Evidence for the Successional Status of Liana Forest (Xingu River Basin, Amazonian Brazil)[1]

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ABSTRACT

Quantitative inventories of two narrowly-rectangular plots of *terra firme* Amazonian rainforest were conducted in the habitats of the Araweté and Asurini Indians, respectively. The samples included all trees with a dbh of ≥10 cm. Relative density, frequency, and dominance are presented for the 20 most important tree species on each plot; species and family importance values are also presented. The Araweté plot had 441 individuals, 142 species, and a total basal area of 22.10 m^2; the Asurini plot had 464 individuals, 137 species, and a basal area of 21.90 m^2. The data suggest that both plots are parcels of a single forest type that conforms to the criteria for Amazonian liana forest. Many of the species on the plots, such as *Orbignya phalerata, Theobroma speciosum, Maximiliana maripa* and *Bertholletia excelsa,* are disturbance indicators in the eastern Amazon. This, and the presence near both sites of Indian black earth (*terra preta do índio*), suggest that much of these forests may have been felled and burned for shifting cultivation at least once in the past.

LIANA FORESTS (OR *MATAS DE CIPÓ*) cover about 100,000 km^2 of Brazilian Amazônia (Pires 1973), occurring most commonly between the Xingu and Tocantins Rivers. The distribution of liana forest within this region is uneven; patches of liana forest tend to be circumscribed by non-lianous *terra firme* forest (Pires & Prance 1985). Few quantitative inventories of trees in Amazonian liana forest have been conducted. Heinsdijk (1957, and cited in Sombroek 1966) conducted forest inventories between the Tapajós and Xingu Rivers, but did not collect voucher specimens and his studies only included trees ≥30 cm diameter at breast height (dbh). Therefore, these inventories are not comparable to more recent ones in Amazônia (*e.g.,* Balée 1986, Boom 1986, Campbell *et al.* 1986), which include all trees ≥10 cm dbh and which involve the rigorous collection of voucher specimens. Liana forest is usually mapped as a primary forest type (*e.g.,* CIPC 1981, IBGE 1985); our findings suggest, however, that liana forest in our region of study is probably late successional forest.

This study presents the first quantitative inventories of liana forest in the Xingu River region: two one-hectare plots in the respective habitats of the Araweté and Asurini Indians of the middle Xingu River basin. These inventories were part of a larger study to determine the utility of the trees in the study sites to the indigenous tribes, like that of Boom's (1986) study of the Chácobo Indians.

Our first objective was to describe species richness, relative density, relative frequency, relative dominance, species importance, and family importance in the two study sites for all individuals ≥10 cm dbh. Our second objective was to show how the adaptations of some of the ecologically most important species in these study sites offer support to the hypothesis that liana forest is not a primary forest type, but rather anthropogenic.

STUDY SITES AND METHODS

The Araweté settlement (4°49'S, 52°31'W) is situated on the left bank of the middle course of the Igarapé Ipixuna, a minor tributary of the right bank of the Xingu. The Asurini settlement (4°45'S, 52°36'W) is located on the right bank of the Xingu itself, about 90 km north of the Araweté settlement.

The annual rainfall of both study sites is approximately 1750 mm (IBGE 1977, Salati 1985). Soils of the region are highly diverse, including oxisols, orthoxic rhodic paleustalf, and the cultural horizon known as *terra preta do índio,* "Indian black earth" (Balée 1989, *cf.* Falesi 1972, Smith 1980).

The Araweté site was surveyed from October–November 1985 and March–April 1986. The Asurini site was surveyed in June 1986. The same methods of inventory and interpretation of data were applied to both sites; these methods are described in detail in Campbell *et al.* (1986) and Campbell (1989). Each study site was a narrowly-rectangular plot of 1000 m by 10 m. All trees and lianas ≥10 cm dbh were measured and permanently

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TABLE 1. *Twenty most important tree species (≥10 cm dbh) in one hectare of liana forest, Araweté, Rio Xingu.*

Species	No. trees	No. S.U.[a]	Basal area[b]	Rel. density[c]	Rel. frequency[d]	Rel. Dominance[e]	Importance Value[f]
Alexa imperatricis	30	11	26,610	6.80	3.09	12.04	21.93
Cenostigma macrophyllum	32	16	17,969	7.26	4.49	8.13	19.88
Euterpe oleracea	22	10	25,425	4.99	2.81	11.50	19.30
Theobroma speciosum	17	12	2920	3.85	3.37	1.32	8.55
Inga 1	14	13	3754	3.17	3.65	1.70	8.52
Orbignya phalerata	8	6	10,854	1.81	1.69	4.91	8.41
Acacia polyphylla	10	10	5397	2.27	2.81	2.44	7.52
Bertholletia excelsa	2	2	13,340	0.45	0.56	6.04	7.05
Sterculia pruriens	12	10	2820	2.72	2.81	1.28	6.81
Trichilia 1	12	9	2340	2.72	2.53	1.06	6.31
Subtotals (10 species)	159	99	111,429	36.05	27.81	50.42	114.28
Maximiliana maripa	9	7	4846	2.04	1.97	2.19	6.20
Protium krukoffii	9	9	2609	2.04	2.53	1.18	5.75
Cassia xinguensis	9	9	2161	2.04	2.53	0.98	5.55
Neea 1	10	9	1456	2.27	2.53	0.66	5.45
Neea 2	10	6	1878	2.27	1.69	0.85	4.80
Eschweilera coriacea	8	6	2397	1.81	1.69	1.08	4.58
Apuleia leiocarpa var. molaris	1	1	7084	0.23	0.28	3.21	3.71
Hirtella tocantina	6	6	1312	1.36	1.69	0.59	3.64
Dialium guianense	6	4	2274	1.36	1.12	1.03	3.51
Astrocaryum munbaca	4	4	3080	0.91	1.12	1.39	3.42
Subtotals (20 species)	231	160	140,526	52.38	44.96	63.58	160.89
Remaining 117 species	210	196	80,492	47.62	55.04	36.42	139.11
Totals	441	356	221,017	100.00	100.00	100.00	300.00

