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Floristic composition and diversity of mixed primary and secondary forests in northwest Guyana

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Abstract. The adequate protection and sustainable management of a tropical rain forest requires a good knowledge of its biodiversity. Although considerable parts of Guyana's North-West District have been allocated as logging concessions, little has been published on the forest types present in this region. The present paper reviews the floristic composition, vegetation structure, and diversity of well-drained mixed and secondary forests in northwest Guyana. Trees, shrubs, lianas, herbs and hemi-epiphytes were inventoried in four hectare plots: two in primary forests, one in a 20-year-old secondary forest and one in a 60-year-old secondary forest. The primary forests largely corresponded with the *Eschweilera–Licania* association described by Fanshawe, although there were substantial variations in the floristic composition and densities of dominant species. The late-succession forest contained the highest number species and was not yet dominated by Lecythidaceae and Chrysobalanaceae. There is a need for updating the existing vegetation maps of northwest Guyana, as they were based on limited information. Large-scale forest inventories may provide a fair indication of species dominance and forest composition, but do not give a reliable insight in floristic diversity. Although previous reports predicted a general low diversity for the North-West District, the forests plots of this research were among the most diverse studied in Guyana so far. These results will hopefully influence the planning of protected areas in Guyana.

Key words: conservation, diversity, floristic composition, forest structure, Guyana, secondary forest, species dominance, vegetation types

Introduction

Guyana harbours one of the world's last large undisturbed tracts of tropical rain forest. To address its need for economic development, however, the Guyanese government has allocated large areas of forest as concessions to foreign logging and mining companies (Sizer 1996; Nasir et al. 1997). At the same time, the country has set up a National Protected Area System (NPAS) to ensure the protection and sustainable use of its natural resources. Some of the objectives of this system include the preservation of viable examples of all natural ecosystems in Guyana and the protection of areas of particular biological significance (Persaud 1997). However, for the conservation and wise use of these forests, a good understanding of their biodiversity is needed (Ek and ter Steege 1998). Unfortunately, there are still many gaps in this knowledge that need to be filled in order to develop a sound protected-area system (Nasir et al. 1997; ter Steege 1998).

Forest inventories in Guyana have mainly focused on the central part of the country (Davis and Richards 1934; ter Steege 1993; Johnston and Gillman 1995; Ek 1997; van der Hout 1999; ter Steege et al. 2000a). In contrast, little (published) quantitative information is available on the forest types in the North-West District (Figure 1), even though a substantial part of this region has been designated as logging concessions. Moreover, the area has not been of major interest to plant collectors (ter Steege et al. 2000b). One of the first accounts of the vegetation of northwest Guyana was given by Anderson (1912), who distinguished two major forest categories: "forests of the swamp lands" and "forests on the slightly elevated or hilly lands", the latter being characterized by Lecythidaceae, Chrysobalanaceae, and *Alexa imperatricis*. More than a decade later, Davis (1929) divided the vegetation of the North-West District into swamp forests, Mora forests and mixed forests. These mixed forests, whether primary or secondary, were all found on higher ground and were dominated by Lecythidaceae, Chrysobalanaceae, *Alexa imperatricis*, and *Catostemma commune*. Davis (1929, p. 126) suggested that they were of "rather poor quality".

In 1968–1969, the Forest Industries Development Surveys (FIDS) sampled a total area of 23.6 ha, divided over 14 different locations in the North-West District. Although all field and location data were lost, a summary was recaptured by ter Steege (1998). It revealed a forest type with high numbers of *Eschweilera*, *Mora excelsa*, *Alexa*, *Eperua*, *Licania*, and *Protium*, but lower in species diversity than southern Guyana (ter Steege 1998). In the early 1990s, numerous permanent sample plots were laid out by the logging company Barama Company Ltd (BCL) and the Edinburgh Centre for Tropical Forests (ECTF). These plots also showed a dominance of Lecythidaceae, Chrysobalanaceae, *Alexa imperatricis* and *Protium* sp. (ECTF 1995). Unfortunately, all of the above-mentioned inventories were based on vernacular (Arawak) plant names.

The only detailed vegetation study of the North-West District was published by Fanshawe in the early 1950s (1952, 1954). He provided exhaustive information on the structure, physiognomy, and floristic composition of various forest types and complemented his findings with extensive plant collections in the region (Ek 1990). Fanshawe established a plot in mixed forest along the Moruca River (Figure 1), which he classified as the *Alexa imperatricis* faciation. This forest type belongs to the *Eschweilera–Licania* association, a type of rain forest typical of the Guyana lowlands (Fanshawe 1954). Various authors have suggested that this well-drained mixed forest growing on brown sands represents a late successional stage of a climax forest dominated by few species, since it is generally favoured by Amerindians for their swidden agriculture (Davis 1929; Fanshawe 1954; Hammond and ter Steege 1998). Little, however, has been documented about succession in *Eschweilera–Licania* forests after slash-and-burn agriculture. In contrast, long-term monitoring of species composition in disturbed and undisturbed primary forests has been done for greenheart forests to measure the (selective) logging damage by timber companies (Ek 1997; van der Hout 1999).

The FIDS surveys resulted in a vegetation map, based their own forest plots, aerial photographs and Fanshawes forest classifications (FIDS 1970). The map dis-

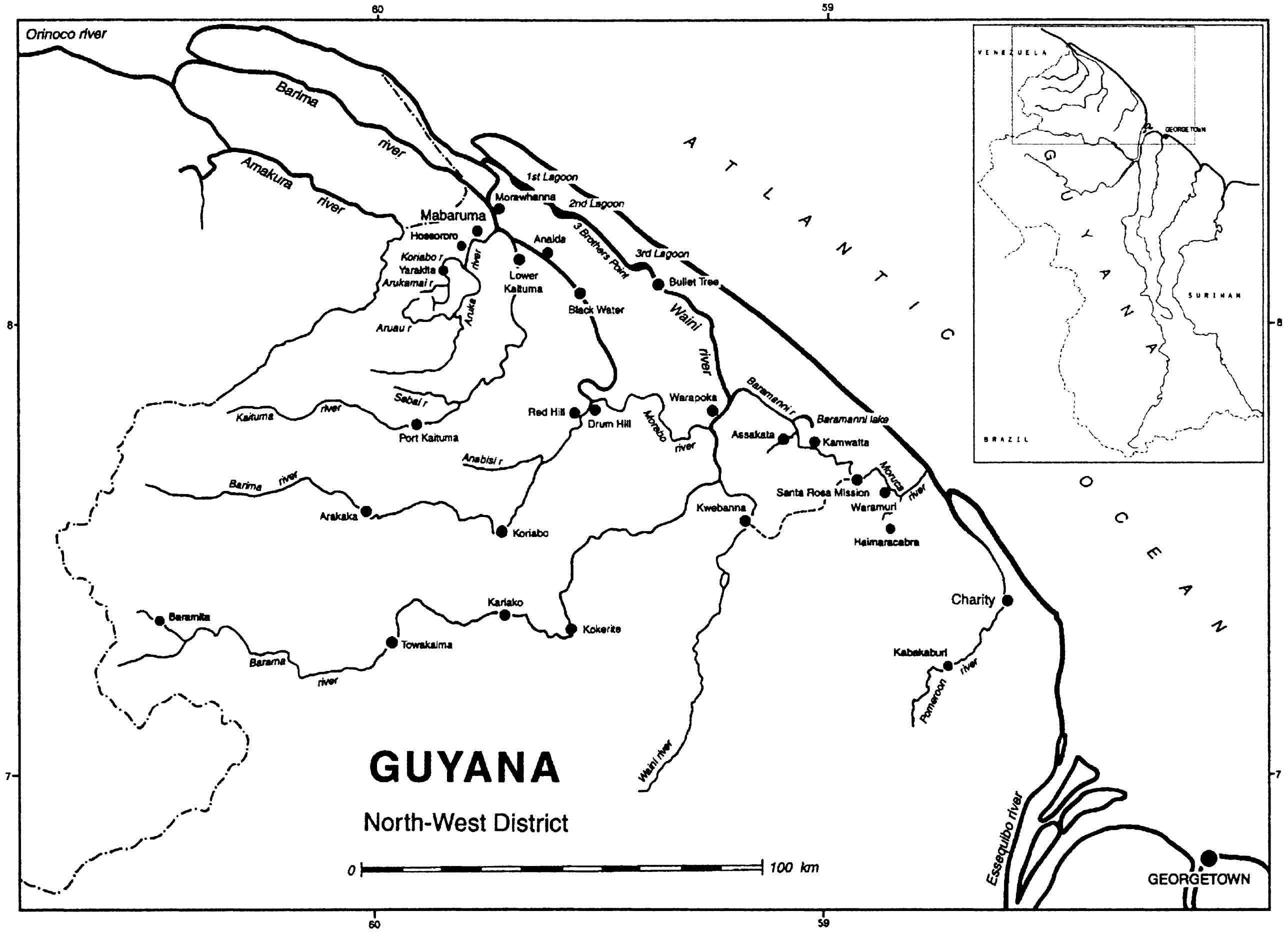

Figure 1. Map of Guyana and the North-West District.

tinguished a mosaic of vegetation types, although no details were given on species composition. The vegetation map drawn by Huber et al. (1995) was also mainly based on Fanshawe's work. The mixed forest type on that map, covering almost half of the North-West District, was thus based on the single plot of 2.1 ha made by Fanshawe in 1954. Ter Steege (1998) concluded from the FIDS results that the forests of the North-West District are quite different from those of central Guyana: because of its lack of legume dominants and the high occurrence of *Alexa*, the district had to be classified as a separate forest region. Such large inventories, however, tend to be crude and underestimate biodiversity (ter Steege et al. 2000a,b). In general, hectare plots give the best estimates of local species diversity and have emerged in the past few years as a popular standard for forest surveys (Martin 1996). Nevertheless, a few plots do not cover the total spatial variation within a forest type. This lack of quantitative data on the distribution and abundance of tree species is one of the main limitations in understanding tropical forest dynamics (Johnston and Gillman 1995).

For the design of appropriate conservation and management plans, quantitative information is required on the diversity, population structure, and distribution patterns of useful (and non-useful) species. Some of the results of an inventory of the major forest types of northwest Guyana will be presented in this paper. This survey formed part of an extensive ethnobotanical study in the region (van Andel 2000). Floristic composition, vegetation structure, and diversity are compared between two well-drained mixed primary forests and two stages of succession forest. Information on the swamp forests of the North-West District will be published elsewhere. The results presented here may contribute to a better understanding of the forests of northwest Guyana, which may in turn be useful in the NPAS programme. It is further hoped that the results of this research will provide baseline data for future sustainable exploitation of both timber and non-timber forest products.

