i>Clathrotropis brachypetala</i> var. <i>brachypetala</i>	2	0.10	2.08	0.62	0.30	1.16
<i>Carapa guianensis</i>	2	0.02	1.86	0.62	0.07	1.16
<i>Hyeronima alchorneoides</i> var. <i>stipulosa</i>	1	0.03	1.56	0.31	0.09	1.16
<i>Ficus maxima</i>	1	0.02	1.54	0.31	0.07	1.16
Total of other species (11)	11	0.11	16.56	3.42	0.34	12.78
Total	321	33.66	300.00	100.00	100.00	100.00

Table 4. Density and frequency of the 10 most common species < 10 cm DBH and ≥ 1.5 m in height in 0.1 ha ('shrub layer') of Mora forest, Barama. Species are ranked in order of decreasing numbers. * Liana; ● hemi-epiphyte.

Mora swamp forest Shrub layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Mora excelsa</i>	1330	83.44	6.34
<i>Duguetia pycnastera</i>	31	1.94	5.63
<i>Tovomita</i> sp. TVA 1020	19	1.19	4.23
<i>Duguetia yeshidan</i>	16	1.00	4.23
<i>Cyclodium meniscioides</i> var. <i>meniscioides</i> ●	10	0.63	4.93
<i>Gustavia augusta</i>	10	0.63	2.82
<i>Philodendron rudgianum</i> ●	10	0.63	2.11
<i>Psychotria bahiensis</i> var. <i>cornigera</i>	10	0.63	2.82
<i>Zygia latifolia</i> var. <i>communis</i>	10	0.63	4.23
<i>Dioclea scabra</i> *	9	0.56	2.11
Total of other species (53)	139	8.72	60.56
Total	1594	100.00	100.00

Table 5. Density and frequency of the 10 most common species < 1.5 m in height in 4×10^{-3} ha ('herb layer') of Mora forest, Barama Species are ranked in order of decreasing numbers. ● Hemi-epiphyte.

Mora swamp forest Herb layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Adiantum latifolium</i>	148	36.36	8.64
<i>Mora excelsa</i>	96	23.59	11.11
<i>Philodendron</i> sp. TVA 1362 ●	19	4.67	1.23
<i>Philodendron rudgeanum</i> ●	18	4.42	4.94
<i>Pterocarpus officinalis</i> ssp. <i>officinalis</i>	14	3.44	4.94
<i>Hyeronima oblonga</i>	13	3.19	2.47
<i>Olyra longifolia</i>	13	3.19	4.94
<i>Hymenocallis tubiflora</i>	10	2.46	1.23
Celastraceae TVA 1364	5	1.23	1.23
<i>Cyclodium meniscioides</i> var. <i>meniscioides</i> ●	5	1.23	4.94
Total of other species (37)	66	16.20	54.31
Total	407	100.00	100.00

Quackal swamp

This dense swamp forest beyond the Moruca savannas continued towards the Atlantic Ocean, where it gradually changed into mangrove forest. The soil consisted of a pegasse layer several meters in thickness. In the wet season, the water level rose to 2 m above the soil, so that the area could only be entered by boat. Access to the forest was easier in the dry season. The canopy was low (12–15 m), with a few emergent *Mauritia flexuosa* palms and *Calophyllum brasiliense* trees (20–25 m tall). The most common woody species were *Tabebuia insignis* var. *monophylla*, *Symphonia globulifera*, *Macrosamanea pubiramea* var. *pubiramea*, *Clusia fockeana*, and *Humiriastrium obovatum* (Table 6). *Marlierea montana*, characteristic of this forest type, was also frequent. Large lianas were rare; the only two individuals ≥ 10 cm DBH were *Machaerium myrianthum* and *Norantea guianensis*.

The shrub layer was characterized by clustered palms, including the spiny *Bactris campestris* and the unarmed *Euterpe oleracea* (Table 7). Neither palms produced stems ≥ 10 cm DBH. *Cassipourea guianensis* and *Marlierea montana* were common in the understorey, as was the shrub *Ischnosiphon obliquus*. Hemi-epiphytes grew abundantly on the lower tree trunks; however, apart from some fertile specimens of *Philodendron fragrantissimum* and *P. linnaei*, most individuals were sterile and could not be identified to the species level. Saplings of the common canopy

species further typified the shrub layer. *Tetracera volubilis* ssp. *volubilis* was one of the few lianas.

The quackal swamp had a dense ground cover of *Rapatea paludosa* ssp. *paludosa* (Table 8). Seedlings of various *Philodendron* species were also common. Juveniles of the common canopy species further occupied the herb layer. Seedlings of *Euterpe oleracea* and *Bactris campestris* were found in small quantities, while seedlings or saplings of *Mauritia flexuosa* were rare.

Savannas

Residents along the Moruca River have been burning the quackal swamp forest for decades. In prolonged dry periods, the pegasse dries out and is easily set on fire. From August 1997 to March 1998, when Guyana suffered from the El Niño droughts, large stretches of savanna were set on fire (Figure 4). The reasons for the burning of swamp forest and the consequences for the collection of NTFP are outlined in detail in van Andel (2000). Half-burnt pieces of quackal forest were observed during this study, with *Mauritia flexuosa* being the only surviving species among the dead stumps. After several fire events, most shrubs and stumps disappear. The vegetation is transformed into an open plain with *Mauritia flexuosa* palms and a ground cover of grasses and sedges (e.g., *Oryza rufipogon*, *Rhynchospora* spp., *Fuirena umbellata*, *Cyperus haspan*). These extensive 'man-made' savannas are found alongside the Moruca and neighbouring rivers. Similar savannas are occasionally found deeper

Table 6. Density, basal area and importance value of the 20 most common species of trees ≥ 10 cm DBH in one hectare of quackal swamp forest, Moruca. Species are ranked in order of decreasing importance value.