[a] S.U. = sampling unit (25 × 10 m).
[b] In cm^2.
[c] Rel. density = relative density (no. of trees in species/total number of trees).
[d] Rel. frequency = relative frequency (no. of sampling units in which species is represented/total no. of sampling units of representation for all species).
[e] Rel. dominance = relative dominance (basal area for species/total basal area for all species).
[f] Importance value = relative density + relative frequency + relative dominance.

tagged. Individuals that straddled the plot boundary were included if their midpoints fell within the boundary. An attempt was made to collect vouchers from all individuals with few exceptions. These included species that had already been repeatedly collected and for which field determination was indisputable (*e.g., Cenostigma macrophyllum*), individuals which lacked leaves, previously-collected palms, and trees whose crowns were inaccessible because of a dense tangle of lianas. Despite these omissions, voucher specimens were obtained for all but two (1.4%) of the species identified in the Araweté study site and three (2.2%) of the species identified in the Asurini plot.

Relative importance value, and its component parts of percent relative density, percent relative frequency, and percent relative dominance, were calculated according to the formulae of Cottam and Curtis (1956) and Curtis and Cottam (1962). The sampling unit for calculation of relative frequency was a 25 m × 10 m subplot, of which there were 40 on each study site. Family importance value was calculated according to the formula of Mori *et al.* (1983).

RESULTS

Among trees ≥10 cm dbh, the Araweté plot had 441 individuals, 142 species, at least 89 genera, and 36 families; the Asurini plot had 464 individuals, 137 species, at least 86 genera, and 38 families (Appendix 1). Despite a high density of lianas on both plots, only three liana genera, *Cydista, Davilla,* and *Acacia,* were ≥10 cm dbh on the Asurini plot and only one liana genus, *Cydista,* was ≥10 cm dbh on the Araweté plot. These values are comparable to those for other eastern Amazonian forests (Campbell *et al.* 1986). The total number of species in the two hectares was 195, of which 43 (22.1%) were shared. Of the total 27 species that comprised the 20 most important species in both plots, sever. were shared. Species–area curves for the two plots (not shown) were still steeply climbing after one hectare, indicating that one hectare is not a sufficient size to sample the species of these forests. As is typical of Neotropical forests, a small number of species in each plot had disproportionately high importance values (Tables 1 and 2).

TABLE 2. *Twenty most important tree species (≥10 cm dbh) in one hectare of liana forest, Asurini, Rio Xingu.*

Species	No. trees	No. S.U.	Basal area	Rel. density	Rel. frequency	Rel. Dominance	Importance Value
Cenostigma macrophyllum	94	35	73,595	20.26	9.92	33.60	63.77
Orbignya phalerata	20	10	26,035	4.31	2.83	11.89	19.03
Alexa imperatricis	17	13	19,748	3.66	3.68	9.02	16.36
Trichilia lecointei	25	14	6805	5.39	3.97	3.11	12.46
Neea oppositifolia	19	13	6290	4.09	3.68	2.87	10.65
Matisia 1	5	5	17,218	1.08	1.42	7.86	10.36
Unonopsis guatterioides	18	14	2046	3.88	3.97	0.93	8.78
Theobroma speciosum	16	14	2815	3.45	3.97	1.29	8.70
Cassia xinguensis	7	7	1726	1.51	1.98	0.79	4.28
Lecythis 1	5	5	3117	1.08	1.42	1.42	3.92
Subtotals (10 species)	226	130	159,395	48.71	36.84	72.78	158.31
Galipea jasminifolia	7	7	847	1.51	1.98	0.39	3.88
Sterculia speciosa	5	5	2797	1.08	1.42	1.28	3.77
Bauhinia acreana	7	6	1003	1.51	1.70	0.46	3.67
Dialium guianense	6	4	2019	1.29	1.13	0.92	3.35
Simaba cedron	6	6	750	1.29	1.70	0.34	3.34
Lindackeria latifolia	5	5	1401	1.08	1.42	0.64	3.13
Eschweilera coriacea	5	5	1205	1.08	1.42	0.55	3.04
Tachigali myrmecophila	5	5	962	1.08	1.42	0.44	2.93
Casearia javitensis	5	4	1409	1.08	1.13	0.64	2.85
Guarea trichilioides	5	4	880	1.08	1.13	0.40	2.61
Subtotals (20 species)	282	181	172,668	60.79	51.29	78.84	190.88
Remaining 117 species	182	172	46,360	39.21	48.71	21.16	109.12
Totals	464	353	219,028	100.00	100.00	100.00	300.00

Although we did not carry out a quantitative inventory of plants <10 cm dbh, both plots are rich in liana and non-woody vine species (Appendix 2). Both plots, moreover, meet the criteria for liana forest as presented by Pires and Prance (1985). This is supported by the relatively low total basal areas for the Araweté and Asurini hectares, which were 22.10 m^2 and 21.90 m^2, respectively. These basal areas are well within the predicted range of liana forest plots of one hectare (18–24 m^2). By contrast, one hectare of non-lianous *terra firme* dense Amazonian forest may have a basal area of more than 40 m^2 (Pires & Prance, 1985). For example, at O Deserto, also in the Rio Xingu, approximately 350 km north of the Asurini site, Campbell *et al.* (1986) found basal areas of 27.6, 28.3 and 32.1 m^2 ha^{-1} among trees ≥10 cm dbh in non-lianous *terra firme* forest. The low basal areas of the Araweté and Asurini plots may reflect past human disturbance of primary forest, as well as high (although as yet unmeasured) density of lianas <10 cm dbh (see below and Boom 1986).

