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# TROPICAL RAIN FORESTS OF KWAKWANI-GUYANA. PART 1: PEDOSPHERE, SEDIMENTS AND VEGETATION STRUCTURE

# BOSQUE LLUVIOSO TROPICAL EN KWAKWANI-GUYANA: PARTE I: PEDOSFERA, SEDIMENTOS Y ESTRUCTURA DE LA VEGETACION

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## ABSTRACT

Soils in Kwakwani (northeastern Guyana) were identified and characterized to establish the patterns of spatial distribution of soil and vegetation and their relationships. The study area is located between 5° 21' 46" - 5° 20' 18" N and 58° 2' 24" - 58° 1' 44" W. Climate is rainy tropical with 2280-2540 mm of annual rainfall and udic soil humidity regime. Thirty observations of soil detail were done in five permanent plots established in Guyana by the Biodiversity Program SI/MAB, and simultaneously the characteristics of the vegetation structure were determined. Data were analyzed by principal component analysis and canonical correlation analysis. In the sandy sediments, Aquoxic Quartzipsamments excessively drained were identified, with Haplorthods inclusions in the more depressed sites. In the loam sediments there was a dominance of Typic Paleudults with Aquic Paleudults inclusions. The forest associated to sandy soils had a similar structure to caatinga forest, presenting a low height and high density of trees (DBH> 10 cm), whereas forests associated to loam soils were characterized by high forests, with a low density (DBH> 10 cm). Soils were acidic with low nutrient levels in the mineral fraction. Nutrient concentration was not related to the mineral fraction characteristic of soils, such as texture and exchangeable aluminum, but it was to organic matter content. Soil variability was related to texture, complex exchange, A horizon thickness, and structure, which also had an influence on the water retention capacity of the soils; these characteristics were associated to forest type.

## RESUMEN

Los suelos de Kwakwani (noreste de Guyana) fueron identificados y caracterizados con la finalidad de conocer el patrón de distribución y las interrelaciones con la vegetación . El área de estudio está localizada entre 5° 21' 46" - 5° 20' 18" Norte y 58° 2' 24" - 58° 1' 44" Oeste. El clima es lluvioso tropical con 2280-2540 mm anual de lluvia y un régimen udico de humedad del suelo. En cinco parcelas permanentes del Biodiversity Program SI/MAB se describieron 30 observaciones de detalles y simultáneamente se determinaron las características de la estructura de la vegetación. La información fue analizada con el uso de componentes principales y correlación canónica. En los sedimentos arenosos fueron identificados Aquoxic Quartzipsamments con inclusiones de Haplorthods en los sitios depresionales. En los sedimentos francos hubo dominancia de Typic Paleudults con Aquic Paleudults como inclusiones. Los bosques en suelos arenosos son similares a la caatinga, con baja altura (15-20 m) y alta densidad de fustes (DBH> 10 cm). Los bosques en suelos francos son altos (25-35 m), con baja densidad de fustes (DBH> 10 cm). Los suelos son ácidos con baja concentración de nutrientes en fracción mineral. El contenido de nutrientes de los suelos no se relacionó con características de la fracción mineral, tales como textura y aluminio intercambiable, pero sí con el contenido de materia orgánica. La variabilidad del suelo está relacionada a textura, CIC, espesor del horizonte A y estructura, las cuales influencian la capacidad de retención de agua de los suelos, y a su vez se relacionan con la presencia de un tipo de bosque específico.

**Key words**: Guyana, pedosphere, soil, tropical rain forest, relationships, vegetation structure.

**Palabras claves**: Guyana, pedósfera, suelo, bosque lluvioso tropical, estructura de vegetación, interrelaciones.

## INTRODUCTION

Pedosphere constitute a hypogeous system with trophic and spatial structure, autoregulation, and functionality. Its function is to provide air, water, nutrients, and mechanical support to plants. It is critical to include the study of soil in ecological research, since soil is responsible for important functions in the flow of energy and matter in the tropical rain forest ecosystems (Stark, 1971a, b; Anderson, 1981; Baille and Ashton, 1985; Mabberley, 1992; Matsumoto, 1995).

Soils of tropical rain forests are acid and oligotrophic, due to the effect of high rainfall on paren-tal material for long periods of time; however, soils that are recent alluvials tend to be more fertile (Sánchez, 1989; Prance, 1989; Whitmore, 1990). The most frequent soil classes are Oxisols and Ultisols (63%), Psamments and Spodozols (7%), and Fluvents and Aquents (12%) (Sánchez, 1989; Whitmore, 1990). Characteristic of rain forest soils is their high sensibility to disturbance, because of their erosivity and nutrient flow dependence of organic matter (Schultz, 1960; Janos, 1985; Jordan, 1989; Tiessen et. al., 1994; ter Steege et. al., 1995; Van Der Meer and Bongers, 1996). Several ecolo-gical studies of tropical rain forests report soil characteristics for some ecosystems near the study area, as Davis and Richards (1934) and ter Steege et al. (1993) in Guyana, Shultz (1960) and Stark (1970) in Suriname, Lescure and Boulet (1985) and Van Der Meer and Bongers (1996) in French Guiana. Soil-vegetation relationships in rain forest have been studied by Johnston (1992) in Tabonuco Forest of Puerto Rico, Oliveira-Filho et al. (1994) in the Brazilian Amazon, ter Steege (1993) in Guyana, Duivenvoorden (1995) in the Colombian Amazon, and Sabatier et al (1997) in French Guiana.

The purpose of this study was to identify and characterize soils of the Kwakwani-Guyana area to establish the patterns of spatial distribution of soil and soil-vegetation relationships. Soil measurements were done in the Biodiversity Permanent Plots established by the Biodiversity Program SI/MAB (Comiskey et al, 1993). In this paper was shown that high forest is restricted to loam soils, and lower forest to sandy soils. However, nutrient concentration in the mineral fraction was not important for forest differentiation.

## METHODS

**Study area:** The study area is located in Kwakwani, northeastern Guyana, near the Berbice River, between 5° 21' 46" - 5° 20' 18" N and 58° 2' 24" - 58° 1' 44" W (Figure 1), with an average altitude of 120-130 m. Geological materials were previously assigned to the Berbice Formation (White Sand Formation) and correspond to the Early Pleistocene (Brown and Sawkins, 1875; Fanshawe, 1952; Sinha, 1968; Berrangé, 1977). The Napi Laterite Formation is present in some locations below the Berbice Formation. It is compose of aluminous laterite or bauxite, with kaolinitic material, which is white or greenish white in color at the base and corresponds to the Oligocene-Eocene. The Berbice Formation has white and brown sands, both overlaying and passing into brown-orange silty and clayey sediments. They are probably sedimentary deposits of the Proto-Berbice River derived from the Roraima Formation (Sinha, 1968; Berrangé, 1977), subject to erosional phases that took place during the Pleistocene.

The well-drained soils of northern Guyana are generally acid, low in nutrients, and highly meteorized (Davis and Richards, 1934; Fanshawe, 1952). In the Berbice Formation, sandy soils and Spodozols predominate, and are related to the caatinga sclerophyll forest vegetation (Richards, 1961). ter Sttege et al. (1993) mention the existence of a soil mosaic in the rain forest.

Climate is tropical with an average temperature of 28°C, and variation lower than 5°C between the rainy and the dry season. Precipitation is distributed in a bimodal pattern with maxima in the months of June and December and minima in September-October and February-March. Largest precipitations occur in June. This bimodal pattern is related to the influence on the intertropical convergence zone by the northeastern and southeastern trade winds (Frost, 1968). Climatological stations in Georgetown (6° 24'N, 58° 8'W) and Ebini (5° 34'N, 57° 47'W), to the north of the study area, show an annual rainfall of 2,358 mm and 2,286 mm, respectively; in September and October, rainfall was less than 100 mm, but more than 30 mm. The Kurupukari Station to the South shows an annual average of 2,540 mm; with more than 100 mm of rainfall each month.

