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DIRECT AND INDIRECT VEGETATION- ENVIRONMENT RELATIONSHIPS IN THE FLOODING SAVANNA OF VENEZUELA

RELACIONES DIRECTAS E INDIRECTAS ENTRE LA VEGETACIÓN Y EL AMBIENTE EN LA SABANA INUNDABLE DE VENEZUELA

Eulogio Chacón-Moreno, María Elena Naranjo and Dimas Acevedo
Instituto de Ciencias Ambientales y Ecológicas (ICAE), Facultad de Ciencias, Universidad de Los Andes, Mérida (5101), Venezuela. Fax: 0274-2401286; E-mail: eulogio@ula.ve

ABSTRACT

The direct and indirect response of vegetation to environmental factors was analyzed in this work. Canonical Correspondence Analysis (CCA), direct gradient analysis technique and Path Analysis, indirect statistical technique, were used to evaluate and understand the response of the vegetation from a flooding savanna in the El Frío area. Data included contain the frequency and cover percentage of plant species, physical and management environmental variables, remote sensed variables and mapping data from 37 sites. Sites were classified in the field as seasonal, hyperseasonal and semiseasonal savannas. Sites were ordered along the first axis. The first ordination axis was mainly associated to relative soil water content, and the second ordination axis was related to grazing intensity. Soil fertility factors presented lowest indirect correlation values with ordination axes. The correlation of topographic features with the first ordination axis, suggest that hydrological dynamics and the capacity to accumulate water in the soil mainly determined the distribution of species in flooding savanna.

Keywords: Tropical savanna, Canonical Correspondence Analysis, Llanos del Orinoco, Venezuela, ordination methods, path analysis, relative soil water content, topography

RESUMEN

Se analizó la respuesta directa e indirecta de la vegetación con los factores ambientales. Se utilizó un Análisis Canónico de Correspondencia (CCA) como técnica de análisis de gradiente, y un análisis de trayectoria (Path Analysis) como técnica estadística indirecta para evaluar y entender la respuesta de la vegetación de una sabana inundable en El Frío. Los datos utilizados contienen información sobre la frecuencia y cobertura de especies de plantas, variables físicas y ambientales, variables de sensores remotos y datos derivados de mapas, sobre 37 censos. Los sitios fueron clasificados en el campo como sabanas estacionales, hiperestacionales y semiestacionales. Los sitios fueron ordenados a lo largo del primer eje. El primer eje de ordenamiento fue principalmente asociado con el contenido relativo de humedad en el suelo, y el segundo eje de ordenamiento fue relacionado con la intensidad de pastoreo. Los factores asociados con la fertilidad de suelo presentaron bajos valores de correlación indirecta con los ejes de ordenamiento. La correlación de las características topográficas con el primer eje de ordenamiento, sugieren que la dinámica hídrica y la capacidad de acumular agua en el suelo determinan principalmente la distribución de especies en la sabana inundable.

Palabras clave: Sabana tropical, Análisis Canónico de Correspondencia, Llanos del Orinoco, Venezuela, métodos de ordenamiento, análisis de trayectoria, contenido relativo de agua en el suelo, topografía

INTRODUCTION

Patterns in plant species composition reflect the response of the vegetation to environmental conditions (Jongman 1995, ter Braak 1987, 1996, Whittaker 1967). In savanna vegetation, climate and soil are mainly responsible for plant species distribution. Climate is the principal influence on plant-available moisture and soil is the main determinant of plant-available nutrients in tropical savannas at the regional scale (Sarmiento 1984, Solbrig *et al*. 1996). The availability of water is controlled by the seasonal rainfall patterns, which determine wet-dry periods. On the other hand, the soils of American tropical savannas are poor in nutrients, and the availability of soil water is related to the geomorphogenic and soil formation processes (Sarmiento 1984).

In the Llanos del Orinoco savanna ecosystem, the availability of water is a variable dependent on the rainfall seasonality and drainage patterns. While the climate determines the regional patterns, the local soil features such as topography, parent of material and age determine the drainage patterns. These features had been used to subdivide the Llanos del Orinoco into regional units. One of these is the flooding savanna located on the alluvial overflow plains. Here, topography and flood of waters interact to form a hydrological environmental gradient ranging from higher areas that remain dry to lower inundated areas. The soil texture along the gradient becomes finer in more frequently flooded areas. The characteristic vegetation of the area is herbaceous, with narrow gallery forest accompanying the watercourses.

Environmental gradients may reflect the gradual changes in a specific factor or a combination of several factors. Patterns of plant species distribution can be observed from continental and regional gradients as well as in latitudinal and altitudinal gradients (Burke 2001, Duckworth *et al.* 2000, Huston 1994). Distribution of plant species into sub-regional gradients is mainly associated to rainfall pattern and geomorphological features (Huston 1994). However, flooding regimes, water availability, and soil texture gradients, explain species distribution at a local scale (Dunham 1989, Huston 1994, Moreno-Casasola and Vásquez 1999, Økland and Odd 1994, Silva and Sarmiento 1976a, b, van Coller *at al*. 2000).

