ECOTROPICOS 18(1):21-29. 2005
Sociedad Venezolana de Ecología

GEOMORPHOLOGY, SOIL TEXTURE AND TREE DENSITY IN A SEASONAL SAVANNA IN EASTERN VENEZUELA

GEOMORFOLOGIA, TEXTURA DEL SUELO Y DENSIDAD DE LEÑOSAS EN UNA SABANA ESTACIONAL EN EL ORIENTE DE VENEZUELA

Susan Smith[1], Juan F. Silva[2] and Mario R. Fariñas[2]

[1]Instituto Forestal Latinoamericano, Vía Chorros de Milla. Núcleo Forestal, Apartado 36.
Mérida, Venezuela. E-mail: ssmith3_9@hotmail.com.
[2]Instituto de Ciencias Ambientales y Ecológicas (ICAE). Facultad de Ciencias.
Universidad de Los Andes. Mérida (5101), Venezuela

ABSTRACT

We studied the relationship between geomorphology, tree density, and soil texture in a seasonal savanna from eastern Venezuela. Six landforms were identified and mapped. Using a regular design, we sampled soils at depths of 0-20 and 20-40 cm, and determined textural fractions. Alternatively, using a stratified procedure, we measured tree densities by counting and identifying all woody individuals disregarding their size in 5x5 m plots. Contrary to our expectations, results showed that total tree density was positively linked to sand content that assures better drainage but lower water retention capacity. Moreover, tree density was also linked to the more stable landforms, suggesting that surface stability is more influential on tree population growth than water availability in the topsoil. Although most species are present in all landforms, the results also showed that three species (*Curatella americana*, *Byrsonima coccolobifolia* and *Casearia sylvestris*) were associated to the more stable depositional surfaces with sandy soils and other three (*Byrsonima crassifolia*, *Roupala complicata* and *Bowdichia virgilioides*) were associated to surfaces undergoing active morphogenesis with clayish top soil.

Key Words: Geomorphology, heterogeneity, seasonal savanna, soil, texture, tree density, Venezuela

RESUMEN

Estudiamos la geomorfología, textura del suelo y densidad de leñosas en una sabana estacional del oriente de Venezuela. Identificamos y mapeamos seis formas de relieve. Usamos un diseño regular para muestrear los suelos a 0-20 y 20-40 cm de profundidad y luego determinar textura. Paralelamente, en un muestreo estratificado en formas de relieve, identificamos y contamos todos los individuos leñosos sin importar tamaño en parcelas de 5x5 m. Los resultados muestran que la densidad total de leñosas está positivamente relacionada con el contenido de arena, que favorece el drenaje pero no la capacidad de retención de agua. Además, la densidad de leñosas aparece relacionada a las formas de relieve más estables, sugiriendo que la estabilidad de las superficies ejerce más influencia que la disponibilidad de agua en los horizontes superiores sobre el crecimiento arbóreo. Aunque la mayoría de las especies están presentes en todos los relieves, tres especies (*Curatella americana*, *Byrsonima coccolobifolia* and *Casearia sylvestris*) aparecen asociadas a las formas más estables con suelos arenosos y otras tres (*Byrsonima crassifolia*, *Roupala complicata* and *Bowdichia virgilioides*) aparecen asociadas a superficies con morfogénesis activas y texturas superficiales arcillosas.

Palabras clave: Geomorfología, heterogeneidad, sabanas estacionales, suelos, textura, densidad arbórea, Venezuela

Ver artículo con figuras a color en: http://ecotropicos.saber.ula.ve

INTRODUCTION

Variations in the physiognomy of Neotropical savannas seem to be largely determined by water availability and fire frequency at several scales (Cole 1982, Medina and Silva 1990). In regions such as the Orinoco Llanos that experience annual fires we would expect open savannas to predominate and tree cover to be of lesser importance. However, we find areas with variable tree density reaching as much as 4000 trees ha^{-1} (Sarmiento 1983). These variations also take place at the site scale with patches of wooded savanna in mosaic with more open savanna and grassland, and are attributed to topographic and edaphic heterogeneity. Moreover, this heterogeneity is the result of geomorphological processes shaping the landscape (COPLANARH 1974a, 1974b).

Rainfall in savannas is seasonally distributed with almost all rains concentrated in a six-month period. During the rest of the year soils run progressively dry until there is no more water available for plant growth. Savanna trees, however, grow actively during the dry season, proving to be somehow independent of rainfall seasonality (Goldstein and Sarmiento 1987, Goldstein *et al*. 1990). Nevertheless, tree seedlings seem to experience drought even during the short lapses with no rain in the wet season, and this has an effect upon tree growth and survival (Hoffman 1996). Provided that in the long run rainfall is evenly distributed at the local scale, we would expect differences in yearly water availability to depend on the capacity of soils to store water. In turn, these differences affect the probabilities for tree individuals to grow and get established.