**Figure 1**. Study area, Kwakwani, Guyana

Evapotranspiration is low (4.2 mm/day) during the maximum precipitation season and high (8.2 mm/day) during the months with lower rainfall (Eden, 1964; Sinha, 1968). The soil humidity regime may be described as udic; it has less than 90 dry days in the control section (Soil Survey Staff, 1994).

**Sampling:** This study was conducted in the rain forest of the Kwakwani, Guyana area. A stratified design was used, where each stratum was one of the permanent biodiversity plots established in Guyana by *The Biodiversity Program SI/MAB*. Five permanent plots of 1-ha each were analyzed, subdivided in 25 quadrates of 20 m x 20 m (Dallmeier et. al., 1992). A systematic sampling was set up within each plot with a fixed distance of 40 m between observations, which correspond to 6 subplots (quadrates) per 1-ha plot (Figure 2). To detect soil variability in forest, it has been proved unnecessary to use a plot size smaller than 20 m x 20 m (Berroterán, 1994). Soil observations were made in the center of quadrate (20 m x 20 m) and vegetation structure data measured in the whole area of the quadrate. A total of thirty observations were described.

Soil observations were of detail (holes of 60 cm wide by 1 m deep). Characteristics of the genetic surface horizon (A) and subsurface horizon (B or C) were performed, because of the importance of considering subsoil in this type of study, as indicated by Berroterán (1994). The soil observations were used to characterize soil variability in the landscape. Thirty observations of detail were described. Representative profile descriptions (5) were made (2 m wide by 2 m deep holes), and morphological and compositional characteristics of each horizon in the soil profile were determined and identified according to the Soil Taxonomy (Soil Survey Staff, 1994).

**Variable Determination:** Morphological characteristics of soil horizons are described according to the Soil Survey Manual (Soil Survey Staff, 1993). Horizon width, HCl reaction, color, structure, inclusions, cracks, rock fragments, and roots were considered. All horizons were considered for taxonomic descriptions of the soils. Means of the A and B or C horizons were used for detail observations.

Granulometric composition was determined by the Bouyoucos's method and organic matter by wet oxidation of the carbon present in the organic fraction of the soil (Jackson, 1984). Availables elements were extracted with North Carolina solution in a 1:4 ratio (weight/volume). Phosphorus was determined colorimetrically (Chapman, 1986), and available cations, calcium, magnesium, and potassium by atomic absorption spectrophotometry. Exchangeable aluminum was estimated with the potassium chloride method (Allen, 1974) and pH using a 1:1 water-soil ratio. Total organic nitrogen was determined by microKjeldal digestion and distillated (Jackson, 1984). Exchangeable bases were determined by extraction with ammonium acetate. Total elements in litter were estimated by digestion with hydrogen peroxide and sulfuric acid (Chapman, 1986).

The characteristics of vegetation structure selected were basal area of trees with diameter at breast

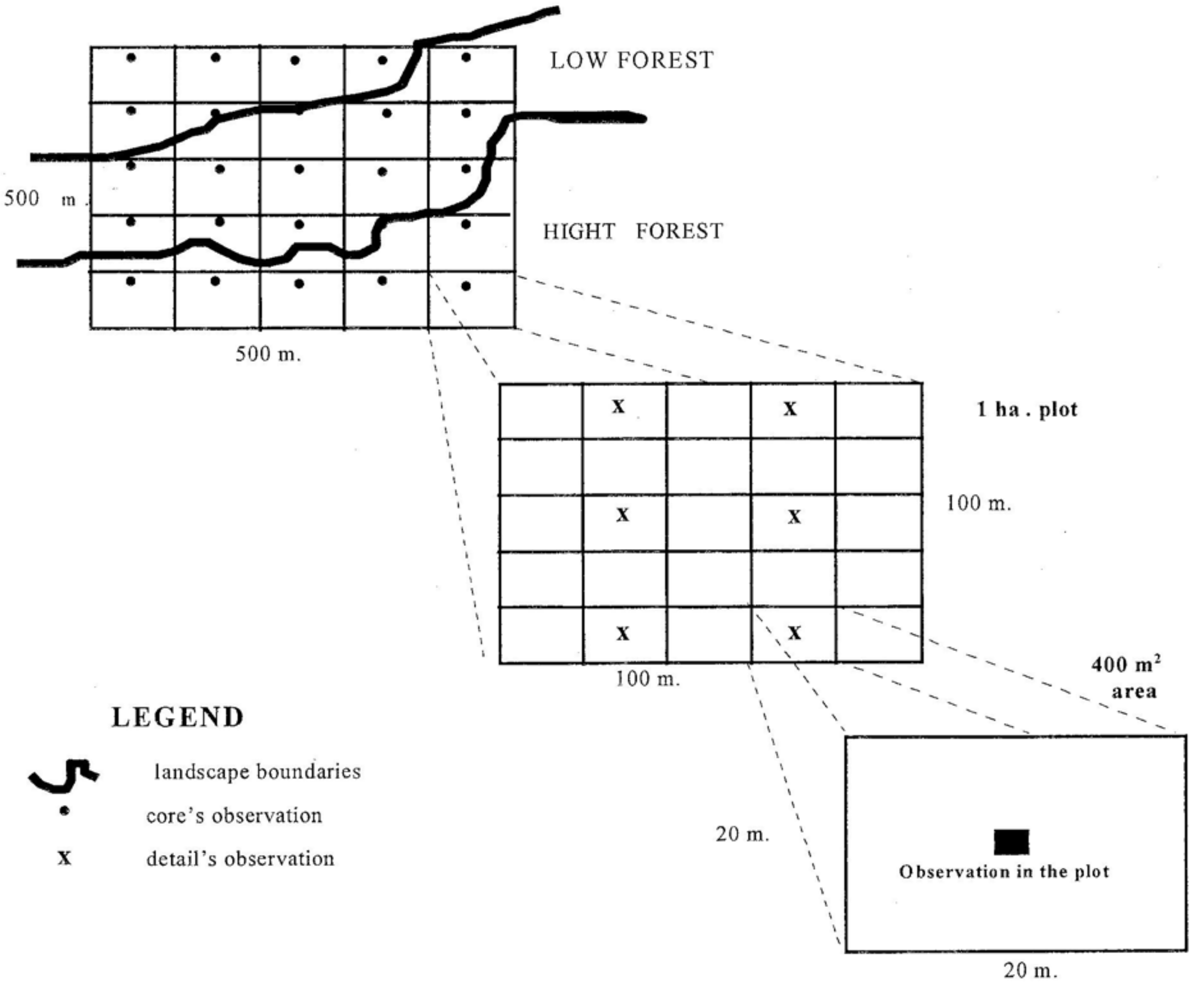

**Figure 2.** Stratified sample design for soils in permanent biodiversity plots established in Kwakwani, Guyana by the SI/MAB Project (Comiskey *et al.*, 1993)

height (DBH >10 cm) or 1.5 m from ground, maximum height of canopy and stem density (DBH>10 cm), emergent trees height, soil cover by trees, and DBH of widest tree in the quadrate.

**Statistical Analyses:** Principal Component Analysis (PCA) was performed with the SAS version 6.1 program. Normality of variables was tested with the Shapiro and Wilk's test, being $p < 0.05$ the acceptable threshold. In the principal component analysis, a variable correlation matrix was used to standardize the unitary variance of the original variables, giving equal importance to each variable. Correlation was determined between the original variables and the principal components (Pla, 1986). The difference between the proportion of the variation in the explained variable for each component or group of components and the maximum variation of the data of that variable (100%) reveals the amount of information loss in the variable for a specific principal component or group of components. This permitted the selection of the variables that explain the information variability.

