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Relationships between Soil and Vegetation in a Tropical Rain Forest in French Guiana¹

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ABSTRACT

We describe a new method to observe and map morphological and functional characteristics of soil. Drainage and surface hydromorphy were mapped in eleven plots including 16.8 hectares. In the same plots, all trees over 20 cm DBH were inventoried. Structural data of the vegetation are correlated to soils characteristics as well as the frequencies and densities of 32 taxa.

FLORISTIC AND PHYSIOGNOMIC HETEROGENEITY of tropical rain forests is often attributed to sylvigenesis (Aubreville 1938, Halle *et al.* 1978, Oldeman 1974). According to Denslow (1980) and Hubbell (1979), floristic patterns result from pattern of colonizing gaps (*i.e.*, the *chablis* of Oldeman, loc. cit.). Changes in the gaps through time lead to a continually evolving forest mosaic. However, the influence of soil on the composition and structure of tropical rain forest is also important (Ashton 1964, Ashton and Brunig 1975, Hase and Folster 1982, Lemee 1960, Richards 1952, Schmid 1958, and Schulz 1960, to mention but a few).

In French Guiana, the ECEREX (ECology, EROsion, EXperimentation) program was initiated in order to study undisturbed rain forest, possibilities for its development, and transformations that follow its modifications by human activities (Sarraiilh 1980). Hydrological, pedological and botanical data were obtained from the study of ten watersheds ranging in size from one to two hectares. Initial observations were made under undisturbed forest, then under diverse methods of cultivation selected by the administration of the Departemental Direction of Agriculture and National Forest Office. A one hectare unit, called the "biomass plot" (Lescure *et al.* 1983) has been added to the initial survey area. We report here preliminary observations dealing with the influence of edaphic factors on the natural forest cover.

MATERIALS AND METHODS

PEDOLOGICAL SURVEY.—A method of observation and mapping of soil mantles was developed by the ORSTOM

(Office de la Recherche Scientifique et Technique Outre-Mer) laboratory in Cayenne (Boulet 1978; Boulet *et al.* 1978, 1979, 1982). This method takes into account the three dimensional organization of the soil. It consists of observing the elementary sampling units of surface-relief (watersheds or interfluves) chosen for their physiographic representativity. Exploratory borings are made along straight lines down the slopes, whose degrees are measured with a clinometer, in order to identify soil morphologies and their respective volumes. Based on these data, soil cross-sections are drawn that show lateral variations in soil morphology and the different pedological volumes (Fig. 1). By additional borings, the projection on the surface of different soil morphologies or soil volumes can be mapped. The points on the map which separate two soil characteristics are linked by "isodifferentiation lines." These lines should not be confused with the classical pedological limits which result in soil maps in two dimensions, dividing the surface in supposed homogeneous areas.

More detailed studies of the soil characteristics are made from within pits which are located by reference to the previously drawn soil cross-sections and map (Fig. 1). Likewise, soil moisture is measured in order to study the water dynamic.

The representation of the soil mantle which results from this approach is made up of a chart of isodifferentiation lines and of vertical cross-sections (Fig. 1). Except in French Guiana, this approach has only been used in Brittany (Al Siddik 1983) and in Brasil (Queiros Neto *et al.* 1981). Therefore it is not possible to foresee all instances where difficulties can appear, for example, when the soil cannot be penetrated with a manual auger. If such obstacles do not appear, the representation with vertical cross-sections and map gives a clear and objective picture of the pedological structure to scientists. These