The patterns of species distribution in seasonal tropical savannas are mainly associated to gradients of soil moisture (Huston 1994, Silva and Sarmiento 1976a, b). At a regional scale the plant species distribution of the Orinoco savannas are related to edaphic controls (topography and soil formation), which determine the water and nutrient status (San José *et al.* 1998). Silva and Sarmiento (1976a, b) found that soil texture and the association with soil series are the principal factors that determine the species distribution in seasonal savanna ecosystems.

A gradual change in species composition has been observed in the flooding savanna, from highest areas located on the river bank, never flooded, dominated by *Paspalum chaffanjonii* Maury, *Axonopus purpusii* (Mex.) Chase, and *Sporobolus indicus* (L.) R.Br. to lowest topographical positions on bottom areas, flooded for longer periods, dominated by *Hymenachne amplexicaulis* (Rudge) Ness and *Leersia hexandra* Swartz; the intermediate positions, flooded during short periods, are dominated by *Panicum laxum* Swartz, *Paspalum chaffanjonii* and *Leersia hexandra* (Medina and Motta 1990). Besides, this change occurs gradually and over extensive, almost flat plains, and a vegetation community border is not observed. However, clear differentiations have been observed for three hydrological conditions, which determine the three main savanna ecosystems defined by Sarmiento (1984, 1990): seasonal, hyperseasonal and semiseasonal savannas.

Flooding savannas are used for extensive cattle grazing. However, secondary production is limited by low vegetation production during the dry period (Tejos *et al*. 1990). Management of water, mainly associated to dike construction, is an important factor which regulates water availability during the dry period, in order to increase primary production. Besides, the abundance of cattle is associated to medium-high topographic positions. Then, grazing could be an important factor for the plant species distribution.

It has been reported that hydrology is the main factor determining species composition in flooding savannas (Castroviejo and López 1985, Silva and Sarmiento 1976a, b, Tejos *et al*. 1990) and also the metabolism and morphological adaptation of the dominant species (Medina and Motta 1990). Further, the flux and accumulation of nutrients in the flooding savanna could be related to their hydrological dynamics. Marked changes in the nutrient budgets were not observed in flooding savannas with dike control, but the increase of biomass due to the dike construction might be responsible for an increased in nutrient uptake and immobilization (López-Hernandez *et al.* 1994).

At present most of the studies in flooding savannas have been about nutrient analysis in the vegetation, however there are no analyses of the relationship between species composition and environmental factors using ordination technique. And there is not evidence of how plant species composition is distributed along the environmental gradient. Even if hydrological factors control the species distribution, how other environmental factors associated to soil fertility are related to species distribution?

It is the objective of this study to analyze the relationship between species composition and physical environmental factors in a Venezuela flooding savanna. To achieve this objective we use species ordering techniques and regression path analysis of environmental variables.

STUDY SITE

The study was carried out in a 5000ha area on the El Frío in the flooding savannas of the Llanos del Orinoco, Venezuela (Figure 1). The area is surrounded by tributaries of the Apure River, which flood the grasslands during and shortly after the rainfall period. Vegetation is used for extensive grazing. Traditionally, the grazing was highly seasonal due to rainfall and flooding. However, construction of dikes, located on the El Frío, has increased productivity during the dry season.

The ecology of the study area has been described by Castroviejo and López (1985), Pereira da Silva and Sarmiento (1997), and Pinillos (1999). Chacón-Moreno (2001) described the regional changes in ecosystems and vegetation following to the construction of the dikes.

METHODS

Data

Thirty seven sites were sampled with 100 m^2 (10m x 10m) quadrats according to a stratified random sampling design. The following variables were recorded at every site at the beginning of dry period between November – December 1997:

Vegetation**:** At each site, 10 plots of 1 m^2 were selected at random. Within plot species were listed and cover % of each species was estimated.

Environmental parameters**:** The following variables were measured in the field: depth of clay pan (cm), soil water content (%), fraction of site covered by water (%), density of earthworm mounds (N°/m^2), presence or absence of dung, grazing intensity inferred from the sward height (classified into: not grazed, some grazing and high grazing), topographical position (upper (river bank), intermediate, and lower position), and geographical position recorded using a GPS. Soil samples were collected from 0-20 and 20-40 cm depths. Sand (%), clay (%), silt (%), total nitrogen (%) and soil organic matter (%), were determined in the soil laboratory of the University of Los Andes, Mérida, using standard methods of soil analysis (González 1980, Guitian and Carballas 1976, Horwitz 1955).

The sites were assigned to savanna ecosystem classes: seasonal, hyperseasonal and semiseasonal savannas (Sarmiento 1984, 1990), considering the soil water availability and flooded condition during the previous wet and dry periods. Additionally, a number of remotely sensed and mapped variables were included: Land ecological map unit derived from Landsat TM image classification, absolute altitude (cm) derived from a digital elevation model, and relative altitude in catena (cm) derived from a slope correction of digital elevation model (Smith *et al.*[a] submitted). Position of each site in relation to the dike (upstream or downstream) was determined (See Figure 1). Flooding condition derived from flood duration map based on radar images classification was determined (Smith *et al.*[b] submitted).