Trees considered to be typical of liana forest (Pires & Prance 1985) are present on one or both plots. These are *Acacia polyphylla, Apuleia excelsa, Astronium gracile, Bagassa guianensis, Bauhinia acreana, Bertholletia excelsa, Castilla ulei, Sapium marmieri,* and *Tetragastris altissima.*

The babassu palm (*Orbignya phalerata*) has been described as the most "frequent" palm in open forest, of which liana forest is a type (Pires & Prance 1985). *O. phalerata* is among the 20 most important species on both plots (Tables 1 and 2). Palms may be particularly well adapted to liana forest because their architecture and periodic shedding of leaves help to exclude lianas (Emmons & Gentry 1983, Putz 1980).

The Caesalpiniaceae and Mimosaceae are the first and second most important families on both plots (Tables 3 and 4). In the Asurini forest, the Caesalpiniaceae (I.V. = 42.41) is significantly more important than any other family.

DISCUSSION

Although they are separated by 90 km, the Araweté and Asurini plots share many species in common. Using Sorenson's index (Greig-Smith 1983), there is a 36 percent coefficient of similarity among all tree species ≥10 cm dbh on the Araweté and Asurini plots. By contrast, at O Deserto, Campbell *et al.* (1986) found much more heterogeneity: only 10 percent, 16 percent and 21 percent similarities among all trees ≥10 cm dbh in three *adjacent* hectares. For the 20 most important species of the Araweté and Asurini plots, the coefficient of similarity is 44 percent. Yet, comparing the 20 most important species of the

TABLE 3. *Ten most important families of trees (≥ 10 cm dbh) in liana forest, Araweté, Rio Xingu.*

Family	No. species	No. trees	Basal area	F. rel. diversity[a]	F. rel. density[b]	F. rel. dominance[c]	F.I.V.[d]
Caesalpiniaceae	11	61	39,124	7.75	13.83	17.70	39.28
Mimosaceae	18	56	26,119	12.68	12.70	11.82	37.19
Arecaceae	5	47	47,737	3.52	10.66	21.60	35.78
Fabaceae	3	33	27,469	2.11	7.48	12.43	22.02
Lecythidaceae	7	15	17,274	4.93	3.40	7.82	16.15
Nyctaginaceae	6	31	5685	4.23	7.03	2.57	13.83
Burseraceae	7	24	7052	4.93	5.44	3.19	13.56
Sterculiaceae	3	32	8797	2.11	7.26	3.98	13.35
Sapotaceae	10	12	6291	7.04	2.72	2.85	12.61
Lauraceae	9	15	5698	6.34	3.40	2.58	12.32

[a] Family relative diversity = the number of species in a family present in the sample/the total number of species in the sample.
[b] Family relative density = the number individuals in a family/total number of trees in the sample.
[c] Family relative density = total basal area for all individuals in a family/total basal area of all individuals.
[d] F.I.V. = family importance value (the sum of family relative diversity, density and dominance).

Araweté and O Deserto plots, at least seven are shared (43% coefficient of similarity), and between the Asurini and O Deserto plots, at least four are shared (21% coefficient of similarity). These similarities suggest that the Araweté and Asurini plots are, in fact, parcels of a single lianous forest community (*cf.* Schulz 1960), and that the Araweté, Asurini, and O Deserto sites are parts of a more wide-spread forest type, which includes both lianous and non-lianous forest, and is characterized by a few shared, ecologically-important species.

Several researchers have hypothesized that liana forests may be partly anthropogenic, *i.e.*, disclimax forests, similar to some savannas and grasslands elsewhere in the tropics (Dodson *et al.* 1985, Flenley 1979, Smith 1980, Sombroek 1966, Whitmore 1975). Many of the most important tree species on both plots are disturbance indicators, "long-lived biological nomads" (van Steenis 1958), adapted to a late-successional disturbance regime of small light gaps (Denslow 1984, Whitmore 1984). They are nomads among other forest species until major disturbance, often fire in the service of man, liberates space for them. These species tend to persist many years once a gap has been filled.

The majority of the 20 most important species on the Araweté and Asurini plots are disturbance indicators (Tables 1 and 2). These include the two most important species on the Asurini plot, *Cenostigma macrophyllum* and *Orbignya phalerata,* which are also among the six most important species on the Araweté plot. Both of these species typify dry forest (Pires & Prance 1985). Although relatively low rainfall characterizes the region of these Xingu inventories (Campbell *et al.* 1986), liana forest itself is not ineluctably associated with low rainfall. Liana forests do not, in fact, catch fire without first being cut down (Pires 1973). *Cenostigma macrophyllum* and *Orbignya phalerata* may be long-lived nomads in liana forest. Certainly this is so with *O. phalerata,* which can readily survive and grow in burned clearings because of its cryptogeal germination and which has an estimated lifespan of 184 years (Anderson 1983, May *et al.* 1985).

