A PRELIMINARY ANALYSIS OF LARGE-SCALE FOREST INVENTORY DATA OF THE GUIANA SHIELD[1]

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Introduction

A neotropical perspective (ter Steege et al. 2000)
Only 16 tree families (Annonaceae, Arecaceae, Bombacaceae, Burseraceae, Chrysobalanaceae, Euphorbiaceae, Lauraceae, Lecythidaceae, Leguminosae, Meliaceae, Moraceae, Myristicaceae, Rubiaceae, Sapotaceae, Sterculiaceae and Violaceae) make up 79% of the tree populations in the Amazonia. Leguminosae dominate the neotropical forests. On average 16% of all individuals are Leguminosae. Leguminosae are especially abundant in the Guianas in floodplain forests and forests on white sand podzols (an average of 164 ind. in three 450-tree samples), and in fact, in the Guiana Shield in general. Over the whole area considered the abundance of Leguminosae is twice as high as that of the next two most abundant families - Arecaceae and Lecythidaceae, with 9% and 8% respectively. These data also show that just three families amount to nearly one third of all trees in Amazonia. In forests on white sand podzols in the Guiana Shield (n = 3), Leguminosae and Bombacaceae are very abundant (163-165 and 72-130 ind. in 450-tree samples respectively). Arecaceae and Moraceae are most abundant in the terra firme forest of Western Amazonia, as are Myristicaceae and Rubiaceae. Sapotaceae are most abundantly found in Central Amazonia and Burseraceae in both Central Amazonia and Eastern Amazonia. Lecythidaceae and Chrysobalanaceae are most abundant in Central Amazonia and Guiana Shield. Arecaceae dominate the floodplain forests in both Western Amazonia and Eastern Amazonia and also the swamp forests in Western Amazonia (data not shown) and Guiana Shield (van Andel, unpublished data)

Average a-diversity is highest in Central Amazonia followed closely by Western Amazonia. The most diverse floodplain forests are found, on average, in Western Amazonia. Plots on the Guiana Shield and Eastern Amazonia have low diversities for terra firme and floodplain forest, as well as forest on white sand podzols and in swamps (as compared to WA and CA). Post-hoc comparison (Scheffé's test) shows that in terms of a-diversity there are two regions. CA and WA plots are not significantly different from each other and neither are EA and GS plots. Between the CA-WA on one hand and EA-GS on the other all combinations are significantly different. Thus, EA and GS plots have significantly lower diversity than WA and CA plots.

[*The above part is merely to show that there is a gradient in forest composition and that despite high rainfall the Guianas have very low alpha diversity. They are presumed to have high beta diversity but analysis at the plot level (unpublished data) does not really suggest this*]

[1] Based on ter Steege and Zondervan 2000, in ter Steege, H. (ed.) (2000). Plant diversity in Guyana. With recommendations for a National Protected Area Strategy. Tropenbos Series 18. The Tropenbos Foundation, Wageningen, The Netherlands. References NOT yet included.

The Guiana Shield

Large scale forest inventories have been carried out in all countries bordering Guyana (Fanshawe 1961, de Milde and de Groot 1970a-f, (Guyana); de Milde and Inglis 1974, Vink 1983 (Suriname); Rollet (1969a, Venezuela); Radambrasil (Leite *et al.* 1974, Veloso *et al.* 1975, Doi *et al.* 1975, (Brasil), see Figure 4.1 for locations) and allow us to study in more detail the composition of Guyana's forest in a regional perspective. There is very little available information on French Guiana, even though some large-scale inventories have been carried out (O.N.F. pers. comm.) Reports or data of the latter were not readily available. For the description of the forests on the southern peneplain we rely mainly on the forest inventories of Guyana and areas bordering the Guianas in Brazil.

[*Note: As to the Guyana Shield areas of Venezuela: several inventories have been carried out but the data are at present not available. Colombian data from INPA 1-3 and ORAM, plus a number of smaller inventories will be available at the workshop*]

The ten most abundant families (based on the average abundance over 24 large-scale forest inventories) are: Caesalpiniaceae (average 24.0%, range 4.9% - 45.3%), Lecythidaceae (9.9, 3.7 - 18.2), Papilionaceae (8.2, 3.5 - 16.5), Sapotaceae (7.9, 2.2 - 14.8), Chrysobalanaceae (7.3, 3.0 - 12.1), Lauraceae (5.3, 0.9 - 17.8), Mimosaceae (5.1, 1.5 - 10.5), Apocynaceae (3.2, 0.7 - 9.0), Burseraceae (3.1, 0.4 - 7.5) and Bombacaceae (2.6, 0.3 - 7.9). These 10 families, out of a total of 73 found, account for 76.5% of all individuals. These 10 families are also among the most species-rich tree families in French Guiana (Sabatier and Prévost 1990). Other species-rich tree families that are not among the top ten abundant ones in the canopy of the forest are Annonaceae and Myrtaceae (mainly small trees) and Moraceae (low densities).

Caesalpiniaceae is the single most dominant tree family in the Guianas, with over 30% of all forest tree individuals over 40 cm in most of north and central Guyana. Caesalpiniaceae is the number one family in each of the large inventory areas in Guyana, Suriname and sub-coastal French Guiana. The high abundance of this tree family is caused by a large number of individuals of species in the genera *Eperua* in all three Guianas, *Dicymbe* in Guyana, *Mora* in Guyana and Suriname and *Dicorynia* and *Vouacapoua* in Suriname and French Guiana. Arguably, *Eperua falcata* is the most abundant tree species in the Guianas (Table 4.1).

Because Caesalpiniaceae can become extremely dominant locally, the abundance of most other families is negatively correlated with the abundance of Caesalpiniaceae (data not shown), except Lauraceae (*Chlorocardium rodiei*) and Bombacaceae (*Catostemma* spp.), which are also common to (co-) dominant in central and NW-Guyana (Chapters 3, 5). Families most negatively correlated with Caesalpiniaceae are Sapotaceae and Mimosaceae. Because of the strong dominance of Caesalpiniaceae, their abundance greatly influences family diversity ($r = 0.95$, $p < 0.001$), with a minimum of family diversity (evenness) in central Guyana. The number of families present in large-scale inventories, however, is rather constant despite great changes in diversity and is thus not a good measure of diversity.

Dominance of Caesalpiniaceae also strongly affects the diversity of tree genera found in large-scale forest inventories ($r = 0.84$, $p < 0.001$). In fact, even the diversity of Caesalpiniaceae itself is (almost significantly) negatively correlated with its own dominance ($r = 0.37$, $p = 0.08$). The main reason for this is that just four genera cause the large dominance of Caesalpiniaceae in Suriname and Guyana: *Eperua, Mora, Dicymbe* in Guyana and *Dicorynia* in Suriname.

Forests of the Guiana Shield

Table 4.1 presents the average composition of large forest areas in the Guiana Shield. A number of genera are clearly more abundant in Guyana than the surrounding countries and these include *Diospyros, Lissocarpa, Pentaclethra, Chlorocardium* and *Emmotum.* A few common genera appear to be characteristic for the forest of the three Guianas – they are much more common than in adjacent Brazil and Venezuela. These genera include *Carapa, Symphonia* (coastal), *Eperua, Mora, Talisia* and *Catostemma*. The southern parts of Guyana and Suriname have a higher proportion of species that may be considered long-lived pioneers (small seeds, light wood, wind or bird dispersal, see also Chapters 5 and 7). Such genera include: *Couratari, Sclerolobium, Jacaranda, Goupia, Cecropia* and *Parkia*. Genera such as *Lecythis, Eschweilera, Licania, Pithecellobium* and *Parinari* are abundant in all areas.