Canonical Correlation (CANOCO) Analysis was performed to study the relationship between the soil variables and vegetation structure. Soil variables used were those selected by principal component analysis. The linear combination for each set of variables was calculated as the maximum correlation between the two sets was obtained (Gittins, 1985). The linear combination of each group of variables is called canonical variable and its correlation coefficient is the first canonical correlation. The other pair of linear combinations not related to the first, and which makes the second largest correlation coefficient is the second canonical correlation. In similar fashion, n variables and canonical correlations may be obtained, depending on the number of variables of the smallest set.

## RESULTS

**Soils:** The study area is a slightly undulated landscape, a product of the dissection of sediments from the Berbice Formation. Slopes are lower than 4% and the difference between the top of the landscape and the drainage border is less than 5 m. Sandy sediments were recognized with a mean of 95% sand and 3.6% clay, with massive relief and less dissected than loam sediments. These latter contain 66% sand and 19.6% clay in the subsurface horizons. No signs of erosion exist at present. Sandy and loam sediments do not overlap, but gradually get in contact, indicating that they are the products of chronologically-related depositions. Sand particle size curves (Figure 3) show a dominance of particles between 500-100 μ (70-75% of the total).

Granulometric curves of the profiles do not vary with depth, suggesting uniformity in the sedimentologic behavior throughout the profile. In the sand fraction, quartz highly resistant to meteorization is the dominant mineral in the two soils, and it is related to deposits coming from quartzic linestones of the Roraima Formation (Sinha, 1968). Below the sandy and loam sediments, at a depth between 2 and 4 m, a clayey deposition with presence of bauxite, related to the Napi Formation (Berrange, 1977) was observed.

In the sandy sediments, Aquoxic Quartzipsamments were identified, excessively drained with Haplorthods inclusions in the more depressed sites. In the loamy sediments there was a dominance of Typic Paleudults with Aquic Paleudults inclusions, the latter associated to clayey sediments above the 2 m of depth. A high acidity and low cation and base exchange capacity are evident in the three profiles (Table 1). All soils are present an organic horizon (O1) that varies between 4 and 5 cm thick, with a high content of fiber material (70%). Total concentration of nitrogen (1.07-0.87%), phosphorus (1500-1600 (g/g), calcium (21,000-35,000 μg/g), magnesium (3,200-5,000 μg/g), and potassium (13,800-19,900 μg/g) in organic horizon does not show a high variability in the profiles (Table 2).

Plots 3 and 6 are located in sandy soils (97-94% sand) and plots 4, 5, and 7 in loamy soils (14-32% clay). Very low concentrations of phosphorus, potassium, calcium as well as strong acidity, were typical in all soils (Table 3). Organic matter, magnesium and potassium concentration in the surface horizon is higher than in the subsuperficial horizon. Sandy soils do not present structure and show less exchangeable aluminum than loam soils. Surface horizon is dark (10YR3/2-5YR3/2) in all soils and subsurface is pinkish gray (7.5YR7/2) in sandy soils and yellowish brown (10YR5/4) to yellow (10YR7/6) in the loam soils.

**Table 1. Analysis of representative soil profiles.** One profile was analyzed for each plot, however, only three were considered in the laboratory. because Paleudults were described in plots 4, 5, and 7.

| Horizon | Depth | Clay | Silt | Sand | Texture | O.M | N | P | Ca | Mg | K | Na | Al | H | CEC | Base saturation | pH |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Name | (cm) | % | % | % | | % | % | ug/g | cmol/k g. of soil | | | | cmol/k g. of soil | | | % | water 1:1 |
| Typic Paleudult (plot 4.22) | | | | | | | | | | | | | | | | | |
| O1 | 0-4 | | | | | 76.5 | | | | | | | | | | | |
| Ah1 | 4-32 | 15.9 | 7.17 | 76.93 | Sandy loam | 1.99 | 0.18 | 5 | 0.12 | 0.06 | 0.05 | 0.02 | 3.24 | 2.36 | 6.7 | 2.39 | 4.4 |
| Ah2 | 62-83 | 19.6 | 5.38 | 75.02 | Sandy loam | 1.64 | 0.14 | 8 | 0.1 | 0.04 | 0.03 | 0.02 | 3.96 | 2.54 | 6.1 | 1.97 | 4.24 |
| Bt1 | 62-83 | 22.7 | 5.07 | 72.23 | Sandy loam clay | 0.71 | 0.09 | 9 | 0.1 | 0.04 | 0.02 | 0.01 | 3.42 | 1.88 | 5.2 | 1.92 | 4.68 |
| Bt2 | 83-125 | 21.4 | 10.44 | 68.16 | Sandy loam clay | 0.43 | 0.07 | 7 | 0.12 | 0.04 | 0.02 | 0.01 | 2.04 | 1.9 | 4.6 | 2.39 | 4.59 |
| Bt3 | 125-180 | 29.6 | 6.1 | 64.3 | Sandy loam clay | 0.43 | 0.09 | 12 | 0.1 | 0.02 | 0.01 | 0.01 | 1.68 | 1.36 | 4.4 | 1.82 | 4.54 |
| Udoxic Quartzipsamment (plot 3.22) | | | | | | | | | | | | | | | | | |
| O1 | 0-5 | | | | | 71.2 | | | | | | | | | | | |
| Ah | 5-26 | 1.7 | 6.86 | 91.44 | Sand | 1.85 | 0.16 | 3 | 0.18 | 0.33 | 0.04 | 0.03 | 0.06 | 1.28 | 2.2 | 10.91 | 4.66 |
| C11 | 26-40 | 1 | 2.62 | 96.38 | Sand | 0.28 | 0.13 | 1 | 0.06 | 0.09 | 0.04 | 0.01 | 0.06 | 0.62 | 1.2 | 8.33 | 5.09 |
| C12 | 40-65 | 0.6 | 4.29 | 95.11 | Sand | 0.14 | 0.1 | 1 | 0.06 | 0.03 | 0.02 | 0.01 | 0.06 | 0.38 | 0.7 | 8.57 | 4.95 |
| C13 | 65-180 | 0.7 | 2.49 | 96.81 | Sand | 0.14 | 0.04 | 1 | 0.03 | 0.03 | 0.02 | 0.02 | 0.06 | 0.24 | 1 | 6.0 | 5.53 |
| Haplorthod (plot 6.17) | | | | | | | | | | | | | | | | | |
| O1 | 0-5 | | | | | 78.2 | | | | | | | | | | | |
| AE | 5-25 | 1.1 | 6.93 | 91.97 | Sand | 1.85 | 0.12 | 1 | 0.24 | 0.12 | 0.02 | 0.02 | 0.06 | 1.04 | 2.3 | 6.96 | 4.62 |
| Bhs11 | 25-40 | 0.9 | 8.27 | 90.83 | Sand | 2.13 | 0.13 | 5 | 0.06 | 0.06 | 0.05 | 0.01 | 2.7 | 1.84 | 4.5 | 2.22 | 4.42 |
| Bhs12 | 40-55 | 1.2 | 2.94 | 95.86 | Sand | 1 | 0.13 | 6 | 0.06 | 0.03 | 0.01 | 0.01 | 0.3 | 0.7 | 2.3 | 2.17 | 5.32 |
| E | 55-75 | 0.6 | 6.7 | 92.7 | Sand | 0.57 | 0.09 | 6 | 0.06 | 0.03 | 0.01 | 0.01 | 0.06 | 0.8 | 1.7 | 2.94 | 4.32 |
| Bhs21 | 75-100 | 0.5 | 10.81 | 88.69 | Sand | 1.71 | 0.12 | 16 | 0 | 0.03 | 0.02 | 0.01 | 1.56 | 1.18 | 7.8 | 0.51 | 5.13 |
| Bhs22 | 100-115 | 1.2 | 3.86 | 94.94 | Sand | 1.85 | 0.1 | 12 | 0 | 0 | 0.01 | 0.02 | 0.24 | 0.88 | 5 | 0.6 | 5.4 |
| C | 115-180 | 1 | 6.46 | 92.54 | Sand | 1.56 | 0.1 | 11 | 0.12 | 0 | 0.01 | 0.01 | 0.06 | 0.4 | 2.8 | 2.14 | 5.55 |