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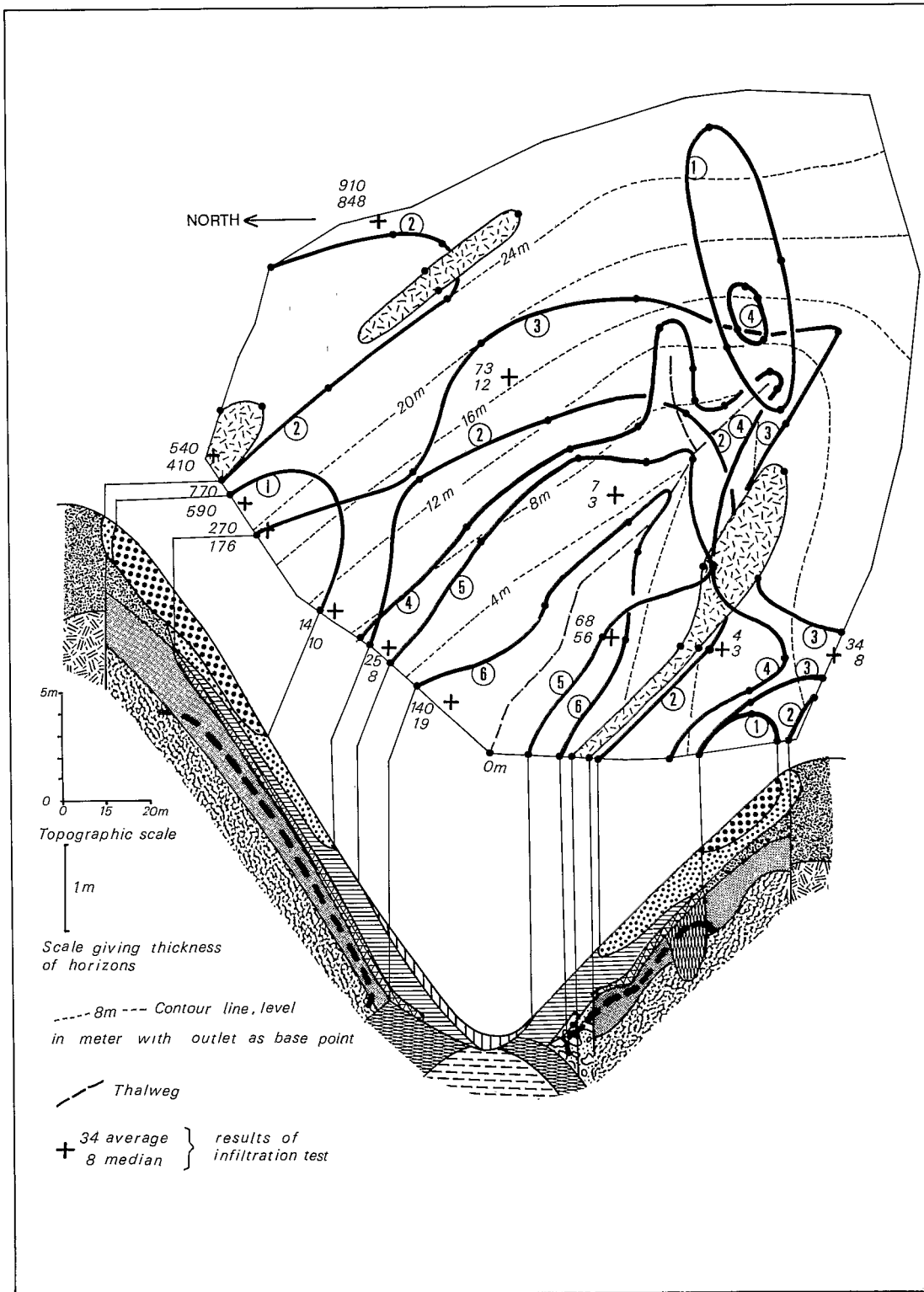
















FIGURE 1. Representation with map and cross-section of "E" ECEREX catchment area.

LEGEND OF VOLUMES AND HORIZONS DRAWN IN SECTION

- (a)  On pegmatite, brownish-yellow (10YR), sandy-clay loamy horizon with rough sand; on schist, strong brown (7.5YR), sandy-clay horizon with fine sand. Massive structure with polyhedral break-up, very rich in micropedic volumes; Well developed porosity, tubular and mainly intermicropedic.
- (b)  Pegmatite weathering material; sandy-clay loam; massive structure; Well developed interstitial porosity.
- (c)  Red (2.5YR) sandy-clay horizon; polyhedral structure; Weak, visible tubular porosity.
- (d)  Red (10R), clay-loamy horizon, with volumes of conserved structure massive structure with polyhedral break-up; weak, visible porosity.
- (e)  Volume differing from (c) by its heterogeneous colour; red (2.5YR) network, on yellow background.
- (f)  Reddish-brown (5YR), sand-clay horizon; polyhedral structure with few micropedic volumes; fairly developed tubular and intermicropedic porosity. This volume reaches the surface where it is little coloured by organic matter
- (g)  Brown (7.5YR) volume enclosing volume (f); colour only distinguishes them
- (h)  Horizon, brownish-yellow (10YR) upslope, becoming olive-yellow (2.5Y) downslope; massive structure with polyhedral break-up; micropedic volumes fairly abundant upslope, strongly diminishing downslope.
- (i)  Horizon characterized by a red (2.5YR), diffused network on brown (7.5YR) background.
- (j)  Weathering material of pegmatite, white with red volumes; sandy-clay massive structure; Weak, visible, tubular porosity.
- (k)  Humiferous, greyish-brown horizon, with grey volumes 5mm ϕ , with ochre-coloured aureole.
- (l)  Horizon with a red network on yellow background becoming white in depth; sandy clay loamy at its top, becoming loamy in depth; polyhedral structure; fairly developed tubular porosity.
- (m)  White horizon with red volumes with ochre-coloured aureole; clay-loamy; fairly developed tubular porosity

 Boundary enclosing material dry to the touch.

