Ecological and spatial modeling

Mapping ecosystems, landscape changes, and plant species distribution in Llanos del Orinoco, Venezuela

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Thesis

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To my late Parents

To Maryelis, Daniela and Rebeca

¡De más allá del Cunaviche, de más allá del Cinaruco, de más allá del Meta! De más lejos que más nunca.

—¿Con quién vamos?
—¡Con Dios!

¡Ancho llano! ¡Inmensidad bravía! Desiertas praderas sin límites, hondos, mudos y solitarios ríos.

...los rumores de la llanura...: el rasgueo del cuatro en el caney de los peones, los rebuznos de los burros que venían buscando el calor de las humaredas, los mugidos del ganado en los corrales, el croar de los sapos en las charcas de los contornos, la sinfonía persistente de los grillos sabaneros, y aquel silencio hondo, de soledades infinitas, de llano dormido bajo la luna, que era también cosa que se oía más allá de todos aquellos rumores.

La llanura es bella y terrible a la vez; en ella caben holgadamente, hermosa vida y muerte atroz.

El Llano asusta; pero el miedo del Llano no enfría el corazón; es caliente como el gran viento de su soleada inmensidad, como la fiebre de sus esteros.

Tierra abierta y tendida, buena para el esfuerzo y para la hazaña, toda horizontes, como la esperanza, toda caminos, como la voluntad.

¡Llanura venezolana! ¡Propicia para el esfuerzo, como lo fue para la hazaña, tierra de horizontes abiertos, donde una raza buena, ama, sufre y espera!

Passages from a novel writing by:
Rómulo Gallegos
"Doña Bárbara", 1929
Venezuelan novel about the live in the Llanos del Orinoco

Table of Contents

Summary

The transformation of Llanos del Orinoco, focused on the flooding savanna, is evaluated in terms of the change and replacement of the savanna ecosystem and the plant species distribution under a Landscape Ecological approach. This research is carried out at three spatial scales: sub-continental, regional and local. At sub-continental scale, monthly composites NOAA-AVHRR normalized vegetation index (NDVI) images were interpreted based on the phenology of savanna ecosystems in the Llanos del Orinoco region in order to produce an ecosystem map of the area.

At regional scale, an analysis and description of the landscape changes derived from the construction of dikes to control inundation in the flooding savanna of the *Llanos del Orinoco* in Venezuela is presented. Elaborations of the landscape ecological maps were based on a land unit approach. An analysis of the landscape transformation derived from the embankment of the flooding savanna is carried out based on the savanna ecosystems replacement. Besides, the hydrological dynamics of the flooding savanna landscape was analyzed through the Digital Elevation Model (DEM) of the El Frío Biological Station as a representative area of flooding savanna. Field measurements were carried out with real time kinematic geographical positioning system and air photographs as well as radar images are used for further interpretation and modelling. The results were a precise digital elevation model, showing distribution of sinks and insight in the process of filling the area in periods of flooding. This DEM was used to obtain a Relative Altitude Model of the study area, and integrated to the soil water relative content field observation in order to produce single spatial models of plant species distribution in a changing flooding savanna landscape by effect of the embankment in the Llanos del Orinoco.

At local scale, the direct and indirect response of vegetation to environmental factors of flooding savanna in the El Frío Biological Station area were analyzed using Canonical Correspondence Analysis (CCA) as direct gradient analysis technique and Path Analysis as indirect statistical technique. Data contain the frequency and cover percentage of plant species, physical and management environmental variables, remote sensed variables and mapping data from 37 sites. The first ordination axis was mainly associated to relative soil water content and the second ordination axis was related to grazing intensity. The hydrological dynamics and the capacity to accumulate water in the soil mainly determined the distribution of species in flooding savanna. Based on environmental-vegetation relationship, Gaussian logistic models were used to evaluate the response of plant species vegetation on environmental gradients of the area. The vegetation data collected contain information about the frequency and percentage of cover for 57 sampling units (sites). The result is that *Leersia hexandra* and *Panicum laxum*, which are the more abundant species, occupy different position into the environmental gradients. These results define the Ecological Model of plant species distribution.

Finally, the analysis and integration of ecological processes into multiple ecological-spatial models were carried out in order to understand, evaluate and predict the distribution of dominant plant species in a changing flooding savanna landscape by effect of the embankment in the Llanos del Orinoco, Venezuela. The models using multiple spatial variables presented best accuracy than models of single variables. The application of ecological integrated model of several spatial variables could be useful to analyze possible changes in the plant species composition on local, regional or global change scenarios. Based on the concepts and main results described and analyzed in this Thesis, an integrated model of ecosystems distribution in the flooding savanna was assembled. This model is based mainly on the spatial distribution of the dominant species and a state and transition ecosystem model.

Samenvatting

De transformatie van de Llanos del Orinoco, gefocusseerd op de savanna die onder water loopt, is geëvalueerd in termen van verandering en vervanging van het savanna ecosysteem en van de verspreiding van de planten soorten onder een Landschaps Ecologische benadering. Dit onderzoek is uitgevoerd op drie verschillende ruimtelijke dimensies: subcontinentaal, regionaal en lokaal. Op subcontinentaal niveau zijn maandelijkse komposities van NOAA-AVHRR genormaliseerde vegetatie index (NDVI) beelden geïnterpreteerd op basis van de phenologie van de savanna ecosystemen in de Llanos del Orinoco regio om een ecosysteem kaart van het gebied te maken.

Op regionaal niveau is een analyse en beschrijving van de veranderingen van het landschap uitgevoerd, gebaseerd op de constructie van dijken om het onderwater lopen van de savanna van de Llanos del Orinoco in Venezuela te controleren. Uitleg van de landschap ecologische kaarten zijn gebaseerd op een land eenheids benadering. Een analyse van de landschap verandering door het bedijken van de savanna is gebaseerd op het 'vervangen van savanna ecosystemen' benadering. Verder zijn de hydrologische veranderingen van het savanna landschap geanalyseerd met behulp van een digitaal hoogte model (DEM) van het El Frio Biological Station waaruit bleek, dat deze savanna is representatief voor een onderwater lopende savanna. Metingen in het veld zijn gedaan met behulp van kinematische geografische positie systemen, met luchtfoto's en met radar beelden om zo het gebied te interpreteren en modelleren. De resultaten zijn een nauwkeurige digitale hoogte model met daarop de verspreiding van de depressies en met een inzicht in het proces hoe het gebied volloopt met water gedurende de natte periode. Deze DEM is gebruikt om een Relatieve Hoogte Model van het studie gebied te maken en is daarna geïntegreerd met de relatieve bodem water gehalte om zo een enkelvoudig ruimtelijk model van de planten verspreiding in een veranderend onderwater lopend savanna ecosysteem te maken, beïnvloed door de bedijking van de Llanos del Orinoco.

Op lokaal niveau zijn de directe en indirecte reacties van de vegetatie op de omgevings factoren van het onderwater lopende savanna in de El Frio Biological Station gebied geanalyseerd met behulp van 'Canonical Correspondence Analysis' (CCA) als een directe gradiënt analyse techniek en 'Path Analysis' als een indirecte statistische techniek. De data bevatte de frequentie en bedekkings percentages van de planten soorten, fysische- en beheers variabelen, 'remote sensing' variabelen en karterings gegevens van 37 locaties. De eerste ordinatie-as was hoofdzakelijk geassocieerd met de relatieve bodem water gehalte en de tweede ordinatie-as was gerelateerd aan de begrazings intensiteit. De dynamiek van de hydrologie en het vermogen om water in de bodem vast te houden bepaalden de verspreiding van de soorten in de savanna. De reacties van de planten soorten op de omgevings gradiënten van het gebied zijn geëvalueerd, gebaseerd op de relatie van de omgeving en vegetatie en met gebruik van

‘Gaussian’ logistieke modellen. De verzamelde vegetatie gegevens van 57 locaties bevatten informatie over de frequenties en bedekkings percentages. De resultaten laten zien, dat *Leersia hexandra* en *Panicum laxum*, die de meest talrijke soorten zijn, langs de omgevings gradiënten in verschillende gebieden voorkomen. Deze resultaten zijn bepalend voor het Ecologisch Model voor de verspreiding van de planten soorten.