A series of studies have documented and described the spatial heterogeneity of the landscape in the Orinoco Llanos, emphasizing the relationships between land forms, soils and vegetation within the same climatic region (Silva and Sarmiento 1976, Silva *et al*. 1971). Together with other evidence (Cole 1982), this suggests that savanna physiognomy is determined by a hierarchical system comprising landform-soil–water availability. At the site scale, water available for plant growth depends on the capacity of the soil to store water, and this is determined by soil texture and structure (Dodd and Lauenroth 1997, Grassi 1998, Sala *et al.* 1992, Sala *et al.* 1997, Saxton *et al.* 1986, Singh *et al.* 1998). In turn, soil texture and structure are the result of the pedogenetic development at a landform scale (Tricart 1964).

There is a scarcity of studies relating geomorphology, soil textures and tree densities at the site scale. Furthermore, we do not know how the different savanna tree species behave in this context. As a contribution on this direction, we studied the relationships between landform, soil texture and tree density at a site scale in an area submitted to the same annual fire regime. Moreover, we compared the behavior of the different tree species present in the area.

METHODS

The study area is a high, dissected plateau of early Quaternary sediments geologically referred as ‘Mesa’ Formation. Here, hydric erosion has been the most important geomorphogenic process (COPLANARH 1974a, 1974b), originating a landscape with erosive surfaces such as the Mesa and its relicts, with steep cliffs in the borders and depositional landforms such as colluvial valleys and cones (Figure 1). The area is located in southeast Anzoátegui State, Venezuela (9º39´N 63º34´W), in an area known as ‘Mesa de Guanipa’, north of the Orinoco River (Figure 2a). Soils are Entisols, Oxisols and Ultisols deep, with good drainage, pH 4.5 to 5.5, generally low water holding capacity and very poor in nutrients. Mean annual rainfall is 1240 mm; mean annual temperature is 25.5 ºC. Land use is currently restricted to very extensive cattle ranching, burnt annually during the dry season from December to April, although not all areas are burnt in the same fire event. Predominant vegetation is open savanna with the grasses *Trachypogon plumosus* (Humb. & Bonpl. ex Willd) Nees, as the dominant species in the upper terrain and *Andropogon selloanus* (Hack.) Hack *and Axonopus canescens* (Nees ex Trin.) Pilg., in the lower terrain. The most important tree species are *Curatella americana* L., *Byrsonima crassifolia* (L.) Kunth, and *Bowdichia virgilioides* Kunth.

We made a photo-interpretation of a pair of aerial photographs, scale 1:25.000 (Mission 040198, 1977). We identified and delimited all landforms according to the Systematic Method (Buzai and Sanchez 1998) and selected a study area of 288 ha which represented the geomorphological heterogeneity found. The whole study area was reticulated with a sampling point every 150 m for a total of 156. At each point, landform was identified