Methodology

Study area

The climate of the North-West District is tropical a mean annual temperature is 26.5 °C, with an average precipitation of 2750 mm per year (Ramdass 1990). There is a distinct dry season from February to April and a less obvious dry period from August to November. The first study site was located at the remote village of Kariako on the Barama River, a few day's journey by boat from the Atlantic coast (Figure 1). 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 about 50 meters. In the dry season, the water level in the river drops significantly, so that the Barama is barely navigable due to fallen trees blocking the waterway. During the rainy season, the forest adjacent to the river is flooded. Behind this floodplain forest, which is dominated by *Mora excelsa*, the vegetation gradually changes into a mixed forest growing on well-drained, sandy-loamy, lateritic soils (Ferralsols or ferralic Arenosols). There is no real dominance of a single species in this mixed forest. The primary forest in the periphery of the village had been replaced by secondary vegetation as a result of shifting cultivation, while the first long stretches of undisturbed forest were found at a distance of only 10 km inland.

The second study site was the Arawak village of Santa Rosa Mission, located along the Moruca River in the coastal swamplands (Figure 1). The Moruca is a black-water river, that flows into the Atlantic Ocean. It is linked to the Waini River by a network of smaller rivers. The Moruca is flanked on both sides by a flooded savanna, in which many small sandy islands arise, remnants of ancient sand dunes (Anderson 1912). Moving inland, these sandy islands gradually merge into a mainland of well-drained, brown loamy sands and red lateritic soils (Ferralsols or ferralic Arenosols), covered with secondary and primary forest. Due to Santa Rosa's growing population and commercial logging activities, the area of undisturbed primary forest is decreasing rapidly. Santa Rosa itself is fringed by a wide zone of disturbed vegetation, varying from shrubland to late secondary forest.

Layout of hectare plots

From July to October 1996, two hectare plots (10 × 1000 m) were laid out at Kariako: one in mixed primary forest (7°25′ N, 59°44′ W) and one in a 20-year-old secondary forest (7°24′ N, 59°43′ W). From July to October 1997, two plots of a similar size were made at Santa Rosa: one in mixed primary forest (7°36′ N, 58°57′ W) and one in a 60-year-old secondary forest (7°38′ N, 58°54′ W). All plots were laid out in areas accessible to local Amerindians to be sure that these forests were subject to NTFP collection. Information about the age and boundaries of the secondary forests was obtained from the former 'owners' of the abandoned farms.

Although neglected in most studies, the undergrowth generally contains between 25 and 46% of the species found in wet tropical forests (Gentry and Dodson 1987), and many useful species as well. Because of this, 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) $\geq$10 cm, and estimating their height. Every 100 m, species with a DBH $<$10 cm and a height $\geq$1.5 m ('shrubs') were sampled in a subplot of 10 ×10. 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 $\geq$10 cm. Care was taken that the hectare plots covered a homogeneous forest area and did not include transitions in vegetation. This was particularly the case in the secondary forests, since the original 'farms' had a circular size rather than an elongated rectangular shape. The mixed forests were frequently traversed by creeks lined with Mora forest. When the vegetation changed along the kilometre line, the shape of the plot was altered (smaller plots were laid out next to each other), in order to still achieve a total surface of one hectare. Natural gaps were included in the plots.

Plant collection

Plant collections, fertile ones when possible, were made of all species occurring in the plots. In addition, flowering and fruiting material was collected outside the plots to match the sterile specimens in the plots. This 'additional collection' method was also successfully implemented in biodiversity studies conducted in the Mabura Hill area (Ek 1997). 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 full list of the identifiable species found in the four hectare plots is given 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 quantitative studies on vegetation structure and NTFPs (Boom 1986; Balée 1994; Comiskey et al. 1994; van Valkenburg 1997; Dallmeijer and Comiskey 1998; Ferreira and Prance 1999). 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.e., I.V. = Rdom + Rden + Rfreq. The last three indices are calculated using the following equations:

Relative dominance (Rdom)

$$= \text{total basal area for a species/total basal area for all species} \times 100\% \text{ (basal area} = \pi \times (\text{DBH}/2)^2)$$

Relative density (Rden)

$$= \text{number of individuals of a species/total number of individuals} \times 100\%$$

Relative frequency (Rfreq)

$$= \text{frequency of a species/sum frequencies of all species} \times 100\%$$

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 defined as a single species accounting for >20% of the total number of individuals. Co-dominance is defined as two or more taxa each representing 10–20% of the trees. To compare the results of the study plots with other forest types, species richness was quantified 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.

Results

General forest composition

A total of 462 plant species (including 10 unidentified specimens) were found in the four hectare plots (see Appendix). A summary of the findings in the four plots is showed in Table 1. The number of tree species and families in 60-year-old

Table 1. Summary of the floristic composition of four hectare plots in mixed and secondary forests in Barama and Moruca. 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	Barama mixed	Moruca mixed	Barama sec. for.	Moruca sec. for.
Floristic composition	Primary	Primary	20 years	60 years
Tree layer $\geq$10 cm DBH				
No. of individuals in 1 ha	496	550	657	528
No. of species in 1 ha	92–93	94–95	78	95
No. of families in 1 ha	39–40	37–38	35	38
Mean diameter trees $\geq$10 cm DBH [cm]	23.6	23.6	18.8	21.0
Canopy height [m]	20–40	30–40	15–20	15–25
α-Diversity	28.2	28.6	21	31.2
Shrub layer $<$10 cm DBH and $\geq$1.5 m				
No. of individuals in 0.1 ha	524	716	590	870
No. of species in 0.1 ha	88	91	139	137
No. of families in 0.1 ha	49	42	57	53
Herb layer $<$1.5 m				
No. of individuals in 4×10^{-3} ha	268	536	431	588
No. of species in 4×10^{-3} ha	50–55	66–68	75–77	65
No. of families in 4×10^{-3} ha	28–33	34–36	40–42	36–41
Total no. of tree species $\geq$10 cm DBH	82–83	86	73	90
Total no. of liana species $\geq$10 cm DBH	10	9	5	5
Total no. of shrub/small tree species $<$10 cm DBH	27	27	56	46
Total no. of liana species $<$10 cm DBH	31	27	38	43
Total no. of species only found in herb layer	17	12	25	20
True herb species	2	0	5	4
Total no. of species found in 1 ha plot	168	161	197	204
Total no. of families found in 1 ha plot	59–62	54	65	61–66

secondary forest equalled that of primary forests. However, even though tree density came within the range of the undisturbed forest, the mean diameter, basal area, and canopy height were lower in the secondary forest. Moreover, there were obvious differences in species composition between the primary and late secondary forests. The 20-year-old forest had the lowest tree diversity, but, due to its open canopy, the lower strata contained more species than the other plots. Because of the dense undergrowth, both secondary forest plots had a higher number of species per hectare than the primary plots. Lianas were particularly common in the succession forests, but most species were <10 cm DBH. True herb species were rare in all plots. It can be deduced from Table 1 that the understorey harboured 41% (Moruca mixed) to 60% (Barama secondary) of the total number of species in the plots. Trees ≥ 10 cm DBH represented 40% (Barama secondary) to 59% (Moruca mixed) of the total number of species. These figures illustrate the importance of nested sampling when studying vegetation structure and species richness in a tropical rain forest.

Lecythidaceae and Chrysobalanaceae clearly co-dominated the canopy of both primary plots (Table 2), representing over 34% of the total number of trees in Barama and almost 49% in Moruca. Chrysobalanaceae were more abundant than Lecythidaceae, and vice versa in Moruca. Papillionaceae ranked third in Barama, but much lower in Moruca. Sapotaceae occupied the third place in Moruca, while

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

Forest type Families	Barama mixed Primary	Moruca mixed Primary	Barama sec. for. 20 years	Moruca sec. for. 60 years
Lecythidaceae	12.7	31.6	2.3	6.3
Leguminosae-Mimos.	5.8	5.1	14.6	23.0
Chrysobalanaceae	21.6	16.9	6.5	1.9
Euphorbiaceae	4.0	2.5	3.3	14.2
Leguminosae-Papil.	11.3	3.3	2.4	5.9
Annonaceae	4.4	1.6	7.2	4.2
Sapotaceae	1.4	10.0	–	1.9
Araliaceae	–	0.2	10.0	1.1
Malpighiaceae	–	–	10.5	0.2
Leguminosae-Caesalp.	3.2	0.9	4.7	1.5
Burseraceae	4.4	1.6	0.9	2.8
Celastraceae	2.8	2.4	0.5	4.2
Melastomataceae	–	–	7.8	1.1
Guttiferae	1.2	3.8	3.2	0.4
Cecropiaceae	0.8	–	6.4	0.9
Unidentified	0.2	–	0.2	–
Total of other families	26.2	20.0	18.7	30.5

only 1.4% belonged to that family in Barama. After 60 years of forest succession, Lecythidaceae and Chrysobalanaceae were still of minor importance compared to Mimosaceae. The high percentage of the latter family can be ascribed to the abundance of *Pentaclethra macroloba* and various *Inga* species, of which *I. alba* was the most common in both secondary plots. The canopy of the 20-year-old forest was dominated by pioneer families like Araliaceae, Malpighiaceae, Melastomataceae and Cecropiaceae. These families had lost most of their importance in the 60-year-old forest and were either absent or rare in the primary forests. The high score for Euphorbiaceae in the 60-year-old forest was largely due to the abundance of *Mabea piriri*. Families like Burseraceae, Celastraceae and Sapotaceae seemed to appear late in the succession stage. Not one plant family dominated all four study plots; however, if the three subfamilies are summed, Leguminosae had a higher overall score than Lecythidaceae and Chrysobalanaceae.

Barama mixed forest

The mixed forest in Barama was characterized by the abundance of *Couepia parillo* Table 3). Other species with a high I.V. were *Eschweilera wachenheimii*, *Licania alba* and *Alexa imperatricis*. Except for a few 40-m-tall emergent trees (mostly *Goupia glabra* or *Inga alba*), the height of the canopy varied between 20 and 30 m. The crown layer was closed except for an occasional gap caused by a fallen tree. Dense clusters of secondary species were found in these openings (e.g., *Senna multijuga* subsp. *multijuga*, *Posoqueria longiflora* and *Olyra longifolia*). The largest diameter (133.5 cm) was recorded for *Goupia glabra*. The few small depressions in the landscape were occupied by some large *Mora excelsa* trees, which, in spite of their low density, attributed to a high basal area. Lianas were common and attained rather large diameters, particularly *Pinzona coriacea* and to a lesser extent *Bauhinia scala-simae* and *Dioclea scabra*.