Quackal swamp forest Tree layer	Absolute density	Basal area	Importance value	Relative density	Relative dominance	Relative frequency
Species	[# ind./ha]	[m ² /ha]	[%]	[%]	[%]	[%]
<i>Tabebuia insignis</i> var. <i>monophylla</i>	122	3.20	30.98	12.90	12.79	5.29
<i>Symphonia globulifera</i>	104	3.63	30.80	10.99	14.52	5.29
<i>Macrosamanea pubiramea</i> var. <i>pubiramea</i>	123	3.02	30.38	13.00	12.09	5.29
<i>Humiriastrum obovatum</i>	76	2.61	23.25	8.03	10.46	4.76
<i>Diospyros guianensis</i> ssp. <i>guianensis</i>	84	1.68	20.91	8.88	6.74	5.29
<i>Pradosia schomburgkiana</i> ssp. <i>schomburgkiana</i>	40	1.54	15.69	4.23	6.17	5.29
<i>Virola elongata</i>	57	1.36	15.68	6.03	5.42	4.23
<i>Marlierea montana</i>	59	0.84	14.89	6.24	3.36	5.29
<i>Humiria balsamifera</i> var. <i>balsamifera</i>	31	1.59	13.89	3.28	6.38	4.23
<i>Clusia fockeana</i>	50	0.70	12.85	5.29	2.81	4.76
<i>Pachira aquatica</i>	21	0.47	8.33	2.22	1.87	4.23
<i>Trattinnickia burserifolia</i>	20	0.26	7.91	2.11	1.04	4.76
<i>Matayba camptoneura</i>	25	0.33	7.68	2.64	1.33	3.70
<i>Tapirira guianensis</i>	15	0.41	6.95	1.59	1.66	3.70
<i>Dulacia</i> cf. <i>guianensis</i>	12	0.25	5.45	1.27	1.00	3.17
<i>Calophyllum brasiliense</i>	7	0.35	5.32	0.74	1.41	3.17
<i>Mauritia flexuosa</i>	6	0.46	4.04	0.63	1.82	1.59
<i>Macoubea guianensis</i>	5	0.18	3.89	0.53	0.72	2.65
<i>Ormosia coutinhoi</i>	13	0.50	3.89	1.37	1.98	0.53
<i>Iryanthera juruensis</i>	10	0.17	3.87	1.06	0.70	2.12
Total of other species (21)	66	1.43	33.33	6.97	5.72	20.65
Total	946	24.99	300.00	100.00	100.00	100.00

Table 7. Density and frequency of the 10 most common species < 10 cm DBH and ≥ 1.5 m in height in 0.1 ha ('shrub layer') of quackal swamp forest, Moruca. Species are ranked in order of decreasing numbers. ● Hemi-epiphyte.

Quackal swamp forest Shrub layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Bactris campestris</i>	214	29.72	5.92
<i>Philodendron</i> spp. ●	52	7.22	2.96
<i>Cassipourea guianensis</i>	44	6.11	5.33
<i>Marlierea montana</i>	34	4.72	3.55
<i>Euterpe oleracea</i>	29	4.03	2.37
<i>Tabebuia insignis</i> var. <i>monophylla</i>	28	3.89	4.14
<i>Diospyros guianensis</i> ssp. <i>guianensis</i>	26	3.61	4.73
<i>Asplundia</i> cf. <i>gleasonii</i> ●	24	3.33	2.96
<i>Humiriastrum obovatum</i>	23	3.19	2.96
<i>Macrosamanea pubiramea</i> var. <i>pubiramea</i>	22	3.06	2.96
Total of other species (39)	224	31.11	62.14
Total	720	100.00	100.00

in the interior, but always close to Amerindian settlements (e.g., Assakata, Koriabo, see Figure 2).

Since juveniles of *M. flexuosa* do not survive repeated burning, these palms gradually disappear from the savannas nearest the human settlements. More-

Table 8. Density and frequency of the 10 most common species < 1.5 m in height in 4×10^{-3} ha ('herb layer') of quackal swamp forest, Moruca. Species are ranked in order of decreasing numbers. ● Hemi-epiphyte.

Quackal swamp forest Herb layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Rapatea paludosa</i> var. <i>paludosa</i>	134	27.86	11.76
<i>Marlierea montana</i>	64	13.31	7.06
<i>Asplundia</i> cf. <i>gleasonii</i> ●	58	12.06	7.06
<i>Diospyros guianensis</i> ssp. <i>guianensis</i>	53	11.02	7.06
<i>Philodendron</i> spp. ●	38	7.90	5.88
<i>Philodendron surinamense</i> ●	26	5.41	3.53
<i>Humiriastrum obovatum</i>	13	2.70	5.88
<i>Symphonia globulifera</i>	11	2.29	4.71
<i>Philodendron lanceolatum</i> ●	9	1.87	2.35
<i>Macrosamanea pubiramea</i> var. <i>pubiramea</i>	9	1.87	3.53
Total of other species (24)	66	13.73	41.18
Total	481	100.00	100.00



Figure 4. Burning savanna along the Moruca River.

over, few herbaceous species can withstand fire very well (e.g., *Eleocharis mitrata*, *Nephrolepis biserrata*, and *Ludwigia nervosa*). In the wet season, *Nymphaea ampla*, *Nepsera aquatica*, *Xyris laxiflora*, *Crinum erubescens*, *Habenaria longicauda*, and *Utricularia foliosa* flower in the flooded savannas. Remnants of tree trunks are found in the pegasse layer. Riverbanks and other parts of savanna that have escaped annual burning quickly become invaded by a dense shrubland of *Montrichardia arborescens*, *Chrysobalanus icaco*, saplings of *Tabebuia insignis* var. *monophylla* and *Virola surinamensis*.

Manicole swamp forest

As its name suggests, the multi-stemmed palm *Euterpe oleracea* (manicole) was the most numerous tree species in the manicole plot (Table 9). In fact,

more than 30% of the individuals ≥ 10 cm DBH were palms. However, since the manicole stems did not attain a diameter over 18 cm, the basal area and importance value of this species were lower than those of *Pentaclethra macroloba* and *Symphonia globulifera*. The canopy of the swamp forest was 15–25 m high, with a few emergents of *Iryanthera juruensis* or *Virola surinamensis*. The latter species achieved a maximum diameter of 153.5 cm, while the mean DBH of all trees was only 20.8 cm. Other common trees included *Tabebuia insignis* var. *monophylla*, *Diospyros guianensis* ssp. *guianensis*, and *Eperua falcata*. The single-stemmed palms *Euterpe precatoria* and *Jessenia bataua* ssp. *oligocarpa* were also frequent. A few scattered individuals of *Mora excelsa* were found; their diameters were not larger than 63 cm. Lianas were poorly represented. Sapindaceae sp. TVA 3056 and *Machaerium myrianthum* were among the few large species encountered in the plot.

The understory was characterized by saplings of *Macrosamanea pubiramea* var. *pubiramea*, *Euterpe oleracea*, and *Pentaclethra macroloba* (Table 10). Large numbers of hemi-epiphytes grew on the lower tree trunks, from the giant *Philodendron melinonii* to the delicate *P. surinamense*. *Tococa aristata* was one of the few true shrubs. Lianas were common in the lower strata (37 species), especially the vigorously climbing palm *Desmoncus polyacanthos*. Other climbers included *Maripa scandens*, *Machaerium* spp., and *Marcgravia coriacea*.

Table 9. Density, basal area and importance value of the 20 most common species of trees ≥ 10 cm DBH in one hectare of manicole swamp, Assakata. Species are ranked in order of decreasing importance value. * Liana.

