

The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest

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Abstract

The impact of soil cover organization on the forest community has been studied in a 19-ha tract at Piste de St Elie station in French Guiana. 195 species each represented by at least 10 individuals were chosen from records of the position, diameter at breast height (dbh) and precise identification by botanical sampling of 12 104 ligneous plants (dbh \geq 10 cm).

Spatial variations in the soil were mapped using the method proposed by Boulet et al. (1982). The soil mapping units correspond to the successive stages of evolution of a currently unbalanced ferralitic cover. These stages describe firstly the thinning by erosion of the microaggregated upper horizon and secondly the mineralogical changes under more or less extended hydromorphic conditions. The degree of evolution of ferralitic cover is also related to the hydrodynamic functioning and chemical properties of the soil. Geological substrate, topography and slope have also been taken into account.

Analysis of the influence of environmental variables on plant cover has been performed using the Ecological Profiles method and Correspondence Analysis (CA) of the table of ecological profiles.

The forest community seems to be dependent on the soil and the topographical features that govern it. There are significant, exclusive soil-species links for each soil functioning mapping unit. However, the highest proportion of significant positive links is connected with a thick microaggregated horizon (25%). Several species are of real value as indicators and more particularly enable differentiation between the forest stands of typical ferralitic soil and the ones of thinned out, transformed and hydromorphic soils. The CA of the species by environmental variables matrices reveals two significant factorial axes. The first can be associated with the drainage mainly related to the thinning of the soil and the second with the hydromorphic conditions related to the topography. The vegetation ordination of the stands (\cong 0.25 ha) delimited in the various soil domains clearly shows that changes in ferralitic cover and in particular the transition from soil with deep vertical drainage to soil with superficial lateral drainage is accompanied by substantial changes in the forest community.

Introduction

The spatial organization of woody tropical forest plant populations can be perceived today as the result of

spatial and temporal interactions between three components, initially described separately in the literature:

- the impact of the physical and chemical features of the environment, especially soil factors (Richards 1952; Lemée 1960);

- the dynamics of each species, related to biotic factors (Janzen 1970; Connell 1971; Harper 1977) and environmental changes in time (Gleason 1926; Leigh 1983);

- the canopy gap processes (Aubréville 1938; Whitmore 1978)

Subsequent works confirmed and attempted to appraise the relative influences of these components, integrating them in more general concepts and models generally used to explain the closely related species richness and diversity in tropical forests (see Huston 1994, for a synthetic review).

In soil factors, there is a clear relationship between the major types of forest vegetation in terms of stature, architecture and species composition, and the main soil classes (see, for example, Davis & Richards 1934, for Guyana; Brunig 1983, for Sarawak; Prance 1987, for Amazonia). Some authors attempted to measure, at a local scale, the impact of topography and certain soil variables such as chemical fertility or drainage on the structure and composition of dense tropical forests (Austin et al. 1972; Newbery & Proctor 1984; Lescure & Boulet 1985; Newbery et al. 1986; Gartlan et al. 1986; Barthès 1991; Basnet 1992; Johnston 1992; Steege et al. 1993; Korning et al. 1994). Newbery (1991) stressed the difficulties, due to the unsuitability of forest inventories which are too small or due to regional and local gradients being mixed in the same set of forest plots encountered in such an operation in 'kerangas forest'. To these are added inadequate knowledge of taxonomy and the difficulties of spatial analysis of soil features. The existence of correlations between catenas or nutrient gradients and forest composition is now well known but as stated by Steege et al. (1993), the relation between soil factors and forest types remains far from clear for many tropical countries. In addition, to the fact that soil factors, and especially nutrient availability as stated by Tilman (1982), can play an important role on species competition in a narrow range of variation close to limiting thresholds (a situation probably dominant in humid tropics) is still a theoretical concept in tropical forest communities.

The first study of the impact of soil on the organization of the tree community in French Guiana was carried out within the framework of the ECEREX program (ECology, ERosion, EXpérimentation) at Piste de St Elie Station (Lescure & Boulet 1985) using an original method of study and mapping of the soil cover (Boulet et al. 1982). Unfortunately, only 32 taxa identified using the vernacular name method were studied.

The same approach was used by Barthès (1991) for the study of the spatial distribution of two species of the genus *Eperua* (Caesalpiniaceae). Following these initial operations, ORSTOM (Institut français de recherche scientifique pour le développement en coopération) did support a study programme on organization factors in the tropical forest community in French Guiana, consisting of sufficiently broad and taxonomically reliable botanical inventories and incorporating recent knowledge of the organization and hydrodynamic functioning of the soil cover, in order to find answers to the questions that led to the first results and in particular:

- to what extent can soil variables account for the heterogeneity of spatial distribution of trees in this tropical forest?

- what is the scale of soil-generated heterogeneity?

- are there any species that operate as indicators of the main soil conditions?

- has species richness been broadly affected by the evolution of the pedological cover and its spatial organization?

- is it possible to use field measurements of soil variables to verify the theory of fine adjustment of ecological niches in tropical forest plants?

Material and methods

Study area

Piste de St Elie Station is located at the northern edge of the Guiana-Amazon forest (5° 18' N, 53° 3' W) on the coast of French Guiana. The climate is the humid tropical type with annual precipitation ranging from 2.5 to 4 m.

The geological substrate belongs to the Palaeoproterozoic 'Armina formation' volcano-sedimentary series (Milési et al. 1995). Very fine micaschist rich in muscovite and quartz is dominant at the station (Grimaldi et al. 1994). It contains veins of pegmatite of very variable size (0.1 to 100 m) made up of phenocrystals of quartz, feldspar, muscovite and tourmaline. The boundary between schist and pegmatite is always very sharp and although the weathered layer of the rock (saprolite) is 20 to 30 m thick, its heterogeneity still shows clearly in the soil in the quartz particle size: fine sand on schist, coarse sand and gravel on pegmatite.

The studied tract comprises 19 one-hectare plots (Figure 3); 17 of them, lying in a 1000 × 1000 m area gridded at 100 m intervals, have been identified according to their Cartesian coordinates (number of the

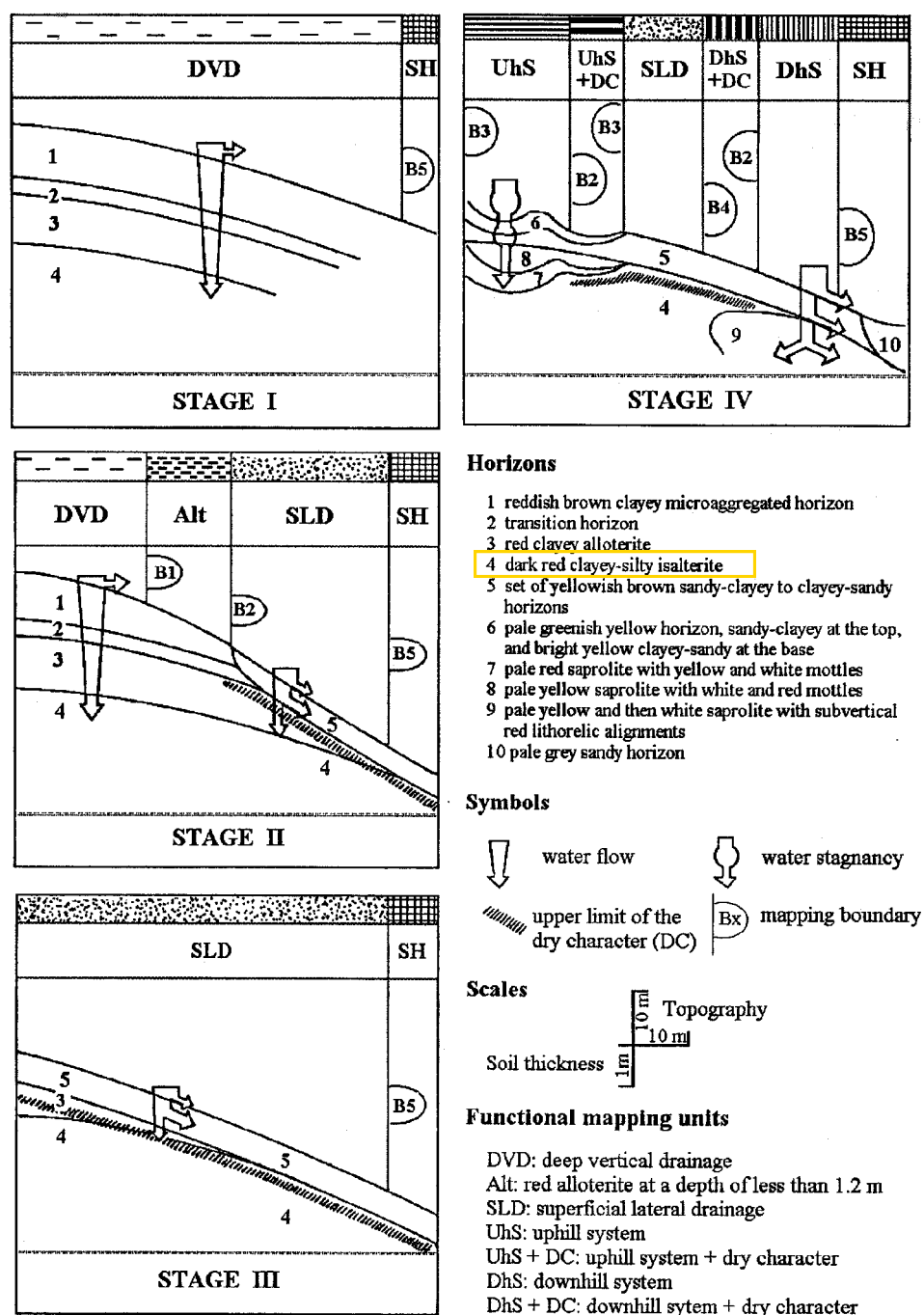


Figure 1. Stages of evolution of the soil cover at Piste de St. Elie station (adapted from Boulet et al. 1993).

N-S line – letter of the E-W line), the two remaining plots (P and R) are located to the east and are at or near the watershed B of the ECEREX programme. Only plot R is shared with the Lescure & Boulet's 1985 study.

Further details of the site and its forest population can be found in Sabatier (1985) and Lescure et al. (1990).

State of knowledge of organization and functioning of the soil cover

The spatial variations of the soil on schist and pegmatite are substantial but ordered on the scale of the landscape unit. Detailed studies of elementary catchments (Boulet 1983; Fritsch et al. 1986) have enabled the identification of several stages of evolution (Boulet et al. 1993; Figure 1) in a currently unbalanced ferrallitic cover. The cover is no longer in phase with present tectonic or climatic constraints which control factors of weathering and pedogenesis (Nahon 1991; Fritsch & Fitzpatrick 1994). The result is an extension of hydromorphic soils from ferrallitic ones. The imbalance has probably been induced by a slight uplift of the Guiana bedrock in reaction to the subsidence of the Amazon and Berbice basins, nevertheless climatic changes cannot be excluded (Boulet et al. 1979).

Stage I consists of the initial ferrallitic cover which successive horizons maintain a constant thickness on the whole of the slope. A reddish brown clayey horizon, 1 to 2 m thick (Figure 1, horizon 1) with a microaggregated structure underlies a thin humic horizon. The microaggregated structure is progressively less developed at depth (horizon 2). The clay content then decreases in favour of fine silt of partially kaolinized muscovites (Tandy et al. 1990) in a red clayey weathering horizon, the 'alloterite' according to Nahon (1991), with a weakly developed medium angular blocky structure (horizon 3), and finally in a dark red clayey silty saprolite, the 'isalterite' (Nahon 1991), rich in muscovite with a massive structure (horizon 4).