We suggest a preliminary division of the major forest regions in the Guianas to be as follows:

1. Forests in the coastal plain (Venezuela-Guyana-Suriname-French Guiana)
2. Forests in the North West District of Guyana and lowland Venezuelan Guyana
3. Forests on White Sands Formation (Guyana-Suriname-French Guiana)
4. Forests in the Pakaraima-Central Guayana Upland region (Guyana-Venezuela-Brazil)
5. Forests on the southern peneplain (Guyana-Suriname-French Guiana-Brazil)

[*It is not known at this time where to put the other forests for which the data has not yet been analysed. A part of Venezuela resembles much the forest of the NW of Guyana and may be one 'forest region'. The forests near San Carlos in Amazonas differ considerable in species composition from that of the Guianas and will be more Amazonian in composition, as is the case with the southern Guianan forests. However, it is interesting to note that the peculiar soil conditions of San Carlos resemble that of Central Guyana (and parts of Suriname and Fr. Guiana) and a number of higher taxa are shared, such as the genus Eperua. In the Colombian part forests are likely to resemble those of WA and indeed share their extremely high diversity. But again on the poorer soils typical Guiana Shield communities appear (Duivenvoorden)*]

These forest regions will be described in detail below.

1 Forests in the coastal plain (Venezuela-Guyana-Suriname-French Guiana)

The coastal zone of the Guianas forms part of the uninterrupted low and wet area that ranges from the Orinoco delta (Delta Amacuro) to the Amazon mouth. The area is for a large part covered with poorly drained (gleyic) soft clay and silt soils of alluvial and marine origin (Gross-Braun *et al.* 1965, de Milde and de Groot 1970c,f). Old beaches (ridges, ritsen in Suriname) occur parallel to the coast. Large areas with peat soils occur, especially in the north west region of Guyana. In eastern Guyana and Suriname the presence of an old coastal plain, the Coropina formation of silty clays and sands is noteworthy (ibid.)
The distribution of forest types in the coastal plain is determined to a large extent by the proximity to the coast or riverbanks. Closer to the sea the sediments are more clayey and flooding duration often increases. Obviously, also salinity, which increases towards the sea, affects the zonation of vegetation types in the coastal area. Below we discuss this zonation from the coastal shore inwards.

There are no typical coastal genera among large trees (Table 4.1). Genera that have dominant species in this area such as *Virola, Iryanthera, Tabebuia, Pterocarpus* and *Macrolobium* also have (often vicariant) species common in the forest on the basement complex, except for the monotypic *Symphonia*.

Mangrove forests

Mangrove forests occur in a narrow belt of a few kilometres wide along the coast and along the banks of the lower reaches of rivers. The mangrove forest along the coast consists mainly of *Avicennia germinans* (Lindeman and Molenaar 1959, de Granville 1986), with occasional undergrowth of the salt fern, *Acrostichum aureum*. With increasing age of the stands, regeneration of *Avicennia* decreases and a low and open mangrove swamp is formed (Lindeman and Molenaar 1959, de Granville 1986). *Rhizophora* occupies the more exposed, soft silts in river mouths and shores. Where the water is distinctively brackish a third mangrove species can be found, *Laguncularia racemosa* (Lindeman and Molenaar 1959). Further inland mangrove species mix with *Euterpe oleracea* palms and such trees as *Pterocarpus officinalis* (Lindeman and Molenaar 1959, Huber 1995a, van Andel 2000) and is still further inland replaced by a mixture of *Pterocarpus officinalis* and *Pachira aquatica* (Fanshawe 1952, Lindeman and Molenaar 1959). Extensive (some 90,000 ha) and well preserved mangrove stands may still be present in Guyana's North West District and Pomeroon area (De Milde and de Groot 1970c,f, Welch 1975). Large tracts of mangrove forest are found also in the Delta Amacuro (4,200,000 ha, Pannier and Fraino Pannier 1989, cited in Huber 1995a) and towards the Amazon mouth in Amapá (Leite *et al.* 1974). *Avicennia* is used extensively as firewood and for tanning in populated areas and this practice has led to the decline of these forests in (eastern) Guyana and in Venezuela (Huber 1995a).

Permanently flooded palm marsh forest (coastal swamp forest)

In permanently flooded, flat plains in the present coastal zone a low (10-20 m tall) swamp forest is found. The soils are often poorly drained peat soils over coastal clay. The most extensive stands are found in the North West District of Guyana and the Orinoco delta in Venezuela (de Milde and de Groot 1970f, Huber 1995a). Characteristic species are *Symphonia globulifera, Tabebuia insignis/fluviatilis, Pterocarpus officinalis* and *Euterpe oleracea*. Species that can become locally dominant in this forest type in Guyana are *Pentaclethra macroloba, Vatairea guianensis, Pterocarpus officinalis* and *Virola surinamensis* (Welch 1975). *Manicaria saccifera* is commonly found as a narrow belt along rivers in Delta Amacuro, Guyana and western Suriname. *Iryanthera macrophylla* and *Tabebuia insignis* form extensive stands behind the *Manicaria* or *Mora excelsa* stands (Fanshawe 1952). *Tabebuia, Virola* and *Symphonia* have been harvested to some extent in the Northwest District of Guyana (Welch 1975). Large-scale extraction of *Euterpe oleracea* is currently taking place (van Andel 2000). *Manicaria* is also in high demand as its entire leaves make very good roof thatch.

Seasonally flooded palm marsh and swamp forest

More inland the duration of flooding is less pronounced and forest composition is slightly different. Common species on peat soils are *Symphonia globulifera, Virola surinamensis, Iryanthera* spp., *Pterocarpus officinalis, Mora excelsa, Pachira aquatica, Manicaria saccifera* and *Euterpe oleracea* (Huber 1995a). Forest dominated by *Triplaris weigeltiana* is commonly found in Suriname (Lindeman and Molenaar 1959). In the *Triplaris* stands in Suriname species of the *Symphonia*-dominated forest are practically absent (Lindeman and Molenaar 1959). In the east of Guyana much land along the rivers was cultivated by the Dutch. Such old plantations are now also covered with *Triplaris weigeltiana* and *Cordia*

tetrandra (Fanshawe 1952). These species are also commonly found on other disturbed or newly sedimented parts of the lower reaches of the rivers (Fanshawe 1952, ter Steege pers. obs.). Repetitive burning has led to large-scale herbaceous and grassy swamps, interspersed with *Mauritia* palms.
In Guyana *Mora excelsa* forms extensive stands along the rivers on alluvial silt up to the confluence of Rupununi and Rewa rivers (Chapter 5). *Mora* forest is low in height close to the coast but grows to magnificent stature more inland, with emergent individuals of over 60 m. Canopy associates of the *Mora* forest are *Carapa guianensis, Pterocarpus officinalis, Macrolobium bifolium, Eschweilera wachenheimii, E. sagotiana, Clathrotropis brachypetala, C. macrostachya, Eperua falcata, E. rubiginosa, Catostemma commune, C. fragrans, Pentaclethra macroloba, Vatairea guianensis, Symphonia globulifera, Terminalia dichotoma* and *Tabebuia insignis* (Fanshawe 1952). Several of the accompanying species are dominant in *Mora* forest in certain areas.