Data analysis

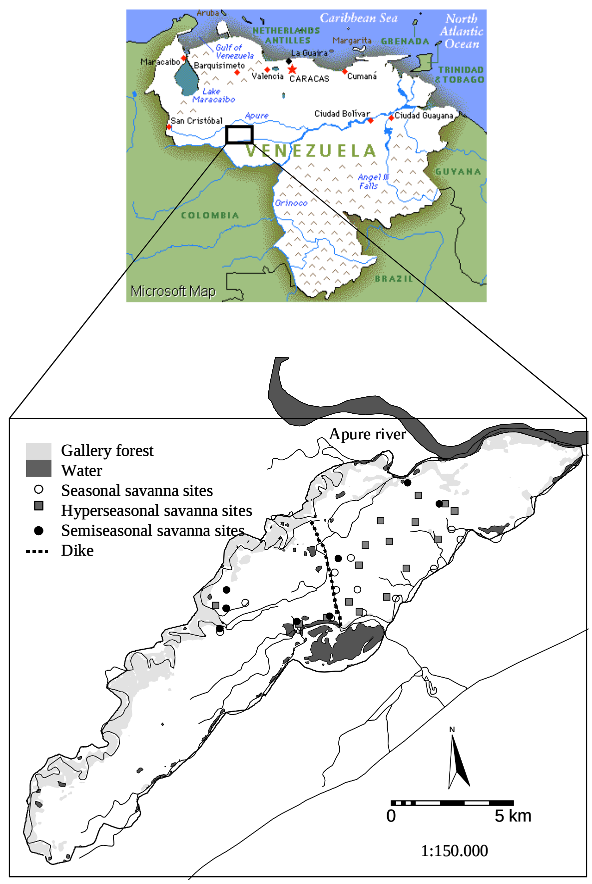

Figure 1. Geographical location of the study area in the flood savanna of El Frío, Venezuela. The sampled sites and dike are indicated.

The relation between species composition and the environmental variables was analyzed using the CANOCO program (ter Braak and Smilauer 1998). A Canonical Correspondence Analysis (CCA) (Jongman *et al.* 1995, ter Braak 1995, 1996, ter Braak and Prentice 1988, ter Braak and Smilauer 1998) was carried out to obtain graphically the relationship between species composition (abundance and frequency) and the environmental variables. The CCA ordinations are scaled based on inter-species distance. The scaling type used was Hill´s (Ter Braak and Smilauer 1998), in order to equalize the average niche breadth for all axes and since it is recommended for long gradients (strong unimodal response) (ter Braak and Smilauer 1998).

Secondly, a Monte Carlo permutation test was used to identify the variables significantly related to species composition. We first investigated the significance of the environmental variables separately. Next, we used a forward selection procedure to select the best environmental variables according to the maximum extra fit and the explained variance (lambda A) (ter Braak and Smilauer 1998).

To determine the indirect relationship of the secondary and not strongly related physical environmental factors to the ordination axis, path analysis models (Legendre and Legendre 1998, Sokal and Rohlf 1981) were used.

RESULTS

Plant species data.

A total of 213 plant species were sampled, of these, 102 species were recorded at one site only. The most frequently recorded species were *Leersia hexandra* (81% of the plots), *Panicum laxum* (72%), *Ipomoea fistulosa* Mart. Ex Choisy (52%), *Paspalum chaffanjonii* (48%), and

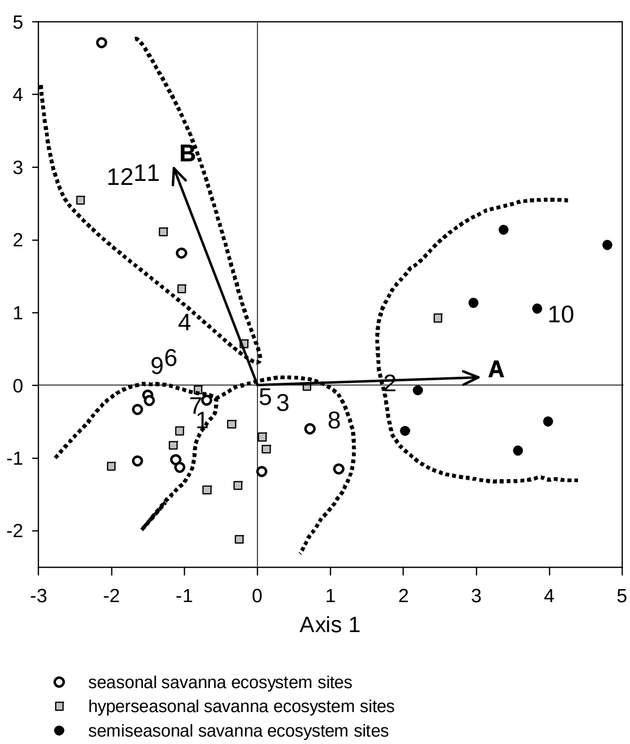

Figure 2. Biplot of sites and most dominant species according to Canonical Correspondence Analysis of cover vegetation data of the El Frío, in the flood savanna area of Llanos del Orinoco, Venezuela. Symbols represent the savanna ecosystems in the area. Arrows show the significant correlation of environmental factors to the ordination axis: A = Relative soil water content, B = Grazing intensity. 1 = Panicum laxum, 2 = *Leersia hexandra*, 3 = *Ipomoea fistulosa*, 4 = *Paspalum chaffanjonii*, 5 = *Mimosa pigra*, 6 = *Sida sp*., 7 = *Hyptis lappacea*, 8 = *Hydrolea spinosa*, 9 = *Dichromena ciliata*, 10 = *Hymenachne amplexicaulis*, 11 = *Axonopus purpusii*, and 12 = *Sporobolus indicus*. Dashed line indicates the site groups.