Tenslotte zijn analyses uitgevoerd en ecologische processen geïntegreerd in multiple ecologisch-ruimtelijke modellen om te begrijpen, te evalueren en om te voorspellen, hoe en waarom de verspreiding van dominante planten soorten in een veranderend onderwater lopend savanna landschap in het Llanos del Orinoco gebied in Venezuela, beïnvloed door bedijking, plaats vindt. De modellen, die multiple ruimtelijke variabelen gebruiken, geven betere en nauwkeuriger resultaten dan modellen, die alleen enkelvoudige variabelen gebruiken. De toepassing van ecologisch geïntegreerde modellen met diverse ruimtelijke variabelen zouden erg nuttig kunnen zijn bij het analyseren en voorspellen van mogelijke veranderingen in soorten samenstellingen voor lokale, regionale of globale veranderingen. Gebaseerd op de concepten en belangrijkste resultaten, zoals beschreven in dit proefschrift, is een geïntegreerd model voor de ruimtelijke weergave van ecosystemen in een onderwater lopend savanna gecompileerd. Dit model is hoofdzakelijk gebaseerd op de ruimtelijke verspreiding van de dominante soorten en op een ‘state and transition’ ecosysteem model.

Resumen

La transformación de los Llanos del Orinoco, con énfasis en la sabana inundable, es evaluada en términos del cambio y reemplazo de los ecosistemas de sabana y de la distribución de especies bajo un enfoque ecológico del paisaje. La investigación es llevada a cabo en tres escalas espaciales: subcontinental, regional y local. En la escala subcontinental, se interpretaron de múltiples imágenes NOAA-AVHRR de índices de vegetación normalizado (NDVI) con base en la fenología de los ecosistemas de sabana en la región de los Llanos del Orinoco, y a partir de esta interpretación se obtuvo un mapa de ecosistemas de sabana.

En la escala regional, se presenta un análisis y descripción de los cambios en el paisaje derivados de la construcción de diques para controlar la inundación en las sabanas inundables de los Llanos del Orinoco, Venezuela. Mapas ecológicos del paisaje fueron elaborados con base en un enfoque de unidades ecológicas. Un análisis de la transformación del paisaje de la sabana inundable derivada del manejo del agua fue realizado con base al reemplazo de los ecosistemas. Además, la dinámica hidrológica del paisaje de sabana inundable fue analizada a través de un modelo digital de elevación (DEM) de la Estación Biológica El Frío como área representativa de las sabanas inundables. Mediciones de campo fueron realizadas con un sistema de posicionamiento geográfico cinemático y fotografías aéreas, así como imágenes de radar para complementar la interpretación y modelización. Los resultados fueron un modelo digital de elevación preciso, que muestra la distribución de sumideros y elevaciones que son importantes en los procesos de llenado durante los períodos de inundación. Este DEM fue usado para obtener un modelo de altitud relativa del área de estudio, el cual fue integrado con las observaciones de campo sobre el contenido relativo de agua en el suelo para producir modelos espaciales simples de distribución de especies de plantas en un paisaje de sabana inundable cambiante por efecto del represamiento en los Llanos del Orinoco.

A escala local se analizó la respuesta directa e indirecta de la vegetación en relación a factores ambientales de la sabana inundable en la Estación Biológica El Frío, utilizando Análisis de Correspondencia Canónica como técnica de análisis de gradiente directo y Análisis de Trayectorias como técnica estadística de análisis indirecto. Los datos utilizados en los análisis corresponden a 37 censos de vegetación que contienen porcentajes de frecuencia y cobertura de plantas, variables ambientales físicas y de manejo, y variables de información de sensores remotos y mapas temáticos. El primer eje de ordenamiento fue principalmente asociado con el contenido de agua en el suelo y el segundo eje de ordenamiento fue relacionado con la intensidad de pastoreo. La dinámica hidrológica y la capacidad de de acumular agua en el suelo determinan principalmente la distribución de las especies en la sabana inundable. Con base en la relación entre el ambiente y la vegetación, se evaluó la respuesta de las especies de plantas sobre gradientes ambientales del área usando modelos

logísticos Gaussianos. Los datos de vegetación contienen información sobre la frecuencia y cobertura de 57 unidades de muestreo (censos). Los resultados muestran que *Leersia hexandra* y *Panicum laxum,* que son las especies mas abundantes, ocupan diferente posición dentro de los gradientes ambientales. Estos resultados definen el Modelo Ecológico de distribución de especies de plantas.

Finalmente, el análisis e integración de los procesos y respuestas ecológicas en combinación con variables espaciales dentro de múltiples modelos espaciales-ecológicos fue desarrollado para entender, evaluar y predecir la distribución de especies de plantas dominantes en un paisaje de sabana inundable transformado por efecto del represamiento en los Llanos del Orinoco, Venezuela. Los modelos que usan múltiples variables espaciales presentaron mejor exactitud que los modelos de simples variables. La aplicación de modelos ecológicos integrados de múltiples variables podría ser útil para analizar los posibles cambios en la composición de especies de plantas en escenarios de cambios locales, regionales o globales. Un modelo integrado de distribución de ecosistemas en la sabana inundable con base en la distribución espacial de las especies dominantes y un modelo de estado y transiciones de los ecosistemas fue elaborado como resultado del acoplamiento de conceptos y principales resultados descritos y analizados en esta Tesis.

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CHAPTER 1

INTRODUCTION

1. INTRODUCTION

1.1 Ecological question

Llanos del Orinoco constitutes one of the largest tropical savanna ecosystems located at the Northern part of South America (PDVSA, 1992; Sarmiento, 1983). It is situated between the Andes Mountains to the north and the Amazonian Tropical Rain Forest to the south. Llanos del Orinoco represents a typical neotropical savanna where climate, soil and fire are the main determinants of this ecosystem (Sarmiento, 1983, 1984; Solbrig *et al.*, 1992, 1996; Silva 1987). But due to this savanna ecosystem is a heterogeneous area, those ecological determinants act at different intensities depending on the observation scale. What is the role of the ecological determinants at each observation scale into the Llanos del Orinoco? and how can the intensity of the ecological determinants be modified by the human impact? These two ecological questions about the savanna ecosystems guide the present research. Those questions will be answered through the explanation and modeling, at different spatial scale, of the relationship between ecological processes, such as the savanna ecosystem distribution and plant species distribution, and the environmental factors; besides, the human influence on the ecological processes will be analyzed.

The ecological determinants have been described and analyzed as the main ecological factors which determine the savanna ecosystem function. Climate is the main determinant in the availability of soil water during the year. The climate seasonality establishes seasonality on soil water availability creating periods of hydrological stress by deficit (or excesses in special cases) where the savanna vegetation is adapted by different ecological mechanism. Soil features establishes the nutrients availability, in the case of the Llanos del Orinoco; this factor presents a remarkable effect because the parental material for the soil genesis is derived from leached and oligotrophic quaternary sediments. Fire eliminates the accumulated herbaceous necromass and does not allow the tree cover regeneration.

On the other hand, the effect of the ecological determinants on the savanna ecosystem has been modified by the human influence, especially by the transformation of the savanna ecosystem into agro ecosystems where the natural characteristics of the savanna are completely replaced as in the case of intensive agriculture. Another human impact is the transformation of the natural system in order to change a part of it, keeping the majority of the ecosystem components, like the use of the savannas for extensive cattle raising or the change in the annual hydrological balance to increase the primary production for cattle forage (López-Hernández and Ojeda 1996).

The two aspects considered above – the ecological determinants and the human influence on savanna ecosystems - are studied in this work under the landscape ecological approach focused on the plant available moisture – plant available nutrient equilibrium at different spatial scale of Llanos del Orinoco.

