THE INFLUENCE OF EDAPHIC CONDITIONS ON THE COMPOSITION, STRUCTURE, AND FOLIAR CHEMISTRY OF FOUR TROPICAL FOREST COMMUNITIES IN NORTHWESTERN BELIZE, CENTRAL AMERICA

by

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INTRODUCTION

A fundamental question in plant ecology is -- what influences the distribution of plants and their communities? In tropical regions, studies investigating this question have frequently found an association between vegetation distribution and environmental factors (Bourgeron 1983; Olsvig-Whittaker 1988). For example, large scale patterns of vegetation distribution are associated with changes in altitude and the resulting gradients in light, temperature, and moisture (Grubb and Whitmore 1966; Webb *et al.* 1970; Gentry 1988; Jeremy 1991). However, expanses of lowland tropical forest also possess a diversity of species and communities across the landscape (Gentry 1990).

In numerous tropical and subtropical forests, species composition and the distribution of individual species are influenced by local changes in topography and soil drainage (Kahan and Castro 1985; Tuomisto and Ruokolainen 1993; Kahn 1987; Ramella and Spichiger 1989; Russell-Smith 1991; Kahn and de Granville 1992). In combination with topography, species composition and species distribution at other locales are influenced by anthropogenic or natural disturbance (Furley and Newley 1979; Basnet 1992a; Basnet 1992b). Still other tropical forests are influenced by a combination of soil moisture, soil fertility, and disturbance (Johnston 1992; Clark *et al.* 1995). It is apparent that multiple environmental factors can influence vegetation distribution in a tropical forest landscape. To better understand these complex interactions, it is necessary to examine local environmental factors to determine the source of regional vegetation patterns.

In the moist subtropical forests of northwestern Belize, broadscale environmental factors do not appear to be responsible for the multiple forest community types that are distributed in a mosaic pattern across the landscape. Annual rainfall is fairly uniform throughout the region (Wright *et al.* 1959), and the topographic relief is less than 200 meters. Most of the elevation change is due to three parallel escarpments that run northeast to southwest (Hartshorn *et al.* 1984).

However, fine scale topographic pattern may exert some influence on the regional pattern of forest development. At the base of the escarpments one finds small rivers, while between the escarpments the terrain slopes gradually or is composed of rolling hills (Hartshorn *et al.* 1984). Upslope sites are characterized by shallow, well drained, gravelly soils, while flat or gently sloping areas have deeper soils of clay and loam with variable hydrology (Wright *et al.* 1959). In addition, maps of the region show a mosaic pattern of both soil and vegetation (Wright *et al.* 1959). These characteristics indicate that topography may influence soil properties and hydrology, thereby influencing vegetation distribution across the landscape.

The goal of this study was to determine whether the mosaic of vegetation types across the landscape was related to the heterogeneity of soil conditions. My approach was to sample the physiognomy, species composition, and foliar chemistry of forest stands which typify the major forest types of the region, and sample the co-occurring soil factors. This approach was taken to answer the following questions: 1) Do the physiognomy and species composition of the overstory tree community vary with respect to the local edaphic conditions (microtopography, soil moisture, soil physical properties, or soil chemistry)? and 2) Is forest structure and composition related to nutrient availability, as indicated by foliar chemistry? An additional objective was to characterize the vegetation and soil of each forest community for use in companion studies.

The forests of northwestern Belize are the ideal location for a study examining the relationship between vegetation and soil characteristics. Unlike similar studies in the Amazon (Clark *et al.* 1995), the same limestone parent material underlies the entire Yucatan peninsula. And although the Yucatan peninsula has been the site for several studies examining the association between the distribution of a few tree species with Mayan ruins (Lambert and Arnason 1982) and the association between species composition and karst topography (Furley and Newley 1979), no studies have systematically examined the relationship between vegetation and soils on relatively flat sites across several forest types.

STUDY SITE

The study is located in northwestern Belize (Figure 1), a region with seasonal rainfall totaling approximately 1600 mm per year (Wright *et al.* 1959; Hartshorn *et al.* 1984;). The seasonal distribution of rainfall is variable from year to year, however in most years the wet season begins in June and rainfall decreases in December and January as the dry season approaches. The dry season occurs from February through March (Brokaw and Mallory 1993).

The region is underlain by Eocene limestone bedrock, which is weathered deeply but incompletely with the upper layer of limestone composed of gravel and boulders (Wright *et al.* 1959). Low karst hills are common to the northwest and south of the study site, whereas the study area is characterized by rolling hills and level areas. Upslope sites generally have a thin, gravelly layer of soil (7 to 15 cm deep), while flat and gently sloping areas have deeper soils (30 to 40 centimeters deep) of calcareous clay and loam. Forests occur on a mosaic of 11 calcareous soil types (Brokaw and Mallory 1990 *from* Wright *et al.* 1959).

The vegetation is classified as sub-tropical moist forest (Holdridge 1971). Approximately ten percent of the tree species are deciduous or partly deciduous, depending on forest type (Brokaw and Mallory 1993). Several forest types occur in the region, with frequent changes in forest type over short distances. The result is a mosaic of vegetation types across the landscape.

Forests throughout the region have been subject to disturbance, both natural (hurricanes and tree fall) and anthropogenic (Mayan settlement). The most significant recent disturbance was selective harvesting of mahogany until the 1950's. In addition, there are occasional small abandoned clearings created by marijuana growers who have now been expelled from the region. Recovery has followed each disturbance, and now most of the region is covered by mature forest (Brokaw and Mallory 1990).

Sampling was done in the southern portion of the Rio Bravo Management and Conservation Area, a 100,000 hectare reserve situated near the Mexican and Guatemalan borders (Figure 1). The four most common forest types were sampled in mature forests with no evidence of logging. Two plots (labeled PC for the nearby Punta de Cacao Mayan ruins) were located in an upland broadleaf forest -- one plot located on a mesic flat site and the other on a drier south sloping hill. All other plots were located on level sites, including three plots in a cohune palm forest (labeled XV for the nearby Xaxe Venic Mayan ruins), one plot in a tall swamp forest (labeled SW), and one plot in a scrub swamp forest locally known as bajo forest (labeled BA).

Forest community descriptions

This study investigated the most common forest types of northwestern Belize -- two seasonally flooded forests and two upland forests. The most abundant forest type is the upland broadleaf forest. Mature forests are usually 20 to 25 meters tall, with an understory of subcanopy palm and broadleaf species (Figure 2). Although these forests have been characterized as semi-deciduous (Wright *et al.* 1959, Beard 1944), only 6-7% of the trees are leafless at any one time (Brokaw and Mallory 1993). Species composition appears to vary with environmental conditions, so that a dry broadleaf forest type (usually occurring on the thin gravelly soils of sloping areas) can be distinguished from a mesic type (generally occurring on level areas with deeper more fertile soils) (Brokaw and Mallory 1993).

Cohune palm forest -- also an upland forest type -- is characterized by an abundance of cohune palms (*Orbignya cohune)* (Brokaw 1990). Although cohune palms are common in the mid-canopy of this forest type (twenty percent or more of the mid-canopy), most of the canopy is occupied by hardwood species. Most mature cohune forests are tall (25-30 meters) with an understory dominated by juvenile palms (Figure 2). Occasionally pure cohune palm stands do occur; dense and short stands (15 meters tall) are probably regrown from abandoned marijuana clearings, whereas those dominated by mature palms appear to be associated with frequently saturated soils (personal observation). This forest type is most common on moist fertile soils (Furley 1975).

The seasonally flooded bajo forest is a short, dense forest with small-diameter xeric tree species (Figure 2). These forests resemble thickets and range in height from 5 to 10 meters. There is no true understory in the bajo forest because stems smaller than 3 centimeters can reach the canopy. The canopy is of even height and somewhat open, with gramnoids dominating the ground cover. Bajo forests occur on infertile clay soils that are flooded for several months during the wet season and are dry and deeply cracked during the dry season. These sites are shallow depressions that are not connected to any input or drainage streams -- thus standing water is common when these sites are flooded.

Swamp forest sites are also flooded for extended periods, but the soils do not shrink and crack like those of the bajo. Swamp forests are taller than bajo forests, and they also have a highly variable canopy height (10-20 meters), with frequent emergent trees and a prominent liana component (Figure 2). The swamp forest sampled in this study drained into an adjacent marsh; variants of this forest type include the taller and better drained lecustrine and riparian swamp forests.

METHODS

Vegetation structure and composition

Field Sampling

Seven permanent plots were established in a total of four forest types. Within each plot, sampling was done in six to nine randomly located subplots (with stratified random sampling used in the flooded forests) (Table 1, Figure 3). One of the subplots (labeled 'A') was larger than the others so it could be detected by airborne remote sensors (part of a companion study). Within all subplots, each tree, palm, and liana with a diameter at breast height (dbh; diameter at 1.34 m) $\geq$ 10 cm was identified to the species, measured for dbh, and measured for height to base of crown. The five tallest trees in each subplot were also measured for height to top of crown. Individuals less then 10 cm but at least 3 cm dbh were sampled in a small (understory) subplot nested within the larger (overstory) subplot (Table 1). Individuals sampled in the bajo plot were not identified to the species, but each species present in the plot was noted.

Some palms had not yet begun their vertical growth, but still contributed to the understory. Palms taller than 3 m were sampled by measuring the stem of the tallest frond (two cross sectional dimensions at dbh height) and counting the number of fronds per plant.

Ground cover estimates of plants $<$ 3 cm dbh were made in a 1.5 meter radius subplot located in the center of the nested overstory and understory subplots. Plants were categorized as grasses, herbs (green stemmed), woody plants (brown stemmed), or palms ($<$ 3 m tall). The percent cover was estimated for each category.

Vertical distribution of foliage was determined at grid points within each overstory subplot by recording the presence of foliage in various height classes. In each overstory subplot designated 'A' there were 100 equally spaced sample points (one per 16 m^2); all other overstory subplots had 16 equally spaced sample points (one per 44 m^2). Leaf area index was determined with a leaf area meter (LAI-2000; LI-COR 1990).

Data Analysis

The three stem size classes -- $<$ 3 cm dbh (ground cover), 3-10 cm dbh (understory), and $\geq$ 10 cm dbh (overstory) -- were analyzed separately to facilitate comparison with other tropical studies, which routinely sample only stems larger than 10 cm dbh. It should be noted that because the criteria for separating 'understory' stems from 'overstory' stems was made on the basis of diameter rather than height, some individuals that were designated 'overstory' actually have their crowns in the understory (or visa-versa for the bajo).

Although lianas were also measured in separate understory and overstory nested subplots, lianas of all diameters grow in the canopy. Consequently, all liana analyses were done on combined 'understory' and 'overstory' data.

For the palms that had not yet begun their vertical growth, plant cover was estimated for comparison with understory basal area. Because cross-sections of palm leaf stems are crescent shaped, the two stem dimensions were multiplied by each other, divided by 2, and then multiplied by the number of fronds on the plant.

Broadleaf and palm tree data were analyzed separately and together. The combined broadleaf and palm tree data illustrate each plot's vegetation structure. Lianas were not included in the calculations of community vegetation structure because the growth of liana foliage is approximately equal to the reduction of foliage in supporting trees (Ogawa *et al.* 1965).

Aboveground biomass was estimated for each tree and palm using allometric relationships (Ogawa *et al.* 1965). Initially, basal area was used to estimate tree height. For each forest community, I chose Ogawa's height equations for stands most similar in height to my sampled forest communities (upland forests ~ dry monsoon forest; swamp forest ~ dipterocarp savanna; bajo forest ~ modified equation from dipterocarp savanna) (Figure 4). Next, the height calculations and measured basal areas were incorporated into Ogawa's biomass equations (for stem, branch, and leaf) to estimate aboveground biomass for each tree. These estimates were summed to determine aboveground biomass (of broadleaf and palm trees) for each subplot.

Each plot was described by the mean and standard deviation of its size or cover measurements. For individuals with stems (lianas, palm trees, broadleaf trees, and combined tree types) the following was calculated: density (stems/ha), basal area (m^2/ha), mean tree basal area (cm^2), quadratic mean diameter (cm), height to base of crown (m), and height to top of crown (m). Aboveground biomass (Mg/ha) and mean tree biomass (kg) were also calculated for combined trees and palms. In the 'per hectare' calculations (i.e.

density, basal area, and biomass), each subplot was an observation. However, in the mean size calculations, each individual was an observation.

Among plot differences in forest community structure (ground cover, lianas, palm trees only, broadleaf trees only, and all tree types) were compared by one-way analysis of variance and contrast analyses (PROC GLM; SAS 1988). Additional structural information was obtained by graphing the vertical stratification of foliage and the diameter distribution in each plot.

Correlations among vegetation structure variables were determined using each subplot as an observation. Principal components of overstory and understory plot means were calculated for comparison with each other and with foliar nutrition and soil properties (see 'Vegetation-Soil Comparisons' in Methods section).

Changes in species composition within and among plots were analyzed by species area curves (Brower *et al.* 1990). Because of the nested sample design, understory and overstory species were both counted as representatives of the overstory subplot area. It should be noted that bajo forest species were only identified from a survey of the plot, not by quantitative sampling -- there are probably many more unidentified species in the bajo forest plot.

To characterize and compare species composition among sample plots, the density and total basal area were calculated for each species in each plot. Plot differences in overstory species composition were analyzed by relative abundance (density) curves, relative dominance (basal area) curves, and detrended correspondence analysis (Brower *et* *al.* 1990; ter Braak 1987). Species composition of the overstory was compared to that of the understory by community similarity coefficient (Jaccard coefficient; Brower *et al.* 1990). Biomass was not used to analyze species composition because height estimate equations were not species specific (i.e. height equations are based on mean community height).

Foliar chemistry of canopy vegetation

Field sampling and laboratory analysis

Five of the most common canopy tree species in each subplot were sampled for foliar chemistry; once a species had been collected in five subplots, the next most abundant species was chosen. Small midcrown branches were harvested using a shotgun. From each branch, five representative leaves were measured for length and width. Disks of leaf material were cut -- avoiding the midvein -- to obtain a sample of approximately 2 grams for determination of specific leaf area. These disks and additional leaf samples were dried at 77° C. Samples were collected in March and May of 1990.

Samples were transported to the Forest Service Laboratory in Research Triangle Park, North Carolina, where the samples were dried again at 70° C for 24 hours. Each field sample was split in two replicates. Standard nutrient analyses and nonstructural carbohydrate concentrations were determined (Table 2). Results were accepted for replicates which were the same at $p < 0.06$.

Data analysis

Because the sampling design limited the number of replicates for each species, investigation of foliar chemistry trends by individual species was not possible. Therefore, species were classified by characteristics that could affect their foliar chemistry. Species were divided among three groups -- palms, nitrogen fixing trees, or other broadleaf trees -- and the foliar composition of these groups was compared.

Because the distribution of nitrogen in vascular plant tissues is dependent in part on the site of active nitrate reduction (Larcher 1983), trees with root nodules that are actively fixing nitrogen may have different concentrations of foliar nitrogen than those without nodules. Nodule formation occurs in species having mutualistic relationships with nitrogen fixing bacteria -- primarily legumes. Species of legumes that were likely to form nodules (96% of species in the Mimosoideae sub-family and 98% in the Papilionaceae sub-family; Jeffrey 1987) were classified as 'nitrogen-fixing trees'. Members of the Caesalpiniodeae sub-family (which have a low frequency of nodulation; Jeffrey 1987) and angiosperms which were not legumes were classified as 'other broadleaf trees'.

The foliar composition of nitrogen fixing trees was compared with that of other broadleaf trees by t-tests (PROC TTEST; SAS 1988). Only swamp forest trees were compared because the swamp forest was the only plot having enough nitrogen-fixing legumes to make statistical comparisons. All of these trees were sampled for foliar chemistry on the same date.

Palms have markedly different leaf morphology and physiology than broadleaf trees, therefore I compared the foliar chemistry of these groups. Most of the sampled palms occurred in the palm forests, thus to minimize the effect of site on the results, comparisons were limited to broadleaf and palm trees growing in the palm forest. Comparisons were done by analysis of variance, blocking for the effect of sample date and sample plot (PROC GLM; SAS 1988).

Among plot differences in foliar chemistry were tested with analysis of variance, blocking for the effect of sample date and tree type. Sample date was used as a blocking variable because seasonality can affect foliar composition in tropical forests (Medina 1984). Tree type was used as a blocking variable because the previous analyses showed that foliar chemistry differed among tree types.

Because the trees sampled for foliage in each plot were not representative of all species found in the plots, the foliar element or compound data for each sample tree was weighted by that species' basal area in the plot. Basal area was chosen as the weighting factor because it is proportional to foliage area (Brower *et al.* 1990). Weighted values were also used to determine correlations among foliar characteristics.

Weighted mean and standard deviation of each foliar parameter was also calculated for each plot (without regard to sample date). Principal components of foliar nutrients (plot means) were calculated for comparison with soil properties, vegetation structure, and species composition (see 'Vegetation-Soil Comparisons' in Methods section).

Soil measurements

Field sampling and laboratory analysis

In order to characterize the soil of each forest community, one soil pit was dug in the largest subplot (A) of each vegetation plot (Soil Conservation Service 1993; Soil Survey Staff 1994). Bulk samples of each horizon were taken from these pits to analyze chemical and physical properties of the soil. *In situ* saturated hydraulic conductivity was measured in each horizon on two dates (Table 3).

Twenty-five meters inside the edge of the PC and XV vegetation plots, cores were taken using an auger to obtain samples for surface horizon (0-10 cm) chemistry and texture (Figure 3). For the BA and SW plots, these cores were taken inside the vegetation subplots.

Bulk and core samples were air dried and transported to the Forest Service Laboratory in Research Triangle Park, North Carolina and the Soil Survey Laboratory in Lincoln, Nebraska. Each field sample was split in two, and standard chemical and texture analyses were performed (Table 3).

Data analysis

Soil pit data from each plot were graphed to illustrate trends in soil characteristics with depth.

Among plot differences in soil surface parameters were investigated with one-way analysis of variance and contrast analyses (PROC GLM; SAS 1988). Correlations between soil surface characteristics were determined using each sample core as an observation.

The mean and standard deviation of each soil parameter was calculated for each plot. Principal components of soil parameters (by plot means) were calculated for comparison to foliar nutrition, vegetation structure, and species composition (see 'Vegetation-Soil Comparisons' in Methods section).

Because most of the surface cores were sampled outside the vegetation subplots, I attempted to estimate what the soil surface values might have been if sampled in the vegetation subplots. Soil surface data was plotted in two dimensions and an interpolated surface was created to look for spatial trends in the data. Attempts were made to fit the data using semivariograms, general additive models, and trend analyses. Because estimations could not be made, comparisons between soil surface properties and vegetation characteristics were made only among plot means.

Vegetation-Soil Comparisons

Plausible associations between vegetation characteristics (structure and foliar chemistry) and soil properties (chemical, physical, and hydrologic) were investigated with scatter graphs and correlation matrices. Foliar chemistry was also compared to vegetation structure by species and plots.

Because many variables were produced from the vegetation structure, foliar chemistry, and soil surface data, principal components analysis was used to summarize the original data with a few principal components. Each principal component is a linear combination of the original variables; the coefficients of each linear combination are the eigenvectors of the correlation matrix (SAS 1988). Because each principal component is orthogonal to the others, principal component scores (coefficients) are uncorrelated. Thus the principal component scores are independent measures of variation, which can be used in subsequent linear analyses.

Separate principal component analyses were performed on variables from overstory vegetation structure, understory vegetation structure, foliar nutrients, soil surface nutrients and pH, and physical properties of the soil surface (PROC PRINCOMP; SAS 1988). Because the scores of the first principal components contain the highest variance of the data set, components having eigenvalues > 1.0 were retained for further analyses (Jackson 1993). Several relationships -- overstory and understory vegetation structure, vegetation structure and soil properties, overstory vegetation structure and foliar properties -- were examined by analysis of variance (PROC REG; SAS 1988).

The variation in species composition across plots was analyzed with detrended correspondence analysis (DCA), as described in the vegetation section of this document. Correlations between the DCA axes and soil surface and foliar characteristics (both individual variables and principal components) were calculated to determine whether the ordination of species and plots was associated with soil or foliar characteristics (CANOCO; ter Braak 1987).

RESULTS

Vegetation Characteristics

Community structure

Communities differed by vertical structure (ground cover, understory, overstory) and by the components (lianas, palms, and trees) of each strata. Structural differences were compared by contrast analyses, testing *a priori* hypotheses that: 1) forest structure differs between the flooded forests (swamp and bajo) and upland forests (broadleaf and palm); 2) forest structure differs between the swamp forest and the bajo forest; 3) forest structure differs between the upland broadleaf forests and the upland palm forests; and 4) forest structure differs between the upland broadleaf forest on a slope and on an adjacent level site. Overall, the analyses of forest structure quantify the observations of forest appearance made in the field (see Forest Community Descriptions section).

Differences in forest structure are illustrated by the ground cover analyses (Tables 4 & 5a). Although ground cover of stemless palms in the upland forests was more than five times that of the flooded forests ($p < 0.001$), the upland forests had 58% of the total ground cover of the flooded forests ($p < 0.001$), primarily because of their relatively low ground cover by woody vegetation ($p < 0.001$).

The large woody ground cover in the flooded forests was influenced by the bajo forest, which had the most woody ground cover of any forest type. Indeed, the bajo forest had twice the woody cover and five times the grass cover of the swamp forest (woody $p=0.006$; grass $p<0.001$). However, the bajo forest was sparsely covered by liana and herbaceous ground cover relative to the swamp forest (liana $p=0.009$; herbaceous $p<0.001$).

Between upland communities there was little difference in ground cover except for the woody component; the ground in the palm forest had half the woody vegetation cover of that in the broadleaf forest ($p=0.044$). Within the broadleaf forest, the sloping site had nearly twice the total ground cover of the level site ($p=0.017$), due in part to its larger herbaceous component ($p=0.063$).

Structural characteristics of lianas in upland forests were not different from those of flooded forests (Tables 4 & 5a). However, within flooded forests, the swamp forest had more than nine times the abundance and basal coverage of lianas than the bajo forest (density $p=0.020$; basal area $p=0.098$). Indeed, in the swamp forest, liana density was nearly equal to understory tree density.

Liana density was also high in upland forests. In two of the palm forest plots and in the level broadleaf forest, liana density was greater than or equal to the density of overstory woody trees. Between upland communities, the palm forest had a slightly lower liana density than the broadleaf forest ($p=0.093$), primarily because of high liana density in the level broadleaf forest site (564 liana stems/ha versus 200 stems/ha on the slope, $p=0.007$). Within the upland broadleaf forest, the level site had larger diameter lianas (mean dbh was over three times larger; mean stem basal area $p=0.060$) and over three times the liana basal area of the sloping site ($p<0.001$).

Overstory palm density and basal area were many times greater in upland forests than in the swamp forest (density $p<0.001$; basal area $p<0.001$; Tables 4 & 5a). In addition, overstory palms in upland forests were more than twice the height (to top) of those in the swamp forest ($p=0.001$). The bajo forest could not be included in the contrast analysis of palms because no palms occurred in the overstory bajo plot.

The differences between upland and flooded forests were the result of high overstory palm density and basal area in the cohune palm forest. When compared to the upland broadleaf forests, overstory palm trees in the palm forests were five times denser ($p<0.001$), had almost twice the mean diameter (mean basal area $p<0.001$), had 18 times more basal area ($p<0.001$), and were appreciably taller than those in the broadleaf forest (height to top $p=0.006$). In addition, within the upland broadleaf forests, palm trees in the sloping forest were taller than those in the level forest (height to base of crown $p=0.040$).

Also of note is the contribution of juvenile palms -- plants that had not yet developed boles -- to understory structure. The density of these plants (referred to as 'palm fronds') is quite high, particularly in the palm forest where their abundance is comparable to that of all plants with stems at dbh (trees, palms, and lianas). The cumulative cross-sectional area of the fronds of these palms is also quite large (Table 5a).

The principal differences in overstory broadleaf tree structure were between upland and flooded forests (Tables 4 & 5b). Although tree density in the upland forests was only

63% of that in the flooded forests ($p < 0.001$), these trees were much larger (mean basal area $p < 0.001$) and had greater basal area per hectare ($p < 0.001$) than those in the flooded forests.

Between flooded forests, there were no differences in size or abundance of broadleaf trees classified as overstory. However, most stems in the bajo sampled in the 'understory' dbh size class actually reached the canopy. Thus the bajo actually had a greater density and smaller trees then the swamp forest (Table 5b).

Between upland forests, broadleaf trees in the palm forest were larger than those in the broadleaf forests (mean basal area $p = 0.006$). However, there were fewer broadleaf trees in the palm forest ($p < 0.001$) because of the presence of canopy palms. In the upland broadleaf forest, broadleaf trees on the slope were similar in size to trees growing on level ground, but the forest on the slope was denser ($p = 0.010$).

Overall, there were large differences in overstory vegetation structure (combined broadleaf and palm trees) between upland and flooded forests (Tables 4 & 5b). Between these forest types, every measurement of vegetation structure was different ($p < 0.001$); stems in upland forests were larger (in both mean basal area and mean biomass), were almost twice the height, and had twice the overstory basal area. In addition, upland forests had four times more aboveground biomass than flooded forests. However, the flooded forests were denser.

Comparisons of overstory structural components between flooded forests found only height differed; bajo trees were shorter than those in the swamp (height to top, $p < 0.001$). However, many structural components differed within the upland forests.

When compared to the broadleaf forests, the overstory stems in the palm forest were larger (mean basal area and mean stem biomass, $p<0.001$) and had a greater basal area ($p=0.024$). However, the broadleaf forest had more overstory stems (density, $p=0.001$) of a slightly greater height (height to base, $p<0.001$). The broadleaf forests were denser because of the forest on the slope (plot PC1); this forest was denser than the level broadleaf forest ($p=0.008$).

Overstory vegetation structure was summarized by one principal component, which contained 0.84 of the total variation in the overstory (Appendix A). The scores of this vector were similar (0.31 to 0.38) for all variables, indicating that the vector describes the overstory plot physiognomy. Understory vegetation was summarized by two principal components, which contained 0.76 and 0.15 of the total variation in the understory. The first vector had scores > 0.35 for all variables except height to base of crown, indicating that the vector describes tree size and height. However, the height of base of crown had a score of 0.92 in the second vector, which effectively describes this variable.

While contrast analyses verified that upland forests were taller than flooded forests (Tables 4 & 5b), vertical stratification of foliage is a more detailed representation of the canopy structure in these forest communities (Figure 5). All upland forests had a similar vertical structure - a ground cover layer, an understory layer at about 2 meters height, an overstory 'layer' between 5 and 25 meters in height, and a few emergent trees over 25 meters tall. Among the palm forest plots there was some variability in overstory foliage cover.