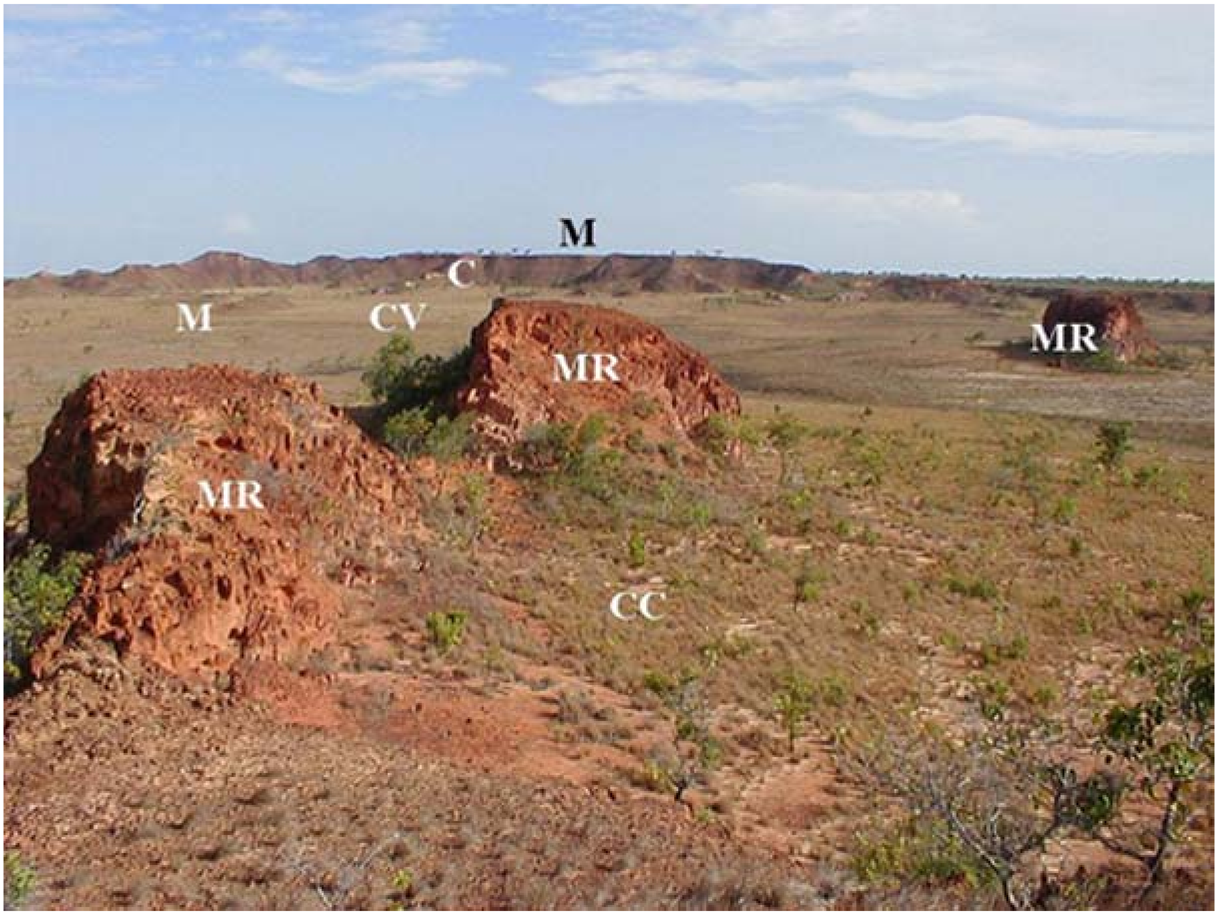

Figure 1. Photograph of the landscape in the study area, showing some of the characteristic landforms. In the background, the mesa (M) and the cliffs (C); in the middle ground, the colluvial valley (CV) with small mounds (M); there are three small relicts of mesa (MR), and in the foreground, a colluvial cone (CC). Photo M. Fariñas.

and soil samples were taken at 0-20 and 20-40 cm depth. This systematic procedure allowed us to assess independently the textural properties of the different landforms. In the laboratory, the different textural fractions were determined using the Bouyucos method (Day 1965). Then, the results for each soil depth were grouped by landform. Sand, silt and clay content were compared using Kruskal-Wallis and Mann-Whitney non-parametric tests.

Vegetation was sampled in each landform using a stratified random procedure. A total of 159 plots (5x5 m) were used. In each plot, all tree individuals (disregarding their size) were counted and identified by species. Results were organized by landform, and mean density values were calculated for total trees, and by species. Non-parametric tests (Kruskal-Wallis, Mann-Whitney) were used to detect significant differences among landforms in terms of total tree density and species density.

We also used Detrended Correspondence Analysis (DCA) to order vegetation plots and integrate results from geomorphology, soils and vegetation. The information for DCA multivariate analysis was obtained from 44 plots (10 x 15 m) distributed among different landforms. Data in each plot included type of landform, slope, tree density and species density according to the procedures mentioned above. A soil sample was taken according to soil sampling procedure. Based on density data, two matrixes were built, one main matrix with the species data and the other with the soil data. This was conformed to quantitative and dummy variables. Additionally, correlation analyses were made with the DCA data to detect relationships between the density of each species and the soil texture.

Indicator Species Analysis (IV) was used to detect the species association with the landforms (Dufrêne and Legendre 1997). The analysis was made with DCA data and the statistic significance was obtained with a Monte Carlo test.

RESULTS

We identified six contrasting landforms: (1) Mesa, (2) Mound, (3) Mesa Relict, (4) Cliff, (5) Colluvial Cone, and (6) Colluvial Valley (Figure 2). 1) 'Mesa', is the largest continuous and the most stable surface except at the borders where active erosive processes are taking place; 2) 'Mound' with a core of lateritic cuirass arise from the plateau or the colluvial valleys as a result of differential erosion; 3) 'Mesa Relict' corresponds to slightly inclined remnants of the Mesa found in depressions; 4) "Cliff" is a steep, rough terrain produced by the intense erosion of the Mesa at the borders, and represent the least stable surfaces; 5) 'Colluvial Cone' formed by the redeposition of sediments from the borders of the Mesa and the Mesa Relict, and conforms to slightly inclined areas; 6) the 'Colluvial Valley' is an extended surface at the lowest level, with a soft rolling relief with flatlands and seasonal lagoons, covered with a thin layer of sediments from the neighboring higher plateaus. Although erosion is taking place in all landforms,