Mimosa pigra L. (47%). *Panicum laxum* (32.3%) and *Leersia hexandra* (26.1%) were the species with the highest average cover. Other species with high cover values included *Paspalum chaffanjonii* (5%), *Hymenachne amplexicaulis* (Rudge) Nees (2.4%) and *Axonopus purpusii* (Mez) Chase (2.3%). Only 15 species had a cover above 1%.

Gradient analysis (CCA).

In the CCA for vegetation cover data (Figure 2) we observed a sites distribution mainly associated to the first axis and some sites associated to the second axis. Four groups of sites can be separated based on a proxy classification. The first group, located to the extreme right of the first axis, contains the wetter semiseasonal savanna site. The second group is located at the middle of the diagram, and is composed mainly of hyperseasonal savanna sites and some seasonal savanna sites. On the left hand side of the plot, is located a third group dominated by seasonal savanna sites. The fourth group is principally associated and distributed along the upper half of the second axis, and contains both seasonal and hyperseasonal savanna sites.

Only two environmental variables were significant correlated to the ordination. The first axis was related to relative soil water content (A), representing a hydrological gradient from lower at the left side to higher water contents and flooded condition to the right side. The second axis was associated with grazing intensity (B), representing a gradient from low grazing intensity at the bottom position and higher grazing intensity at the top of the diagram.

Relative to the species distribution, on the first axis clearly separates the 12 dominant species in a sequence starting from the extreme right with *Hymenachne amplexicaulis*, a typical semiseasonal savanna species, followed by *Leersia hexandra*, also known to prefer wetter sites, and ending at

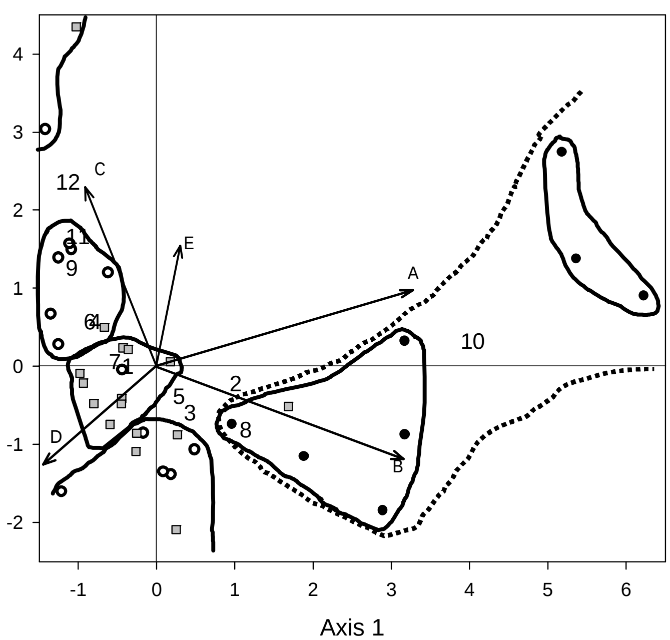

Figure 3. Biplot of sites and most frequents species according to Canonical Correspondence Analysis of frequency vegetation data of the El Frío, in the flood savanna area of Llanos del Orinoco, Venezuela. Symbols represent the savanna ecosystems in the area. Arrows show the significant correlation of environmental factors to the ordination axis: A = Depth of floods, B = Relative soil water content, C = Grazing intensity, D = Micro-relief, and E = Sand % (0-20 cm). 1 = *Panicum laxum*, 2 = *Leersia hexandra*, 3 = *Ipomoea fistulosa*, 4 = *Paspalum chaffanjonii*, 5 = *Mimosa pigra*, 6 = *Sida sp.*, 7 = *Hyptis lappacea*, 8 = *Hydrolea spinosa*, 9 = *Dichromena ciliata*, 10 = *Hymenachne amplexicaulis*, 11 = *Axonopus purpusii*, and 12 = *Sporobolus indicus.* Dashed and solid lines indicate the site groups.

Table 1. Cumulative percentage variance explained by the four principal ordination axes of Canonical Correspondence Analyses (CCA) (frequency and cover) of the El Frío, Apure State, Venezuela. In brackets the variance percentage per axis. P > 0.0050 (Monte Carlo test).