Vertical structure of the flooded forests was dramatically different from that of the upland forests. The swamp forest had a ground cover layer but no distinct canopy layer; the foliage was dense between 2 and 8.5 meters and gradually tapered off above that height. The bajo forest also had a ground cover layer but a more defined canopy layer from 4 to 8.5 meters.

Leaf area indexes of the swamp and bajo were considerably lower than those of the upland forests. However, among all plots, leaf area index had a weak relationship to total basal area ($r=0.59$, $p=0.163$, $n=7$) and biomass ($r=0.77$, $p=0.043$, $n=7$). Leaf area index in the palm forest was relatively low compared to its biomass; perhaps the leaf area meter did not accurately measure the leaf area of palms because of the unusual geometry of their leaves.

Frequency distributions of diameters showed an inverse J-curve (Figure 6). In the bajo forest over 70 % of the stems were in the smallest size class (<6.5 cm dbh), while in the swamp and upland broadleaf forests almost half of the stems were in that size class. However, in the palm forests a more even distribution of diameters was found, with almost half the stems of diameters $\geq$ 10 cm.

Community composition

The species-area relationship among all plots showed progressive decrease in species accumulation from dry to wet upland forests (Figure 7a). However, there was a sharp increase in the slope of the curve when the species of the flooded forests were added.

Species area curves within plots were ordered along the apparent moisture gradient within each plot, thereby minimizing the change in slope along each curve (Figure 7b). Curves began to level off between 0.1 and 0.3 hectares, but showed a continued accumulation of species with additional area. However, most curves (except for XV2) appear to have a point at which the slope of the curve changes from a relatively slow accumulation of species to a more rapid one, indicating a change in species composition within the plots.

To compare species diversity among plots, the number of species per half-hectare was estimated from the species-area curves (Table 5c). Half of a hectare was used as the standard of comparison because it was the area sampled by the smallest plot. The swamp had the highest diversity (64 species/half-hectare). The upland forests varied from 43 to 55 species per half-hectare. The level upland broadleaf forest was more diverse than the forest on the slope (55 species/half-hectare versus 47 species/half-hectare).

To compare species diversity of a plot with other characteristics of that plot, the species richness (number of species sampled in the plot) was determined. Among all plots, there appeared to be an inverse relationship between species richness and species dominance (Figures 8 & 9). When fewer species dominated a plot (i.e. more species comprised the 'top' half of the overstory basal area or density), the diversity of that plot increased (Table 5c). When dominance was determined by basal area, this relationship was particularly strong.

Within the palm forest there also appeared to be a relationship between the dominance (basal area) of overstory palms and species richness. As the basal coverage of overstory palms increased (from plot XV3 to XV1), the species richness decreased (Table 5c). In addition, the most common palm species in these plots, *Orbignya cohune*, comprised less than 20% of the basal area in the most diverse plot (XV3) but over 26% of the basal area in the other plots (Figure 8). This same species comprised only 12% of the stems in the more diverse plot, but around 20% of the stems in the less diverse plots (Figure 9).

In addition to *Orbignya cohune*, the palm forests had a few other overstory species that were also dominant and/or abundant (comprising $\geq$ 9% of the plot basal area or density; Table 6). *Spondias mombin* and the *Ficus* genus (*Ficus glabrata* and *Ficus* sp.) were dominant species, while *Spondias mombin* (in all three plots), *Guarea excelsa* (in XV1 and XV2), and *Dendropanax arboreus* (in XV3) were abundant species. Of note is that an abundant tree (10-18% of stems) of relatively small diameter - *Guarea excelsa* - does not dominate the basal area, while an infrequent tree (about 1% of stems) which is very large - *Ficus glabrata* - can dominate the basal area.

The overstory of the upland broadleaf forests was also dominated by a few species (Table 6). *Drypetes brownii* was the most common species in the upland broadleaf forests; on the slope it comprised 31% of the basal area and 30% of the stems, while on the level forest it comprised 8% of the basal area and 14% of the stems. *Brosiumum alicastrum* was also dominant (22% and 17% of basal area) and abundant (12% and 9% of stems) in these forests. In addition, the level broadleaf forest also had two other important species; *Celtis* *schippii* (20% of basal area; 10% of stems) and *Vateria lundeii* (11% of basal area; 2% of stems).

Compared to the upland broadleaf forests, the high species richness in the swamp forest resulted in the dominant and abundant overstory species comprising less of the plot density and basal area. The most abundant species (*Margaritaria nobilis*) was only found in the swamp forest, and the second most abundant species (*Simira salvadorensis*) was not abundant in the upland forests. However, most of the dominant species - *Vateria lundeii*, *Spondias mombin*, and *Swietenia macrophylla* - were more common in the upland forests.

Also of note is the dominance of a few species in the understory of these forests (Table 6). In the broadleaf forests (both upland and swamp) *Cryosophila argentea* was the dominant understory species (comprising over 30% of the basal area) and the most abundant understory species (comprising over 25% of the stems). However in the palm forests, regenerating *Orbignya cohune* (individuals that had not yet grown a stem) had many times the cross sectional area and generally higher density than the highest ranked species that had stems. In fact, in the palm forests there were 0.8 to 1.3 times more regenerating *Orbignya cohune* plants than understory plants with stems, and the total cross sectional area of these *Orbignya cohune* plants was 1.6 to 2.9 times the total basal area of understory plants with stems.

Detrended correspondence analysis (DCA) ordinates species by their similarities in abundance and center-weights each sample plot among its species scores (Jongman *et al.* 1995; Figure 10). Species and plots with similar scores have similar abundances and species composition, respectively, while species and plots occurring at opposite ends of an axis are most different (Figure 11). The eigenvalue associated with each DCA axis is a measure of the proportion of the variability in species or sample dispersion explained by that axis (Jongman *et al.* 1995; Gauch 1982). Eigenvalues closer to 1 indicate that the axis captures more of the variability in the data.

The first DCA axis of overstory tree species density had an eigenvalue of 0.6804, indicating that this axis contained most of the variability in the species abundance relative to the second axis (eigenvalue = 0.0786). In fact, the sample plots followed a trend along the first axis (PC1 < PC2 < XV1,XV2 < XV3 < SW). The more common species appear to group around or parallel to this axis as determined by the plot density of these species.

Foliar chemistry

Analyses comparing the foliar chemistry of groups of species -- palms, nitrogen fixing trees, or other broadleaf trees -- demonstrated that legumes had a higher concentration of foliar N than non-legumes ($p=0.003$) and therefore a lower C:N ratio ($p=0.005$) (Table 7). These analyses also showed that palm tree foliage had a higher C:N ratio than that of broadleaf trees ($p<0.001$). However, all foliar nutrients were lower in the palms (N $p<0.001$; P $p=0.004$; K $p=0.004$; Ca $p<0.001$; Mg $p=0.003$). In addition, none of the carbohydrates were significantly different between the two tree types ($p<0.1$).

Analysis of variance (blocked for the effect of sample date and tree type) revealed that plots differed by all measured foliar compounds (hexose $p=0.012$, starch $p=0.003$, all others $p<0.001$) (Tables 4 & 8). There was no interaction between date and type or plot ($p<0.1$).

Contrast analyses revealed that upland forests had higher concentrations of foliar N, P, Ca, ($p<0.001$) and specific leaf area ($p=0.006$) than flooded forests. However, carbon concentration ($p<0.001$) and C:N ratio ($p=0.009$) were higher in flooded forests.

Within flooded forests, the bajo foliage had greater Ca ($p<0.001$) and Mg ($p=0.016$) concentrations than the swamp forest. In addition, the bajo had a higher C:N ratio but a lower carbon concentration than the swamp forest (C:N $p=0.003$; C $p<0.001$).

Within upland forests, the broadleaf forests had higher concentrations of foliar K and Mg than the palm forests (K $p=0.018$; Mg $p<0.001$). It was the high Mg in the broadleaf forests that differentiated the upland forests from the flooded forests for this foliar element ($p=0.010$ for contrast between broadleaf and flooded forests, $p=0.103$ for contrast between palm and flooded forests). However, the broadleaf forests had lower foliar P ($p<0.001$), C ($p=0.012$), N ($p<0.001$), C:N ratio ($p=0.033$), specific leaf area ($p=0.040$), and carbohydrate concentrations (all, $p<0.008$) than the palm forest. In fact, it was the high values of these measurements in the palm forest foliage that differentiated the upland forests from the flooded forests foliage (all contrasts of these characteristics between broadleaf and flooded forests, $p\geq0.109$; all contrasts of these characteristics between palm and flooded forests, $p\leq0.004$).

Within the upland broadleaf forests, the forest on the slope had higher foliar C ($p=0.027$), C:N ratio ($p=0.082$), and Ca ($p=0.001$) but lower foliar Mg ($p<0.001$).

Foliar nutrients were summarized by two principal components, which contained 0.60 and 0.30 of the total variation in foliar nutrition (Appendix A). The first vector scores were > 0.42 for P and all cations, indicating that the vector describes overall cation nutrition. The second vector had scores > 0.50 for foliar N and P concentrations; this vector describes the variation in these nutrients.

Soil Chemistry, Texture, and Hydrology

Soil profile

Profile patterns of soil texture appear to cluster by community type (Figure 12). Profiles of the upland broadleaf forests had a similar pattern: the surface was mostly clay and silt, with the profile becoming sandier with depth. However, the profiles differed in the proportion of each particle size; a large proportion of the soil from the plot on the slope was sand size particles, while the level plot at the base of the slope had a much higher proportion of clay. The palm forest soils were composed primarily of clay and silt at the surface, with increased proportions of silt at greater depth. Both flooded forests had very high clay concentrations throughout the profile, except that in the bajo silt (and to a lesser degree, sand) replaced clay at 1 m. Bulk density decreased as the clay content increased, although this relationship is opposite that normally expected.

Saturated hydraulic conductivity (K_{sat}) was measured during a wet period (March 1990) and dryer period (May 1990) -- months that are usually at the end of the dry season and the beginning of the wet season, respectively. When the soil was wet, the K_{sat} on the slope in the upland broadleaf forest was very high (44.5 cm/hr at 10-15 cm depth) -- two orders of magnitude greater than that of the level site (0.2 cm/hr at 10-15 cm depth; Figure 13). The K_{sat} in the palm forest soil was similar to that of the level upland broadleaf forest, with values ranging from 1.77 cm/hr and 4.75 cm/hr (at 10-25 cm depth). The bajo had the lowest K_{sat} of all plots (0.03 cm/hr at 10-25 cm depth). Thus K_{sat} was related to the bulk density and relative proportions of sand and clay in these soils, because the soils' ability to transport water is dependent on the size and arrangement of soil pores (Amoozegar and Warrick 1986; Rundel and Wesley 1991).

After the soil had dried somewhat, K_{sat} was measured again. Measurements in the C horizons of the plots (Bg in plot PC2) were comparable to K_{sat} values obtained on the earlier sample date. However, in the upper horizons, K_{sat} could not be measured in because the constant head permeameter could not produce saturated soil conditions (i.e. a constant head could not be maintained). This occurred because the rate of lateral flow and percolation into the dry soil was faster than the rate of water supply by the constant-head permeameter. Nonetheless, the rates of flow from the permeameter, recorded for these horizons, are an indicator of the rate of soil drying and amount of soil cracking that occurred over a three month period. In addition, these flow rates indicate the relative rate at which rainwater will percolate through the upper horizon when the soil is dry. They show that drying and rainwater percolation were very rapid in the bajo, moderately rapid in the swamp and upland forests, and generally slow in the palm forests. (The high flow rate in the upper horizon of XV3 appears to be an anomaly - perhaps the result of a root channel - and thus will not be considered in later comparisons.)

The major differences in the soil chemistry profiles among the plots were between upland and flooded forest types. The pH was lower through much of the swamp and bajo profiles, compared to most of the upland forests that were alkaline throughout the soil profile (except the level upland broadleaf forest; Figure 13). Soil Ca concentration followed a pattern similar to that of pH; the swamp, bajo, and level broadleaf plots had lower Ca concentrations through most of the profile (Figure 14). Soils in the upland and flooded forest communities also exhibited different K and Mg profiles. Although the absolute concentrations of these cations appeared to differ among the upland forest soils, all concentrations of K and Mg decreased with depth - evidence of upper horizon nutrient cycling. However, in the flooded forests K (below 20 cm) and Mg concentrations increased with depth - indicating that parent materials influence the concentration of these cations.

Community trends in inorganic and organic forms of N and P were not directly apparent (Figures 15 & 16). Total N and to a lesser degree total P were highly variable throughout the profile in most plots, but mineralizable N and extractable P -- better indicators of the concentrations available to plants -- decreased rapidly below the surface. These profiles show that the top ten centimeters of the profile appear to contain 1/2 to 2/3 of the available soil pool of these important plant nutrients -- supporting my comparison of soil surface properties (0-10 cm cores) with vegetation and foliar characteristics.

Soil surface

Among plot differences in soil surface properties were similar to those of the soil profiles, indicating that the soil surface data is a good proxy for the trends occurring throughout the profile. The one-way analysis of variance of soil surface properties revealed that plots differed by all soil surface measurements ($p=0.082$ for total P, $p<0.001$ for all others) (Tables 4 & 8).

The major differences in soil surface chemistry and texture were between upland and flooded forests (Tables 4 & 8). Upland forests had higher pH than flooded forests (both pH measurements, $p<0.001$) and almost double the concentrations of K ($p<0.001$), Ca ($p<0.001$), and extractable P ($p=0.015$). However, upland forests had a much lower concentration of soil Mg (0.07% versus 0.17%, $p=0.006$). As for texture, upland forests had more sand ($p=0.015$) and less clay ($p=0.052$) than flooded forests.

Soil chemistry also differed between the two flooded forest communities. The bajo had slightly higher pH (laboratory pH, $p<0.001$), Ca ($p<0.001$), and total N concentration ($p=0.016$) than the swamp forest. However, the bajo had lower concentrations of Mg ($p<0.001$), extractable P ($p=0.004$), and mineralizable N ($p<0.001$). Texture differences between the soils were not large - only the proportion of sand was larger in the bajo ($p=0.013$).

Within upland forests, the soils of the broadleaf forests had lower pH (laboratory pH, $p=0.001$) and less than half the K concentration ($p=0.003$) of the palm forest soils. However, the broadleaf forest soils were higher in C ($p=0.002$), total N ($p=0.086$), and

Mg ($p=0.053$) concentrations. In fact, it was the high concentration of carbon in the broadleaf forests and the low concentration of Mg in the palm forests which caused upland forests to differ from flooded forests for these soil constituents ($p=0.008$ for contrast of C between broadleaf and flooded forests, $p=0.679$ for contrast of C between palm and flooded forests; $p=0.305$ for contrast of Mg between broadleaf and flooded forests, $p=0.007$ for contrast of Mg between palm and flooded forests).

As for soil texture, the broadleaf forests had twice the sand ($p<0.001$) and slightly less clay ($p=0.002$) than the palm broadleaf forests. In fact, it was the low clay and high sand content of the broadleaf forest soils that differentiated the upland soils from the flooded soils for these particle sizes ($p=0.001$ for contrast of clay between broadleaf and flooded forests, $p=0.715$ for contrast of clay between palm and flooded forests; $p<0.001$ for contrast of sand between broadleaf and flooded forests, $p=0.785$ for contrast of sand between palm and flooded forests).

Several of the differences between the soils of the broadleaf forest and the palm forest were actually due to the dramatic effect of slope on the soils of the broadleaf forests. All soil surface parameters except for total P were different between the two broadleaf forest plots. The sloping site had higher concentrations of soil C, N, Ca, Mg, extractable P, and pH (Mg $p=0.003$, all others $p<0.001$). Only mineralizable N and soil K were lower ($p<0.001$) in the sloping site. The sloping site also had less clay ($p<0.001$), but more silt ($p=0.009$) and sand ($p<0.001$). It appears that the difference between the sloping site and all other upland forest plots (all on relatively level sites) caused the difference between broadleaf and palm forest soils for total C, total N, extractable P, percent clay, and percent sand as supported by least significant difference t-tests ($p<0.05$) among these five plots.

As expected, many soil parameters were correlated (for example, clay and sand, mineralizable N and total N). There was also a strong correlation between pH and total Ca concentration ($r=0.85$, $p<0.001$, $n=65$); indicating the role of calcium carbonate in raising soil pH.

Soil chemistry (nutrients and pH) was summarized by two principal components (S1 and S2) that contained 0.64 and 0.22 of the total variation in soil chemistry (Appendix A). The first vector scores were > 0.37 for pH, total Ca, total Mg, mineralizable N, and extractable P; this vector describes general soil nutrition and pH. The second vector had scores > 0.59 for total N and total K; this vector describes the variation in these nutrients.

Soil physical properties (texture and bulk density) were summarized by one principal component (T1) which contained 0.92 of the total variation. As all scores were > 0.48, the vector describes the physical structure of the surface soils. This principal component (T1) was correlated to the first principal component of soil chemistry (S1, $r=0.81$, $p=0.027$, $n=7$).

Attempts were made to estimate values for the soil properties of each vegetation subplot. Semivariograms, general additive models, and trend analyses were employed, but estimates were unobtainable because the variability in soil values was unrelated to direction or distance. In other words, the soil surface properties were spatially independent at a distance of 50 meters or more. Because subplot estimates were unobtainable, I could not evaluate the correlation between foliar chemistry and soil chemistry at the subplot level.

The spatial independence of soil properties indicates that the actual concentration of nutrients that an individual tree encounters may be quite variable. Because the roots of canopy trees are spread out over large distances (probably larger than the subplot area) the plot means of soil properties are better indicators of the conditions a stand of trees experience -- supporting the plot level comparisons between the soil and vegetation characteristics.

Vegetation-Soil Relationships Across Communities

Relationship between soil chemistry and chemistry of canopy foliage

I hypothesized that canopy foliage chemistry (N, P, Ca, Mg, K) is related to the concentration of these nutrients in the surface soil or to soil characteristics that may effect the uptake of nutrients (pH). Contrast analyses confirmed some of the hypothesized relationships.

Contrast analyses showed that when compared to flooded forests, upland forests had higher concentrations of soil Ca and extractable P, corresponding to higher concentrations of foliar Ca and P (Table 4). Within flooded forests the bajo forest had higher soil and foliar Ca but lower mineralizable-N and foliar N concentrations than the swamp forest. Within upland forests, the broadleaf forest had higher soil and foliar Mg concentrations than the palm forest. And in the upland broadleaf forests, the forest on the slope had higher soil and foliar Ca concentrations than the level forest.

Some nutrients were significantly different in both soil and foliage contrasts, but the directions of the trends were opposite. These opposite trends occurred for the following contrasts: the bajo forest had lower soil Mg but higher foliar Mg than the swamp forest; the upland broadleaf forest had lower soil K but higher foliar K than the palm forest; the upland broadleaf forest had higher soil N but lower foliar N than the palm forest; and the broadleaf forest on the slope had higher soil Mg but lower foliar Mg than the level forest.

Among all plots, there were no relationships between individual soil properties and foliar nutrient concentrations. In addition, neither the multivariate analysis of variance (MANOVA) between the principal components of foliar nutrition and soil properties, nor the univariate analyses of variances (ANOVAs) of the MANOVA were significant ($p<0.1$; Appendix B.1).

Relationship between soil characteristics and vegetation structure

I hypothesized that the growth of forest vegetation (as indicated by leaf area index, overstory basal area, or total aboveground biomass) is related to the concentrations of soil elements essential for plant nutrition (N, P, Ca, Mg, K) or to soil conditions which could affect nutrient uptake (pH). In addition, I hypothesized that vegetation growth might be associated with the physical and hydrologic condition of the soil because these conditions can influence plant water relations.

Although no continuous relationships were found by the graphical comparison of vegetation structure with soil chemistry, several vegetation-soil relationships appeared as clusters of data points. The flooded forest plots formed one cluster while the upland forests formed another, and there was some separation among upland communities (Figure 17). Aboveground biomass (overstory and understory combined), total basal area, and leaf area index had similar relationships with the soil variables, but the relationships with biomass were generally stronger (the clusters were smaller). Leaf area index was positively correlated to mineralizable N ($r=0.91$, $p=0.004$, $n=7$). Aboveground biomass was positively correlated to soil Ca ($r=0.89$, $p=0.008$, $n=7$) and pH ($r=0.96$, $p<0.001$, $n=7$). Aboveground biomass was also negatively related to soil Mg ($r=-0.98$, $p<0.001$, $n=7$).

These associations were summarized by the ANOVA of the principal components. The vector representing overstory plot physiognomy (V1O) was dependent on the vectors describing soil texture (T1) and general soil nutrition and pH (S1; $p=0.001$, $R^2 = 0.965$, Appendix B.2). Graphs of these relationships show that most of variability in the relationship is between the upland and flooded forests.

Relationship between soil characteristics and species composition

To test the hypothesis that environmental gradients may be related to the trends observed in species composition, I calculated the correlation coefficients between plot soil surface properties and each DCA axis (Table 9). Mineralizable N, pH, and bulk density were positively correlated with the first DCA axis. The same axis had weaker correlations with additional soil nutrients (positively correlated with total N, PO_4P, and Ca, and negatively correlated with Mg) and soil texture (positively correlated with sand and negatively correlated with clay). In addition, the principal component vectors of soil texture (T1) and general soil nutrition and pH (S1) were both negatively correlated to the first DCA axis.

Relationship between foliar nutrition and vegetation structure

I hypothesized that overstory vegetation growth (as indicated by total basal area) is related to foliar nutrition (P, N, Ca, Mg, and K). When the accumulation of overstory vegetation (i.e. total basal area, total biomass, and leaf area index) was compared to the weighted mean of foliar chemistry, no relationships were found. However, when just the upland communities were analyzed, foliar P was associated with aboveground biomass (Figure 17). In addition, ANOVA of principal components demonstrated that the vector representing overstory plot physiognomy (V1O) was dependent on the vector of foliar N and P (F2; $p=0.038$, $R^2 = 0.612$, Appendix B.3). However, this relationship is based primarily on the low nutrient status of the bajo foliage.

Relationship between foliar nutrition and species composition

Foliar chemistry can be a good indicator the nutrients available to the species composing a forest community. Therefore mean foliar nutrient concentrations were compared to each DCA axis (Table 10). Although no foliar nutrients were strongly associated with the gradient in soil moisture along the first DCA axis, the principal component vector representing foliar N and P (F2) was negatively correlated to the first DCA axis (r=-0.86)

DISCUSSION

A basic tenet of autecology is that plant community structure and composition are linked to the underlying abiotic environment. This study suggests that the major differences among the forests in northwestern Belize are the result of underlying hydrologic conditions. The analyses demonstrate that the largest differences in edaphic conditions and vegetation characteristics occur between the seasonally flooded forests and the upland forests. By comparison, the magnitude of changes within either of these forest groupings is much smaller.

Topography may also influence edaphic conditions, as evidenced by the characteristics of the upland broadleaf forest growing on a slope. The soils of this forest not only differed in chemistry, texture and hydrology from those of the level forest, but they also differed from the other upland forest type -- the cohune palm forest. However, slope was not strongly associated with forest structure or foliar chemistry, but was reflected more in changes in species composition. As such, the species composition of the forest on the slope is similar to what has been classified as 'dry' upland forest (Brokaw and Mallory 1993), while that on the level site is indicative of a more 'mesic' upland forest.

Other differences among upland forests were found between the broadleaf forests and the palm forest. The soils of the palm forest have chemical, textural, and hydrological characteristics indicative of higher site productivity. This is reflected in larger aboveground biomass and tree size, as well as greater concentrations of foliar N and P.

The *a priori* contrast hypotheses, that the soils and vegetation of the broadleaf forests would differ from the palm forests, assumed a discontinuity between the forest types. However, there is a gradient across these forest types, with intermediate characteristics represented by the mesic broadleaf forest. This forest has some edaphic conditions that are more similar to the dry broadleaf forest and others that are closer to the palm forest soils. This intermediate condition is also reflected in the vegetation characteristics of this forest, including its species composition. Recall that a forest stand can be classified as "cohune palm forest" with less then 20% of its overstory canopy composed of *Orbignya cohune*; the mesic broadleaf forest has 2% of its overstory basal area composed by this species. These results support my field observations that there is a gradient in soil moisture and species composition from dry upland forest, to mesic upland forest, to cohune palm forest.

This gradient in soil moisture and species composition appears to continue from the upland forests into the swamp forest. However, most of the other soil properties of the flooded forests differ greatly from that of the upland forests, with a concurrent difference in forest stature.

Although many soil chemical properties are statistically different between the two flooded forests, the magnitude of these differences is small. The chief difference between the soils of these forests is the influence that the physical soil properties have on the soil hydrology. In the dry season, the bajo soil develops deep cracks and the forest experiences severe drought, but the swamp forest does not. These differences in soil hydrology do not translate into large differences in vegetation stature, but are reflected in smaller mean tree diameter in the bajo and different species composition (such as the absence of palms and lianas in the bajo). Although species composition was not quantitatively measured for the bajo forest, the general survey of the forest shows many species that are unique to this forest type.

Environmental conditions

In these forests, topography and soil texture influence the water holding capacity of the soil. Seasonal changes occur in water holding capacity because the soils contain montmorillonite clay, which swell when wet and shrink when dry (Troeh and Thompson 1993). The combination of soil texture and montmorillonite clay content results in a broad gradient in soil moisture from the dry upland broadleaf forest (relatively dry) to the mesic broadleaf forest to the palm and flooded forests (wettest). However, the actual gradient is dependent on the season.

Total soil moisture available to plants is also constrained by the depth of the rooting zone. In this region, the mineral soil in the upland forests ranges in depth from 0.1 to 0.5 meters, overlaying a weathered karst that is relatively inhospitable to roots (Brokaw and Mallory 1990). On my upland sites, depth to the C horizon karst ranges from 0.35 to 0.58 meters, and few roots are found below these depths (Appendix C). Thus a relatively small volume of soil moisture is available to plants in these forests.

In the dry upland broadleaf forest, it appears that water carried fine clay particles off the slope, leaving a high fraction of sand. This high proportion of sand facilitates the rapid percolation movement of water through the profile even when the soils are saturated (as indicated by the high K_{sat}). These conditions, along with the shallow rooting zone, result in relatively limited plant available moisture throughout the year.

Down slope from this site, the level surface of the mesic upland broadleaf forest appears to accumulate fine clay particles transported from the slope. These clay particles increase soil moisture retention, so that when the soil is saturated during a wet season rain event, water movement through the profile is relatively slow (as indicated by the low K_{sat}). Thus soil water remains on site and soil moisture levels are fairly high in the wet season. However, during the dry season, the soils dry fairly rapidly and form small cracks. Despite these dry season conditions, over the course of a year, the soil of this forest type provides more plant available moisture than that of the dry upland forest.