The shrub and herb layers of this forest were quite open and hardly formed well-marked strata. Although some true shrub species were common (*Tabernaemontana undulata*, *Psychotria astrellantha*), most individuals in the shrub layer were saplings of the canopy species (Table 3). Understorey palms like *Bactris humilis* and *B. oligoclada* were found every now and then. Common hemi-epiphytes included *Evodianthus funifer* subsp. *funifer* and the climbing fern *Cyclodium meniscioides* var. *meniscioides*. Their seedlings were also frequent on the forest floor. Occasional hemi-epiphytes were *Heteropsis flexuosa*, *Thoracocarpus bissectus*, and *Clusia grandiflora*. The long aerial roots of these species often reached the forest floor.

Although tree seedlings were locally abundant (*Eschweilera wachenheimii*, *Quiina guianensis*, *Paypayrola longifolia*), the herb layer was poor in true herbaceous species. This group was represented by only two species: *Costus erythrothyrsus* and the fern *Triplophyllum funestum* var. *funestum*. The lowest stratum further consisted of shrub and liana seedlings.

Table 3. Density, basal area, and importance value of the 15 most common species in the tree layer, and the 10 most common species in the shrub and herb layer in mixed forest, Barama. Species are ranked in order of decreasing importance value. [a]Liana; [b]hemi-epiphyte.

Barama mixed forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Couepia parillo	89	6.00	40.23
Alexa imperatricis	43	3.06	22.03
Eschweilera wachenheimii	45	1.70	17.87
Mora excelsa	8	3.86	14.57
Goupia glabra	6	2.79	10.90
Licania alba	16	1.35	10.57
Protium decandrum	17	0.74	8.90
Neea cf. *constricta*	14	0.57	8.20
Inga alba	7	1.56	8.17
Inga rubiginosa	12	0.76	7.97
Catostemma commune	15	0.80	7.89
Eschweilera pedicellata	14	1.08	7.74
Unonopsis glaucopetala	15	0.38	7.00
Mabea piriri	12	0.31	5.37
Paypayrola longifolia	9	0.09	4.91
Total of other species (78)	174	7.87	117.66
Total	496	32.91	300.00
Shrub layer species (0.1 ha)	Absolute density (# ind./0.1 ha)	Relative density (%)	Relative frequency (%)
Tabernaemontana undulata	45	8.59	4.27
Paypayrola longifolia	41	7.82	3.85
Protium decandrum	37	7.06	2.99
Quiina guianensis	36	6.87	3.42
Alexa imperatricis	32	6.11	3.42
Psychotria astrellantha	26	4.96	3.85
Couepia parillo	20	3.82	3.42
Anaxagorea dolichocarpa	19	3.63	3.42
Paullinia cf. *rufescens*[a]	19	3.63	2.14
Myrcia graciliflora	11	2.10	2.99
Total of other species (78)	238	45.41	66.23
Total	524	100.00	100.00
Herb layer species (4×10^{-3} ha)	Absolute density (# ind./4×10^{-3} ha)	Relative density (%)	Relative frequency (%)
Paypayrola longifolia	28	10.45	5.31
Psychotria apoda	23	8.58	1.77
Quiina guianensis	19	7.09	6.19
Triplophyllum funestum var. *funestum*	18	6.72	3.54
Protium decandrum	13	4.85	3.54
Bauhinia guianensis[a]	12	4.48	3.54
Cyclodium meniscioides var. *meniscioides*[b]	12	4.48	3.54
Psychotria astrellantha	11	4.10	5.31
Philodendron rudgeanum[b]	10	3.73	4.42
Eschweilera wachenheimii	10	3.73	3.54
Total of other species (55)	112	41.81	59.28
Total	268	100.00	100.00

Moruca mixed forest

The primary forest in Moruca showed a strong dominance of Lecythidaceae and Chrysobalanaceae, in particular large numbers of *Eschweilera sagotiana*, *E. wachenheimii*, and *E. decolorans* (Table 4). The canopy of this forest was ca. 30 m high, with a few emergents growing to 45 m, such as *Aspidosperma excelsum*, *Hymenolobium flavum* and *Peltogyne venosa* subsp. *venosa*, which had the largest diameter (159.7 cm). The mean diameter of trees ≥10 cm DBH was the same in the two study sites (23.6 cm). *Couepia parillo*, which was abundant at Barama, was totally absent at Moruca, not only from the plot but also from the surrounding area. In contrast, *E. sagotiana*, dominant in Moruca, was infrequently collected in the mixed forest in Barama and was not found in the hectare plot. The importance of Sapotaceae was noticeable in Moruca, represented by six species of *Pouteria*, with *P. durlandii* being the most common. *Alexa imperatricis* played a less important role in Moruca, while late secondary species like *Goupia glabra*, *Jacaranda copaia* subsp. *copaia*,

Table 4. Density, basal area, and importance value of the 15 most common species in the tree layer, and the 10 most common species in the shrub and herb layer in mixed forest, Moruca. Species are ranked in order of decreasing importance value. [a]Liana; [b]hemi-epiphyte.

Moruca mixed forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Eschweilera sagotiana	62	3.66	25.67
Eschweilera wachenheimii	60	3.28	24.23
Licania alba	49	1.83	16.88
Eschweilera decolorans	28	2.06	14.86
Pouteria durlandii	17	1.55	11.02
Licania heteromorpha var. *perplexans*	24	0.53	9.33
Peltogyne venosa subsp. *venosa*	3	2.66	9.00
Alexa imperatricis	15	0.74	7.92
Goupia glabra	9	1.54	7.61
Pentaclethra macroloba	14	1.00	7.34
Tovomita cf. *schomburgkii*	17	0.25	7.25
Aspidosperma excelsum	6	1.00	5.90
Pouteria cf. *coriacea*	11	0.29	5.90
Licania sp. TVA 2332	13	0.43	5.89
Inga alba	6	0.83	5.40
Total of other species (80)	217	12.91	135.98
Total	550	34.55	300.00
Shrub layer species (0.1 ha)	Absolute density (# ind./0.1 ha)	Relative density (%)	Relative frequency (%)
Quiina guianensis	64	8.94	3.60
Tabernaemontana undulata	63	8.80	4.00
Alexa imperatricis	56	7.82	2.00
Licania alba	32	4.47	4.00

Table 4. Continued.

Moruca mixed forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Trichilia schomburgkii subsp. *schomburgkii*	32	4.47	3.60
Licania heteromorpha var. *perplexans*	31	4.33	3.20
Bactris oligoclada	31	4.33	2.80
Connarus perrottetii var. *rufus*[a]	30	4.19	1.20
Duguetia pauciflora	22	3.07	2.80
Tovomita cf. *schomburgkii*	20	2.79	3.20
Total of other species (81)	335	46.78	69.60
Total	716	100.00	100
Herb layer species (4×10^{-3} ha)	Absolute density (# ind./4×10^{-3} ha)	Relative density (%)	Relative frequency (%)
Eschweilera wachenheimii	129	24.07	4.64
Thoracocarpus bissectus[b]	61	11.38	0.66
Rourea pubescens var. *spadicea*[a]	60	11.19	5.30
Tabernaemontana undulata	24	4.48	3.31
Eschweilera cf. *sagotiana*	20	3.73	2.65
Quiina guianensis	18	3.36	5.30
Paypayrola longiflora	16	2.99	1.99
Trattinnickia cf. *lawrancei* var. *boliviana*	14	2.61	3.31
Licania heteromorpha var. *perplexans*	12	2.24	3.97
Unidentified liana seedling TVA 2394[a]	11	2.05	1.99
Total of other species (58)	171	31.91	66.89
Total	536	100.00	100.00

and *Inga alba* were common in both primary plots. Large lianas were less frequent in the mixed forest in Moruca. *Tetracera volubilis* subsp. *volubilis* was present with five individuals over 10 cm; of the six other large climbing species, only *Dicranostyles guianensis* was represented by more than one individual. Some of the large hemi-epiphytes (*Clusia palmicida* and *C. grandiflora*) had aerial roots with a diameter greater than 10 cm.

The shrub layer in this forest was denser and richer in species than in Barama: 716 individuals belonging to 91 species in 0.1 ha, vs. 524 individuals and 88 species in Barama. The most abundant species in the understorey, the small tree *Quiina guianensis* and the shrub *Tabernaemontana undulata*, accounted for only 17.7% of the individuals. The small palm *Bactris oligoclada* was common. Major hemi-epiphytes in this stratum included *Clusia palmicida* and *C. grandiflora*. *Connarus perrottetii* var. *rufus* was the most important woody climber ($n = 30$) in the shrub layer, followed by *Tetracera volubilis* subsp. *volubilis* with ten individuals.

No true herb species were found in the herb layer, just seedlings of trees, shrubs, hemi-epiphytes and lianas. Juveniles of *Eschweilera wachenheimii* were the most abundant, followed by the hemi-epiphyte *Thoracocarpus bissectus* and the liana *Rourea pubescens* var. *spadicea*. Seedlings of more than 20 liana species were found in the herb layer.

20-year-old secondary forest (Barama)

The young secondary forest plot in Barama had an irregular, open canopy 15–20 m high, with several emergents of *Schefflera morototoni*, *Miconia fragilis*, and *Jacaranda copaia* (Table 5). The tree layer mainly consisted of secondary pioneer species (e.g., *S. morototoni*, *Byrsonima stipulacea*, *Cecropia sciadophylla* and *J. copaia* subsp. *copaia*) and other light-demanding species like *Pentaclethra macroloba*, *Inga alba* and *Bellucia grossularioides*. The largest diameter recorded was 47.5 cm for *Tapirira guianensis*, while the mean diameter was only 18.8 cm. Because of their valuable bark, some of the large *I. alba* trees had been spared when the original primary forest was felled, thus attributing to the relatively high basal area. Some of the dominant species in the Barama primary forest (*Couepia parillo*, *Alexa imperatricis*) were already common in the 20-year-old forest, while other typical species of the mature forest (*Eschweilera wachenheimii*, *Licania alba*) were only represented by a few individuals, three and one respectively. No large palms were found. Only five

Table 5. Density, basal area, and importance value of the 15 most common species in the tree layer, and the 10 most common species in the shrub and herb layer in 20-year-old secondary forest, Barama. Species are ranked in order of decreasing importance value. [a]Liana; [b]hemi-epiphyte.