Type of factors	Type of vegetation data	Axis 1	Axis 2	Axis 3	Axis 4
Physical and management factors	Frequency	8.6	14.1 (5.5)	18.8 (4.7)	22.7 (3.9)
Physical and management factors	Cover	11.9	20 (8.1)	25.2 (5.2)	29.3 (4.1)
Remote sensed variables	Frequency	5.8	9.2 (3.4)	12.3 (3.1)	15.1 (3.1)
Remote sensed variables	Cover	7.3	11.3 (4)	13.8 (2.5)	15.4 (1.6)
Physical, management and remote sensed variables	Frequency	8.7	14.3 (5.6)	19.1 (4.8)	23.5 (4.4)
Physical, management and remote sensed variables	Cover	12.1	20.6 (8.5)	26.6 (6)	32.1 (5.5)

the extreme left with *Axonopus purpusii* and *Sporobolus indicus* (L.) R.Br. These two species are the only ones clearly separated by the second axis that locates both at its upper section. The species *I. fistulosa, M. pigra* and *H. spinosa* are associated to the second group, while the other five species *P. laxum, P. chaffanjonii, Sida sp., H. lappacea, D. ciliata*, are more related to the third and fourth groups, jointly on the first ordination axis.

This analysis allow a clear differentiation of the semiseasonal savanna sites which also are represented by *H. amplexicaulis* and *L. hexandra*, and correlated with the wettest environmental gradient.

In CCA for frequency vegetation data (Figure 3), the sites had a similar distribution pattern that the CCA for cover data; however the differentiation between the classified ecosystems was more evident. A first cluster (doted line) very spread along the first ordination axis contain all the semiseasonal savanna sites which also are split in two groups (black line); this axis is mainly related to relative soil water content and depth of flood which are hydrological variables.

Other four groups can be separated presenting more differentiation on the second ordination axis than the first. One of these group of sites, mainly composed of seasonal and hyperseasonal savanna is located in the lower section of the second axis, is associated to non-grazing areas, while on the opposite side of the second axis, two other groups of sites, mainly composed by seasonal savanna sites, are associated to medium and elevated grazing intensity. The second axis is also related to sand % (0 - 20 cm). A group of sites in the middle of two axes is almost totally composed by hyperseasonal savanna sites and is related to high presence of micro-relief.

The species distribution in the Figure 3 followed a similar pattern as in Figure 2; however, *D. ciliate* is more associate to grazing intensity and *H. spinosa* is associated to semiseasonal savanna sites.

Ordination analysis of frequency vegetation data shows a better definition of group into the field classes than the ordination analysis with cover data, and the gradient of grazing intensity represented by the second axis is more clear. Also the number of significant environmental variables correlated with the axes was larger. However, the long of both ordination axes in the CCA with cover vegetation data is larger than the CCA with frequency data.

Table 1 shows the cumulative percentage variance of the species composition data explained by the four CCA axes. The first four axes of the

Table 2. Results of the Monte Carlo permutation test of the relation between species composition and twenty-three environmental factors (physical, management, remotely sensed and ancillary geographical data) of El Frío, Venezuela. Lambda-1 is the proportion of variance explained by each single environmental variable, and Lambda-A is the proportion of conditional variance explained by the variable in forward selection. ns = not significant.

Environmental factors	Frequency				Cover			
	Lambda-1		Lambda-A		Lambda-1		Lambda-A	
	Variance	P	Variance	P	Variance	P	Variance	P
Soil water content (%)	0.56	0.005	0.35	0.005	0.62	0.005	0.62	0.005
Grazing intensity	0.31	0.015	0.29	0.005	0.40	0.005	0.37	0.005
Depth of floods	0.57	0.005	0.57	0.005	0.48	0.005	-	ns
Micro-relief	0.32	0.01	0.26	0.010	0.25	0.020	-	ns
Soil water saturation-class	0.53	0.005	-	ns	0.61	0.005	-	ns
Cover by water	0.43	0.005	-	ns	0.36	0.010	-	ns
Relative altitude in catena	0.35	0.005	-	ns	0.34	0.01	-	ns
Depth of hard pan	0.24	ns	-	ns	0.28	0.025	-	ns
Sand % (0-20 cm)	0.21	ns	0.24	0.050	0.10	ns	-	ns
Nitrogen % (0-20 cm)	0.23	ns	-	ns	0.23	ns	-	ns
Soil Organic Matter (20-40 `	0.23	ns	-	ns	0.23	ns	-	ns
Land Ecological Unit	0.25	ns	-	ns	0.21	ns	-	ns
Flooding condition	0.21	ns	-	ns	0.18	ns	-	ns
Presence of animals (dung)	0.20	ns	-	ns	0.18	ns	-	ns
Soil Organic Matter (0-20 `	0.19	ns	-	ns	0.18	ns	-	ns
Relative position to dike	0.25	ns	-	ns	0.15	ns	-	ns
Sand % (20-40 cm)	0.19	ns	-	ns	0.15	ns	-	ns
Silt % (20-40 cm)	0.25	ns	-	ns	0.14	ns	-	ns
Absolute altitude	0.22	ns	-	ns	0.14	ns	-	ns
Silt % (0-20 cm)	0.20	ns	-	ns	0.14	ns	-	ns
Clay % (20-40 cm)	0.22	ns	-	ns	0.13	ns	-	ns
Clay % (0-20 cm)	0.20	ns	-	ns	0.10	ns	-	ns
Nitrogen % (20-40 cm)	0.17	ns	-	ns	0.09	ns	-	ns

CCA with physical environmental factors and land management data explains 29.3 % of the variance in species composition using cover data and 22.7 % using frequency data. The first four axes of similar models with remotely sensed and mapping information accounted for 15.4 and 15.1 % of the variance in species composition for cover and frequency data respectively. However, when all the factors (physical, management and remote sensed variables) were considered, the total variance explained by the four axes reached 32.1 % for cover data and 23.5 % for frequency data; however the difference with CCA of physical and management factors is not higher. The variance values for the second axis when the cover data and physical and management factors are considered, is larger and is almost the same value than the first axis.