In stage II, a set of yellowish brown horizons (5), sandy-clayey with a polyhedral structure at the top and clayey-sandy to clayey with a compact appearance at the base, appears downslope and develops from all horizons (1 to 4) of the initial ferrallitic cover. From downslope to upslope, microaggregated horizons 1 and 2 thin out and then disappear. They only remain upslope. Weathering horizons (3 and 4) are then at a depth of less than one metre and become 'dry to the touch' in all seasons.

In stage III, horizons 1 and 2 disappear throughout the slope.

The main horizons of these three stages of evolution of the soil cover differ markedly in pore space (Grimaldi & Boulet 1990). The porosity of the microaggregated horizon (1) is equally distributed between two categories of pores with very distinct sizes (Figure 2): micropores of uniform size (modal size: 10 to 20 nm) resulting from the association of clay particles

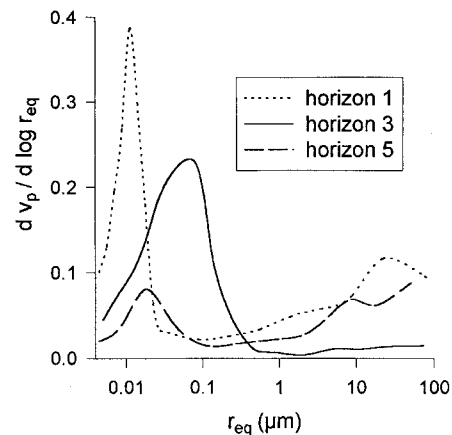


Figure 2. Distribution of pore volume (v_p , $\text{cm}^3/\text{g}^{-1}$) according to pore size (r_{eq}) in horizons 1, 3 and 5.

in the microaggregates, and a macropore category with a broad spread of sizes, grouping intermicroaggregate pores, and channels and vughs of biological origin. The pore size distribution of the red clayey 'alloterite' (3) is practically unimodal (Figure 2), with a single class of fairly varied pores (10 nm to 1 μm) resulting from the association of heterogeneous elementary particles. The sandy-clayey horizon with a polyhedral structure (5) has a bimodal pore size distribution in which macropores are dominant (Figure 2).

The organization of the soil cover along the slope was used to establish its functioning, taking mineralogical composition and pore space characteristics into account. The volume and continuity of macropores provide the microaggregated horizon with a water absorption capacity according to its thickness. Filtration of water is slowed in the horizon with unimodal pore size distribution. When this horizon approaches the surface, a perched water table is formed above it during heavy rains. The result is lateral saturated throughflow (Chorley 1978) in the macroporous sandy-clayey horizon (5). Drainage is superficial and lateral (SLD: Superficial Lateral Drainage) whereas it is deep and vertical (DVD: Deep Vertical Drainage) when the microaggregated horizon is thick (Humbel 1978; Guehl 1984). Transformation of the ferrallitic cover is caused by chemical erosion, i.e. dissolution of minerals in the perched water table with lateral flow (Grimaldi 1988), whereas conditions are favourable to the continuation of weathering by neoformation of kaolinite when vertical drainage slows (Grimaldi et al. 1992).

In stage IV (Figure 1), transformation continues under more or less extended hydromorphic condi-

tions causing a redistribution or export of iron. Fritsch (1984) makes a distinction between two hydromorphic systems, the uphill system and the downhill system. In the uphill system (UhS), soil saturation between precipitations lasts longer when the slope is more gentle on flat-topped hills. This saturation affects the top of the dark red saprolite (4), which becomes pale red (7) and pale yellow with white and red mottles (8). The soil is a bright yellow and sandy clay above this heterogeneous saprolite and then becomes a pale greenish yellow and clayey sand near the surface (6). The uphill system is associated with closed depressions from one to several metres in diameter and as much as 0.70 m deep; these finally interconnect to form channels. Stagnant water in the depressions of the uphill system during the rainy season indicates a confined environment. In the downhill system (DhS), lateral saturated throughflow in horizon 5 feeds the groundwater that flows slowly along the main drainage axes several days after rain fall. The possibility of discharge of groundwater during the rainy season characterizes a more open environment than the uphill system. This groundwater transforms the dark red 'isalterite' (4) from downslope into heterogeneous saprolite that is yellow and then white with red mottles (9); the 'dry to the touch' character disappears. In lowland, the superficial grey horizon (10) has low iron and clay contents.

Soil mapping

Knowledge of the successive stages of evolution of the ferralitic cover is used to retain features of pedogenetic significance and those related to the dynamics of water in the soil for soil mapping. The soil mapping method used had been proposed by Boulet et al. (1982). This method does not refer to a pre-established soil classification and aim to provide ecologists with a representation of the organization and functioning of the soil cover (Lescure & Boulet 1985). The results of auger borings along several transects were used to delimit the following soil morphological characters or sets of characters (Guillaume 1992):

- *Boundary 1*: appearance of the red alloterite (3) characterized by abundant muscovite particles at a depth of less than 1.2 m (Alt). This is the first sign of the thinning out of the initial ferralitic cover. Boundary 1 delimits the 'Alt' mapping unit from ferralitic soil with Deep Vertical Drainage (DVD).
- *Boundary 2*: appearance of the 'dry to the touch' character (DC) at a depth of less than 1.2 m. This criterion was very clear as mapping had been performed

during the rainy season. The 'dry' character appears after more marked thinning out of the initial ferralitic cover. Boundary 2 delimits the Superficial Lateral Drainage mapping unit (SLD).

- *Boundary 3*: appearance of pale red saprolite (7), the first sign of the uphill system (UhS) at a depth of less than 1.2 m. When associated with the 'dry to the touch' character, it delimits the UhS + DC mapping unit.

- *Boundary 4*: appearance of yellow, red mottled saprolite (9), the first sign of the downhill system (DhS) at a depth of less than 1.2 m. When associated with the 'dry to the touch' character, it delimits the DhS + DC mapping unit.

- *Boundary 5*: surface hydromorphy (SH) with more than 10% grey and rusty mottles in the humic horizon. This character is associated with thalwegs in a manner that is relatively independent of the stage of evolution of the ferralitic cover.

Physical measurements and chemical analyses

We have aimed to specify the relations between soil mapping units and the water regime and chemical properties of soil in terms of soil constraints for plants. In order to show excess or shortage of water, the variations in the soil water potential according to rainfall were monitored at five tensiometer stations representative of the main mapping units described above: DVD, SLD, UhS, DhS and SH. Five to ten tensiometers, depending on the station, were installed at depths of 0.1 to 2 m.

Classical chemical analyses of soil samples were performed on the fraction < 2 mm at four depths (0–10, 10–20, 20–30, 30–40 cm) in DVD and SLD mapping units. Ten boreholes were drilled at these two pedological domains to take into account the spatial variability of the soil. The total carbon content was determined by the Walkley & Black method (Dabin, 1965), the total nitrogen and phosphorus contents respectively by the Kjeldhal and Duval methods (*in* Dabin, 1967). Soil pH was measured in a 1:2.5 soil:water suspension. Exchangeable cations (Ca^{++} , Mg^{++} , K^+ , Na^+) were extracted with 1M ammonium acetate solution and Cation exchangeable capacity (CEC) was determined at pH 7 (Pelloux et al. 1971). Exchangeable aluminium was extracted with 1M KCl solution.

Botanical observations

The botanical data cover all ligneous plants with a dbh of 10 cm or more in the 19 one-hectare plots. A total

of 11 905 trees, 184 lianas and 15 hemiepiphytes were recorded and measured (dbh) and their positions noted to within one metre. Identification was performed by the collection of a botanical sample when a plant was not identified *in situ* with certainty by one of the team's botanists. A total of 550 species were identified, with 195 species represented by 10 or more individuals and 112 species represented by 20 or more individuals. These subsets were subsequently used for statistical analysis of the behaviour of species. Nomenclature follows the Checklist of the Plants of the Guianas (Boggan et al. 1992). Variations in stem density, dbh and basal area distributions and the specific richness of the main pedological mapping units have been examined.

Statistical analysis

Environmental descriptors

The forest community was plotted using a grid of 5×5 m quadrats to relate environmental and botanical data. Several environmental descriptors were allocated to each quadrat (Table 1). Geomorphology was described by two descriptors: the topographic situation and slope class. The two geological substrate classes, schist or pegmatite, were identified by the size of the quartz and muscovite particles. Soil descriptor classes are the mapping units, except for the SLD unit which was divided in two classes according to the appearance depth of the 'dry to the touch' character. Since it may occur in all stages of evolution, SH (presence or absence) is potentially a second soil descriptor. However, in our study, SH conditions have been found almost exclusively related to stage IV (Figure 3b) except for two very small pockets in 10-B and 6-F with 48 and 30 trees respectively. SH was thus handled as a soil descriptor class. For quadrats including several mapping units, the broadest gives the descriptor class.

Quadrats were not useful in the study of the locations, since 5×5 m grid units contained only 1 to 3 trees, and the largest quadrats frequently include two or more environmental classes. The various pedological domains were therefore divided into 0.2 to 0.3 ha stands (i.e., 120–200 trees) that were as square as possible according to the size and shape of the mapped area. The smallest entities were not considered in further analysis, except for UhS + DC in 4-B (91 trees), SLD2 in 6-J (87 trees) and SH in 6-B (90 trees) and 9-B (77 trees). This provided the following set of stands

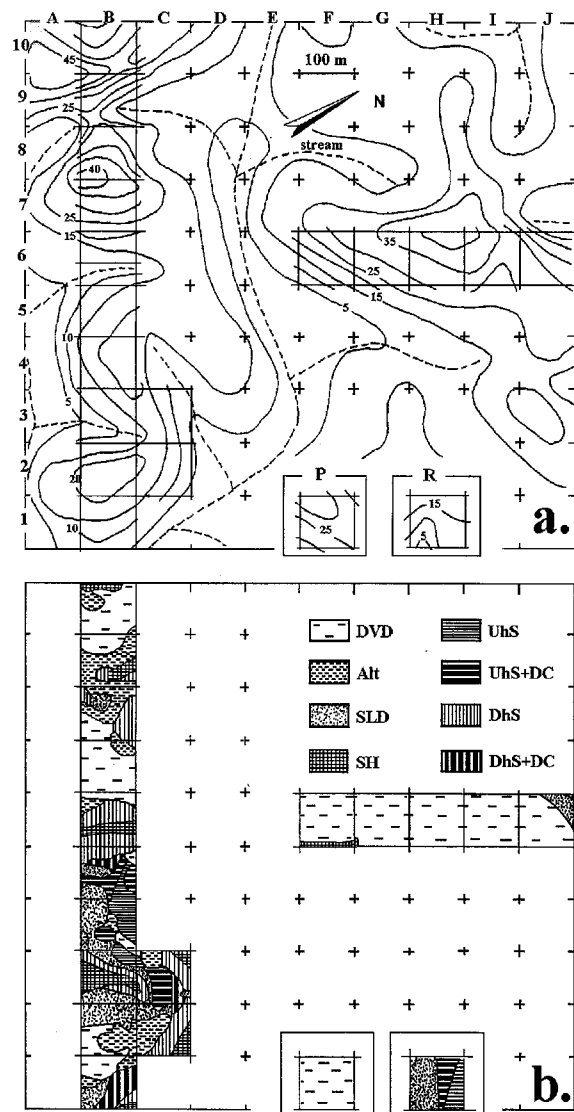


Figure 3. Topography of the areas studied (a) and Soil mapping used in analysis of soil-population relations (b). The 1 ha plots (squares) are numbered according to the Cartesian coordinates of their bottom left-hand corner, except for P and R plots that are apart from the main area.

for analysis: DVD: 34; Alt: 7; SLD: 9; UhS: 7; DhS: 8; SH: 4.