Manicole swamp forest Tree layer	Absolute density	Basal area	Importance value	Relative density	Relative dominance	Relative frequency
Species	[# ind./ha]	[m ² /ha]	[%]	[%]	[%]	[%]
<i>Pentaclethra maculoba</i>	116	3.90	34.82	17.47	10.86	6.49
<i>Symphonia globulifera</i>	65	4.96	30.11	9.79	13.82	6.49
<i>Euterpe oleracea</i>	124	1.37	28.99	18.67	3.82	6.49
<i>Virola surinamensis</i>	7	7.58	26.08	1.05	21.12	3.90
<i>Tabebuia insignis</i> var. <i>monophylla</i>	40	2.84	19.79	6.02	7.92	5.84
<i>Diospyros guianensis</i> ssp. <i>guianensis</i>	36	2.04	17.61	5.42	5.70	6.49
<i>Eperua falcata</i>	49	2.03	16.29	7.38	5.66	3.25
<i>Macrobium</i> cf. <i>angustifolium</i>	32	1.48	14.80	4.82	4.14	5.84
<i>Iryanthera juruensis</i>	16	2.67	14.41	2.41	7.45	4.55
<i>Euterpe precatoria</i>	45	0.86	14.36	6.78	2.39	5.19
<i>Pterocarpus officinalis</i> ssp. <i>officinalis</i>	21	1.56	13.35	3.16	4.35	5.84
<i>Jessenia bataua</i> ssp. <i>oligocarpa</i>	33	0.61	12.52	4.97	1.71	5.84
<i>Tapirira guianensis</i>	23	0.83	11.63	3.46	2.32	5.84
<i>Alchorneopsis floribunda</i>	12	0.87	9.43	1.81	2.42	5.19
<i>Inga marginata</i>	13	0.30	7.99	1.96	0.84	5.19
<i>Mora excelsa</i>	6	0.54	3.70	0.90	1.49	1.30
<i>Micropholis venulosa</i>	4	0.11	3.51	0.60	0.31	2.60
<i>Ficus gomelleira</i>	1	0.88	3.26	0.15	2.46	0.65
<i>Sapindaceae</i> sp. TVA3056 *	4	0.05	2.70	0.60	0.14	1.95
<i>Inga</i> cf. <i>java</i>	3	0.04	2.50	0.45	0.10	1.95
Total of other species (10)	14	0.34	12.18	2.10	0.98	9.10
Total	664	35.88	300.00	100.00	100.00	100.00

Table 10. Density and frequency of the 10 most common species < 10 cm DBH and ≥ 1.5 m in height in 0.1 ha ('shrub layer') of manicole swamp, Assakata. Species are ranked in order of decreasing numbers. * Liana; ● hemi-epiphyte.

Manicole swamp forest Shrub layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Macrosamanea pubiramea</i> var. <i>pubiramea</i>	303	18.90	3.40
<i>Philodendron surinamense</i> ●	216	13.47	3.02
<i>Euterpe oleracea</i>	170	10.61	3.40
<i>Pentaclethra maculoba</i>	92	5.74	3.40
<i>Philodendron scandens</i> ●	57	3.56	2.64
<i>Philodendron linnaei</i> ●	54	3.37	1.89
<i>Desmoncus polyacanthos</i> *	39	2.43	2.26
<i>Evodianthus funifer</i> ssp. <i>funifer</i> ●	39	2.43	1.89
<i>Ischnosiphon obliquus</i>	34	2.12	2.26
<i>Philodendron</i> sp. TVA 3007 ●	33	2.06	1.51
Total of other species (72)	566	35.30	11.70
Total	1603	100.00	100.00

The fleshy herb *Dieffenbachia paludicola* formed a dense ground cover in the manicole swamp (Table 11). Juveniles of hemi-epiphytes and lianas were

also numerous in the herb layer. The seedling density of *Euterpe oleracea* was not very high; this was probably caused by the selective cutting of mature indi-

Table 11. Density and frequency of the 10 most common species < 1.5 m in height in 4×10^{-3} ha ('herb layer') of manicole swamp forest, Assakata. Species are ranked in order of decreasing numbers. * Liana; ● hemi-epiphyte.

Manicole swamp forest Herb layer	Absolute density	Relative density	Relative frequency
Species	[# ind.]	[%]	[%]
<i>Dieffenbachia paludicola</i>	83	15.15	8.62
<i>Sapindaceae</i> sp. TVA 3056 *	59	10.77	0.86
<i>Philodendron</i> sp. TVA 3007 ●	44	8.03	5.17
<i>Spathiphyllum cannaefolium</i>	44	8.03	3.45
<i>Philodendron surinamense</i> ●	32	5.84	3.45
<i>Machaerium myrianthum</i> *	29	5.29	1.72
<i>Macrosamanea pubiramea</i> var. <i>pubiramea</i>	25	4.56	6.03
<i>Philodendron scandens</i> ●	22	4.01	3.45
<i>Pterocarpus officinalis</i> ssp. <i>officinalis</i>	21	3.83	2.59
<i>Monstera adansonii</i> var. <i>klotzschiana</i> ●	20	3.65	0.86
Total of other species (38)	169	30.84	63.78
Total	548	100.00	100.00

viduals for their palm heart (van Andel et al. 1998). Other herb species were *Rapatea paludosa* var. *paludosa* and *Spathiphyllum cannaefolium*. The most common tree seedlings were *Pterocarpus officinalis* and *Macrosamanea pubiramea* var. *pubiramea*.

Discussion

Classification of Mora forest

As previously reported by Davis (1929) and Anderson (1912), the Mora forest along the Barama and Barima Rivers only started to develop fully above the tidal influence. Going upriver, the numbers of *Euterpe oleracea* decreased as did the typical brackish swamp species of *Symphonia globulifera*, *Pterocarpus officinalis*, and *Pachira aquatica*. Fanshawe (1952) did not include Mora forest in his inventories, but did briefly mention that this forest was co-dominated by *Carapa guianensis*, *Clathrotropis brachypetala*, and *Eschweilera sagotiana* above the tidal limits. The Barama plot, however, was not consistent with this description, as *C. guianensis* and *C. brachypetala* were only represented by two individuals per ha and *E. wachenheimii*, not *E. sagotiana*, was the third most important species. The low density of *C. guianensis* (crabwood) might be attributed to a patchy distribution (Davis 1929) or to past logging activities. Before gold mining became their major source of income a few decades ago (Forte 1999), local Amerindians used to float crabwood logs down the Barama to a sawmill

along the Waini. At the beginning of the previous century, almost all crabwood in the riverine forest along the Barama and Barima Rivers had been felled for timber (Anderson 1912).