Table 2 presents the correlation among environmental factors in the ordination analyses for frequency and cover data. The Monte Carlo permutation test of frequency data showed that

Table 3. Correlation matrix between environmental factors of a flood savanna, Venezuela . ** = 95% significant, * = 90% significant, ns = not significant

	Sand % (0-20 cm)	Clay % (0-20 cm)	Silt % (0-20 cm)	Soil Organic Matter (0-20 cm)	Nitrogen % (0-20 cm)	Sand % (20-40 cm)	Clay % (20-40 cm)	Silt % (20-40 cm)	Soil Organic Matter (20-40 cm)	Nitrogen % (20-40 cm)	Micro-relief	Depth of hard pan	Depth of floods	Cover by water	Grazing intensity	Presence of animals (dung)	Soil water content (%)	Soil water saturation-class	Relative position to dike	Absolute altitude	Relative altitude in catena	Flooding condition	Land Ecological Unit
Sand % (0-20 cm)	1	*-0.71	*-0.67	**-0.41	ns	*0.84	*-0.81	ns	ns	*-0.59	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Clay % (0-20 cm)		1	ns	**0.39	*0.45	*-0.53	*0.79	ns	ns	*0.74	ns	ns	ns	ns	ns	ns	ns	ns	**-0.33	**-0.40	ns	ns	**0.35
Silt % (0-20 cm)			1	ns	ns	*-0.63	ns	*0.56	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**0.33	ns	ns	**-0.39
Soil Organic Matter (0-20 cm)				1	ns	*-0.45	*0.46	ns	ns	**0.39	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Nitrogen % (0-20 cm)					1	ns	**0.36	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**0.36
Sand % (20-40 cm)						1	*-0.77	*-0.53	**-0.40	*-0.49	ns	ns	ns	ns	ns	**-0.34	ns	ns	ns	ns	ns	ns	ns
Clay % (20-40 cm)							1	ns	*0.43	*0.75	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Silt % (20-40 cm)								1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Soil Organic Matter (20-40 cm)									1	**0.35	ns	ns	ns	**-0.36	ns	ns	*-0.43	**-0.42	ns	ns	ns	ns	ns
Nitrogen % (20-40 cm)										1	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	**-0.37	ns	ns
Micro-relief											1	ns	ns	**-0.34	ns	ns	*-0.46	*-0.50	ns	ns	ns	ns	ns
Depth of hard pan												1	ns	ns	ns	ns	*-0.44	*-0.45	ns	ns	ns	ns	ns
Depth of floods													1	ns	ns	ns	*0.69	*0.65	*0.44	ns	*-0.37	ns	ns
Cover by water														1	ns	ns	*0.74	*0.70	**0.33	ns	**-0.33	**0.37	ns
Grazing intensity															1	ns	ns	ns	ns	ns	ns	ns	ns
Presence of animals (dung)																1	ns	ns	ns	ns	ns	ns	ns
Soil water content (%)																	1	*0.98	ns	ns	*-0.60	**0.33	**0.36
Soil water saturation-class																		1	ns	ns	*-0.57	ns	**0.41
Relative position to dike																			1	*0.78	ns	ns	ns
Absolute altitude																				1	ns	ns	*-0.48
Relative altitude in catena																					1	ns	ns
Flooding condition																						1	ns
Land Ecological Unit																							1

Table 4. Total correlation values between environmental variables and the first ordination axis of CCA, using path analysis.

Environmental variable	r	Environmental variable	r
Relative altitude in catena	- 0.563	Nitrogen % (20-40 cm)	- 0.065
Micro-relief	- 0.449	Land Ecological Unit	0.155
Depth of hard pan	- 0.495	Clay % (0-20 cm)	- 0.133
Soil Organic Matter (20-40 cm)	- 0.251	Silt % (0-20 cm)	- 0.064
Sand % (20-40 cm)	- 0.036	Nitrogen % (0-20 cm)	0.236
Clay % (20-40 cm)	- 0.053		

only seven of the 23 environmental variables presented significant lambda-1 values ($P < 0.05$), and for conditional variance only six variables presented significant values. For the cover data, eight factors had significant correlation, however, in the conditional analysis the number of significant factors is reduced to two.