**Table 2**. Total concentration of elements in superficial organic horizon of representative profile.

| | Depth (cm) | N % | P ug/g | Ca ug/g | Mg ug/g | K ug/g |
|---|---|---|---|---|---|---|
| Typic Paleudult (plot 4.22) | 0-4 | 1.07 | 1600 | 35000 | 3200 | 16200 |
| Udoxic Quartzipsamment (plot 3. 22) | 0-5 | 0.87 | 1500 | 21000 | 5000 | 13800 |
| Aquic Haplorthod (plot 6.17) | 0-5 | 0.89 | 1500 | 22000 | 3800 | 19900 |

**Table 3.** Soil characteristics of detail observations. Horizon thickness, pH, organic material, exchangeable aluminum, available nutrient (phosphorus, potassium, calcium, magnesium), color (Munsell table values), size and type structure, and root number/area for each plot with 6 replicates (detail observations).

| **VEGETATION PLOTS** | Low, dense forests | | | | High forests | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 3 | | 6 | | 4 | | 5 | | 7 | |
| | Ave | sd | Ave | sd | Ave | sd | Ave | sd | Ave | sd |
| **SUPERFICIAL HORIZON** | | | | | | | | | | |
| Thickness (cm) | 25.67 | 2.94 | 22.00 | 3.46 | 47.83 | 12.62 | 48.00 | 5.76 | 46.33 | 11.31 |
| pH | 4.17 | 0.29 | 3.92 | 0.42 | 4.21 | 0.16 | 4.22 | 0.12 | 4.23 | 0.24 |
| Sand (%) | 97.41 | 3.16 | 97.00 | 2.77 | 81.49 | 7.87 | 74.10 | 1.90 | 78.13 | 8.21 |
| Silt (%) | 0.28 | 0.69 | 0.18 | 0.45 | 5.65 | 5.08 | 5.00 | 2.45 | 1.93 | 1.14 |
| Clay (%) | 2.31 | 2.53 | 2.82 | 2.38 | 12.86 | 7.32 | 20.90 | 2.21 | 19.93 | 8.75 |
| Organic material (%) | 1.79 | 1.01 | 1.87 | 0.53 | 1.94 | 0.36 | 2.26 | 0.86 | 1.78 | 0.95 |
| Aluminum (cmol/kg.) | 0.60 | 0.13 | 0.18 | 0.08 | 4.53 | 0.26 | 4.62 | 0.23 | 4.32 | 0.36 |
| Nitrogen (%) | 0.15 | 0.14 | 0.07 | 0.03 | 0.08 | 0.01 | 0.08 | 0.02 | 0.05 | 0.04 |
| Phosphorus (µg/g) | 5.05 | 6.83 | 10.43 | 8.73 | 3.70 | 0.78 | 2.80 | 1.02 | 6.12 | 7.48 |
| Potassium (µg/g) | 14.09 | 4.03 | 11.21 | 1.46 | 11.07 | 2.86 | 7.93 | 1.86 | 15.43 | 5.45 |
| Calcium (µg/g) | 28.74 | 7.13 | 31.15 | 4.59 | 32.37 | 2.62 | 27.19 | 3.72 | 49.63 | 11.02 |
| Magnesium (µg/g) | 23.45 | 10.39 | 23.84 | 6.00 | 15.51 | 4.09 | 13.44 | 1.78 | 30.40 | 22.22 |
| Value (color) | 3.67 | 1.63 | 3.17 | 0.98 | 3.00 | 0.00 | 3.00 | 0.00 | 3.42 | 0.49 |
| Chroma (color) | 2.00 | 0.00 | 2.17 | 0.41 | 2.83 | 0.41 | 2.92 | 0.20 | 2.83 | 0.75 |
| Fine roots (n/100 $cm^2$) | 27.33 | 5.92 | 22.50 | 9.85 | 17.00 | 6.63 | 11.00 | 2.76 | 17.17 | 3.49 |
| Coarse roots (n/100 $cm^2$) | 1.00 | 0.89 | 1.50 | 1.76 | 0.17 | 0.41 | 0.33 | 0.52 | 1.00 | 1.10 |
| Structure | no | | no | | Medium Blocky | | Fine Blocky | | Medium Blocky | |
| **SUB-SUPERFICIAL HORIZON** | | | | | | | | | | |
| pH | 4.82 | 0.20 | 4.61 | 0.32 | 4.57 | 0.14 | 4.54 | 0.17 | 4.73 | 0.13 |
| Sand (%) | 98.05 | 1.53 | 93.28 | 3.15 | 72.17 | 1.83 | 66.93 | 0.93 | 59.40 | 19.78 |
| Silt (%) | 0.72 | 1.75 | 0.43 | 0.80 | 13.12 | 4.80 | 12.67 | 2.42 | 8.20 | 10.56 |
| Clay (%) | 1.23 | 0.61 | 6.28 | 2.79 | 14.71 | 5.09 | 20.40 | 2.11 | 32.40 | 22.74 |
| Organic material (%) | 0.28 | 0.14 | 0.24 | 0.16 | 0.71 | 0.09 | 1.23 | 0.36 | 1.53 | 1.14 |
| Aluminum (cmol/kg.) | 0.30 | 0.07 | 0.21 | 0.10 | 3.06 | 0.10 | 3.03 | 0.23 | 2.32 | 0.09 |
| Nitrogen (%) | 0.08 | 0.06 | 0.04 | 0.03 | 0.05 | 0.02 | 0.05 | 0.01 | 0.03 | 0.02 |
| Phosphorus (µg/kg) | 4.16 | 4.62 | 9.21 | 5.19 | 4.36 | 2.79 | 9.98 | 15.15 | 2.50 | 3.44 |
| Potassium (µg/kg) | 6.28 | 2.46 | 5.13 | 1.55 | 8.82 | 8.63 | 7.15 | 6.47 | 5.14 | 1.86 |
| Calcium (µg/kg) | 27.99 | 8.31 | 28.81 | 3.94 | 30.72 | 7.05 | 39.76 | 20.09 | 22.46 | 5.97 |
| Magnesium (µg/kg) | 12.07 | 3.84 | 10.05 | 0.77 | 11.98 | 3.50 | 15.14 | 4.62 | 19.81 | 17.95 |
| Value (color) | 7.00 | 0.00 | 6.33 | 1.63 | 5.33 | 0.82 | 6.33 | 1.03 | 5.50 | 1.52 |
| Chroma (color) | 2.00 | 0.00 | 2.00 | 0.00 | 4.33 | 1.51 | 5.33 | 1.03 | 3.33 | 2.07 |
| Coarse roots (n/100 $cm^2$) | 0.17 | 0.41 | 0.17 | 0.41 | 0.17 | 0.41 | 0.00 | 0.00 | 0.00 | 0.00 |
| Fine roots (n/100 $cm^2$) | 19.33 | 6.09 | 12.17 | 8.50 | 6.67 | 10.48 | 5.33 | 2.80 | 3.50 | 1.64 |