Forests on the old coastal plain: the 'Coropina formation'
There is little specific information on the forests of the old coastal plain. *Nectandra rubra* is a species considered typical for this area in Guyana (I. Welch, pers. comm.). In Suriname *Parinari campestris* is common on old ridges (Lindeman 1953, Lindeman and Molenaar 1959, Theunissen 1980). Other common trees are *Tetragastris* spp., *Goupia glabra, Pouteria* spp., *Eschweilera* spp. and *Antonia ovata*. Marsh forest on silty clay in Suriname is not very different from Marsh forest of the young coastal plain with species such as: *Euterpe oleracea, Eschweilera* spp., *Parinari campestris, Carapa guianensis, Copaifera guianensis, Qualea caerulea* and *Pithecellobium jupunba* (Lindeman and Molenaar 1959, Theunissen 1980)

[*Other vegetation types in the coastal plain are wet savannahs and swamps. Huge wetland areas are found in the NW of Guyana and in Suriname and in Venezuela (to check)*]

2 Forests in the Northwest District of Guyana and lowland Venezuelan Guayana

The upland forests in the north west of Guyana (and bordering Venezuela), are found both on soils developed on the crystalline shield, such as Granites and Greenstones (Gibbs and Baron 1993) and on pockets of Plio-Pleistocene sediments (see Gross-Braun *et al.* 1965).

Rainforests of the Northwest District
The dry land forest of the Northwest District of Guyana and eastern Venezuela are characterised by a high abundance of *Eschweilera sagotiana, Alexa imperatricis, Catostemma commune, Licania* spp. and *Protium decandrum.* These species are found abundantly in almost every dry land forest type in this region (de Milde and de Groot 1970f, Huber 1995a, Barama Company Ltd. unpublished data). Most of these species belong to genera of the 'Lowland Guianas Dominants' of Table 4.1. Upland forests dominated by *Alexa, Eschweilera, Licania* and *Catostemma* continue far into Venezuela (Huber 1995a). Poor mono-dominant stands of *M. gonggrijpii* are found on the (probably) more clayey soils between the Cuyuni and Mazaruni. *M. gonggrijpii* dominated stands are also found in the eastern parts of Venezuelan Guyana (Rollet 1969b, Finol Urdaneta undated).
Extraction of plywood species (mainly *Catostemma, Alexa* and *Mouriri*) has risen quite substantially over the last years in the area.

3 Forests on the White Sands Formation (Guyana-Suriname-French Guiana)

Extensive sediments have been deposited in the late Tertiary-Pleistocene in the Guianas. These sediments form the so-called White Sands Formation, in Guyana known as 'Berbice formation'. The formation is found from the Cuyuni-Waini waterdivide in Guyana to western French Guiana (Figure 4.6). It extends furthest inland in Guyana (Berbice-Corantyne waterdivide) and is over 2000 metres thick in the coastal area near the mouth of the Berbice river (Gibbs and Barron 1993). The formation gradually becomes less wide in Suriname and occupies only a small, narrow portion in coastal western French Guiana (ibid.). Soils in the Berbice formation consist of pure white sands to loamy sands. Dolerite intrusions (Dykes) are common in Guyana and are usually covered with lateritic soils. In creek valleys peat is commonly formed.
The forests are often dominated by a few or only one species (Davis and Richards 1934, Fanshawe 1952, ter Steege *et al.* 1993) and consequently have a low α-diversity (ter Steege 1998a, Chapters 5, 7, 8). The main forests in the region were classified as belonging to the *Eschweilera-Licania* association, which occurs on the brown sands and the *Eperua-Eperua* association on the white sands (Fanshawe 1952).
Genera typical of the Berbice formation are *Campsiandra, Emmotum, Dimorphandra, Chlorocardium, Talisia* and *Diospyros/Lissocarpa,* as are the typical lowland Guianas dominants (Table 4.1). There are gradual shifts in species composition from west to east (Table 4.1) but these also correspond with increased area of soils formed on the basement complex, included in the inventories in Suriname. The best examples of forests on the Berbice formation are found in central Guyana, in Table 4.1 exemplified by the Mazaruni-Essequibo, Essequibo-Demerara and Demerara-Mahaicony waterdivides. Palms are rare in the forests on the Berbice formation (Chapter 3). Most of the understorey palms belong to the genus *Bactris*. In swampy areas *Jessenia* and *Mauritia* may be dominant.

Rain forests on Pleistocene brown sands in central Guyana
In Guyana forests on the brown sands of the Berbice formation are almost invariably characterised by species of *Eschweilera* and *Licania*. Species, which may be locally dominant are *Eschweilera sagotiana, E. decolorans, E. confertiflora, Licania alba, L. majuscula, L. laxiflora, Chlorocardium rodiei, Mora gonggrijpii, Alexa imperatricis, Swartzia schomburgkii, S. leiocalycina, Catostemma commune, Eperua falcata, Pouteria guianensis, P. cladantha, Aspidosperma excelsum* and *Pentaclethra macroloba* (Fanshawe 1952). Mono-dominance is common in forests on brown sands in central Guyana and tends to get less in an eastward direction (see above). Mixed forests on brown sands have traditionally been the main targets for timber extraction in Guyana, with main emphasis on *Chlorocardium rodiei*.

Rain forests on Pleistocene brown sands in eastern Guyana, Suriname and French Guiana
Towards the east in Guyana and across the border in Suriname the species mix changes slightly and the more common species are *Goupia glabra, Swartzia leiocalycina, Aspidosperma excelsum, Manilkara bidentata, Terminalia amazonica, Parinari campestris, Vochysia surinamensis, Emmotum fagifolium, Humiria balsamifera, Catostemma fragrans, Hymenaea courbaril, Licania densiflora* and *Eperua falcata* (Fanshawe 1952, Maas 1971). In Guyana, this forest on light brown sands extends south towards the Kanuku mountains, where it grades into semi-evergreen forest of the Rupununi district (see below). Species common in these forests in Suriname are *Peltogyne* spp., *Loxopterygium sagotii, Platonia insignis, Vochysia* spp., *Protium* spp., *Aspidosperma marcgravianum* and *Andira inermis* (Lindeman and Molenaar 1959). In transition to forests on the basement complex, e.g in the Coesewijne and Wayombo areas, *Dicorynia guianensis, Nectandra rubra, Goupia glabra, Eperua falcata* and *Chaetocarpus schomburgkianus* are commonly found (Schulz 1960). Due to the

occurrence of high value timber species, such as *Dicorynia, Nectandra* and *Goupia*, this area has been heavily exploited in Suriname. The Pleistocene sediments become a very narrow band in French Guiana. Gazel (1981) reports on the composition of a few plots near St. Laurent. Common species here are: *Eschweilera odora, Licania* spp., *Eperua falcata, Dicorynia guianensis, Virola melinonii, Iryanthera sagotiana* and *Goupia glabra*. As in the transition forest in Suriname species common on the basement complex (*Dicorynia, Virola, Iryanthera*) are more abundantly present here than in central Guyana.

Dry evergreen forest on white sands
Dry evergreen forest (Wallaba forest in Guyana, Savannah forest in Suriname) on bleached white sands (albic Arenosols) occurs from the Pakaraima escarpment (see below), through central Guyana and northern Suriname into a small narrow portion of French Guiana. The distribution of this forest type follows the Berbice-Zanderij formation very closely. The forest type can also be found on white sands with impeded drainage (gleyic Arenosols).