Study of ecological profiles

According to the null hypothesis (H_0) of random distribution of a species among the classes of a descriptor, there is equality of the relative frequencies observed for a class of this descriptor (rf) and for all the records (Rf);

Table 1. Environmental descriptors.

Topography	Soil descriptor
1 – lowland	1 – deep vertical drainage (DVD)
2 – foot-slope	2 – weathered material at less than 1.2 m (Alt)
3 – middle-slope	3 – dry character between 1 and 1.2 m (SLD1)
4 – upper-slope	4 – dry character at less than 1 m (SLD2)
5 – flat hilltop	5 – uphill system (UhS)
6 – ridge	6 – uphill system and dry character at less than 1.2 m (UhS+DC)
	7 – downhill system (DhS)
Slope:	8 – downhill system and dry character at less than 1.2 m (DhS+DC)
1 – level land (0–5%)	9 – surface hydromorphy (SH)
2 – gentle slope (5–15%)	
3 – steep slope (15–30%)	
4 – very steep slope (>30%)	
Substrate:	
1 – schist	
2 – pegmatite	

the absolute frequency of the species is then its expected frequency (Ef) (Appendix 1). The corrected frequency (Cf) is the ratio of the observed rf and Rf ; thus, it is also the ratio of observed frequency and expected frequency (Appendix 1). It can be understood as the number of times that a species is represented in relation to its expected frequency according to its random distribution (e.g., 0.5: half; 2.0: twice). The profiles of corrected frequencies (Godron 1966) were calculated in order to analyse the distribution of the occurrences of each taxon in the descriptor classes.

When observed frequency is higher than expected frequency, it is interesting to test the hypothesis of 'attraction' of the species by environmental characteristics and, conversely, if the observed frequency is lower, it is interesting to test the hypothesis of 'repulsion'. In both cases the test is Fisher's exact test of proportions (Siegel 1956; Sokal & Rohlf 1969), referring to one tail of the hypergeometric distribution (Appendix 1). This test works with the 2×2 contingency tables associated with the frequencies observed in each descriptor class. It is well suited to finite populations and exclusive pairs of characters (Dagnelie, 1970) and leads to the indexed profile (Gauthier et al. 1977) when systematically applied.

The mutual information (MI) between descriptor and taxon (Godron, 1968) has been calculated. The strength of the connection between descriptor and frequency of a taxon can be assessed. The degree of significance and the corrected frequency give this informa-

tion for each descriptor class while mutual information between the descriptor and the taxon show the whole profile. The ratio $Q(L)$ of measured entropy (function of the actual distribution of samples in the descriptor classes) and maximum entropy (equal distribution of samples in the descriptor classes) of a descriptor (Daget & Godron, 1982) shows the quality of sampling; the latter is better when the value approaches 1.

Correspondence analysis of the ecological profile table

Analysis of species-environment relationships can be performed by correspondence analysis of the table of profiles of absolute frequencies. This procedure proposed by Romane (1972) was used and completed by Bonin & Roux (1978). Montaña & Greig-Smith (1990) and Mercier et al. (1992) showed that the procedure is a convenient alternative to the canonical correspondence analysis of Braak (1986). They showed the fundamental properties and extended application to quantitative data, which is more convenient in cases of very low beta diversity with relevés differing mostly in species abundances. The method enables the simultaneous ordination of species, environmental classes and stands. The scores of the sites are computed as additional columns after correspondence analysis of the ecological profile table with species as rows and environmental classes as columns (Bonin & Roux 1978).

As indicated by the authors and mentioned by Mercier et al. (1992), 'the scores of species are computed according to their relationships with the environmental classes and the scores of the sites are computed subsequently as a function of the species which occur in each stand'. The property of 'équivalence distributionnelle' (Bonin & Roux 1978) enabled use of stands of unequal size.

Results

Pedology

The experimental layout crosses several hills with very different topographic and soil characteristics (Figures 3a and 3b). Thus, the hill with a broad flat area at the top (coordinates 4-B to 5-C, Figure 3b) displays uphill and downhill transformation systems whereas the large elongated hill (coordinates 6-F to 6-J) is almost entirely covered by DVD soils. The various stages of transformation of the ferrallitic cover have been observed on both types of bedrock. However, when pegmatite and schist are found on the same slope, the transformation is one stage ahead on pegmatite, whose weathered material has a lower iron content than the one of schist (Fritsch 1984).

Tensiometer measurements show the substantial differences between the hydrodynamic functioning of the five soil mapping units considered. The results presented to illustrate the water status of the soil during the rainy season (Figure 4a) are for the day after rainfall (25 mm) after a fairly wet period during the rainy season (330 mm during the 10 days preceding the measurements). The water status of the soil in the dry season is illustrated by two successive records (Figures 4b and 4c) after 25 and 47 days respectively with practically no rainfall (43 and 57 mm respectively of cumulated precipitation).

The day after rainfall (Figure 4a), the positive values of the matric potential of the water show prolonged saturation (> 24 h) of the soil cover, with the exception of the soil with deep vertical drainage (DVD) in which saturation is always short-lived (a few hours after the heaviest rainfall). The records at the tensiometer station for the downhill system (DhS) also differ from those of the other stations, with water matric potentials that were close to 0, as much as 0.8 m and then negative. This can be explained by the strong slope near the station, which facilitates the lateral flow of water accumulated above the weathered material. At

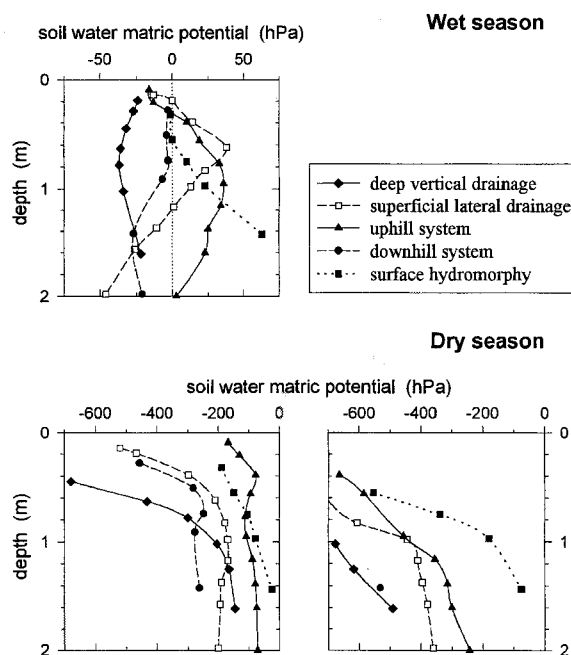


Figure 4. Seasonal variations of the matric water potential profiles at five stations representative of the main soil mapping units: one day after a 25 mm rainfall (a); after a 25-day dry period (b); after a 47-day dry period (c). Values above zero indicate soil water saturation.

the other stations, saturation starts at a depth of 0.2 or 0.3 m. The shallowest soil layer with very strong root density (Humbel 1978) was thus not subjected to this excess water phenomenon. Saturation reached a maximum depth according to the soil type. It attained 2 m or more in the uphill system (UHS) and thalweg soil with a surface hydromorphy (SH), about 1 m in the soil with superficial lateral drainage (SLD), that is to say the depth at which the 'dry to the touch' (DC) phenomenon appears.

The five pedological situations also differ in the rate of drying of the soil (Figures 4b and 4c). The soil with deep vertical drainage (DVD) dries the fastest, at least in the layer between the surface and a depth of 0.6 m. The store of water that can be used by the plants is therefore rapidly exhausted at the top of the microaggregated horizon. In contrast, after 25 days with practically no precipitation (Figure 4b), the tensiometer stations showed that there was still substantial moisture in the thalweg soil with surface hydromorphy (SH) and in the uphill system (UHS). The surface lateral drainage soil (SLD) and the downhill system (DhS) behaved in an intermediate manner. After a 47-day dry period (Figure 4c), behaviour of the uphill system soil

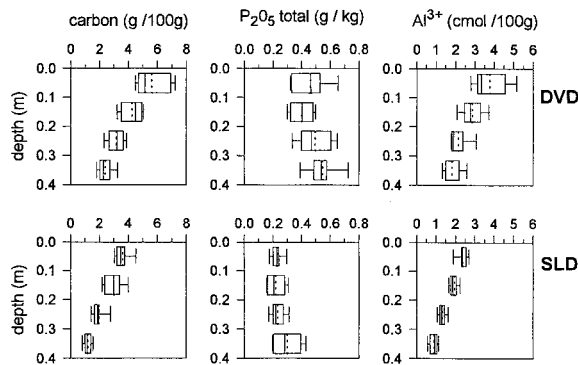


Figure 5. Comparison of soils with deep vertical drainage (DVD) and superficial lateral drainage (SLD) for three chemical elements that are important for soil fertility (carbon and P₂O₅) or toxicity (Al³⁺).

(UhS) was similar to the one of the superficial lateral drainage soil (SLD).

These differences in hydrodynamic behaviour are accompanied by differences in chemical properties, as verified for two soil units (DVD and SLD) (Figure 5 and Table 2). The soil with deep vertical drainage (DVD) displayed significantly higher carbon, nitrogen, total phosphorus and exchangeable aluminium contents than SLD soil; the cation exchange capacity was also higher (Mann-Whitney U test, $P = 0.002$). The difference was only substantial for depths of 25 and 35 cm for all the exchangeable bases ($P = 0.02$, Mann-Whitney). The pH values only diverged significantly at depths of 15 and 25 cm ($P = 0.05$ and $P = 0.02$ respectively, Mann-Whitney).

Impact of the environmental variables on the occurrence of taxa

Analysis of the ecological profiles (see Appendix 2 for species represented by 20 individuals or more) shows that a substantial proportion of the species display a significant reaction to the environmental descriptors.

The soil descriptor was satisfactorily sampled: $Q(L) = 0.85$. A large proportion of profiles with a significant response (positive or negative) was obtained in at least one of the descriptor classes for species with a minimum of 10 individuals (i.e. 68% – $P < 0.05$; 44% – $P < 0.01$; 28% – $P < 0.001$; $N = 195$); this proportion increased distinctly when there were at least 20 individuals (i.e., 78% – $P < 0.05$; 57% – $P < 0.01$; 39% – $P < 0.001$; $N = 111$). Corrected frequencies and MI values showed that many species had weakly contrasted profiles (i.e., tending

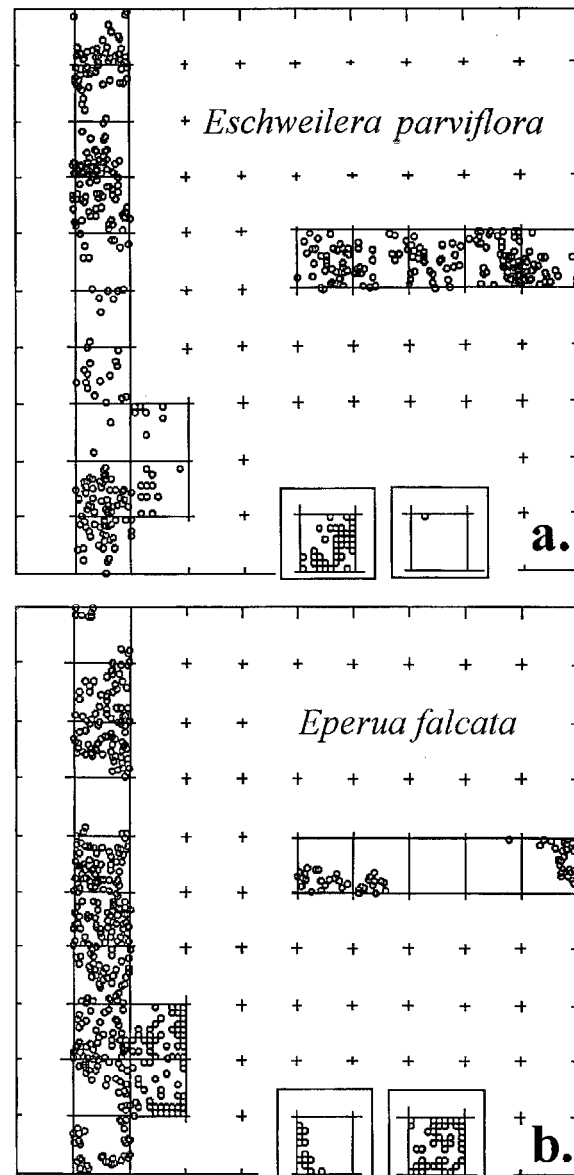


Figure 6. Spatial distribution of two species well correlated to the type of soil drainage. *Eschweilera parviflora* (a) is found almost only on DVD and Alt soils whereas *Eperua falcata* (b) is found almost only on thinned soils. The distribution patterns of the two species are thus complementary.

to be present everywhere). This was the case, for example, of *Eperua grandiflora*, whose presence was significantly higher in UhS+DC soils but which was also observed in all the other types of soil. However, some were observed very locally, such as *Abarema mataybifolia* on DVD soils and *Euterpe oleracea* on SH soils. A small number of species displayed partic-

Table 2. Chemical characteristics of DVD and SLD soils.