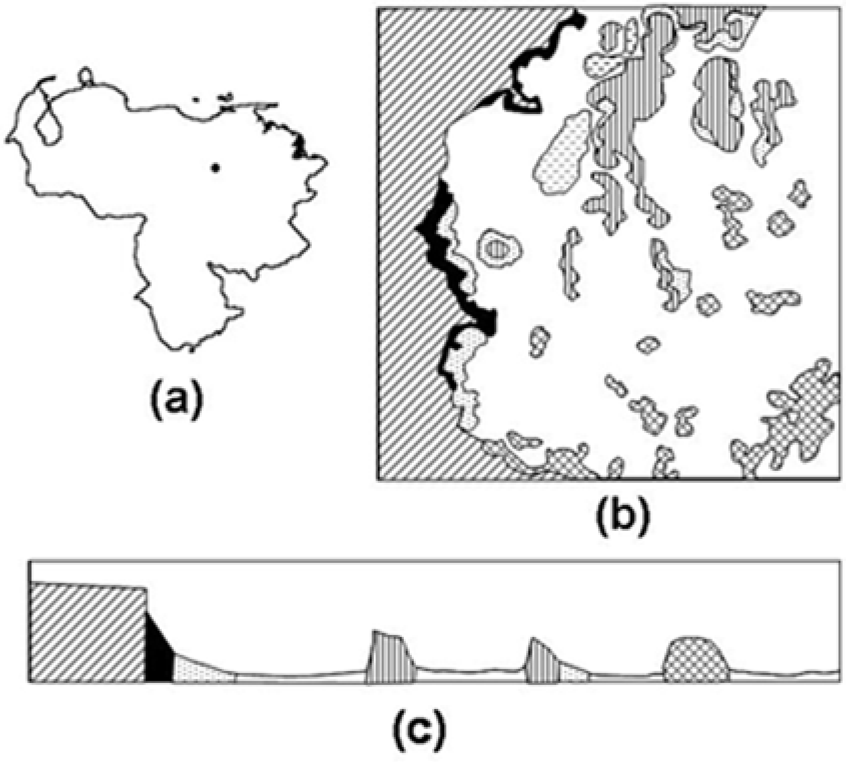

Figure 2. Diagram representing the location of the area of study area in Venezuela (a); the spatial distribution of the landforms within the study area (b); and an idealized cross-section with the relative position of each landform (c, vertical scale exaggerated). Diagonally hatched= Mesa; vertically hatched= Mesa Relict; black= Cliff; stippled= Colluvial Cone; crossed hatched= Mound; white= Colluvial Valley; horizontally dashed= seasonal lagoon.

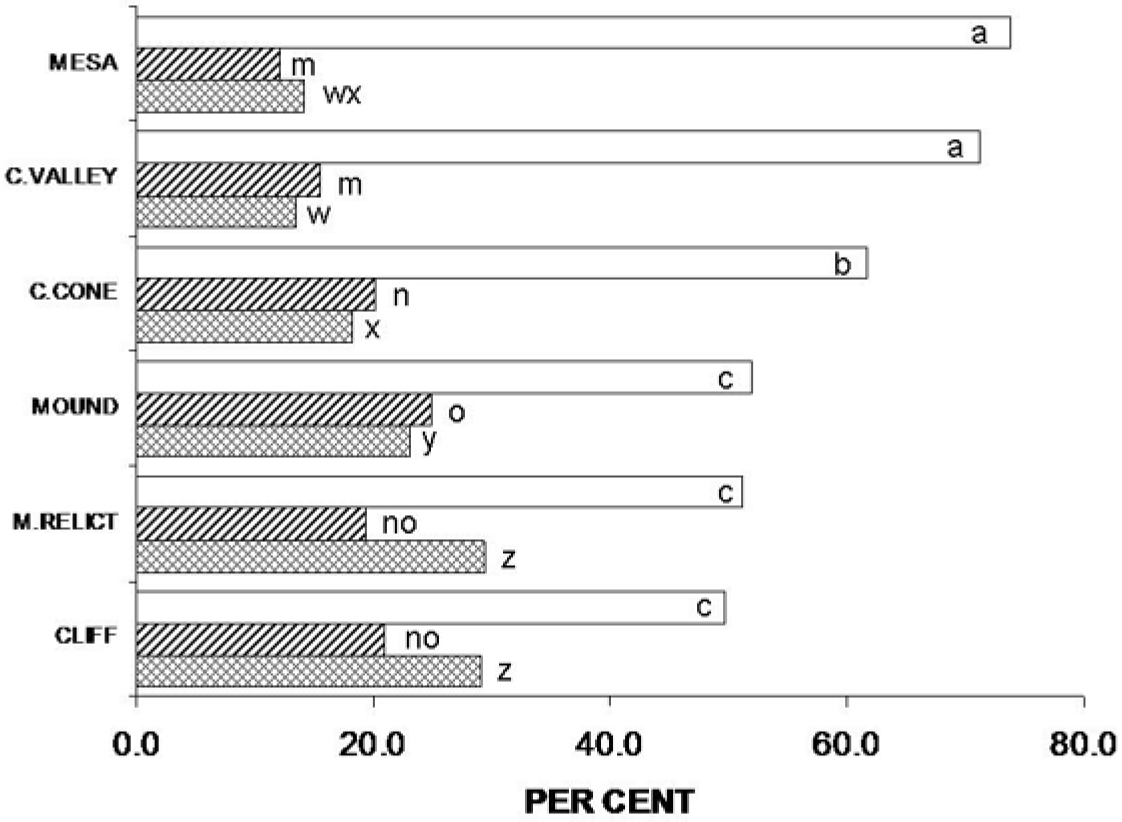

Figure 3. Mean per cent of sand (empty bar), silt (hatched bar), and clay (crossed hatched bar) in each landform. Different letters indicate significant differences between landforms for each soil fraction. Landforms are organized from more stable to less stable types.

these differ by origin and relative stability, which depends on the balance between morphogenesis and pedogenesis. Surfaces where pedogenesis is predominant are more stable than surfaces where morphogenesis still prevails. Mesa and Colluvial Valley are depositional in origin and more stable; Cliff and Mesa Relict are erosional in origin and more dynamic; whereas Colluvial Cone, of depositional origin, and Mound, of erosional origin are intermediate landforms in terms of relative stability.