LEGEND OF ISODIFFERENTIATION CURVES

The definition of each curve is given for an observer who crosses it in the direction of the numbered side.









-  - Appearance on surface of the (f) reddish-brown horizon.
-  - Appearance on surface of the (g) brown horizon.
-  - Appearance of the diffuse horizon.
-  - Appearance on the surface of first hydromorphic features: Heterogeneous distribution of organic matter.
-  - Appearance on surface of accentuated features of hydromorphy.
-  - Disappearance of (c) red, sandy-clay horizon through the upward climb of horizon (1)
-  Point where the isodifferentiation curve was located.
-  Pegmatite

FIGURE 1, continued. Legend for symbols used in Figure 1.

maps are useful to botanists in particular because they allow correlations of soil properties and plant distribution.

BOTANICAL SURVEY.—The botanical data were collected by CTFT (Centre Technique et Forestier Tropical) and ORSTOM. The CTFT inventory included all trees in the ten watersheds with a DBH greater than 20 cm (Guiraud and Sarrailh 1980). Each watershed was divided into plots of 400 square meters (20 × 20 m). The tree-plotter spoke *Djuka*, a language widely used locally. The meaning of the vernacular names used by the tree-plotter was discussed by Lescure (1981).

In turn, ORSTOM inventoried all trees and shrubs over 1 cm DBH in watersheds A, B, C and I as well as in biomass plot. This inventory was based on 100 m² subplots which were located within the CTFT plots. The tree-plotter was an Amerindian from the Wayãpi tribe, whose botanical nomenclature was documented by Grenand (1980). Botanical vouchers were collected for many species and deposited in the ORSTOM herbarium of Cayenne. Both CTFT and ORSTOM measured DBH for each inventoried tree.

RESULTS AND DISCUSSION

PEDOLOGICAL RESULTS.—The soil mantles of the 11 ECEREX plots are representative of those in neighboring areas. These soil mantles indicate different stages in the evolution of an initial cover which changed because of a slight upthrust of the basement rock, resulting in a relative drop in the base level (Boulet *et al.* 1979). During this transformation, both the organization and functioning of the soil mantle changed, and soil properties were modified. The evolution of the soil mantle, based on current soil cross-sections made in the ECEREX area is illustrated in Figure 2.

The first stage (Fig. 2.1) corresponds to the initial soil mantle. This mantle is characterized by a top set of horizons that are brown, porous, microaggregated, very rich in ferruginous lithorelictual nodules, and more than a meter thick. This porous set overlays and gradually intergrades with another set which is characterized by much less visible porosity of tubular type, and by the lack of microaggregates. This compact set is subdivided into a red, clay-rich top horizon, and a bright red, micaceous silt-clayey bottom horizon. The nodules which are formed out of *lithorelictual*, *ferruginised* uncemented volumes, becomes indurated on the top of the compact set. In this first stage, water flow is deep and vertical. This is known as a free vertical drainage (FVD). However, downslope where the water table fluctuates, drainage is hindered when the water level is high. Hydromorphic characteristics only appear at the bottom of the slope.

In the second stage (Fig. 2.2), the porous set becomes thinner downslope. When its thickness is less than 70 cm,

the compact bottom set becomes dry to the touch and its top is slightly hydromorphic (presence of a red network against a yellow background). Filtration tests (Humbel 1978) and tensiometric measures (Guehl 1981) show that the dry horizon becomes impermeable, and the water flow becomes superficial and lateral which leads to a higher runoff. The rest of the water drains shallowly under the surface. This is known as a blocked vertical drainage (BVD). Surface hydromorphy advances upslope and surface permeability suddenly decreases after the drainage is blocked. The nodules which are dispersed in the porous set are concentrated in the horizon where the water circulates laterally.

In the third stage (Fig. 2.3), the porous set completely disappears and dry to the touch horizons are present throughout the slope. The water-flow, therefore, becomes entirely superficial and lateral. The surface hydromorphy invades a large part of the slope and the nodular horizon is omnipresent.

In the fourth stage (Fig. 2.4), the red, clay-rich horizon of the compact set begins to regress upslope. Dry to the touch horizons disappear downslope where a shallow water table is present. The nodules present above the red clayey horizon disappear downslope. The surface hydromorphy keeps the same extension as in the third stage with a few variations related, perhaps, to the degree of sloping.