The palm forest sites are generally level and have intermediate clay content. Thus, when wet season rains saturate this soil, water movement through the profile is relatively slow (as indicated by the low K_{sat}). During the transition from the wet to dry seasons, these soils appear to crack and dry less than those of the mesic broadleaf forest. As a result, soil moisture is generally available to plants in these forests throughout the year.

Both flooded forests are on very flat sites with deep soil profiles composed mostly of clay, probably deposited during annual flooding. Soil moisture content is very high during the wet season because soils are saturated or inundated. However, during the dry season the flooded forests deviate from the gradient of increasing soil moisture.

The swamp forest exhibits rates of soil drying and cracking similar to that of the upland broadleaf forests. Because soil moisture retention increases with organic matter content (Troeh and Thompson 1993), the higher levels of soil organic matter in the swamp forest soil (as indicated by the darker soil color, Appendix C) may cause the observed moisture retention and lack of severe cracking. However, during the dry season, the bajo forest soil is very dry and forms deep cracks -- some observed to be over 2 meters deep -- which minimize water retention in the rooting zone. Consequently, the moisture conditions in the bajo soil change from saturation to extreme drought over the short period between the wet and dry seasons.

Along the gradient of increasing soil moisture, there is a concurrent gradient in edaphic factors (pH, soil texture, mineralizable N, and to some extent extractable P; Table 9). Of particular note is the inverse relationship between soil moisture and soil fertility (plant available P and N). Concentrations of extractable P are highest in the soils of the dry upland forest, intermediate in the other upland forests (mesic broadleaf and palm forests), lower in the swamp forests, and lowest in the bajo forest. Concurrently, concentrations of mineralizable N are highest in the upland broadleaf forests, intermediate in the palm forests, and lowest in the flooded forests.

There is also a gradient in soil fertility through the soil profiles. The rapid decrease in mineralizable N and extractable P with depth indicates that these nutrients are cycled in the upper horizon. The decrease with depth of these important plant available nutrients appears to be associated with the decline of fine roots. At depths greater than 50 cm below the surface -- where the mineral soil ends -- the concentration of mineralizable N is near zero and most profiles are described as having few fine roots (Appendix C).

Vegetation response

Community composition

The gradient in soil moisture, pH, and fertility is closely followed by a gradient in species composition. Detrended correspondence analysis shows a gradient in species composition from dry upland broadleaf forest to swamp forest, with a concurrent change in the physical characteristics of the soil that influence soil moisture retention (sand content decreases while clay increases). Other Belizean forests, species composition is also related to soil moisture and nutrient status (Furley and Newey 1979).

Species in each forest type must be adapted to the particular availability and seasonality of soil moisture. For example, species of the dry broadleaf forest need to tolerate lower year-round soil moisture, while species of the mesic broadleaf forest and palm forest do not. Swamp species must be adapted to flooding, but are not necessarily drought tolerant. However, bajo species must tolerate both flood and drought conditions. In fact, some bajo trees are species found in the driest upland broadleaf forests of the region, however in the bajo forest they never attain the same stature. Overall, trees in the flooded forests must be able to survive physiologically stressful conditions -- flooding, low nutrient concentrations, and relatively low pH -- thus many species in the flooded forests are unique to these forests (Appendix D, Figure 7a). Flooded forests elsewhere in the Yucatan also display a relationship between species distribution and hydroperiod (Olmstead and Duran 1986).

There appears to be a relationship between species richness and dominance across all the forest communities (except the bajo). As diversity increases, overstory dominance decreases. These relationships are to be expected -- more species result in greater competition for common resources, decreasing the ability of any one species to dominate (Whittaker 1965). The high diversity in the swamp forest may be the result of this dominance-diversity relationship, or may be due to the frequent formation of canopy gaps that provide greater microsite variability (Denslow 1987; van der Maarel 1988; Brown 1993).

Species diversity is dependent on the size of the area sampled. Species-area relationships show a change in species composition within the plots, indicating that the plots actually encompassed more than one variant of the community type sampled. The number of species sampled in all the subplots of each plot are expected to be representative of the forest enclosed by the dimensions of the plot -- ranging from 2.5 to 4.0 ha, depending on the plot. This expectation is reasonable because the number of species found in these plots is similar to that in a contiguous hectare located in similar forest communities (Brokaw and Mallory 1993).

Overstory community structure and foliar nutrition

Structural characteristics of these forests are also related to edaphic conditions (overall soil texture, nutrients, and pH). However, unlike species composition, overstory structure does not follow a gradient in soil moisture, but groups by soil properties characteristic of flooded or unflooded forests. In addition, structural characteristics are related to foliar chemistry, particularly N and P concentrations. As a whole, it appears that the conditions in the middle of the soil moisture gradient are optimal for plant growth; the largest trees, greatest aboveground biomass, and highest concentrations of foliar N and P were produced under these conditions.

Whittaker *et al.* (1974) showed that aboveground biomass of climax forests is positively correlated with net primary productivity. In addition, it generally understood that foliar nutrition of trees is related to plant productivity (Perry 1994). Thus in this study, it appears that the soil moisture gradient is paralleled by a gradient in productivity; productivity is highest in the palm forests, lower in the upland broadleaf forests, and lowest in the flooded forests. Similar relationships -- between foliar nutrient concentration and basal area (Shariff and Miller 1990) and between soil moisture and productivity (Lugo *et al.* 1978) -- have been found in other tropical and subtropical forests.

Although the large difference in productivity between upland and flooded forests is associated with soil fertility, within these groupings there is no such association. For example, the palm forest has the highest productivity, but intermediate soil concentrations of total Ca, total Mg, mineralizable N, and extractable P, while the broadleaf forests have intermediate productivity, but the highest concentrations of mineralizable N and exchangeable P (dry broadleaf forest only). Within the flooded forests, the swamp forest has a leaf area index and foliar nutrient concentrations similar to the upland forests, but other indicators of productivity (biomass and tree size) and soil fertility are not different from the bajo forest. For all forest types, it appears that productivity is most strongly related to soil moisture availability.

Seasonal flooding limits height and size of trees, thereby having a large influence on forest physiognomy. Flooding in the swamp forest results in a relatively shallow rooting zone; coarse roots -- which assist in anchoring the trees -- are limited to the top 12 cm of the profile (Appendix C). The shallow rooting zone, in addition to promoting tree fall, probably limits the height of trees in the swamp.

The bajo is even more limited in height and tree size. Some of the species in the bajo also grow in dry upland forests, although in the bajo they attain smaller diameter and stature. In addition, the bajo has the lowest specific leaf area and leaf area index. In most forest ecosystems, leaf area index and average specific leaf area are positively correlated; however the low specific leaf area in the bajo foliage indicates that the seasonal drought in the bajo selects for xeromorphic species with sclerophyllous leaves (Larcher 1983).

My estimates of aboveground biomass in the upland forests (213 to 294 Mg/ha) using derived allometric equations are similar to those reported elsewhere. Overstory biomass in other subtropical moist forests have been estimated between 157 to 291 Mg/ha (Brown and Lugo 1984). Aboveground biomass in ten sites classified as subtropical or tropical montane (27.5° C, 1350 mm/yr) averaged 291 Mg/ha (±29 std) (Brown and Lugo 1982). Aboveground biomass of two dense upland forests in the Brazilian Amazon were reported at 198 Mg/ha and 388 Mg/ha (Fearnside *et al.* 1993).

My estimates of aboveground biomass in the flooded forests (92 Mg/ha) are similar to the 89 Mg/ha estimated for unproductive broadleaf forests in tropical America (Brown and Lugo 1984; forests were classified as unproductive if they occurred on rough terrain or were flooded). My estimates are also comparable to those of subtropical dry forests (80 ± 22 Mg/ha; Brown and Lugo 1982).

In northwestern Belize, the aboveground biomass of a young (45 year old) dry upland broadleaf forest was reported to be 56 Mg/ha ('high bush forest'; Lambert *et al.* 1980). The biomass of a young (65 year old) palm forest was reported to be 183 Mg/ha ('cohune ridge'; Arnason and Lambert 1982). The forests in my study have considerably higher biomass because they are mature undisturbed forests. However, it should be noted that the biomass of the palm forest and mesic broadleaf forest may be slightly overestimated; separate allometric equations were not available to calculate the biomass of palms, which probably have wood of lower specific weight then broadleaf trees.

Overstory palms and lianas

Although the canopy trees in the palm forest community had the highest mean concentrations of foliar N and P, overstory palm foliage had lower concentrations of all measured nutrients when compared to broadleaf tree foliage. Similar results were found by Arnason *et al.* (1984). Low nutrient concentrations are associated with long leaf life span and evergreeness in general (Ca, Mg, P, and K, Chabot and Hicks 1982; N, Reich *et al.* 1992). Low concentrations of nutrients in palm foliage may indicate longevity of palm leaves.

The high C:N ratio in the palm foliage results in a slow decomposition rate of palm litter. I have observed a very thick layer of undecomposed palm leaf litter in forests dominated by *Orbignya cohune*; other researchers have measured slow decomposition rates in these forests (Arnason and Lambert 1982, Ewel 1969). In addition, both *Orbignya cohune* and *Sabal morrisiana* are used in Belize for thatch because of their resistance to decay (Hartshorn *et al.* 1984).

In this study, overstory palms - *Orbignya cohune* and *Sabal morrisiana* - were most abundant and had the largest diameters in forests where the soil had high moisture availability but did not flood. These species of arborescent palms are common in the cohune palm forest, less abundant in the broadleaf forests, infrequent in the swamp forest, and do not grow in the bajo forest. However, some tropical forests have high densities of arborescent palms on poorly drained or flooded soils (Kahn and Castro 1985; Kahn and de Granville 1992; Tuomisto and Ruokolainen 1993), while others have an abundance of tall palms along slope crests (Kahn and de Granville 1992; Clark et al. 1995). In addition, other species in the *Orbignya* genus are found in upland forests as well as seasonal swamp forests (Kahn and de Granville 1992). One can only surmise that the influence of soil moisture availability on canopy palm distribution is species specific.

The distribution of lianas among these forest types appears to be related to their vessel size and water use. Lianas have long xylem vessels of large diameter (Ewers *et al.* 1990) and higher specific hydraulic conductivity than similar diameter trees (Gartner *et al.* 1990). Lianas in the palm forest (plot XV1) had 3 to 4 times the mean annual sap flux density of nearby trees, regardless of the season (Billings 1991). Gartner *et al.* (1990) found that lianas with these characteristics occurred on wetter sites and were more active in wetter seasons. Thus it is no surprise that we find more lianas in forest stands where there is ample water supply. Lianas are uncommon in the bajo because of the extremely limited availability of water during the dry season, and liana abundance is relatively low in the dry upland forest because of the lower year round soil moisture. However, lianas are a significant component of the forest community at sites where the soils do not dry out as quickly -- i.e. in the mesic broadleaf, palm, and swamp forests.

Woody lianas require high light conditions to establish and thrive (Walter and Breckle 1985). Consequently, they grow where radiation levels are higher (Chazdon and Fetcher 1984) -- in forest canopies and gaps. The particularly high liana component in the swamp forest is related to the higher percentage of canopy openness (Table 5c), which results from high levels of disturbance and uneven canopy height. Although, the basal area of lianas does not appear to dominate the plot, the leaf area to basal area ratio in lianas is much greater than that of trees (Putz 1983). Thus the relatively small liana basal area could represent a significant portion of the foliar coverage in the swamp.

Understory composition and structure

Understory species composition is associated with overstory species composition. Community similarity indices indicate that many species occur in both the understory and overstory - 26 to 50% of species were found in both strata (Table 5c). Approximately half of the species in each plot were found only in the overstory size class, indicating that they regenerate in canopy gaps. A small proportion of species were found only in the understory size class, indicating that they are mature understory species. However, forests with higher irradiance in the understory -- dry broadleaf forest on the slope and swamp forest -- had a larger proportion of mature understory species.

Understory structure does not appear to be associated with soil properties (Appendix B.4), but is more closely associated with overstory structure (Appendix B.5). This is also demonstrated by the frequency distribution curves, which show proportionately more large sized trees as one progresses to sites with larger overstory biomass. Trends in understory composition and structure across all sites suggest that the forests were mature and relatively undisturbed.

Ground cover composition also appears to be related to the amount of light that penetrates to the understory. Light penetration is determined by the characteristics of the canopy and the vertical structure of the forest. For example, the short stature and low leaf area index of the bajo forest minimize light attenuation; high irradiance on the forest floor are reflected in the ubiquitous nature of ground cover vegetation. The extensive grass cover in the bajo has probably resulted from these high light levels coupled with the drought tolerant nature of some grasses. Many savanna grasses have C_4 pathways; because C_4 plants can effectively utilize CO_2 even at low concentrations, they can optimize photosynthesis in high light environments while reducing water loss through stomatal closure (Larcher 1983). In addition, graminoid plants have a competitive advantage over herbaceous dicots where light penetration is high and arid conditions prevail (Schulze

1981). By comparison, the swamp forest has an uneven canopy and higher leaf area, which results in lower light levels on the forest floor. Coupled with the lack of severe drought, these lower light levels result in proportionately more herbaceous and woody plants than grasses.

Compared to the flooded forests, the upland forests have a higher leaf area index and very different vertical structure. The result is lower total ground cover and different ground cover composition in the upland forests. However, within the upland forests, communities have similar vertical structure and height, resulting in similar total ground cover and composition (only woody cover differed). The greater ground cover in the dry upland forest was not due to vertical structure (which was similar to other plots) but may result from the south facing slope, an aspect which allows for greater light penetration to the forest floor for a large part of the year.

Understory light levels may also play a role in the distribution of understory palm species. Unlike the overstory palms, the understory palm *Cryosophila argentea* was not limited in distribution to wetter sites. This species occurred in the understory of all plots, indicating its adaptation to the lower light levels in the understory. Survival in low light environments is a necessary adaptation of understory palms (Chazdon 1985; Chazdon 1986).

CONCLUSION

The results of this study support my hypothesis that the heterogeneous distribution of vegetation in northwestern Belize is related to variability in edaphic conditions. Species composition, forest physiognomy, and canopy foliage chemistry are all associated with edaphic conditions, particularly gradients in soil moisture. Moreover, these results illustrate the relationship between geomorphology, soil formation, and the development of forest vegetation.

The geomorphology of a landscape can influence soil characteristics (Gerrard 1981; Swanson *et al.* 1988). Differences in soil characteristics may be due to: variation in parent materials associated with topographic features; or variation in topographic features that influence soil-formation processes (Jeffery 1987). The latter is the factor most influencing soil development in northwestern Belize; all soils in the region have developed over a base material of fractured calcareous limestone (King *et al.* 1992; Wright *et al.* 1959). The resulting variation in soil properties appears to influence the distribution of species and forest physiognomy, to produce a mosaic of forest types across the landscape.

However, the influence of soil properties on vegetation is not unidirectional. Vegetation, especially trees, affects the development and properties of forest soils (Binkley 1994; Perry 1994; Silver 1994). A case in point, Furley (1975) concluded that the leaf litter of cohune palms (*Orbignya cohune*) promotes the development of moist organic soil conditions which are ideal for the growth of this species. Thus biotic and abiotic components of forests ecosystems develop in concert.

I conclude that the development of forest ecosystems of this region are neither strongly directional (such as primary succession along a floodplain forest illustrated by Terborgh *et al.* 1996), nor due primarily to random processes (as proposed by the non-equilibrium hypothesis of Hubbel *et al.* 1979), but develop -- with some variability -- along a topographic gradient which influences soil formation and consequently, development of forest vegetation.

Table 1 - Subplot dimensions

Plot ID	Subplot ID	Subplot	
		Understory	Overstory
PC1,PC2,XV1,XV2,XV3	A	26 m x 26m (= 676 m^2)	40 m x 40 m (= 1600 m^2)
	B-I	10 m radius (= 314 m^2)	15 m radius (= 707 m^2)
SW	A	19 m x 19 m (= 361 m^2)	28 m x 28 m (= 784 m^2)
	B-G	10 m radius (= 314 m^2)	15 m radius (= 707 m^2)
BA	A	19 m x 19 m (= 361 m^2)	28 m x 28 m (= 784 m^2)
	B-I	7 m radius (= 154 m^2).	10.5 m radius (= 346 m^2)

Table 2 - Foliar nutrient and carbohydrate analyses

Analysis	Units	Technique
C, N	%	Carlo-Erba C/N/S analyzer on dry material (Carlo-Erba 1986)
P, K, Ca, Mg	%	Dried, ashed, acidified with HF, analyzed with Perkin-Elmer ICP (Wallace and Barret 1981)
hexose, sucrose, starch	%	enzymatic conversion of carbohydrates to glucose units, indirect measurement by assay conversion of NADP to NADPH (Schoenberger 1989)

Table 3 - Soil analyses

Analysis	Parameter	Units	Technique
Soil Chemistry	total C, total N	%	Carlo-Erba C/N/S analyzer on dry soil (Carlo-Erba 1986)
	mineralizable N	% of total N	anaerobic incubation, 7 days at 40°C (Keeney & Bremner 1966)
	total P, K, Ca, Mg	%	Perkin-Elmer ICP (Wallace and Barrett 1981)
	extractable P	%	extractable PO_4-P at pH 8.5 (Watanabe and Olsen 1965)
	pH (laboratory)		pH meter: KCl, H_2O (Soil Conservation Service 1992)
	pH (field)		colorimetric soil reaction (Hellige-Truog kit; OREBCO)
Soil Physics	bulk density[1]	g/cm^3	core sampler (Soil Conservation Service 1992)
	texture[2]	%	particle size analysis with hydrometer (Soil Conservation Service 1992)
Soil Hydrology	saturated hydraulic conductivity (K_{sat})	cm/hr	constant-head well permeameter (Amoozegar 1989)

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[1] Analyzed for pit bulk samples only.

[2] Analyzed for both pit bulk samples and surface core samples.

Table 4 - Summary of ANOVA and contrast analyses (p-values $\leq$ 0.1)

CONTRASTS	SOIL	FOLIAR	TREES & PALMS Overstory	TREES Overstory	PALMS Overstory	LIANAS	GROUND COVER
Upland vs. Flooded	<0.001 Ca <0.001 K <0.001 pH 0.006 Mg 0.015 extract-P 0.005 sand 0.052 clay	* <0.001 Ca <0.001 C <0.001 N 0.009 C:N * <0.001 P 0.006 specific leaf area	<0.001 density <0.001 total basal area <0.001 mean basal area <0.001 height to base <0.001 height to top <0.001 total biomass <0.001 mean stem biomass	<0.001 density <0.001 total basal area <0.001 mean basal area <0.001 height to base <0.001 height to top	<0.001 density <0.001 total basal area 0.002 height to base 0.001 height to top		<0.001 total cover <0.001 woody <0.001 palms 0.089 herbaceous
Between Flooded Communities (Swamp & Bajo)	<0.001 Ca <0.001 Mg <0.001 mineral-N <0.001 pH (lab) 0.004 extract-P 0.016 N 0.013 sand	* <0.001 Ca * 0.016 Mg <0.001 C 0.003 C:N	0.030 height to top	<0.001 height to top		0.020 density 0.098 total basal area	0.006 woody 0.009 lianas <0.001 herbaceous <0.001 grass
Between Upland Communities (Broadleaf & Palm)	0.001 pH (lab) 0.002 C 0.003 K 0.086 N 0.053 Mg <0.001 sand 0.002 clay	<0.001 P * 0.012 C * 0.018 K * <0.001 N * <0.001 Mg 0.033 C:N <0.001 tot soluble <0.001 tot nonstructural 0.001 starch 0.007 sucrose 0.002 hexose 0.040 specific leaf area	0.011 density <0.001 mean basal area 0.024 total basal area <0.001 height to base <0.001 mean stem biomass	<0.001 density <0.001 mean basal area <0.001 height to base	<0.001 density <0.001 mean basal area <0.001 total basal area 0.006 height to top	0.093 density	0.044 woody
Slope vs. Level (Dry & Mesic)	0.003 Mg <0.001 Ca <0.001 C <0.001 K <0.001 N <0.001 mineral-N <0.001 extract-P <0.001 pH <0.001 clay <0.001 sand 0.009 silt	* <0.001 Mg * 0.001 Ca * 0.027 C 0.082 C:N	<0.001 height to base 0.008 density	<0.001 height to base 0.010 density	0.040 height to base	0.007 density <0.001 total basal area 0.060 mean basal area	0.017 total cover 0.063 herbaceous

Model / plot effect of each one-way ANOVA was significant (p<0.05) for all measurements except: soil P (p=0.082) and % lianas in ground cover (p=0.158).
Type effect of foliar chemistry ANOVA was significant (p<0.05) for foliar C, N, C:N, P, Ca, Mg, specific leaf area, and sucrose.
Date effect of foliar chemistry ANOVA was significant (p<0.05) for foliar C, N, C:N, P, K, Ca, and specific leaf area.
Foliar carbohydrates were only measured in upland communities.
Biomass was only calculated for combined broadleaf and palm trees.
No overstory palms occurred in the bajo forests.
* = Significant contrast for nutrient in both soil and foliage.

Table 5a - Summary of Vegetation Structure (means and std)

		units	PC1	PC2	XV1	XV2	XV3	SW	BA
Ground Cover									
	grass	%	0.00	0.00	0.00	0.00	0.00	6.43	31.89
		(std)	0.00	0.00	0.00	0.00	0.00	9.45	30.40
	herbaceous	%	11.00	3.50	4.11	5.86	4.75	17.14	1.72
		(std)	4.15	1.87	3.02	6.59	3.49	16.04	1.80
	lianas	%	11.08	3.25	7.39	6.64	3.44	15.43	0.39
		(std)	21.60	3.57	9.91	10.39	6.89	13.95	0.70
	woody	%	30.00	21.00	11.89	16.14	3.81	28.14	57.00
		(std)	9.35	9.51	11.94	26.30	2.45	11.94	35.33
	palms	%	20.60	13.17	29.11	25.14	20.25	8.71	0.56
		(std)	27.90	10.61	20.67	11.23	11.61	10.56	1.67
	total	%	74.10	40.92	52.50	53.79	32.25	75.86	91.56
		(std)	20.54	11.50	17.87	21.79	15.57	17.72	35.38
Lianas									
	density	lianas/ha	199.76	563.67	114.74	309.81	297.92	948.28	104.24
		(std)	129.96	433.36	103.58	207.40	222.62	360.67	160.71
	basal area	m^2/ha	0.38	1.41	0.32	0.78	0.60	1.43	0.14
		(std)	0.29	1.09	0.27	0.81	0.49	0.26	0.24
	mean basal area	cm^2	23.33	41.77	44.34	42.84	35.28	18.44	13.71
		(std)	20.06	48.18	30.38	83.54	54.30	22.62	5.84
	quadratic mean dbh	cm	5.45	7.29	7.51	7.39	6.70	4.85	4.18
Palms									
overstory									
	density	palms/ha	17.53	15.58	111.63	76.35	85.59	15.92	0.00
		(std)	15.90	17.42	44.63	69.06	51.96	17.22	0.00
	basal area	m^2/ha	0.53	0.44	10.17	9.15	7.45	0.66	--
		(std)	0.54	0.63	4.61	7.67	4.43	0.66	--
	mean basal area	cm^2	301.91	256.97	876.61	1227.28	811.73	414.39	--
		(std)	187.57	117.76	522.48	739.13	615.56	169.85	--
	quadratic mean dbh	cm	19.61	18.09	33.41	39.53	32.15	22.97	--
	mean height to base	m	12.32	7.58	10.60	11.85	9.85	4.11	--
		(std)	6.40	2.45	5.38	4.89	4.13	1.55	--
	mean height to top	m	15.63	9.17	23.02	19.09	15.34	6.71	--
		(std)	10.31	3.13	5.47	8.21	5.43	1.38	--
understory									
	density	palms/ha	507.57	636.69	109.79	191.41	69.59	436.53	31.39
		(std)	146.70	219.27	92.88	113.35	64.43	332.45	108.23
	basal area	m^2/ha	1.72	2.39	0.39	0.69	0.22	1.42	0.08
		(std)	0.61	1.05	0.35	0.41	0.17	1.11	0.29
	mean basal area	cm^2	33.03	36.66	35.96	34.99	32.30	32.57	26.50
		(std)	12.62	13.74	13.45	14.41	17.32	13.78	8.01
	quadratic mean dbh	cm	6.48	6.83	6.77	6.67	6.41	6.44	5.81
	mean height to base	m	4.37	4.50	4.38	4.50	3.73	3.17	3.10
		(std)	2.69	2.34	1.77	2.43	1.68	1.25	0.89
	mean height to top	m	5.65	5.68	3.00	5.06	4.57	4.14	--
		(std)	3.13	2.66	1.15	1.86	1.92	1.40	--
palm fronds									
	density	plants/ha	75.72	89.09	664.79	480.28	577.39	93.50	0.00
	cross section area	m^2/ha	0.04	0.27	3.95	2.64	3.62	0.96	0.00
	mean cross section	cm^2/plant	5.68	30.14	68.76	55.02	54.42	41.86	--