Another nomad species which occurs on both plots is *Bertholletia elcelsa,* with an estimated lifespan of hundreds

TABLE 4. *Ten most important families of trees (≥ 10 cm dbh) in liana forest, Asurini, Rio Xingu.*

Family	No. species	No. trees	Basal area	F. rel. diversity	F. rel. density	F. rel. dominance	F.I.V.
Caesalpiniaceae	12	133	10,916	8.76	28.66	4.98	42.41
Mimosaceae	19	33	6463	13.87	7.11	2.95	23.93
Arecaceae	3	24	27,104	2.19	5.17	12.37	19.74
Meliaceae	7	37	8046	5.11	7.97	3.67	16.76
Bombacaceae	4	11	18,497	2.92	2.37	8.45	13.74
Moraceae	10	15	5616	7.30	3.23	2.56	13.10
Lecythidaceae	7	18	7191	5.11	3.88	3.28	12.27
Fabaceae	3	19	10,004	2.19	4.09	4.57	10.85
Nyctaginaceae	3	24	7159	2.19	5.17	3.27	10.63
Sapindaceae	7	10	3055	5.11	2.16	1.39	8.66

of years (J. M. Pires, pers. comm.). This species readily grows where intentionally planted (Posey 1985) and occurs spontaneously in previously-burned forest (Balée 1989, S. Mori, pers. comm.). Various species of *Inga* are well-known successional species (Huber 1909, Schulz 1960); and, 12 and 15 species of *Inga* occur on the Araweté and Asurini plots, respectively. The congeneric of cacao, *Theobroma speciosum,* which ranks among the ten most important species on both plots, appears to be successional in old fallow elsewhere in Amazônia, and is even cultivated in dooryard gardens by several lower Amazonian Indian peoples (Balée 1989). The palm, *Maximiliana maripa,* which is the eleventh most important species on the Araweté plot, is known to be a disturbance indicator elsewhere in Amazônia (Pesce 1985, Schulz 1960). *Neea, Simaba, Lindackeria* and *Hirtella* are genera which commonly occur as successional species and are found among the top 20 most important species on one or both plots. Many other well-known successional taxa, such as *Cecropia, Cedrela, Ceiba, Jacaranda,* and *Zanthoxylum* are represented in the inventories.

Shifting cultivation is increasingly seen as being widespread in pre-Columbian Amazônia. For example, Fanshawe (1954) pointed out that shifting cultivation was once so widespread in what is now Guyana that it was hazardous to consider *any* forest there as being primary. In particular, the *Alexa* faciation of the generalized *Eschweilera/Licania* association of the region (named for its dominant species, *Alexa imperatricis*) is seen to represent a "late stage in the succession." Significantly, *A. imperatricis* is the most important species on the Araweté plot and the third most important on the Asurini plot. Other species of Fanshawe's *Alexa* faciation which occur on one or both of the plots are *Casearia javitensis, C. combayensis* and *Trichilia guianensis.*

Although the Araweté and Asurini Indians consider liana forest to be primary forest ("ka'ã-hete" in Araweté; "ka'a-ete" in Asurini), we conclude that the Araweté and Asurini liana forest plots are probably recovering from past disturbance, very likely fire. Moreover, there is compelling evidence to suggest the cultural origin of these fires. One frequently encounters artifacts of prehistoric ceramic-making peoples at both present settlement sites. The Indians regard potsherds and polished stone axeheads (which indicate swidden cultivation) found at these sites to be of divine origin. At both sites one encounters *terra preta do índio,* black earth indicating long periods of prior human occupation (Smith 1980, Balée 1989). Given this long-term human occupation and the nearness of the inventory plots to the respective settlements, it is likely that most of the forest has been felled and burned at least once for shifting cultivation. As such, the liana forests, and their associated species compositions, are likely to be late-successional residue of prior cultures, and should no longer be *a priori* mapped as climax vegetation.

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APPENDIX 1 Species (≥10 cm dbh) in two one-hectare plots of *terra firme* liana forest, Araweté and Asurini, Rio Xingu.