Considering that Llanos del Orinoco is a large area constituted by a general type of sediments (Quaternary parent materials) and a uniform climate (typical savanna climate Aw), the main differences, which determine the landscape heterogeneity at different scales, will be related to the processes which can modified the plant available moisture and the plant available nutrients. At subcontinental scale, the main processes which might be operating on the savanna ecosystems are the differentiation in soil water accumulation associated to the geomorphological dynamics, and a particular zonal soil differentiation. At the regional scale, and focused on the flooding savanna, the soil water availability is modified by the human influence. At the local scale, into the flooding savanna (Figure 1.1), the plant available moisture – plant available nutrient equilibrium could be addressed to mask the nutrients availability by the flooding condition. If this assumption is accepted, then, how the plants have been replaced in relation to the water availability change? These three scales and issues will be analyzed through the whole work.

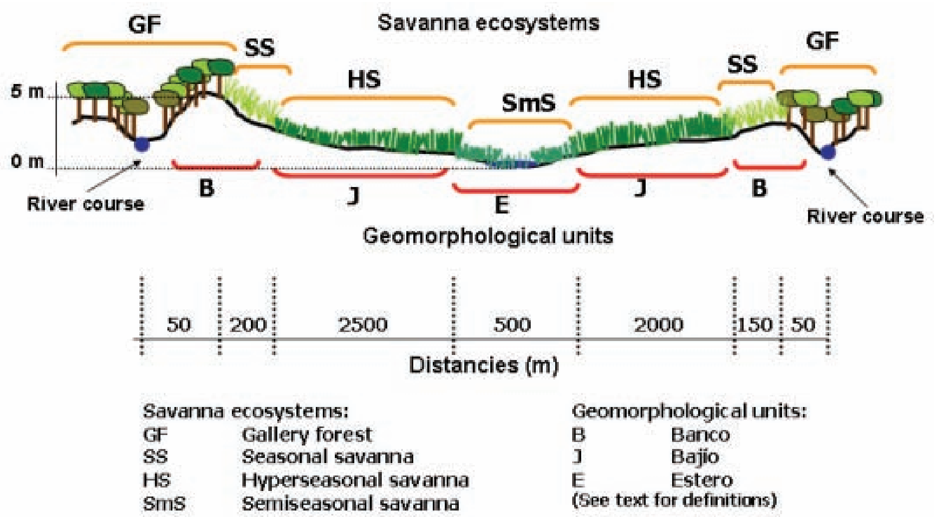


Figure 1.1 Idealized profile of the flooding savanna showing the ecosystem distribution in relation to the topographical gradient on the geomorphological units. Approximate distances between different units and relative altitude are showed.

1.2 Transformation of the Llanos del Orinoco

Venezuela has an extension of almost one million square kilometres, and the Llanos del Orinoco occupies more than a quarter of the territory on the lowest land of the Orinoco river basin (240,000 km2)(PDVSA, 1992). Processes of intense transformation, such as agriculture and cattle raising, have developed throughout the territory. Consequently, the original ecosystems have tended to disappear rapidly, resulting in a mosaic of land cover. Government policies are focused on increasing the use and exploitation of the Llanos areas in order to elevate the quality of life of the Venezuelan people, but most of the time, these policies lack environmental controls.

Traditionally, the use of the savanna ecosystems in Venezuela was for extensive cattle raising, but due to increasing population densities, agriculture use is intensifying. The natural ecosystem is being replaced in two different directions (Silva and Moreno, 1993): 1) Transformation for intensive or semi-intensive cattle raising where the natural plant species are replaced with cultivated pasture. This kind of use requires many inputs (fertilizer and water supply) to sustain production. 2) Transformation to agriculture. As a result, vegetation cover is replaced with crops, and soil properties are modified, requiring large quantities of fertilizer to maintain production. These two transformations were supported by the government which built much of the irrigation infrastructure and subsidizes fertilizer.

The processes of transformation and replacement of natural ecosystems of the Venezuelan savannas have occurred without planning, and some areas of so called “flooding savanna” (they are not permanently flooded), have been transformed in order to maximize economic benefits. There is no clear evidence what the consequences of those transformations are, as well as on species distribution, biodiversity and the ecosystem function.

The impact of these transformations on the natural ecosystem can be analyzed in order to determine the magnitude of the change and the influence on the ecological processes. The definition and mapping of ecosystems, and the modeling of the species distribution related to ecological conditions are two important aspects to be considered in order evaluate the landscape change. The change and transformation processes of ecosystems produce important changes in the species composition and distribution. These changes include the disappearance as well as the appearance of species. Such changes are related to environmental factors; the characterization of the pattern distribution of these environmental factors will contribute, in the spatial context, to explain the possible changes in the species and ecological processes distribution.

1.3 Objective of the research

The objective of this study is to develop and test methodologies for the definition, characterization, analyses, and modeling of the ecological processes associated to the principal ecological determinants of the savanna ecosystem in a spatial context into the Llanos del Orinoco, Venezuela.

Methodologies are developed at three different spatial scales (subcontinental, regional and local) of the savanna ecosystem; at each scale, different specific objectives and methodological approaches are used. At a subcontinental scale, the Llanos del Orinoco are analyzed focusing on savanna ecosystem definition and mapping based on the phenological responses of plants, which also are associated to the climate seasonality as the principal criterion to determine the savanna ecosystems. At a regional scale, the flooding savanna is analyzed in relation to landscape change, making emphasis on the effect of the landscape transformation on the hydrological balance. Particular attention is paid to the local scale and the specific objective is to develop a spatial ecological model in order to analyze the relationship among ecological processes, the hydrological dynamics, and the pattern of species and plant community distribution in flooding savanna.

1.4 Methodological approach

Ecological processes such as plant succession, biodiversity, herbivory patterns, predator interaction, dispersion, nutrient dynamics, species distribution and productivity have an important spatial component. In this thesis, the methodological approach is conformed by the analysis of the savanna landscape through the use and application of ecological tools: Landscape Ecology concepts, vegetation analysis and modeling to understand the processes into the spatial context. The methodological approach require the use of remote sensing techniques, the application of Radar image interpretation as well as the Digital Elevation Model to evaluate the hydrological dynamics.

1.4.1 Savanna ecosystems

The Llanos del Orinoco constitutes the largest area of savanna in Venezuela. This area presents a variety of tropical ecosystems and replacement agroecosystems: semiseasonal forest, gallery forest, seasonal savanna, semiseasonal savanna, hyperseasonal savanna, irrigated crops, rainfed crops and land are grassed. There are several classification systems for savanna ecosystems based on density of vegetation, sociological relation, climatic features, nutrients status, and ecosystem functioning (Bourliere and Hadley, 1983; Huber, 1990; Huntley and Walker, 1982; San José *et al.* 1982; Sarmiento, 1984; Sarmiento, 1990; Sarmiento and Monasterio, 1969). In this study, the savanna classification system to be used takes into account the ecological criterion which considers the hydrological conditions in the soil (Sarmiento, 1990).

Soil water condition is mainly determined by two factors: the rainfall seasonality and the drainage and percolation of water (Sarmiento, 1984). The rainfall seasonality is associated with the Aw climate as defined by the Köppen Climate System (Strahler and Strahler, 1997), with an important dry period of 3-4 months which causes stress through water deficit (Monasterio, 1970; Sarmiento, 1984). The drainage and percolation of water in the soil which is also associated with soil texture and relief (Sarmiento, 1984, 1990; Silva and Sarmiento, 1976a, 1976b). It is important to remark that the other factor influencing the savanna ecosystem is the poor soil fertility associated with a low availability of nutrients in the soil generated under seasonal rainfall climate and Quaternary geological sediments (Sarmiento, 1984; Silva and Sarmiento, 1976b).

Four large sub-regions of savanna ecosystem are recognized based on the particular differentiation of the main determinants of the savanna. According to the age of parental material, landform, and soil, the savannas ecosystems in the Llanos del Orinoco can be classified as the piedmont or footslope savanna, the high plains or tertiary plateau, the alluvial overflow plains and the aeolian plains (Sarmiento, 1983). Particular savanna ecosystems predominate in each sub-regions, therefore, the footslope savanna is characterized by the presence of seasonal savanna on well drained soil; the high plains are characterized by seasonal savanna on very poor soils; the aeolian plains are associated with seasonal and hyperseasonal savanna, of poor and sandy soils, and the alluvial overflow plains are characterized by hyperseasonal and semiseasonal savanna ecosystems (Sarmiento, 1983).