Table 5b - **Summary of Vegetation Structure** (means and std)

	units	PC1	PC2	XV1	XV2	XV3	SW	BA
Broadleaf Trees								
overstory								
density	trees/ha	**519.96**	**377.80**	**254.96**	**287.57**	**326.77**	**519.30**	**588.40**
	(std)	71.74	71.86	75.06	98.47	110.87	103.00	177.32
basal area	m^2/ha	**27.11**	**26.65**	**25.08**	**25.84**	**24.55**	**15.56**	**14.02**
	(std)	7.32	9.93	10.19	6.63	10.68	2.9	3.96
mean basal area	cm^2	**523.01**	**642.81**	**1015.05**	**1026.21**	**772.36**	**299.72**	**238.01**
	(std)	710.58	1027.77	1892.60	2035.96	1384.7	318.78	268.68
quadratic mean dbh	cm	**25.81**	**28.61**	**35.95**	**36.15**	**31.36**	**19.53**	--
mean height to base	m	**14.27**	**11.82**	**11.84**	**10.39**	**11.91**	**6.66**	**6.29**
	(std)	4.39	4.26	5.02	3.60	4.01	1.98	1.95
mean height to top	m	**24.73**	**26.18**	**26.29**	**23.81**	**25.01**	**15.21**	**11.03**
	(std)	2.89	3.28	5.40	3.37	4.98	2.86	2.81
understory								
density	trees/ha	**1157.61**	**841.50**	**334.03**	**335.94**	**361.86**	**1051.22**	**4369.11**
	(std)	543.57	267.08	276.14	184.71	166.97	474.16	1037.99
basal area	m^2/ha	**2.92**	**2.30**	**1.04**	**0.78**	**1.01**	**2.93**	**9.51**
	(std)	1.36	1.22	0.83	0.37	0.38	1.45	2.58
mean basal area	cm^2	**25.23**	**27.40**	**31.63**	**22.97**	**29.01**	**27.88**	**21.44**
	(std)	18.15	19.00	19.38	17.73	17.26	18.19	15.80
quadratic mean dbh	cm	**5.67**	**5.91**	**6.35**	**5.41**	**6.08**	**5.96**	**5.23**
mean height to base	m	**5.59**	**5.35**	**4.84**	**4.37**	**6.04**	**3.83**	**4.36**
	(std)	3.05	2.47	1.93	2.01	2.91	1.24	1.79
mean height to top	m	**9.46**	**14.13**	--	**5.00**	--	**6.35**	**7.28**
	(std)	5.66	6.99	--	--	--	3.08	2.85
Broadleaf and Palm Trees								
overstory								
density	stems/ha	**537.49**	**393.38**	**366.59**	**373.16**	**403.11**	**535.22**	**588.40**
	(std)	68.14	81.66	96.63	84.45	70.20	108.77	177.32
basal area	m^2/ha	**27.63**	**27.09**	**35.25**	**36.10**	**31.20**	**16.22**	**14.02**
	(std)	7.48	10.00	12.21	9.60	10.18	3.25	3.96
biomass	Mg/ha	**200.37**	**257.45**	**285.18**	**289.83**	**244.33**	**81.89**	**62.68**
	(std)	60.98	118.27	103.83	91.97	95.49	16.43	19.09
mean basal area	cm^2	**517.24**	**626.05**	**970.94**	**1071.00**	**779.63**	**303.11**	**238.01**
	(std)	700.69	1010.77	1603.31	1824.65	1275.07	315.76	268.68
quadratic mean dbh	cm	**25.66**	**28.23**	**35.16**	**36.93**	**31.51**	**19.65**	--
mean stem biomass	kg	**374.40**	**535.35**	**783.30**	**869.26**	**606.89**	**151.89**	**106.31**
	(std)	623.59	924.04	1546.15	1805.11	1212.88	201.69	132.04
mean height to base	m	**14.22**	**11.63**	**11.45**	**10.72**	**11.53**	**6.58**	**6.29**
	(std)	4.47	4.27	5.14	3.95	4.08	2.01	1.95
mean height to top	m	**23.78**	**23.68**	**25.32**	**21.22**	**20.82**	**13.81**	**11.03**
	(std)	10.31	3.13	5.47	8.21	5.43	1.38	--
understory								
density	#/ha	**1665.18**	**1478.18**	**410.92**	**527.34**	**431.45**	**1487.75**	**4369.11**
	(std)	575.67	387.31	346.20	257.34	180.82	522.91	1037.99
basal area	m^2/ha	**4.64**	**4.69**	**1.34**	**1.47**	**1.23**	**4.34**	**9.51**
	(std)	1.53	1.63	1.09	0.64	0.40	1.41	2.58
biomass	Mg/ha	**13.02**	**14.74**	**4.26**	**4.51**	**3.81**	**10.58**	**29.76**
	(std)	2.99	5.49	3.52	1.88	1.25	3.37	8.31
mean basal area	cm^2	**27.77**	**31.46**	**32.85**	**27.39**	**29.55**	**29.25**	**21.44**
	(std)	17.11	17.66	18.03	17.67	17.27	17.11	15.80
quadratic mean dbh	cm	**5.95**	**6.33**	**6.47**	**5.91**	**6.13**	**6.10**	**5.23**
mean stem biomass	kg	**8.55**	**9.83**	**10.46**	**8.38**	**9.18**	**7.10**	**6.70**
	(std)	6.79	7.12	7.46	7.03	6.84	5.41	6.11
mean height to base	m	**5.19**	**4.98**	**4.72**	**4.42**	**5.65**	**3.64**	**4.36**
	(std)	2.99	2.43	1.90	2.16	2.87	1.28	1.79
mean height to top	m	**5.74**	**6.91**	**3.00**	**5.06**	**4.57**	**4.39**	**7.28**
	(std)	3.13	2.66	1.15	1.86	1.92	1.40	--

Table 5c - Summary of Vegetation Structure

	units	PC1	PC2	XV1	XV2	XV3	SW	BA
Plot Size								
plot dimension		200x120	200x120	200x200	180x160	180x200	150x150	150x150
number of subplots		6	6	9	7	8	7	9
total area of all subplots								
overstory	hectares	0.5134	0.5134	0.7255	0.5841	0.6548	0.5025	0.3555
understory	hectares	0.2245	0.2245	0.3189	0.2561	0.2875	0.2246	0.1592
Number of trees (broadleaf and palm)								
overstory	stems/plot	277	204	267	219	265	271	209
understory	stems/plot	338	333	130	135	125	334	696
Number of species (overstory and understory)								
	species/plot	48	56	50	53	61	68	--
	species/0.5ha	47	55	43	49	51	64	--
Similarity between species composition of overstory and understory								
percent similarity		44.7	39.3	34.7	26.4	42.6	50.0	--
number of unique overstory species		14	26	23	27	26	12	--
number of unique understory species		12	8	9	12	9	22	--
Species dominance (overstory)								
1/2 plot density	no. species	3	6	4	4	7	6	--
1/2 plot basal area	no. species	2	4	4	3	5	6	--
Leaf Area Index								
leaf area index		7.5	7.3	6.0	7.5	6.2	6.2	4.1
	(std)	0.2	0.2	0.2	0.2	0.3	0.2	0.1
proportion open sky	%	1	1	2	1	2	4	6

Table 6 - Abundance and Dominance of Species (species $\geq$ 5% of plot total)

	PC1			PC2			XV1			XV2			XV3			SW		
	Species	value	%	Species	value	%	Species	value	%	Species	value	%	Species	value	%	Species	value	%
Density (plants/ha)																		
overstory																		
	DRBR E	159.71	29.5	DRBR E	56.48	13.9	ORCO P	84.08	22.8	ORCO P	73.62	19.7	ORCO P	48.87	12.1	MANO E	79.10	14.2
	BRAL M	64.27	11.9	CESC U	40.90	10.1	GUEX M	38.59	10.4	GUEX M	68.48	18.3	DEAR AR	36.65	9.1	SISA R	55.13	9.9
	PORE SA	64.27	11.9	BRAL M	37.01	9.1	SPMO AA	35.84	9.7	SPMO AA	41.09	11.0	SPMO AA	36.65	9.1	COBE PO	45.00	8.1
	PS MO	31.16	5.8	PS MO	25.32	6.2	SAMO P	27.57	7.5	TRMI ME	18.83	5.0	CUBE S	29.02	7.2	Unknown spp	36.02	6.5
	ASCR AP	29.22	5.4	PODU SA	21.42	5.3	STDS AP	22.05	6.0				SAMO P	25.96	6.4	SWMA ME	34.59	6.2
				ASCR AP	21.42	5.3										VALU F	29.24	5.3
understory																		
	CRAR P	502.94	33.5	CRAR P	596.40	40.7	CRAR P	103.47	25.4	CRAR P	187.43	35.0	RI V	69.56	16.0	CRAR P	384.01	26.0
	PORE SA	195.83	13.1	RI V	186.93	12.8	GUEX M	56.44	13.8	RI V	62.48	11.7	CRAR P	55.65	12.8	MANO E	170.82	11.6
	PIPS PI	129.07	8.6	FAOC R	173.58	11.9	RI V	53.30	13.1	TRMI ME	50.76	9.5	Unknown spp	41.74	9.6	RI V	82.42	5.6
	TRPA ME	102.37	6.8	PORE SA	89.02	6.1	PIGI MI	31.36	7.7	GUEX M	42.95	8.0	PIGI MI	34.78	8.0	COBE PO	81.43	5.5
	RI V	102.37	6.8							PIPS PI	39.05	7.3						
										PORE SA	27.33	5.1						
palm fronds																		
							ORCO P	548.8		ORCO P	413.9		ORCO P	528.70		SAMO P	89.0	
							SAMO P	109.8		SAMO P	66.38		SAMO P	48.70				
Basal Area (m2/ha)																		
overstory																		
	DRBR E	8.63	31.2	CESC U	6.49	19.8	ORCO P	9.28	26.3	ORCO P	10.02	27.7	ORCO P	6.04	19.3	VALU F	2.19	13.2
	BRAL M	6.07	21.9	BRAL M	5.42	16.6	SPMO AA	3.85	10.9	FIGL MO	5.65	15.6	FI MO	3.10	9.9	SPMO AA	1.63	9.8
	PORE SA	1.79	6.5	VALU F	3.44	10.5	POCA SA	3.01	8.5	SPMO AA	4.96	13.7	SPMO AA	2.87	9.1	SWMA ME	1.60	9.6
	POAM SA	1.67	6.0	DRBR E	2.57	7.8	FIGL MO	2.99	8.5	GUEX M	3.15	8.7	FIGL MO	2.86	9.1	COBE PO	1.37	8.2
							FI MO	2.00	5.7	PIAR MI	1.91	5.3	DEAR AR	2.49	7.9	MANO E	1.20	7.2
							GUEX M	1.84	5.2				LOCA F	1.80	5.7	PTHA	0.96	5.8
													CEME ME	1.62	5.2	LOCA F	0.95	5.7
																Unknown spp	0.89	5.3
understory																		
	CRAR P	1.69	40.2	CRAR P	2.26	49.3	CRAR P	0.37	28.2	CRAR P	0.68	46.5	CRAR P	0.21	17.3	CRAR P	1.33	31.2
	PORE SA	0.55	13.0	RI V	0.47	10.3	GUEX M	0.16	11.8	TRMI ME	0.17	11.4	RI V	0.15	12.0	MANO E	0.53	12.3
	TRPA ME	0.25	6.0	FAOC R	0.43	9.4	PIGI MI	0.12	9.2	GUEX M	0.13	9.1	Unknown spp	0.12	9.8	COBE PO	0.22	5.1
	BRAL M	0.21	5.1				RI V	0.10	7.8	RI V	0.09	6.3	TRMI ME	0.07	5.8			
							TRPA ME	0.07	5.7				GUEX ME	0.07	5.5			
							PORE SA	0.07	5.5				ACCO MI	0.07	5.4			
							ASCR AP	0.07	5.5				PIGI MI	0.06	5.1			
palm fronds																		
							ORCO P	3.07		ORCO P	2.32		ORCO P	3.55		SAMO P	0.96	
							SAMO P	0.53		SAMO P	0.32		SAMO P	0.39				

Table 7 - Foliar chemistry of groups of species

Nitrogen fixation vs. other broadleaf species

		N-fixers	Others	p-value
Swamp				
		(n=5)	(n=26)	
N	%	2.8	2.1	0.003
C:N		17.2	24.4	0.005

Palm trees vs. broadleaf species

		Palms (n=30)	Others (n=109)	type effect p-value	date effect p-value	plot effect p-value	type*date interaction p-value
Palm Forest							
C:N		18.0	27.9	0.001	0.001	0.009	---
N	%	1.71	2.73	0.001	0.004	---	---
P	%	0.11	0.15	0.004	---	---	---
K	%	5.43	9.44	0.006	---	---	0.022
Ca	%	0.47	2.34	0.001	0.001	0.015	---
Mg	%	0.17	0.26	0.003	---	0.001	---

--- = not significant $p > 0.1$

Table 8 - Summary of Foliar and Soil Measurements (means and std)

	units	PC1	PC2	XV1	XV2	XV3	SW	BA
Canopy Foliage								
C	%	**42.8**	**39.4**	**46.6**	**45.5**	**45.2**	**48.9**	**47.7**
	(std)	4.3	5.0	3.4	3.2	3.3	2.2	2.4
N	%	**2.09**	**2.00**	**2.13**	**2.16**	**2.15**	**2.16**	**1.41**
	(std)	0.48	0.39	0.72	0.60	0.54	0.55	0.33
C:N		**21.2**	**20.0**	**24.1**	**22.5**	**22.0**	**24.1**	**35.8**
	(std)	6.3	4.2	6.1	5.0	5.2	5.5	9.1
P	%	**0.082**	**0.088**	**0.121**	**0.121**	**0.117**	**0.094**	**0.056**
	(std)	0.026	0.027	0.057	0.039	0.046	0.027	0.016
K	%	**8.21**	**9.48**	**5.67**	**7.19**	**5.67**	**5.64**	**7.21**
	(std)	4.03	3.80	3.84	4.02	3.36	2.40	4.04
Ca	%	**3.55**	**5.16**	**1.16**	**1.84**	**2.31**	**1.70**	**2.08**
	(std)	2.03	2.43	1.25	2.00	1.32	0.91	1.29
Mg	%	**0.60**	**0.45**	**0.19**	**0.21**	**0.29**	**0.26**	**0.28**
	(std)	0.29	0.19	0.15	0.20	0.19	0.09	0.10
specific leaf area	cm^2/g	**127.4**	**120.9**	**147.3**	**172.0**	**163.9**	**150.3**	**107.2**
	(std)	47.3	30.6	51.3	55.0	40.9	62.0	25.5
hexose	%	--	**1.34**	**2.09**	**1.90**	**2.89**	--	--
	(std)	--	0.47	1.43	0.99	2.36	--	--
sucrose	%	--	**2.29**	**4.02**	**2.57**	**3.88**	--	--
	(std)	--	0.81	1.80	1.76	2.40	--	--
total soluble carbon.	%	--	**3.63**	**6.11**	**4.47**	**6.77**	--	--
	(std)	--	1.15	2.75	2.14	4.53	--	--
starch	%	--	**0.88**	**1.43**	**1.07**	**1.41**	--	--
	(std)	--	0.38	1.20	0.68	0.72	--	--
total nonstructural	%	--	**4.51**	**7.54**	**5.54**	**8.18**	--	--
	(std)	--	1.21	3.61	2.38	5.17	--	--
Soil Surface (0-10cm)								
total C	%	**15.38**	**7.20**	**8.05**	**7.61**	**9.02**	**5.25**	**7.37**
	(std)	2.58	2.62	3.66	1.47	2.24	2.19	1.77
total N	%	**0.88**	**0.65**	**0.54**	**0.51**	**0.46**	**0.44**	**0.44**
	(std)	0.31	0.19	0.19	0.11	0.11	0.18	0.08
mineralizable-N	% of total N	**7.04**	**7.08**	**6.25**	**6.32**	**6.05**	**3.89**	**3.33**
	(std)	1.56	1.32	1.88	1.33	1.45	1.57	0.91
total P	ppm	**20.81**	**10.27**	**19.48**	**20.86**	**13.86**	**11.86**	**16.37**
	(std)	10.11	5.88	8.07	9.43	7.00	6.61	2.86
exchangeable-P	ppm	**9.95**	**6.03**	**6.42**	**6.73**	**6.45**	**5.04**	**2.55**
	(std)	3.71	2.45	2.80	1.52	2.03	3.28	0.93
total K	%	**0.011**	**0.013**	**0.029**	**0.038**	**0.026**	**0.013**	**0.014**
	(std)	0.004	0.002	0.008	0.004	0.005	0.004	0.004
total Ca	%	**2.07**	**1.40**	**1.92**	**1.95**	**1.95**	**0.95**	**0.95**
	(std)	0.06	0.57	0.24	0.10	0.10	0.08	0.19
total Mg	%	**0.086**	**0.079**	**0.045**	**0.061**	**0.069**	**0.169**	**0.165**
	(std)	0.026	0.032	0.022	0.015	0.037	0.011	0.034
pH field		**7.8**	**5.8**	**7.5**	**7.3**	**7.0**	--	**6.0**
	(std)	0.3	0.3	0.4	0.4	0.5	--	0.4
pH lab		**7.4**	**7.1**	**7.5**	**7.6**	**7.7**	**6.3**	**6.4**
	(std)	0.1	0.3	0.2	0.2	0.1	0.2	0.1
clay	%	**34.87**	**70.70**	**59.19**	**66.54**	**55.73**	**88.27**	**75.00**
	(std)	8.70	7.92	19.28	13.81	18.44	2.38	4.17
silt	%	**34.37**	**18.36**	**28.10**	**22.56**	**34.78**	**10.58**	**20.53**
	(std)	9.22	3.60	14.47	11.37	15.28	2.23	3.64
sand	%	**30.77**	**10.94**	**12.71**	**10.60**	**9.49**	**1.15**	**4.47**
	(std)	7.83	5.69	7.00	4.23	3.82	0.29	1.21
bulk density	g/cm^3	**1.23**	**1.05**	**1.02**	**1.07**	**1.08**	**0.81**	**0.94**
Ksat-wet	cm/hr	**44.49**	**0.18**	**3.06**	**4.75**	**1.77**	--	--
Ksat-dry	cm/hr	**66.57**	**17.31**	**18.54**	**10.29**	**77.71**	**19.81**	--
change Ksat	cm/hr	**22.08**	**17.13**	**15.48**	**5.54**	**75.94**	--	--

Table 9 - Correlation between soil characteristics and DCA axes

Parameter	Correlation with Axis 1 (r > 0.7)
mineralizable N	-0.98
pH (field)	-0.87
S1 (chemistry) principal component vector	-0.86
total nitrogen	-0.81
extractable P	-0.77
total calcium	-0.75
total magnesium	0.74
total carbon	-0.74
bulk density	-0.92
sand	-0.84
T1 (texture) principal component vector	-0.82
clay	0.81

Table 10 - Correlation between foliar characteristics and DCA axes.

Parameter	Correlation with Axis 1 (r > 0.7)
F2 (N&P) principal component vector	-0.86
% C	0.85
% K	-0.77
leaf area index	-0.71

Table 11 - Classification of soil profiles

Forest Community	**Plot**	**Slope (degrees)**	**Soil Order**	**Soil Suborder**
Upland Broadleaf	PC2	0	Mollisol	Aquoll
	PC1	20	Mollisol	Rendoll
Cohune Palm	XV1	<5	Mollisol	Rendoll
	XV2	<5	Vertisol	Udert
	XV3	<5	Vertisol	Udert
Bajo	BA	0	Vertisol	Aquert
Swamp	SW	0	Mollisol	Aquoll

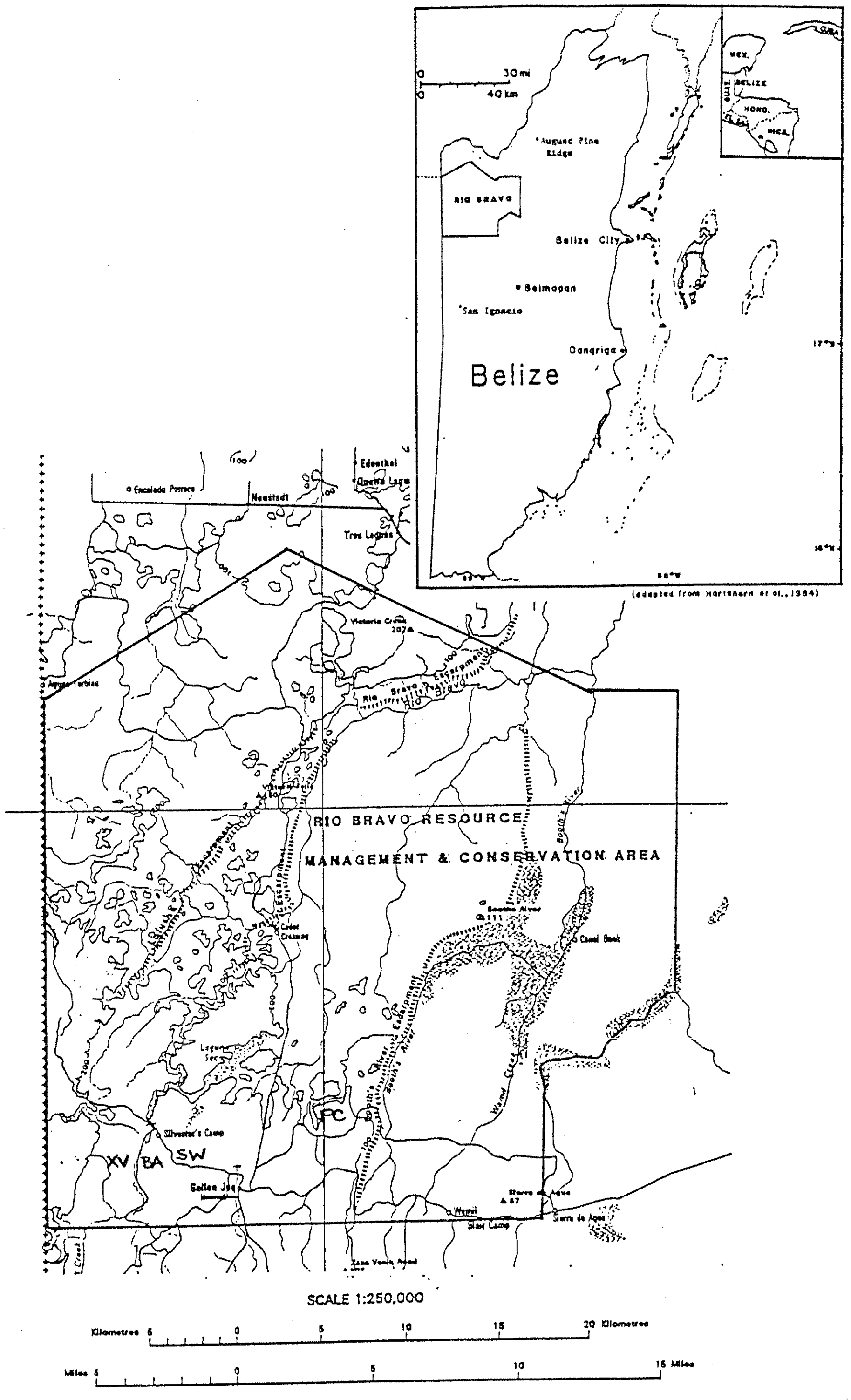


Figure 1 - Location of study sites in Belize, Central America
(adapted from Brokaw and Mallory 1993, based on map by Edward Stanford, Ltd.)
PC1, PC2 = upland broadleaf forest; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

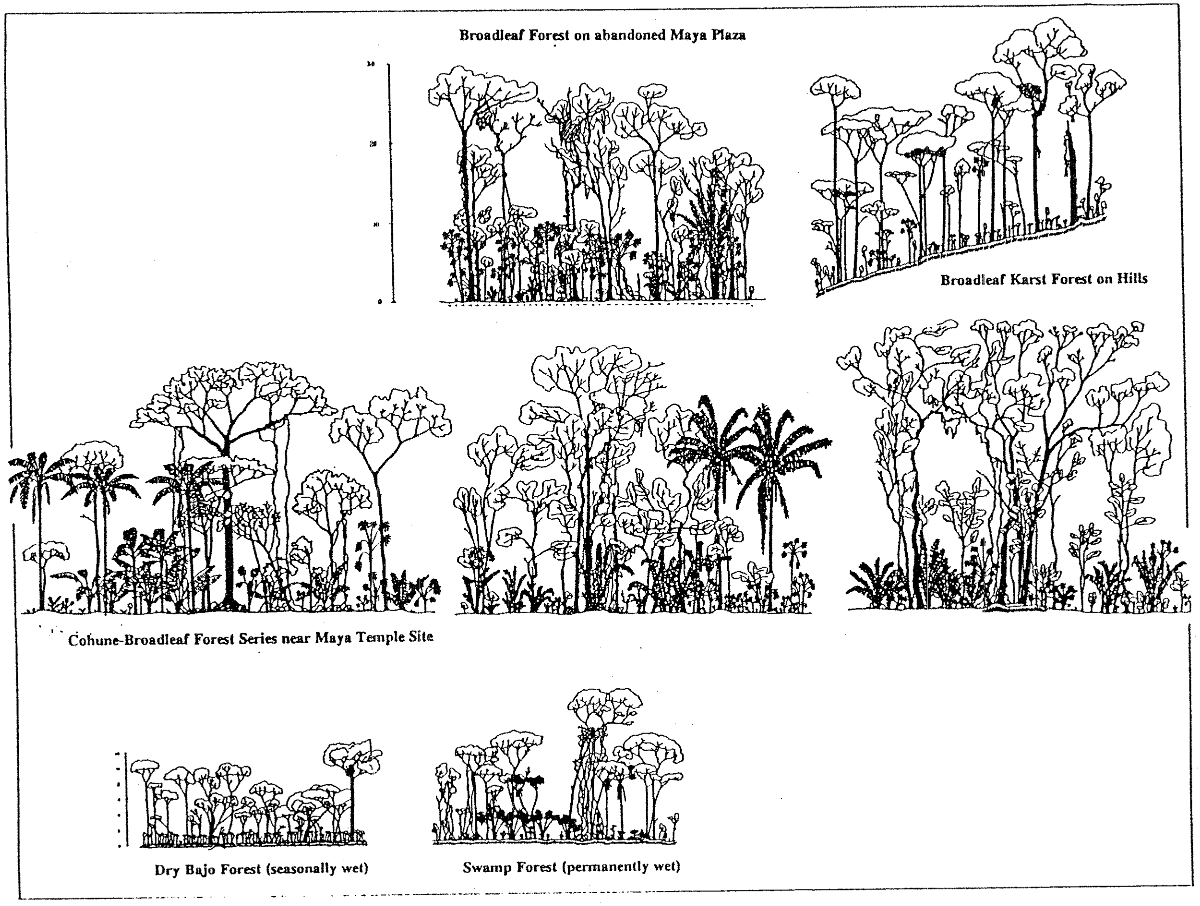
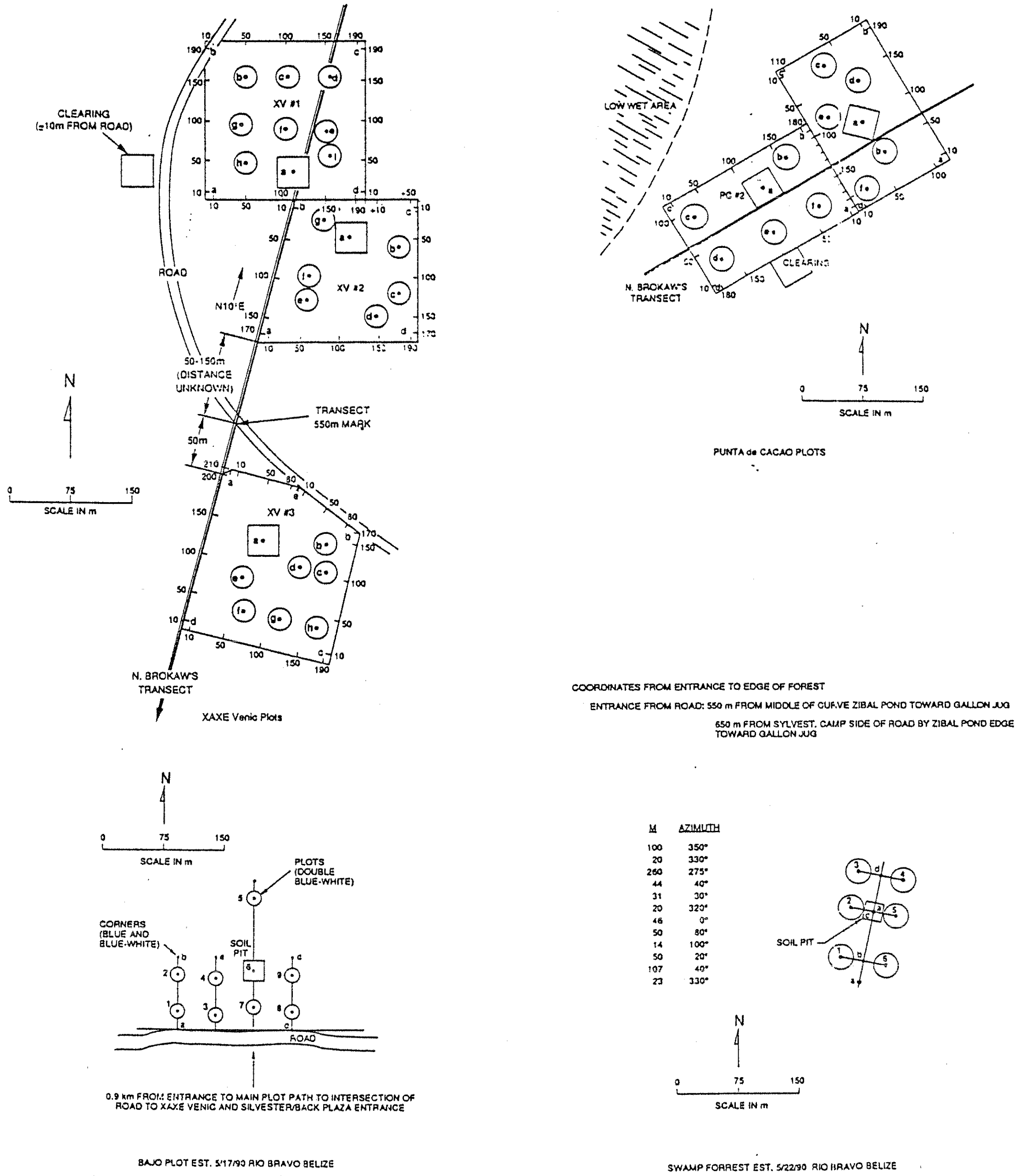