Landforms are significantly different in soil texture ($p<0.0001$). The soils in the depositional landforms (Mesa, Colluvial Valley and Colluvial Cone) have significantly higher sand content than the soils of the other landforms ($P< 0.05$, Figure 3). Conversely, the erosional landforms (Cliffs, Mesa Relicts and Mounds) have soils with significantly higher proportions of clay ($P< 0.05$). In landforms of intermediated stability, silt content reaches significantly higher values ($P< 0.05$).

Mean total tree density in the whole area is 4582 ind.ha^{-1} and there are significant differences between landforms ($p<0.05$). However, according to the non-parametric analysis, the pattern of variation in total tree density is not related to the geomorphic dynamics of the area. Contrasting landforms such as Mesa, Cliff, Colluvial Valley and Mound do not differ significantly in tree density. Similarly, there was no significant correlation between total tree density and soil texture.

Curatella americana, Byrsonima crassifolia, Bowdichia virgilioides, Palicourea rigida Kunth, and *Byrsonima coccolobifolia* Kunth, were present in all landforms and in the whole range of soil textures. *Casearia sylvestris* Sw. was absent in the Mesa Relicts and *Roupala complicata* Kunth was absent in the Colluvial Valley.

The most abundant tree was *C. americana* with a mean density of 1817 ind. ha^{-1}, and the least abundant was *B. coccolobifolia* with 139 ind.ha^{-1}. Although the non-parametric tests revealed significant differences in density of individual species between landforms (Table 1) these differences do not seem to have any meaning in terms of origin and stability of the landforms.

Two species showed a significant association with landform: *Casearia sylvestris* (IV = 22.1, $p < 0.001$), with its highest mean density in the Colluvial Valley (1836 ind.ha^{-1}) and *Byrsonima coccolobifolia* (IV = 12.3 $p < 0.001$) with its highest mean density in the Mesa (733 ind.ha^{-1}).

Density was significantly correlated to texture in three species as follows. Density of *C. sylvestris* was positively correlated to sand ($r= 0.41$, $p<0.05$) and negatively correlated to silt ($r= -0.38$, $p<0.01$) and clay ($r= -0.39$, $p<0.008$). Density of *R. complicata* was negatively correlated to sand ($r= -0.32$, $p<0.03$) and positively correlated to silt ($r= 0.36$, $p<0.01$). Density of *B. virgilioides* was positively correlated to clay ($r= 0.34$, $p<0.02$). Although there was no significant correlation between *C. americana* and texture, this species only reaches higher density in soils with sand higher than 50%.

A clearer picture of the links between landform, soil texture, slope and vegetation was obtained from the multivariate analyses. Although it does not discern each landform, DCA neatly separates two land form groups (Figure 4). On the right the more stable landforms (Mesa, Colluvial Valley), on the left the less stable forms (Mesa Relict, Cliff). Intermediate landforms (Mound, Colluvial Cone) are spread throughout the ordination space. Three species (*B. coccolobifolia*, *C. americana* and *C. sylvestris*) are clearly associated to the more stable group, whereas another three (*R. complicata*, *B. crassifolia* and *B. virgiliodes*) are associated to the less stable group. *P. rigida* is poorly associated to either group.

In Figure 5, we present the results of the correlation analysis of the DCA. The limit of significance for ‘r’ ($p<0.05$, n-2 degree of freedom) is drawn as a circle, and the variables that fall outside the circle are significantly correlated to either axis; also, the lower the angle between two vectors the higher the positive correlation between them (Benzécri and Benzécri 1980, Lebart *et al*. 1979). The first axis is strongly correlated to soil texture, with Cliff, and Mesa Relict linked to clay, silt and slope, whereas Colluvial Valley is linked to sand. The second axis is correlated to topographic position, with Mesa (high) and Colluvial Valley (low) on opposite extremes, and Cliff and Mesa Relict (transitional). Tree density is correlated to sand and lower positions. Colluvial Cone and Mound did not have a significant correlation to the first two axes of the ordination.

Table 1. Mean tree density (plants.ha^{-1}) measured in each of the six landforms. Different letters indicate significant differences between landforms.