The four sub-regions and the main savanna ecosystems are analyzed at the sub-continental scale, while the regional and local studies are focused on flooding savanna. The flooding savanna ecosystem is an area where the hydrological dynamics plays an important role in the functioning and ecological processes; moreover, it is responsible for the distribution of plants and animals.

1.4.2 Landscape Ecology

Landscape Ecology has developed its main concepts and methodologies during the last three decades (Haines-Young *et al.*, 1994; Wiens, 1999; Zonneveld, 1995). Although studies about the landscape were considered by Humboldt and Darwin, it was the geographer C. Troll who used the term “Landscape Ecology” in 1939 (Zonneveld, 1995). From this date, research about Landscape Ecology has increased in methodological concepts as well as in its applications for planning and conservation.

There is no consensus about conceptual unity of Landscape Ecology as different visions and schools have been developed (Wiens, 1999). However, a clear objective of Landscape Ecology has been set as the relationship between the ecological processes and the spatial configuration in which those processes are developed.

Three phases in the growth and strength of Landscape Ecology can be established. The first phase is characterized by the observation and description of the ecological processes in relation to the environment into the spatial context (Forman and Godron, 1986). Important contributions of this phase are the community studies developed by Braun-Blanquet (1932), and the ecological succession theory proposed by Clements (Clements, 1928).

The second phase starts with the Troll definition, from 1950 to 1980, and the development of concepts and methodologies incorporated from others disciplines, specifically geography and ecology (Forman, 1995). It is important to note the formation of schools and thinking trends in Landscape Ecology. Studies in North America are focused on the ecology of the landscape, while in Eastern Europe the studies centred on social and economic components for planning (Forman and Godron, 1986). In Western Europe, studies focused on different fields such as architecture, planning, conservation, land evaluation, forestry development and include the consideration of humans as an integral part of the landscape (Forman and Godron, 1986; Wiens, 1999; Zonneveld, 1995).

From the 1980s, a great methodological and conceptual advance of Landscape Ecology was developed (Forman, 1995; Forman y Godron, 1986; Klopatek and Gardner, 1999; Naveh and Lieberman, 1984; Turner and Gardner, 1990; Turner *et al*. 2001; Zonneveld, 1995). The methodological development evolved from qualitative analysis and descriptions, to quantitative analysis such as geostatistics, as well as ecological process modeling (Dale, 1999; Klopatek and Gardner, 1999; Turner and Gardner, 1990; Turner *et al*. 2001). Much of these methodological contributions are a consequence of the accessibility to spatial data and information from remote sensing technologies, Geographical Information Systems (GIS), and improved spatial mathematical and statistical models.

During the last years, and from the application point of view, Landscape Ecology has played a very important role as a tool for solving problems about resource management and conservation (Hobbs, 1999). This role is mainly due, to its integration with other disciplines in the study of different processes at the spatial scale, and not only the ecological vision. Because of the diversity of definitions and methodologies derived from different trends and schools, Landscape Ecology has become one of the most inter-disciplinary of sciences (Hobbs, 1999; Zonneveld, 1995), making it perhaps superfluous as a discipline.

Landscape definitions, concepts and characteristics had been described and analyzed in Forman (1995), Forman and Godron (1986), Klopatek and Gardner (1999), Naveh and Lieberman (1984), Turner and Gardner (1990), Turner et al. (2001), and Zonneveld (1995). All these definitions and features emphasize that the landscape is formed by spatial units or elements which are homogeneous in structure and function.

1.4.3 Ecological analysis

To understand the processes and ecosystem dynamics, and the response and distribution of the individuals to the environment, specific analytical tools are required. For vegetation composition and distribution, the plants responses have been studied using a simple series of analyses; from description of plant distribution (e.g., linear regression), to the use of complex statistical analyses (canonical correspondence analysis). These analyses allow us to understand the relationship between plant pattern distribution and the environmental factors that determined such pattern.

On the other hand, ecological processes, such as productivity, are often analyzed based on the phenology dynamics (Azzali and Menenti 1999; Menenti *et al.* 1991). Productivity is a dynamic and changing process which could be monitored when the vegetation phenology changes are observed and associated to the climatic seasonality of the study zone. In this study, the phenological dynamics may be analyzed through the normalized difference vegetation index (NDVI) derived from temporal NOAA satellite images. This index allows to discriminate different production periods for large areas.

Regarding the vegetation-environment relationship, research on vegetation can be divided into two large groups or schools. The first group emphasizes the classification of vegetation based on its floristic composition, whereas the second group highlights quantitative studies and gradient analysis (Fariñas, 2001; Jongman, *et al*. 1995; ter Braak, 1987, 1996). The first group focuses on cluster analysis tools, while the gradient analysis is associated with ordination and regression techniques (Fariñas, 2001; Jongman *et al*., 1995). The classification school focuses strongly on typology. This typology does not take into account real world fuzziness and ever changing arrays of species assemblages.

In this work, ecological analysis is centred on the gradient analysis technique because it usefully links the spatial component within models. Depending on the type of data, the gradient analysis is conformed by two kinds of analysis tools. Ordination techniques are applied to multivariate data, and regression techniques for individual responses (Jongman *et al*., 1995). The analysis of the response of the species to the environmental gradient is based on unimodal response model (Ter Braak and Prentice, 1988; Ter Braak and Smilauer, 1998).

For regression techniques, data are analyzed for each particular species in relation to environmental variables (Ter Braak and Looman, 1995). Although, different types of regression models can be applied to the species-environmental studies, the more simple regression analysis, such as the linear regression, is not a good estimator of the behaviour of the species about environmental variables because the species response in long gradients presents limits at the extreme of gradient where the species fitness is low. In these situations, a unimodal model, such as ordination methods, is better to represent the response of the species to environmental variables, having a maximum of the expression in an optimal point of the gradient, and expressing a tolerance where the species can have a relative high fitness.

1.4.4 Spatial and ecological modeling

In Landscape Ecology, the use of modeling has become an important tool to understand and analyze the relationship between the spatial heterogeneity and the ecological resources (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Guisan, *et al.,* 1998; Turner *et al*., 2001; Zimmermann and Kienast, 1999). Landscape Ecological models can be grouped in three types according to the use or final objective of the model: a) Descriptive models of spatial patterns, b) Models which express the spatial context in the temporal dimension, and c) Predictive models (Turner *et al.* 2001). Descriptive models of spatial patterns include the thematic maps which describe a spatial pattern as the vegetation units or the species abundance, or the relationship between the

species distribution and the environment, as well as the abundance distribution of species related to such habitat characterization and determination.
Models express the spatial context of the changes occurring in the landscape for different time periods. Examples of these models are the spatial expressions of deforestation, where not only the percentage of change area or the change rate is taken, but also the spatial structure of change.
Predictive models are those in which the changes and factors that can affect the pattern of species distribution, vegetation, population, etc., are introduced into the model. It is important to consider the use of prediction models for Global Change scenarios.

In many of the models mentioned before, some authors define them as spatially explicit models (Withers and Meentemeyer, 1999).

The development and conception of spatial models have been enhanced by use of Geographical Information Systems (GIS) that connect spatial data bases with ecological processes. This integration becomes one of the more important objectives in Landscape Ecology (Gustafson, 1998). In this case, the GIS function as a platform on which the diverse ecological information derived from different entities is manage, related and analyzed in the spatial context.

When the spatial information is associated to discrete homogeneous units which define the ecosystem function and structure, it is necessary to use the concept of Landscape Ecological Unit (LEU) or Land Unit (LU) from Landscape Ecology (Forman and Godron, 1986; Turner and Gardner, 1990; Zonneveld, 1989, 1995, 1998). A LEU is the result of combining the features of the landscape spatial structure and the ecological processes associated with the landscape units. The LEU shows the spatial features of the landscape: vertical structure (features of each landscape ecological unit), the horizontal structure (neighbour relationships), as well as the processing dynamics of the ecosystem (Zonneveld, 1989, 1995, 1998).