Family & species	Araweté				Asurini			
	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]
Anacardiaceae								
Astronium gracile Engl.	1775	1	1	510				
A. lecointei Ducke					2449	1	1	311
Spondias mombin L.					2569	1	1	113
Tapirira guianensis Aubl.	1669	1	1	829				
Thyrsodium paraense Aubl.					2364	2	2	441
Annonaceae								
Guatteria chrysopetala (Steud.) Miq.	1752	1	1	123				
G. rigida R. E. Fries	1742	2	2	805				
Unonopsis guatterioides (A. DC.) R. E. Fries					2324	18	14	2046
Xylopia nitida Dun.	1693	2	2	294	2366	1	1	87
Apocynaceae								
Aspidosperma auriculatum Markgr.					2491	1	1	113
A. desmanthum Benth.					2313	1	1	201
A. ulei Markgr.	1651	1	1	383				
Himatanthus sucuuba (Spruce) Woodson					2578	1	1	531
Tabernaemontana angulata Mart.	1759	1	1	79				
Araliaceae								
Didymopanax morototoni (Aubl.) Decne. & Planch.	1709	2	2	344				
Arecaceae								
Astrocaryum munbaca Mart.	1672	4	4	3188				
Astrocaryum 1	1773	2	2	3080				
Euterpe oleracea Mart.	1833	22	10	25,425	2568	1	1	95
Maximiliana maripa Mart.	1637	9	7	4846				
Oenocarpus distichus Mart.					2500	3	2	884
Orbignya phalerata Mart.	1776a	8	6	10,854	none	20	10	26,035
Bignoniaceae								
Cydista 1					2452	1	1	79
Jacaranda copaia (Aubl.) D. Don					2565	4	4	2501
Tabebuia serratifolia (Vahl) Nichols.					2347	1	1	201
Bombacaceae								
Bombax paraense Ducke					2407	3	3	729
Bombax 1					2533	1	1	95
Ceiba pentandra (L.) Gaertn.					2446	2	2	455
Matisia 1					2428	5	5	17,218
Boraginaceae								
Cordia bicolor A. DC.	1776	3	3	481				
C. lomatoloba Johnston	1686	1	1	394				
C. nodosa Lam.	1827	1	1	79				
C. sagotii Johnston	1674	1	1	193	2431	2	2	228
C. scabrifolia DC.					2567	1	1	154
Cordia 1	1799	2	2	960				
Burseraceae								
Crepidospermum rhoifolium (Benth.) Tr. & PL.	1774	1	1	356				
Protium apiculatum Swart	1723	1	1	129				
P. crenatum Sandw.	1688	2	2	698				
P. heptaphyllum (Aubl.) March.	1650	1	1	79				
P. krukoffii Swart	1645	9	9	2609	2572	1	1	104
P. robustum (Swart) Porter					2435	1	1	113
Protium 1					2506	2	2	1515
Protium indet.	none	1	1	434				
Tetragastris altissima (Aubl.) Swart	1769	5	3	1459				
Trattinnickia 1	1779	1	1	829				

APPENDIX 1 Continued.

Family & species	Araweté Voucher no.[a]	Araweté No. trees	Araweté No. S.U.[b]	Araweté Basal area[c]	Asurini Voucher no.[a]	Asurini No. trees	Asurini No. S.U.[b]	Asurini Basal area[c]
Trattinnickia 1					2369	1	1	210
Burseraceae indet.	none	1	1	459				
Caesalpiniaceae								
Apuleia molaris Spruce ex Benth.	1811	1	1	7084				
Bauhinia acreana Harms	1778	1	1	298	2498	7	6	1003
B. guianensis Aubl.	1808	1	1	317				
B. macrostachya Ducke					2416	3	3	277
Cassia fastuosa Willd.	1748	1	1	2921				
C. xinguensis Ducke	1673	9	9	2161	2520	7	7	1726
Cenostigma macrophyllum Tul.	1668	32	16	17,969	2335	94	35	73,595
Crudia oblonga Benth.	1869	3	1	3615				
C. tomentosa (Aubl.) Macbr.					2382	3	1	226
Dialium guianense (Aubl.) Sandw.	1676	6	4	2274	2325	6	4	2019
Swartzia arborescens (Aubl.) Pittier	1648	3	2	528	2339	2	2	192
S. auriculata Poepp. & Endl.					2434	1	1	95
S. flaemingii Cowan					2587	4	4	624
S. laurifolia Benth.	1763	2	2	1519				
Swartzia 1					2492	1	1	214
Swartzia 2					2497	1	1	79
Swartzia indet.	none	1	1	353				
Zollernia paraensis Hub.	1791	1	1	85	2350	4	4	866
Capparidaceae								
Capparis coccolobifolia Mart.	1828	2	1	192				
Capparis 1					2534	2	1	182
Caricaceae								
Jacaratia spinosa (Aubl.) A. DC.	1691	2	2	416				
Cecropiaceae								
Cecropia obtusa Trécul	1830	1	1	283				
Cecropia palmata Willd.					2373	2	2	1335
Chrysobalanaceae								
Hirtella tocantina Ducke	1656	6	6	1312				
Licania apetala (E. Meyr.) Fritsch	1861	1	1	143	2499	1	1	95
L. heteromorpha Benth.	1804	1	1	1029				
Licania 1	1806	1	1	380				
Clusiaceae								
Rheedia gardneriana Miers ex Planch. & Trécul	1647	4	3	493	2319	1	1	363
Dilleniaceae								
Davilla 1					2463	1	1	95
Ebenaceae								
Diospyros aranthifolia Mart.					2360	1	1	79
Elaeocarpaceae								
Sloanea garckeana K. Schum.					2342	1	1	113
S. grandiflora J. E. Smith	1643	3	3	382				
S. obtusa (Spltz.) K. Schum.	1636	1	1	227				
Euphorbiaceae								
Conceveiba guianensis Aubl.					2570	3	2	518
Pera 1					2408	1	1	95
Sapium ciliatum Hemsley	1757	1	1	380				
S. lanceolatum (Markg.) Huber					2528	2	2	173
S. marmieri Huber					2355	1	1	855
Sapium indet.					none	3	3	409
Fabaceae								
Alexa imperatricis (Schom.) Baill.	1634	30	11	26,610	2391	17	13	19,748

APPENDIX 1 Continued.