On the Pleistocene white sands *Eperua falcata* and *E. grandiflora* are strongly dominant and may form, alone or together, more than 60% of the canopy individuals (Fanshawe 1952). Common other species in the canopy layer are *Catostemma fragrans, C. altsonii, Licania buxifolia, Talisia squarrosa, Ormosia coutinhoi, Eschweilera corrugata, Aspidosperma excelsum, Terminalia amazonia, Chamaecrista adiantifolia, Chamaecrista apocouita, Swartzia* spp., *Dicymbe altsonii* (west Guyana only), *D. corymbosa* (ibid.), *Manilkara bidentata* (Pomeroon-Waini waterdivide) and *Pouteria* (Fanshawe 1952).
Forest dominated by *Dimorphandra conjugata* (Dakama forest) is common on the higher parts of waterdivides from central Guyana to western Suriname. This forest type is characterised by very high standing litter crop (up to 800 ton/ha, Cooper 1982) and is very fire prone. Other species, characteristic for Dakama forests, are *Eperua falcata, Talisia squarrosa, Emmotum fagifolium* and *Swartzia bannia* (Fanshawe 1952, Lindeman and Molenaar 1959). *Humiria balsamifera* (Muri) co-dominates the degraded Dakama forest (Dakama-Muri scrub) with *Dimorphandra*. Other common species in this scrub are *Swartzia bannia, Clusia fockeana, Licania incana, Bombax flaviflorum, Ocotea schomburgkiana, Trattinickia burserifolia, Ternstroemia punctata* and *Byrsonima crassifolia* (Lindeman and Molenaar 1959, Cooper 1982). In areas where fires are very regular, e.g. along the road from Soesdyke to Linden in Guyana, Dakama forest degrades into Muri-scrub and finally into unproductive grassland (pers. obs.).

Creek forest of the white sands formation
The White Sands Area has a gently rolling aspect with a drainage pattern of many small creeks. The water table in the heads of such creeks is perpetually high and often a swamp forest is found on a layer of peat soil (pegasse). Dominant species are *Jessenia bataua, Mauritia flexuosa, Tabebuia insignis, Clusia* spp., *Symphonia, Iryanthera, Couratari, Eperua falcata* and *Diospyros ierensis* (Fanshawe 1952, ter Steege *et al.* 1993, Chapter 5, 8). The forest is very open and a dense layer of herbs is found. This layer is often dominated by *Rapatea paludosa*. In the lower reaches of creeks a variety of soils is found ranging from redistributed sands to clays. Common tree species in these creek forests are *Mora excelsa, Eperua rubiginosa, E. falcata, Pterocarpus officinalis, Carapa* spp., *Inga* spp. and *Pentaclethra macroloba* in central Guyana (Chapter 8).

Rain forest and evergreen forest on laterite ridges
Throughout the Berbice formation Dolerite dykes penetrate through the sediments (Daniel and Hons 1984). These dykes, varying in heights between 100 to 400 m, are covered with

lateritic soils of rocky, gravelly to clayey constitution (van Kekem *et al.* 1996). There is little quantitative information available on the forest composition on these soils (but see Chapters 5, 8). Common trees are *Eschweilera* spp., *Licania* spp., *Swartzia* spp., *Mora gonggrijpii* (Guyana), *Chlorocardium rodiei* (Guyana). On lateritic soils in central Guyana a local endemic, *Vouacapoua macropetala*, forms extensive stands with *Eschweilera sagotiana, Licania laxiflora, Sterculia rugosa, Poecilanthe hostmanii* and *Pentaclethra macroloba* (Chapter 8). On lateritic soils in Suriname its vicariant, *V. americana*, is often dominant (Schulz 1960).

On the rocky phase of laterite, which has low water retention capacity and consequently is characterised by periods of water shortage a low shrubby forest is found. Myrtaceae (*Eugenia* spp., *Calycolpes, Marlierea*) and Sapotaceae (*Ecclinusa, Manilkara*) dominate here (e.g. Chapter 8).
Because of the occurrence of steep slopes landslides are not uncommon on laterite ridges. Often liana forest is encountered on such landslides. Pioneers, such as *Cecropia* spp., *Schefflera morototonii, Jacaranda copaia* and *Pentaclethra macroloba* are also abundantly present on such sites in central Guyana (ter Steege pers. obs.).

[*Other interesting vegetation types in C-Guyana and likely the other areas as well are the shrubby vegetation types on rocky islands in the large rivers. In Guyana they are characterised by the occurrence of a few endemic species*]

4 Forests in the Pakaraima-Central Guayana Upland region (Guyana-Venezuela-Brazil)

The forests of the uplands of west central Guyana are part of the central Guayana province (Berry *et al.* 1995). The lowland forests of this region have been classified as belonging to the *Eschweilera-Dicymbe* association (Fanshawe 1952). The major soils in the region are shallow and rocky (Gross-Braun *et al.* 1965) having formed on steep volcanic mother material (basic and acidic) and on sandstone.
In Guyana, *Dicymbe*, which is practically restricted to the Guiana Shield (Berry *et al.* 1995), is the most characteristic genus for the lowland forests of this area (Table 4.1). *D. altsonii* and *D. corymbosa* are (absolutely) dominant over large stretches of forest from the Pakaraimas to the Essequibo (Fanshawe 1952, ter Steege 1998a). Genera, common to the southern upland region (crystalline shield), are common in the Pakaraimas as well (Table 4.1). *Podocarpus, Ragala, Micrandra* and a few other are characteristic for the montane forests in this area. These forests are the least known in Guyana but are also very small in extent. Most of our information is from bordering Venezuela and Brazil, where the areas with montane forests are much larger and also our knowledge is more advanced (Veloso *et al.* 1975, Huber 1995b, Chapter 10).

Lowland and lower montane forests of the Pakaraima uplands on brown sands
Dicymbe altsonii (endemic to Guyana) is the main characteristic and most common canopy species in the 'mixed forests' of the lowland eastern Pakaraima Mountains. *Dicymbe* may be absolutely dominant over large areas. Co-dominants are *Eperua falcata, Eschweilera sagotiana, E. potaroensis, Mora gonggrijpii, Alexa imperatricis, Licania laxiflora, Swartzia leiocalycina, Vouacapoua macropetala* and *Chlorocardium rodiei*. *Eschweilera potaroensis,* an endemic of this region, may be co-dominant in forests around the confluence of the Potaro and Essequibo Rivers (Chapters 5, 6).

Lowland and lower montane forests of the Pakaraima uplands on white sands
On the white sand derived from the weathering table mountains Legumes are a strongly dominant feature (Fanshawe 1952, Whitton 1962). The main dominant species are *Eperua falcata, Eperua grandiflora, Dicymbe altsonii, D. corymbosa* and *Dimorphandra davisii* (endemic to the Pakaraima Mts.). On isolated spots forest dominated by *Dimorphandra polyandra* is found (Fanshawe 1952). Several other species, associated with the white sands in Guyana (see below) are common in this region such as *Chamaecrista adiantifolia, Chamaecrista apoucouita, Talisia squarrosa* and *Ocotea schomburgkiana*. *Cunuria glabra* is widespread and dominant on poorly drained soils, along rivers, notably the Kako River (I. Welch, perscomm., see also Chapter 8), often together with *Dimorphandra macrostachya*. Forest with abundance of *D. macrostachya* is also found over large areas of the Gran Sabana in Venezuela (Hernández 1992, 1994, Huber 1995a). *Ormosia coutinhoi* is typical for the areas bordering swamps and *Aldina insignis* is found on the edges with *Mora excelsa* forest (Fanshawe 1952). Forests with *D. davisii, D. polyandra* and *D. cuprea* are characterised by thick litter layers, comparable to the forest of *D. conjugata*. Whitton (1962) reported that all *Dimorphandra* forest of the Pakaraimas showed signs of burning, with almost single dominance of *Dimorphandra* regenerating through clumping.