Ave= average, sd= standard deviation

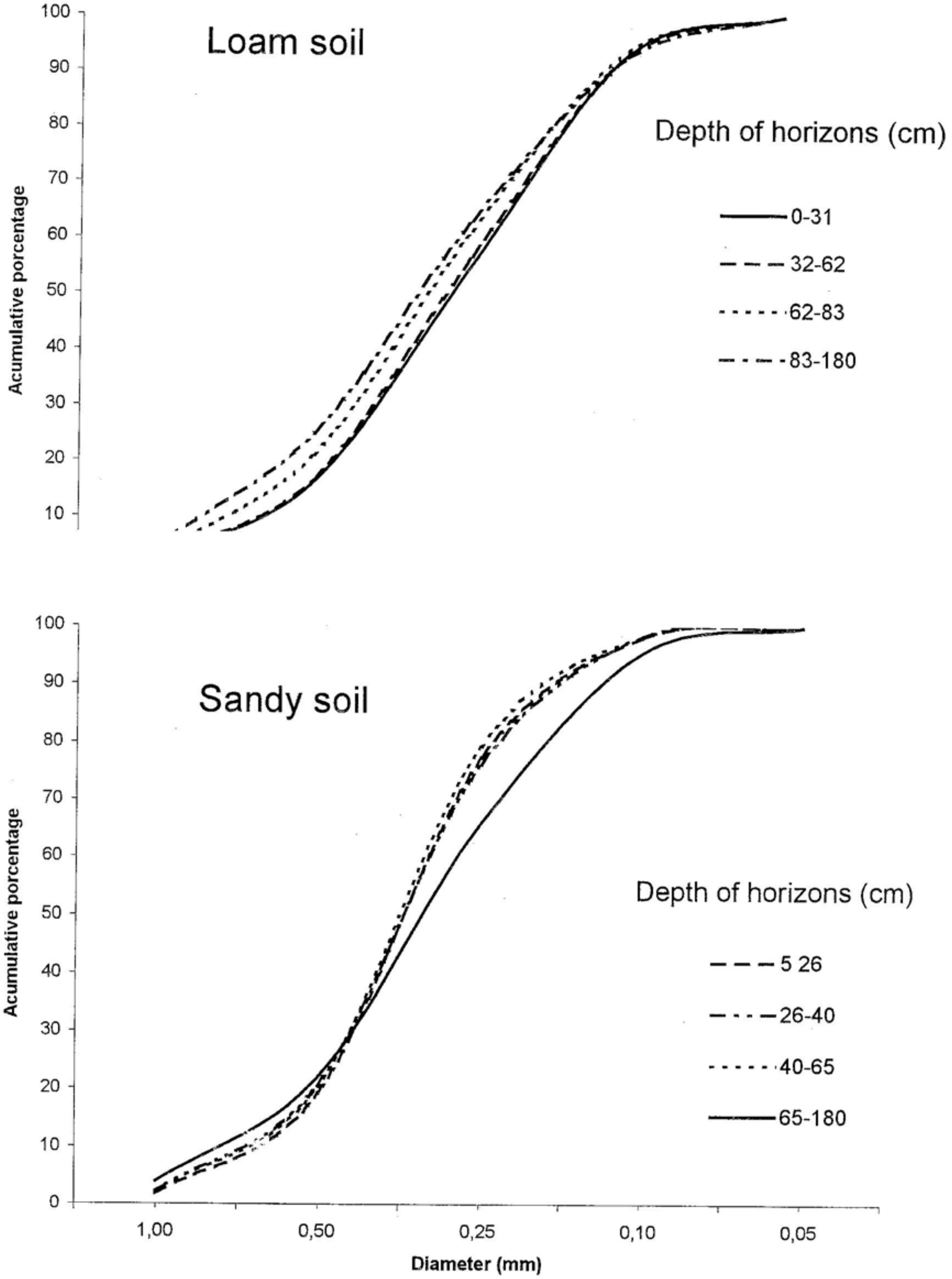

**Figure 3.** Sand particle size distribution curve in sandy and loam soils. It shows the dominance of medium and fine sands (between 0.5-0.1 mm) in all soil horizons

In the principal component analysis of the soil characteristics, the first component had an eigenvalue of 11.3 and explained 37.7% of the information variability; the second an eigenvalue of 3.8 and explained 12.6% of the variability. The total of principal components were 30, the first 5 explained 70% of the information variability, and the remaining 25 components had very low values (<1) and each explained less than 5% of the information, thus they were omitted from the analysis.

In the first principal component the particle size distribution (sand, silt and clay) and the aluminum are the characteristics with more weight in the distribution of the others characteristics. In the component 2 axis the available nutrient distribution predominates (Figure 4). Texture, cation exchange capacity, aluminum, and A horizon thickness, were not related to the concentration of available nutrient in the surface and subsurface horizons. These nutrients are more associated to the content of organic matter of the surface horizon. Magnesium, calcium, potassium, and phosphorus did not show significant correlation with texture, structure, A horizon thickness, and A horizon aluminum (Figure 4).

Aluminum, clay, silt, chroma and structure are characteristics that make up a highly correlated group (Figure 4). Clay and aluminum are positively correlated for both surface (r=0.52) and subsurface (r=0.8) horizons. Structure is correlated positively with exchangeable aluminum (r=0.9) and clay (r=0.77), and negatively with sand (r=-0.81). Sand correlates negatively with the former characteristics (> -0.68 in all cases) and in sandy soils there is a larger root content.

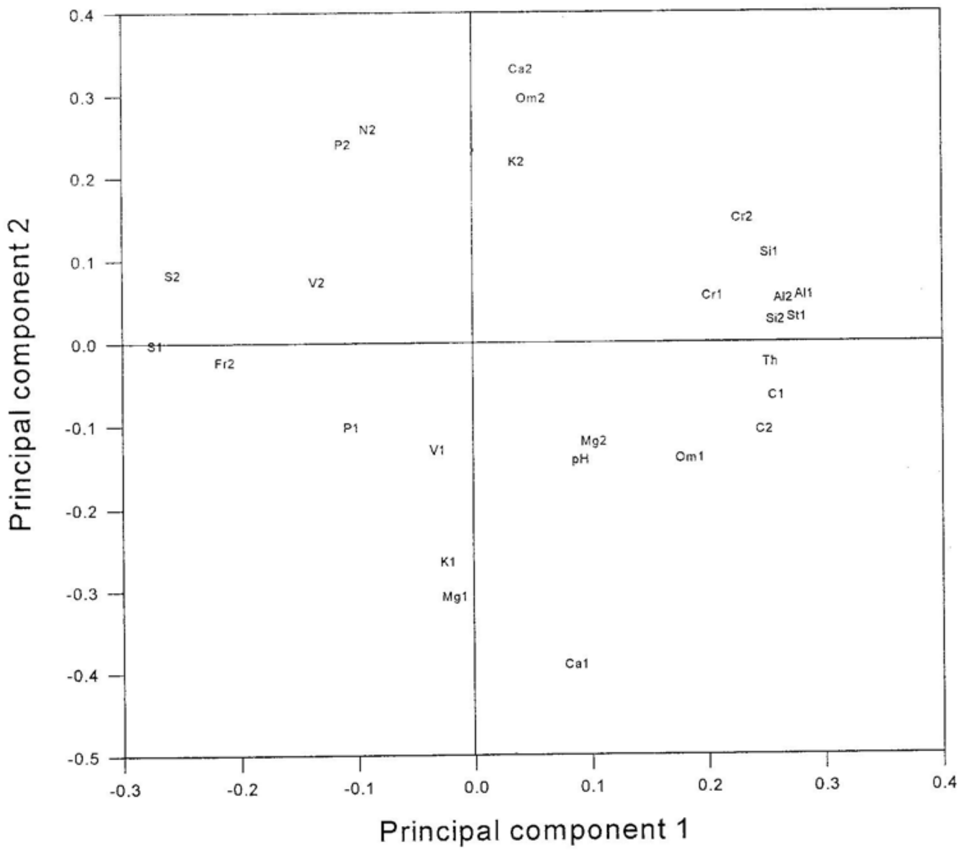

**Figure 4.** Soil characteristic eigenvectors for the first 2 principal component with 50% of the information variability. In the first principal component the particle size distribution, A horizon thickness, structure of superficial horizon and aluminium are the characteristics with more value. In the component 2 axis there is predominance of the available nutrient. **Superficial horizon symbols: Th.** Thickness; pH, **S1**: Sand, **Si**: Silt, **Cl**: Clay, **Oml**: Magnesium, **Vl**: value (color), **Crl**: chroma (color), **Stl**: structure. **Subsuperficial horizon symbols: S2**: sand, **Si2**: silt, **C2**: clay, **Om2**: organic material, **Al2**: aluminium, **N2**: nitrogen, **P2**: phospohorus, **K2**: potassium, **Ca2**: calcium, **Mg2**: magnesium, **V2**: value (color), **Cr2** chroma (color), **Fr2**: fine roots.