Pterocarpus officinalis and *Pentaclethra macroloba* ranked as second and third canopy species in the central Guyanan Mora forest studied by Davis and Richards (1934). They ranked second and fourth in the present study. Moreover, various Annonaceae were present in the understorey of both forests. Even though *M. excelsa* accounted for only 24% of the species in central Guyana and several minor tree species (e.g., *Aldina insignis* and *Eschweilera pedicellata*) were not found in the North-West District, the central Guyanan Mora forest seems to correspond better with the Barama Mora forest than Fanshawe's description. The Mora forest in Iwokrama (Johnston and Gillman 1995) also had much less in common with the Barama plot than the central Guyanan forest. There, *M. excelsa* made up only 20% of the species, and *Eperua* spp. and *Myrcia phaeoclada* were subdominant. Fanshawe (1952) described another Mora forest co-dominated by *E. wachenheimii* along the Mazaruni River; the densities of the other common trees in that forest, however, differed again from those in the forest in Kariako. Nevertheless, since more than 56% of the individuals ≥ 10 cm DBH in the Barama plot were *M. excelsa*, there is no doubt that this vegetation type belongs to the *Mora excelsa* con-sociation (Fanshawe 1952). Mora-dominated forest occurs from Venezuelan Guayana to Western Suriname (Huber 1995a; Lindeman 1953; Lindeman and

Moolenaar 1959), but there seems to be a substantial geographical variation in species composition and density.

Classification of manicole swamp

Forests dominated by *Euterpe oleracea* are widely distributed in swamplands in northern South America and attain their greatest concentration in the Amazon Estuary (Henderson and Galeano 1996). The vegetation of the manicole swamp in this study was quite consistent with Fanshawe's description of the 'palm marsh forest on pegasse' (Fanshawe 1952). This climax swamp forest, 30–40% of which was made up of palms, is typical of the delta area of the North-West District and belongs to the *Symphonia-Tabebuia-Euterpe* association. Fanshawe sketched several subdivisions of this vegetation type: his *Pentaclethra macroloba* community corresponded best to our manicole swamp in Assakata as this species had the highest in I.V. in the plot. A manicole swamp with *Virola surinamensis* as the characteristic emergent was also noted by Fanshawe (1952) along creeks in the Courantyne-Canje district. That forest had more aspects in common with the Assakata plot, such as the abundance of *Diospyros guianensis* and *Macrosamanea* and a ground cover of *Dieffenbachia paludicola* and *Rapatea paludosa*.

Not a single individual of *Manicaria saccifera* (troolie) was found in the Assakata plot, while it was very abundant (ca. 120 mature palms per ha) in other *Euterpe* swamps in the North-West District (van Andel et al. 1998). Except for the absence of troolie, however, the species composition of the Assakata plot did not differ much from the other coastal *Euterpe* swamps. Troolie swamp has been classified as the *Manicaria saccifera* faciation, occurring in narrow belts along rivers where alluvial silt mixes with pegasse. (Fanshawe (1952): 96) noted that 'for some obscure reasons, this faciation only occurs in patches along the lower Waini, instead of in a solid belt as it does on other rivers'. Along the middle and lower Barima, the majority of *Euterpe oleracea* was found just behind the mangrove belt to about 100 m inland. In contrast, troolie grew up to 300 m from the river, after which the vegetation changed to a dense, thin-stemmed swamp of *Macrosamanea pubiramea* var. *pubiramea* and *Symphonia globulifera*, probably a form of quackal forest. Deeper inland, the swamps gave way to well-drained mixed forest. This zonation from riverbank to watershed did not quite correspond

with the transition reported for this region by Fanshawe (1952).

Classification of quackal swamp

The quackal swamp showed traits common to several of Fanshawe's forest types, but did not fully coincide with one particular community or assemblage. For example, Fanshawe described a 'manni-dalli swamp' along the Moruca River, which he classified as the *Symphonia globulifera* community within the *Symphonia-Tabebuia-Euterpe* association. That community also contained *Clusia fockeana* and *Pradosia schomburgkiana*, with *Euterpe oleracea* as canopy dominant. It belonged, therefore, to the palm marsh forests. In contrast, *Euterpe* was only present in the understorey in our quackal swamp. Moreover, less than one percent (six individuals) of the tree layer was occupied by palms (*Mauritia flexuosa*). The quackal swamp, therefore, bore more resemblance to a marsh forest, in which palms only account for 5% of the stand, lianas are few, and epiphytes frequent (Fanshawe 1952).

The *Iryanthera-Tabebuia* assemblage, with a few scattered *Mauritia* palms, has been said to cover most of the pegasse forest behind the riverine palm swamps along the lower Barima (Davis 1929; Fanshawe 1954; Ramdass 1990). This assemblage, especially the *Iryanthera macrophylla* facies or 'kirikaua forest', had several features in common with our quackal swamp. They both contained *Diospyros guianensis*, *Humiriastrum obovatum*, *Humiria balsamifera*, *Bactris* sp., *Tapirira guianensis*, and *Marlierea montana*. However, the Myristicaceae species typical of a kirikaua forest were missing from the quackal forest. Instead of *Iryanthera macrophylla* and *I. lanceifolia*, the species *I. juruensis*, *I. sagotiana*, *Virola surinamensis*, and *V. elongata* were found in Moruca. None of them, however, were dominant. The Arawak name 'kirikaua' was not used in the Moruca area, while it is used elsewhere in the country for *I. sagotiana* (Mennega et al. 1988).

Fanshawe (1952) and Davis (1929) also described a 'palm marsh woodland' occurring contiguous to the flooded savannas. It was a small-stemmed, dense forest, with *Mauritia* as sole emergent along with *Tabebuia*, *Ilex martiana*, *Pradosia schomburgkiana*, and *Marlierea montana*, species also common to our quackal swamp. Their forest, however, was consistently dominated by *Clusia fockeana*, a tree that ranked only tenth in the Moruca swamp plot (Ta-

ble 6). A 'kwako community' was also found in a few places on the Essequibo, with a couple of *Mauritia* palms towering over a 5 m high shrub layer of *M. montana*, *Tabebuia*, *Bactris*, and *Symphonia* (Fanshawe 1952). This community seems to be a less-developed stage of the quackal forest in Moruca. Then again, the marsh forest on pegasse has been said to vary from place to place in floristic composition, dominants, and physiognomy (Fanshawe 1954).

The composition of our quackal swamp coincided with the 'flooded shrublands of the coastal plains', with *Mauritia flexuosa*, *Clusia*, and *Pradosia* distinguished by Huber et al. (1995) as small patches on their vegetation map. The swamp woodland containing *Bombax*, *Pterocarpus*, *Croton*, and *Inga* that covers the entire Moruca area on Hubers' map was not, however, found in the present study. The marsh forest along the Surinamese coast, described by Lindeman (1953) and Lindeman and Moolenaar (1959), also had several species in common with our quackal forest (e.g., *M. flexuosa*, *Virola surinamensis*, *Tabebuia insignis*, and *Symphonia globulifera*), but differed substantially in other aspects. The 'permanently flooded swamp and palm forests' of Huber (1995a) along the lower Orinoco delta were not treated in such detail that an adequate comparison could be made.