In this work, the models are based in the analysis of the ecological response in relation the spatial heterogeneity. The ecological response is the central component of the model, and after determining the species-environment relationship, which represents the ecological model, a spatial explicit model is created about the environmental heterogeneity and variables. Then these ecological relationships are expressed into this environmental spatial model.

1.5 Outline of the thesis

The thesis is structured in four parts and follows a hierarchical organization (Figure 1.2). The first part (Chapters 1, 2 and 10) corresponds to a theoretical consideration and description of the general methodological approach, a presentation of the study area, and a synthesis of the work. Chapter one contains the research problems, the objectives of the research and the general description of the methodological approach. In chapter 2, the environment of Llanos del Orinoco is described, the landscape, the hierarchical structure and classification, and how the concept of Landscape Ecological Map is applied to understand the dynamics of the Llanos del Orinoco. Chapter 10 presents the general synthesis and conclusions drawn from the whole work, including an integrating model for plant species and ecosystems distribution.

The second part is developed at sub-continental scale. In chapter 3, the savanna ecosystem definition is linked to a spatial distribution through the analysis of phenological dynamics derived from the interpretation of NOAA satellite imagery time series in order to elaborate an Ecosystem map of the Llanos del Orinoco. At this scale, the relationship between the phenological dynamics and the soil water availability derived from the climate seasonality is the main criterion which leads the discussion.

The third part corresponds to chapters 4 and 5. The hydrological dynamics and the ecosystems changes in the flooding savanna, as the result of the embankment of the area, are evaluated and analyzed through the interpretation of Landsat and radar imagery and DEM, using a framework of Land Ecology Unit. These two chapters are based on the criterion that the change in soil water availability is determinant in the establishment of plants communities.

The fourth part is focused on the study, integration and application of spatial and ecological modeling to determine the vegetation species distribution in the flooding savanna into a local hierarchical level (Chapters 6, 7, 8 and 9). Chapter 6 analyzes the plants species distribution and such distribution with respect to the environmental factors at a local scale of the flooding savanna. Chapter 7 presents the ecological models of distribution for the main dominant species of flooding savanna into the topographical and hydrological gradients. Chapter 8 presents the final ecological and spatial modeling of vegetation species distribution in the flooding savanna based on a single spatial variable, and chapter 9 explains the plant species model distribution based on integration of multiple spatial variables.

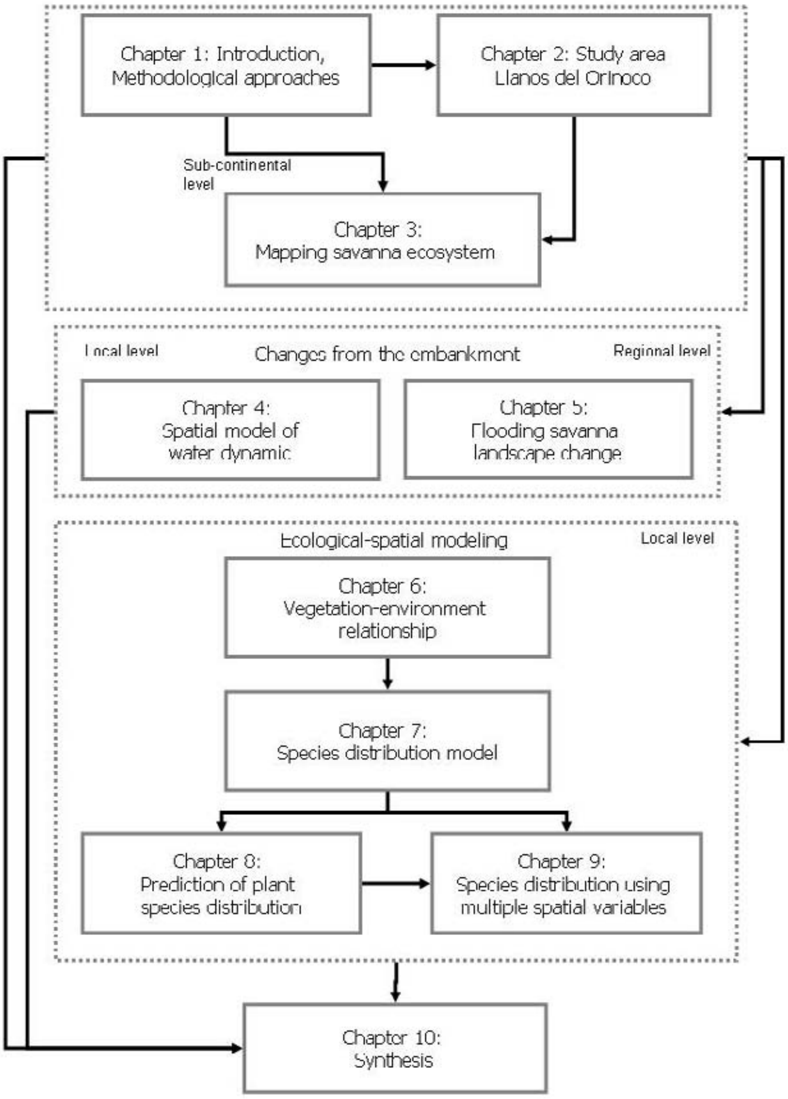


Figure 1.2 Scheme for thesis organization

CHAPTER 2

LLANOS DEL ORINOCO, VENEZUELA

2. LLANOS DEL ORINOCO, VENEZUELA

2.1 Abstract

Llanos del Orinoco represents one of the most beautiful and extensive areas of semi-natural landscape in Venezuela; it represent an area with predominance of savanna ecosystems. The Llanos del Orinoco comprises four sub-regions differentiated according to the geomorphological features: piedmont, high plains, alluvial overflow plains, and aeolian plains. The main tropical savannas ecosystem classes based on the durations of soil water availability, deficit or excess, which are also associated to the climatic conditions, are the seasonal, hyperseasonal and semiseasonal savannas. Seasonal savannas are the areas with herb cover, mainly grasses, with two hydrological seasons. The vegetation responds to one long period of stress. Hyperseasonal savannas are ecosystems with four different hydrological conditions during the year. Plants suffer from two different stress conditions; caused by dry soil and by excess of water. Semiseasonal savannas are ecosystems with two periods. Species distribution and response are driven by excess water during a long period. The diversity and abundance of animal species is associated to the different savanna ecosystems, and the main uses of the Llanos del Orinoco are the extensive cattle raising and agriculture. In this chapter an ecological overview to set the knowledge of the main issues that will be board in the following chapters will be presented.

2.2 Study area

Savanna is one of the most important ecosystem in the Neotropical region. It is found at the northern part of South America in the Llanos del Orinoco, the Guayana Shield and other areas as the valley of Magdalena river and the southern part of Maracaibo lake. In Venezuela, the Orinoco Llanos represents a quarter of the territory and is located on the large sedimentary basin. This region comprises the major savanna area in the northern part of South America (PDVSA, 1992; Sarmiento 1983, 1990) (Fig 2.1).

2.3 Llanos del Orinoco savanna regions

The *Llanos del Orinoco* can be divided according to the age of parent materials, landforms and soil into four principal sub-regions: the piedmont, the high plains, the alluvial overflow plains and the aeolian plains (Chacón-Moreno, 1991; MARNR, 1985; Sarmiento, 1983) (Fig.2.2).

2.3.1 The piedmont (footslope savanna).

This sub-region is located at the bottom of the Andes footslope, and it is characterized by large alluvial fans and a system of alluvial terraces. Savannas occupy the major part of the area and semideciduous tropical forests are widespread on this landform (Monasterio *et al.*, 1971; Sarmiento 1983, Sarmiento *et al.*, 1971a, Silva *et al.*, 1971).