Barama secondary forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Schefflera morototoni	66	2.96	27.40
Byrsonima stipulacea	69	2.18	24.20
Cecropia sciadophylla	35	1.63	17.27
Pentaclethra macroloba	41	1.14	15.47
Couepia parillo	41	1.16	14.78
Alexa imperatricis	29	1.42	14.56
Inga alba	22	1.37	12.48
Jacaranda copaia subsp. *copaia*	29	1.10	12.30
Bellucia grossularioides	25	0.70	10.19
Miconia fragilis	18	0.44	7.92
Tapirira guianensis	16	0.67	7.92
Hyeronima alchorneoides var. *stipulosa*	15	0.37	7.13
Xylopia surinamensis vel. aff	15	0.36	6.31
Cordia tetrandra	15	0.24	6.14
Vismia guianensis	18	0.25	5.47
Total of other species (63)	203	5.34	110.44
Total	657	21.33	300.00

Table 5. Continued.

Barama secondary forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Shrub layer species (0.1 ha)	Absolute density (# ind./0.1 ha)	Relative density (%)	Relative frequency (%)
Couepia parillo	36	6.10	3.51
Scleria secans	36	6.10	0.70
Tabernaemontana undulata	26	4.41	2.11
Inga umbellifera	23	3.90	1.40
Pentaclethra macroloba	18	3.05	1.75
Neea cf. *floribunda*	15	2.54	2.11
Aciotis sp. cf. TVA 1384	14	2.37	1.40
Bactris humilis	14	2.37	3.16
Bauhinia guianensis[a]	13	2.20	2.11
Dioclea cf. *scabra*[a]	13	2.20	1.75
Total of other species (127)	382	64.73	79.99
Total	590	100	100.00
Herb layer species (4×10^{-3} ha)	Absolute density (# ind./4×10^{-3} ha)	Relative density (%)	Relative frequency (%)
Pourouma guianensis subsp. *guianensis*	64	14.85	3.23
Leandra divaricata	61	14.15	3.23
Bauhinia guianensis[a]	31	7.19	4.03
Triplophyllum funestum var. *funestum*	16	3.71	2.42
Miconia ceramicarpa var. *ceramicarpa*	16	3.71	0.81
Selaginella parkeri	15	3.48	0.81
Psychotria poeppigiana var. *barcellana*	14	3.25	4.03
Philodendron rudgeanum[b]	13	3.02	3.23
Inga melinonis	12	2.78	1.61
Piper nigrispicum	11	2.55	2.42
Total of other species (167)	178	41.29	74.19
Total	431	100.00	100.00

liana species were present in this size class, of which only *Bauhinia guianensis* was represented by more than one individual. Large hemi-epiphytes were absent.

The shrub layer did not contain that many individuals, but was very dense because of the numerous lianas (38 species <10 cm), impenetrable patches of razorgrass (*Scleria secans*), and Melastomataceae shrubs. The most common small tree was *Couepia parillo*, a species that was dominant in the primary forest (Table 3). The highest diversity was scored by the genus *Inga* with eight species, of which *I. umbellifera* was the most abundant. The families Rubiaceae and Melastomataceae were also represented by eight species. Hemi-epiphytes were occasionally found, mainly *Evodianthus funifer* subsp. *funifer* and *Philodendron rudgeanum*.

The herb layer was characterized by liana seedlings, large patches of the herb *Leandra divaricata* and juveniles of trees and shrubs typical of a secondary forest (*Pourouma guianensis* subsp. *guianensis*, *Miconia* spp., and *Inga* spp.). Five true herb species were recorded.

60-year-old secondary forest (Moruca)

The canopy of the late secondary forest plot in Moruca was more closed than that of the younger forest in Barama. The crown layer was 15–25 m high, with several large emergents (*Simarouba amara*, *Pentaclethra macroloba* and *Inga alba*). The diversity, density, and mean diameter of this late secondary forest were almost equal to that of the primary forest, but the floristic composition was different (Table 6). *Mabea piriri* had the greatest number of individuals. Due to its much larger trunks, *P. macroloba* had the highest I.V. score. A maximum diameter of 67.8 cm was recorded for *Goupia glabra*, while the mean diameter was 21.0 cm. Several large palms were present: *Jessenia bataua* subsp. *oligocarpa*, *Maximiliana maripa* and *Astrocaryum aculeatum*; the latter being a clear sign of previous human occupation (Wessels Boer 1965). Except for *Alexa imperatricis*, characteristic species of the mature mixed forest (*Eschweilera* spp., *Licania* spp.) were either absent or present with few individuals. Just five woody climbers over 10 cm DBH were present, of which *Tetracera volubilis* subsp. *volubilis* was the largest.

The shrub layer in the 60-year-old forest was very dense (with 870 individuals in 0.1 ha) and mainly composed of small trees (*Paypayrola longiflora* and *Mabea piriri*) and the shrub *Tabernaemontana undulata*. Lianas were common (43 species), both as saplings in the shrub layer and as seedlings on the forest floor; however, besides *Bauhina* spp. and *Dichapetalum pedunculatum*, most climbing species were represented by few individuals. Six species of the genus *Inga* were noted. Except for *Alexa imperatricis* and *Pentaclethra macroloba*, saplings of trees common in primary forests were not abundant in the shrub layer.

Mabea piriri was again numerous in the herb layer, followed by juveniles of *Tabernaemontana undulata*. Numerous *Inga* seedlings were found, but many were impossible to identify to the species level at this early stage. Lianas and hemi-epiphytes were particularly common. Only four true herbs were found, of which the small fern *Triplophyllum funestum* var. *funestum* was the most frequent. Just a few seedlings of primary tree species were found in the herb layer.

Discussion

Classification of mixed forest

Although no more than 10 km apart, the hectare plot in the Moruca mixed forest and mixed forest plot of Fanshawe (1954) differed in several ways. Fanshawe's mixed

Table 6. Density, basal area, and importance value of the 15 most common species in the tree layer, and the 10 most common species in the shrub and herb layer in 60-year-old secondary forest, Moruca. Species are ranked in order of decreasing importance value. [a]Liana; [b]hemi-epiphyte.

Moruca secondary forest: tree layer species (1 ha)	Absolute density (# ind./ha)	Basal area (m^2/ha)	Importance value (%)
Pentaclethra macroloba	55	3.45	28.07
Mabea piriri	62	1.28	20.01
Goupia glabra	22	1.87	15.69
Inga alba	13	1.85	12.24
Alexa imperatricis	23	1.04	12.05
Lecythis cf. *chartacea*	19	0.84	9.63
Laetia procera	12	0.89	8.89
Inga cf. *acreana*	23	0.41	7.74
Cordia sericicalyx	13	0.65	6.84
Cupania hirsuta	20	0.30	6.72
Jacaranda copaia subsp. *copaia*	9	0.59	6.25
Protium unifoliolatum	7	0.66	5.77
Schefflera morototoni	6	0.66	5.55
Brosimum guianense	10	0.22	5.35
Carapa guianensis	8	0.37	5.15
Total of other species (80)	226	9.06	144.06
Total	528	24.14	300.00
Shrub layer species (0.1 ha)	Absolute density (# ind./0.1 ha)	Relative density (%)	Relative frequency (%)
Paypayrola longiflora	84	9.66	1.45
Mabea piriri	79	9.08	2.32
Tabernaemontana undulata	73	8.39	2.32
Pentaclethra macroloba	55	6.32	2.90
Lecythis corrugata subsp. *corrugata*	30	3.45	0.87
Alexa imperatricis	29	3.33	2.03
Protium unifoliolatum	20	2.30	0.87
Dichapetalum pedunculatum[a]	19	2.18	2.32
Duguetia pauciflora	19	2.18	2.03
Trichilia schomburgkii subsp. *schomburgkii*	18	2.07	0.58
Total of other species (127)	445	51.83	82.90
Total	870	100.00	100.00
Herb layer species (4×10^{-3} ha)	Absolute density (# ind./4×10^{-3} ha)	Relative density (%)	Relative frequency (%)
Mabea piriri	182	30.95	5.13
Tabernaemontana undulata	104	17.69	4.49
Inga spp. (various)	30	5.10	5.77
Paypayrola longiflora	24	4.08	3.21
Philodendron surinamense[b]	24	4.08	2.56
Pentaclethra macroloba	21	3.57	2.56
Rourea surinamensis[a]	17	2.89	3.21
Virola elongata	12	2.04	2.56
Paullinia cf. *rufescens*[b]	10	1.70	1.92
Unidentified seedling TVA2160	10	1.70	0.64
Total of other species (55)	154	26.19	67.94
Total	588	100.00	100.00

forest plot was laid out on a sandy island at the headwaters of the Moruca River, probably near the village of Kamwatta (Figure 1). The Moruca mixed forest plot was established on the brown loamy sands and lateritic soils of the mainland. *Alexa imperatricis* was the second most abundant tree species in Fanshawe's plot (with a relative density of 13%), while it ranked eighth in the Moruca plot (Rden = 2.73%). *Eschweilera wachenheimii* was an important species in the plots of this study (ranking second in Moruca and third in Barama), but was not found by Fanshawe. *Licania heteromorpha* var. *perplexans*, a species noted by Fanshawe (1952) to occur in every known faciation of the *Eschweilera–Licania* association, was a common species in Moruca, but present with only few individuals in the Kamwatta plot. *Licania alba* (syn. *L. venosa*), quite common in both the Moruca and Barama mixed forests, was mentioned by Fanshawe as a characteristic species in this association, but did not occur in his Kamwatta plot. In contrast, *Hebepetalum humiriifolium*, a tree common in Fanshawe's plot, was not observed anywhere in the study area.

The Barama plot, located almost 100 km further inland, differed from the Moruca and Kamwatta plots by the abundance of *Couepia parillo* (number one in the tree layer of the mixed forest and also frequent in the young secondary forest). *Alexa imperatricis* ranked second in Barama mixed forest, following Fanshawe's definition of the faciation named after that species. *Eschweilera sagotiana* and *Licania heteromorpha* var. *perplexans* were both present, but not common, in Barama primary forest.

Besides the geographical variations in floristic composition and densities of dominant species, the two mixed forest plots showed a great overlap with Fanshawe's plot (1954). Therefore, it is likely that both the Barama and the Moruca mixed forests are members of the same *Alexa imperatricis* faciation, and consequently correspond with the *Eschweilera–Licania* association, although 'Lecythidaceae–Chrysobalanaceae association' would be a better term for this vegetation type. No direct comparisons could be made with Fanshawe's plot, as the islands behind Kamwatta had been transformed into coconut plantations.