	Landform					
Species	**Mesa**	**Colluvial Valley**	**Colluvial Cone**	**Mound**	**Mesa Relict**	**Cliff**
Curatella americana	2978^{a}	1497^{a}	1750^{ab}	2019^{ab}	1886^{bc}	693^{c}
Byrsonima crassifolia	822^{a}	246^{b}	1200^{ac}	1048^{a}	2305^{c}	1200^{a}
Bowdichia virgilioides	156^{a}	31^{b}	300^{ac}	152^{a}	495^{c}	453^{c}
Byrsonima coccolobifolia	733^{b}	51^{ac}	117^{c}	57^{ac}	19^{a}	80^{ac}
Roupala complicata	44^{c}	0^{b}	783^{ad}	667^{a}	971^{d}	880^{d}
Palicourea rigida	89^{a}	21^{b}	633^{c}	562^{ac}	400^{c}	347^{ac}
Casearia sylvestris	44^{a}	1836^{b}	283^{c}	67^{a}	0^{a}	27^{a}
Tree density	4867^{abc}	3682^{a}	5067^{bc}	4571^{a}	6076^{bc}	3688^{a}

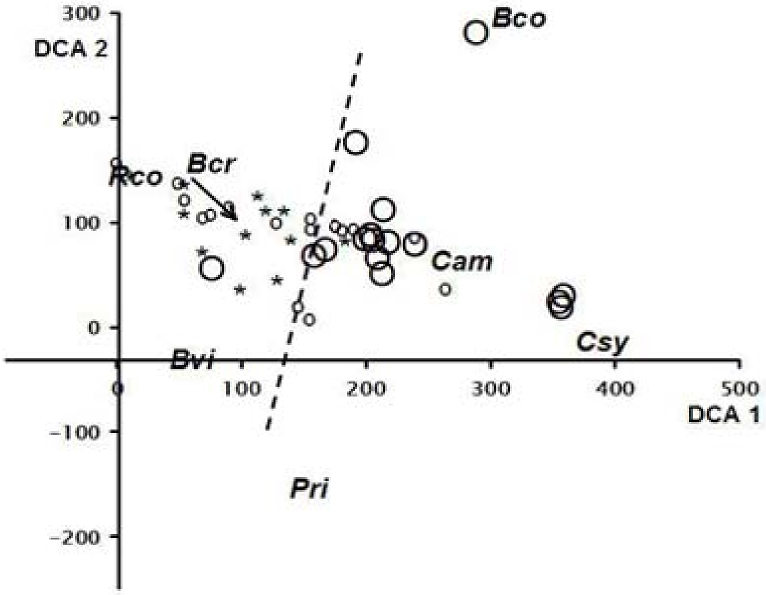

Figure 4. First two axes of the Lineal Correspondence Analysis showing the position of the plots and the species. Bco= *Byrsonima coccolobifolia*; Cam= *Curatella americana*; Csy= *Casearia sylvestris*; Bcr=*Byrsonima crassifolia*; Rco= *Roupala complicata*; Bvi= *Bowdichia virgilioides*; Pri= *Palicourea rigida*. Stars identify less stable landforms; large circles identify the most stable landforms, and small circles identify Colluvial Cone and Mound. The broken line separates the first two groups.

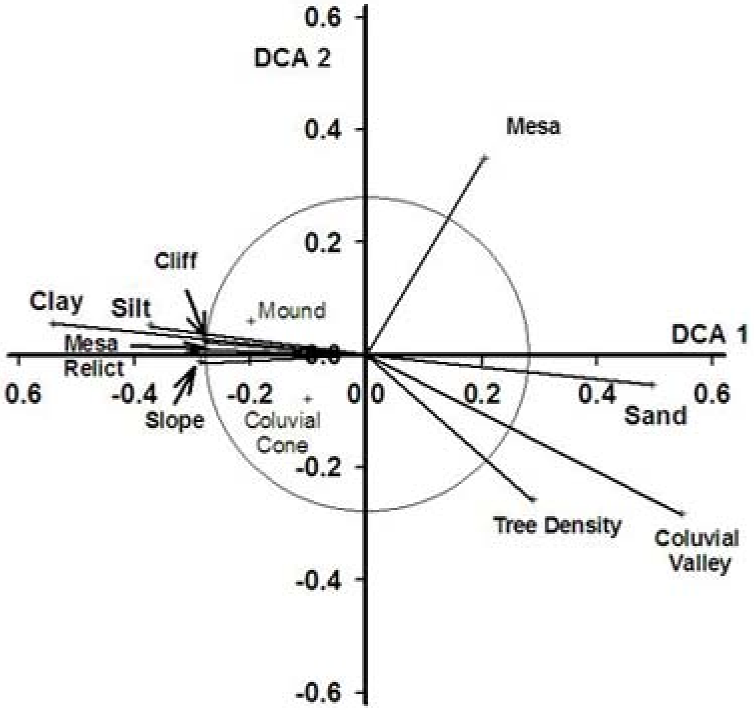

Figure 5. Results of the correlation analysis on the DCA. Variables outside the correlation circle are significantly correlated to the axes (r = 0.294, p<0.05).