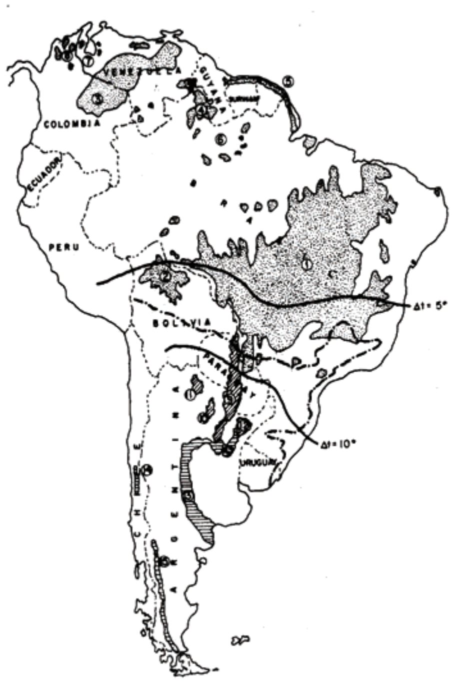


Figure 2.1 Major tropical savanna regions in South America. The Orinoco Llanos are located in the northern part of South America (3). From Sarmiento (1990).

2.3.2 The high plains (Mesas)

The Mesas are low plateaus, at an elevation of 200 to 300 m (Sarmiento, 1983; Sarmiento and Monasterio, 1971) formed during the Late Pliocene or Early Pleistocene. The parent material of this region is somewhat coarse alluvium characterised by hard lateritic layers.

2.3.3 The alluvial overflow plains (flooding savanna).

The alluvial overflow plains or flooding savannas occupy a vast depression in the central part of the Llanos del Orinoco. Their geomorphological dynamics are characterised by many rivers, which transport the Andean sediments, overflow and change their courses during the rainy months. Therefore, the dynamic system effects change with the geomorphology and the pattern of relief that results from these dynamics is characterised by the presence of a topographic catena with natural levees or river banks, intermediate shallow and extensive topographic positions, and low areas or swamps. The difference in height between banks and lowest areas is approximately 3 meters (Sarmiento, 1983; Sarmiento *et al*, 1971b), although it can be less than one meter.

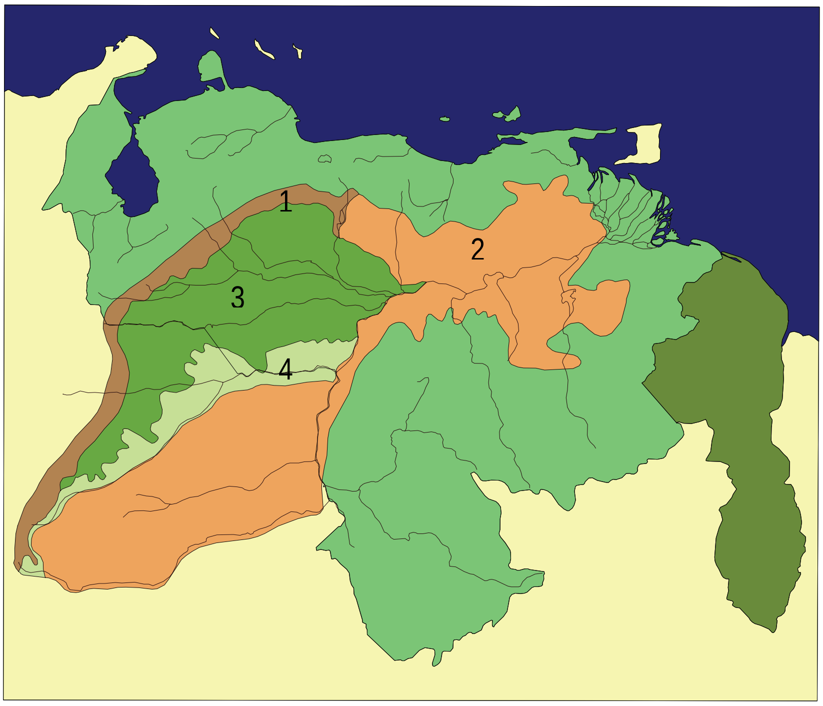


Figure 2.2 Llanos del Orinoco main sub-regions of savanna: 1) Footslope savanna (brown), 2) High plain savanna (orange), 3) Alluvial overflow savanna (dark green), 4) Savannas on aeolian plains (light green). From Sarmiento 1983.

2.3.4 The aeolian plains (aeolian savanna)

These landforms represent the remainder of a former arid morphogenesis that took place during the Wurm glacial period when the Alisios winds took sediments from no vegetated areas during a drier period than that of the current time (Vivas, 1992). The extensive dune relief occurs in areas which are superimposed on larger areas of loess-like material that was partly covered by younger alluvia (Ramia, 1959; Sarmiento, 1983).

2.4 Savanna classes

Savannas are defined as a tropical formation where the grass stratum is continuous and dominant. Occasionally, this formation could be interrupted by trees or shrubs, where fires occur frequently and the growing patterns are associated with the climate seasonality (Bourliere and Hadley, 1983).

The classification, or typology, for savanna areas in Venezuela corresponds to different criteria. From the point of view of the climate, the Llanos del Orinoco presents a regular seasonality, but precipitation shows a gradient which increases from East to West; the areas located in the West have more total annual precipitation than the areas situated in the East. Generally, the Neotropical savannas are considered to be wetter than the African or Australian savannas (Bourliére and Hadley, 1983; Sarmiento, 1983). African savannas have a annual rainfall between 600 to 1500 mm, while the American savanna presents a gradient from 1000 to 1700 mm for the Venezuelan Llanos del Orinoco. The quantity of rainfall has a tight relation to the soil nutrient content because the wet savannas are submitted to more leaching of nutrients, then its have oligotrophic condition with areas which present a sum of exchangeable bases < 5 meq. $100g^{-1}$ soil (Huntley and Walker, 1982; Sarmiento, 1983, 1990).

Regarding the geographic location of savannas and the political division of the country, the Llanos del Orinoco has been classified into three areas: Western Llanos, Central Llanos and Eastern Llanos. The Eastern Llanos correspond with the Mesas type, and Central Llanos correspond with part of the piedmont (footslope savanna) and the the Western Llanos to the alluvial savanna. This typology is mostly used in the economic or regional context because each one is related to the economic development. Eastern savanna is an area where the economy is dominated by the petroleum exploration and exploitation; the Central Llanos, located at the Northern part of the country, is the area with more agricultural development influenced by the fast population growth; the Western Llanos are located between the Andes Region and the Colombia frontier.

Another criterion used to classify savannas in Venezuela is based on the physionomic features emphasizing the proportion of woody elements into the herbaceous matrix. Using these criterion, five different types of savannas can be discerned: 1) grass savanna, where the predominant life form is the herbaceous element (grasses and sedges) without woody elements; 2) open savanna with predominance of the herbaceous strata and a tree cover of 2%; 3) closed savanna, where the woody element occupies 15% of cover; 4) forest savanna, where the woody and herbaceous elements have the same importance in cover, and 5) park savanna is a open savanna where patch or island of woody species area distributed in the landscape, in Venezuela this isolated group of trees is denominated “matas”.

Another classification is based on the floristic composition of savanna, due by the dominance of one or more species, the fytosociological association of the species. Commonly, savannas are classified in relation to the dominance of one species. In Venezuela, savannas are classified as *Trachipogon* savannas because this species is the most dominant in almost all savanna regions (San José *et al.,* 1982; Sarmiento and Monasterio, 1969).

Regarding thermal criteria, it is possible to differentiate regions or savanna landscape that exist at different altitudes, presenting differences in temperature along the altitudinal gradient. Huber (1990) classified the savannas (Venezuelan Guiana region) into two main types: Macrothermic savannas with a average annual temperature over 24ºC and an altitudinal range between 0 and 500 m.a.s.l., and Submesothermic savannas with an average annual temperature between 18 and 24ºC and an altitudinal gradient between 500 and 1400 m.a.s.l. Related to Llanos del Orinoco, the Macrothermic savanna could be an equivalent class.