Chlorocardium rodiei (greenheart) was not found in any of the plots or in their surroundings, although it was noted by Huber et al. (1995) on their vegetation map as growing in the mixed forests of the North-West District. Fanshawe (1952) had cited the northern limit of greenheart around the Pomeroon River, even though it had been found around St Bedes (lower Barama) and the Aruka River by Davis (1929) and Anderson (1912). There is a great need for updating the existing vegetation maps of northwest Guyana, as they were based on limited information.

In general, the plots of this study seem to correspond with the mixed forest as described by Davis (1929), even though many of the scientific names used in his article have been changed and a number of trees were listed by family or local names only. Less overlap was found between the plots of the North-West District and the mixed forest in central Guyana (Davis and Richards 1934; ter Steege 1993; Johnston and Gillman 1995; Ek 1997; ter Steege et al. 2000a). The forest in Barama, in particular, differed substantially in floristic composition and species dominance. The central Guyana mixed forest is dominated by other species of Chrysobalanaceae and Lecythidaceae; *E. wachenheimii* and *Couepia parillo* play a much less prominent role in the canopy. The *Eschweilera–Licania* dominance also seems to change in species composition along the geographical range (ter Steege et al. 2000b). For example, mixed forests dominated by Chrysobalanaceae and Lecythidaceae continue far into Venezuelan Guayana, but *E. decolorans*, *Gustavia poeppigiana*, and *Licania densiflora* take over the leading part there (Huber 1995).

Disturbance and succession

If the mixed forests in Barama and Moruca are regarded as the same forest type, putting aside some regional differences like the abundance of *C. parillo*, then the secondary plots may be considered as two different stages of succession. This being the case, we then see that 60 years since abandonment is not long enough for Lecythidaceae and Chrysobalanaceae to become dominant. The canopy of the late succession forest was occupied by different species and families than the primary forest, while pioneer species were present in much lower numbers than in the early secondary forest. The basal area of the 60-year-old forest (24.14 m^2/ha) was much lower than that found in the Moruca primary plot (34.55 m^2/ha), indicating that after 60 years of succession the forest still has not attained a forest structure similar to that of primary forest. This does not correspond with the conclusions of Aide et al. (1996), who suggested that 60 years was sufficient for abandoned pastures to regain a basal area comparable with that of primary forest. In fact, with regard to floristic composition, it may take more than a century before a secondary forest resembles the surrounding primary forest (Ferreira and Prance 1999).

The Moruca area has a long history of Amerindian occupancy (Schomburgk 1848; Atkinson 1990). The frequent findings of stone axes and potsherds in the primary forest in Barama also point towards the presence of humans in the past. The large individuals of late successional species (*Goupia glabra*, *Inga alba*) further suggest that both areas of mixed forest were subjected to disturbance in the past, although local Amerindians considered the forest as ‘high bush’ or primary forest. Fanshawe discovered charcoal traces at a depth of 30–70 cm in the soil of his Kamwatta plot, which he related to prior slash-and-burn cultivation. He concluded that: “With the evidence of a once numerous Amerindian population and consequent widespread shifting cultivation, it is extremely difficult not to be suspicious of the primeval state of any forest type encountered” (Fanshawe 1954, p. 80). He assumed that the *Eschweilera–Licania* association represented a late stage of succession to the climax rain forest, “more or less indistinguishable from primary forest”, but did not give an example of how this undisturbed forest should look like. No soil samples were taken during the present study, so verification of whether burning had occurred in the past was not possible. Nevertheless, it is to be expected, since charcoal traces (from natural forest fires) have been found in even the little-disturbed forests in central Guyana (Hammond and ter Steege 1998), and there is evidence that the North-West District acted as an important centre for pre-Columbian peoples (Williams 1989).

In comparison to the Moruca plot, the mixed forest in Barama contained fewer *Eschweilera*, but more *Alexa imperatricis*, *Goupia glabra*, and *Mabea piriri*, and more large lianas (29 vs. 17 individuals over 10 cm). The overall dominance of Lecythidaceae and Chrysobalanaceae in Barama was lower than in Moruca. Following the theory of Hart (1990), who proposed that high species dominance might be achieved during early and late successional stages and co-dominance during mid-successional stages, this might indicate that the Barama forest represents a slightly earlier stage of succession than the Moruca forest. Davis (1929) stated that the abundance of Sapotaceae (as was the case in Moruca) almost certainly indicates primary forest. However, the present data offer only a snapshot in forest succession. The real patterns of regeneration and dynamic change within these forests can only be assessed after long-term monitoring of regrowth in permanent sample plots.

Biodiversity

Except for the 20-year-old secondary forest, the study plots appeared to have a relatively high diversity when comparing their Fisher's α values with those of more or less similar forest types in Guyana (Table 7). Plant diversity and forest composition strongly correlate with geographical location, soil type and disturbance (ter Steege 1998). The high species-richness of the forest plots in Moruca and Barama might be explained by the fact that the North-West District has been subjected to extensive and frequent human disturbance (Williams 1989). According to the

Table 7. Comparison of density and diversity (Fisher's α) of trees $\geq$10 cm DBH in forest plots in Guyana and Peru: 1) This study; 2) Fanshawe (1954); 3) Johnston and Gillman (1995); 4) Davis and Richards (1934); 5) R.C. Ek (unpublished data); 6) Comiskey et al. (1994); 7) Philips et al. (1994); 8) Boom (1986).

Location	Forest type	No. of plots	Plot size (ha)	No. of individuals	No. of species	Fisher's α
Northwest Guyana[1]	Mixed	2	1	467–533	83–86	28.2–28.6
Northwest Guyana[1]	20 years old	1	1	650	73	21
Northwest Guyana[1]	60 years old	1	1	524	90	31.2
Northwest Guyana[2]	Mixed	1	2.1	744	52	13.1
Iwokrama[3]	Mixed	1	1	459	71	23.5
Moraballi Creek[4]	Mixed	1	1.5	644	91	28.9
Mabura Hill[5]	Mixed	1	1	459	71	23.5
Kwakwani[6]	Mixed	1	1	493	59	17.5
Kwakwani[6]	Mixed	1	1	504	85	29.3
Tambopata, Peru[7]	Tierra firme	1	1	575	172	83.1
Alto Ivon, Bolivia[8]	Tierra firme	1	1	649	94	30.2

intermediate-disturbance theory, a high dominance of species indicates a low rate of disturbance (Hart 1990; Huston 1994). Short intervals between slash-and-burn cultivation certainly reduce species-richness, but a longer return time between fire events may promote diversity by facilitating a re-establishing process driven by colonisation rather than competition (Hammond and ter Steege 1998). The 60-year-old secondary forest plot had the highest α-diversity of all plots studied in Guyana so far. Since it was surrounded by both older and younger forests, the plot contained elements from early and late secondary forests, as well as from primary forests. Comparisons with similar succession forests could not be made, since no other plots of secondary forest have yet been studied in Guyana.

The central Guyana forests have only recently been disturbed by logging and mining. Because of their low soil fertility, the white sands in this region are less favoured for shifting cultivation. Hammond and ter Steege (1998) suggested that for this reason, the region was never inhabited by a substantial Amerindian population. The low rate of large-scale disturbances may have led to competitive exclusion and to the higher dominance of few, often Caesalpinoid, species (ter Steege 2000). This was illustrated in Table 7 by the lower α-diversity scores for the central Guyana mixed forest plots in Iwokrama and Mabura Hill (Johnston and Gillman 1995; R.C. Ek, unpublished).

In contrast, the mixed forest in Moraballi Creek had an α-diversity comparable to the northwestern forests (Table 7). According to Davis and Richards (1934), there was reason to believe that the indigenous population of that area was once greater than at the time of their research. One of the mixed forest plots in Kwakwani, also an area with a long history of human intervention, was even more species-rich than those in the North-West District, but another plot in the same forest type was much pooorer in species. However, both plots were different in species composition than the northwestern forests and were less dominated by Lecythidaceae and Chrysobalanaceae (Comiskey et al. 1994). It remains unclear, then, why Fanshawe's mixed forest in Kamwatta had such a conspicuous low diversity when compared to the nearby plots on the Moruca mainland. One explanation might be low colonization through inadequate seed dispersal. Studies have shown that the distance from a primary forest is an important factor of forest regeneration (Ferreira and Prance 1999). Fanshawe's plot was laid out on a relatively small island, surrounded by a wide area of marsh forest. Moreover, the islands in the vicinity of Fanshawe's plot were already cultivated at the time of Fanshawe's research (1954) and the first patch of well-drained primary forest was situated several kilometres away.

Ter Steege (1998) suggested a geographical decline in tree diversity from southern Guyana northward, implying that the forests of the North-West District were among the most species-poor of the country. The results of this study, however, contradict that hypothesis, since the Barama and Moruca plots rank among the most diverse in Guyana so far. One reason for this phenomenon might be that although ter Steege left out two coastal swamp forest plots in his analysis of the FIDS inventories, he may have included the extremely species-poor Mora forests, thus reducing the overall diversity in the northwestern region. Another explanation for the suggested low diversity in northwest Guyana might be the FIDS' inclusion of only those trees >30.5 cm DBH. The mean diameter in the Barama mixed plot was 23.6 cm: only 22% of the individuals and 31% of the total number of species had a DBH >30.5 cm. Thus, 78% of the individuals and 69% of the tree diversity at that site were represented by species with a DBH below the diameter threshold of the FIDS inventories.

The large-scale inventories of the Barama Company Ltd and the FIDS also underestimated diversity as they were based on vernacular (Arawak) plant names, which often included several species within one name (ECTF 1995; ter Steege 1998). Although many commonly used vernacular names in forestry come from Arawak, the language itself is hardly spoken anymore (Fanshawe 1949). Enumeration by native names is not a rigidly accurate nor an absolutely satisfactory method of working out the floristic composition of a tropical forest, but it is often the only method available to third-world forestry officers (Davis and Richards 1934). This system can give useful results as long as the indigenous tree spotters are familiar with the particular forest region. However, using Arawak plant names for species identification in remote interior (non-Arawak) areas might lead to unreliable results, especially when sterile individuals of different species within a genus are not easily distinguishable in the field (e.g., *Licania*, *Swartzia*, *Protium* and *Pouteria*). This has become obvious from the sample plots of the BCL, where *Licania* species were listed as either 'kauta' or 'kairiballi', all *Inga* species were summed as 'waikey', and various *Eschweilera* species were called 'kakaralli' (ECTF 1995). Barama Caribs involved in the present research had separate names for 19 different *Inga* species and also made a clear distinction between the various *Licania* and *Eschweilera* species. Unfortunately, Carib names are hardly ever used in forestry in Guyana and Carib informants are less familiar with Arawak and Creole names. Moreover, many species restricted to remote (Carib) areas do not even have an Arawak name. These aspects may also have played a role in the low estimation of plant diversity of the northwest forests. Forest inventories should, therefore, always be combined with plant collection and local indigenous informants should be involved as much as possible.