The variables that lost less than 20% of the information in the 5 selected principal components of the explained variance percentage are sand, clay, silt, and aluminum content for the surface and subsurface horizons; and structure, thickness, and magnesium content of the surface horizon (Appendix 1). These are the most important characteristics for the study of soil variability and interpreting their relationships.

Figure 5 confirms that there are differences between the two big groups of sandy and loam soils. Component 1, where sandy soils (plots 3 and 6) are clearly separated from loamy soils (plots 4, 5, and 7) is related to texture dominance in the soil information variability and the behavior of the other characteristics. The high relationship between the sandy soils of plots 3 and 6 is clear, as well as that of loam samples from plots 4 and 5. Principal component 2 separates plots 4 and 5 from 7. This last plot shows the greatest dispersion in soil variability, with Typic Paleudults and Aquic Paleudults. In component 2, a soil from plot 3 located far from the rest of sandy soils, corresponds to a Spodosol inclusion. In plot 4, there are soils tending to sandy loam and associated with the sandy soils of plots 3 and 6.

**Vegetation and soil-vegetation relationships:** The forest associated to sandy soils had emergent heights between 14-21 m, upper canopy limit between 13-20 m, mean density for individuals with diameter >10 cm is 763-879 stem/ha, basal mean area of individuals with diameter >10 cm is 22.6 m²/ha (Table 4). These characteristics help identify these forests as similarly structured as the caatinga or wallaba forest (Davis and Richards, 1934; Fanshawe, 1952; Klinge and Medina, 1979, Johnston and Gillman, 1995). In the study it is classified as a low forest, with high density of thin stems (DBH> 10 cm).

The forest associated to loam soils had emergent heights between 26-40 m, upper canopy limit between 18-38 m, mean density for individuals with diameter >10 cm is 442-525 stem/ha, and basal mean area of individuals with diameter >10 cm is 28.7 m²/ha. These characteristics help identify these forests as a high forest, with low density of thin stems (DBH> 10 cm).

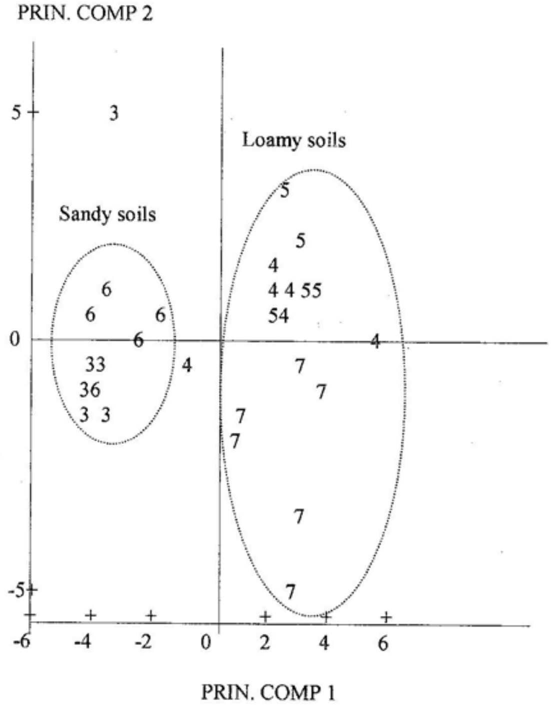

**Figure 5** Principal Components 1 and 2 of soil detail observations in Kwakwani-Guyana. Numbers 3, 4, 5, 6 and 7 are plot numbers in permanent biodiversity plots of SI/MAB. In component 1, sandy soils (plot 3 and 6) are clearly separated from loamy soils (plots 4, 5 and 7). There are 2 hidden observations.

For CANOCO, 8 variables of vegetation and 9 of soil were included. The multivariate statistics tests of Wilks' lambda, Pillai Trace, Hotelling-Lawley, Trace and Roy's Greatest Root give values of Pr>F less than 0.001. It was shown that there was a highly significant correlation between soil and vegetation characteristics. Using the F approximation with the Ho (null hypothesis) test, it was shown that the canonical variable 1 is highly related (p>0.001) in linear fashion to the soil and vegetation variables (Table 5). With a canonical correlation of 98.5%, an eigenvalue of 32.7, representing 85% of the information variance. The second canonical correlation has an F value greater than 0.05, and is included in the analysis because it has an eigenvalue greater than 1 (2.09) and a canonical correlation between soil and vegetation variables of 82.7%. These first two canonical variables represent 90.7% of the information variance.

**Table 4.** Structural characteristics of forest vegetation in Kwakwani-Guyana. Average characteristic /plot with 6 replicates (n=6) or quadrate (20 mx 20 m).

| **VEGETATION PLOTS** | Low, dense forests | | | | High forests | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 6 | | 3 | | 4 | | 5 | | 7 | |
| **Characteristics** | average | sd | average | sd | average | sd | average | sd | average | sd |
| Emergent trees height (m) | 21.00 | 2.00 | 17.75 | 2.27 | 37.17 | 2.48 | 37.50 | 4.32 | 36.33 | 6.02 |
| Maximum canopy height (m) | 20.50 | 0.84 | 17.50 | 2.51 | 34.17 | 3.76 | 33.00 | 7.48 | 32.17 | 5.15 |
| Minimum canopy height (m) | 15.17 | 2.71 | 11.00 | 2.76 | 10.33 | 10.39 | 7.00 | 7.04 | 6.75 | 9.41 |
| Thickness between maximum and minimum canopy (m) | 5.33 | 3.27 | 6.50 | 1.76 | 23.83 | 11.37 | 26.00 | 8.39 | 25.42 | 9.00 |
| Stem density, BH>10 cm (stem/ha) | 763 | 100.9 | 879 | 182.6 | 525 | 11.8 | 49.2 | 84.7 | 442 | 163.3 |
| Stem density, BH>30 cm (stem/ha) | 38 | 31.1 | 21 | 24.6 | 83 | 49.2 | 95.8 | 36.8 | 91.7 | 40.8 |
| DBH of widest tree in the quadrat (cm) | 35.70 | 10.21 | 29.18 | 9.89 | 58.94 | 26.48 | 54.86 | 8.96 | 71.20 | 29.48 |
| Soil cover by trees (%) | 77.00 | 6.32 | 78.33 | 8.16 | 74.00 | 17.82 | 79.17 | 10.21 | 73.33 | 20.66 |
| Basal area of trees, DBH> 10 cm ($m^2$/ha) | 24.8 | 12.08 | 21.35 | 8.32 | 30.08 | 14.82 | 25.83 | 13.21 | 29.3 | 17.21 |