Dry submontane forests of the Pakaraima uplands
Xeromorphic woodland with *Dicymbe jenmanii* (endemic to the Kaieteur region), *Moronobea jenmanii, Humiria balsamifera, Chrysophyllum beardii, Tabebuia* spp., *Anthodiscus obovatus, Saccoglottis, Dimorphandra cuprea, Clusia* spp., *Oedimatopus, Archytaea, Bonettia, Didimopanax, Poecilandra retusa, Pradosia schomburgkiana, Pagamea guianensis* and *Chaetocarpus stipularis* is found on shallow soils. On areas with impeded drainage epiphytes of Araceae, Bromeliaceae, Cyclanthaceae and Rapateaceae cover the forest floor (Fanshawe 1952).
Much of this forest area is in a seral stage (scrub) recovering from fires (Fanshawe 1952). Such xeromorphic scrub vegetation is characterised by *Humiria balsamifera, Dimorphandra cuprea, Bonettia, Poecilandra retusa, Pradosia schomburgkiana, Pagamea guianensis* and *Chaetocarpus stipularis.*

Montane forests of the Pakaraima highlands
The montane forests (800-1500m) in Guyana are small in extent (see Chapter 10). In Venezuela just across the border montane forest is found with *Dimorphandra macrostachya, Byrsonima stipulacea, Sloanea pittieriana, Platycarpum rugosum, Enlicheria nilssonii, Sterigmapetalum guianense, Caryocar montanum, Moronobea ptaritepuiana* and *Podocarpus magnifolius* (Huber 1995a). It is very likely that elements of this forest also occur on the Guyanan slopes of Mt. Roraima. The only numerical data we have are from Brazil (Table 4.1, Veloso *et al.* 1975). The most abundant species in this area are *Micrandra lopesii, Nectandra rubra, Eschweilera odora, Elizabetha* sp., *Licaria canella, Micropholis guianensis, Ormosia flava, Caraipa grandiflora, Mezilaurus itauba* and *Cariniana micrantha.* Sapotaceae and Lauraceae, in general, are overwhelmingly abundant at higher elevations.

Upper montane forests of the Pakaraima highlands
Upper montane forests (1500-2000m) are only found on the high table mountains, such as Mts. Roraima, Ayanganna and Wokomung. Huber *et al.* (1995) and Huber (1995a) list: *Bonnetia tepuiensis, Schefflera, Podocarpus, Magnolia* and *Weinmannia*. The cloud forests are rich in cryptogamic and vascular epiphytes (Huber 1995a). The forest finally grades into tepui scrub (2200-2700m) with *Bonnetia roraimae, Schefflera, Clusia* and *Ilex*, which, in Guyana, is probably only found on Mts. Roraima and Ayanganna (Huber *et al.* 1995). On the

Brazilian slopes of Mt. Roraima, Veloso *et al.* (1975) do not describe any forests with *Bonnetia*, but low scrubs with Melastomataceae, Rubiaceae, *Ilex* and *Podocarpus steyermarkii*.

[*If I am correct Otto was going to deal with the areas over 1500m*]

5 Forests on the southern peneplain (Guyana-Suriname-French Guiana-Brazil)

The forests in the southern regions of the Guianas are situated on soils developed on the crystalline shield, known as the 'Guiana peneplain' (Gross-Braun *et al.* 1965; Gibbs and Barron 1993). This peneplain extends from (east Colombia-) Venezuela, through the Guianas to Amapá (Brazil). These forests are among the least known in the Guianas, mainly due to their remote location. The few systematic inventories in the southern areas were carried out in Guyana (de Milde and de Groot 1970g, see also ter Steege 1998, Chapter 5) and further south just across the border in Brazil (Leite *et al.* 1974, Veloso *et al.* 1975, Doi *et al.* 1975). Several inventories were carried out on the crystalline shield in Suriname, near the coastal area. Thus, our knowledge in Suriname is restricted to the areas in the near interior. In French Guiana too, several inventories were carried out in the near interior (Fleury 1994). These data were unavailable but some incomplete summaries exist. Our knowledge of French Guiana is thus very restricted to a number of descriptive accounts (de Granville 1990, Sabatier and Prévost 1990) and a few detailed studies of relatively small areas (Mori and Boom 1987, Sabatier 1990).
The forests on the crystalline shield are more diverse than those of the white sands formation (Lindeman and Molenaar 1959, Fanshawe 1952, ter Steege 1998a, Chapter 5). Genera that are more common on the shield in south Guyana, Suriname, Brazil and Venezuela (Imataca) compared to central and north-west Guyana include (Table 4.1) *Anacardium, Andira, Bagassa, Cecropia, Couratari, Dipteryx, Geissospermum, Laetia, Micropholis, Parkia, Pourouma, Pseudopiptadenia, Qualea, Sclerolobium, Simarouba, Tetragastris, Virola* and *Vochysia*. Typical for Suriname (and French Guiana) are *Dicorynia, Andira, Dipteryx, Trichilia* and *Lueheopsis*. Further south still (Brazil) *Hymenolobium, Bertholletia, Cynometra, Dialium* and *Clarisia* become more abundant (Table 4.1). Several of these genera (and also of the non-mentioned genera) are comprised of species with medium to light wood and characteristic of late succession (Chapter 7).

Sub-coastal French Guiana and Brazil.
Six species: *Eperua falcata, Dicorynia guianensis, Eschweilera odora, Eschweilera amara, Chrysophyllum prieurii* and *Qualea albiflora* are responsible for 50% of the individuals in the forest of sub-coastal French Guiana (Fleury pers. comm, see Table 4.1). In Paracou, where intensive silvicultural studies are being carried out, the forest on the schist soils have an abundance of *Eperua, Licania, Parinari, Eschweilera, Dicorynia guianensis, Inga, Goupia glabra, Bocoa prouacencis, Symphonia globulifera, Qualea rosea, Ruizterania, Vouacapoua americana, Ocotea rubra* and *Virola* (Schmitt 1985, Bergonzini 1989). The most common taxa at the ECEREX station on the Piste de St. Elie, slightly more inland and in the Bonidoro schists area, (Lescure and Boulet 1985, Sabatier *et al.* 1997) on variably drained Ferralitic soils are Lecytidaceae (*Eschweilera*), Caesalpiniaceae (*Eperua*), Chrysobalanaceae (*Licania*) and Sapotaceae.

Just over the border in Brazil, in Amapá (Leite *et al.* 1974) *Eschweilera* is the most abundant genus followed by *Pouteria, Inga, Minquartia, Licania, Protium, Manilkara, Vouacapoua, Virola, Chrysophyllum, Vochysia, Pentaclethra, Qualea, Ocotea* and *Tachigali*. These genera

together account for 50% of all individuals over 30 cm. Areas on the basement complex are characterised by *Dinizia excelsa, Manilkara, Minquartia, Pouteria, Protium, Tetragastris, Eschweilera, Couma, Iryanthera* and *Geissospermum sericeum*.

Dry to moist forests in the southern Guyana-Brazil border area
The North- and South-Rupununi savannah cover a fairly large part of the southern region. Dry (deciduous) forest types fringe these savannahs. Due to repeated burning of the savannah the forest edges in this region retreat further and further each year. Most of the dry forest stands show high presence of *Goupia glabra, Couratari, Sclerolobium, Parinari, Apeiba, Peltogyne, Catostemma, Spondias mombin* and *Anacardium giganteum* (Fanshawe 1952, ter Steege 1998a, Chapter 5). *Couratari guianensis, Terminalia dichotoma, Tetragastris panamensis* and *Licania* spp. form stands in the eastern part. These dry mixed forests extend far into Brazil (Veloso *et al.* 1975) and Venezuela (see Huber 1995a). Forests along the foothills of the Kanuku mountains are characterised by *Cordia alliodora, Centrolobium paraense, Apeiba schomburgkii, Acacia polyphylla, Pithecellobium* s.l., *Peltogyne pubescens, Manilkara* spp., *Cassia multijuga* and *Vitex* spp. (Fanshawe 1952, ter Steege 1998a). The first two species are sought after timber species within the local Amerindian communities. *Cochlospermum vitifolium* (and *orinocense*) is a conspicuous member of this forest. Similar forests with *Centrolobium, Cordia, Peltogyne, Vitex, Inga, Protium, Tetragastris, Parkia, Pseudopiptadenia, Spondias* and *Genipa* have also been found along the footslopes of the Acarai Mts. in Brazil (Veloso *et al.* 1975, Doi *et al.* 1975).