	DVD (N = 10)				SLD (N = 10)			
Depth	5 cm	15 cm	25 cm	35 cm	5 cm	15 cm	25 cm	35 cm
Exch. bases (meq/100 g)	0.91 0.15–2.56	0.56 0.36–1.09	0.38 0.20–0.61	0.30 0.16–0.52	0.71 0.21–1.13	0.54 0.31–1.73	0.22 0.13–0.86	0.17 0.13–0.22
CEC (meq/100 g)	10.46 8.0–16.25	7.00 5.25–9.00	5.77 3.75–8.00	4.40 3.25–5.75	6.03 5.00–7.75	4.58 3.25–6.75	2.25 1.50–3.25	1.42 0.75–2.25
Tot. carbon (%)	5.59 4.46–7.45	4.25 3.18–5.09	3.16 2.04–4.01	2.42 1.67–3.63	3.61 2.94–7.72	2.99 2.18–4.09	1.93 1.28–2.98	1.17 0.72–1.60
Tot. nitrogen (%)	3.12 2.52–4.55	2.33 1.79–2.73	1.83 1.23–2.09	1.43 1.06–2.11	2.24 1.84–2.65	1.93 1.30–2.64	1.27 1.03–1.91	0.89 0.52–1.90
Exch. AL ³⁺ (meq/100 g)	3.77 2.60–5.24	2.85 1.86–3.81	2.15 1.77–3.14	1.81 1.30–2.67	2.36 1.86–2.79	1.93 1.67–2.33	1.33 1.02–1.67	0.87 0.56–1.13
Tot. phosphorus (%)	0.46 0.31–0.71	0.40 0.29–0.50	0.50 0.33–0.67	0.55 0.33–0.79	0.23 0.16–0.33	0.22 0.15–0.31	0.23 0.16–0.31	0.30 0.19–0.45
Water pH	4.23 3.96–4.52	4.39 4.18–4.89	4.57 4.40–4.69	4.74 4.59–4.90	4.28 4.06–4.50	4.57 4.36–4.96	4.77 4.45–4.97	4.87 4.66–5.15

Upper value: mean; lower left: min.; lower right: max.

ularly high mutual information in comparison with the others; the species concerned have the most significant profiles overall: *Eperua falcata*, *Eschweilera parviflora*, *Lecythis idatimon*, *Euterpe oleracea*, *Licania alba*, etc. They are of greater value as indicators. It is also possible to appraise the coherence of the results by examining the homogeneity of the positive or negative results for related soil descriptor classes. *Eschweilera sagotiana* is thus significantly related to the two classes associated with the DhS.

A large number of species (48%) reacts significantly to DVD. Many are positively related to this soil descriptor class alone (25% – $P < 0.05$; 16.5% – $P < 0.01$; 12% – $P < 0.001$; $N = 195$), such as *Ecclinusa guianensis* and *Geissospermum laeve*. Only *Bocoa prouacensis* extends this positive link to the DhS + DC, the second well drained soil. No other soil descriptor category appears to be positively linked in an exclusive way to such a large number of species. However, each class has this type of significant link, which may be exclusive or only shared with related classes, e.g.: *Licania canescens* – Alt; *Cru-dia bracteata*, *Hebepetalum humiriifolium*, *Morono-bea coccinea* – SLD1 or SLD2; *Sagotia racemosa*, *Symphonia* sp.1 – SLD2 and DhS + DC; *Duguetia calycina* – UhS and UhS + DC; *Eschweilera sagotiana*, *Pachira dolichocalyx* – DhS and DhS + DC.

Significant negative links display the same pattern. In a few cases, the positive or negative relations cover a large number of classes, accompanied by high mutual information. For example, there is a significant negative link ($Cf = 0.31$; $P < 0.001$) between *Eperua falcata* and DVD soils and a positive link with almost all the other soil classes. Symmetrical behaviour is observed in *Eschweilera parviflora*, which is limited to DVD soils ($Cf = 1.52$; $P < 0.001$) and significantly absent from 6 of the 9 other classes. The spatial distributions of the two species are perfectly complementary (Figures 6a and 6b). They are the most abundant species and the taxa whose behaviour has been described best by the sampling used in this work. *Lecythis persistens* and *Licania alba* display a substantial behavioural link with *Eperua falcata*.

The geological substrate (schist or pegmatite) was the least well-sampled descriptor, $Q(L) = 0.65$ (i.e., 83% of the specimens studied were on schist). In addition, as mentioned above, pedogenesis is always more advanced on pegmatite than on schist. As a result, there are very few cases of DVD on pegmatite (21 individuals). Much caution is therefore required concerning the significance of the relations observed (many species positively related to schist also seem to be positively related to DVD soils). Nevertheless, reaction to the substrate can be assessed in situations independent

from evolution or at more advanced pedological stages. For example, among the species related to SH soils – *Caraipa racemosa*, *Paramachaerium ormosioides* and *Tabebuia insignis* – seem to be significantly related to schist, whereas *Sclerolobium melinonii* would be better represented on pegmatite; other species such as *Carapa procera*, *Eschweilera coriacea*, *Iryanthera hostmanii* and *Jessenia bataua* are not significantly influenced by the substrate.

The topographic and the slope descriptors were well sampled (0.89 and 0.90 respectively for $Q(L)$). The rates of significant responses (positive or negative) were distinctly lower than for the soil descriptor with 52% for topography and 40% for the slope ($P < 0.05$, $N = 195$). The species already mentioned for their links with SH soils were found to be positively related to lowland and gentle slopes. *Eperua falcata* and *Eschweilera parviflora* were also found to be complementary on gentle slopes, lowlands, footslopes and flat areas on hilltops in the first case and on steep slopes, upper slopes and ridges in the second. The strong similarity of the behaviour of *Lecythis persistens* and *Eperua falcata* has been confirmed.

Correspondence analysis of the ecological profiles table

Analysis of correspondence in the table of ecological profiles was performed on 98 species for which 20 individuals or more had been counted and that had at least one significant link (positive or negative) with one of the classes of one of the four descriptors (CA1). Only axes 1 and 2 were significant, accounting for 47% and 20% of the total inertia respectively; this range fell to 8% for the third axis. The vegetation ordination of the stands (Figure 7) revealed three different groups: DVD, thinned-transformed and SH soils, but displayed a horseshoe effect. As mentioned by Montaña & Greig-Smith (1990), problems may arise in correspondence analysis of species by environmental variable matrices if certain variable states are linked to only few species. Thus, a single species (*Euterpe oleracea*) accounted for 30% of axis 1 and 25% of axis 2 inertia. Moreover, CA1 showed three groups of variables, one of them including seven of the nine soil states in a very crowded clump (not represented). In order to improve the resolution of the CA, the surface hydromorphy soils in lowland – the outermost position linked with the very marked behaviour of a few species – were excluded from the pool of data for a second correspondence analysis (CA2). Analysis was then applied to 95 spe-

cies; SH stands were drastically reduced in number and size (85 and 75 trees in 2-C and 3-B, respectively).

In CA2 only axes 1 and 2 were significant with 47% and 12% of the total inertia respectively, this range fell to 7% for the third axis (eigenvalues 0.07, 0.02, 0.01). Processing the variables and species readily showed the relations between environmental variables, the species associated with them and the variability of the species composition at the locations (Figures 8, 9 and 10). Vegetation ordination of stands shows a clear segregation of DVD (Figure 9); the latter is related to a large number of species (Figure 10) and to upper slopes and ridges (Figure 8). Likewise, the segregation of the SH soils is verified; they are related to a small number of species and, as expected, to foot-slope. Between the extremities of the scatter of points, thinned and transformed soils form a fairly distinct group. Transformation systems (UhS and DhS) seem very close to superficial laterally drained (SLD) soil. However, vegetation ordination of stands (Figure 9) indicates that species mixture on stands on UhS is different to that on DhS; the latter is closely related to SH in a catena-like pattern. The two very small pockets of SH soils out of stage IV (in 10-B and 6-F) were displayed tentatively. Their positioning seems to be related to their respective evolution stage. The stands on soil with 'alloterite' (Alt) at a depth of less than 1.2 m are very dispersed; they do not form a definite group of stands and do not appear to be linked to any other.

In axis 1 (Figure 11), there is opposition between the DVD, upper slopes and ridges group of environmental classes on the positive side (28, 6 and 14% of the axis inertia respectively) and all the other environmental classes, particularly the SLD2, DhS, SH soils and foot-slope, level land and pegmatite on the negative (5, 10, 4 and 10, 7, 6% of the inertia). In axis 2 (Figure 11), there is opposition between UhS, UhS+DC associated with flat hilltop and level land in the positive side (13, 7 and 16, 4% of the inertia) and Alt, DhS, SH associated with ridges, gentle slope, steep slope and pegmatite in the negative (4, 10, 4 and 11, 4, 7, 10% of the inertia). The strongest contributions to axis 1 are the DVD soil and ridge states. They are opposed to all other features that limit to varying degrees internal or external drainage. Axis 2 combines on the negative side apparently contradictory features like gentle slope and steep slope, DhS and ridge; they characterize an open environment and are opposed to UhS, flat hilltop and level land on the positive side that characterize a confined environment.