These classifications are based mainly on the environmental conditions or descriptive features of the savannas, however they do not reflect the functionality of the ecosystems. Sarmiento (1983, 1990) developed a typology of savannas ecosystems using the seasonality of the hydrological regime of soil water availability as the main criterion which will be described in detail in the next section.

2.5 Seasonality and savanna ecosystems

Tropical savannas can be divided into four major categories from an ecological point of view: Tropical Seasonal Savanna, Tropical Hyperseasonal Savanna, Tropical Semiseasonal Savanna, and Swampland (Sarmiento, 1983, 1990) (Fig 2.3).

In the savanna ecosystem, both seasonality and geomorphological conditions determine the dynamics of water in the soil. This can be seen as an ecological criterion more than a simple climate condition (Sarmiento, 1990). The hydrological seasonality determines three intervals with different soil moisture and different ecological function. The first interval is when the content of water in the soil is a limiting factor to natural vegetation or the soil is ecologically dry. The second interval corresponds to the period in which the soil has water to maintain the natural vegetation, but without reaching levels of soil water saturation; this period is called ecologically favorable or wet. The third interval occurs with a situation of water excess in the soil (bad drainage, retention of gravitational water, reduction situations, and hydromorph environment); this period is called water excess or perhydric season.

As a consequence of the annual sequence of wet and dry seasons, the savanna ecosystem can be classified into three main types (Sarmiento, 1983, 1990) (Fig. 2.3): Seasonal savannas (SS) are the areas with herb cover mainly grasses with two hydrological seasons: one dry season which lasts between 4 to 6 months, and another season ecologically favorable with soil water availability. The vegetation, in this ecosystem, responds to one long period of stress, with different pattern of species distribution than the other two ecosystems.

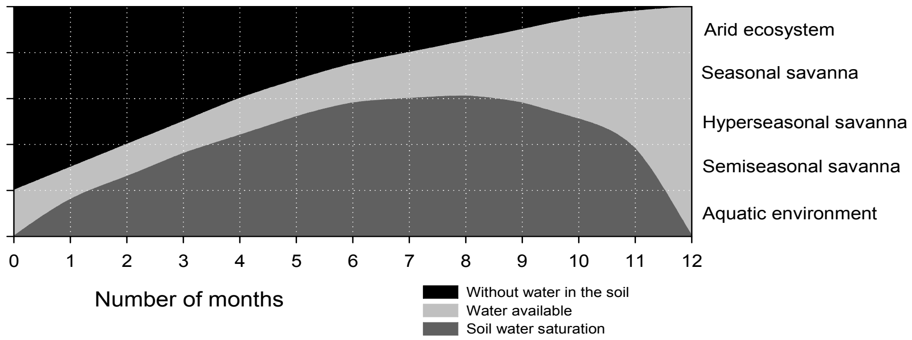


Figure 2.3. Representation of the annual hydrological regime in different kinds of savanna ecosystems. Three situations can be differentiated: without water in the soil, Water available, and soil water saturation. From Sarmiento (1990).

Hyperseasonal savanna (HS) is the ecosystem with four different hydrological conditions during the year: a first dry period of approximately two or three months; a second period with availability of water in the soil which lasts one or two months; a third period with excess of water in the soil, with a duration of 6 to 7 months approximately, and a fourth period with availability of water in the soil, like in the second period, with a duration of one month. The plant communities in this ecosystem respond to two different stress conditions: a) stress caused by dry soil and b) stress caused by excess of water.

Semiseasonal savanna (SS) is the ecosystem with two periods: a favorable one which lasts two or three months, and a long period with excess of water in the soil of approximately 9 months. The plant communities in this ecosystem have a response to environmental stress of excess of water during a long period, which determine almost mono specific flora.

Related to the diversity of species and other ecological features, the seasonal savanna exhibit a high diversity of plants with predominance of grasses (C4), leguminous, and large number of woody species. On the other hand, in the hyperseasonal savanna, the predominant vegetation are grasses and sedges with few species of trees and leguminous. The proportion of species of type C3 is larger than the C4 species. In the semiseasonal savanna, the grass (C3) and sedges species are predominant with almost mono specifics communities (Sarmiento, 1990).

In the flooding savanna, plant communities do not have a specific border of separation because the species are distributed following the hydrological gradient. Then the borders between the seasonal and hyperseasonal savanna as well as the contact area between hyperseasonal and semiseasonal savanna are not very clear (Sarmiento, 1990).

2.6 Climate

The Llanos del Orinoco has a typical tropical wet and dry climate which is classified as wet seasonal tropical (Aw Köppen Climate System) (Strahler and Strahler, 1997); generally, the climate in savanna is tropical macrothermic with an average of temperature for the coolest month above 18 ºC and a noticeable seasonality in the rainfall regime (Nix, 1983; Sarmiento and Monasterio, 1975). The annual precipitation in the Llanos del Orinoco increases from about 1000 mm in the eastern border to 2000 mm close to the Andes Cordillera in the western border (Sarmiento, 1983). Calabozo city, which is located at the Central Llanos, has a annual total rainfall average of 1367 mm, San Fernando, located at South of Llanos del Orinoco, has a average of 1412 mm, and Barinas city, which is on piedmont sub-region (western zone), has a rainfall average of 1688 mm. In Barinas city, the annual average of temperature is 26°C with a difference between the hot and cool months of 5°C; the rainfall distribution has a biseasonal pattern (unimodal) with a period of rain or wet season of 7-8 months from April to October, and other period with little rain or seasonal dry of 3-4 months from December to March; the same pattern of rainfall distribution is observed for san Fernando city (Fig. 2.4) (Acevedo, 1988). During the seasonal wet occurs the 70% of the total rainfall, while during the seasonal dry occurs only 10% of the total rainfall (Acevedo, 1988; Sarmiento, 1984).

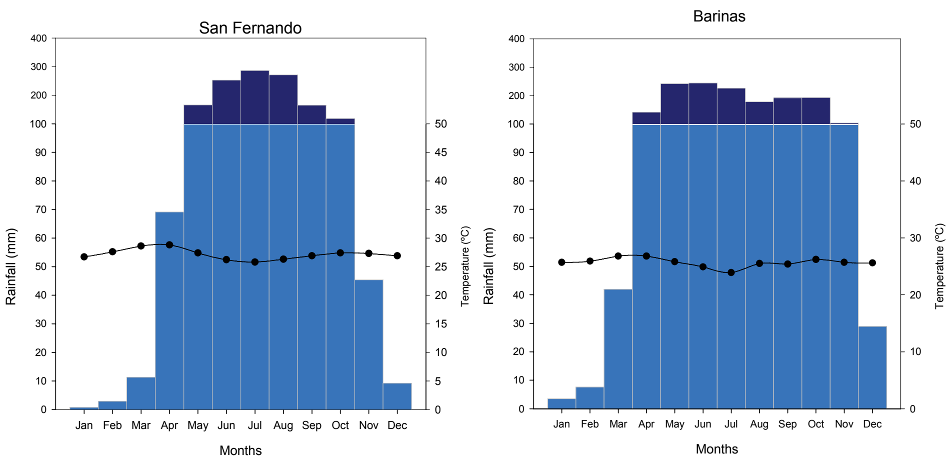


Figure 2.4 Climographs (monthly rainfall and temperature average) of San Fernando and Barinas cities, located in the Central and Western Llanos del Orinoco respectively.

In figure 2.5, a comparison between the annual evaporation and rainfall distribution for Mantecal town, located in the middle of the flooding savanna, is showed. In this figure, we can observe the unimodal pattern of rainfall distribution as that observed in Barinas and San Fernando, and the distribution of the evaporation during the year, in the dry period, when the rainfall is low, the values of evaporation are higher than in the rainy period because the solar radiation is intercepted by the clouds during this period.