Family & species	Araweté				Asurini			
	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]
Machaerium quinata (Aubl.) Sandw.					2541	1	1	133
Platymiscium ulei Harms	1844	1	1	95	2436	1	1	123
Pterocarpus amazonicus Huber	1835	1	1	660				
Fabaceae indet.	none	1	1	104				
Flacourtiaceae								
Casearia arborea (Rich.) Urb.					2490	1	1	189
C. combayensis Tul.					2489	1	1	113
C. javitensis HBK.	1722a	1	1	117	2460	5	4	1409
C. mariquitensis HBK.	1649	3	2	1150				
C. pitumba Sleumer	1819	1	1	113				
Eichlerodendron 1	1705	3	3	1077				
Lindackeria latifolia Benth.	1652	4	4	1052	2337	5	5	1401
L. paraensis Kulm.	none	2	2	321				
Lindackeria 1	1867	1	1	227				
Flacourtiaceae 1					2717	1	1	104
Lauraceae								
Aiouea piauhyensis (Meisn.) Mez.	1865	1	1	707				
Aniba burchellii Kosterm.					2588	1	1	79
Licaria brasilensis (Nees) Kosterm.	1787	4	4	911				
Mezilaurus itauba (Meisn.) Taubert ex. Mez.	1750	4	3	682	none	1	1	113
Nectandra 1					2315	1	1	79
Nectandra cuspidata Nees					2573	2	2	523
Ocotea caudata (Nees) Mez.	1662	1	1	527	2383	1	1	79
O. opifera Mart.	1780	1	1	594				
Ocotea 1	1728	1	1	207				
Ocotea 2	1803	1	1	1126				
Ocotea 3	1812	1	1	829				
Ocotea 4	1848	1	1	115				
Lecythidaceae								
Bertholletia excelsa Humb. & Bonpl.	1770	2	2	13,340	2579	1	1	434
Couratari guianensis Aubl.	1855	1	1	907				
Eschweilera blanchetiana Miers					2439	2	2	1075
E. coriacea Mart. ex Berg (A. P. Candolle) Mori	1701	8	6	2397	2329	5	5	1205
E. ovata (Cambess) Miers					2380	1	1	363
Eschweilera 1					2493	3	3	699
Gustavia augusta L.	1841	1	1	156				
G. hexapetala (Aubl.) Smith	1654	1	1	79	2344	1	1	298
Lecythis lurida (Miers) Mori	1852	1	1	289				
L. pisonis Cambess.	1802	1	1	106				
Lecythis 1					2406	5	5	3117
Melastomataceae								
Mouriri cauliflora D.C.	1640	1	1	97				
Meliaceae								
Cedrela fissilis Vell.					2574	1	1	189
Guarea carinata Ducke					2576	1	1	104
G. guidonia (L.) Sleumer	1717	3	3	730	none	1	1	79
G. trichilioides L.					2564	5	4	880
Guarea 1	1642	1	1	115				
Trichilia guianensis Kl. ex C.D.C.	1714	1	1	219				
T. lecointei Ducke	1698	2	2	272	2323	25	14	6805
T. montealegrensis Sandw. & A. Lima	1687	1	1	95				
T. quadrijuga Kunth in HBK.	1671	1	1	149	2330	3	3	645
Trichilia 1	1700	12	9	2340				
Meliaceae 1					2530	1	1	104
Mimosaceae								
Acacia multipinnata Ducke					2531	2	2	191

APPENDIX 1 Continued.

Family & species	Araweté				Asurini			
	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]
Acacia polyphylla DC.	1696	10	10	5397	2359	4	3	1147
Acacia 1					2525	1	1	95
Inga alba (Sandw.) Willd.	1744	1	1	430	2510	2	2	340
I. auristellae Harms	1730	4	4	1084	2584	1	1	133
I. capitata Desv.	1725	2	2	486	2352	4	4	543
I. crassiflora Ducke	1818	1	1	232				
I. edulis Mart.	1751	4	4	1481				
I. macrophylla H. & Benth.					2429	1	1	113
I. marginata Willd.					2378	1	1	95
I. nobilis Willd.	1782	1	1	333	2527	2	2	355
I. rubiginosa (Rich.) DC.	1665	1	1	82	2427	1	1	201
I. subsericantha Ducke	1736	1	1	109	2553	1	1	154
I. thibaudiana DC.	1756	4	4	960	2545	2	2	246
Inga 1	1864	14	13	3754				
Inga 1					2372	1	1	240
Inga 2					2488	1	1	177
Inga 3	1767	1	1	131				
Inga 3					2522	1	1	829
Inga 4					2526	1	1	214
Inga 5	1733	3	3	626				
Inga 5					2544	1	1	201
Inga 6					2509	1	1	227
Parkia pendula Benth.	1850	1	1	1134				
Pithecellobium amplum Spruce ex Benth.	1639	2	1	3655				
P. jupunba (Willd.) Urb.	1851	1	1	4594				
P. latifolium (L.) Benth.	1664	3	2	1446				
Tachigali myrmecophila Ducke	1795	2	2	185	2481	5	5	962
Moraceae								
Bagassa guianensis Aubl.	1771	1	1	330	2370	1	1	154
Brosimum acutifolium Huber					2432	2	2	2249
B. rubescens Taub.					2311	2	2	990
Castilla ulei Warb.	1762	3	3	1222				
Chlorophora tinctoria (L.) Guad.	1697	1	1	1625				
Clarisia ilicifolia (Spreng.) Lanj. & Rossb.	1826	1	1	95	2426	3	3	306
Clarisia 1	1683	1	1	131				
Helicostylis pedunculata R. Ben.	1738	1	1	201				
Maquira guianensis Aubl.					2451	1	1	154
Naucleopsis glabra Spruce ex Baill.					2457	2	1	322
Perebea guianensis Aubl.					2468	1	1	573
P. mennegai C. C. Berg					2448	1	1	95
P. mollis (P.U.E.) Huber	1813	1	1	397	2312	1	1	572
Pseudolmedia murure Standl.					2508	1	1	201
Moraceae indet.	none	1	1	320				
Myristicaceae								
Iryanthera paraensis Huber	1684	2	2	267				
Virola melinonii A.C. Smith	1741	1	1	97				
Myrtaceae								
Calyptranthes cuspidata Mart.	1776	2	2	216				
Eugenia feijoii Engl.	1809	1	1	158				
E. macrocalyx (Rusby) McVaugh					2386	1	1	254
E. omissa McVaugh					2314	1	1	79
Eugenia 1					2317	1	1	95
Myricaria floribunda (West ex Willd.) Berg					2516	1	1	452
M. tomentosa (Aubl.) DC.					2318	1	1	227
Psidium acutangulum DC.	1836	1	1	117				
Nyctaginaceae								
Neea divaricata Poepp. & Endl.	1703	1	1	939				