**sd**= Standard deviation; **DBH**= diameter at breast height (1.5 m from ground)

**Table 5.** Canonical Correlation Analysis. 30 observations, 8 vegetation variables and 9 soil variables.

| | **Canonical Correlations** | | | **Eigenvalues** | | | | **Test of H0** |
|---|---|---|---|---|---|---|---|---|
| | Canonical Correlation | Adjusted Canonical Correlation | Squared Canonical Correlation | Eigenvalue | Difference | Proportion | Cumulative | Pr> F |
| 1 | 0.985035 | 0.977549 | 0.970295 | 32.6638 | 30.4949 | 0.8502 | 0.8502 | 0.0001 |
| 2 | 0.827308 | 0.696867 | 0.684439 | 2.1690 | 0.6555 | 0.0565 | 0.9066 | 0.0878 |
| 3 | 0.775982 | 0.671054 | 0.602148 | 1.5135 | 0.5056 | 0.0394 | 0.9460 | 0.2209 |
| 4 | 0.708499 | 0.617889 | 0.501970 | 1.0079 | 0.3730 | 0.0262 | 0.9722 | 0.4250 |
| 5 | 0.623166 | 0.550497 | 0.388336 | 0.6349 | 0.2407 | 0.0165 | 0.9888 | - |
| 6 | 0.531723 | - | 0.282730 | 0.3942 | 0.3652 | 0.0103 | 0.9990 | - |

Canonical variable 1 sums up two large groups of variables (Figure 6). One group where the vegetation variables of emergent tree, density of woody stratum (DBH>30 cm), canopy heights, canopy thickness and greater diameter interrelate with the soil variables clay, aluminum and structure. The opposing group shows density of woody stratum (DBH>10 cm) related to the surface and subsurface sand.

## DISCUSSION

The sand particle size sigmoidal curves (Figure 3) with a dominance of particles between 500-100 µ, indicate a distribution corresponding to an alluvial high-energy deposition, similar to those shown by Glennie (1970) for alluvial environments with little selection. Then, depositions are confirmed to be alluvial and not marine as suggested by Prance (1989). It is shown that the white sands are not the product of granitic rock meteorization or podzol pedogenesis, as indicated by Schultz (1960) for the white sands of Suriname and by Anderson (1981) for the Amazon caatinga. According to Brown and Sawkins (1875), Fanshawe (1952) and Berrangé (1977), these alluvial sediments are from the beginning of the early Pleistocene.

In sandy and loam sediments, sands show prevalence of particles between 100-500µ, which indicates that the alluvial depositions came from sediments of the same source of the Proto-Berbice River derived from the Roraima Formation. Although in the case of more sandy sediments, the environment was more turbulent and the deposited particles thicker, which is explained by a transversal ranking in a high competition environment. Matsumoto (1995) found similar results in the Amazon basin, and reported an average of 320µ in the sandy sediments and 300µ in the loam, confirming the similarity of the alluvial depositional process in the areas with dry paleoclimates.

The percolated water of 1090 mm/year in the Guyana forests (ter Steege et al, 1995) is considered sufficient for a high soil lixiviation. All soils analyzed in the study area are acidic and with low nutrient levels in the mineral fraction. This might be explained by the action of a wet climate over rich quartz sediments and a relief favoring free drainage for base leaching in material with sustained mineral transformation and decomposition. Whitmore (1990) reports that soils with low fertile levels, such as Oxisols, Ultisols, Psamments, and Spodozols represent 70% of the soils of the humid tropics. According to Sánchez (1989) and Mabberley (1992), the soils of the humid tropical regions tend to be acidic and pedogenetically developed, which is favored by the wet climate.

PCA showed that nutrient concentration is not related to the mineral fraction characteristic of the soils, such as texture and exchangeable aluminum, but to its organic matter concentration. This fact explains the little difference in content of available phosphorus, nitrogen, calcium, magnesium, and potassium in the Kwakwani soils, since organic matter content in the mineral horizons and litter shows no significant difference. Scott et al. (1992) in Maracá, Brazil and Tiessen et al. (1994) in the Venezuelan Amazon also indicated the relationship of nutrients and organic matter concentration in forest soils.

The high concentration of available bases (calcium, potassium, and magnesium), phosphorus, and nitrogen in litter, and the high density of roots in the organic horizons in the soils studied, guarantee the nutrient supply to the forest vegetation, since levels in the mineral fraction of these soils are quite low to explain the presence of vegetation in the Kwakwani rain forest.

This high litter in the acidic soils of tropical rain forests has been reported also by Stark (1970, 1971a, 1971b) in Suriname and the Brazilian Amazon, by Scott et al. (1992) in the Maracá island of Brazilian Amazon, and by Coomes and Grubb (1996) in the Orinoco Basin. Also, Stark (1970, 1971a, b), Janos (1985), Jordan (1989), Scott et al. (1992), and Thompson et al. (1994) state that in the acidic soils with low cation content in the mineral fraction, the mechanisms of direct nutrient absorption from litter through mycorrhizae and a high root density are important for the mineral nutrition of the rain forests.

Texture of parent material is the major factor determining soil variability between forest types (Figure 6). Partial drainage restriction is the major factor of soil variability within a forest type. Sandy sediments are related to Quartzipsamments with

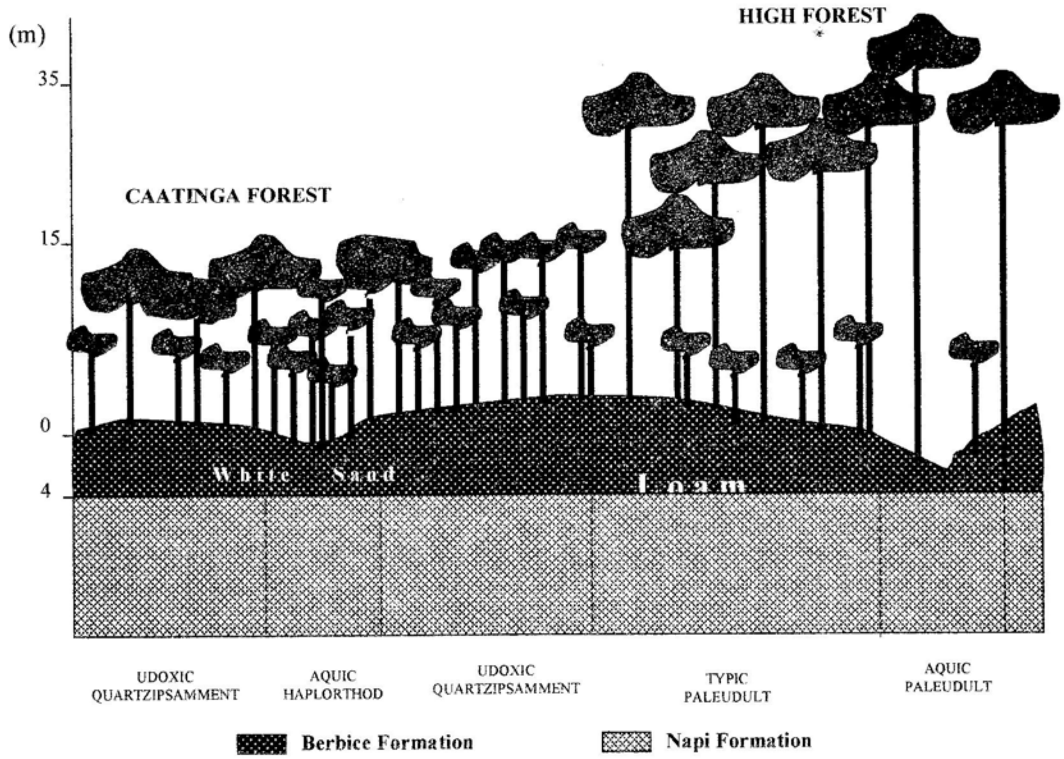

**Figure 6.** Canonical correlation between vegetation and soil for their variable canonicals 1 and 2. **Symbols:B Et**: emergent trees height, **Ch**: maximum height canopy, **Ct**: thickness between maximum and minimum canopy, **D30**: stem density (DBH>30 cm), **D10**: stem density (DBH>10 cm), **Co**: soil cover by trees, **Dtt**: DBH of widest tree in the quadrate, **Ba**: basal area of trees (DBH>10 cm), **S**: sand of superficial horizon, **S**: sand od subsuperficial horizon, **c**: clay of superficial horizon, **C**: clay of subsuperficial horizon, **al**: aluminium superficial horizon, **AL**: aliminium subsuperficial horizon, **H**: A horizon thickness, **st**: structure of superficial horizon