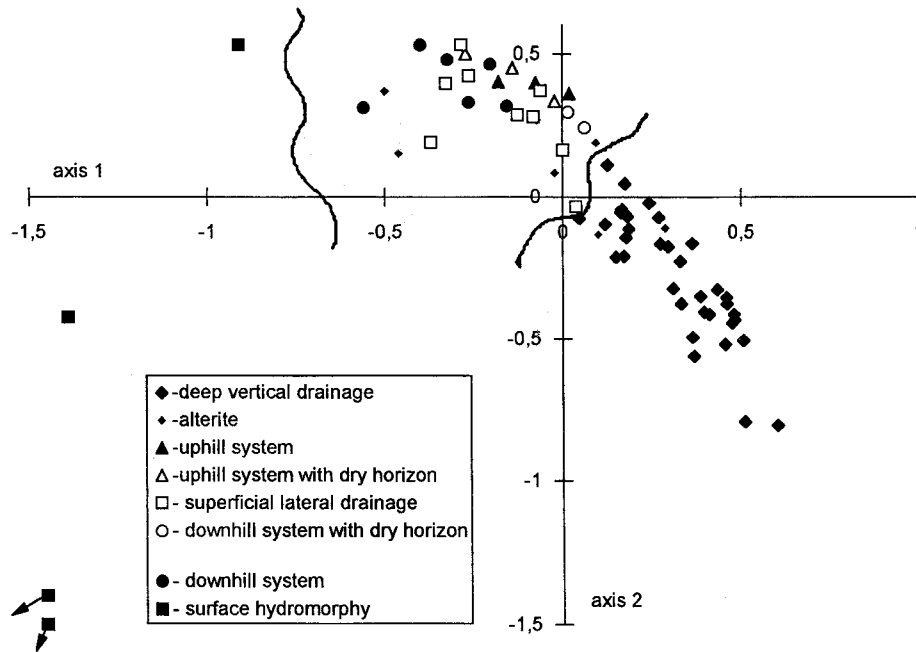


Figure 7. Vegetation ordination diagram of stands after the CA of the complete data set (CA1).

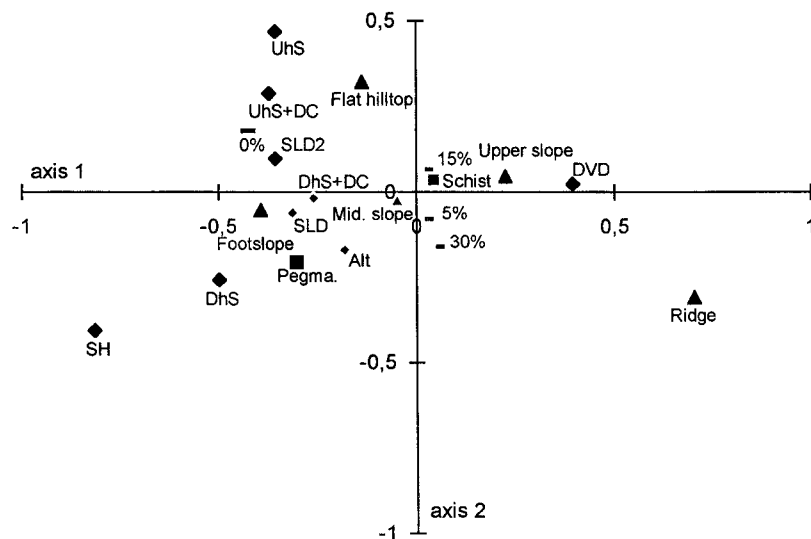


Figure 8. Ordination diagram using the normalised scores associated to the environmental classes in the CA of the reduced data set (CA2). ♦ soil domain; ■ substrate; — slope; ▲ topography. Small symbols indicate a weak correlation to first two axes.

Figure 10 shows the position of species along axes 1 and 2. Nineteen species are necessary to explain 75% of the axis 1 inertia and twenty three do the same for axis 2. However, only two species (*Eperua falcata* and *Eschweilera parviflora*) account for 28% of axis 1 inertia. Both were found to be good indicators of soil thinning by the profile analysis. Two families

display several taxonomically related species in a complementary pattern of soil affinities: the Lecythidaceae with five species of the genus *Eschweilera* and the Sapotaceae with five species of the genus *Pouteria*.

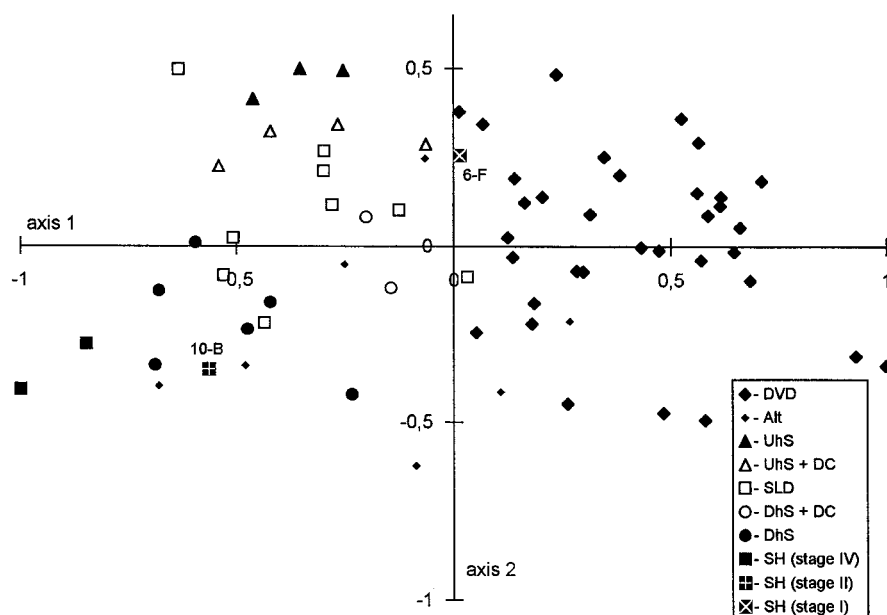


Figure 9. Vegetation ordination diagram of stands after the CA of the reduced data set (CA2). The positioning of the two very small SH stands on stage I (6-F plot) and II (10-B plot) are shown tentatively.

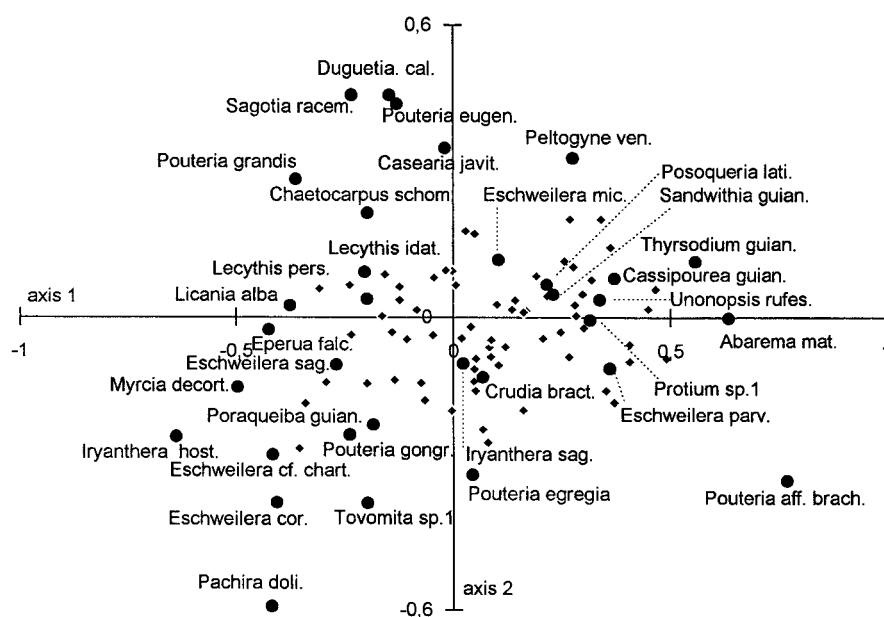


Figure 10. Ordination diagram using the normalised scores of each species in the first two axes of CA of the reduced data set (CA2). Closed circles and abbreviated names indicate the species necessary to explain 75% of axis inertia.

Structural parameters of the community according to the soil classes

The densities and basal areas (Figure 12 (a) and 12b) are not significantly different from one pedological

stage to the next, except for the SH stands where the values are significantly smaller (Mann-Whitney U test, $P < 0.05$). Considerable dispersion of values has been observed in all cases; densities ranged from 470 to 840 trees per hectare and basal area ranged from 19 to 52

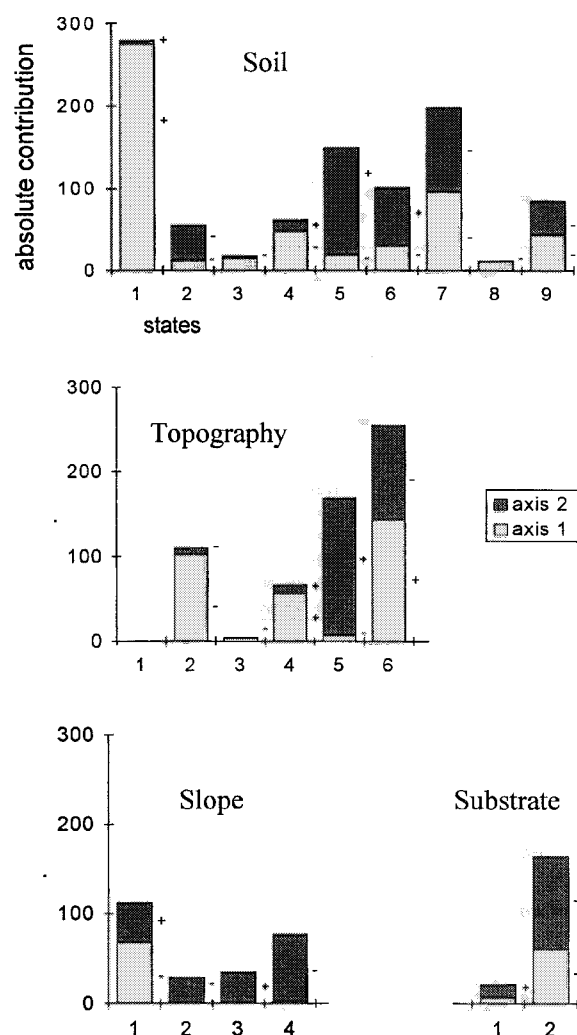


Figure 11. Absolute contributions of states of variables to the first two axes of the CA2. Sign of the position of the coordinate in the axis is shown at the right-hand side.

m² per hectare. This is caused partially by the small area of the stands but also by the sylvigenesis.

The distribution of diameters according to soils can be tested by Fisher's exact test of proportions (Table 3). Individuals were separated into three diameter categories (10–15 cm; > 15 – 35 cm; > 35 cm). Although the corrected frequencies indicate deficits or excesses in one or other of the size categories of certain classes of the soil variable, these differences between the observed and the expected number of individuals are never significant except for SH soils where small diameters are significantly more abundant than expected ($P < 0.05$). It will nevertheless be noted that other

Table 3. Distribution of individuals in the soil variable states according to diameter.

Classes	10–15 cm	>15–35 cm	>35 cm	Total
DVD	2464	2460	835	5759
	1.00	1.00	1.00	
	*	*	*	
Alt	510	539	198	1247
	0.96	1.01	1.09	
	*	*	*	
SLF1	195	196	69	460
	0.99	1.00	1.03	
	*	*	*	
SLD2	532	513	161	1206
	1.03	1.00	0.92	
	*	*	*	
UhS	183	201	66	450
	0.95	1.05	1.01	
	*	*	*	
UhS+DC	275	265	95	635
	1.01	0.98	1.03	
	*	*	*	
DhS	510	533	180	1223
	0.98	1.02	1.01	
	*	*	*	
DhS+DC	225	223	83	531
	0.99	0.98	1.07	
	*	*	*	
SH	274	243	76	593
	1.08	0.96	0.88	
	+	*	*	
Total	5168	5173	1763	12104

Line 1 abs. freq.; line 2 corrected freq.; line 3 probability + $P < 0.05$; * not significant.

well marked differences are the result of a shortage of large trees on SLD2 and SH soils.