DISCUSSION

The relationships between landform and soil texture found in the study area showed that soils in the depositional and more stable landforms are richer in sand whereas the more dynamic landforms are richer in clay. Similar results have been reported for other areas in the Orinoco Llanos (Ponce *et al*. 1994, Sarmiento 1990, Escobar *et al*. 1995, Fassbender *et al*, 1979). In the more stable landforms, pedogenesis is the dominant process and the eluviation of clay progresses without disturbance. That is not the case in the more dynamic landforms originated by erosive processes that removed the upper, sandy layers exposing the clayish layer below. Furthermore, the active morphogenesis hinders the pedogenetic processes to take place (Elizalde and Jaimes 1989).

Total tree density is high and varies significantly between landforms. Although the non-parametric statistics did not show that differences were related to the land dynamics described, the DCA showed a clear link between tree density and the more stable landforms. By the same token, although the direct correlation analysis of total tree density and soil texture was not statistically significant, the multivariate analysis showed landforms and tree density were associated to per cent of sand. Direct, simple correlations between vegetation variables and physical determinants may be difficult to find since there are many explanatory variables and they are not independent. In this context, the results of the multivariate analysis are of greater importance. There are alternative explanations to the lack of significance in the direct correlation analyses between soil texture and tree density. It may be that the change in species dominance occurring along the texture-geomorphological gradient introduces a compensatory effect. In addition, the fact that soil sampling and vegetation sampling were conducted independently may have foiled any direct correlation.

The multivariate and the correlation analyses coincide to show differences in the behavior of individual species. Within the range of textures found, three species (*R. complicata, B. crassifolia* and *B. virgiliodes*) are more abundant on the heavier soils whereas the other three (*B. coccolobifolia*, *C. americana* and *C. sylvestris*) favour sandy soils.

The above mentioned species are widely distributed in the Neotropical savannas. *C. americana*, *B. crassifolia* and *B. virgilioides* are probably the most common tree species in the northern savannas of the Neotropics from Central America and the Caribbean to the northern Amazon region (Sarmiento 1983), but they are also common in the savannas of the Brazilian Shield (Ratter and Dargie 1992). However, their spatial distribution at large or local scale remains unexplained.

In these well drained savannas, higher clay content is related to higher water retention capacity; therefore we expected the clayish soils to have higher tree density. Our results showed the opposite. Tree density was positively associated to sand contents, but also to more stable surfaces. Too active morphogenesis is likely to hinder tree population growth whereas more stable surfaces allows for higher tree density despite lower water retention capacity in the top soil. In addition to this trade-off, drainage may be more influential than water retention capacity on savanna tree growth. Other variables such as soil depth, soil structure, coarse fraction, etc., were not measured. A modeling effort to explain changes in tree density as a result of variations in water available for plant growth should indeed include those variables.

ACKNOWLEDGEMENTS

This study was funded by FONACIT (Venezuela) Grant # 98003404 and by IAI Grant CRN #040. Thanks to P. Alvizu, D. Thielen, J. Smith, and N. Smith for assistance in data analysis. We are grateful to A. Azocar, G. Silva, and K. Kaylor, as well as to two anonymous reviewers for comments and critiques to earlier versions of the manuscript.

LITERATURE CITED

BENZÉCRI, J. P. and F. BENZÉCRI. 1980. Pratique de l´analyse des donnés. 1. Analyse des correspondances.

DUNOD, P, G. D. BUZAI y X. SANCHEZ. 1998. Análisis regional y métodos geoestadisticos de regionalización. Pp. 249-270, *in* Matteucci, S. D. y Buzai, G. D. (Comp.): Sistemas ambientales complejos: herramientas de análisis espacial. Eudeba, Buenos Aires.

COLE, M. M. 1982. The Influence of soil, geomorphology and geology on the distribution of plant, communities. P.p. 145-174 *in* Huntley, B.J. & Walter, B.H. (eds.): Ecology of Tropical Savannas. Springer-Verlag, Berlin.

COPLANARH. 1974a. Estudio Geomorfológico de los Llanos Orientales. Regiones 7 y 8, Sub-regiones 7C, 8A, 8B. Zonas 7C2, 8A2, 8A3, 8B1 y 8B2. Comisión del Plan

Nacional de Aprovechamiento de Recursos Hidráulicos. Caracas.

COPLANARH. 1974b. Estudio Geomorfológico de los Llanos Orientales. Regiones 7 Sub-regiones 7C. Zonas 7C1 y 7C2. Comisión del Plan Nacional de Aprovechamiento de Recursos Hidráulicos. Caracas.

DAY, P.R. 1965. Particle fractionation and particle size analysis. P.p. 545-567, *in* Black, C.A. (ed.): Methods of soil analysis. American Society for Agronomy, Wisconsin.

DODD, M. B. and W. K. LAUENROTH. 1997. The influence of soil texture on the soil water dynamics and vegetation structure of a shortgrass steppe ecosystem. Plant Ecology 133:13-28.