In the fifth stage (Fig. 2.5), the red compact horizon disappears, the bright red micaceous one is replaced by a reticulate horizon subjacent to it. Downstream of the thalweg, the water table rises to the surface. Usually, the nodules remain upslope. This evolution appears to be the result of a depression in the initial soil mantle. From downstream to upstream, and from downslope to upslope, this depression induces the disappearance of the higher horizons of the initial soil mantle (*i.e.*, the porous set) and considerably modifies the type of drainage in the soil mantle. Finally, this depression allows the thalweg to incise the general water table store until water table rises to the surface level.

This evolution has been established for soil mantles on the Bonidoro-schists. These schists are penetrated by large pegmatitic veins which, because of their thick texture, may induce soil behaviour very different from that observed in the schists. However, soils on pegmatites present the same types and determination of drainage, although possessing a different morphology from those on schists. This shows the importance of the elementary organization (types of assemblage of the elementary particles among themselves) on such characters as texture; this elementary organization plays a critical role in the hydrodynamic behavior of the soil.

Hydrological and hydrodynamical studies confirmed the above proposed water dynamics. The existence of the two types of drainage appeared at the level of one hectare

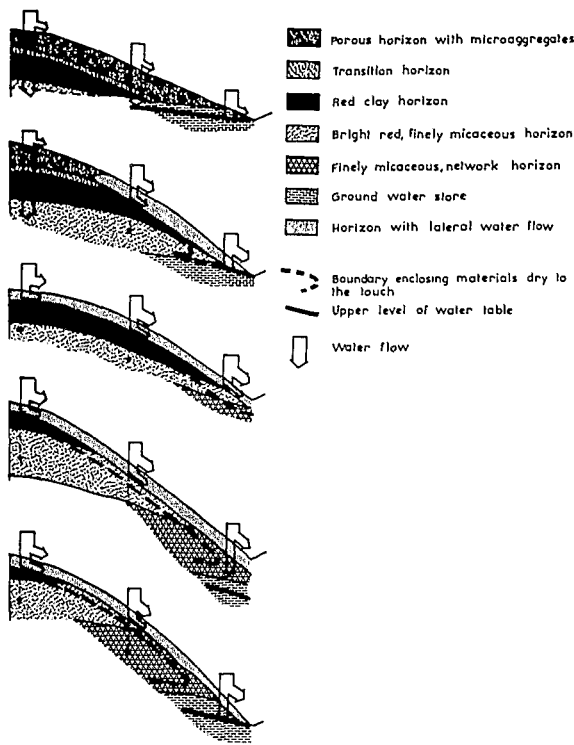


FIGURE 2. Stages of development of the soil mantle on Bonidoro schists.

plot (watersheds) as well as a hundred square meter one (runoff and erosion plots). Thus, the correlation between runoff in the watersheds and the percentage of the surface where blocked vertical drainage occurs is 0.99 (Fritsch 1981). Similarly, Sarrailh (1981), points out large differences in runoff between soils affected by one or another type of drainage. Under forest cover, the annual runoff, in percent of the total amount of precipitation, ranges from 0.6 to 1.4 percent in FVD soils and from 15 to 22 percent in BVD soils. Finally, using tensiometric and neutronal humidimetry, a precise study of the areas where the drainage changes, supports the above mentioned interpretation (Guehl 1981).

Although physical soil properties are variable, Table 1 demonstrates that variation in soil fertility is very low. Most exchange mineral reserves are concentrated in the upper twenty centimeters and especially in the upper five centimeters. Under thirty centimeters, chemical properties are uniform. However, we note higher amounts of superficial organic matter in FVD than in BVD soils. In FVD soils, the amount of organic matter decreases toward the lower part of the slope, and the amount of exchangeable bases varies in the same way. In BVD soils, we cannot observe any variation from up- to downslope, or only a very slight decrease.

TABLE 1. Chemical properties of four soils representative of the different categories affected by the examined physical characteristics.