Savannas

Fanshawe mentioned in one of his studies that the pegasse of the kirikaua forest can dry out to the underlying clay pan during a drought and burn easily. Although the vast savannas between the Essequibo and the Courantyne Rivers probably have an edaphic-biotic origin, there are signs that fire has been partly responsible for their development along the Moruca River (Fanshawe 1952). Besides the fires during the latest El Niño droughts, when rainfall was the lowest in over a century (Hammond and ter Steege 1998), large forest fires are known to have occurred around Moruca in 1898, 1912, 1926, and 1940 (Fanshawe 1954). When R.H. Schomburgk visited the Moruca area, he also noted the occurrence of extensive savanna fires (Schomburgk 1842). Moving from the populated islands towards the (uninhabited) coast, the swamp vegetation in Moruca seems to follow a man-made zonation: aquatic swamp → flooded savanna → palm marsh → marsh forest (quackal) → mangrove forest. This sequence is slightly different than the transition found by Fanshawe (1952) in the delta area of the North-West District.

The savannas of the North-West District do not appear on the vegetation map by Huber et al. (1995). As there are clear indications that they are of recent, man-made origin, one should wonder if they should be called 'savannas' at all. They do not form part of the coastal savanna belt of the Guianas, which stretches from the Berbice River to Amapá (Brazil) and consists mostly of coarse (white) sands (Sarmiento 1983). Vegetation types similar to the Moruca savanna, with extensive colonies of *Mauritia flexuosa* towering over a thick, floating peat layer of Cyperaceae, are also found in coastal Suriname. These open swamps have been thought to result from peat fires, facilitated by lightning, excessive droughts, and man (Lindeman 1953; Lindeman and Moolenaar 1959; Theunissen 1993). As the germination of *M. flexuosa* is enhanced in open grounds (Hiraoka 1999) and adult palms are fire-resistant, burning may ultimately result in pure stands of the species. However, *M. flexuosa* is not tolerant to even periodic brackish conditions (Theunissen 1993), which may explain its absence in the *Euterpe*-dominated swamps. The lowland plains of the Orinoco delta have a similar appearance: large *Mauritia* colonies standing out above a herbaceous layer with flood-resistant grasses and sedges (Huber 1995a). The species in the herb layer there, however, were different from the Moruca savanna. No reference has been made to fire, although the Orinoco savannas have long been inhabited by Arawak and Warao Indians (Huber 1995b) and peat fires are thought to have taken place at least since the arrival of Amerindians in South America (Janssen 1974; Theunissen 1993).

Comparison with other Amazonian floodplain forests

There is a considerable variation in Amazonian forest types subject to inundation (Prance 1979). Not only the length and frequency of the flooding, but also water chemistry and acidity are very important for the floristic differentiation of these forests (Kubitzki 1989; Rosales Godoy et al. 1999). Following the terminology of Prance (1979), a Mora forest can be classified as a seasonal várzea, i.e., a forest flooded by regular annual cycles of white water rivers. The Mora plot in this study contained the typical seasonal várzea species *Gustavia augusta* and *Carapa guianensis*. A manicole swamp, on the other hand, represents a tidal várzea, inundated and drained twice daily, as high tides temporarily block the flow of the

ivers in the estuarine region. Typical species of this forest type, such as *Virola surinamensis*, *Euterpe oleracea*, and *Manicaria saccifera*, were also common elements in the plots in the North-West District. Finally, a quackal forest can be considered as a permanent swamp forest, occurring behind the main riverbanks in depressed areas that rarely fully drain in the dry season (Prance 1979). In the present study, the quackal swamp was flooded by excessive rain or black water from the Moruca River. For this reason, the quackal swamp shows some traits similar to the Amazonian igapó forest, e.g., the abundance of *Virola elongata*. In addition, it shares a few species with extremely nutrient-poor white sand forests, such as *Humiria balsamifera* (Kubitzki 1989) and *Pradosia schomburgkiana* (ter Steege 1998). That *Mauritia flexuosa* more or less replaced *E. oleracea* may be explained by the fact that *M. flexuosa* can withstand a terrain with poorer drainage better than *E. oleracea* (Hiraoka 1999).

Usefulness of one-hectare plots

The question remains whether a one-hectare sample is sufficient to detect the major variations in a particular vegetation type. Looking at the species-area curves for trees ≥ 10 cm DBH in the three hectare plots (Figure 5), we can see that the curves of the three swamp plots quickly level off. This means that one hectare gives a rather complete view of the tree diversity in these forest types. Increasing the sample area would yield only a few more species. This is not the case for all vegetation types since the natural ranges for many taxa in the Guianas are not yet fully known (ter Steege 1998) and other vegetation studies (van Andel 2000) have shown that the curves do not always level off. Therefore, hectare plots may give a fair estimate of the local diversity, but one plot is certainly not enough to classify an entire vegetation community.

Biodiversity

When the Fisher's α values of the three study plots were compared with more or less similar forest types in Guyana, the Barama Mora forest emerged as extremely species-poor (Table 12). In addition, the plots of Johnston and Gillman (1995) and Davis and Richards (1934) in central Guyana were much less dominated by *M. excelsa* than the Barama plot. Mora forests are considered to represent relatively established

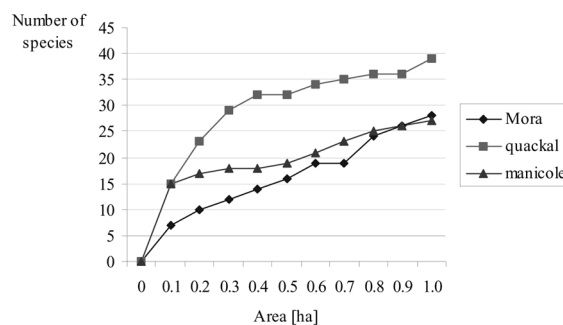


Figure 5. Species area curves of trees ≥ 10 cm DBH in the three hectare plots.

forests (Davis and Richards 1934; Hammond and ter Steege 1998), although little is known about their succession. Data from this research offer no further explanation for the striking differences in diversity and species composition between northwest and central Guyanan Mora forests.

With regard to species richness, all three swamps in the North-West District were clearly much poorer in species than better-drained forests (van Andel 2000). The two swamp plots on pegasse were comparable to the swamp plots studied by Fanshawe (1954). Low diversity is a general pattern in Neotropical swamp forests, since living conditions are quite extreme in these seasonally and permanently flooded habitats (Hiraoka 1999). Inundated forests are exposed to severe oxygen stress in the root zone, especially when the duration of the annual flood lasts up to 10 months. Moreover, one must keep in mind that the water quality of a river can change during the course of a year (Kubitzki 1989). This is particularly important in the delta of the North-West District, where the salt content of the large rivers rises not only twice a day during high tide, but also throughout the year in periods with low rainfall. These severe conditions may possibly explain the exceptionally low diversity of the manicole swamp: it ranked among the least diverse of all swamp forests studied in Guyana so far (Table 12).