In the frequency analysis, the maximum individual lambda-1 value observed correspond to the depth of flood. However, relative soil water content and soil water saturation-class presented similar high lambda values. Each one of these three variables explains more than 50% of the variance in the ordination analysis. Conversely, when the conditional effects were calculated, the number of significant variables decreases to only five, but a new soil physical variable (Sand% 0-20) was included into the model. Also the variance for relative soil water content decreased 21%. Grazing intensity was the fourth important factor explaining 31% of the variance; furthermore, when lambda conditional values were calculated the value remained almost similar, only a 2% decrease, due by the independence from the first ordination axis, which is represented by the other factors.

In the cover analysis, relative soil water content and soil water saturation-class presented the highest individual lambda-1 values, above 60%. These values were 10% higher than the values presented by the other five significant variables. For conditional effects, only two variables presented significant variance: relative soil water content and grazing intensity. The first one explained 62% and the second one explained 37% of the variance.

In both analyses, the conditional effects show a reduction in the number of significant variables, mainly due to the covariance between the variables associates to the same axis. Then, in the conditional analyses remaining factors represent the two main axes. This effect is remarkable for the cover data, where the number of significant variables is reduced to two, each one for each ordination axis

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Environmental correlations

Table 3 presents a matrix of correlations among the 23 environmental factors considered in the CCA analysis. Many of the soil physical features presented significant negative and positive correlation values among them. Percent of soil organic matter (20-40 cm) and nitrogen content (20-40 cm) present significant negative correlation with hydrological (soil water content and soil water saturation-class) and topographical (relative altitude in catena) variables. Significant correlations were found between clay, silt and nitrogen content (0-20 cm) with the Land Ecological Unit map variable. On the other hand, hydrological variables present significant correlations between them. The relative soil water content shows correlations with almost all hydrological variables (micro-relief, depth of hard pan, relative altitude in catena, and Land Ecological Unit), but not with soil texture variables. The highest correlation of relative soil water content with non-hydrological variables was with relative altitude in catena (60%). Grazing intensity was the unique environmental variable that did not present a correlation with any other variable.

These results confirm the highest relationship among the hydrological variables determining the first ordination axis. Besides the independence and not relation of the grazing intensity variable with the hydrology component highlighted by the association of it with the second ordination axis.

Table 4 shows the results of path analysis as the direct and indirect correlation between selected environmental variables with the first ordination axis from CCA. Relative altitude in catena, micro-relief and depth of hardpan variables presented higher correlation values with the ordination axis. More over these percentages of correlation increase compared to those presented in Table 2. Soil fertility factors presented lower total (indirect plus direct relation) correlation coefficients than direct correlation coefficients calculated in the ordination analysis (Lambda-1 values in Table 2). Only the soil organic matter (20-40 cm) remained with similar percentage value. Land Ecological Unit presented a lower correlation value than in Table 2.

DISCUSSION

The distribution of species in the flooding savanna was related to a hydrological gradient, which is described by the first ordination axis, whereas grazing intensity was related to the second ordination axis. For cover vegetation data, the analysis of the conditional effects shows that only these two factors presented significant relations, which explained a high percentage of the variance. But other factors; mainly associated with hydrological conditions, were particularly significant in explaining the relation of plant distribution in the ordination analysis. The analysis of frequency vegetation data revealed that sand % (0-20 cm) was associated to the second axis, and micro-relief was related to both ordination axes.

analyses which included physical variables and variables associated to management as grazing intensity explained more variance than the analyses which included only remotely sensed and ancillary geographical data. Nevertheless, when all types of environmental variables were included, the variance explained increased. This suggests that some of the remotely sensed and ancillary geographical data could contribute to the explanation of species composition.

Ordination diagram shows that the sites distributed in the diagram are mainly derived by species composition, and especially with dominant species like *L. hexandra, P. laxum, P. chaffanjonii*, *H. amplexicaulis* and *A. purpusii*. The ordination analysis suggests that the species are responding to the hydrological gradient, and the response model follow a unimodal pattern. Along this hydrological gradient, the separation of semiseasonal savanna sites is very clear, however the seasonal and hyperseasonal savanna sites did not present a clear boundery; but we can group the sites associated to different variables. A similar pattern of plant species has been described by Medina and Motta (1990). In flooded savannas of northern Bolivia, the plant communities are mainly associated with water conditions, and the topographically lowest areas are dominated by *Hymenachne amplexicaulis* and *Leersia hexandra* (Haase 1989).

The explained variance was greater for the cover analysis than the frequency analysis, suggesting that species cover differences are larger than species frequency differences between sites. Frequency analysis shows major similarity between the groups separated in the diagram and the ecosystem classes defined. Differences between the cover and frequency analyses could be explained because species like *P. laxum*, and *L. hexandra*, presented a wide distribution along the gradients. These plants, which are dominant in particular ecosystems, could be found with low cover in other ecosystems or transitional areas. Then, frequency analysis reflects the wide distribution of the species in the middle of the gradient and major overlapping of the dominant species. For this reason separation of communities between seasonal and hyperseasonal savanna ecosystems followed a gradual transition between these two types of ecosystems. On the other hand, cover analysis reflects the importance value of the species in each ecosystem, and hence the greater variance explained.