DUFRÊNE, M. and P. LEGENDRE. 1997. Species assemblages and indicator species: the need for a flexible asymetrical approach. Ecological Monographs 67(3):345-366.

ELIZALDE G. y E. JAIMES. 1989. Propuesta de un modelo pedogeomorfológico. Revista Geográfica Venezolana (30):5-36.

ESCOBAR, R., W. FRANCO y A. TORRES-LEZAMA. 1995. Régimen hídrico en plantaciones de Pino Caribe, morichal y sabana al sur del Estado Monagas, Venezuela. Revista Forestal Venezolana 39(1):49-65. 1995.

FASSBENDER, H.W., J. A. COMERMA, P. BRITO and F. SALAS. 1979. Retención y disponibilidad de agua en los suelos de las plantaciones de *Pinus caribaea* en el oriente de Venezuela. Acta Científica Venezolana 30:577-581.

GRASSI, C. 1998. Fundamentos del riego. CIDIAT, Mérida.

GOLDSTEIN, G. and G. SARMIENTO. 1987. Water relation of trees and grasses and their consequences for the structure of savanna vegetation. Pp. 13-37, *in* Walter, B.H. (ed.): Determinants of tropical savannas. IUBS Monograph Series No. 3. Oxford.

GOLDSTEIN, G., F. RADA, M. CANALES y A. AZÓCAR. 1990. Relaciones hídricas e intercambio de gases en especies de sabanas americanas. Pp. 219-241, *in* Sarmiento, G. (ed.): Las Sabanas Americanas. Aspectos de su Biogeografía, Ecología y Utilización. Fondo Editorial Acta Científica Venezolana, Caracas, Venezuela.

HOFFMAN, W. A. 1996. The effects of fire and cover on seedling establishment in a neotropical savanna. Journal of Ecology 84: 383-393.

LEBART, L., A. MORINEAU and J. P. FENELÓN. 1979. Traitament des donnés statistiques. Methods et programmes. Dunod, Paris.

MEDINA, E.and J. F. SILVA. 1990. Savannas of Northern South America: a steady state regulated by water-fire interactions on a background of low nutrient availability. Journal of Biogeography 17: 403-413.

PONCE, M., V. GONZÁLEZ, J. BRANDÍN y M. PONCE. 1994. Análisis de la vegetación asociada a una toposecuencia de los Llanos centro orientales de Venezuela. Ecotropicos 7(2):11-22.

RATTER, J. A. and T. C. DARGIE. 1992. An analysis of the floristic composition of 26 cerrado areas in Brazil. Edinburgh Journal of Botany 49(2): 235 - 250.

SALA, O. E., W. K. LAUENROTH and R. A. GOLLUSCIO. 1997. Plant functional types in temperate arid regions. Pp. 217-233, *in* Smith, T.M., Woodward, I.A. and H.H. Shugar, (eds): Plant Functional Types. Cambridge University, Cambridge.

SALA, O. E., W. K. LAUENROTH and W. J. PARTON. 1992. Long-term soil water dynamics in the shortgrass steppe. Ecology 73(4):1175-1181.

SARMIENTO, G. 1983. The savannas of tropical America. Pp. 245-288, *in* Bourliere, F. (ed): Tropical Savannas. Elsevier. Amsterdam.

SARMIENTO, G. 1990. Ecología comparada de ecosistemas de sabanas en América del Sur. Pp. 15-56, *in* Sarmiento, G. (ed): Las Sabanas Americanas, Aspectos de su Biogeografía, Ecología y Utilización. Fondo Editorial Acta Científica Venezolana, Caracas, Venezuela.

SARMIENTO, G. y M. MONASTERIO. 1971. Ecología de las Sabanas de America Tropical: Análisis macroecológico de los Llanos de Calabozo, Venezuela. Cuadernos Geográficos 4: 7-126.

SAXTON, K. E., W. J. RAWLS, J. S., ROMBERGER and R. I. PAPENDICK. 1986. Estimating generalized soil-water characteristics from texture. Soil Science Society of America Journal 50(4):1031-1036.

SILVA, J. F., M. MONASTERIO y G. SARMIENTO. 1971. Reconocimiento ecológico de los llanos occidentales. II El norte del Estado Barinas. Acta Científica Venezolana 22:60-71

SILVA, J. F. y G. SARMIENTO. 1976. Influencia de factores edáficos en la diferenciación de las sabanas. Análisis de componentes principales y su interpretación ecológica. Acta Científica Venezolana 27: 141 - 147.

SINGH, J. S., D. G. MILCHUNAS and W. K. LAUENTROTH. 1998. Soil water dynamics in vegetation patterns in a semiarid grassland. Plant Ecology 134:77-89.

TRICART, J. 1964. Geomorfología y pedología. Revista Geográfica Venezolana 30:5-36.

Recibido 14 de enero 2005; revisado 18 de julio 2005; aceptado 05 de septiembre 2005.