According to Prance (1979) and Kubitzki (1989) local species diversity in várzeas is higher than in igapós, because soils frequently inundated by white water are supposedly relatively richer in nutrients than those of forests flooded by black water. The results of the present study, however, do not agree with this theory, since the nutrient-poor quackal plot had a higher tree diversity than the Mora and manicole plots, which were both flooded by relatively nutrient-

Table 12. Comparison of density and diversity of trees ≥ 10 cm DBH in 1 ha study plots in Guyana and Peru. (1) This study; 2) van Andel (2000); 3) Fanshawe (1954); 4) Johnston and Gillman (1995); 5) Davis and Richards (1934); 6) ter Steege et al. (2000); 7) Dallmeijer et al. (1996); 8) Philips et al. (1994).

Location	Forest type	No. of plots	Plot size [ha]	No. of individuals	No. of species	Fisher's alpha
Northwest Guyana ¹	Mora	1	1	314	28	7.4
Northwest Guyana ¹	quackal	1	1	942	39	8.2
Northwest Guyana ¹	manicole	1	1	657	27	5.7
Northwest Guyana ²	mixed	2	1	467–533	83–86	28.2–28.6
Northwest Guyana ³	kirikaua	1	1.5	1034	29	5.6
Northwest Guyana ³	troolie	1	1.5	1057	30	5.8
Iwokrama ⁴	Mora	1	1	357	64	22.7
Moraballi ⁵	Mora	1	1.5	462	60	18.4
Mabura Hill ⁶	palm swamp	6	–	–	–	12.6
Manu, Peru ⁷	swamp	1	1	668	73	20.9
Tambopata, Peru ⁸	swamp	1	1	713	60	15.6

rich water. Fanshawe's kirikaua forest was indeed quite species-poor, but the troolie swamp (inundated by brackish water) had a similar low diversity (Fanshawe 1954). Another reason for the low species diversity in the swamp forests in Guyana may be that they form a heavily fragmented habitat (ter Steege, personal communications). In contrast, swamp and floodplain forests in Western Amazonia generally have a higher diversity than those in the North-West District (Philips et al. 1994; Dallmeijer et al. 1996). This could be because these forests are less fragmented, but it might also be linked with a higher habitat complexity, such as oxbow lakes, floodplain depressions, ridges, and river terraces (Salo et al. 1986). To date, the underlying causes of the diversity and vegetation gradients in the North-West District remain poorly understood. More quantitative data on swamp forest communities, flood periods, and the nutrient contents of soils and rivers are needed to fully comprehend the conditions which lead to the formation of a particular kind of swamp forests.

Appendix

Table A1. Species found in the three hectare plots, North West district, Guyana.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
ADIANTACEAE			
<i>Adiantum latifolium</i> Lam.	x		
AMARYLLIDACEAE			
<i>Hymenocallis tubiflora</i> Salisb.	x		
ANACARDIACEAE			
<i>Spondias mombin</i> L.	x		
<i>Tapirira guianensis</i> Aubl.		x	x

Acknowledgements

This study was carried out as part of the Tropenbos-Guyana Programme and was funded by the European Union. MSc students M. Smeets, A. de Jagher, S. Smedema, S. Groenewegen, K. Bröker, and P. Huyskens assisted the author with the data collection in the hectare plots. We are most grateful to everyone in northwest Guyana who offered their collaboration and hospitality. Special thanks are given to the indigenous 'botanists' of the families Samuels, George, Tony, Abrahams, Gomes, and Daniels. I would also like to thank J. Forte (University of Guyana) and R. Zagt (Tropenbos-Guyana) for their support. Various specialists in herbaria all over the world helped me identify the plant specimens. At Utrecht University, Prof. Dr P.J.M. Maas, Dr H. ter Steege, Dr R. Ek, Drs. M.J. Jansen-Jacobs, Drs. L. Cobb and two anonymous reviewers are acknowledged for critically reviewing this manuscript. Mr. H. Rypkema is thanked for his fine maps.

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
ANNONACEAE			
<i>Anaxagorea dolichocarpa</i> Sprague & Sandw.	x		
<i>Duguetia megalophylla</i> R.E. Fr.	x		
<i>Duguetia pycnastera</i> Sandw.	x		
<i>Duguetia yeshidan</i> Sandw.	x		
<i>Guatteria schomburgkiana</i> Mart.		x	
<i>Guatteria</i> sp. (TVA666)	x		
APOCYNACEAE			
<i>Macoubea guianensis</i> Aubl.		x	
<i>Malouetia flavescens</i> (Willd.) Müll. Arg.	x		
<i>Tabernaemontana disticha</i> A. DC.			x
<i>Tabernaemontana</i> sp. (TVA1593)	x		
<i>Apocynaceae</i> sp. (TVA3045)			x
ARACEAE			
<i>Dieffenbachia paludicola</i> N.E. Br.			x
<i>Monstera adansonii</i> Schott var. <i>klotzschiana</i> (Schott) Madison			x
<i>Philodendron</i> cf. <i>brevispathum</i> Schott			x
<i>Philodendron fragrantissimum</i> (Hook.) Kunth		x	
<i>Philodendron lanceolatum</i> (Vell.) Schott		x	
<i>Philodendron linnaei</i> Kunth		x	x
<i>Philodendron megalophyllum</i> Schott	x		x
<i>Philodendron</i> cf. <i>melinonii</i> Brongn. ex Regel			x
<i>Philodendron pedatum</i> (Hook.) Kunth		x	x
<i>Philodendron quercifolium</i> Engl.		x	
<i>Philodendron rudgeanum</i> Schott	x		x
<i>Philodendron scandens</i> K. Koch & Sello			x
<i>Philodendron surinamense</i> (Schott) Engl.		x	x
<i>Philodendron</i> spp. (unidentified seedlings)		x	x
<i>Philodendron</i> sp. (TVA1362)	x		
<i>Philodendron</i> sp. (TVA3007)			x
<i>Spathiphyllum cannifolium</i> Schott	x		x
<i>Syngonium</i> sp. (TVA1447)	x		
ARECACEAE			
<i>Bactris campestris</i> Poepp. ex Mart.		x	x
<i>Desmoncus polyacanthos</i> Mart.	x		x
<i>Euterpe oleracea</i> Mart.		x	x
<i>Euterpe precatoria</i> Mart.			x
<i>Geonoma baculifera</i> (Poit.) Kunth	x		
<i>Jessenia bataua</i> (Mart.) Burret ssp. <i>oligocarpa</i> (Griseb. & H.Wendl.) Balick			x
<i>Mauritia flexuosa</i> L.		x	
ASPLENIACEAE			
<i>Asplenium serratum</i> L.			x
<i>Asplenium</i> sp. (TVA3058)			x
BIGNONIACEAE			
<i>Anemopaegma paraense</i> Bureau & K. Schum.	x		
<i>Anemopaegma</i> sp. (TVA1394)	x		
<i>Ceratophytum tetragonolobus</i> (Jacq.) Sprague & Sandw.	x		
<i>Mansoa kerere</i> (Aubl.) A.H. Gentry			x
<i>Schlegelia violacea</i> (Aubl.) Griseb.			x