Inundated areas are characterised by *Orbignya* spp., *Maximiliana regia, Mauritia flexuosa* (Fanshawe 1952, Veloso *et al.* 1975). The latter is also a typical feature along creeks and depressions in the savannahs. Common trees are *Protium* spp., *Licania canella, Eschweilera* spp., *Macrolobium acaciifolium, Clathrotropis, Elizabetha, Simarouba, Inga* and *Couepia* (Veloso *et al.* 1975).

South of the Cuyuwini river to east of the New River the forest is characterised by a high presence of *Geissospermum sericeum, Eschweilera* cf. *pedicellata, Lecythis corrugata, Pouteria coriacea* and *Pourouma* spp. Several other taxa, characteristic of late secondary forest, have fairly high presence this region: *Parkia, Ficus, Sclerolobium, Trichilia, Parkia, Parinari* and *Goupia*. *Eperua rubiginosa, Pterocarpus* and *Macrolobium acaciifolium* are common in forests along the rivers in this area.

Moist forests on the basement complex in Suriname and French Guiana
Eperua falcata is the most abundant species in soils of the Zanderij formation and the soils on the basement complex in the near interior in Suriname. Other common species in these forests are *Dicorynia guianensis, Tetragastris altissima, Couratari stellata, Eschweilera odora, Iryanthera sagotiana, Virola melinonii, Parinari campestris, Mora gonggrijpii, Manilkara bidentata* and *Goupia glabra* (Schulz 1960). Other *Eschweilera* spp. and *Licania* spp. are also abundantly present. In comparison with the forests of the near interior of Guyana, Vochysiaceae, Myristicaceae, Mimosaceae, are more prominent in Suriname than in Guyana. There are clear trends from west to east: e.g. *Mora gonggrijpii* is not uncommon in certain areas in the west but is absent in the east, while *Dicorynia guianensis* increases in abundance toward the east. *Qualea rosea* is quite abundant in the somewhat drier sandier areas, whereas *Vouacapoua americana* in combination with *Eschweilera* spp. is characteristic of the lateritic hills (Schulz 1960). Comparable hill forest is found over large stretches in the further interior (e.g. Goliath creek, Stofbroekoe Mt., Voltz Mt.). On the higher portions of mountains Myrtaceae, Sapotaceae and lianas are conspicuous (Lindeman and Molenaar 1959,

Schulz 1960). Liana forest is likely an indication of disturbance and species such as *Laetia procera* and *Goupia glabra* are common. No information could be found on the large mountain stretches in central to southern Suriname (a.o. Wilhelmina Mts., Eilerts de Haan Mts., Oranje Mts. but see below).

In Nouragues, central French Guiana, Lecythidaceae, Sapotaceae, Caesalpiniaceae, Chrysobalanaceae, Burseraceae are among the most common families (Poncy *et al.* 1998). The most abundant species in a 100-ha sample were *Vouacapoua americana, Eperua falcata, Bocoa prouacensis, Dicorynia guianensis, Sclerolobium, Pseudopiptadenia* and *Inga* spp. Large local differences were noted and *Tetragastris altissima* was extremely abundant in a forest area only 7 km away from the 100-ha sample. Granitic outcrops in the area are dominated by Myrtaceae (*Myrcia, Myrciaria, Eugenia*) with some *Eriotheca, Inga* spp., *Terminalia amazonica* and *Clusia* spp. Several species common on these rocks are also common in dry savannahs.

In Saül, *Tetragastris altissima* is by far the most abundant species, followed by *Quararibea turbinata, Protium apiculatum, Eschweilera coriacea, Virola michelii, Eperua falcata* and *Chimarris microcarpa* (Mori and Boom 1987). The leading families around Saül are Burseraceae (*Tetragastris altissima*), Sapotaceae, Lecythidaceae, Caesalpiniaceae and Mimosaceae. The terrain around Saül is relatively dissected with peaks of just over 400m.

Further down south close to the Brazilian border the forest at Trois Sauts, Oyapoque R., also shows a high abundance of Burseraceae (23% of all individuals, Sabatier 1990). Lecythidaceae are the second family, followed by Meliaceae, Mimosaceae and Lauraceae. Chrysobalanaceae and Caesalpiniaceae are 8th and 10th in rank respectively.

Forests south of the Brazilian border
It is reasonable to assume that the forest at the southern Suriname and French Guiana border will not be unlike the forest in bordering Brazil, which is dominated by *Licania* and *Pouteria* and with *Cynometra, Dialium, Protium, Eschweilera, Tabebuia* and *Manilkara* (Table 4.1). More easterly the forests are more dominated by *Eschweilera*, with *Vochysia, Manilkara, Tetragastris* and *Pouteria* (Table 4.1).

Submontane forest (200 - 600 m altitude) is found close to the border with Suriname and Guyana. Montane forest is found in the Acarai Mts from 600-800 m. Forests on the mountain tops are dominated by Myrtaceae and *Clusia* on Sierra do Acarai (Doi *et al.* 1975).

[*The data of the Brazilian part may need to be reanalysed. I was supposed to receive digital RADAM data but is has not yet been forthcoming. Data of the area of Neblina is still to be types in but will be available before the workshop. I have no indication of extra data from Amazonian Venezuela*]

Conclusions

There are clear differences in forest composition over large areas in the three Guianas. Because several species have restricted ranges at the species level this is obvious but several large range species can be found nearly everywhere (e.g. *Goupia glabra*). There are also clear differences in composition at the genus and family level (Table 4.1).

Areas that stand out in terms of their forest composition are:

1. Forests in the sub-coastal Guianas, that may have the largest number of species/ genera typical of the three Guianas
2. Forests on the Berbice Formation (Guyana mainly) with unique high dominance of Caesalpiniaceae and endemics (see also Chapters 5 and 6)
3. Forests of the Pakaraima highlands (see also Chapters 5 and 6)

SAVANNAHS OF SOUTHWEST GUYANA[2]

Marion Jansen-Jacobs, Hans ter Steege

Introduction

In the southern part of Guyana the largest savannah area of the country is found: the Rupununi Savannah, which covers approximately 13,000 km^2 (Daniel and Hons 1984). The Kanuku Mts., a mainly forested mountain range, divides the Rupununi Savannah in a northern and southern part. The Rupununi Savannah is in fact an extension of the larger Rio Branco Savannahs of Brazil. Phytogeographically the area belongs to the Amazon Region and not to the Eastern Guayana Province of the Guayana Region, such as the rest of Guyana (Berry *et al.* 1995, see also Chapter 10). As was suggested in Chapter 6 the approximate boundary may be around 4° N, just north of the savannah area.

There are several publications on the vegetation in Southwest Guyana (Schomburgk 1847, 1848, Davis 1936, Myers 1936, Smith 1939, Fanshawe 1952, Eden 1964, 1973; Goodland 1966, Anonymous 1966) but no clear synthesis. Southwest Guyana differs substantially from central and north Guyana in terms of climate, geomorphology and population. Because these factors are important for the understanding of the vegetation they are briefly discussed below.