Depth in cm	Soil with free vertical drainage (FVD)												Soil with blocked vertical drainage (BVD)											
	Upper part of the slope						Lower part of the slope with surface hydromorphy						Upper part of the slope						Lower part of the slope with surface hydromorphy					
	0-5	5-20	80-90	150-160	0-5	5-20	80-90	150-160	0-5	5-20	80-90	150-160	0-5	5-20	80-90	150-160	0-5	5-20	80-90	150-160				
Carbon %	61	34			46	36			39	20			41	22			22	1.6			5.4			
Nitrogen %	3.3	2.2			2.4	1.9			2.6	1.4			2.2	1.6			2.2	1.6			5.4			
PH water 1/25	4.4	4.7			4.7	4.8			4.7	4.9			4.6	4.9			4.6	4.9			5.2			
Exchangeable bases M.E.																								
Ca	0.31	0.06			0.16	0.08			0.23	0.04			0.23	0.08			0.23	0.08			0.01			
Mg	0.47	0.02			0.44	0.29			0.62	0.20			0.55	0.21			0.55	0.21			0.02			
K	0.22	0.13			0.19	0.14			0.12	0.07			0.17	0.07			0.17	0.07			0.01			
Na	0.17	0.06			0.10	0.07			0.08	0.07			0.11	0.06			0.11	0.06			0.05			
Exchange capacity ME	15.8	9.2			9.8	8			8.7	5.1			13	5.8			13	5.8			3.2			
Degree of saturation %	7.4	4.9			9.1	7.3			12	7.5			8	7.3			8	7.3			5.4			
Total phosphorus %	0.29	0.28			0.2	0.27			0.26	0.25			0.15	0.13			0.15	0.13			0.13			

TABLE 2. *Structural characteristics of the vegetation in the 11 sample areas and in the four plot-populations; relative cover of the types of soil in the sample area.*

Watersheds or plots	Basal area m ² ·ha ⁻¹	Density N·ha ⁻¹	log N = aD + log b			Total area Ha	FVD area in % of total area	BVD area in % of total area	H+ area in % of total area	H- area in % of total area
			a · 10 ⁻³	log b	R					
A	24.49	236	-29	2.765	-0.97	1.24	0	100	9.8	90.2
B	24.88	193	-29	2.667	-0.96	1.76	10.2	89.8	8.7	91.3
C	22.74	195	-25	2.495	-0.99	1.72	100	0	6.7	93.3
D	21.12	146	-23	2.249	-0.92	1.60	71.9	28.1	10.5	89.5
E	18.50	142	-19	2.163	-0.96	1.80	47.2	52.8	29.0	71.0
F	18.76	190	-26	2.527	-0.95	1.72	0	81.8	45.9	54.1
G	17.62	186	-34	2.862	-0.98	1.80	0	88.6	59.6	40.4
H	20.02	200	-38	2.051	-0.86	1.28	0	90.9	63.5	36.5
I	20.40	212	-30	2.767	-0.98	1.28	61.7	38.3	11.3	88.7
J	18.96	195	-46	2.346	-0.86	1.60	8.8	90.1	72.1	27.9
Biomass plot	32.80	286	-27	2.758	-0.97	1.00	100	0	0	100
	21.47	193	-29	2.700	-0.99	16.80	34.7	60.6	30.1	69.9
Plot-populations										
FVD	22.86	197	-25	2.752	-0.99	5.12				
BVD	20.46	192	-32	2.810	-0.99	8.98				
H+	17.75	177	-33	2.843	-0.99	3.32				
H-	22.27	191	-26	2.651	-0.99	9.92				

The contrast between the great variations of the flow patterns, involving variations of water reserves as well as variations of soil's thickness usable by roots, and the slight variations of chemical fertility, justifies that we mainly study the effects of physical properties of the soil. At most, the slightly lower chemical fertility of the BVD soils and its diminution from up- to down-slope will increase the effects of physical characteristics studied here.

Therefore, we shall limit our discussion to the variations to the physical properties of the soil especially those concerning the air-water balance. The influence on the vegetation of other pedological factors—presence of nodules, schists versus pegmatite parent rock—was also studied but revealed no significant correlations. We will examine the following characteristics of the soil's air-water balance: free vertical drainage (FVD); blocked vertical drainage (BVD); presence (H+) or absence (H-) of hydromorphic characters in the upper horizons of the soil.

STRUCTURAL PARAMETERS OF THE TOTAL POPULATION.—We utilize here the data concerning all trees over 20 cm in DBH, and the 20 × 20 m CTFT plots. We examine three aspects of the structure: density, basal area and the absolute value of the calculated constant "a" of the semi-logarithmic distribution of the diameter classes.

Following Rollet (1969) we refer to the diameter class distribution of the entire population calling it total structure, and estimate that the semi-logarithmic adjustment proposed here gives a satisfactory linear transformation on condition that the population is small enough (covering a few hectares) and that its lower limit is high enough (over 20 cm DBH). We use:

$$\log N_i = a D + \log b$$

in which

N_i = number of trees per hectare for each class of DBH,

D = median value of the class measured in cm, a and b being calculated constant values.

The "a" value determines the slope of the adjusted line and thus illustrates the tendency of population to produce large trees; the stronger this tendency, the smaller the absolute "a" value.