The forests of the North-West District are nevertheless poor in species when compared to many other well-drained mixed forests in western Amazonia (Philips et al. 1994 (Table 7); for further comparisons, see ter Steege 2000). However, not all tierra firme forests in western Amazonia have such a high species diversity (Boom 1986). With markedly fewer than 100 species $\geq$10 cm DBH per ha, the forests in the Guiana Shield may have the lowest diversity in Neotropical forests. This may be caused by low soil fertility, low rates of disturbance, and a relative isolation (Connel and Lowman 1989; Johnston and Gillman 1995; ter Steege 2000).

Except for a small fringe of mangrove forest, none of the NPAS' existing proposals for protected areas include a significant portion of northwest Guyana, even though the NPAS programme aims to preserve viable examples of all natural ecosystems in

Guyana. In addition, the forests in this region are under serious threat from logging and mining concessions. In the periphery of the larger Amerindian settlements, the need for agricultural land is transforming large areas of primary forest into secondary shrubland. Ter Steege (1998) has already urged that rapid action be taken to preserve a portion of the northwest primary forest, which is possibly unique to South America. The fact that these forests rank among the most species-rich of Guyana, and thus are of particular biological significance, should also influence the planning of protected areas in Guyana.

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Appendix. Species identified in the four hectare plots, North-West District, Guyana. Specimens unidentified at family level ($n = 10$) are omitted. TVA + A64 = authors' initials. Life forms: T = tree, S = shrub, H = herb, HE = hemi-epiphyte.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Acanthaceae						
Mendoncia hoffmannseggiana Nees	1358	L			X	
Anacardiaceae						
Astronium cf. *lecointei* Ducke	955	T	X			X
Tapirira guianensis Aubl.	729	T		X	X	X
Tapirira cf. *obtusa* (Benth.) J.D. Mitch.	1402	T	X			
Annonaceae						
Anaxagorea dolichocarpa Sprague & Sandw.	607	T	X		X	
Annona symphyocarpa Sandw.	918	T	X			
Bocageopsis multiflora (Mart.) R.E. Fr.	2000	T				X
Duguetia calycina Benoist	1883	T		X		
D. megalophylla R.E. Fr.	1021	T			X	
D. pauciflora Rusby	643	T		X		X
D. pycnastera Sandw.	601	T	X			
D. yeshidan Sandw.	723	T	X		X	
Guatteria schomburgkiana Mart.	2268	T		X		
Guatteria sp.	1127	T			X	
Rollinia exsucca (DC. ex Dunal) A. DC.	641	T	X	X	X	X
Unonopsis glaucopetala R.E. Fr.	885	T	X	X	X	X
Xylopia cayennensis Maas	2209	T				X
Xylopia aff. *surinamensis* R.E. Fr.	1122	T			X	
Xylopia sp.	1176	T			X	
Xylopia sp.	1165	T			X	
Apocynaceae						
Ambelania acida Aubl.	1749	S		X		
Aspidosperma excelsum Benth.	1897	T		X		
Aspidosperma marcgravianum Woodson	639	T		X		X
Aspidosperma sp.	1583	T	X			
Forsteronia guyanensis Müll. Arg.	662	L			X	
Forsteronia sp.	2460	L		X		
Himatanthus articulatus (Vahl) Woodson	2169	T		X		X
Odontadenia puncticulosa (Rich.) Pulle	2168	L				X
Odontadenia sp.	1401	L			X	
Odontadenia sp.	2178	L				X
Parahancornia fasciculata (Poir.) Benoist	2370	T		X		
Tabernaemontana heterophylla Vahl	716	S			X	X

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Tabernaemontana aff. *siphilitica* (L.f.) Leeuwenb.	2154	S		X		X
Tabernaemontana undulata Vahl	708	S	X	X	X	X
Araceae						
Heteropsis flexuosa (Kunth) G.S. Bunting	1039	HE	X	X		
Philodendron fragrantissimum (Hook.) Kunth	953	HE	X			
Philodendron rudgeanum Schott	845	HE	X	X	X	
Philodendron scandens K. Koch & Sello	602	HE	X		X	
Philodendron surinamense (Schott) Engl.	2001	HE		X		X
Philodendron spp. (unidentified seedlings)		HE		X		
Araliaceae						
Dendropanax sp.	2414	T		X		
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	603	T			X	X
Aristolochiaceae						
Aristolochia daemoninoxia Mast.	1269	L			X	
Bignoniaceae						
Anemopaegma sp.	1661	L	X			
Arrabidaea sp.	2357	L		X		
Clytostoma binatum (Thunb.) Sandw.	1505	L			X	
Distictella magnoliifolia (H.B.K.) Sandw.	2117	L				X
Jacaranda copaia (Aubl.) D. Don subsp. *copaia*	1582	T		X	X	X
Jacaranda copaia subsp. *spectabilis* (DC.) Gentry	934	T	X	X		
Memora flavida (DC.) Bureau & K. Schum.	2114	L		X		X
Musatia prieurei (DC.) Bureau ex K. Schum.	1460	L	X			
Parabignonia steyermarkii Sandw.	1102	L			X	
Tabebuia insignis (Miq.) Sandw. var. *monophylla* A169	901	T			X	
Bignoniaceae sp.	2099	L				X
Bombacaceae						
Catostemma commune Sandw.	604	T	X	X	X	X
Pachira aquatica Aubl.	2011	T		X		X
Pachira insignis (Sw.) Savigny	2468	T		X		

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama-20-year-old forest	Moruca 60-year-old forest
Boraginaceae						
Cordia nodosa Lam.	635	S	X	X	X	X
Cordia sericicalyx A. DC.	2034	T		X		X
Cordia tetrandra Aubl.	646	T	X	X	X	
Bursereae						
Protium decandrum Marchand	1955	T	X		X	X
P. guianense Marchand	2059	T	X		X	X
P. heptaphyllum March. subsp. *heptaphyllum*	1555	T			X	
Protium sp.	931	T	X			
P. unifoliolatum Engl.	2033	T				X
Tetragastris altissima (Aubl.) Swart	967	T	X		X	
Trattinnickia cf. *lawrancei* var. *boliviana* Swart	2388	T		X		
Burseraceae sp.	1464	T	X			
Cecropiaceae						
Cecropia peltata L.	2707	T			X	X
Cecropia sciadophylla Mart.	1506	T	X		X	X
Pourouma guianensis Aubl. subsp. *guianensis*	589	T	X		X	X
Celastraceae						
Goupia glabra Aubl.	748	T	X	X	X	X
Maytenus cf. *guyanensis* Klotzsch ex Reissek	992	T	X	X		X
Maytenus sp.	958	T	X	X		
Chrysobalanaceae						
Couepia parillo DC.	1663	T	X		X	
Hirtella racemosa L. var *racemosa*	1178	T			X	
Licania alba (Bernoulli) Cuatrec.	1977	T	X	X	X	X
L. cf. *divaricata* Benth.	2398	T		X		
L. heteromorpha Benth. var. *perplexans* Sandw.	1570	T	X	X	X	
L. kunthiana Hook.f.	2040	T				X
L. micrantha Miq.	1918	T		X		
L. persaudii Fanshawe & Maguire	991	T	X			
Licania sp.	2324	T		X		
Licania sp.	2332	T		X		
Parinari rodolphii Huber	647	T		X		X
Combretaceae						
Combretum laxum Jacq.	2081	L				X
Combretum rotundifolium Rich.	1160	L				X
Terminalia cf. *amazonia* (J.F. Gmel.) Exell	1778	T		X		X
Terminalia dichotoma G. Mey.	2218	T				X
Compositae						
Mikania cf. *psilostachya* DC.	1463	L			X	

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Connaraceae						
Connarus perrottetii var. *rufus* Forero	2395	L		X		
Connarus sp.	2350	L		X		
Pseudoconnarus cf. *macrophyllus* Radlk.	977	L	X		X	
Rourea pubescens (DC.) Radlk. var. *spadicea*	1488	L	X	X	X	X
Rourea surinamensis Miq.	1532	L		X	X	X
Convulvulaceae						
Dicranostyles ampla Ducke	2714	L				X
Dicranostyles guianensis Mennega	2444	L		X		
Dicranostyles sp.	2364	L		X		
Dicranostyles sp.	2407	L		X		
Maripa scandens Aubl.	1417	L	X			
Maripa sp.	2009	L				X
Costaceae						
Costus erythrothyrsus Loes.	861	H	X			
Costus scaber Ruiz & Pav.	627	H			X	
Cucurbitaceae						
Cayaponia jenmanii C. Jeffrey	994	L	X			
Helmontia leptantha (Schltdl.) Cogn.	1580	L			X	
Cyclanthaceae						
Evodianthus funifer (Poit.) Lindm. subsp. *funifer*	610	HE	X			X
Thoracocarpus bissectus (Vell.) Harling	608	HE	X	X	X	X
Cyclanthaceae sp.	2471	HE		X		
Cyperaceae						
Scleria secans (L.) Urb.	1087	H			X	X
Dichapetalaceae						
Dichapetalum pedunculatum (DC.) Baill.	1502	L	X	X	X	X
Tapura guianensis Aubl.	1641	T	X	X	X	
Dilleniaceae						
Davilla kunthii A. St. Hil.	989	L	X	X		X
Doliocarpus brevipedicellatus subsp. *brevipedicellatus*	2142	L		X		X
Doliocarpus cf. *dentatus* (Aubl.) Standl.	1403	L	X			
Pinzona coriacea Mart. & Zucc.	1659	L	X			
Pinzona sp.	2509	L		X		
Tetracera volubilis L. subsp. *volubilis*	651	L	X	X	X	X