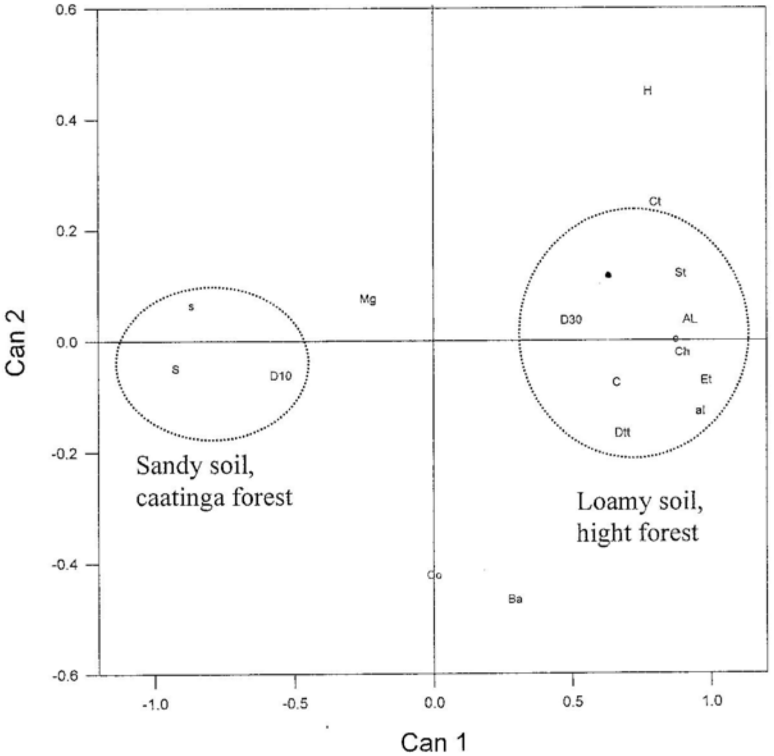

**Figure 7.** Diagram block of landscape in Kwakwani-Guyana. It shows soil taxonomy, vegetation structure and geology.

high quartz content, poor in bases and cation retention capacity. They correspond with white sand soils reported by Davis and Richards (1934) in Guyana, by Schultz (1960) in Suriname, and by Matsumoto (1995) in northeastern Brazil. Spodosol and lowest forest inclusions were identified in low positions, due to fluctuations in the water table with leaching of organic matter and iron and aluminum sesquioxides from the upper horizons of the profile. Anderson (1981) and Matsumoto (1995) in Brazil have reported dominance of Quartzipsamments in the sand deposits of the rain forests. However, the presence of Spodosols has been reported for San Carlos de Río Negro, Venezuela (Klinge and Medina, 1979) and in the white sand of many places in Brazil (Stark, 1971a). However, chemical analysis shows that Psamments and Spodosols are quite similar from a nutrient viewpoint, so soil variability in this forest type derives from drainage. Sabatier et al (1997) reported that changes in soil drainage are accompanied by substantial changes in the forest community, similar to this study.

Typic Paleudults dominate in loam sediments, coincident with the brown sand soils reported by Richards (1961), Fanshawe (1952), and Johnston and Gillman (1995) for Guyana. Aquic Paleudult and highest forest inclusions were observed in low positions or with clayey horizons that restrict drainage. Paleudults show greater thickness in A horizon, aluminum and clay, and a larger cation retention capacity than Quartzipsamments. Soil taxonomy reflected differences shown at the level of soil ordination by PCA into a forest type.

Multivariate analyses show the high relationship between soil and vegetation structure. Clay and exchangeable aluminum contents are the soil characteristics more related to forest height, although thickness and structure type of A horizon are also important. The greater clay content increases the cation exchange capacity and water retention with free drainage, which enhace soil-plant relationship in soils with thicker and better structured A horizon. This is expressed in both canopy and emergent individuals height, and stem thickness.

The high sand content is closely related to the high density of trees with DBH>10 cm, which is explained by a lower height in the formation and a negative correlation between height and woody stratum density. These close relationships between granulometric composition, A horizon thickness, and vegetation characteristics, as determinant factors for the distribution pattern of ecological systems, have not been quantitatively demonstrated for rain forests.

## CONCLUSION

Following analysis of soils, parental material, and vegetation of systems under a specific mesoclimate, ecosystems can be identified and their functionality partly understood. In the well-drained oligotrophic soils of the rain forests of Guyana, the nutrient concentration in the mineral fraction is not determinant for defining the characteristics of vegetation structure. There were no significant differences in nutrient concentration between these forest types, due to its dependence on the organic fraction in litter. Texture, aluminum content, A horizon thickness, and structure are associated to distribution of forest types. Soil drainage was very important in determining within forest type variation.

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**Appendix 1.** Percentage of Information loss in soil characteristics for 5 firsts principal components

| | % information in original variable | % information loss in variable |
|---|---|---|
| **SUPERFICIAL HORIZON** | | |
| Tickness | 80.77 | 19.23 |
| pH | 74.94 | 25.06 |
| Sand | 92.8 | 7.2 |
| Silt | 84.32 | 15.68 |
| Clay | 93.59 | 6.41 |
| Organic material | 63.73 | 36.27 |
| Aluminum | 92.12 | 7.88 |
| Nitrogen | 69.51 | 30.49 |
| Phosphorus | 64.98 | 35.02 |
| Potassium | 64.91 | 35.09 |
| Calcium | 70.6 | 29.4 |
| Magnesium | 81 | 19 |
| Value | 39.57 | 60.43 |
| Chroma | 69.54 | 30.46 |
| Fine roots | 68.66 | 31.34 |
| Structure | 87.62 | 12.38 |
| **SUBSUPERFICIAL HORIZON** | | 100 |
| pH | 44.36 | 55.64 |
| Sand | 95.2 | 4.8 |
| Silt | 95.22 | 4.78 |
| Clay | 80.22 | 19.78 |
| Organic material | 60.16 | 39.84 |
| Aluminium | 84.6 | 15.4 |
| Nitrogen | 72.09 | 27.91 |
| Phosphorus | 67.3 | 32.7 |
| Potassium | 42.63 | 57.37 |
| Calcium | 70.6 | 29.4 |
| Magnesium | 73.87 | 26.13 |
| Value | 57.72 | 42.28 |
| Chroma | 69.96 | 30.04 |
| Fine roots | 70.9 | 29.1 |

**Appendix 2.** Multivariate Statistics and F Approximations

| Statistic | Value | F | Num DF | Den DF | Pr > F |
|---|---|---|---|---|---|
| Wilks' Lambda | 0.00078 | 2.6954 | 72 | 86.65 | 0.0001 |
| Pillai's Trace | 3.46682 | 1.6995 | 72 | 160.0 | 0.0031 |
| Hotelling-Lawley Trace | 38.42105 | 6.0033 | 72 | 90.0 | 0.0001 |
| Roy's Greatest Root | 32.66383 | 72.5863 | 9 | 20.0 | 0.0001 |