In each plot under study, we established by use of the pedological map, the percentage of surface covered by each of the edaphic factors. Variations of the structural data with these percentages were correlated using Spearman's non-parametric correlation coefficient (r_s). We also superimposed the inventory-plot maps on the pedological ones, thus edaphically characterizing each of the 400 m² plots. Next, we regrouped the plots into plot-populations, FVD, BVD, H+, H-, and calculated the values of the three structural parameters under consideration for each of these plot-populations.

Table 2 gives the following data for each studied watershed as well as for each plot-population: tree-population density expressed in number of trees per hectare; total basal area; "a" and log b values as well as r coefficient of correlation of the graphs adjusted to the observed total structure; surface of each studied watershed; and percentage of this surface occupied by FVD, BVD, H+, H- edaphic factors.

TABLE 3. Absolute frequencies and densities of the studied taxa in different soil's conditions.

Taxa	Frequencies				Densities			
	FVD	BVD	H+	H-	FVD	BVD	H+	H-
<i>Bocopa prouacensis</i> (Aubl.) Amsch.	14	19	1	28	14	19	1	28
<i>Brosimum guianense</i> (Aubl.) Hub.	7	7	1	14	7	7	1	14
<i>Carapa guianensis</i> Aubl.	9	14	5	18	10	15	5	19
<i>Chrysophyllum prieurii</i> A.DC.	11	24	4	30	14	27	4	35
<i>Dicorynia guianensis</i> Amsh.	8	52	12	16	8	58	13	16
<i>Eschweilera chartacea</i> (Berg.) Eyma	62	114	36	118	105	165	55	186
<i>Eschweilera corrugata</i> (Poi.) Miers.	57	132	51	126	92	261	73	235
<i>Licania canescens</i> R.Ben.	14	13	3	28	15	16	4	32
<i>Licania heteromorpha</i> Benth.	40	113	42	97	49	165	63	132
<i>Manilkara bidentata</i> (A.DC.) Chev.	0	9	9	6	0	11	10	6
<i>Micropholis guyanensis</i> (A.DC.) Pierre	18	43	20	42	18	44	21	42
<i>Ocotea guianensis</i> Aubl.	11	6	1	15	11	8	1	17
<i>Ocotea rubra</i> Mez.	6	8	4	11	6	11	4	11
<i>Parabancornia amapa</i> (Aubl.) Ducke	5	9	1	14	6	12	1	16
<i>Parkia nitida</i> Miq.	4	8	6	4	4	9	6	4
<i>Peltogyne paniculata</i> Benth.	6	11	2	13	7	11	2	15
<i>Pouteria guianensis</i> Aubl.	16	13	1	24	17	13	1	24
<i>Pouteria melanopoda</i> Eyma	5	12	2	13	5	12	2	13
<i>Pouteria ptychandra</i> Eyma.	9	8	3	28	11	8	3	33
<i>Priourella cuneifolia</i> (Rudge) Pierre	10	8	4	17	12	8	4	17
<i>Protium</i> sp.	22	13	1	33	27	15	1	42
<i>Qualea</i> sp.	7	2	0	8	7	2	0	8
<i>Sclerolobium melinonii</i> Harms.	4	10	1	12	5	11	1	14
<i>Swartzia remiger</i> Amsch.	5	15	5	16	6	15	5	16
<i>Swartzia tomentosa</i> DC.	5	10	4	11	5	10	4	11
<i>Symphonia globulifera</i> L.	9	37	17	24	9	42	18	27
<i>Tovomita</i> sp.	9	14	6	14	10	14	6	14
<i>Virola melinonii</i> R. Ben.	13	12	0	25	13	12	0	25
<i>Youacapoua americana</i> Aubl.	25	25	5	41	26	25	5	44
<i>Xylopia nitida</i> Dun.	8	6	1	12	9	6	1	14
<i>Eperua</i> spp.	42	161	65	92	62	268	126	195
<i>Sterculia</i> spp.	5	8	5	9	5	8	5	9

Total number of trees: FVD: 1294; BVD: 1703; H+: 589; H-: 1996.

Total number of 400 m² plots: FVD: 128; BVD: 224; H+: 83; H-: 223.

TAXONOMIC DISTRIBUTION.—One should keep in mind that the method used here for inventory, widely employed in tropical forest botany (Maas 1971, Prance *et al.* 1976, Richards 1952, Rollet 1969, Schulz 1960), leads to some taxonomic uncertainty. It therefore becomes difficult to compare populations of all taxa encountered. On the other hand, one can positively identify several taxa at either the specific or generic level. With a sufficient sample size, we can compare the response of these taxa to the different types of soil. We chose 32 taxa, 30 identified at the level of species, and two at the genus one. For each of these taxa, the absolute frequency and the density were calculated, regrouping the plots in populations FVD, BVD, H+, H-, as mentioned above (Table 3).