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Dioscoreaceae						
Dioscorea pilosiuscula Bert. ex Spreng.	1558	L	X			
Dryopteridaceae						
Cyclodium meniscioides var. *meniscioides*	1820	HE	X	X	X	
Polybotrya caudata Kuntze	663	HE	X		X	
Ebenaceae						
Diospyros cf. *ierensis* Britton	756	T		X		
Diospyros tetrandra Hiern	941	T	X	X	X	
Elaeocarpaceae						
Sloanea grandiflora Sm.	638	T	X		X	
S. cf. *guianensis* (Aubl.) Benth.	986	T	X	X		X
S. latifolia (Rich.) K. Schum.	1615	T			X	X
S. obtusifolia (Moric.) K. Schum.	1999	T		X		
S. cf. *parviflora* Planch. ex Benth.	2340	T		X		
S. cf. *schomburgkii* Benth.	1404	T	X	X		
S. aff. *synandra* Spruce ex Benth.	932	T	X		X	
Sloanea sp.	2006	T				X
Sloanea sp.	2195	T				X
Erythroxylaceae						
Erythroxylum macrophyllum Cav.	1170	S	X		X	X
Euphorbiaceae						
Alchornea schomburgkii Klotzsch	983	T	X			
Alchorneopsis floribunda (Benth.) Müll. Arg.	1668	T			X	
Chaetocarpus schomburgkianus (Kuntze) Pax & Hoffm.	990	T	X	X		X
Conceveiba guianensis Aubl.	974	T	X			X
Drypetes fanshawei Sandw.	2475	T		X		
Hyeronima alchorneoides Allemao var. *stipulosa* Franco	1321	T	X		X	X
Hyeronima oblonga (Tul.) Müll. Arg.	2095	T	X	X		X
Mabea piriri Aubl.	731	T	X	X	X	X
Maprounea guianensis Aubl.	2042	T				X
Pausandra hirsuta Lanj.	1655	T	X			
Pausandra sp.	2058	T				X
Pera glabrata (Schott) Baill.	2036	T				X
Sandwithia guyanensis Lanj.	1411	T	X	X	X	X
Sapium jenmanii Hemsl.	938	T	X			
Senefeldera sp.	1621	T	X			
Senefeldera sp.	1369	T			X	
Flacourtiaceae						
Casearia aff. *acuminata* DC.	1241	T			X	
Casearia aff. *arborea* (Rich.) Urb.	2190	T				X

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Casearia javitensis Kunth	1219	T	X	X	X	X
Casearia cf. *ulmifolia* Vahl ex Vent.	1528	T	X			
Caesearia sp.	1522	T	X			
Caesearia sp.	2334	T		X		
Laetia procera (Poepp.) Eichl.	857	T			X	X
Flacourtiaceae sp.	2448	T		X		
Gesneriaceae						
Paradrymonia maculata (Hook. f.) Wiehler	733	HE			X	
Gnetaceae						
Gnetum sp.	1612	L	X			
Graminae						
Olyra longifolia Kunth	987	H	X			X
Guttiferae						
Clusia grandiflora Splitg.	1814	HE	X	X		
Clusia palmicida Rich. ex Planch. & Triana	671	HE	X	X		X
Symphonia globulifera L.f.	755	T		X		X
Tovomita cf. *brevistaminea* Engl.	927	T	X		X	
T. calodictyos Sandw.	2484	T		X		
T. cf. *choisyana* Planch. & Triana	993	T	X			
T. cf. *obscura* Sandw.	3081	T	X		X	X
T. schomburgkii Planch. & Triana	3040	T		X		
Vismia guianensis (Aubl.) Choisy	619	T			X	
Vismia macrophylla Kunth	621	T			X	
Hernandiaceae						
Sparattanthelium guianense Sandw.	2119	L				X
Hippocrateaceae						
Hippocratea volubilis L.	2463	L		X		
Salacia sp.	1498	L			X	
Salacia sp.	1584	L	X			
Tontelea coriacea A.C. Sm.	1372	L	X			
Tontelea cf. *glabra* A.C. Sm.	933	L	X		X	
Humiriaceae						
Humiria balsamifera (Aubl.) A. St. Hil. var. *balsamifera*	2273	T		X		
Sacoglottis aff. *cydonioides* Cuatrec.	2347	T		X		
Sacoglottis guianensis Benth. var. *guianensis*	2393	T		X		
Icacinaceae						
Casimirella ampla (Miers) R.A. Howard	1449	L				X
Discophora guianensis Miers	2061	T				
Leretia cordata Vell.	2073	L		X		X

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Lacistemataceae						
Lacistema aggregatum (Bergius) Rusby	1995	T	X		X	
Lauraceae						
Aniba cf. *guianensis* Aubl.	1785	T		X		X
A. hostmanniana Mez	1123	T			X	
A. cf. *kappleri* Mez	981	T	X			
A. cf. *riparia* (Nees) Mez	968	T			X	X
Aniba sp.	988	T	X			
Nectandra cf. *cuspidata* Nees	1234	T			X	
Nectandra sp. aff.	1421	T			X	
Ocotea cernua (Nees) Mez	969	T			X	
O. schomburgkiana (Nees) Mez	1779	T		X	X	X
O. splendens (Meisn.) Mez	3010	T			X	X
O. tomentella Sandw.	2424	T	X	X		X
Ocotea sp.	2182	T				X
Ocotea sp.	2111	T				X
Ocotea sp.	2710	T			X	
Lecythidaceae		T				
Eschweilera alata cf. A.C. Sm.	1443	T		X		
E. decolorans Sandw.	2429	T		X		
Lecythidaceae						
E. pedicellata (Rich.) S.A.Mori	1613	T	X			
E. sagotiana Miers	1908	T		X	X	
E. wachenheimii (Benoist) Sandw.	750	T	X	X	X	X
Eschweilera sp.	2144	T				X
Lecythis cf. *chartacea* Berg	2035	T		X		X
Lecythis corrugata Poit. subsp. *corrugata*	806	T		X	X	X
Lecythis zabucajo Aubl.	620	T	X	X	X	X
Lecythis sp.	2380	T		X		
Lecythidaceae sp.	1348	T	X			
Leguminosae-Caesalpiniaceae						
Bauhinia guianensis Aubl. var. *guianensis*	584	L	X	X	X	X
Bauhinia scala-simiae Sandw.	1596	L	X			X
Brownea latifolia Jacq.	1669	T				X
Dicorynia cf. *guianensis* Amshoff	2124	T				X
Eperua falcata Aubl.	1007	T		X		
Hymenaea courbaril L. var. *courbaril*	1784	T				X
Mora excelsa Benth.	585	T	X			X
Peltogyne venosa (Vahl) Benth. subsp. *venosa*	2411	T		X		
Sclerolobium micropetalum Ducke	2706	T	X		X	
Senna bacillaris (L.f.) H.S. Irwin & Barneby	1624	T			X	

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Senna multijuga (Rich) Irwin & Barneby var. *multijuga*	691	T	X			X
Tachigali paniculata Aubl.	2392	T		X		
Leguminosae-Mimosaceae						
Abarema jupunba var. *trapezifolia* (Vahl) Barn. & Grim.	649	T		X	X	X
Hydrochorea cf. *corymbosa* (Rich.) Barneby & Grimes	1684	T	X			
Inga cf. *acreana* Harms	2166	T				X
I. cf. *acrocephala* Steud.	2121	T		X		X
I. alba (Sw.) Willd.	598	T	X	X	X	X
I. capitata Desv.	1398	T		X	X	X
I. edulis (Vell.) Mart.	587	T	X		X	
I. graciliflora Benth.	883	T	X	X	X	X
I. huberi Ducke	1418	T	X	X		X
I. lateriflora Miq.	1768	T		X		X
I. leiocalycina Benth.	1261	T			X	
I. marginata Willd.	2284	T		X		
I. melinonis Sagot	1132	T			X	X
I. pezizifera Benth.	1062	T			X	
I. rubiginosa (Rich.) DC.	749	T	X		X	X
I. splendens Willd.	686	T			X	
I. thibaudiana DC. subsp. *thibaudiana*	819	T			X	
I. umbellifera (Vahl) Steud. ex DC.	1459	T			X	
Inga sp.	1352	T	X			
Inga sp.	1535	T			X	
Inga sp.	2463	T		X		
Inga sp.	920	T	X			
Inga spp. (unidentified seedlings)		T	X	X	X	X
Pentaclethra macroloba (Willd.) Kuntze	707	T	X	X	X	X
Zygia cataractae (Kunth) L. Rico	1736	T				X
Leguminosae-Papilionaceae						
Alexa imperatricis (R.H. Schomb.) Baill.	600	T	X	X	X	X
Clathrotropis brachypetala var. *brachypetala*	632	T	X	X	X	X
Clitoria sp.	2008	L				X
Dioclea scabra (Rich.) R.H. Maxwell	668	L	X		X	
Leguminosae-Papilionaceae						
Diplotropis purpurea (Rich.) Amshoff	2369	T		X		X
Dipteryx odorata (Aubl.) Willd.	2511	T				X
Hymenolobium flavum Kleinhoonte	2417	T		X		
Lonchocarpus cf. *heptaphyllus* (Poit.) DC.	834	L	X			

Appendix. Continued.

	Col-lection number TVA	Life form	Bar-ama mixed forest	Mor-uca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Lonchocarpus negrensis Benth.	2153	L		X		X
Lonchocarpus sp.	2113	L				X
Machaerium ferox Ducke	945	L	X		X	
M. kegelii Meisn.	2007	L				X
M. madeirense Pittier	1210	L	X	X	X	X
M. myrianthum Spruce ex Benth.	2186	L		X		X
M. quinata (Aubl.) Sandw. var. *quinata*	2645	L			X	X
Machaerium sp.	2072	L				X
Machaerium sp.	2082	L				X
Machaerium sp.	2172	L				X
Ormosia nobilis Tul.	1164	T			X	
Pterocarpus officinalis Jacq. subsp. *officinalis*	1658	T			X	
Pterocarpus cf. *rohrii Vahl*	960	T	X			
Swartzia arborescens (Aubl.) Pittier	2202	T		X		X
S. grandifolia Bong.	2171	T		X		X
S. guianensis (Aubl.) Urb.	1086	T	X		X	
Swartzia sp.	1654	T	X			
Leguminosae-Papil. sp.	2180	T				X
Loganiaceae						
Strychnos glabra Sagot ex Progel	2078	L				X
S. cf. *melinoniana* Baill.	2442	L		X		
S. mitscherlichii Schomb. var *mitscherlichii*	752	L				X
Strychnos sp.	2479	L		X		
Malpighiaceae						
Banisteriopsis sp.	2132	L				X
Byrsonima aerugo Sagot	1789	T				X
Byrsonima stipulacea A. Juss.	886	T			X	
Heteropterys multiflora Hochr.	2644	L				X
Hiraea affinis Miq.	1456	L	X			X
Hiraea sp.	1534	L			X	
Mezia cf. *includens* (Benth.) Cuatrec.	1016	L	X		X	
Tetrapterys crispa A. Juss.	1390	L	X			
Malpighiaceae sp.	2360	L		X		
Marantaceae						
Ischnosiphon arouma (Aubl.) Körn.	810	S			X	X
Ischnosiphon foliosus Gleason	738	S	X	X	X	X
Maranta sp.	2217	H				X
Monotagma spicatum (Aubl.) J.F. Macbr.	1410	H			X	
Melastomataceae						
Aciotis sp.	1384	S			X	
Bellucia grossularioides (L.) Triana	1029	T			X	