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
Tabebuia insignis (Miq.) Sandw. var. monophylla Sandw.		x	x
Bignoniaceae sp.	x		
BOMBACACEAE			
Pachira aquatica Aubl.		x	
BORAGINACEAE			
Cordia nodosa Lam.		x	
BROMELIACEAE			
Araeococcus sp.			x
BURSERCEAE			
Trattinnickia burserifolia Mart.		x	
CECROPIACEAE			
Cecropia peltata L.	x		
CELASTRACEAE			
Celastraceae sp. (TVA1364)	x		
CHRYSOBALANACEAE			
Licania alba (Bernoulli) Cuatrec.		x	
Licania heteromorpha Benth. var. perplexans Sandw.			x
Licania incana Aubl.		x	
Licania persaudii Fanshawe & Maguire	x		
Parinari rodolphii Huber		x	
CLUSIACEAE			
Calophyllum brasiliense Cambess.		x	
Clusia fockeana Miq.		x	
Clusia grandiflora Splitg.	x	x	x
Clusia palmicida Rich. ex Planch. & Triana		x	x
Clusia sp.		x	
Symphonia globulifera L.f.		x	x
Tovomita schomburgkii Planch. & Triana			x
Tovomita sp. (TVA1020)	x		
COMBRETACEAE			
Combretum cacoucia Exell			x
COMPOSITAE			
Mikania gleasonii B.L. Rob.			x
CONVULVULACEAE			
Maripa scandens Aubl.			x
COSTACEAE			
Costus arabicus L.	x		
CUCURBITACEAE			
Cucurbitaceae sp. (TVA1696)	x		
CYCLANTHACEAE			
Asplundia cf. gleasonii Harling		x	x
Evodianthus funifer (Poit.) Lindm. ssp. funifer		x	x
Thoracocarpus bisectus (Vell.) Harling	x	x	x
CYPERACEAE			
Hypolytrum longifolium (Rich.) Nees ssp. longifolium	x		
Rhynchospora gigantea Link		x	
DENNSTAEDTIACEAE			
Lindsaea lancea (L.) Bedd. var. lancea			x

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
DICHAPETALACEAE			
Tapura sp. (TVA1466)	x		
DILLENACEAE			
Tetracera volubilis L. ssp. volubilis		x	
DIOSCOREACEAE			
Dioscorea amazonum Mart. ex Griseb.			x
DRYOPTERIDACEAE			
Cyclodium meniscioides (Willd.) C. Presl var. meniscioides	x		x
Elaphoglossum sp. (TVA2309)		x	
EBENACEAE			
Diospyros guianensis (Aubl.) Gürke ssp. guianensis		x	x
Diospyros tetrandra Hiern	x		
ELAEOCARPACEAE			
Sloanea grandiflora Sm.	x		
EUPHORBIACEAE			
Alchorneopsis floribunda (Benth.) Müll. Arg.			x
Amanoa guianensis Aubl.			x
Hieronyma alchorneoides Allemão var. stipulosa Franco	x		
Hieronyma oblonga (Tul.) Müll. Arg.	x	x	
Mabea piriri Aubl.	x		
Sandwithia guyanensis Lanj.	x		
Euphorbiaceae sp. (TVA1481)	x		
FLACOURTIACEAE			
Casearia guianensis (Aubl.) Urb.	x		
Homalium guianense (Aubl.) Oken	x		
GESNERIACEAE			
Codonanthe crassifolia (Focke) C.V.Morton			x
GRAMINAE			
Olyra longifolia Kunth	x		
HAEMODORACEAE			
Xiphidium caeruleum Aubl.	x		
HIPPOCRATEACEAE			
Cheiloclinium cognatum (Miers) A.C. Sm.	x		
HUMIRIACEAE			
Humiria balsamifera (Aubl.) A. St.-Hil. var. balsamifera		x	
Humiristrum obovatum (Benth.) Cuatrec.		x	
LAURACEAE			
Aniba cf. guianensis Aubl.			x
Aniba jenmanii Mez		x	x
Aniba cf. terminalis Ducke	x		
Licaria sp. (TVA2251)		x	
Ocotea schomburgkiana (Nees) Mez		x	x
Ocotea splendens (Meisn.) Mez			x
LECYTHIDACEAE			
Eschweilera wachenheimii (Benoist) Sandw.	x		
Gustavia augusta L.	x		
LEGUMINOSAE-CAESALPINIACEAE			
Bauhinia guianensis Aubl. var. guianensis	x		
Brownea latifolia Jacq.	x		