Species richness and evenness of the community according to the soil classes

The species richness of the forest community according to the nature of the soil has been examined by grouping the neighbouring sectors in the same pedological domain in plots of increasing size and calculating the number of species for each. Species recruitment curves (Figure 13) were plotted using average values. Comparison of these curves suggests that the thinning

of the soil profile (Alt and SLD) might enhance a species-rich mixture. In contrast, hydromorphy in any form and to any extent seems to limit the number of species making up the community. The differences to the DVD values for samples of 150 individuals are not significant for Alt and SLD values (Mann–Whitney U test, $P \gg 0.05$, $N_{\text{DVD}} = 38$, $N_{\text{Alt}} = 8$, $N_{\text{SLD}} = 10$), but are significant for UhS, DhS and SH ($P < 0.05$, $N_{\text{DVD}} = 38$, $N_{\text{UhS}} = 7$, $N_{\text{DhS}} = 12$, $N_{\text{SH}} = 2$, Mann–Whitney); for 300 individuals, only the difference between DVD and UhS is significant ($P = 0.05$, $N_{\text{DVD}} = 19$, $N_{\text{UhS}} = 3$, Mann–Whitney). With more than 300 individuals, no significant differences have been found between the distributions of the values of species richness.

Evenness based upon the Shannon index (H/H_{max} according to Pielou, 1966) has been calculated for each of the stands. No significant differences appear between DVD and Alt or SLD values (mean evenness: 0.775, 0.777 and 0.778 respectively; Mann–Whitney U test, $P \gg 0.05$). However differences are always significant when DVD values are compared to UhS, DhS or SH ones (mean evenness: 0.747, 0.743 and 0.723 respectively; Mann–Whitney U test, $P < 0.05$).

Discussion

The data presented here, based upon detailed botanical survey and soil mapping, clearly show that the soil is an important factor in the composition of the forest community at Piste de St Elie station. They are consistent with Lescure & Boulet's results (1985), and extend them considerably. It can be seen clearly that species mixture and richness are related to the edaphic characteristics of the site. Soil-population relationships have been analysed by drawing up ecological profiles of species on the one hand and the study of small homogeneous stands ($\cong 0.25$ ha), delimited *a posteriori*, on the other. As is mentioned by Newbery (1991), the use of such small sampling units is not entirely satisfactory for analysis of tropical forest communities, mainly because small areas promote within group variation, since the species-area curve stabilizes at over several hectares even when rare species are excluded (Newbery et al. 1992). In spite of this, one of the most conclusive results of this study is the demonstration of a species composition with characteristic frequencies enabling clear differentiation between the group of quarter-hectare areas on ferralitic soil and those in which the soil has been modified by erosion or by

erosion and hydromorphy. This is all the more significant as the comparison is not between soils that are remote from each other, as would be the case for example of a ferralitic soil and a podzol.

The change in drainage from deep vertical to superficial lateral and the soil transformation processes that accompany or follow these induce different floristic composition, species frequency and species richness of the forest community: the frequencies of *Eperua falcata*, *Lecythis idatimon*, *Licania alba* and many other species associated with thinned out soils increase considerably while *Eschweilera parviflora* and the numerous species associated with deep drainage become more scarce or disappear. The structure is of little concern. Only SH conditions, as mentioned by Lescure & Boulet (1985), showed significant differences (i.e., shortage of density and basal area, more small trees and fewer large trees). Structure on SLD soils seems to be affected, with fewer large trees, but not significantly.

The time scale of the soil thinning is still unknown, but forest renewal, which takes place on the scale of several centuries, is probably considerably faster.

The vegetation ordination of stands, separates them according to the type of transformation system; hydromorphy in the confined uphill environment does not result in the same species mixture as hydromorphy in the open environment of the downhill system. Stands on thinned soil (SLD) broadly cover the latter two categories; this leads on the one hand to the expectation that there is a tendency for this soil to become oriented towards one or other of the transformation systems and on the other hand that very fine differences in population would not appear in such a limited number of small areas of forest. Stands on Alt display considerable dispersion according to vegetation. This may be a true characteristic of stands on this soil type, with an enhanced versatility of the species mixture, mainly influenced by the neighbourhood and related to low levels of edaphic constraints, or it may reveal a failure in the detection of horizon 3. Further investigation is needed.

The differences in chemical properties and hydrodynamic behaviour revealed are related to the successive evolution stages of the soil cover. It is delicate in this context to isolate the determinant factor/s for vegetation. The phosphorus content has been mentioned by several authors as being a key factor. It appears here, like many other potentially determinant chemical variables (carbon, nitrogen or other nutrients, exchangeable aluminium, pH, etc.), to be related to the pedocli-

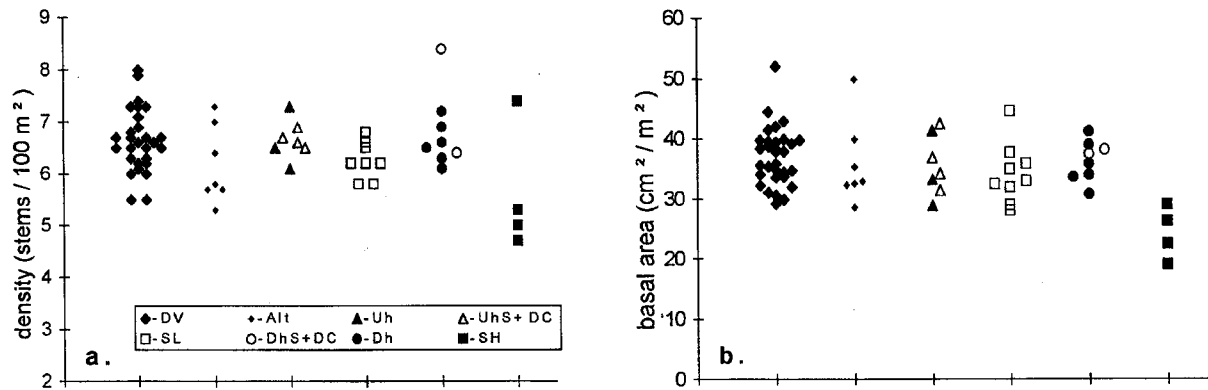


Figure 12. Comparison of stem densities (a) and basal areas (b) according to soil classes for stands of about 0.25 ha.

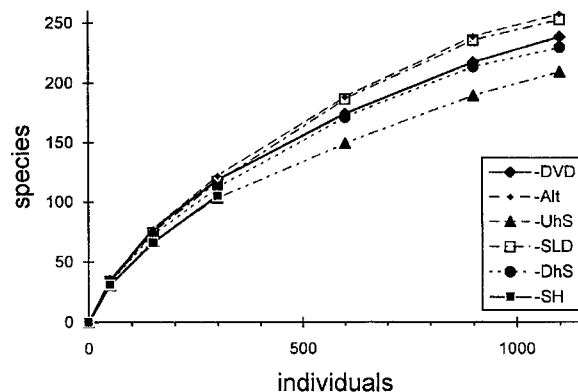


Figure 13. Comparison of the cumulative number of species for increasing number of individuals according to the main soil mapping units.

mate, that is to say the availability of water and air for plants.

Interpretation of factorial axes, according to the absolute contribution of each state of the variables (Figure 11), suggests that drainage is of great importance for axis 1 (the strongest gradient) which contains contrasted groups of states with enhanced or poor internal and external drainage for the soil. Thus axis 1 reflects mostly the first process of soil evolution, i.e., the thinning of the microaggregated horizon. Interpretation of axis 2 is more difficult; it might be dominated by pedoclimate, with UhS soil and flat hill top at the positive side with the most confined environment (limited water flow during periods of excess water); in contrast, the DhS and SH soils in foot-slopes or the ridges and steep slopes would be on the negative side of the axis with the most open environment (considerable water flow during the rainy season). The soil variable is clearly

linked to the topography, but analysis of the pedological processes shows that the link is complex and that the main gradient is not a simple catena.

The differences in rooting depths measured by Humbel (1978) in DVD and SLD soils (5% of roots in the 0 to 2 m layer observed at deeper than 1 m in DVD soil in comparison with 0.5% in SLD), suggest that plants growing in DVD soil are deeper rooted than in SLD soil to compensate for the serious shortage of water occurring in the surface layer of the thick micro-aggregated horizon (Figure 4c). The critical moment for the plants would be the establishment phase when plantlets with small root systems must survive periods with little rainfall. Moreover, periods of excess water and related bad aeration occurring in the thinned out soils (Figure 4a) may limit the depth of soil accessible to the roots (80 to 90% of roots in the 0 to 2 m layer observed at a depth of less than 20 cm in SLD soil in comparison with 40 to 70% in DVD).

In a different context, in Guyana, where there is a main soil and vegetation gradient between brown sands and white sands, Steege et al. (1993) reported also that 'most dominant and sub-dominant tree species have a clear association with a distinct soil type or hydrology class'. Some species of our study are well represented in this area and show similar behaviour, such as the greater tendency of *Eperua grandiflora* to be present in 'excessively drained' soils than *Eperua falcata* or the optimum of *Eschweilera sagotiana* in well drained conditions (in our study, this species is related to DhS soils, which are the second best drained soils). At one extremity of the gradients, several dominant species are shared by our lowland hydromorphic stands and their palm-swamp forest (*Euterpe oleracea*, *Jessenia bataua*, *Tabebuia insignis*). However, our drainage

gradient is longer and the secondary gradients are very different.

The larger number of species observed in DVD soils than in more or less hydromorphic ones (see Appendix 2 and Figure 13) suggests that the water shortage plays a smaller negative role in the success of species than an unfavourable air / water ratio and related chemical properties. Nevertheless, the history of the local flora might be of major importance in the absolute richness of the guilds. On the other hand, the richness of the species mixture seems to be enhanced by thinning of the microaggregated superficial horizon (Figure 13). This would be related to a lower risk of water shortage during the dry season (Figure 4c).

However, the spatial distribution of soil categories in the form of a mosaic might be an important factor in local plant combinations and species richness. Indeed, the juxtaposition of soils favourable for a species and soils that are less so may enable its simultaneous presence in both types of environment by maintaining a high level of seminal potential through the specimens growing in the most favourable soils. Such an expectation refers to the great importance of chance in encountering a suitable regeneration site. This process is related to certain aspects of the 'neighbourhood effects' described by Dunning et al. (1992). It might account for the increase in species richness observed in the broken up areas of thinned out soils.

Finally, the assumption that 'soil heterogeneity ... shows little relation to tree distribution in tropical forests' (Huston 1994, p. 85), apparently supported by many field studies, is not true. In our study (see also Steege et al. 1993), most species have a clear optimum of soil characteristics, few of them are dominant in the area of this optimum and all the others are scattered or very localized in it. We may therefore expect that some soil features form the bounds of the qualitative and quantitative variability of the species mixture of tropical forest stands.

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Appendix 1

Statistical analysis of the ecological profiles: the 2×2 contingency table associated with the absolute frequency (a) of a focal species in class k of an nk class descriptor and calculation of (1) the expected frequency (Ef) under the null hypothesis H_0 of random distribution, (2) the corrected frequency (Cf), (3) the probability of the actual value of a ($P_0(a)$), (4) and (5) the probability (P) of either attraction or repulsion and (6) the mutual information (MI) between species and descriptor.

Classes:	k	Others	Total
Focal species	a	b	m
Others	c	d	n
Total	r	s	N

Under H_0

$$rf = Rf \Leftrightarrow \frac{a}{r} = \frac{m}{N} \Rightarrow a = \frac{r \cdot m}{N} = Ef \quad (1)$$

then, for observed values:

$$Cf = \frac{a/r}{m/N} = \frac{a}{r \cdot m/N} = \frac{a}{Ef} \quad (2)$$

$$P_0(a) = \frac{\binom{r}{a} \cdot \binom{s}{b}}{\binom{N}{m}} = \frac{m!n!r!s!}{N!a!b!c!d!} \quad (3)$$

To test 'attraction' or 'repulsion':

if $a > Ef$ then

$$P = P_0(\geq a) = P_0(a, a+1, \dots, \text{Min}(m, r)), \quad (4)$$

if $a < Ef$ then

$$P = P_0(\leq a) = P_0(\text{Max}(m-s, 0), \dots, a-1, a), \quad (5)$$

(4) and (5) are computed according to (3).