Figure 2 - Cross sectional view of forest communities.
Transect through A subplot of each sample plot. (drawings by P.Strohmeir and R. Zimmermann)

broadleaf forest on abandoned Maya Plaza = PC2
broadleaf karst forest on hills = PC1
cohune-broadleaf forest series = XV1, XV2, XV3
dry bajo forest = BA
swamp forest = SW



\+ = location of surface soil sample

Figure 3 - Arrangement of vegetation subplots and soil surface cores within sample plots (maps drawn by Michele Schoenberger)

Xaxe Venic plots (XV1, XV2, XV3) = cohune palm forest
Punta de Cacao plots (PC1, PC2) = upland broadleaf forest
Bajo plot (BA) = bajo forest
Swamp plot (SW) = swamp forest

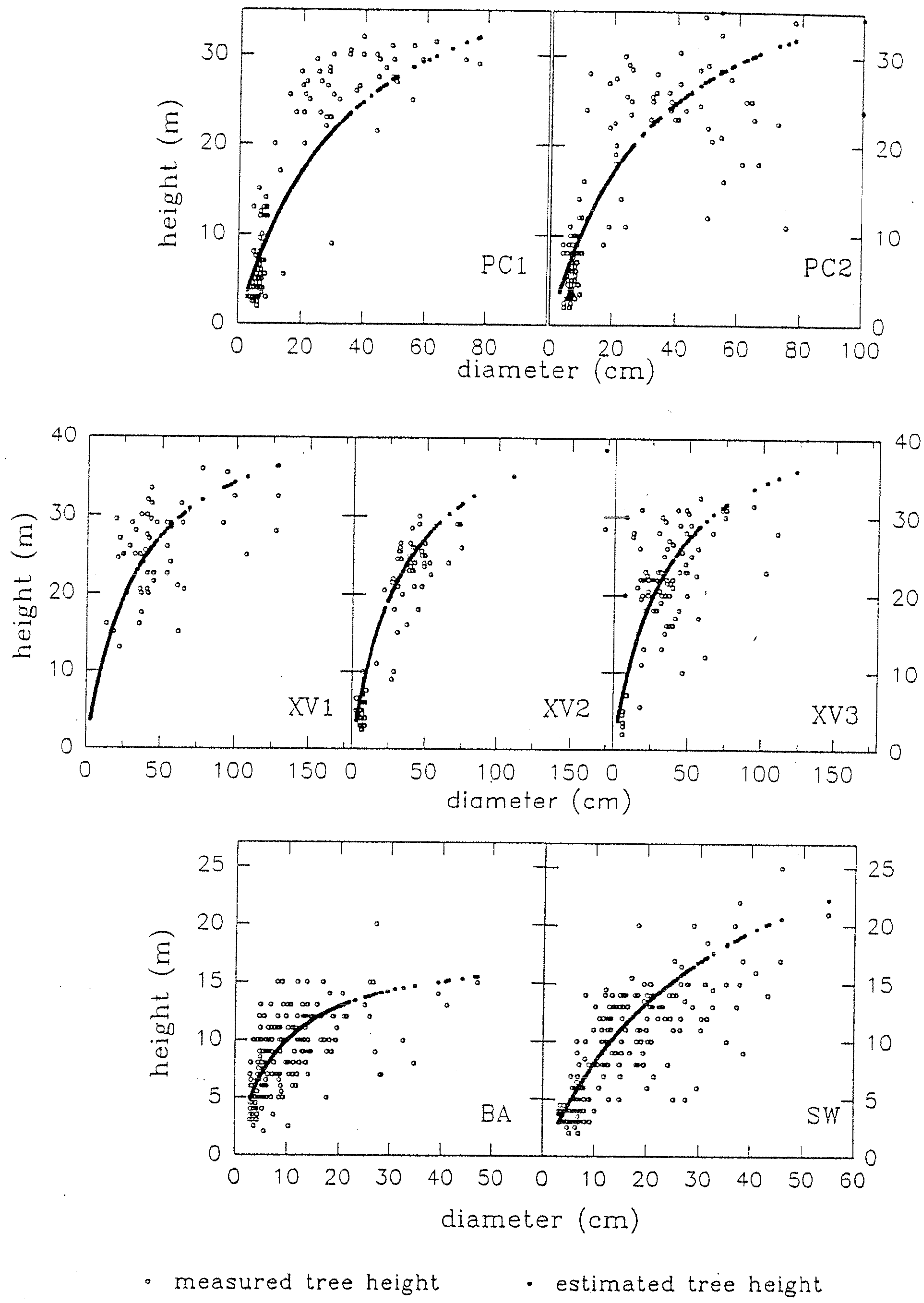


Figure 4 - Height estimated from stem diameter (dbh)
Equation from Ogawa (1965), chosen or modified to match height of forest canopy trees.

PC1, PC2, XV1, XV2, XV3: $1/H = 0.944/DBH + 0.0278$
SW: $1/H = 0.739/DBH + 0.0217$
BA (modified): $1/H = 0.450/DBH + 0.0550$

H= height (m); DBH= diameter at breast height (cm)
PC1, PC2 = upland broadleaf forest; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

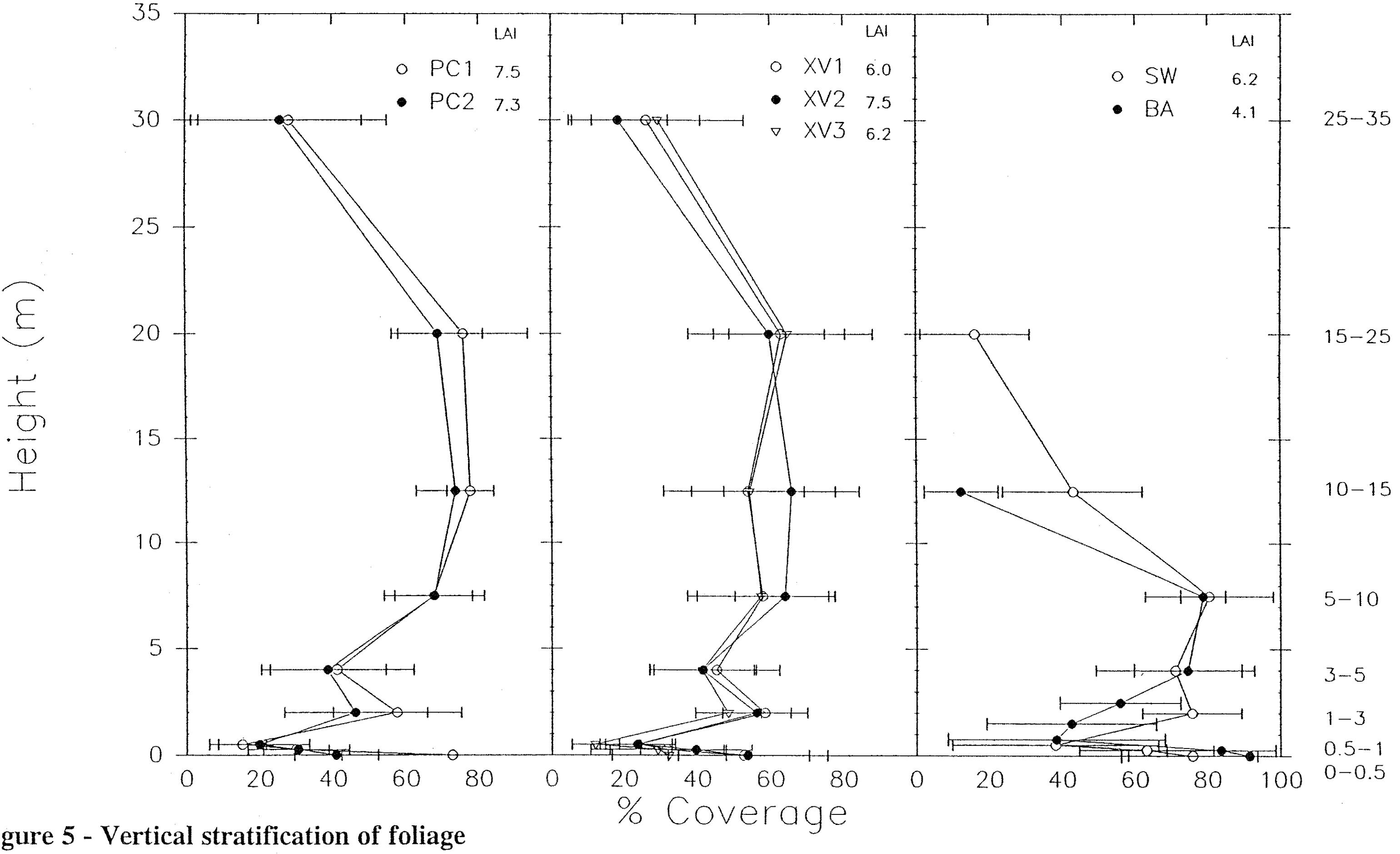


Figure 5 - Vertical stratification of foliage
Percentage cover calculated from the proportion of points with foliage present, in each height range. Error bars are standard deviation of subplot values. LAI = leaf area index

PC1, PC2 = upland broadleaf forest; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

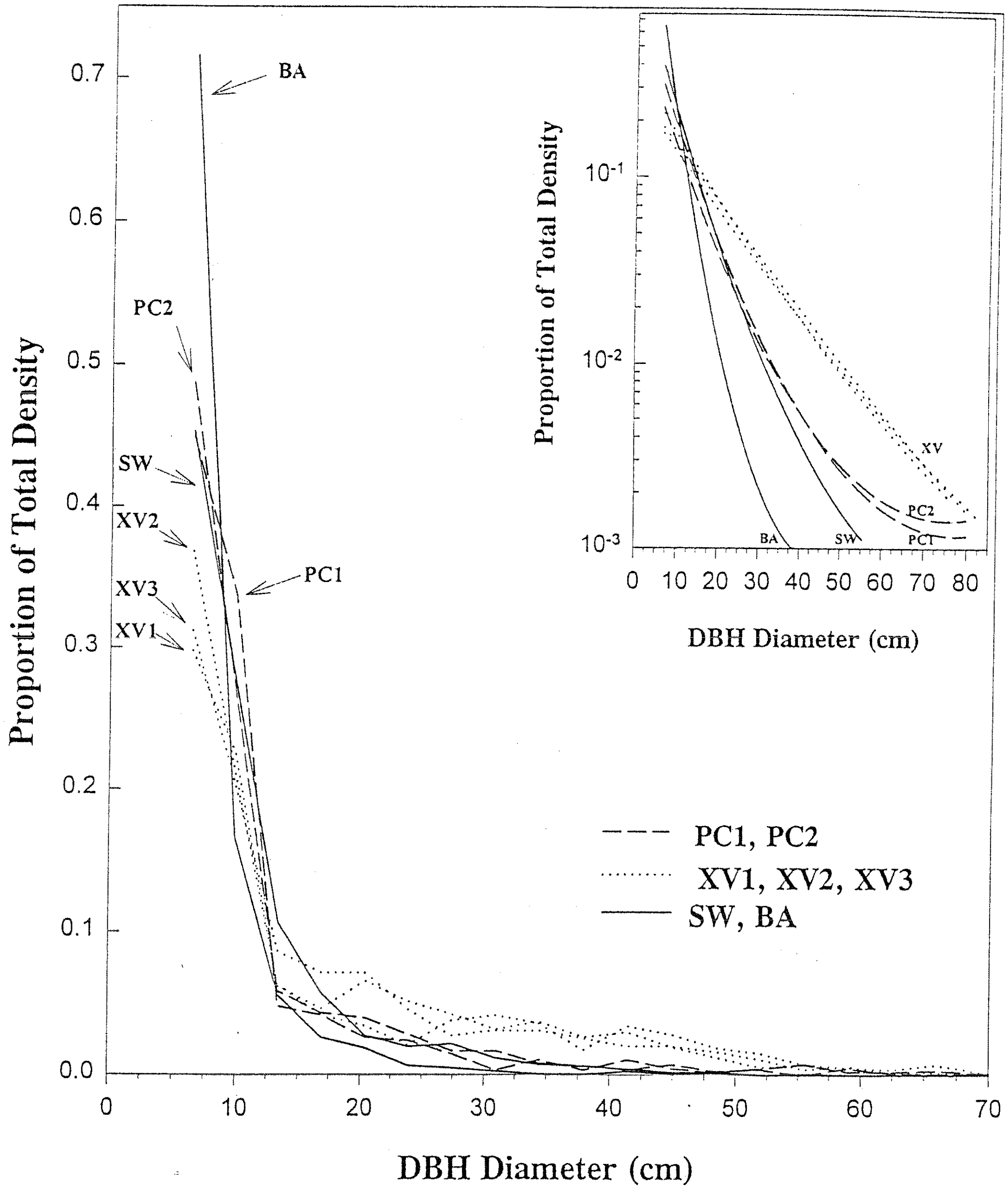


Figure 6 - Frequency distribution of diameters.
Size classes are in increments of 3.5 cm. Lowest diameter class (plotted as 6.4 on x-axis) represents size class $3 \leq \text{dbh} < 6.5$. Inset shows second order regressions of frequency distributions. R^2 of second order regressions are: PC1 $r^2 = 0.95$; PC2 $r^2 = 0.88$; XV1 $r^2 = 0.93$; XV2 $r^2 = 0.85$; XV3 $r^2 = 0.93$; SW $r^2 = 0.99$; BA $r^2 = 0.96$. Confidence intervals (95%) overlap between the PC plots and between the XV plots.

PC1, PC2 = upland broadleaf forest; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

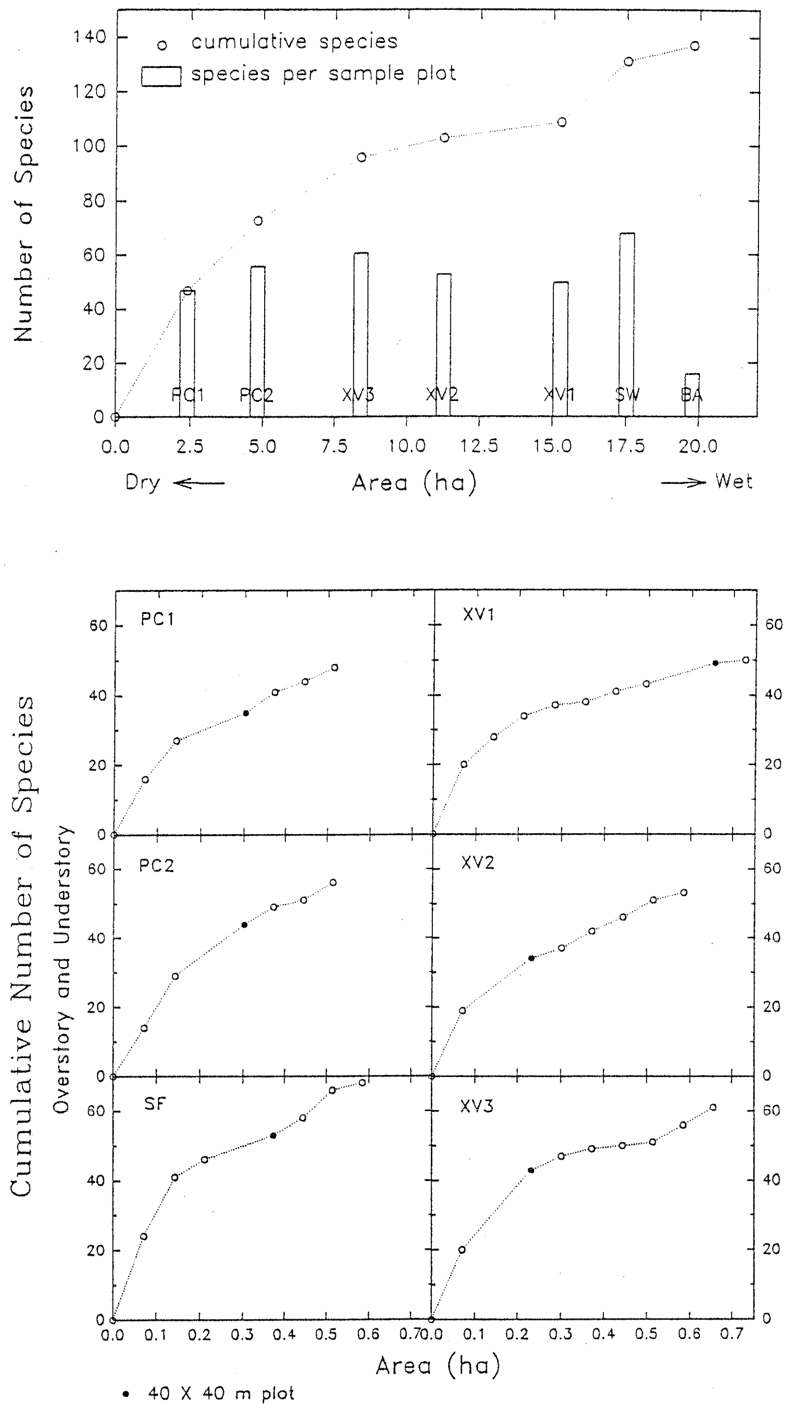


Figure 7 - Species-area relationships along a soil moisture gradient
7a) Relationships among plots 7b) Relationships among subplots
Includes overstory and understory species. Species sampled in understory nested plots are assumed to be representative of those present in the area of overstory plots.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site;
XV1, XV2, XV3 = palm forest; SW = swamp forest

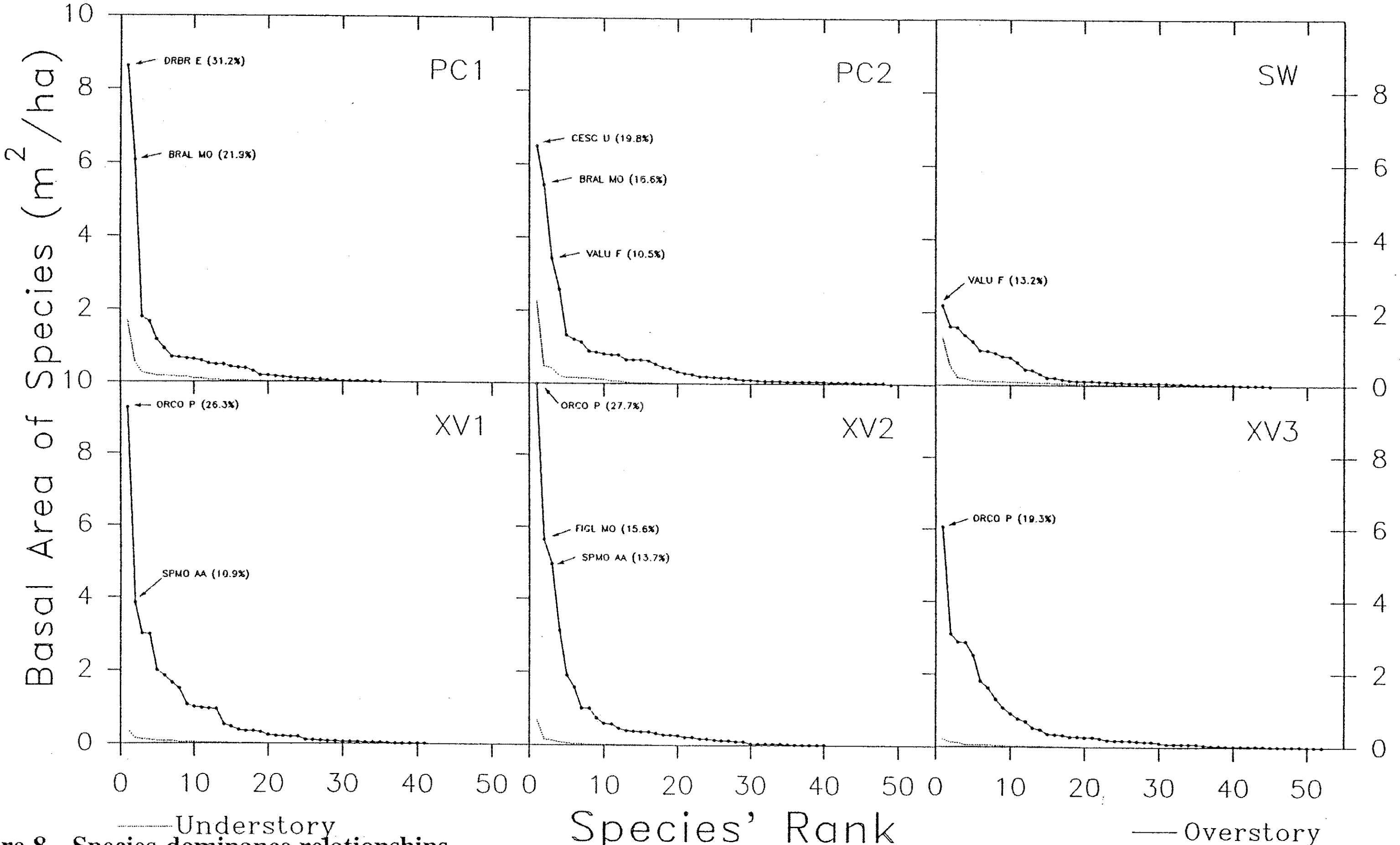


Figure 8 - Species-dominance relationships
Species are ranked by their basal area along X-axis. Points are labeled for species comprising > 10% of the plot basal area. (see Appendix D for species abbreviations; Table 6 for species comprising > 5% of basal area)

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site; XV1, XV2, XV3 = palm forest; SW = swamp forest

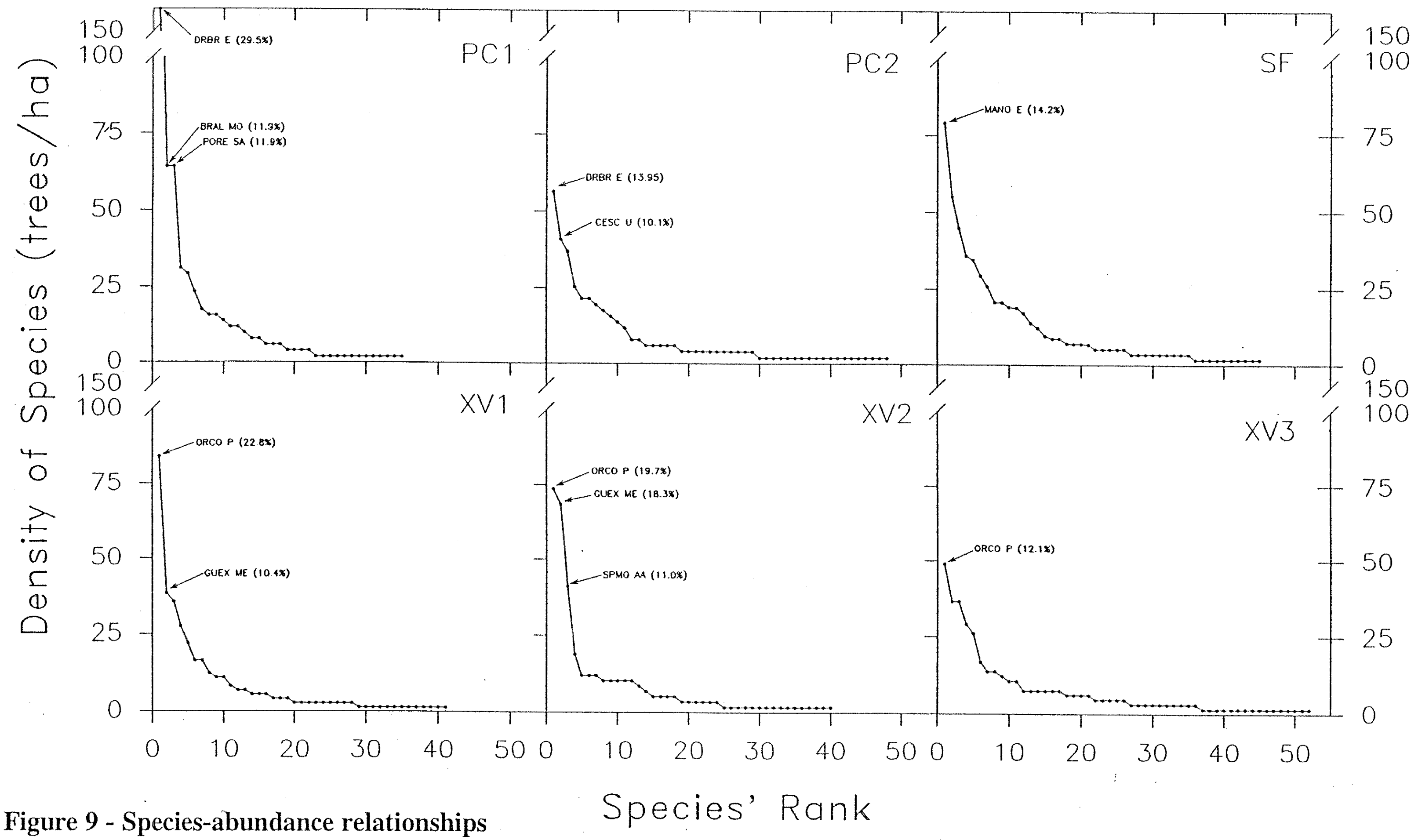


Figure 9 - Species-abundance relationships

Overstory species are ranked by their density per hectare along X-axis. Points are labeled for species comprising > 10% of the plot stems. (see Appendix D for species abbreviations; Table 6 for species comprising > 5% of stems)