No significant direct relations were found between physical soil properties and the ordination gradient. Path analysis revealed the percentage of indirect relations between the selected variables that were significantly correlated to relative soil water content, with the main species ordination axis. The lowest path correlation values for fertility soil features, and the increment in the correlation of topographic and relief properties with the main ordination axis, suggest that hydrological dynamics associated to the topographic position and the capacity or possibility to accumulate water in the soil determine mainly the distribution of species in flooding savanna. These results coincide with studies about the relationship between geomorphology and hydrology which determine the vegetation type in the area (Sarmiento and Pinillos 2001) and the vegetation diversity and production as result of the soil water content (Sarmiento *et al.* 2004).

On the other hand, the relative altitude in catena factor was significantly correlated to relative soil water content. Both the hydrological gradient and relative altitude presented highest correlations mainly because the topographic position determines the areas more susceptible to flooding.

The depth of hardpan factor was also negatively correlated to relative soil water content, this since the hardpan determines part of the soil water storage capacity because of its impermeability. When the hardpan is almost superficial, storage of water in the soil is lowest and flood conditions occur faster.

The two factors mentioned above, are related to two important aspects associated to the hydrological conditions. The first one is the order in which the study area start to be flooded, because when the rainy season begins the deepest areas will be flooded first and during more time than the relatively higher areas. On the other hand, the presence of hardpan and the depth of it will determine the water storage capacity in the soil.
Higher areas, like the banks do not present hardpan and are also the last areas in getting water, which is not retained for long time in the soil, and flooding does not occur.

Flooding and soil water storage capacity are the determinant factors in these savannas. However, it is very important to remark that the remaining of water in the soil during the dry season will depend on the depth of the hardpan, that is because the total quantity of water that evaporates will be in accordance to the depth of hardpan- the larger the depth of the hardpan, the slower the time of evaporation and vice versa.

In the flooding savannas of El Frío, it is important to remark that the semiseasonal savanna ecosystems are mainly derived as a consequence of the dike construction, then many of the sample areas present a similar geomorphology (Sarmiento and Pinillos 2001). This means that hyperseasonal and semiseasonal savanna ecosystems are situated on the same geomorphological pattern.

On the other hand, the origin of the parental material for the soil genesis is the same for whole area and it determines the low soil fertility of the Neotropical savannas. The semiseasonal savanna derived from the continuous flooding from dike construction, despite of the fact that it shows sediments accumulation dynamics different from the original semiseasonal savanna, there is no enough time for this savanna to generate or modify the soil.

These two facts - the similar geomorphology for both hyperseasonal and semiseasonal savanna ecosystems, and the no formation of new soil type – together with the lack of nutrients, suggest and explain the no correlation or low correlation between the environmental factors associated to the soil physical properties with the ordination axes.

Similar conclusions were reported on tropical dune slacks, where spatial and temporal fluctuations of the water table are strongly related to weather oscillation and topography (Moreno-Casasola and Vásquez 1999).

Comparable results and observations have been made in areas associated with flooding, where the soil moisture regime is the main factor determining the distribution of plants (Dunham 1989, Moreno-Casasola and Vásquez 1999, van Coller *et al.* 2000).

El Frío has a large tradition on extensive cattle grazing. This kind of use is carried out on semiseasonal and hyperseasonal ecosystems during the dry period, but during the wet period the cattle is moved towards the seasonal ecosystem. Many of the native grasses species in the seasonal ecosystem class are non-palatable for cattle, and few palatable species could determining special areas preferred by cattle. Species like *H. amplexicaulis* in the flooding areas and *L. hexandra*, in the hyperseasonal areas did not present grazing signs because the collecting period did not coincide with the grazing period on those areas; however this species are very palatable for grazing.

The second ordination axes reflects the grazing processes mainly on the seasonal and hyperseasonal savanna. The areas associated to grazing intensity showed a relationship to the palatable species like *A. purpusii* and *S. indicus*, while the areas with less grazing intensity were related to species like *M. pigra* and *H. lappacea* which are species favored by overgrazing, where there is not pasture and cattle can not graze. Therefore, this second ordination axes is in fact dividing the preferred areas from grazing from those overgrazing areas. Duckworth *et al*. (2000) showed that one of the more important environmental variables correlated to the first ordination axis in calcareous grassland was grazing intensity. Moreover, grassland communities in a tidal area of The Netherlands presented differences in vegetation structure on the first ordination axes which was highly correlated to grazing intensities (van de Rijt 1996).

In the seasonal savanna areas of Venezuela outside of the flooding savannas, Silva and Sarmiento (1976a, b) found that the main environmental factor associated to the distribution of plants in different soil series is soil texture, which is also related to the infiltration of water in the soil. San José et al. (1998) found that at a regional scale in the Orinoco savannas, the moisture regime and hydrological features are the major determinants of the species, however, flooding savanna areas were not included in this study.

Plant-available moisture and plant-available nutrients are considered the two main determinants of tropical savannas at regional scale (Sarmiento 1984, 1996, Solbrig et al. 1996). At sub-regional or local scale, other factors could be playing important role as determinants of species distribution. In the flooding savanna ecosystems we found that the main factor, which determines species composition, was relative soil water content, related to the topographic position.

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