Mutual information between the focal species and the descriptor (according to Godron, 1968):

$$MI = \sum_1^{nk} \frac{a}{N} \log_2 \frac{N}{r} \cdot \frac{a}{m} + \sum_1^{nk} \frac{c}{N} \log_2 \frac{N}{r} \cdot \frac{c}{n} \quad (6)$$

Appendix 2. Table of ecological profiles of the most abundant species ($f \geq 20$) for the four environmental variables. Line 1, absolute frequencies; line 2, corrected frequencies; line 3, sign and significance of the link: + + + - - - $P < 0.001$; + + - - $P < 0.01$; + - $P < 0.05$; • not significant; MI : mutual information (10^{-2}).

Descriptor:	Soil										Topography						Slope					Substrate						
	1	2	3	4	5	6	7	8	9	MI	1	2	3	4	5	6	MI	1	2	3	4	5	6	MI	1	2	MI	
Classes:																												
<i>Abarema mataphylla</i> (Sandw.) Barneby & Grimes MIMOS.	20	1	0	0	0	0	0	0	0	0	0	1	4	11	1	4		0	6	10	5				21	0		
	2.00	0.46	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.27	0.61	1.83	0.49	2.38		0.00	0.93	1.13	1.36			1.20	0.00		
<i>Aspidosperma</i> sp.1 APOCYN.	20	0	0	1	0	0	1	1	0			0	9	10	2	2		0	5	12	6			22	1			
	1.83	0.00	0.00	0.44	0.00	0.00	0.43	0.99	0.00			0.00	0.00	1.25	1.52	0.90	1.09		0.00	0.71	1.24	1.49			1.15	0.26		
<i>Astrocaryum sciophilum</i> (Miq.) Pulle AREC.	+++									0.12																	0.02	
	117	25	5	29	4	10	9	13	3			3	33	91	57	12	19		13	71	84	47			177	38		
<i>Bocoea prouacensis</i> Aubl. CAESAL.	1.14	1.13	0.61	1.35	0.50	0.89	0.41	1.38	0.28			0.29	0.87	1.35	0.93	0.58	1.10		0.62	1.08	0.93	1.25			0.99	1.04		
	1.07	0.32	0.29	0.89	0.90	0.85	1.21	0.51	2.72			--		+++													0.00	
<i>Carapa procera</i> A. DC. MELIA.	102	15	4	18	5	9	4	17	1			3	23	60	50	19	20		15	57	72	31			150	23		
	1.23	0.83	0.60	1.03	0.77	0.98	0.23	2.21	0.12			0.36	0.74	1.09	1.00	1.12	1.43		0.88	1.06	0.98	1.01			1.03	0.84		
<i>Caryocarp glabrum</i> (Aubl.) Pers. CARYOC.	46	3	1	8	3	4	11	2	12			11	17	26	16	9	11		11	30	34	15			80	10		
	1.07	0.32	0.29	0.89	0.90	0.85	1.21	0.51	2.72			2.58	1.07	0.92	0.62	1.03	1.53		1.25	1.09	0.90	0.95			1.07	0.65		
<i>Caryocarp glabrum</i> (Aubl.) Pers. CARYOC.	+	--	--	--	--	--	--	--	--	0.11		++		--	--	--	--										0.01	
	18	5	2	3	1	2	0	0	0			1	3	7	16	2	4		2	16	10	5			28	5		
<i>Cassaria javitensis</i> Kunth FLAC.	1.15	1.47	1.59	0.91	0.82	1.16	0.00	0.00	1.24			0.64	0.51	0.68	1.70	0.62	1.51		0.62	1.59	0.72	0.87			1.02	0.89		
	11	0	0	3	3	1	1	1	0			0	3	6	6	4	1			+	+	+			18	2		
<i>Casipourea guianensis</i> Aubl. RHIZO.	1.16	0.00	0.00	1.51	4.03	0.95	0.49	1.14	0.00			0.00	0.85	0.96	1.05	2.06	0.62		2.56	0.65	0.83	1.14			1.08	0.59		
	120	3	2	12	4	8	19	6	6			7	27	51	56	17	22		11	56	99	14			170	10		
<i>Catostemma fragrans</i> Benth. BOMBAC.	1.40	0.16	0.29	0.67	0.60	0.85	1.04	0.76	0.68			0.82	0.85	0.90	1.09	0.97	1.53		0.63	1.02	1.30	0.44			1.14	0.33		
	+++	--	--	--	--	--	--	--	--	0.26		1	0	10	13	5	4			+	+	+	---		31	2		
<i>Chaetocarpus schomburgkianus</i> (Kuntze) Hoffm.	20	5	1	3	0	3	0	0	1			0.64	0.00	0.97	1.38	1.56	1.51		0.93	1.29	0.86	0.87			1.13	0.36		
	1.27	1.47	0.80	0.91	0.00	1.73	0.00	0.00	0.62			--	--	--	--	--	--										0.02	
<i>Chrysophyllum argenteum</i> Jacq. subsp. nitidum (Meyer) Pennington SAPOT.	16	8	5	5	7	4	6	1	0			0	7	17	15	11	2		11	17	19	5			43	9		
	0.65	1.49	2.53	0.97	3.62	1.47	1.14	0.44	0.00			0.00	0.76	1.04	1.01	2.18	0.48		2.17	1.07	0.87	0.55			1.00	1.02		
<i>Chrysophyllum sanguinolentum</i> (Pierre) Baehni SAPOT.	4	7	2	6	0	4	3	1	0			2	8	8	9	3	2		4	8	16	4			30	2		
	0.31	2.52	1.95	2.23	0.00	2.82	1.10	0.84	0.00			1.32	1.41	0.80	0.98	0.97	0.78		1.28	0.82	1.19	0.71			1.13	0.37		
<i>Couepia caryophyllioides</i> R. Benoist CHRYSO.	15	4	1	4	2	2	4	2	0			0	3	15	11	4	1										0.00	
	0.93	1.14	0.77	1.18	1.58	1.12	1.16	1.34	0.00			0.00	0.50	1.41	1.13	1.21	0.37		0.90	0.96	0.91	1.35			0.96	1.21		
<i>Couepia guianensis</i> Aubl. CHRYSO.	19	3	0	1	0	2	1	0	1			0	5	4	9	2	7		2	8	10	7			22	3		
	1.48	1.08	0.00	0.37	0.00	1.41	0.37	0.00	0.76			0.00	1.05	0.47	1.17	0.76	3.24		0.76	0.97	0.88	1.48			1.06	0.71		
<i>Couratari oblongifolia</i> Ducke & Knuth LECYTH.	+	0	0	3	2	1	0	2	0			0	2	8	4	2	6										0.01	
	1.34	0.00	0.00	1.37	2.45	0.87	0.00	2.07	0.00			0	2	8	4	2	6		2	10	3	7			21	1		
										0.10		0.00	0.51	1.16	0.64	0.94	3.40		0.93	1.49	0.32	1.82			1.15	0.27		
																		++									0.02	

[illegible]

<i>Licania alba</i> (Bernoulli) Cuatr. CHRYSO.	34	22	15	34	12	23	37	3	17		13	54	60	46	21	3	30	59	82	26	159	38
	0.36	1.08	2.00	1.73	1.64	2.23	1.86	0.35	1.76	0.61	1.39	1.55	0.97	0.82	1.10	0.19	1.56	0.98	0.99	0.75	0.97	1.13
<i>Licania canescens</i> R. Benoit CHRYSO.	43	19	4	4	2	2	2	3	0		0	10	20	37	7	10	8	28	39	9	62	22
	1.08	2.20	1.25	0.48	0.64	0.45	0.82	0.81	0.00	0.14	0.00	0.67	0.76	1.54	0.86	1.49	0.98	1.09	1.10	0.61	0.89	1.54
<i>Licania densiflora</i> Kleinboote CHRYSO	19	4	2	1	0	3	9	0	1		1	8	11	13	4	2	3	13	18	5	28	11
	1.02	1.00	1.35	0.26	0.00	1.47	2.28	0.00	0.52		0.54	1.16	0.90	1.17	1.06	0.64	0.79	1.09	1.09	0.73	0.87	1.66
<i>Licania granvillei</i> G.T. France CHRYSO.	33	6	2	6	5	3	4	7	1		1	13	23	17	7	6	7	24	30	6	57	10
	1.04	0.87	0.79	0.90	2.01	0.85	0.59	2.38	0.30		0.31	1.10	1.10	0.89	1.08	1.12	1.07	1.17	1.06	0.51	1.03	0.88
<i>Licania heteromorpha</i> Benth. var. <i>heteromorpha</i> CHRYSO	27	7	1	7	5	3	2	6	1		0	8	18	21	8	4	6	26	23	4	47	12
	0.96	1.15	0.45	1.19	2.28	0.97	0.34	2.32	0.35		0.00	0.77	0.97	1.25	1.40	0.85	1.04	1.44	0.92	0.39	0.96	1.20
<i>Licania laxiflora</i> Frisch CHRYSO	14	3	5	2	1	4	7	0	0		1	6	14	13	1	1	3	11	18	4	28	8
	0.82	0.81	3.65	0.56	0.75	2.12	1.92	0.00	0.00		0.59	0.94	1.24	1.26	0.29	0.35	0.85	1.00	1.19	0.64	0.94	1.31
<i>Licania membranacea</i> Sagot ex Lanessan CHRYSO.	34	7	4	5	2	0	8	5	5		5	10	20	23	4	8	6	21	36	7	54	16
	1.02	0.97	1.50	0.72	0.77	0.00	1.13	1.63	1.46		1.51	0.81	0.91	1.15	0.59	1.43	0.88	0.98	1.22	0.57	0.93	1.34
<i>Licania spucei</i> (Hooker f.) Frisch CHRYSO	8	0	0	4	0	1	5	2	1		1	8	4	3	2	3	1	9	9	2	20	1
	0.80	0.00	0.00	1.91	0.00	0.91	2.36	2.17	0.97		1.00	2.16	0.61	0.50	0.98	1.78	0.49	1.40	1.02	0.54	1.15	0.28
<i>Licania chrysophylla</i> (Meisn.) LAUR.	21	0	0	0	0	0	1	0	0		0	3	5	11	1	3	0	6	9	8	21	2
	1.92	0.42	0.00	0.00	0.00	0.00	0.43	0.00	0.00		0.00	0.74	0.69	1.67	0.45	1.63	0.00	0.85	0.93	1.99	1.10	0.51
<i>Micropholis guyanensis</i> (A. DC.) P. subsp. <i>duckiana</i> SAPOT.	23	3	2	2	2	2	6	1	3		2	9	14	9	6	4	5	16	15	8	34	10
	1.10	0.66	1.20	0.46	1.22	0.87	1.35	0.52	1.39		0.96	1.16	1.02	0.72	1.41	1.13	1.16	1.19	0.81	1.04	0.93	1.34
<i>Micropholis guyanensis</i> (A. DC.) Pierre subsp. <i>guyanensis</i> SAPOT.	10	1	0	5	0	0	5	0	2		4	6	7	2	2	2	1	9	7	6	20	3
	0.91	0.42	0.00	2.18	0.00	0.00	2.15	0.00	1.77		3.67	1.48	0.97	0.30	0.90	1.09	0.45	1.28	0.72	1.49	1.05	0.77
<i>Micropholis obscura</i> Pennington SAPOT.	26	4	2	0	0	1	0	0	0		0	2	11	14	5	1	2	9	13	9	30	3
	1.66	1.18	1.59	0.00	0.00	0.58	0.00	0.00	0.00		0.00	0.34	1.06	1.49	1.56	0.38	0.62	0.89	0.93	1.56	1.10	0.53
<i>Minquartia guyanensis</i> Aublet OLACA.	6	5	0	3	0	0	5	0	2		2	5	7	4	0	3	2	12	4	3	13	8
	0.60	2.31	0.00	1.43	0.00	0.00	2.36	0.00	1.94		2.01	1.35	1.06	0.67	0.00	1.78	0.98	1.87	0.45	0.82	0.75	2.24
<i>Moronebea coccinea</i> Aublet CLUSIA.	11	3	5	2	0	2	5	0	0		0	6	1	7	10	5	4	8	15	1	23	5
	0.83	1.04	4.70	0.72	0.00	1.36	1.77	0.00	0.00		0.00	1.21	0.80	1.25	1.84	0.00	1.46	0.93	1.27	0.20	0.99	1.05
<i>Mouriri crassifolia</i> Sagot MELAST.	16	2	1	5	3	2	3	2	1		0	7	10	12	5	1	3	10	18	4	31	4
	0.96	0.55	0.75	1.43	2.31	1.09	0.85	1.30	0.58		0.00	1.13	0.91	1.20	1.47	0.36	0.88	0.93	1.22	0.65	1.07	0.67
<i>Myrcia decorticans</i> De Candolle MELAST.	3	4	0	5	1	2	4	4	6		4	11	7	3	3	1	4	11	11	3	21	8
	0.22	1.34	0.00	1.73	0.93	1.31	1.37	3.14	4.22		2.91	2.15	0.77	0.36	1.07	0.43	1.41	1.24	0.90	0.59	0.87	1.62
<i>Neea floribunda</i> Poeppig & Endlicher NYCTA.	24	0	2	1	0	0	1	0	0		0	2	7	5	7	7	1	14	9	4	27	1
	1.80	0.00	1.88	0.36	0.00	0.00	0.35	0.00	0.00		0.00	0.40	0.80	0.63	2.58	3.12	0.37	1.63	0.76	0.82	1.16	0.21
	++	-																+			+	0.03