The homogeneity of these plot-populations were tested with chi-square tests by comparing the frequencies and the densities of different species according to different soil factors. Differences in relative densities were tested by *t*-tests. Analyses are presented in Table 4.

SOIL AND VEGETATION STRUCTURE CORRELATIONS.—In the 11 sampling stations, densities ranged from 142 to 286 trees per hectare, but the calculated r_s values show no significant correlation between density and cover area for any of the edaphic factors. Basal areas ranged from 18.5 to 32.8 m²/ha, but we found no correlation between basal area and the FVD and BVD cover area. On the other hand basal area and H+, H- cover area were correlated ($r_s = -.83$, $P < .01$); this correlation being negative demonstrates that the surface hydromorphy does not favor large basal areas.

The three structural parameters being closely linked, a difference in basal area without changes in density indicates that the population with the higher basal area produces more big trees than the other one. This is confirmed by the correlation test with the "a" value of the total structure; r_s values show a correlation between "a" and the cover area variation of FVD ($r_s = -.50$), BVD ($r_s = .52$), H+ ($r_s = .70$) and H- ($r_s = -.70$); the di-

TABLE 4. Behavior of the taxa in different soil conditions: results of the Chi-square tests on frequencies and t -tests densities for the studied taxa, situated in FVD versus BVD and in H+ versus H- conditions.

	Drainage (FVD vs. BVD)		Hydromorphy (H+ vs. H-)	
	Fre- quency	Density	Fre- quency	Density
<i>Bocopa prouacensis</i>			+	+
<i>Brosimum guianense</i>			+	
<i>Carapa guianensis</i>				
<i>Chrysophyllum prieurii</i>			+	(+) ^b
<i>Dicorynia guianensis</i>	+	+	+	+
<i>Eschweilera chartacea</i>				
<i>Eschweilera corrugata</i>	+	+		
<i>Licania canescens</i>			+	(+)
<i>Licania heteromorphba</i>	+	+		+
<i>Manilkara bidentata</i>	- ^c	-	+	+
<i>Micropholis guyanensis</i>		+		+
<i>Ocotea guianensis</i>	+		+	(+)
<i>Ocotea rubra</i>				
<i>Parahancornia amapa</i>			+	(+)
<i>Parkia nitida</i>			+	+
<i>Peltogyne paniculata</i>				
<i>Pouteria guianensis</i>	(+)		+	+
<i>Pouteria melanopoda</i>				
<i>Pouteria ptychandra</i>			+	+
<i>Priourella cuneifolia</i>				
<i>Protium</i> sp.	+	+	+	+
<i>Qualea</i> sp.	+	+	-	+
<i>Sclerolobium melinonii</i>			(+)	
<i>Swartzia remiger</i>				
<i>Swartzia tomentosa</i>				
<i>Symphonia globulifera</i>	+	+	+	+
<i>Tovomitza</i> sp.			-	
<i>Virola melinonii</i>				+
<i>Vouacapoua americana</i>	(+)		+	+
<i>Xylopia nitida</i>			(+)	
<i>Eperua</i> spp.	+	+	+	+
<i>Sterculia</i> spp.				

^a $P < .05$.

^b $P < .10$.

^c Insufficient sample size for this comparison.

rections of the correlations indicate that FVD and H- factors contribute to the presence of large trees.

The means of the densities of the FVD, BVD, H+ and H- plot-populations indicated no influence of these edaphic factors on tree density. The t -values of 1.27 for FVD versus BVD and of 1.31 for H+ versus H- were not significant.

The characteristics of the different types of soil help explain observed correlations. In the FVD soils, aeration is always satisfactory. Roots penetrate more than two meters deep. The layer between one and two meters contains, under natural forest, 5 percent of all the roots found in the top two meters (Humbel 1978). In the dry season, the thickness of soil accessible to the roots compensates

TABLE 5. Behavior of the studied taxa according to the pedological climate.

Species	Sign of correlation with:	
	H+	BVD
<i>Bocopa prouacensis</i>	-	
<i>Brosimum guianense</i>	-	
<i>Chrysophyllum prieurii</i>	-	
<i>Licania canescens</i>	-	
<i>Parahancornia amapa</i>	-	
<i>Pouteria ptychandra</i>	-	
<i>Sclerolobium melinonii</i>	-	
<i>Virola melinonii</i>	-	
<i>Xylopia longifolia</i>	-	
<i>Parkia nitida</i>	+	
<i>Dicorynia guianensis</i>	+	+
<i>Licania heteromorphba</i>	+	+
<i>Manilkara bidentata</i>	+	+
<i>Micropholis guianensis</i>	+	+
<i>Symphonia globulifera</i>	+	+
<i>Eperua</i> spp.	+	+
<i>Ocotea guianensis</i>	-	-
<i>Pouteria guianensis</i>	-	-
<i>Protium</i> sp.	-	-
<i>Qualea</i> sp.	-	-
<i>Vouacapoua americana</i>	-	-
<i>Eschweilera corrugata</i>		+