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site; XV1, XV2, XV3 = palm forest; SW = swamp forest

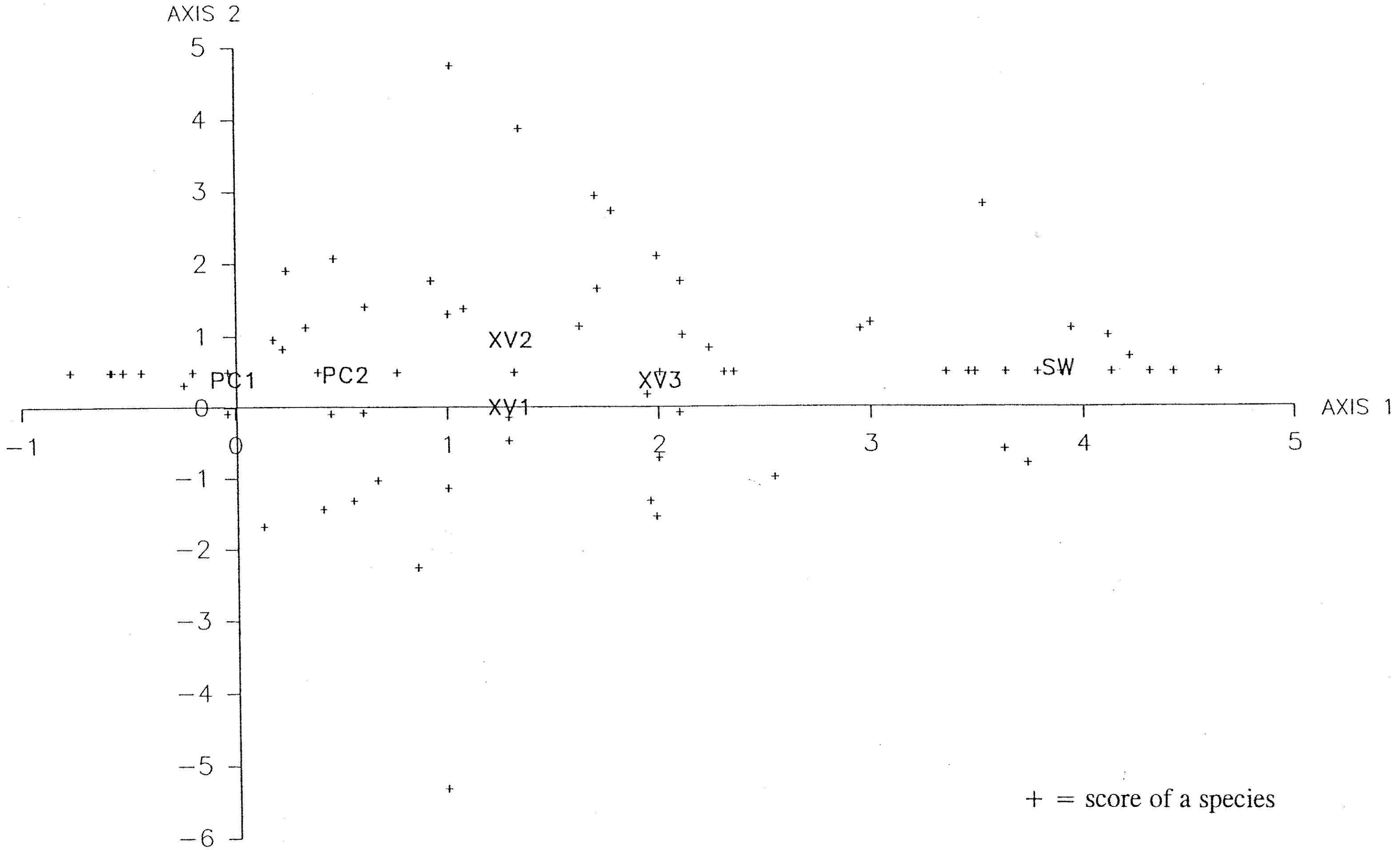


Figure 10 - Detrended correspondence analysis - plot scores
Plot scores center-weighted by the scores of species found in the plot. Species scores determined from their abundance in each sample plot.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site; XV1, XV2, XV3 = palm forest; SW = swamp forest

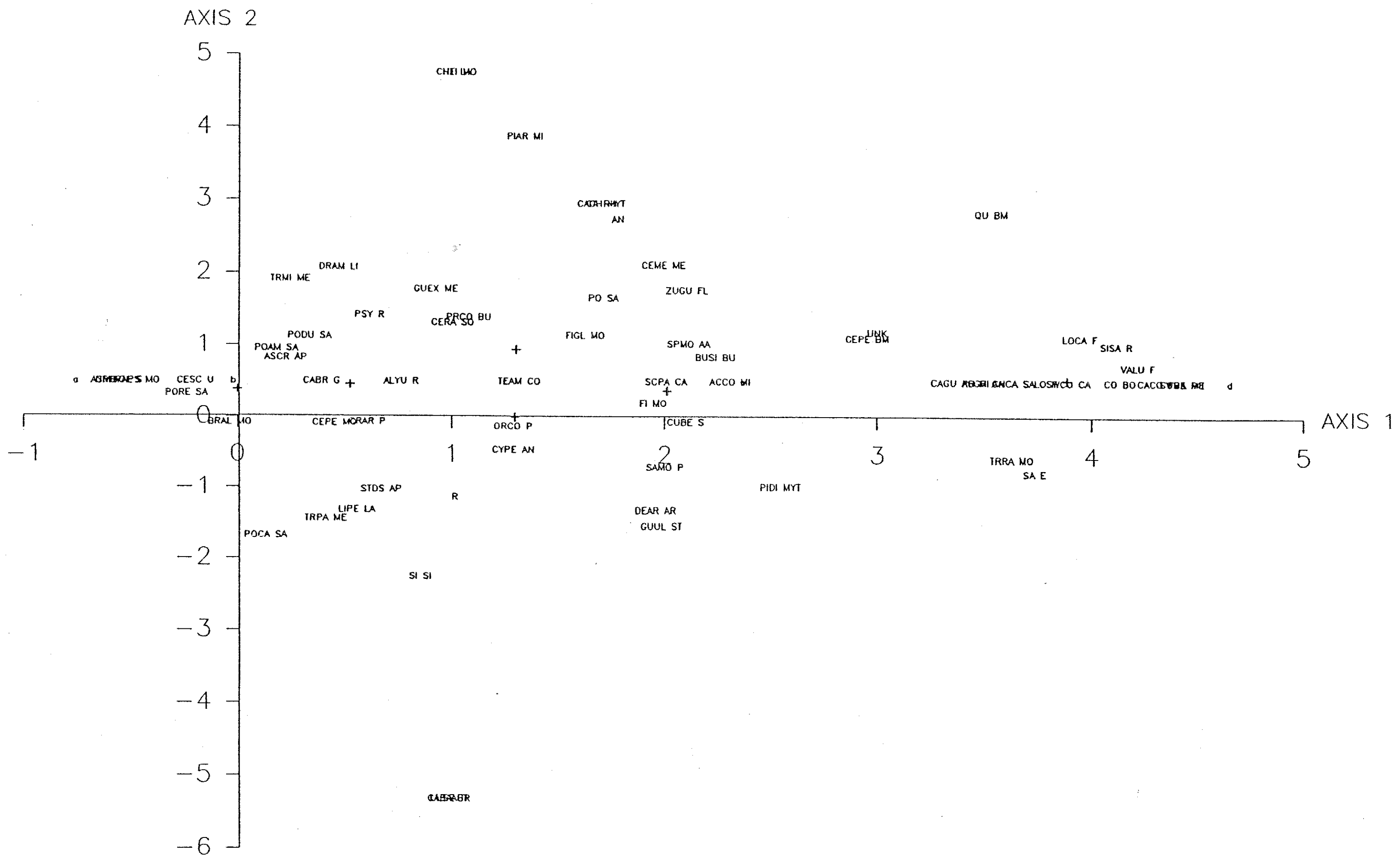


Figure 11 - Detrended correspondence analysis - species scores
Species scores determined from their abundance in each sample plot.

(see Appendix D for species abbreviations and Appendix E for codes of species with similar scores)

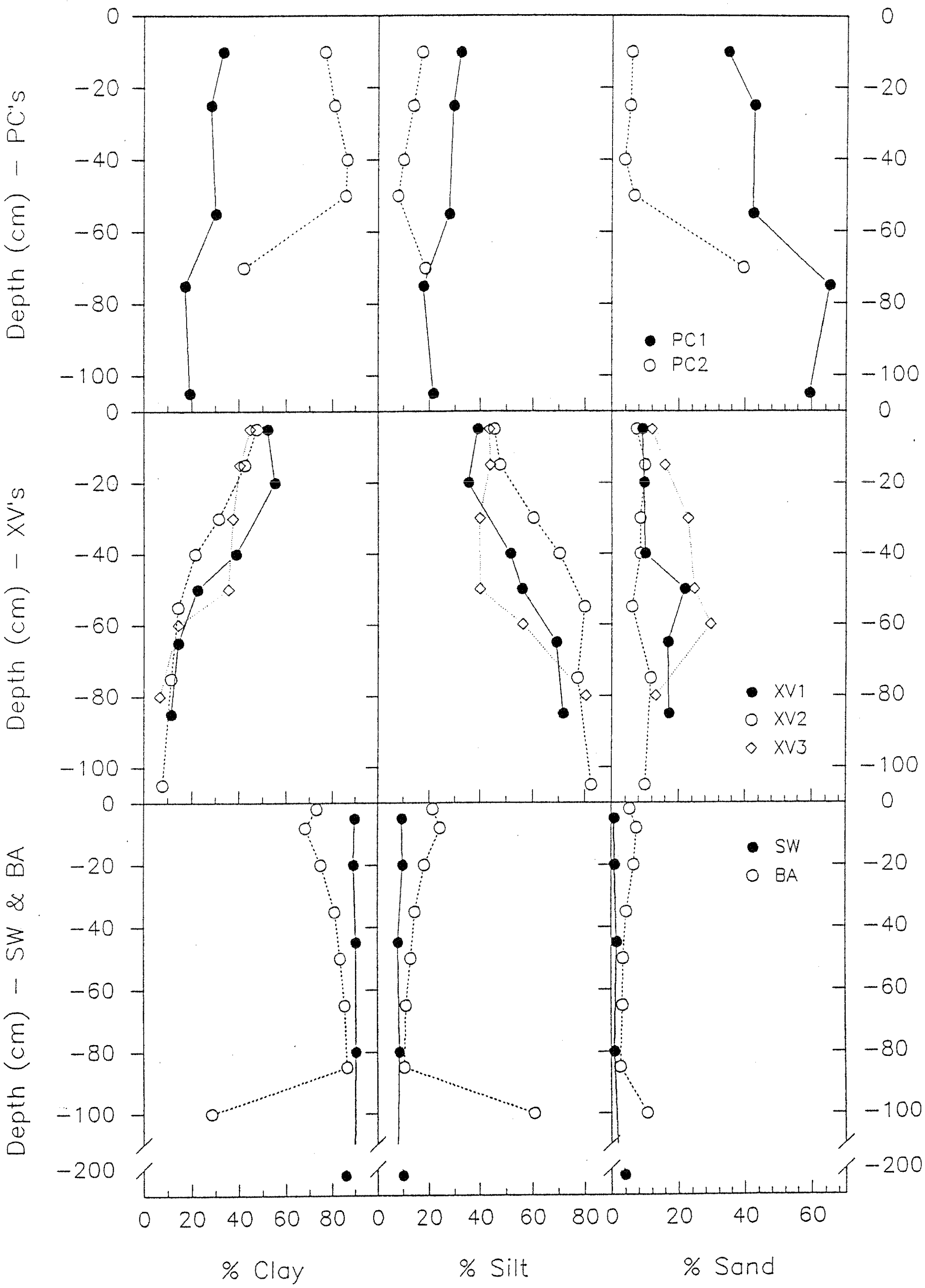


Figure 12 - Profiles of soil texture
Each point represents the mean depth of a bulk sample.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

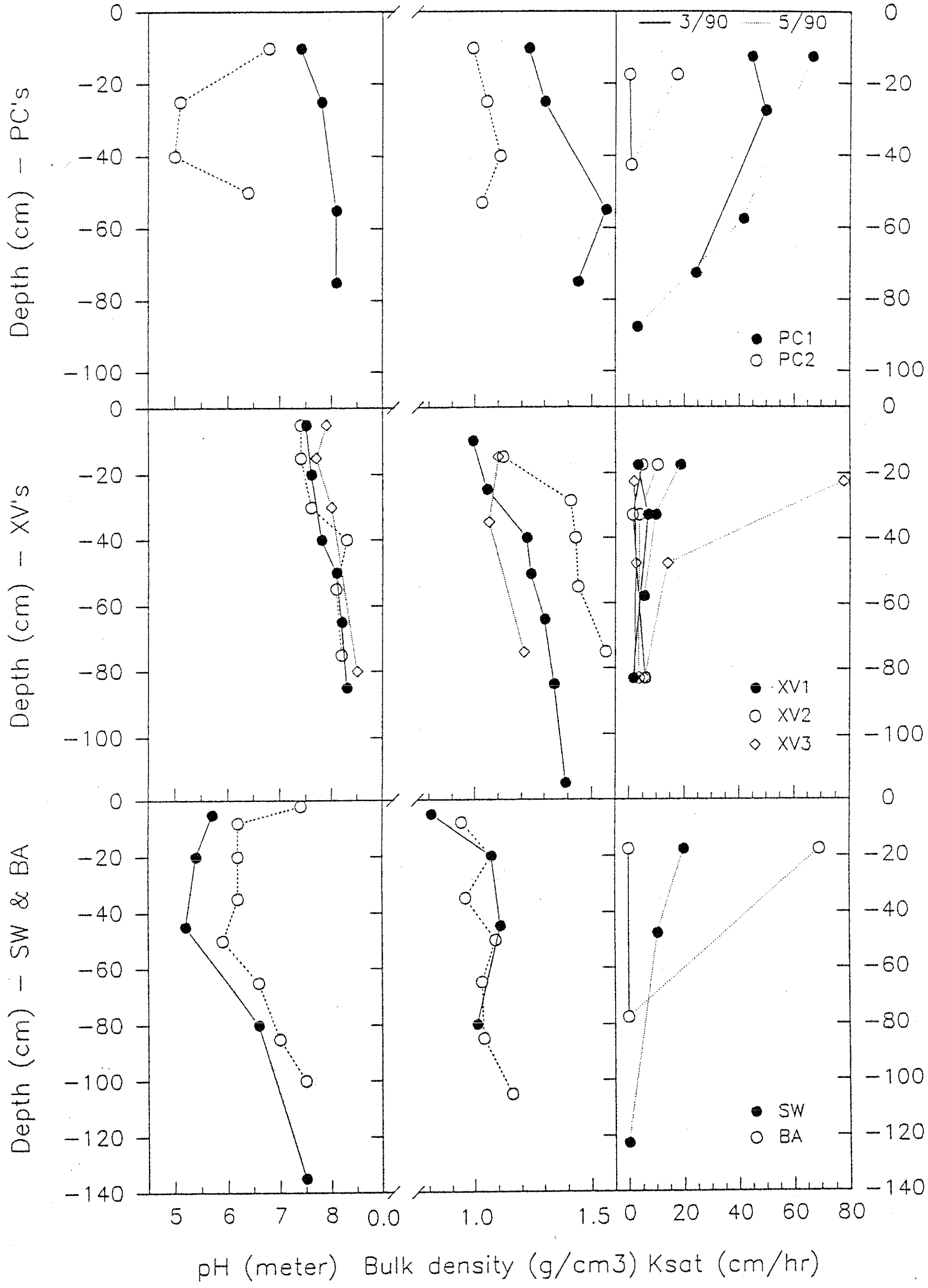


Figure 13 - Profiles of soil pH, bulk density, and K_{sat}
Each point represents the mean depth of a bulk sample. Upper horizon K_{sat} values for 5/90, which are greater then those taken on 3/90, are not accurate measures of saturated hydraulic conductivity. See text for detailed explanation.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site;
XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

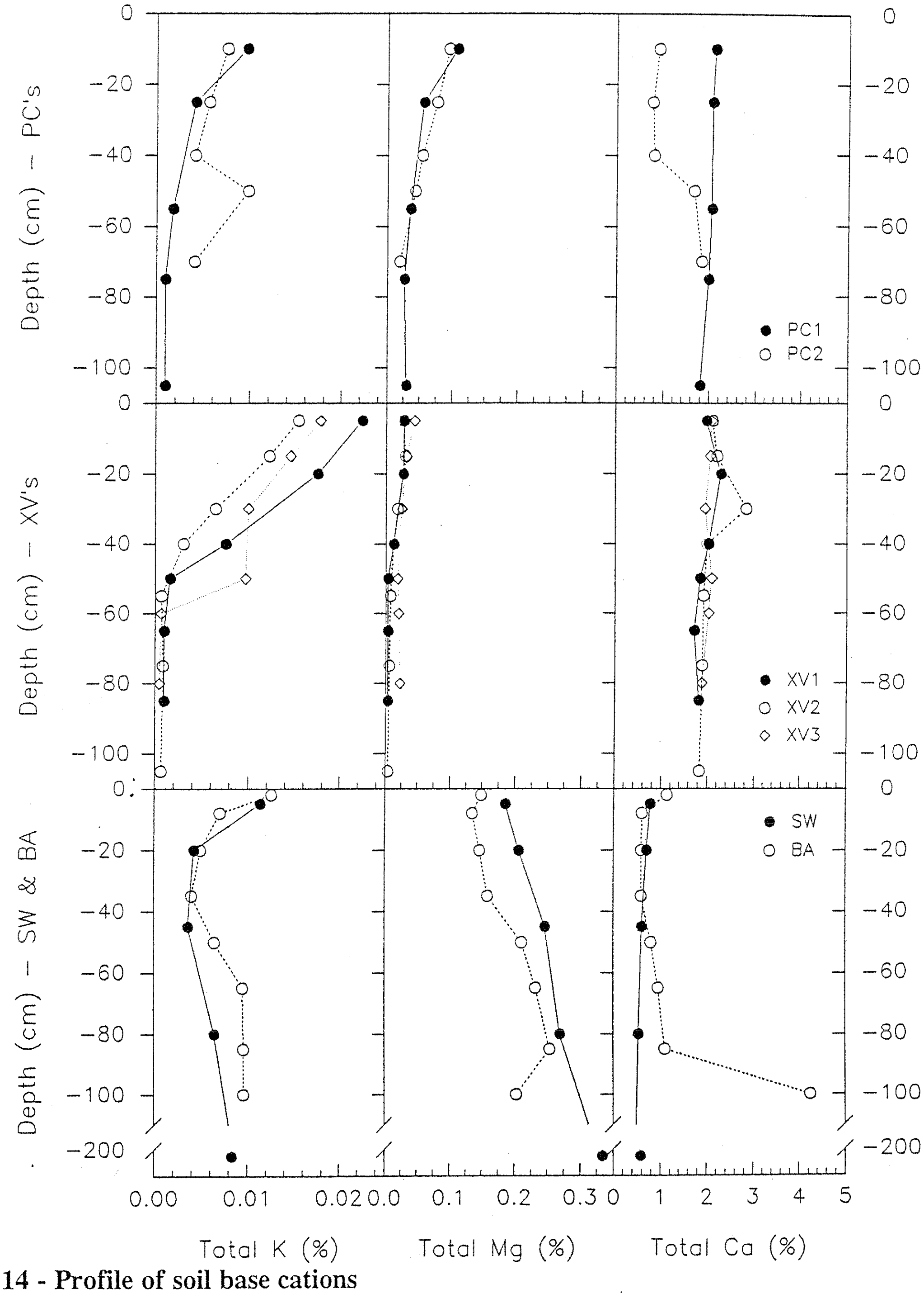


Figure 14 - Profile of soil base cations
Each point represents the mean depth of a bulk sample.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site;
XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

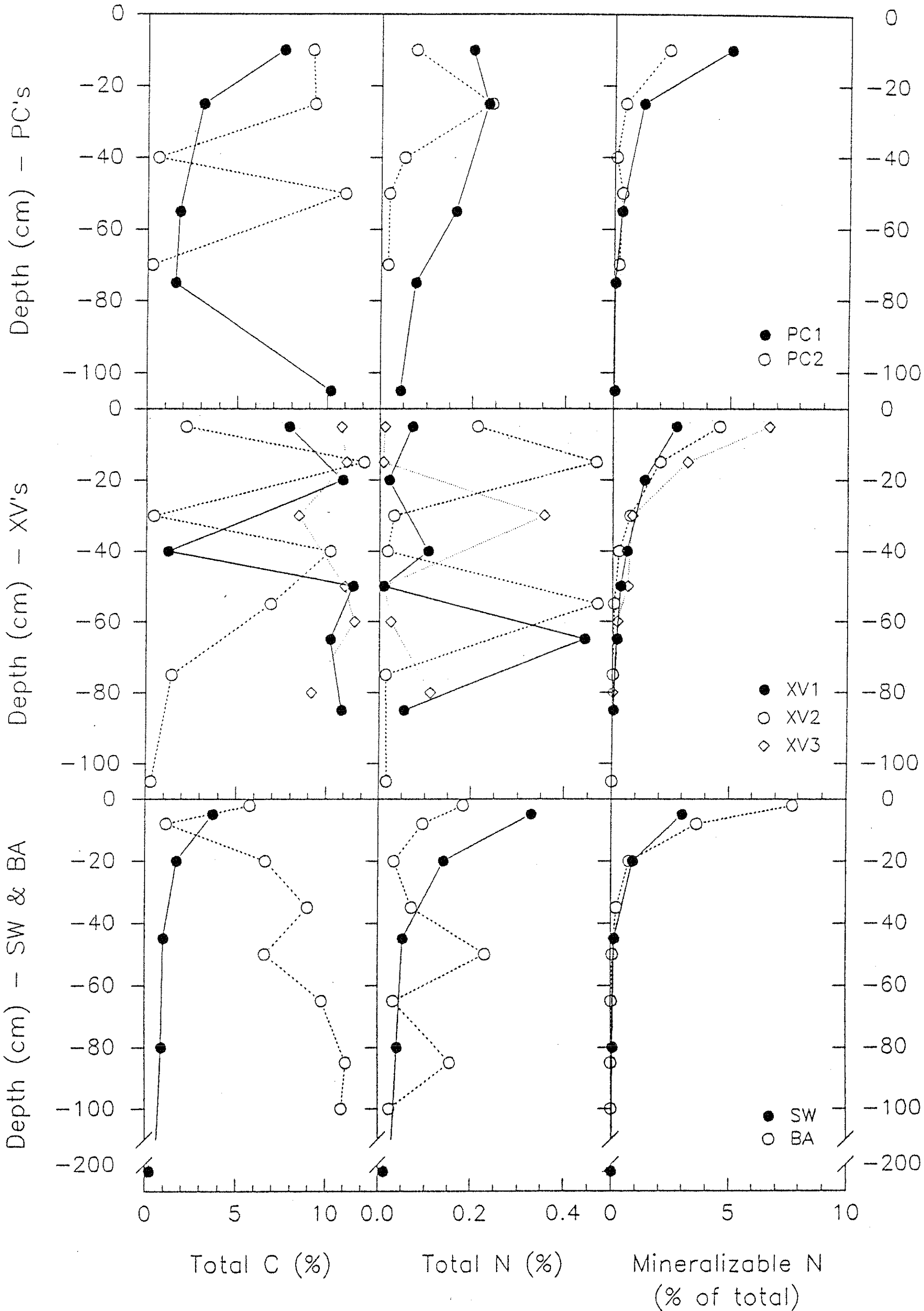


Figure 15 - Profile of total soil carbon and soil nitrogen
Each point represents the mean depth of a bulk sample.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site;
XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

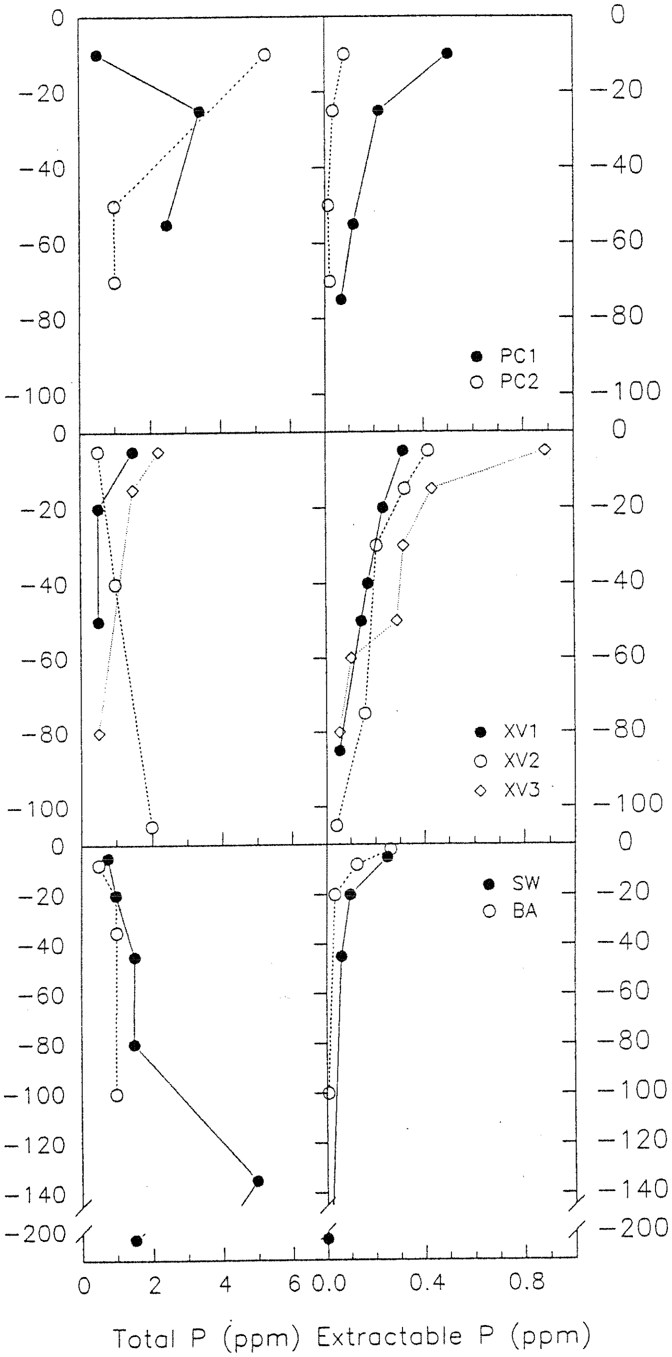


Figure 16 - Profile of soil phosphorus concentrations
Each point represents the mean depth of a bulk sample.