Climate
In contrast to central and north Guyana, with two dry and two wet seasons, the Rupununi area experiences only one wet and one dry season (Persaud 1994). The annual rainfall in the Rupununi Savannah is between 1500-2000 mm y^{-1}, of which ca. 70-80 % falls during the wet season from May-August (Persaud 1994). The savannah areas also have the highest amount of sunshine hours of the country (8 h day^{-1}, Persaud 1982). The mean annual daily temperature is 27.5 ° C (Persaud and Persaud 1993). Rainfall increases towards the south because of the orographic uplift caused by the Acarai Mts. (Persaud 1994, see also Figures 6.3, 6.4). The drainage system of the Rupununi Savannahs is unable to carry a high volume of surface runoff. As a result most rivers flood in the wet season. In a few places ground water drainage is impeded by clay, and ponds and lakes persist for several months (Hills 1969).

Geomorphology and soils
Geomorphologically SW Guyana belongs to the Precambrian Lowlands (Daniel and Hons 1984), which derives its name from the underlying Precambrian crystalline basement rocks. These rocks are exposed in the Kanuku Mts. and over a wide area in the South Rupununi Savannah. In the North Rupununi Savannah the Precambrian rocks are covered by the sedimentary rocks of the Takutu Formation (Sinha 1968).

The landscape of the North Rupununi Savannah is gently undulating. Domes and ridges with porous laterite on top are mostly forested, in-between seasonally waterlogged flats with sandy clay are found (Daniel and Hons 1984, Sinha 1968, Eden 1973). The Kanuku Mts. are a large outcrop of granite. The slopes have a thin layer of sandy-clayey lithosol and are covered with forest. In the south Rupununi Savannah the granitic bedrock is close to the surface. It is visible as inselbergs - summits of the bedrock that dominate the landscape (Frost 1968, Eden

[2] [2] Based on Jansen and ter Steege 2000, in ter Steege, H. (ed.) (2000). Plant diversity in Guyana. With recommendations for a National Protected Area Strategy. Tropenbos Series 18. The Tropenbos Foundation, Wageningen, The Netherlands. References NOT yet included.

1973). The slopes of the higher inselbergs are steep and strewn with boulders. The thin sandy soil that develops on the slopes supports a moderately thick forest. The pediments have thin soil with lateritic tendencies (Daniel and Hons 1984). In the depressions, "groundwater laterites" are formed which act as a partially impermeable layer (Frost 1968). In general the soils of the Rupununi Savannah are highly acidic and poor in nutrients (Goodland 1966).

Savannah fires

The vegetation of the Rupununi Savannahs is mostly burned once a year to promote the growth of pasture grasses for the cattle but also to keep vegetation around dwellings short. Hence, fire is usually of human origin, but it may also have natural causes (Hills 1969). Due to lack of combustible material, the total area burned by one single fire is usually not large. Fire is important in the maintenance of savannahs - it enables fire-resistant plants (pyrophytes) to grow and increase in numbers. One of the widespread species of sparse woody plants in the Rupununi Savannah is the fire-resistant treelet *Curatella americana*, with a thick corky bark and xerophytic leaves. Importantly, fires are a direct threat to bush-islands and forest at the savannah edge and notable decreases of forest cover appear to have occurred on the forested mountains over the last decades (B.J.H. ter Welle pers. comm., M.J. Jansen-Jacobs pers.obs., H. ter Steege pers. obs.). Especially during severe El Niño years, such as the 1997-1998 event, fires may cause substantial damage to forest in and around the savannah (Hammond and ter Steege 1998).

Flora of Southwest Guyana

The floristic composition of SW Guyana is known to some extent as a result of activities of botanical collectors since the 19th century, notably Robert Schomburgk between 1835-1843, Richard Schomburgk in 1840-44, A.C. Smith in 1937-38, G. Wilson-Browne in 1948, and R.J.A. Goodland in 1963 (Ek 1990).

Since 1979 the Utrecht Herbarium conducts systematical botanical explorations of the southern part of Guyana in the framework of the 'Flora of the Guianas' project (Appendix 5). The explorations resulted in a database of 6333 specimens of vascular plants from this area. The aim of this chapter is to describe the floristic composition of the northern and southern Rupununi and the forests surrounding them on the basis of this database and to shed light on the position/significance of the flora of the Rupununi Savannah in Guyana.

The 6333 records of vascular plants in SW-Guyana represent 3618 species belonging to 150 families, 65% of all species collected in Guyana so far (see Table 2.1). The families, best represented in terms of species are: Fabaceae (131 species), Rubiaceae (131), Poaceae (124), Pteridophyta (111), Cyperaceae (107), Orchidaceae (90), Melastomataceae (89), Caesalpiniaceae (72), Euphorbiaceae (70), Mimosaceae (52) and Asteraceae (51). The most species-rich genera are: *Miconia* (28), *Psychotria* (26), *Rhynchospora* (26), *Piper* (24), *Utricularia* (24) and *Polygala* (21). The largest number of species (1165) was found in the South Rupununi Savannah (2281 collections), against 713 species from the North Rupununi Savannah (1149 collections). The difference is partly due to the more intensive collecting activity in the South Savannah, but probably also to the presence of the inselbergs in the South Savannah (a random sample of 1149 collections yields 764 species). Comparing those two samples from the two areas shows that of a total of 1203 species only 23% were common to the North and South Rupununi, 40% has been collected only in the South Rupununi and 36

% only in the North Rupununi. Thus, the two areas are either severely under-collected or substantially different in floristic terms.

In the Kanuku Mountains, 929 species were found/collected (1644 collections). It is expected that many more species will be recorded in the future once collecting of the taller, inaccessible trees progresses. In the Upper Essequibo Region 813 species were collected (1249 collections). This number will also increase with increased collecting effort, as the area is still very much 'under-collected' (Chapter 6).

Vegetation types of the Savannah area

The main savannah area is divided by the Kanuku Mountains in the North and South Rupununi Savannah. The border between the, mostly forested, Kanuku Mountains and the savannah area is not sharp. In this zone, mostly at lower altitudes, some small savannahs pockets surrounded by forest exist. The southern border of the Rupununi Savannah is situated more or less around the Cuyuwini River. Here, the savannah landscape is interrupted by bush islands, which gradually coalesce into the extensive Amazonian forest of South Guyana.

Savannah
Fanshawe (1952) classified the fire-climax savannah vegetation as the *Curatella-Byrsonima* association, with contains characteristic species such as: *Curatella americana, Byrsonima crassifolia, Byrsonima coccolobifolia, Antonia ovata, Palicourea rigida, Tibouchina aspera* and *Amasonia campestris*. The main grasses belong to the genera *Trachypogon, Paspalum, Axonopus* and *Andropogon* and the main sedges to the genera *Rhynchospora* and *Bulbostylis* (Myers 1936, Fanshawe 1952, Jansen-Jacobs pers. obs.). Some species tend to appear and flower only after substantial rain, such as the herbs: *Schultesia benthamiana*, *Schiekia orinocensis*, *Polygala* spp., *Abolboda pulchella* and the bulbous herbs: *Curculigo scorzonerifolia*, *Alophia drummondii* and *Cipura paludosa*. In other herbs flowering is induced by fire. These species often have a subterraneous woody stem, such as: *Byrsonima verbascifolia, Clitoria guianensis,* and *Cissampelos ovalifolia*. In the whole savannah area the parasite *Cassytha filiformis* is common.

Bush islands
Small forest patches, locally called 'bush islands', are found commonly within the savannah. The bush-islands vary in size, the larger ones are found on the more elevated places in the landscape and sometimes are rocky. The latter type of bush-island is more frequent in the South than in the North Rupununi Savannah. The height of the trees in larger bush-islands is not more than 10 m. Several tree species, which are common in bush-islands, also occur in the more open savannah area as solitary trees: *Himatanthus articulatus, Curatella americana, Humiria balsamifera, Byrsonima* spp., *Palicourea rigida, Tocoyena neglecta* and *Vitex schomburgkiana*. *Curatella americana,* the most common woody plant in the savannah area, has only been collected a few times.