APPENDIX 1 Continued.

Family & species	Araweté				Asurini			
	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]	Voucher no.[a]	No. trees	No. S.U.[b]	Basal area[c]
N. floribunda Poepp. & Endl.	1699	4	3	454	2503	2	1	173
N. glomeruliflora Neimer	none	1	1	93				
N. oppositifolia R. & P.	2126	4	4	748	2320	19	13	6290
Neea 1	2121	10	9	1456				
Neea 1					2411	3	3	696
Neea 2	2111	10	6	1878				
Olacaceae								
Heisteria ovata Benth.					2560	1	1	314
Polygonaceae								
Coccoloba latifolia Lam.					2519	1	1	87
Quiinaceae								
Lacunaria jenmani (Oliv.) Ducke	1814	1	1	201	2340	1	1	314
Rubiaceae								
Simira japurensis Schum.					2413	1	1	154
Rutaceae								
Galipea jasminifolia (St. Hil.) Engl.	1718	2	1	190	2514	7	7	847
Sohnreyia excelsa Krause	1715	1	1	491				
Zanthoxylum pentandra Aubl.					2521	1	1	201
Z. rhoifolium Lam.					2586	1	1	133
Zanthoxylum 1	1727	2	2	246				
Sapindaceae								
Cupania cinera Peopp. & Endl.					2501	1	1	254
C. hirsuta Radlk.					2389	1	1	143
C. scrobiculata Rich.	1678	2	2	276				
Matayba arborescens Radlk.					2310	1	1	1107
Pseudima frutescens (Aubl.) Radlk.					2477	3	3	549
Talisia 1					2309	2	2	240
Toulicia guianensis Aubl.					2511	1	1	79
Toulicia 1					2308	1	1	683
Sapotaceae								
Micropholis acutangulum Ducke					2582	1	1	314
Richardella macrophylla Pierre					2327	2	2	714
Sapotaceae 1	1689	3	3	297				
Sapotaceae 2	1860	1	1	181				
Sapotaceae 3	1732	1	1	21				
Sapotaceae 4	1815	1	1	227				
Sapotaceae 5	1834	1	1	227				
Sapotaceae 6	1840	1	1	82				
Sapotaceae 7	1846	1	1	412				
Sapotaceae 8	1849	1	1	98				
Sapotaceae 9	1860	1	1	4416				
Sapotaceae 10	1876	1	1	330				
Simaroubaceae								
Simaba cedron Planch.					2345	6	6	750
Simarouba amara Aubl.					2566	1	1	346
S. guianensis Aubl.					2557	1	1	79
Sterculiaceae								
Sterculia pruriens (Aubl.) K. Schum.	1740	12	10	2820				
S. speciosa K. Schum.					2316	5	5	2796
S. striata St. Hil. & Naud.	1805	3	3	843				
Theobroma speciosum Willd. ex Spreng.	1670	17	12	2920	2338	16	14	2815
Tiliaceae								
Apeiba 1	1820	2	2	2214				
Luehea duckeana Burret					2456	2	2	2704
Mollia lepidota Spruce ex Benth.					2577	3	1	2475

APPENDIX 1 Continued.

Family & species	Araweté Voucher no.[a]	Araweté No. trees	Araweté No. S.U.[b]	Araweté Basal area[c]	Asurini Voucher no.[a]	Asurini No. trees	Asurini No. S.U.[b]	Asurini Basal area[c]
Ulmaceae								
Ampelocera edentula Ducke	1816	1	1	201	2379	2	2	296
Verbenaceae								
Aegiphila intermedia Mold.	1743	1	1	383				
Vitex compressa Turcz.	1682	4	3	572				
V. triflora Vahl					2348	3	3	311
Vitex 1					2437	2	2	201
Violaceae								
Amphirrhox longifolia (St. Hil.) Spreng.	1646	6	6	683				
Vochysiaceae								
Erisma bracteosum Ducke	1633	1	1	2921				
Vochysia floribunda Mart.	1661	1	1	107				
Totals	142 species	441	356	221,017	137 species	464	353	219,028

[a] Voucher specimens, on W. Balée's number series, are deposited in N.Y.
[b] S.U. = sampling units (1 S.U. = 25 × 10 m).
[c] In cm^2.