PC1 = upland broadleaf forest on slope; PC2 = upland broadleaf forest on level site; XV1, XV2, XV3 = palm forest; SW = swamp forest; BA = bajo forest

```
         ALL SAMPLE PLOTS
            (r²=0.84)

   8 +
     |                     X  P
     |                        P
LAI  |
     |
     |                   X
   6 +                    X
     |
     |        S
     |
     |
     |
   4 +      B
    -+---------+---------+---------+-
     2         4         6         8
             Mineralizable N
               (% of total N)
```

```
             ALL SAMPLE PLOTS
                 (r²=0.79)
            (NOTE: 1 obs hidden.)
    300 +                  X
Above-  |                 XX
 ground |
Biomass |
(Mg/ha) |             P
        |                   P
    200 +
        |
        |
        |
        |
        |
    100 +         B
        -+--------+--------+--------+
         0        1        2        3
               Total Soil Ca (%)
```

```
              ALL SAMPLE PLOTS
                 (r²=0.97)

    300 +         X
Above-  |      X  X
 ground |
Biomass |
(Mg/ha) |          P
        |           P
    200 +
        |
        |
        |
        |
        |
    100 +                     BS
        -+------------+------------+-
        0.0          0.1          0.2
              Total Soil Mg (%)
```

```
               ALL SAMPLE PLOTS
                   (r²=0.92)

    300 +                    X
Above-  |                   X  X
 ground |
Biomass |
(Mg/ha) |              P
        |                  P
    200 +
        |
        |
        |
        |
        |
    100 +    SB
        -+------------+------------+-
         6            7            8
                    Soil pH
```

```
               ONLY UPLAND PLOTS
                 (r²=0.99)

    300 +
Above-  |                  XX
 ground |
Biomass |                 X
(Mg/ha) |
        |
    250 +
        |
        |
        |    P
        | P
        |
    200 +
        -+--------+--------+--------+
       0.08     0.10     0.12     0.14
                  Foliar P (%)
```

Figure 17 - Relationships between soil and vegetation characteristics
Comparison of plot means.

P = upland broadleaf forest plots; X = palm forest plots; S = swamp forest plot; B = bajo forest plot

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Appendix A - Principal components analysis

A.1 Overstory vegetation structure by plot

```
7 Observations
8 Variables

                     Principal Component Analysis
                 Eigenvalues of the Correlation Matrix

             Eigenvalue      Difference      Proportion      Cumulative
  PRIN1         6.69966         5.81285        0.837458         0.83746
  PRIN2         0.88681         0.66055        0.110851         0.94831
  PRIN3         0.22626         0.07719        0.028282         0.97659
  PRIN4         0.14907         0.11270        0.018633         0.99523
  PRIN5         0.03637         0.03453        0.004546         0.99977
  PRIN6         0.00183         0.00183        0.000229         1.00000
  PRIN7         0.00000         0.00000        0.000000         1.00000
  PRIN8         0.00000          .             0.000000         1.00000


                     Principal Component Analysis
                             Eigenvectors

                     PRIN1          PRIN2          PRIN3          PRIN4
      TOTBA       0.379769       -.143384       0.115567       0.277228
      DENS        -.336631       0.417091       0.284311       0.655647
      QDBH        0.382929       -.094284       0.104809       0.213695
      AVGBA       0.355389       -.384684       -.066623       0.329293
      AVGHTB      0.319636       0.555032       0.398986       0.036384
      AVGHTT      0.357755       0.282736       0.260447       -.544066
      BIOMAS      0.378287       -.161587       0.164317       0.144530
      LAI         0.310262       0.484247       -.797725       0.144749


              Sample points listed by principle component 1

PLOT        PRIN1       PRIN2       PRIN3       PRIN4       TOTBA        DENS

BA       -4.19757    -0.40772     0.30519     0.15400     14.0228     588.401
SW       -3.10413    -0.12583    -0.41980    -0.11205     16.2205     535.217
PC1       0.64276     1.89373     0.25444     0.30290     27.6347     537.488
PC2       0.94715     0.53180    -0.43611    -0.65574     27.0891     393.379
XV3       1.20182    -0.41209     0.30828     0.04741     31.1951     403.115
XV1       2.15955    -0.78945     0.60151    -0.25518     35.2547     366.593
XV2       2.35043    -0.69044    -0.61351     0.51867     36.0990     373.160

PLOT       QDBH       AVGBA      AVGHTB      AVGHTT      BIOMAS      LAI

BA       13.2746      238.01      6.2876     11.0344      62.627     4.1
SW       14.2770      303.11      6.5808     13.8141      81.909     5.4
PC1      18.6351      517.24     14.2171     23.7795     200.410     7.5
PC2      18.4502      626.05     11.6334     23.6817     212.720     7.3
XV3      19.7992      779.63     11.5318     20.8192     273.944     6.2
XV1      21.0481      970.94     11.4464     25.3195     285.224     6.0
XV2      21.2987     1071.00     10.7187     21.2207     289.885     7.5
```

A.2 Understory vegetation structure by plot

```
      7 Observations
      7 Variables

                         Principal Component Analysis
                      Eigenvalues of the Correlation Matrix

                  Eigenvalue      Difference      Proportion      Cumulative
   PRIN1             5.31229         4.26992        0.758899         0.75890
   PRIN2             1.04238         0.64014        0.148911         0.90781
   PRIN3             0.40224         0.18655        0.057462         0.96527
   PRIN4             0.21569         0.18845        0.030813         0.99609
   PRIN5             0.02724         0.02708        0.003892         0.99998
   PRIN6             0.00016         0.00016        0.000023         1.00000
   PRIN7             0.00000          .             0.000000         1.00000


                         Principal Component Analysis
                                 Eigenvectors

                 PRIN1        PRIN2        PRIN3        PRIN4

TOTBA         0.428802     -.026647     0.170922     0.219059
DENS          0.427427     -.025889     -.070243     0.328188
QDBH          0.419584     -.042215     0.337314     0.111470
AVGBA         -.356922     0.004517     0.890841     0.112683
AVGHTB        -.133668     0.916692     -.075385     0.350539
AVGHTT        0.359158     0.391707     0.191578     -.804381
BIOMAS        0.427936     0.055301     0.126837     0.221983


              Sample points listed by principle component 1

 PLOT       PRIN1        PRIN2        PRIN3        PRIN4       TOTBA        DENS

 XV1     -2.41168     -0.53772      0.23793      0.63632     1.33518      410.92
 XV3     -1.94163      1.18515     -0.49641      0.18188     1.22770      431.45
 XV2     -1.22824     -0.43117     -0.75822     -0.74586     1.46507      527.34
 SW       0.08911     -1.76623      0.30440     -0.02913     4.34386     1487.75
 PC1      0.49355      0.78023      0.01311      0.16619     4.64310     1665.18
 PC2      0.49531      0.80323      1.12362     -0.45788     4.69328     1478.18
 BA       4.50358     -0.03349     -0.42443      0.24847     9.50545     4369.11

 PLOT       QDBH      AVGBA      AVGHTB      AVGHTT      BIOMAS

 XV1      4.0961    32.8454     4.71991     3.00000      4.2610
 XV3      3.9278    29.5537     5.65349     4.57143      4.2723
 XV2      4.2908    27.3872     4.42096     5.05595      4.5101
 SW       7.3883    29.2534     3.63528     4.38543     10.5741
 PC1      7.6385    27.7694     5.19219     5.74325     13.0213
 PC2      7.6797    31.4583     4.97926     6.90746     14.7497
 BA      10.9293    21.4433     4.36496     7.28261     29.7766
```

A.3 Foliar nutrients by plot

```
     7 Observations
     5 Variables

                     Principal Component Analysis
                 Eigenvalues of the Correlation Matrix

            Eigenvalue      Difference      Proportion      Cumulative

  PRIN1        2.99560         1.48408        0.599120         0.59912
  PRIN2        1.51152         1.15476        0.302304         0.90142
  PRIN3        0.35676         0.27055        0.071352         0.97278
  PRIN4        0.08621         0.03631        0.017242         0.99002
  PRIN5        0.04991          .             0.009981         1.00000

                     Principal Component Analysis
                             Eigenvectors

              PRIN1         PRIN2         PRIN3         PRIN4

FOLN       -.244927      0.719974      -.226033      -.040430
FOLP       -.423168      0.512101      0.352615      0.177826
FOLK       0.523233      0.168487      0.540751      0.584981
FOLCA      0.505416      0.325870      0.270967      -.740140
FOLMG      0.481375      0.291223      -.677301      0.277009


                       Foliar nutrients by plot
               Sample points listed by principle component 1

     PLOT       PRIN1        PRIN2        PRIN3        PRIN4        FOLN

     XV1     -1.96223      0.06174      0.11863      0.11494     2.13042
     XV3     -1.14269      0.51507     -0.21061     -0.34348     2.15440
     XV2     -1.11073      0.50100      0.68754      0.38493     2.15584
     SW      -1.08875     -0.15955     -0.53183     -0.24384     2.15715
     BA       1.00530     -2.64903      0.10751      0.02818     1.40987
     PC1      1.87873      0.80037     -0.89196      0.32620     2.08676
     PC2      2.42037      0.93039      0.72072     -0.26693     2.00369

     PLOT      FOLP        FOLK        FOLCA       FOLMG

     XV1     0.12126     5.66349     1.15800     0.18724
     XV3     0.11697     5.67084     2.31040     0.29194
     XV2     0.12083     7.19487     1.84500     0.20921
     SW      0.09446     5.64349     1.69551     0.26161
     BA      0.05576     7.21316     2.08034     0.27737
     PC1     0.08238     8.20818     3.55242     0.60131
     PC2     0.08781     9.47993     5.16565     0.45210
```

A.4 Soil nutrient and lab pH properties by plot

```
     7 Observations
     8 Variables

                        Principal Component Analysis
                    Eigenvalues of the Correlation Matrix

              Eigenvalue      Difference      Proportion      Cumulative

  PRIN1          5.12541         3.38993        0.640676         0.64068
  PRIN2          1.73547         0.88890        0.216934         0.85761
  PRIN3          0.84657         0.67694        0.105821         0.96343
  PRIN4          0.16963         0.06657        0.021204         0.98463
  PRIN5          0.10306         0.08320        0.012883         0.99752
  PRIN6          0.01986         0.01986        0.002483         1.00000
  PRIN7          0.00000         0.00000        0.000000         1.00000
  PRIN8          0.00000          .             0.000000         1.00000


                        Principal Component Analysis
                                Eigenvectors

                         PRIN1        PRIN2        PRIN3        PRIN4

      SOILN           0.257304     0.594540     0.179777     -.328220
      MINN            0.397645     0.181325     -.345571     -.329166
      PO4P            0.373536     0.326998     0.088230     0.662057
      PH              0.414936     -.172008     -.187765     0.172401
      SOILP           0.257075     -.148983     0.850075     -.251082
      SOILK           0.213913     -.649078     0.034791     0.031609
      SOILCA          0.432912     -.068549     0.054868     0.282960
      SOILMG          -.405849     0.170093     0.279951     0.414454


                 Sample points listed by principle component 1

PLOT       PRIN1        PRIN2        PRIN3        PRIN4       SOILN        MINN

BA      -3.22799     -0.31231      0.83362     -0.37760     0.44410     3.33375
SW      -3.04056      0.34867     -0.02616      0.51881     0.44288     3.89000
PC2     -0.08682      1.13309     -1.51528     -0.47601     0.64906     7.07800
XV3      0.89871     -0.83152     -0.92946      0.51301     0.46442     6.04727
XV1      1.46772     -0.93733      0.17392     -0.30295     0.54279     6.24700
XV2      1.70962     -1.59241      0.48382     -0.02900     0.50670     6.32400
PC1      2.27932      2.19181      0.97955      0.15374     0.87888     7.04429

PLOT        PO4P           PH        SOILP        SOILK     SOILCA      SOILMG

BA      .00025538     6.38750     .0016367     0.013869    0.95029     0.16451
SW      .00050442     6.30000     .0011863     0.013359    0.94672     0.16904
PC2     .00060256     7.08000     .0010268     0.012930    1.40419     0.07897
XV3     .00064535     7.70909     .0013860     0.025646    1.94582     0.06887
XV1     .00064222     7.45455     .0019478     0.029356    1.92316     0.04537
XV2     .00067273     7.56000     .0020858     0.038218    1.94557     0.06130
PC1     .00099509     7.38889     .0020805     0.010704    2.07271     0.08609
```

A.5 Soil physical properties by plot - no Ksat

```
   7 Observations
   4 Variables


                        Principal Component Analysis
                     Eigenvalues of the Correlation Matrix

               Eigenvalue       Difference       Proportion       Cumulative

 PRIN1          3.66181          3.36441          0.915453          0.91545
 PRIN2          0.29740          0.25664          0.074351          0.98980
 PRIN3          0.04076          0.04073          0.010190          0.99999
 PRIN4          0.00003           .               0.000007          1.00000


                        Principal Component Analysis
                                Eigenvectors

                     PRIN1          PRIN2          PRIN3          PRIN4

    CLAY            -.521527       0.023468       0.307081       0.795714
    SILT            0.480745       0.709798       -.307596       0.412863
    SAND            0.481678       -.703747       -.276367       0.443111
    BULKDEN         0.514665       0.019404       0.857151       0.005959


                 Sample points listed by principle component 1

PLOT   PRIN1    PRIN2     PRIN3     PRIN4     CLAY     SILT     SAND  BULKDEN

SW   -2.79749 -0.32354 -0.10079  0.001836 88.2667 10.5833  1.1500    0.81
BA   -1.16198  0.23040  0.06672  0.002522 75.0000 20.5286  4.4714    0.94
PC2  -0.61970 -0.42516  0.20291  0.003746 70.7000 18.3600 10.9400    0.99
XV2  -0.20027 -0.06444  0.12179 -0.011203 66.5400 22.5600 10.6000    1.01
XV1   0.35829  0.21115 -0.39869 -0.000941 59.1909 28.1000 12.7091    0.99
XV3   1.09950  1.00069  0.12167  0.002224 55.7273 34.7818  9.4909    1.10
PC1   3.32165 -0.62910 -0.01361  0.001817 34.8667 34.3667 30.7667    1.23
```

Appendix B - ANOVAs of principal components

B.1 Foliar nutrients versus soil chemistry and texture

```
Model: F1 F2 = S1 S2 T1

Dependent Variable: F1

                         Analysis of Variance

                             Sum of          Mean
   Source           DF      Squares        Square      F Value       Prob>F

   Model             3     11.27393       3.75798        1.683       0.3397
   Error             3      6.69970       2.23323
   C Total           6     17.97363

       Root MSE       1.49440     R-square       0.6272
       Dep Mean       0.00000     Adj R-sq       0.2545
       C.V.      4.7111282E18


                         Parameter Estimates

                   Parameter      Standard    T for H0:
 Variable  DF       Estimate         Error   Parameter=0    Prob > |T|

 INTERCEP   1  9.865027E-17    0.56483044         0.000        1.0000
 S1         1     -0.166230    0.52622397        -0.316        0.7728
 S2         1      0.950890    0.56246419         1.691        0.1895
 T1         1      0.163562    0.66021391         0.248        0.8203

Dependent Variable: F2

                         Analysis of Variance

                             Sum of          Mean
   Source           DF      Squares        Square      F Value       Prob>F

   Model             3      7.54272       2.51424        4.941       0.1111
   Error             3      1.52642       0.50881
   C Total           6      9.06914

       Root MSE       0.71331     R-square       0.8317
       Dep Mean      -0.00000     Adj R-sq       0.6634
       C.V.      -49931531.11


                         Parameter Estimates

                   Parameter      Standard    T for H0:
 Variable  DF       Estimate         Error   Parameter=0    Prob > |T|

 INTERCEP   1  -0.000001429    0.26960493        -0.000        1.0000
 S1         1      0.845460    0.25117729         3.366        0.0435
 S2         1      0.537675    0.26847547         2.003        0.1390
 T1         1     -0.655965    0.31513338        -2.082        0.1288
```

```
               Foliar nutrients vs soil chemistry and texture

Multivariate Test:

                                Adjusted        Approx        Squared
                 Canonical     Canonical       Standard      Canonical
                Correlation   Correlation       Error       Correlation

           1      0.930547      0.897925       0.054739      0.865918
           2      0.770078       .             0.166149      0.593020

                             Eigenvalues of INV(E)*H
                               = CanRsq/(1-CanRsq)

                 Eigenvalue    Difference    Proportion    Cumulative

            1      6.4581        5.0010        0.8159        0.8159
            2      1.4571         .            0.1841        1.0000


               Test of H0: The canonical correlations in the current row
                              and all that follow are zero

               Likelihood
                 Ratio        Approx F      Num DF      Den DF     Pr > F

          1    0.05456857      2.1872          6           4      0.2344
          2    0.40697971      2.1857          2           3      0.2596


                Multivariate Statistics and F Approximations

                             S=2     M=0     N=0

 Statistic                     Value           F       Num DF     Den DF   Pr > F

 Wilks' Lambda              0.05456857      2.1872         6          4   0.2344
 Pillai's Trace             1.45893849      2.6964         6          6   0.1263
 Hotelling-Lawley Trace     7.91525875      1.3192         6          2   0.4913
 Roy's Greatest Root        6.45813377      6.4581         3          3   0.0799

         NOTE: F Statistic for Roy's Greatest Root is an upper bound.
                NOTE: F Statistic for Wilks' Lambda is exact.
```

B.2 Overstory structure versus soil chemistry and texture

```
Model: V10 = T1 S1 S2

Dependent Variable: V1O

                          Analysis of Variance

                               Sum of         Mean
     Source          DF       Squares       Square      F Value       Prob>F

     Model            3      38.82111     12.94037       28.195       0.0107
     Error            3       1.37689      0.45896
     C Total          6      40.19800

         Root MSE        0.67747     R-square       0.9657
         Dep Mean        0.00000     Adj R-sq       0.9315
         C.V.       47422796.397


                          Parameter Estimates

                      Parameter      Standard    T for H0:
   Variable  DF        Estimate         Error   Parameter=0    Prob > |T|

   INTERCEP   1     0.000001429    0.25605903         0.000        1.0000
   T1         1       -0.712420    0.29929997        -2.380        0.0976
   S1         1        1.549070    0.23855726         6.493        0.0074
   S2         1       -0.045043    0.25498632        -0.177        0.8710


Model: V1O = T1 S1
Dependent Variable: V1O

                          Analysis of Variance

                               Sum of         Mean
     Source          DF       Squares       Square      F Value       Prob>F

     Model            2      38.80679     19.40339       55.788       0.0012
     Error            4       1.39121      0.34780
     C Total          6      40.19800

         Root MSE        0.58975     R-square       0.9654
         Dep Mean        0.00000     Adj R-sq       0.9481
         C.V.       41282382.611

                     ANOVA of Principle Components
               Overstory structure vs soil chemistry and texture


                          Parameter Estimates

                      Parameter      Standard    T for H0:
   Variable  DF        Estimate         Error   Parameter=0    Prob > |T|

   INTERCEP   1     0.000001429    0.22290391         0.000        1.0000
   T1         1       -0.742425    0.21452229        -3.461        0.0258
   S1         1        1.569612    0.18132458         8.656        0.0010
```

```
          Overstory structure vs soil chemistry and texture


          Plot of T1*V1O.  Symbol is value of PLOT.

 5 +
   |
T1 |                                             P
   |
   |                                                 X
 0 +                                                       XX
   |              B                                P
   |
   |                     S
   |
-5 +
   ---+------------+------------+------------+------------+------------+--
     -6           -4           -2            0            2            4

                                   V1O
```

```
          Plot of S1*V1O.  Symbol is value of PLOT.

 5 +
   |
S1 |
   |                                             P          X
   |                                                 X     X
 0 +                                               P
   |
   |
   |              B      S
   |
-5 +
   ---+------------+------------+------------+------------+------------+--
     -6           -4           -2            0            2            4

                                   V1O
```

B.3 Overstory structure versus foliar nutrients

```
Model: V1O = F1 F2

Dependent Variable: V1O

                           Analysis of Variance

                               Sum of         Mean
       Source          DF     Squares        Square      F Value       Prob>F

       Model            2    26.33344      13.16672        3.799       0.1190
       Error            4    13.86456       3.46614
       C Total          6    40.19800

           Root MSE       1.86176     R-square       0.6551
           Dep Mean       0.00000     Adj R-sq       0.4826
           C.V.      130323008.24


                           Parameter Estimates

                      Parameter      Standard    T for H0:
     Variable  DF      Estimate         Error   Parameter=0    Prob > |T|

     INTERCEP   1   0.000003782    0.70367810         0.000        1.0000
     F1         1     -0.309439    0.43914218        -0.705        0.5199
     F2         1      1.647382    0.61821553         2.665        0.0561


Model: V1O = F2

Dependent Variable: V1O

                           Analysis of Variance

                               Sum of         Mean
       Source          DF     Squares        Square      F Value       Prob>F

       Model            1    24.61242      24.61242        7.896       0.0375
       Error            5    15.58558       3.11712
       C Total          6    40.19800

           Root MSE       1.76554     R-square       0.6123
           Dep Mean       0.00000     Adj R-sq       0.5347
           C.V.      123587474.86


                           Parameter Estimates

                      Parameter      Standard    T for H0:
     Variable  DF      Estimate         Error   Parameter=0    Prob > |T|

     INTERCEP   1   0.000003782    0.66730964         0.000        1.0000
     F2         1      1.647381    0.58626407         2.810        0.0375
```

```
           Overstory structure vs foliar nutrients

          Plot of F2*V10.  Symbol is value of PLOT.
F2 |
 2 +
   |
   |                                             P P X      X
 0 +                     S                                 X
   |
   |
-2 +
   |              B
   |
-4 +
   ---+------------+------------+------------+------------+------------+--
     -6           -4           -2            0            2            4
                                   V10
```

B.4 Understory structure vs soil chemistry and texture

```
Model: V1U V2U = S1 S2 S3 T1

Dependent Variable: V1U

                         Analysis of Variance

                              Sum of         Mean
       Source          DF    Squares       Square      F Value       Prob>F

       Model            4   23.44601      5.86150        1.391       0.4589
       Error            2    8.42779      4.21390
       C Total          6   31.87380

           Root MSE       2.05278     R-square       0.7356
           Dep Mean       0.00000     Adj R-sq       0.2068
           C.V.              .


                         Parameter Estimates

                       Parameter       Standard    T for H0:
     Variable  DF       Estimate          Error   Parameter=0    Prob > |T|

     INTERCEP   1   -0.000000789     0.77587695        -0.000        1.0000
     S1         1      -1.135990     0.78400171        -1.449        0.2844
     S2         1       0.268207     0.80182088         0.334        0.7698
     S3         1       0.552144     1.01386701         0.545        0.6406
     T1         1       0.656596     1.00949876         0.650        0.5822

Dependent Variable: V2U

                         Analysis of Variance

                              Sum of         Mean
       Source          DF    Squares       Square      F Value       Prob>F

       Model            4    5.41112      1.35278        3.209       0.2514
       Error            2    0.84314      0.42157
       C Total          6    6.25426

           Root MSE       0.64928     R-square       0.8652
           Dep Mean       0.00000     Adj R-sq       0.5956
           C.V.              .


                         Parameter Estimates

                       Parameter       Standard    T for H0:
     Variable  DF       Estimate          Error   Parameter=0    Prob > |T|

     INTERCEP   1    0.000001036     0.24540600         0.000        1.0000
     S1         1      -0.344805     0.24797583        -1.390        0.2989
     S2         1      -0.184778     0.25361194        -0.729        0.5420
     S3         1      -0.725014     0.32068107        -2.261        0.1522
     T1         1       0.823121     0.31929942         2.578        0.1233
```

B.5 Understory structure vs overstory structure

```
Model: V1U V2U = V1O

Dependent Variable: V1U

                          Analysis of Variance

                               Sum of         Mean
       Source          DF     Squares       Square      F Value       Prob>F

       Model            1    20.66663     20.66663        9.220       0.0289
       Error            5    11.20717      2.24143
       C Total          6    31.87380

           Root MSE       1.49714     R-square       0.6484
           Dep Mean       0.00000     Adj R-sq       0.5781
           C.V.                 .


                          Parameter Estimates

                        Parameter       Standard    T for H0:
     Variable  DF        Estimate          Error   Parameter=0    Prob > |T|

     INTERCEP   1   0.000001024     0.56586637         0.000        1.0000
     V1O        1     -0.717022     0.23613518        -3.036        0.0289

Dependent Variable: V2U

                          Analysis of Variance

                               Sum of         Mean
       Source          DF     Squares       Square      F Value       Prob>F

       Model            1     0.93636      0.93636        0.880       0.3912
       Error            5     5.31790      1.06358
       C Total          6     6.25426

           Root MSE       1.03130     R-square       0.1497
           Dep Mean       0.00000     Adj R-sq      -0.0203
           C.V.                 .

                     ANOVA of Principle Components
                Understory structure vs overstory structure


                          Parameter Estimates

                        Parameter       Standard    T for H0:
     Variable  DF        Estimate          Error   Parameter=0    Prob > |T|

     INTERCEP   1  -0.000000218     0.38979470        -0.000        1.0000
     V1O        1      0.152623     0.16266073         0.938        0.3912
```

```
                 Understory structure vs overstory structure

Multivariate Test:

                                Adjusted       Approx       Squared
                 Canonical      Canonical      Standard     Canonical
                Correlation    Correlation      Error      Correlation

           1      0.893367       0.889565      0.082424      0.798104

                                Eigenvalues of INV(E)*H
                                  = CanRsq/(1-CanRsq)

                 Eigenvalue    Difference    Proportion    Cumulative

            1       3.9531          .           1.0000        1.0000

               Test of H0: The canonical correlations in the current row
                             and all that follow are zero

               Likelihood
                  Ratio          F         Num DF      Den DF     Pr > F

          1    0.20189557      7.9061          2           4     0.0408

               Multivariate Statistics and Exact F Statistics

                              S=1    M=0    N=1

Statistic                    Value           F      Num DF    Den DF  Pr > F

Wilks' Lambda             0.20189557     7.9061          2         4  0.0408
Pillai's Trace            0.79810443     7.9061          2         4  0.0408
Hotelling-Lawley Trace    3.95305566     7.9061          2         4  0.0408
Roy's Greatest Root       3.95305566     7.9061          2         4  0.0408


            Plot of V1O*V1U.  Symbol is value of PLOT.
        (NOTE: 1 obs hidden.)
     5 +
       |
   V1O |
       |           X     X
       |              X              P
     0 +
       |
       |
       |                            S
       |                                                            B
    -5 +
       --+------------+------------+------------+------------+------------+--
        -4           -2            0            2            4            6

                                       V1U
```

Appendix C - Soil pit classifications.