Rocks
The South Rupununi Savannah in particular has many places with bare rock . These rocks can vary from small flat plates to large outcrops, up to 50-80 m high. On such rocks typical 'rock vegetation' occurs in the small patches wherever some soil substrate is present. The species present on the smallest rock plates are: *Cereus hexagonus, Melocactus smithii, Cnidoscolus urens, Cyrtopodium glutiniferum* and *Portulaca sedifolia*. On more extended rocks *Furcraea*

foetida is found too, as are woody species such as *Cyrtocarpa velutinifolium*, *Clusia* spp., *Mimosa brachycarpoides, Bredemeyera floribunda* and *Cestrum latifolium*. On the slopes of Shea Rock and Mt. Shiriri, well-known rocky outcrops in the South Rupununi Savannah, mats formed by *Pepinia geyskesii*, and on places with running water *Sinningia incarnata* and *Anemia* species occur.

Bare rock is also found on the highest peaks (ca. 800-900 m) of some mountains (primarily the Kanuku Mts. and Mt. Makarapan). Woody elements here are a.o. *Clusia palmicida, Erythroxylum mucronatum* and *Myrcia sylvatica.*

Wet savannah and ponds
Ponds are a common feature of the Rupununi Savannahs. They are fully extended in the wet season and dry up gradually in the dry period, although some have water the year round. Except of real aquatic plants, of which the common ones are listed in Table 11.6, there exists a broad variety of plants adapted to wet and dry circumstances. These plants, nearly all herbaceous, are mostly in flower when the ponds are drying up and the soil is still muddy. Some genera, or even families, are represented with several species in the wet savannah, such as *Cyperaceae, Eriocaulaceae, Aeschynomene, Utricularia, Acisanthera, Sauvagesia, Ludwigia, Polygala*, *Bacopa* and *Xyris*.

Oxbow lakes and ponds near Karanambo
Some ponds in the surroundings of Karanambo are isolated parts of the meandering Rupununi R., so-called oxbow lakes. The water level in these ponds varies with the level of the river. The vegetation along the ponds has much in common with the forest along the Rupununi R. but remarkable is the abundance here of *Cordia grandiflora, Bothriospora corymbosa, Chomelia angustifolia*, and *Simaba orinocensis*. The famous *Victoria amazonica* is common in the aquatic vegetation of the ponds. Eight other real aquatic plants have been collected here, of which *Polygonum acuminatum* and *Eichhornia azurea* have not been recorded from other ponds in the area.

Rivers and creeks
The main river system in southern Guyana belongs to the Essequibo drainage basin, including the Rupununi R. that drains most of the Rupununi Savannahs. The Takutu R. and Ireng R., which drain the westernmost parts of the savannah, are part of the Amazon basin. The water-divide between these drainage systems lies in north-south direction in the Rupununi area. When the Savannah is flooded waters from both river basins merge.

The rivers in the savannah area are bordered by gallery forest, which is inundated during part of the year. The height of the vegetation mostly does not exceed 10 m. The forest along the river and larger creeks in the Kanuku Mts. is somewhat higher, 15-20 m. Trees species such as *Caryocar microcarpum, Macrolobium acaciifolium, Senna latifolia, Zygia cataractae* and *Genipa spruceana* occur along all the rivers in S-Guyana. Common liana species are *Cydista aequinoctialis* and *Memora schomburgkii*. *Mauritia flexuosa* is the most common tree along rivers and creeks. In the open savannah *Mauritia* is a dominating element in the landscape. Some woody species are present only along the rivers in savannah area, such as *Faramea crassifolia, Genipa americana, Rosenbergiodendron densiflorum, Waltheria involucrata*, and *Clerodendrum aculeatum*; others are confined to the wetter environment of the Kanuku Mts. and Upper Essequibo Region, such as *Duguetia quitarensis, Licania leptostachya, Zygia inaequalis*, and *Mouriri acutiflora*. Some species tend to a more northern distribution, such as *Lecythis schomburgkiana, Pouteria glomerata, Crateva tapia*, and *Chomelia angustifolia*;

others to a more southern distribution, such as *Alchornea schomburgkii, Andira surinamensis, Etaballia dubia*, and *Swartzia panacoco*.

The Rupununi Savannahs in a regional context

It is remarkable that species that are dominant in the Rupununi Savannahs such as *Curatella americana, Byrsonima crassifolia*, and *Palicourea rigida* occur in all savannahs in northern South America, but most of the other species are less widespread. Genera are often similar, but the species differ. Comparable savannahs are the Gran Sabana in Venezuela (Huber 1995a), the Rio Branco Savannah in Brazil (see Takeuchi 1960, Milliken & Ratter 1998) and the Sipaliwini Savannah in Suriname (van Donselaar 1969). Also the Intermediate Savannah, although on the Berbice Formation, shares most of the common species with the Rupununi savannahs (see e.g. Fanshawe 1952).

[*This is obviously an area where we have to expand a bit more*]

The savannah region of Southern Guyana contributes a very distinct floristic element to Guyana's [*and the Guiana shield*] plant species-richness. The composition of the flora differs substantially at the species, genus and family level. The Intermediate Savannah, on the Berbice Formation, shares many of its common species with the southern savannahs but a complete floristic inventory was not possible at present.

The Southern Rupununi has a, for Guyana, unique rock vegetation that is quite vulnerable to disturbance.

Fire is important in the maintenance of low savannah vegetation. Recurrent fire, however, is one of the most important threats to the forests surrounding the savannahs but possibly also for the herbaceous savannah itself. Protection of this unique area should therefore include strict fire management.

The forests of the Kanuku Mts. differ substantially in their composition from the forests in central and south Guyana. At present we have very little quantitative and qualitative data to make a good comparison, however.

The savannahs with their forest edges, and surrounding mountains are one of the most impressive landscapes in Guyana.

Implications for conservation:

Because of its unique contribution to the flora of Guyana and its unique landscape, the savannahs in southern Guyana have considerable conservation potential. The south Rupununi Savannah may be the least disturbed, a fact already noted by (Myers 1936).

There are considerable potential conflicts between utilisation and conservation in the savannah area, due to the relatively high concentration of people living and utilising the area. Conservation in this area will have to be achieved by finding a good balance between protection and utilisation by the people living in it. While it may be relatively easy to

preserve the vastness or impressiveness of the landscape, protection of the unique flora may be more difficult. Recurrent fire is considered one of the most important threats of the savannah system, although paradoxically, it may also be necessary for the maintenance of that same savannah. The effect of fire on the savannah ecosystem and its surrounding forests should therefore be considered an important issue.

Fire is also a threat to the forests surrounding the savannahs and considerable changes have already taken place at the forest-savannah interface. Here, stricter fire control measures should be put into place, if these forests are to be protected.

The rock vegetation in the south Rupununi Savannah is quite vulnerable to disturbance. Although this unique vegetation type may be little endangered at present, increased visits to rocky areas may damage the vegetation beyond the capacity to recover. Hence, in order to protect this vegetation somewhat stricter rules are necessary.

The Kanuku Mts. are an impressive part of the southern landscape and have forests not found in abundance elsewhere in Guyana, such as dry deciduous forests (see also Chapter 5). Together with the slightly wetter forests in the east, which continue towards the south, some of the least disturbed forests can be found. Possible the best wilderness protection opportunities exist in an area from the eastern Kanuku Mts. towards the east and south.