APPENDIX 2 Lianas and non-woody vines <10 cm dbh on two one-hectare plots of *terra firme* tropical forest, Rio Xingu.[a]

A. Araweté

Apocynaceae; *Allamanda cathartica* L. (2090), *Odontadenia macarantha* (Roem. & Schult.) Maf. (2139): **Araceae;** *Heteropsis jenmanii* Oliv. (2014), *Monstera obliqua* Miguel (1974), *Philodendron distantilobium* K. Krause (1985), *P. ochrostemon* Schott. (1959), *P. pedatum* (Hook.) Kunth. (2023), *Philodendron* 1 (2073), *Anthurium clarrgerum* P. & E. (1975): **Asclepiadaceae;** indt. (2020), *Metaslema stenolobum* Decne. (2079): **Bignoniaceae**; *Amphilophium aschersonii* Ule. (1980), *Arrabidaea frailii* Sprague (1968), *A. selloi* (Spreng.) Sandw. (1956), *Lundia erionema* DC. (1964), *Martinella ovata* (HBK.) Bur. & K. Schum. (1966), *Martinella* 1 (1963), *Memora racemosa* A. Gentry (1958), *M. schomburgkii* Miers (1961), *Mussatia prieurei* Bur. ex K. Schum. (1977), *Mansoa standleyi* (Steyerm.) A. Gentry (2021), *Pryostegia dichotoma* Miers (1976), Bignoniaceae indet. (1981): **Caesalpiniaceae**; *Bauhinia corniculata* Benth. (2018), *B. coronata* Benth. in Mart. (1973), *B. guianensis* Aubl. (1808), *B. platycalyx* Benth. (1880), *Derris amazonica* Killip. (2010): **Combretaceae**; *Combretum rotundifolium* Rich. (1951), *Combretum* 1 (2017): **Commelinaceae**; *Commelina longicaulis* Jacq. (2075): **Convolvulaceae**; *Dicranostyles* 1 (2080), *Merremia macrocalyx* (R. & P.) O'Donnell (2000): **Cucurbitaceae**; *Gurania cissoides* Berg. (1972): **Dilleniaceae**; *Doliocarpus guianensis* Aubl. (1957): **Dioscoreaceae**; *Dioscorea* 1 (1992), *Dioscorea* 2 (2016), *Dioscorea* 3 (2025), *Dioscorea* 4 (2081): **Fabaceae**; indt. (1971), *Dioclea* 1 (1979), *Machaerium leiophyllum* (DC.) Benth. (1982), *Machaerium lerox* (Mart. ex Benth.) Ducke (2011), *Mucuna altissima* (Jacq.) DC. (2043), *Mucuna* 1 (2057): **Loganiaceae**; *Strychnos guianensis* (Aubl.) Mart. (2098): **Malpigiaceae**; *Banisteriopsis pubipetala* (Adr. Juss.) Cuatr. (2101): **Menispermaceae**; *Abuta imene* (Mart.) Eichl. (2009), *Abuta* 1 (2088): **Mimosaceae**; *Acacia multipinnata* Ducke (1960), *Mimosa allamandiflora* (1962): **Passifloraceae**; *Passiflora* 1 (2070): **Polygonaceae**; *Symmeria paniculata* Benth. (2013): **Rubiaceae**; *Geophila* 1 (2027), *Sabicea aspera* K. Schum. (1970), *Uncaria guianensis* (Aubl.)Gmel. (2097): **Sapindaceae**; *Paullinia pinnata* L. (1882), *P. rugosa* Benth. ex Radlk. (1945), *Serjania paucidentata* DC. (1984), *Paullinia* 2 (2024): **Vitaceae**; *Cissus erosa* L.C. Rich. (1993), *C. sicyoides* L. (1952).

B. Asurini

Araceae; *Philodendron leucanthum* Krause (2598), *Philodendron* 1 (2610): **Bignoniaceae**; *Tanaecium nocturnum* (Barb. Rodr.) Bur. & K. Schum (2442), *Melloa quadrivalvis* (Jacq.) A. Gentry (2606), *Cydista lilacina* A. Gentry (L.) Miers (2596), *xylophragma pratense* (Bur. & Schum. ex Schum.) Sprague (2452), *Memora flaviflora* (Miq.) Pulle (DC.) Bur. & K. Schum. (2595), *Adenocalymma impressum* (Rusby) Sandw. (2607), *Mansoa kerere* (Aubl.) A. Gentry (2602), *Tynanthus polyanthus* (Bur.) Sandw. (2597), *Mansoa alliacea* (Lam.) A. Gentry (2471), *Stizophyllum riparium* (HBK) Sandw. (2611): **Caesalpiniaceae**; *Bauhinia* 1 (2608): **Combretaceae**; *Combretum lanceolatum* Pohl. ex Eichl. (2616): **Convolvulaceae**; *Ipomoea* 1 (2599): **Fabaceae**; *Canavalia grandiflora* Benth. (2550), *Dioclea virgata* (Rich.) Amsh. (2617), *Dioclea* 1 (2600), *Machaerium aristulatum* (Spruce ex Benth.) Ducke (2620), *M. floribundum* Benth. (2648), *M. quinata* (Aubl.) Sandw. (2541), *Mucuna* 1 (2647): **Malphigiaceae**; *Heteropterys aceroides* Gris. (2619): **Menispermaceae**; *Vigna caracalla* (L.) Verde aff. *Caryomene* (2594): **Mimosaceae**; *Acacia multipinnata* Ducke (2531), *Mimosa rufescens* Benth. (2605): **Rhamnaceae**; *Gouania polygama* (Jacq.) Urb. (2618): **Sapindaceae**; *Paullinia spicata* Benth. (2604), *P. pinnata* L. (2612), *Puallinia* 1 (2613).

[a] Voucher specimens, on W. Balée's number series, are deposited at N.Y.