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Clidemia japurensis DC. var. japurensis	702	S			X	
Henriettea cf. *multiflora* Naudin	2592	T				X
Leandra divaricata (Naudin) Cogn.	1423	H			X	X
Loreya mespiloides Miq.	591	T			X	
Miconia ceramicarpa (DC.) Cogn. var. *ceramicarpa*	859	S			X	
M. fragilis Naudin	952	T			X	
M. hypoleuca (Benth.) Triana	753	T			X	
M. nervosa (Sm.) Triana	2076	S				X
M. plukenetii Naudin	1673	T			X	
M. punctata D. Don.	2106	T				X
M. cf. racemosa (Aubl.) DC.	1367	S			X	
M. cf. ruficalyx Gleason	1167	T			X	X
M. cf. traillii Cogn.	1587	S			X	
Miconia sp.	1752	S				X
Melastomataceae sp.	1130	T			X	
Meliaceae						
Carapa guianensis Aubl.	628	T	X	X	X	X
Cedrela odorata L.	1000	T			X	
Guarea cf. *guidonia* (L.) Sleumer	919	T	X			
Guarea sp.	1125	T			X	
Trichilia schomburgkii C. DC. subsp. *schomburgkii*	2054	T	X	X		X
Trichilia sp.	2116	T				X
Menispermaceae						
Abuta barbata Miers	2188	L				X
Anomospermum grandifolium Eichler	2174	L				X
Cissampelos cf. *andromorpha* DC.	1542	L			X	
Curarea candicans (Rich.) Barneby & Krukoff	11554	L		X		
Odontocarya sp.	1545	L	X			
Telitoxicum krukovii Moldenke	2456	L		X		
Telitoxicum sp.	1265	L			X	
Monimiaceae						
Siparuna guianensis Aubl.	653	S	X		X	
Moraceae						
Brosimum guianense (Aubl.) Huber	2038	T				X
Ficus broadwayi Urb.	1129	T			X	
Helicostylis tomentosa (Poepp. & Endl.) Rusby	1598	T			X	
Naucleopsis cf. *guianensis* (Mildbr.) C.C. Berg	2130	T				X
Pseudolmedia laevis (Ruiz & Pav.) J.F. Macbr.	1531	T	X			

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Sorocea hirtella subsp. *oligotricha* Akkermans & C.C. Berg	1363	T	X		X	
Musaceae						
Heliconia acuminata Rich. var. *acuminata*	797	S	X			X
Myristicaceae						
Iryanthera juruensis Warb.	3049	T		X		
Virola calophylla Warb.	2152	T		X		
V. elongata (Benth.) Warb	2062	T			X	X
V. sebifera Aubl.	999	T	X		X	
V. surinamensis (Rol.) Warb.	2293	T		X		
Myristicaceae sp.	956	T	X			
Myrsinaceae						
Cybianthus cf. *surinamensis* (Spreng.) G. Agostini	2258	T		X		
Stylogyne surinamensis (Miq.) Mez	965	T				X
Myrtaceae						
Calycolpus goetheanus (Mart. ex DC.) O. Berg	1751	T				X
Eugenia patrisii Vahl	637	T	X		X	
Marlierea schomburgkiana O. Berg	959	T		X	X	X
Myrcia graciliflora Sagot	898	T	X			
Myrcia cf. *guianensis* (Aubl.) DC. var. *guianensis*	2122	T				X
Nyctaginaceae						
Neea cf. *constricta* Spruce ex J.A. Schmidt	1242	T	X			
Neea cf. *floribunda* Poepp. & Endl.	1608	T			X	
Ochnaceae						
Ouratea guianensis Aubl.	1451	S			X	
Olacaceae						
Minquartia guianensis Aubl.	2489	T		X		
Palmae						
Astrocaryum aculeatum G. Mey.	642	T				X
Astrocaryum gynacanthum Mart.	645	T			X	X
Bactris humilis (Wallace) Burret	727	S	X	X	X	X
Bactris oligoclada Burret	616	S	X	X	X	X
Bactris simplicifrons Mart.	664	S	X			
Euterpe oleracea Mart.	615	T				X
Euterpe precatoria Mart.	1041	T	X			
Geonoma maxima (Poit.) Kunth	658	S	X	X		
Jessenia bataua (Mart.) Burret subsp. *oligocarpa*	732	T		X		X
Maximiliana maripa (Correa) Drude	746	T		X		X

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Passifloraceae						
Passiflora nitida Kunth	875	L				X
Piperaceae						
Piper adenandrum (Miq.) C. DC.	1524	S		X	X	X
P. aequale Vahl	1264	S			X	
P. arboreum Aubl.	1353	S	X			X
P. avellanum (Miq.) C. DC.	1250	S				X
P. hostmannianum (Miq.) C. DC.	1103	S			X	
P. vs. *humistratum* Görts & K.U. Kramer	2430	S		X		
P. nigrispicum C. DC.	3013	S			X	
P. vs. *oblongifolium* (Klotzsch) C. DC.	1667	S			X	
Piper sp.	2098	S				X
Piper sp.	2170	S				X
Polygalaceae						
Moutabea guianensis Aubl.	1516	L	X	X		
Polygonaceae						
Coccoloba gymnorrachis Sandw.	3077	L	X			
C. cf. *lucidula* Benth.	1388	L			X	
C. marginata Benth.	1760	S				X
C. cf. *parimensis* Benth.	1443	L			X	
Pteridophytae						
Triplophyllum funestum (Kunze) Holttum v. *funestum*	1088	H	X		X	X
Quiinaceae						
Quiina guianensis Aubl.	614	T	X	X	X	X
Q. indigofera Sandw.	2037	T	X	X	X	X
Q. obovata Tul.	2185	T				X
Quiinaceae						
Quiina sp.	1360	T			X	
Rubiaceae						
Amaioua corymbosa Kunth	948	T	X			
Amaioua guianensis Aubl.	930	T	X		X	
Faramea aff. *guianensis* Bremek. (poss. sp. nov.)	2094	S		X		X
Faramea quadricostata Bremek.	1638	S	X			
Faramea sp.	1380	S			X	
Palicourea crocea (Sw.) Roem. & Schult.	742	S			X	
Palicourea cf. *guianensis* Aubl.	1538	S			X	
Posoqueria longiflora Aubl.	984	T	X			X
Psychotria apoda Steyerm.	1374	S	X	X	X	
P. astrellantha Wernham	1370	S	X			
P. brachybotrya Müll. Arg.	1431	S			X	
P. poeppigiana Müll. Arg. var. *barcellana*	581	S			X	

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Psychotria sp.	1368	S			X	
Rubiaceae sp.	1173	T			X	
Rubiaceae sp.	1416	S			X	
Rubiaceae sp.	1440	S	X			
Rubiaceae sp.	1476	S	X			
Rubiaceae sp.	1618	S			X	X
Sabicea glabrescens Benth.	667	L			X	
Uncaria guianensis (Aubl.) J.F. Gmel.	846	L	X		X	
Rutaceae						
Zanthoxylum sp.	2333	T		X		X
Sapindaceae						
Cupania hirsuta Radlk.	951	T	X		X	X
Cupania scrobiculata var. *reticulata* (Cambess.) Radlk.	1919	T		X		X
Matayba guianensis Aubl.	2064	T				X
Paullinia cf. *capreolata* (Aubl.) Radlk.	1439	L	X	X	X	X
Paullinia cf. *rufescens* Rich. ex Juss.	928	L	X			X
Paullinia sp.	2131	L				X
Talisia cf. *guianensis* Aubl.	2397	T		X	X	
Talisia hexaphylla Vahl	975	T	X	X		
Sapotaceae						
Chrysophyllum pomiferum (Eyma) T.D. Penn.	2079	T		X		X
Chrysophyllum sanguinolentum (Pierre) Baehni	2319	T		X		
Micropholis venulosa (Mart. & Eichler) Pierre	2607	T	X		X	X
Pouteria bilocularis (Winkl.) Baehni	2343	T		X		
P. caimito (Ruiz & Pav.) Radlk.	1628	T	X			X
P. cf. coriacea (Pierre) Pierre	2323	T		X		
P. cuspidata (A. DC.) Baehni	2255	T		X		
P. durlandii (Standl.) Baehni	2440	T		X		
P. guianensis Aubl.	611	T	X	X	X	X
P. hispida Eyma	1135	T		X		
Pouteria sp.	1525	T			X	
Pouteria sp.	2151	T				X
Pouteria sp.	2359	T		X		
Pouteria venosa (Mart.) Baehni subsp. *amazonica*	2041	T				X
Schizaeaceae						
Lygodium volubile Sw.	1863	L				X
Selaginellaceae						
Selaginella parkeri (Hook. & Grev.) Spring	1270	H			X	

Appendix. Continued.

	Collection number TVA	Life form	Barama mixed forest	Moruca mixed forest	Barama 20-year-old forest	Moruca 60-year-old forest
Simaroubaceae						
Simarouba amara Aubl	856	T		X	X	X
Smilacaceae						
Smilax cumanensis Willd.	2107	L				X
Smilax schomburgkiana Kunth	677	L			X	
Smilax syphilitica Willd.	3071	L	X			
Solanaceae						
Markea coccinea L.C. Rich.	1660	L	X			
Markea sp.	2466	L	X	X		
Sterculiaceae						
Herrania kanukuensis R.E. Schult.	622	T			X	
Sterculia pruriens (Aubl.) K. Schum.	982	T	X		X	
Sterculia sp.	1753	T	X			X
Sterculia sp.	2372	T		X		
Sterculia sp.	2709	T	X		X	
Tiliaceae						
Apeiba petoumo Aubl.	1602	T	X		X	X
Turneraceae						
Turnera aff. *rupestris* Aubl.	1361	H			X	
Verbenaceae						
Petrea bracteata Steud.	1650	L			X	
Vitex compressa Turcz.	1023	T	X		X	X
Violaceae						
Paypayrola longifolia Tul.	759	T	X	X	X	X
Vitaceae						
Cissus descoingsii Lombardi	1657	L			X	
Zingiberaceae						
Curcuma cf. *xanthorrhiza* Roxb.	2089	H				X
Renealmia alpinia (Rottb.) Maas	736	S			X	
Renealmia orinocencis Rusby	1475	H	X		X	

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