Appendix 2. Continued

<i>Licania alba</i> (Bemoulli) Cuat. CHRYSO.	34 0.36 ---	22 1.08 ++	15 2.00 ++	34 1.73 ++	12 2.23 +++	23 1.86 +++	37 1.76 ++	3 0.61 +	17 1.76 +	13 1.39 0.00	54 1.55 0.67	60 0.97 0.76	46 0.82 1.54	21 1.10 0.86	3 0.19 1.49	30 1.56 0.98	59 0.99 1.10	82 0.99 1.00	26 0.75 0.61	159 0.97 0.89	38 1.13 1.54
<i>Licania canescens</i> R. Benoist CHRYSO.	43 1.08 +	19 2.20 +++	4 1.25 +	4 0.48 +	2 0.64 +	2 0.45 +	7 0.82 +	3 0.81 +	0 0.00 -	0 0.00 -	10 0.67 1.16	20 0.76 0.90	37 1.54 1.13	7 0.86 1.06	10 1.49 0.64	8 0.98 0.79	28 1.09 1.09	39 1.10 1.09	9 0.61 0.73	62 0.89 0.87	22 1.54 1.66
<i>Licania densiflora</i> Kleinboonte CHRYSO	19 1.02 +	4 1.00 +	2 1.35 +	1 0.26 +	0 0.00 +	3 1.47 +	9 2.28 +	0 0.52 +	1 0.52 +	1 0.54 0.31	8 1.16 1.10	11 0.90 1.10	13 1.17 0.89	4 1.06 1.08	2 0.64 1.12	3 0.79 1.07	13 1.09 1.17	18 1.09 1.06	5 0.73 0.51	28 0.87 1.03	11 1.66 0.88
<i>Licania granvillei</i> G.T. France CHRYSO.	33 1.04 +	6 0.87 +	2 0.79 +	6 0.90 +	5 2.01 +	3 0.85 +	4 0.59 +	7 2.38 +	1 0.30 +	1 0.31	13 1.23 1.10	23 1.10 1.10	17 0.89 1.08	7 1.08 1.12	6 0.51 1.02	7 1.07 1.01	24 1.17 1.06	30 1.06 0.51	6 0.02 0.02	57 1.03 0.96	10 0.88 1.20
<i>Licania heteromorpha</i> Benth. var. <i>heteromorpha</i> CHRYSO	27 0.96 +	7 1.15 +	1 0.43 +	7 1.19 +	5 2.28 +	3 0.97 +	2 0.34 +	6 2.32 +	1 0.35 +	0 0.00 -	8 0.77 0.59	21 0.97 1.25	8 1.40 0.85	4 0.85 0.35	0 0.00 -	6 1.04 0.85	26 1.44 1.18	23 0.92 1.18	4 0.39 0.64	47 0.96 0.94	12 1.20 1.31
<i>Licania laxiflora</i> Fritsch CHRYSO	14 0.82 +	3 0.81 +	5 3.65 +	2 0.56 +	1 0.75 +	4 2.12 +	7 1.92 +	0 0.00 +	0 0.00 +	1 0.59 0.51	6 1.24 0.94	14 1.26 1.24	13 0.29 0.35	1 0.35 0.03	1 0.00 -	3 0.85 0.6	11 1.00 1.19	18 1.19 0.64	4 0.64 0.01	28 0.94 0.54	8 1.31 1.6
<i>Licania membranacea</i> Sagot ex Lanessan CHRYSO.	34 1.02 +	7 0.97 +	4 1.50 +	5 0.72 +	2 0.77 +	0 0.00 -	8 1.13 +	5 1.63 +	5 1.46 +	5 1.51 0.81	20 0.91 0.91	23 1.15 1.15	4 0.59 1.43	8 1.43 0.02	8 0.02 0.02	6 0.88 0.98	21 0.98 1.22	36 1.22 0.57	7 0.57 0.02	54 0.93 0.93	16 1.34 1.34
<i>Licania sprucei</i> (Hooker f.) Fritsch CHRYSO	8 0.80 +	0 0.00 +	4 0.00 +	4 1.91 +	0 0.00 +	1 0.91 +	5 2.36 +	2 2.17 +	1 0.97 +	1 1.00	8 2.16 0.61	4 0.50 0.98	3 1.78 0.05	3 0.05 0.05	3 0.05 0.01	1 0.49 0.49	9 1.40 1.02	9 1.02 0.54	2 0.54 0.01	20 1.15 0.93	1 0.28 1.34
<i>Licania chrysophylla</i> (Meissn.) Kostermans LAUR.	21 1.92 +++	1 0.42 +	0 0.00 +	0 0.00 +	0 0.00 +	0 0.00 +	1 0.43 +	0 0.00 +	0 0.00 +	0 0.00 -	3 0.74 0.69	11 1.67 0.45	1 1.63 0.04	3 0.04 0.04	3 0.04 0.01	0 0.00 -	6 0.85 0.93	9 1.99 1.49	8 0.00 0.77	21 1.10 1.05	2 0.51 0.01
<i>Micropholis guyanensis</i> (A. DC.) P. subsp. <i>duckiana</i> SAPOT. (Baillon) Pennington	23 1.10 +	3 0.66 +	2 1.20 +	2 0.46 +	2 1.22 +	2 0.87 +	6 1.35 +	1 0.52 +	3 1.39 +	2 0.96	14 1.16 1.02	9 0.72 1.41	6 1.13 0.01	4 0.01 0.01	4 0.01 0.01	1 0.45 0.45	16 1.19 0.81	15 0.81 1.04	8 1.04 0.01	34 0.93 1.10	10 1.34 0.51
<i>Micropholis guyanensis</i> (A. DC.) Pierre SAPOT.	10 0.91 +	1 0.42 +	0 0.00 +	5 2.18 +	0 0.00 +	0 0.00 +	5 2.15 +	0 1.77 +	2 1.77 +	4 3.67	6 1.48 0.97	2 0.30 0.90	2 1.09 0.06	2 0.06 0.06	2 0.06 0.06	1 0.45 0.45	9 1.28 0.72	7 1.49 0.02	6 1.49 0.02	20 1.05 1.05	3 0.77 0.00
<i>Micropholis obscura</i> Pennington SAPOT.	26 1.66 +++	4 1.18 +	2 1.59 +	0 0.00 +	0 0.00 +	1 0.58 +	0 0.00 +	0 0.00 +	0 0.00 +	0 0.00 -	2 0.34 1.06	11 1.49 1.56	5 0.38 0.06	1 0.06 0.06	1 0.06 0.06	2 0.62 0.89	13 0.93 1.56	9 1.56 0.01	9 1.56 0.01	30 1.10 0.93	3 0.53 0.03
<i>Minqvaria guianensis</i> Aublet OLACA.	6 0.60 +	5 2.31 +	0 0.00 +	3 1.43 +	0 0.00 +	0 0.00 +	5 2.36 +	0 1.94 +	2 1.94 +	2 2.01	5 1.35 1.06	7 0.67 0.00	4 1.78 0.04	3 0.04 0.04	3 0.04 0.06	2 0.98 1.87	12 0.45 0.82	4 0.82 0.04	3 0.82 0.04	13 0.75 0.75	8 2.24 0.03
<i>Moronobea coccinea</i> Aublet CLUSIA.	11 0.83 +	3 1.04 +	5 4.70 +	2 0.72 +	0 0.00 +	2 1.36 +	5 1.77 +	0 0.00 +	0 0.00 +	0 0.00 -	6 1.21 0.80	10 1.25 1.84	5 0.00 0.00	0 0.00 0.06	0 0.06 0.06	4 1.46 0.93	8 1.27 1.05	15 1.27 1.05	1 0.00 0.00	23 0.99 0.99	5 1.05 1.05
<i>Mouriri crassifolia</i> Sagot MELAST.	16 0.96 +	2 0.55 +	1 0.75 +	5 1.43 +	3 2.31 +	2 1.09 +	3 0.85 +	2 1.30 +	1 0.58 +	0 0.00 -	7 1.13 0.91	12 1.20 1.47	5 0.36 0.04	1 0.04 0.04	1 0.04 0.01	3 0.88 0.93	18 1.22 1.05	4 1.22 1.05	4 0.01 0.01	31 1.07 0.87	4 0.67 1.62
<i>Myrcia decorticans</i> De Candolle MELAST.	3 0.22 ---	4 1.34 +	0 0.00 +	5 1.73 +	1 0.93 +	2 1.31 +	4 1.37 +	4 4.22 +	6 4.22 +	4 2.91	11 2.15 0.77	7 0.36 1.07	3 0.43 0.09	1 0.09 0.09	1 0.09 0.01	4 1.41 1.24	9 0.90 0.59	5 0.59 0.01	5 0.01 0.01	21 0.87 0.87	8 1.62 0.01
<i>Neea floribunda</i> Poeppig & Endlicher NYCTA.	24 1.80 +++	0 0.00 +	2 1.88 +	1 0.36 +	0 0.00 +	0 0.00 +	1 0.35 +	0 0.00 +	0 0.00 +	0 0.00 -	2 0.40 0.80	7 0.63 2.58	7 3.12 0.11	7 0.11 0.11	7 0.11 0.03	1 0.37 0.63	9 0.76 0.82	4 0.82 0.03	4 0.03 0.03	27 1.16 1.16	1 0.21 0.03

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