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
<i>Eperua falcata</i> Aubl.			x
<i>Eperua rubiginosa</i> Miq. var. <i>rubiginosa</i>	x		
<i>Macrolobium</i> cf. <i>angustifolium</i> (Benth.) Cowan			x
<i>Mora excelsa</i> Benth.	x		x
<i>Sclerolobium</i> sp. (TVA2282)		x	
LEGUMINOSAE-MIMOSACEAE			
<i>Abarema jupunba</i> var. <i>trapezifolia</i> (Vahl) Barneby & J.W. Grimes			x
<i>Inga capitata</i> Desv.		x	
<i>Inga edulis</i> (Vell.) Mart.	x		
<i>Inga</i> cf. <i>java</i> Pittier			x
<i>Inga marginata</i> Willd.		x	x
<i>Inga splendens</i> Willd.	x		
<i>Inga thibaudiana</i> DC. ssp. <i>thibaudiana</i>		x	
<i>Inga</i> sp. (TVA2283)		x	
<i>Macrosamanea pubiramea</i> (Steud.) Barneby & J.W. Grimes var. <i>pubiramea</i>		x	x
<i>Pentaclethra macroloba</i> (Willd.) Kuntze	x	x	x
<i>Zygia latifolia</i> (L.) Fawc. & Rendle var. <i>communis</i> (Benth.) Barneby & Grimes	x		x
LEGUMINOSAE-FABACEAE			
<i>Alexa imperatricis</i> (R.H. Schomb.) Baill.	x		
<i>Clathrotropis brachypetala</i> (Tul.) Kleinhoonte var. <i>brachypetala</i>	x	x	
<i>Crudia</i> sp. (TVA1468)	x		
LEGUMINOSAE-FABACEAE			
<i>Dioclea scabra</i> (Rich.) R.H. Maxwell	x		
<i>Dioclea</i> sp. (TVA3064)			x
<i>Machaerium leiophyllum</i> var. <i>leiophyllum</i> (DC.) Benth.			x
<i>Machaerium myrianthum</i> Spruce ex Benth.		x	x
<i>Machaerium quinata</i> (Aubl.) Sandw. var. <i>quinata</i>	x		x
<i>Ormosia coccinea</i> (Aubl.) Jackson			x
<i>Ormosia coutinhoi</i> Ducke		x	
<i>Pterocarpus officinalis</i> Jacq. ssp. <i>officinalis</i>	x		x
<i>Swartzia guianensis</i> (Aubl.) Urb.	x		
<i>Vatairea guianensis</i> Aubl.		x	
Fabaceae sp. (TVA1426)	x		
Fabaceae sp. (TVA1444)	x		
Fabaceae sp. (TVA2276)		x	
Fabaceae sp. (TVA2302)		x	
LOGANIACEAE			
<i>Strychnos mitscherlichii</i> M.R. Schomb. var. <i>mitscherlichii</i>	x		
MALPIGHIACEAE			
<i>Hiraea affinis</i> Miq.			x
<i>Mezia</i> cf. <i>includens</i> (Benth.) Cuatrec.	x		
<i>Spachea elegans</i> (G. Mey.) A. Juss.	x		
<i>Tetrapteryx crispa</i> A. Juss.	x		
<i>Malpighiaceae</i> sp. (TVA2277)		x	
MARANTACEAE			
<i>Calathea</i> cf. <i>micans</i> (Mathieu) Körn.	x		
<i>Ischnosiphon foliosus</i> Gleason	x		
<i>Ischnosiphon obliquus</i> (Rudge) Körn.			x
<i>Ischnosiphon</i> sp. (TVA3016)			x

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
MARCGRAVIACEAE			
Marcgravia coriacea Vahl			x
Marcgravia sp. (TVA3061)			x
Norantea guianensis Aubl.		x	
MELASTOMATACEAE			
Bellucia grossularioides (L.) Triana	x		
Clidemia japurensis DC. var. japurensis	x		
Miconia serrulata (DC.) Naudin	x		
Miconia sp. (TVA3053)			x
Tococa aristata Benth.		x	x
MELIACEAE			
Carapa guianensis Aubl.	x		x
Trichilia rubra C. DC.	x		
Trichilia sp. (TVA3046)			x
MENISPERMACEAE			
Orthomene schomburgkii (Miers) Barneby & Krukoff			x
MORACEAE			
Ficus maxima Mill.	x		
MORACEAE			
Ficus paraensis (Miq.) Miq.	x		
Ficus vs. roraimensis C.C. Berg			x
Sorocea hirtella Mildbr. ssp. oligotricha Akkermans & C.C. Berg	x		
MYRISTICACEAE			
Iryanthera juruensis Warb.		x	x
Iryanthera sagotiana (Benth.) Warb.		x	
Virola elongata (Benth.) Warb	x	x	
Virola surinamensis (Rol.) Warb.		x	x
MYRSINACEAE			
Cybianthus aff. surinamensis (Spreng.) G. Agostini		x	
Stylogyne surinamensis (Miq.) Mez	x		
MYRTACEAE			
Calyptanthus sp. (TVA2239)		x	
Marlierea montana (Aubl.) Amshoff		x	
OCHNACEAE			
Ouratea guianensis Aubl.	x		
OLACACEAE			
Dulacia cf. guianensis (Engl.) Kuntze		x	
Heisteria cauliflora Sm.	x		
ORCHIDACEAE			
Catasetum sp. (TVA1927)			x
Epidendron anceps Jacq.			x
PASSIFLORACEAE			
Passiflora garckeii Mast.			x
Passiflora cf. laurifolia L.			x
PIPERACEAE			
Peperomia glabella (Sw.) A. Dietr.			x
Peperomia rotundifolia (L.) Kunth			x
Piper vs. berbicense Miq.			x
Piper nigrispicum C. DC.			x

Table A1. Continued.

Species unidentified at the family level (n = 3) have been omitted.	Barama Mora	Moruca quackal	Assakata manicole
Piper sp. (7M4H7)	x		
POLYGALACEAE			
Moutabea guianensis Aubl.	x		
POLYGONACEAE			
Coccoloba densifrons Mart. ex Meisn.		x	x
POLYPODIACEAE			
Campyloneurum repens (Aubl.) C. Presl	x		
RAPATAACEAE			
Rapatea paludosa Aubl. var. paludosa		x	x
RHIZOPHORACEAE			
Cassipourea guianensis Aubl.		x	x
RUBIACEAE			
Alibertia acuminata (Benth.) Sandw.	x		
Duroia eriopila L.f. var. eriopila		x	x
Geophila repens (L.) L.M. Johnst.	x		
Gonzalagunia dicocca Cham. & Schltd.	x		
Palicourea sp. (TVA3012)			x
Psychotria bahiensis DC. var. cornigera (Benth.) Steyerf.	x		
Randia armata (Sw.) DC.	x		
Rubiaceae sp. (TVA1651)	x		
Rubiaceae sp. (TVA2257)		x	
Schradera polycephala A.DC.		x	
Uncaria guianensis (Aubl.) J.F. Gmel.	x		
SAPINDACEAE			
Allophylus racemosus Sw.		x	
Matayba camptoneura Radlk.		x	
Paullinia calopectera Radlk.	x		
Sapindaceae sp. (TVA3056)			x
SAPOTACEAE			
Chrysophyllum argenteum Jacq. ssp. auratum (Miq.) T.D. Penn.	x		
Micropholis guyanensis (A.DC.) Pierre ssp. guyanensis		x	
Micropholis venulosa (Mart. & Eichl.) Pierre	x		x
Pouteria bilocularis (Winkler) Baehni			x
Pouteria cuspidata (A. DC.) Baehni		x	x
Pouteria guianensis Aubl.	x		
Pouteria sp. (TVA3070)			x
Pradosia schomburgkiana (A. DC.) Cronq. ssp. schomburgkiana		x	
SCHIZAEACEAE			
Schizaea fluminensis Miers ex J.W. Sturm		x	
SMILACACEAE			
Smilax syphilitica Willd.			x
STERCULIACEAE			
Sterculia sp. (unidentified seedling)			x
VERBENACEAE			
Vitex compressa Turcz.	x		
VIOLACEAE			
Paypayrola longifolia Tul.	x	x	
Rinorea cf. flavescens (Aubl.) Kuntze	x		

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