the small quantity of available moisture per unit-volume, and probably of available nutrients. Moreover, even during the dry season, these soils retain moisture below one meter. In BVD soils, water availability is extremely variable. In the rainy season, a fugacious "perched" water table circulates between 30 and 50 cm in depth. However, water pockets trapped by the subjacent impermeable horizon persist longer than the rainy season. Soil aeration becomes insufficient, at least in some of the horizons. The layer on which roots depend is limited in depth. Humbel (1978) showed that under natural forest, the 1-2 meter layer of BVD soils contains only 0.5 percent of the total amount of the roots present in the 0-2 meter one; this ratio is ten times smaller than the one observed in the FVD soils. In addition, available moisture decreases considerably in dry season.

Surface hydromorphy may also influence root development. It affects more roots in BVD soils, where 80 to 90 percent of the total amount of the roots present in the 0-2 meter layer is situated between 0 and 20 cm in depth, than in FVD soils where this upper layer only contains 40 to 70 percent of the total amount of the roots present in the 0-2 meter layer. Moreover, it appears that this surface hydromorphy is not independent of the type of drainage since it covers a smaller area in the FVD watersheds than in the BVD ones where it can extend itself over a considerable area even when the slope is steep (30%).

SOIL AND TAXONOMIC DISTRIBUTION.—Table 6 summarizes the responses of the studied taxa to pedoclimate. Some species were more successful on surface hydromorphy and BVD soils, and while others did better on FVD soils without surface hydromorphy. Some species were insensitive to BVD conditions but reacted to surface hydromorphy. Ten of the 32 studied taxa (31%) do not react in any way, either to drainage conditions or presence of surface hydromorphy. Perhaps a larger sample could differentiate patterns.

We note that nine taxa (28%) react negatively to the surface hydromorphy without being affected by BVD conditions. These are *Bocoa prouacensis*, *Brosimum guianense*, *Chrysophyllum prieurii*, *Licania canescens*, *Parahancornia amapa*, *Pouteria ptychandra*, *Sclerolobium melinonii*, *Virola melinonii*, *Xylopia longifolia*. On the other hand, only one taxon *Parkia nitida*, prefers surface hydromorphic soils.

The densities and frequencies of *Ocotea guianensis*, *Pouteria guianensis*, *Protium* sp., *Qualea* sp., *Vouacapoua americana* are lower under BVD conditions as well as under surface hydromorphic soils. Inversely, these same edaphic conditions favor the development not only of *Symphonia globulifera*, *Eperua* spp. which are well known in French Guiana for their presence in low, flat, hydromorphic zones, but also of *Dicorynia guianensis*, *Licania heteromorpha*, *Manilkara bidentata* and *Micropholis guianensis*. It is interesting to note, though the present data can not demonstrate it, that in the case of *Eperua*, certain species may prefer FVD soils (*Eperua grandiflora*) but these species are in minority compared with the dominant *Eperua falcata*, and do not present enough statistical weight to influence the result obtained at the genus level. Finally, only one taxon, *Eschweilera corrugata*, prefers BVD soils, but the advantage that this type of soil offers is lost when the surface hydromorphy takes place. Once

again, we note that the influence of surface hydromorphy is greater than that of the BVD factor: 37 percent of the studied taxa respond to differences in drainage conditions, and 59 percent to the apparition of surface hydromorphy.

CONCLUSION.—Even the species reacting to the edaphic factors of drainage and surface hydromorphy are not restricted to only one condition. Only *Manilkara bidentata* shows a zero-density under FVD conditions in our sample area, but we only found 11 trees of this species, and we have observed this species growing on FVD soils outside of the sample area. We used frequency and density to measure the reactions of species to pedological factors, but according to Finkelstein (1983), Puig and Prevost (1983), Sabatier and Puig (1983), those variations are probably accompanied by other manifestations, particularly in growth and phenology.

Finally, our results show that the method of pedological investigation used here, which emphasizes lateral functional variations in soils by the mean of easily observed morphological characteristics, is of great help to botanists. In analysing species distribution and forest structure, this approach should be followed by more extensive studies taking into account on one hand, a larger number of taxa each represented by more individuals, and on the other hand, the analysis of other structural characteristics of the vegetation such as frequencies and size of the gaps, growth of the trees and architectural pattern.

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