Site: Punta de Cacao #1 (PC1)
Setting; Upland hillside; mixed deciduous forest
Classification: loamy, mixed, isohyperthermic Eutropeptic Rendoll

Oi 0-0.3 cm. Slightly decomposed branch and leaf litter.

A1 0.3-2 cm. Very dark gray (10YR 3/1) silty clay loam; moderate fine, granular structure; friable, non-sticky - slightly plastic; many very fine, fine, and medium roots throughout; pH 7.4; abrupt wavy boundary.

A2 2-17 cm. Very dark brown (10YR 2/2) gravelly clay; moderate medium sub-angular blocky structure; firm, sticky, plastic; common discontinuous, faint clay films and pressure faces on ped faces; many very fine and fine, common medium and few very coarse roots throughout; 20% subrounded, weathered gray (2.5YR 6/1) gravels; pH 7.4; gradual wavy boundary.

Bw 17-45 cm. Very dark grayish brown (10YR 3/2) extremely gravelly clay loam; moderate fine subangular blocky structure; friable, slightly sticky, slightly plastic; few patchy faint clay films on ped and pressure faces; common very fine and fine, few medium and coarse roots throughout; 75% subrounded, weathered gray (7.5YR 6/1) gravels; pH 7.8, abrupt irregular boundary.

C/B 45-80 cm. Pale yellow (2.5Y 7/4) extremely gravelly loam; massive structure; friable, non-sticky, slightly plastic; and dark grayish brown (10YR 4/2) very gravelly clay loam; moderate fine subangular blocky structure; friable, slightly sticky, slightly plastic; common very fine and fine, few coarse roots throughout; 61% subrounded, weathered light gray (2.5Y 7/1) saprolite gravels; pH 8.1; gradual wavy boundary.

C 80-110 cm. Pale yellow (2.5Y 8/4) extremely gravelly loam; massive parting to weak very coarse subangular blocky structure; very friable, non-sticky, non-plastic; common very fine and fine, few coarse roots throughout; 61% subrounded, weathered, pale yellow (2.5Y 8/2) and yellow (2.5Y 8/8) gravels; pH 8.1; diffuse wavy boundary.

Site: Punta de Cacao #2 (PC2)
Setting: Valley floor (plaza); mixed deciduous forest
Classification: fine, mixed, isohyperthermic Vertic Epiaquoll (modal Yalbak soil)

A 0 - 48 cm. Black (5YR 2.5/1) clay; moderate, fine sub-angular blocky structure, very firm, sticky, plastic; many continuous distinct pressure faces on ped faces; many very fine, fine, and coarse roots throughout; pH 5.1; gradual wavy boundary.

Bg 48 - 58 cm. Gray (10YR 5/1) clay loam; weak medium subangular blocky structure; firm, sticky, plastic; common discontinuous distinct pressure faces on ped faces; few very fine, fine, and coarse roots, common medium roots throughout; common, rounded, medium black (10YR 3/1) masses of iron-manganese accumulation in the matrix; pH 6.4, abrupt irregular boundary.

Cr 58 - 110+ cm. Pale brown (10YR 6/3), very dark gray (10YR 3/1), and dark yellowish brown (10YR 4/6) extremely gravelly clay; massive structure with moderate, coarse joint fractures; firm, slightly sticky, slightly plastic; few fine and common medium roots that decrease continuously with depth; 85% subrounded, slightly weathered pale brown (10YR 6/3) gravels and cobbles that are slightly weathered calcite and limestone bedrock carapace.

Site: Xaxa Venic #1 (XV1)
Setting: Valley floor (plaza); mixed deciduous forest
Classification: fine-loamy, mixed, isothermic Typic Rendoll

Oi 0 - 1 cm. Slightly decomposed leaf and branch litter.

A1 1 - 3 cm. Dark brown (7.5YR 3/1) loam; weak fine, granular structure; firm slightly sticky, plastic; few faint, patchy, pressure faces on ped faces; many very fine, fine, medium, and common roots throughout; pH 7.5, abrupt wavy boundary.

A2 3-33 cm. Dark brown (7.5YR 3/2) clay, moderate medium subangular blocky structure, very firm, slightly sticky, plastic; many continuous pressure faces on ped faces; many very fine, fine, medium, and common coarse roots throughout; 5% subrounded, weathered, very pale brown (10YR 7/3) gravels, pH 7.6; gradual wavy boundary.

BC 33-46 cm. Dark grayish brown (10YR 4/2) clay loam; moderate medium subangular blocky structure; friable, slightly sticky, slightly plastic; common faint discontinuous pressure faces on ped faces; many very fine, fine, medium, and coarse roots throughout with an intermittent root mat of very fine and fine roots at the lower (BC - C/B) boundary; 12% subrounded, weathered very pale brown (10YR 7/3) gravels; pH 7.8, clear wavy boundary.

C/B 46-56 cm. Pale yellow (2.5Y 8/2) silt loam and light gray (10YR 7/2) loam; weak, coarse subangular structure parting to massive structure; very friable, slightly sticky, slightly plastic; common very fine, fine, medium roots throughout; 13% subrounded, weathered pale yellow (2.5Y 8/2) gravels; pH 7.8; gradual wavy boundary.

C1 56-100 cm. Pale yellow (2.5Y 8/2) loam saprolite; massive structure; very friable, non-sticky, non-plastic; few very fine, fine, and coarse and common medium roots throughout; 14% subangular, slightly weathered, pale yellow (2.5Y 8/2) gravels; pH 8.2; gradual wavy boundary.

C2 100-110 cm. Pale yellow (2.5Y 8/2) very gravelly loam saprolite; massive structure; very friable, non-sticky, non-plastic; few fine, medium, and coarse roots throughout; 40% subangular, slightly weathered, pale yellow (2.5Y 8/2) gravels; pH 8.2.

Site: Xaxa Venic #2 (XV2)
Setting: Valley floor (plaza); mixed deciduous forest
Classification: loamy, mixed, isohyperthermic Typic Hapludert

Oi --- Intermittent, slightly decomposed leaf, palm leaf, and branch litter.

A1 0-22 cm. Dark brown (7.5YR 3/2) clay; moderate fine, granular structure; very firm, slightly sticky, plastic; common discontinuous, faint pressure faces on ped faces; many very fine, fine, and medium roots throughout; pH 7.4, clear wavy boundary.

Bw 22-35 cm. Brown (10YR 5/3) clay loam; moderate fine subangular blocky structure; firm, slightly sticky, slightly plastic; common, discontinuous, faint pressure faces on ped faces; many very fine, fine, and medium roots throughout; 3% subrounded, weathered, light gray (2.5Y 7/2) gravels; pH 7.6, clear wavy boundary.

C/B 35-45 cm. Light gray (2.5Y 7/2) and pale brown (10YR 6/3) silt loam and clay loam; massive structure; firm, slightly sticky, slightly plastic; common very fine, fine, medium roots throughout; 5% subrounded, weathered light gray (2.5Y 7/2) gravels; pH 8.3; gradual wavy boundary.

C1 45-100 cm. Light gray (2.5Y 7/2) silt loam saprolite; massive structure; friable, slightly sticky, nonplastic; common very fine, fine, and few medium roots throughout; 7% subangular, slightly weathered, white (2.5Y 8/1) gravels; pH 8.2; gradual wavy boundary.

90-97 cm. Thin strata of iron stained gravels and cobbles which appear to be residual from bedrock, not recently transported material.

C2 100-125 cm. White (5Y 8/1) cobbly silt loam saprolite; massive structure; friable, slightly sticky, non-plastic; few very fine, fine, medium roots throughout; 34% subangular, slightly weathered, white (2.5Y 8/1) gravels and cobbles; pH 8.2

Site: Xaxa Venic #3 (XV3)
Setting; Valley floor (plaza), mixed deciduous forest
Classification: fine-loamy, mixed, isohyperthermic Typic Hapluderts

A1 0-24 cm. Very dark grayish brown (10YR 3/2) clay; moderate medium, granular structure; very firm, slightly sticky, plastic; common, faint pressure faces on ped faces; many very fine, fine medium, and common coarse roots throughout; 5% subrounded, weathered, pink (7.5YR 7/4) gravels; pH 7.8, gradual wavy boundary.

A2 24-56 cm. Brown (7.5YR 4/2) clay; moderate fine subangular blocky structure; very firm, slightly sticky, plastic; common, faint, discontinuous pressure faces on ped faces; common, very fine, fine, medium, and few coarse roots throughout; 13% subrounded, weathered, pink (7.5YR 7/4) limestone gravel; pH 8.0, abrupt wavy boundary.

C/B 56-66 cm. Pinkish white (7.5YR 8/2) and brown (7.5YR 5/2) loam saprolite; massive structure; friable, slightly sticky, non-plastic; few very fine, fine, medium roots throughout; 5% subrounded, weathered pinkish white (7.5YR 7/2) cobbles; pH 8.2; clear wavy boundary.

C 66-84+ cm. White (10YR 8/1) silt loam limestone saprolite; massive structure; friable, slightly sticky, nonplastic; 7% subrounded, weathered white (10YR 8/1) cobbles; pH 8.5.

Site: Swamp Forest
Setting: Swamp margin on valley floor; mixed deciduous swamp forest
Classification: fine, mixed, isohyperthermic, Fluvaquentic Vertic Endoquoll

A 0-12 cm. Very dark gray (10YR 3/1) clay; moderate, coarse, prismatic parting to strong medium subangular blocky structure; very firm, sticky, plastic; common discontinuous, faint, pressure faces on ped faces; many very fine, fine, medium, and coarse roots throughout; pH 5.7, clear wavy boundary.

Cg1 12-130 cm. Very dark gray (2.5Y 3/1) clay; weak coarse prismatic parting to moderate medium subangular blocky structure; firm, slightly sticky, plastic; faint pressure faces on ped faces and common, continuous distance, nonintersecting slickensides (spread 5-20 cm apart at oblique angles of 20-45 degrees); common very fine, fine, medium, and few coarse roots throughout; common, rounded, medium masses of iron accumulation in the matrix; common, fine rounded black (N 2/5Y/-) noncemented iron-manganese short concretions in the matrix; pH 5.6; clear wavy boundary.

Cg2 130-160 cm. Bluish gray (5B 6/1) clay; weak coarse prismatic parting to moderate medium and coarse subangular blocky structure; firm, slightly sticky, plastic; few very fine and fine roots throughout; common, rounded, medium and coarse yellowish brown (10YR 5/6) masses of iron accumulation in the matrix; few fine and medium rounded black (N 2/5Y/-) noncemented iron-manganese short concretions in the matrix; pH 7.5, gradual wavy boundary.

Cg3 160-230+ cm. Light greenish gray (5GY 7/1) clay; weak medium and coarse subangular blocky structure; firm, slightly sticky, plastic; few very fine and fine roots throughout; common, rounded medium, and coarse yellowish brown (10YR 5/6) accumulations of iron in the matrix; few, fine and medium rounded black (N 2.5Y/-) noncemented, iron-manganese concretions in the matrix; 2% hard chert and soft, weathered limestone bodies (residuum) throughout; pH 8.0.

Site: Bajo

Setting: Seasonal swamp on flat valley floor; small trees and brush swamp forest
Classification: fine, mixed, isohyperthermic Endoaquert

Oi 0-0.5 cm. Intermittent, slightly decomposed leaf litter.

Oa 0.5-2.0 cm. Humus layer.

A 2.0-6 cm. Very dark grayish brown (10YR 3/2) clay; moderate fine, subangular structure; very firm, sticky, plastic; few patchy, faint pressure faces on ped faces; many very fine, fine medium, and coarse roots throughout; pH 7.4, clear wavy boundary.

Ag 6-14 cm. Dark grayish brown (10YR 4/2) clay, moderate medium subangular blocky structure, very firm, sticky, plastic; common discontinuous, faint pressure faces on ped faces; many very fine, fine, medium, coarse roots throughout; few rounded, medium black (N 2.5Y/-) moderately cemented, iron-manganese, concretions in the matrix; 1% subangular, hard, chert gravels, pH 6.2; gradual wavy boundary.

Cg1 14-56 cm. Grayish brown (10YR 5/2) clay; weak medium subangular blocky structure; firm, sticky, plastic; many continuous distinct pressure faces on ped faces and common continuous distance nonintersecting slickensides (spaced 7-20 cm apart at oblique angles); many very fine, fine, and common medium roots throughout; common, rounded, medium, black (N 2.5Y/-), moderately cemented, iron-manganese concretions in the matrix; pH 6.2, gradual wavy boundary.

Cg2 56-96 cm. Gray (5Y 6/1) clay; massive structure; firm, sticky, plastic; many continuous, distinct pressure faces on fracture faces; common continuous, faint nonintersecting slickensides (spaced 7-20 cm apart, at oblique angles); common very fine, fine, and few medium roots throughout; many fine, and common medium rounded black (N 2.5Y/-) moderately cemented, iron-manganese concretions in the matrix; 1% angular, hard chert gravels; pH 7.8; gradual wavy boundary.

Cg3 96-110+ cm. Light gray (%Y 7/2) clay; massive structure; firm, sticky, plastic; common discontinuous, faint pressure faces on ped faces, and a few discontinuous, faint, nonintersecting slickensides on fracture faces (spaced 15-20 cm apart at oblique angles); few fine roots throughout; common rounded, medium black (N 2/5Y/-), moderately cemented, iron-manganese concretions in the matrix; pH 7.5.

Appendix D - Species presence

FAMILY	SPECIES	PC1	PC2	XV1	XV2	XV3	SW	BA	Abbreviation	
Acanthaceae		+/+								AC
Anacardiaceae	*Astronium graveolens*		+/			/+	/+		ASGR	AA
	Metopium brownei							+	MEBR	AA
	Spondias sp.						+/		SP	AA
	Spondias mombin	/+	/+	/+	/+	/+	+/+		SPMO	AA
Annonaceae					/+	/+				AN
	Cymbopetalum penduliflorum		/+	/+	/+	+/+			CYPE	AN
Apocynaceae				/+					AS	AP
	Aspidosperma cruenta	+/+	+/+	+/+	/+		+/+	+	ASCR	AP
	Aspidosperma megalocarpon	/+	/+		/+				ASME	AP
	Stemmadenia donnell-smithii	+/+	/+	+/+	/+	/+			STDS	AP
	Tabernaemontana chrysocarpa						+/		TACH	AP
	Thevetia ahoui		+/						THAH	AP
Araliaceae	*Dendropanax arboreus*			/+	/+	+/+			DEAR	AR
Bignoniaceae	*Tabebuia* sp.					+/			TA	BI
	Tabebuia rosea						+/+		TARO	BI
Bombacaceae	*Ceiba pentandra*			/+	/+	/+	/+		CEPE	BM
	Quararibea sp.				+/+		+/+		QU	BM
Boraginaceae	*Cordia* sp.		+/+				+/+		CO	BO
	Cordia dodecandra		/+						CODO	BO
Burseraceae							+/+			BU
	Bursera simaruba	/+		/+	/+	/+	/+		BUSI	BU
	Protium copal	+/	+/+	+/+	+/+	+/+	+/		PRCO	BU
Caesalpiniaceae	*Haematoxylon campechianum*							+	HACA	CA
	Schizolobium parahybum		/+				/+		SCPA	CA
	Swartzia belizensis					/+			SWBE	CA
	Swartzia cubensis		/+			+/+	+/+		SWCU	CA
Capparidaceae	*Forchammeria trifoliata*			+/					FOTR	CP
Caricaceae	*Carica papaya*			/+					CAPA	CR
Chrysobalanaceae	*Hirtella americana*	+/+							HIAM	CH
Clusiaceae	*Clusia* sp.							+	CL	CL
Combretaceae	*Bucida buceras*					/+			BUBU	CO
	Terminalia amazonia		+/+				/+	+	TEAM	CO
Euphorbiaceae	*Alchornea latifolia*						+/		ALLA	E
	Croton pyramidalis						+/+	+	CRPY	E
	Drypetes brownii	+/+	+/+		+/				DRBR	E
	Margaritaria nobilis						+/+		MANO	E
	Sapium sp.			/+		/+	+/+		SA	E
Fabaceae	*Erythrina folkersii*					+/			ERFO	F
	Gliricidia sepium						+/+	+	GLSE	F
	Lonchocarpus sp	/+					+/+		LO	F
	Lonchocarpus castilloi				/+	/+	+/+		LOCA	F
	Lonchocarpus rugosus						+/+		LORU	F
	Platymiscium yucatanum						+/		PLYU	F
	Pterocarpus hayesii						+/+		PTHA	F
	Vatairea lundellii		/+	+/+	/+	/+	+/+		VALU	F
Flacourtiaceae	*Casearia bartlettii*	+/							CABA	FL
	Casearia corymbosa					+/+	+/+		CACO	FL
	Homalium racemosum						+/+		HORA	FL
	Laetia thamnia							+	LATH	FL
	Xylosma sp.						+/+		XY	FL
	Zuelania guidonia				/+	+/+			ZUGU	FL
Guttiferae	*Calophyllum brasiliense*	/+	/+			/+		+	CABR	G
Lauraceae							+/+			LA
	Beilschmiedea sp.						+/		BE	LA
	Licaria peckii	/+	/+	/+	+/+		+/		LIPE	LA
	Nectandra salicifolia				/+				NESA	LA
Leguminosae						/+				LE
Liliaceae	*Dracaena americana*	/+		+/+	/+				DRAM	LI
Malpighiaceae	*Byrsonima bucidaefolia*							+	BYBU	MAL
Malvaceae	*Hampea trilobata*							+	HATR	MA
Melastomataceae	*Miconia impetiolaris*		+/						MIIM	MEL
	Mouriri myrtilloides		+/+						MOMY	MEL
Meliaceae		/+								ME
	Cedrela mexicana				/+	+/+			CEME	ME
	Guarea excelsa	+/+	/+	+/+	+/+	+/+	+/		GUEX	ME
	Swietenia macrophylla		/+			+/+	+/+		SWMA	ME
	Trichilia havenensis			+/					TRHA	ME

+/+ = present in understory / present in overstory

FAMILY	SPECIES	PC1	PC2	XV1	XV2	XV3	SF	BA	Abbreviation	
	Trichilia minutiflora	+/+	/+	+/+	+/+	+/+	+/		TRMI	ME
	Trichilia pallida	+/+	+/+	+/+	+/+	+/	+/		TRPA	ME
Mimosaceae	*Acacia* sp.		+/+			/+	+/+		AC	MI
	Acacia cookii	+/+	+/+	+/	+/	+/+	+/+		ACCO	MI
	Acacia glomerosa						/+		ACGL	MI
	Pithecellobium sp.	+/					/+		PI	MI
	Pithecellobium arboreum				/+	/+			PIAR	MI
	Pithecellobium gigantifolium			+/	+/	+/+	+/		PIGI	MI
Moraceae						+/				MO
	Brosimum alicastrum	+/+	+/+	+/+	/+	+/	/+		BRAL	MO
	Cecropia peltata	+/+		/+	+/+		/+		CEPE	MO
	Chlorophora tinctoria				/+				CHTI	MO
	Ficus sp.	+/	/+	/+	/+	+/+	/+		FI	MO
	Ficus glabrata			+/+	/+	/+			FIGL	MO
	Ficus oerstediana	/+							FIOE	MO
	Pseudolmedia sp.	+/+	+/+	+/	+/				PS	MO
	Trophis racemosa		/+	/+		+/+	+/+		TRRA	MO
Myrsinaceae	*Ardisia* sp.	+/					+/		AR	MY
Myrtaceae		+/					+/+	+		MYT
	Calyptranthes chytraculia		+/		/+	+/+	+/		CACH	MYT
	Pimenta dioica		/+	/+		+/+	/+		PIDI	MYT
Ochnaceae	*Ouratea lucens*							+	OULU	O
Palmae				+/						P
	Bactris sp.		+/	+/	+/	+/	+/		BA	P
	Bactris major					+/	+/		BAMA	P
	Cryosophila argentea	+/+	+/+	+/+	+/+	+/+	+/+		CRAR	P
	Orbignya cohune	/+	+/+	+/+	+/+	+/+			ORCO	P
	Roystonea oleracea						+/		ROOL	P
	Sabal morrisiana	+/+	+/+	+/+	+/+	+/+	+/+		SAMO	P
Piperaceae	*Piper* sp.	+/							PI	PI
	Piper auritum			+/					PIAU	PI
	Piper psilorhachis	+/	+/	+/	+/	+/			PIPS	PI
	Piper sempervirens				+/				PISE	PI
Polygonaceae	*Coccoloba* sp.						+/+		CO	PO
	Coccoloba belizensis				+/	+/+	+/+	+	COBE	PO
Rhizophoraceae	*Cassipourea* sp.				/+	/+			CA	RH
	Cassipourea guianensis		/+			+/+	+/+		CAGU	RH
Rubiaceae		+/		/+	+/+		+/			R
	Alibertia edulis		+/				+/		ALED	R
	Alseis yucatanensis	+/	/+			/+			ALYU	R
	Exostema mexicanum		/+						EXME	R
	Faramea occidentalis		+/+						FAOC	R
	Guettarda combsii					+/+			GUCO	R
	Psychotria sp.		+/+	+/+	+/+	/+			PSY	R
	Randia sp.						+/		RA	R
	Simira salvadorensis	/+	+/+	/+	/+	/+	+/+		SISA	R
Rutaceae	*Amyris belizensis*						+/		AMBE	RT
	Zanthoxylum procerum	/+							ZAPR	RT
Sapindaceae	*Allophylus cominia*						+/+		ALCO	S
	Cupania belizensis	+/+		/+		+/+			CUBE	S
	Cupania rufescens						/+		CURU	S
	Matayba oppositifolia					/+			MAOP	S
	Talisia oliviformis	+/+	+/+						TAOL	S
Sapotaceae	*Chrysophyllum cainito*		/+				+/+	+	CHCA	SA
	Manilkara zapota	/+			+/			+	MAZA	SA
	Pouteria sp.		/+	+/+	/+	/+			PO	SA
	Pouteria amygdalina	+/+	/+	+/+	/+	+/+			POAM	SA
	Pouteria campechiana	+/+	+/+	/+	+/	+/+			POCA	SA
	Pouteria durlandii	+/+	+/+	+/+	+/+	+/+			PODU	SA
	Pouteria reticulata	+/+	+/+	+/+	+/+	/+			PORE	SA
	Pouteria sapota		/+						POSA	SA
Simaroubaceae	*Simarouba* sp.	+/	/+	/+		/+			SI	SI
Solanaceae	*Cestrum racemosum*			/+	/+				CERA	SO
Sterculiaceae	*Guazuma ulmifolia*			/+		+/+			GUUL	ST
Tiliaceae	*Luehea seemannii*			/+					LUSE	TI
Ulmaceae	*Celtis schippii*	+/+	+/+						CESC	U
Urticaceae	*Urera baccifera*				+/				URBA	UR
Verbenaceae	*Vitex gaumeri*		/+				+/		VIGA	VE
Violaceae	*Rinorea* sp.	+/	+/+	+/	+/	+/	+/		RI	V
Unknown	Unknown	+/+	+/+	+/+	+/+	+/+	+/+		UNK	

+/+ = present in understory / present in overstory

Appendix E - Codes for species with identical DCA scores

Score symbol	Species abbreviation	Axis 1	Axis 2
a			
	AC	-0.7700	0.4982
	FIOE MO	-0.7700	0.4982
	HIAM CH	-0.7700	0.4982
	MAZA SA	-0.7700	0.4982
	ME	-0.7700	0.4982
	ZAPR RT	-0.7700	0.4982
b			
	CODO BO	-0.0318	0.4982
	EXME R	-0.0318	0.4982
	FAOC R	-0.0318	0.4982
	MOMY MEL	-0.0318	0.4982
	POSA SA	-0.0318	0.4982
	RI V	-0.0318	0.4982
	VIGA VE	-0.0318	0.4982
c			
	BUBU CO	2.3556	0.4982
	GUCO R	2.3556	0.4982
	LE	2.3556	0.4982
	MAOP S	2.3556	0.4982
	PIGI MI	2.3556	0.4982
	SWBE CA	2.3556	0.4982
d			
	ACGL MI	4.6400	0.4982
	ALCO S	4.6400	0.4982
	BU	4.6400	0.4982
	CO PO	4.6400	0.4982
	CRPY E	4.6400	0.4982
	CURU S	4.6400	0.4982
	GLSE F	4.6400	0.4982
	HORA FL	4.6400	0.4982
	LA	4.6400	0.4982
	LORU F	4.6400	0.4982
	MANO E	4.6400	0.4982
	MYT	4.6400	0.4982
	PI MI	4.6400	0.4982
	PTHA F	4.6400	0.4982
	TARO BI	4.6400	0.4982
	XY FL	4.6400	0.4982

Appendix F - Relative abundance of species analyzed for foliar chemistry

Plot	Relative density	Relative basal area	Number of species sampled
PC1	0.692	0.704	9
PC2	0.486	0.537	7
XV1	0.799	0.780	20 (1 near but not in plot)
XV2	0.697	0.662	12
XV3	0.689	0.796	17
SW	0.317	0.356	13 (3 near but not in plot)

Appendix G - Literature supplement

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