2.7 Vegetation

Venezuela, as a tropical country, has a high diversity of plants. The major quantity of diversity is found in the Guayana zone where the tropical rain forest, Tepuy vegetation and savannas predominate, but the highest diversity per area is found in the Andes because the environmental gradient and the isolation determine a high variety of habitats and species (Aguilera *et al*., 2003). The diversity in the Llanos del Orinoco is not so high compared with Guayana or Andes; however, due to the large extension, the Llanos del Orinoco represents an important reservoir of biodiversity. In this region, savanna ecosystems are the predominant as a plant cover, even though there are several large areas covered by various kinds of tropical forests, and almost every watercourse is bordered by a fringe of gallery forest. Other large areas are also covered by swampland (esteros) which are frequently inundated areas (Ramia, 1959; Sarmiento, 1983; Sarmiento *et al*., 1971b).

An important ecosystem in the area is the Tropical Forest which has a large specific diversity. This diversity is constituted by a high number of species used for timber exploitation. In the forest, we may find evergreen, semideciduous and deciduous species (Aguilera *et al*., 2003; Sarmiento *et al.,* 1971b). Vegetation communities of wetland on permanently inundated areas ("esteros"). The vegetation is characteristic for the area, with different kinds of plants species (grasses, sedges and palms).

2.7.1 Seasonal savanna vegetation:

The seasonal savanna is one of the savanna types with more extension in the Llanos del Orinoco and it is present in all of the sub-regions mentioned above. The principal features and ecological considerations are described and analyzed by Sarmiento (1990). The plants in the seasonal savanna for the piedmont sub-region is mainly located on terraces, alluvial fan or piedmont hill, the plants communities are dominated by species as *Axonopus purpusii*, *Elyonurus tripsacoides*, *Paspalum plicatulum* and *Trachipogon plumosus*, and the woody strata is dominated by evergreen species as *Curatella americana, Byrsonima crassifolia, Bowdichia virgilioides* and *Palicourea rigida* (Monasterio *et al.,* 1971; Sarmiento, 1983; Sarmiento *et al.,* 1971a, 1971b; Silva *et al.,* 1971). The floristic composition in this sub-region is related to the features of the soil, especially to the drainage gradient associated to the soil texture and topographic position (Silva and Sarmiento, 1976a, 1976b).

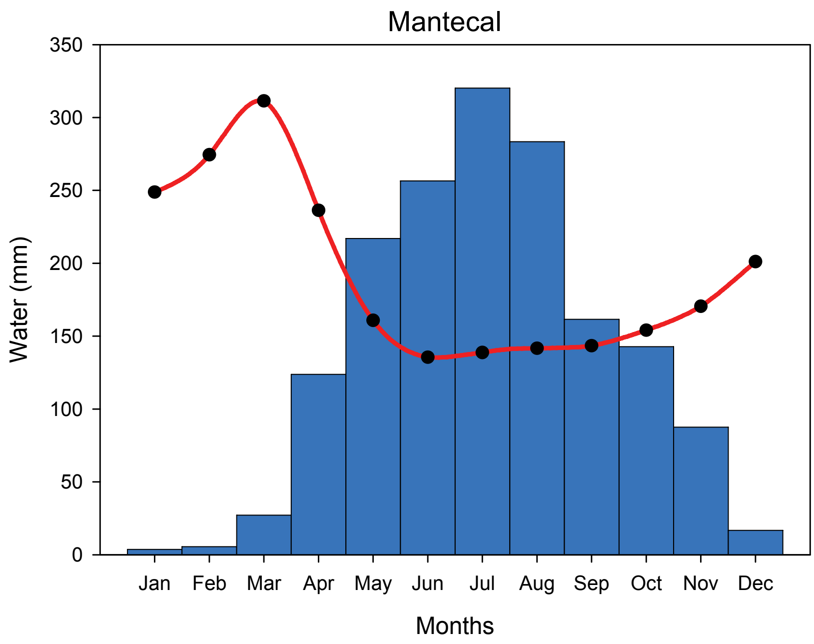


Figure 2.5. Monthly rainfall and evaporation for Mantecal town, located in the flooding savanna area, Venezuela.

In the Mesas sub-region, the seasonal savanna is the more extend ecosystem. The main feature of the mesas relief is the type of sediment and the presence of a latherithic layer, which determine the open structure of the savannas; on the colluvial deposits, however, the savanna is closer and the woody strata is more developed. The dominant herb species on this sub-region are *Trachipogon plumosus* and *Trachipogon vestitus*, and *Andropogon selloanus,* whereas *Axonopus canescens* and *Leptocoryphium lanatum* are subdominant species. For the woody strata, the dominant species are *Bowdichia virgilioides*, *Byrsonima crassifolia* and *Curatella americana* (Monasterio and Sarmiento, 1968; Sarmiento, 1983; Sarmiento and Monasterio, 1969).

In the flooding savanna area, the seasonal savanna ecosystem is only observable on the highest topographic, the woody strata is almost absent, and the herb dominant species are *Axonopus purpusii, Paspalum plicatulum Sporobolus indicus* and *Imperata contracta* (Monasterio *et al.,* 1971; Ramia, 1959; Sarmiento, 1983; Sarmiento *et al.,* 1971). According to the vegetation data for the flooding savanna in El Frío Biological Station described in Chacón-Moreno *et al.*, 2004), the number of species from 20 sites was 141, the most common species being *Panicum laxum, Paspalum chaffanjonii* and *Axonopus purpusii.*

In the aeolian plains, the seasonal savanna is observable on the top of the dune and the density of the vegetation decrease with the height of the dune; some higher dunes are almost without vegetation (Ramia, 1959). The dominant species are: *Trachipogon plumosus, Axonopus purpusii, Trachipogon montufari* and *Paspalum carinatum* (Ramia, 1959).

2.7.2 Hyperseasonal savanna vegetation

The hyperseasonal savanna shows a grassland physiognomy where the woody element is absent, except for some particular areas where the palms are present as *Copernicia tectorum*. In the piedmont sub-region, hyperseasonal savanna is located at the bottom of the different soil units described for Western Llanos and the terraces with high accumulation of water (Silva *et al.,* 1971). The principal dominant species are: *Andropogon bicornis* and *Sorgastrum parviflorum*.

In the Mesas area, the hyperseasonal savanna is located in the valleys between the hills of the Mesas relief occupying the wetter places. The main species are: *Leersia hexandra, Mesosetum loliiforme, Sorghastrum parviflorum* and some species of *Andropogon* and *Panicum*. In the aeolian plains, the Hyperseasonal savanna does not has much cover, it is only present in the flat areas and transitional zones between the lagoon and the dune.

In the alluvial overflow plains, the hyperseasonal savanna is the most representative type of savanna vegetation; the main feature of this area is the topographic catena derived from the geomorphological processes when the rivers overflow and deposit a layer of fine sediments. The highest part of the topographic catena is called “banco”, the middle part “bajío”, and the lowest part “estero”. The “bajío” is the most extensive area where hyperseasonal savanna is developed. The main species are *Andropogon bicornis, Leersia hexandra*, and *Panicum laxum*. After dike construction, however, the areas of hyper-seasonal savanna were replaced by semi-seasonal savannas, which still have water available in the soil during the dry period. The vegetation is herbaceous, with a few low shrubs but almost no trees. The number of species is quite high, but not higher than that found in the seasonal ecosystem. According to the vegetation data for the study area of El Frío Biological Station, the number of species collected in this ecosystem was 118 over 18 sites and the species most frequently encountered were *Panicum laxum, Leersia hexandra, Ipomoea fistulosa, Mimosa pigra, Hydrolea spinosa* and *Hyptis lappacea* (Chacón-Moreno *et al*., 2004). Of these species, the first two are the most dominant grasses in the zone.

2.7.3 Semiseasonal savanna vegetation

In this ecosystem, the vegetation is green during the whole year; and is important supply of forage to maintain cattle. The semiseasonal savanna can be derived from two different classes: The first are the areas which occupy the lower topographic position in the Alluvial overflow plains, and it is called "estero"; these areas receive water mainly from the rainfall and remain flooded during the rainy season with water available in the soil during the dry period. The vegetation is almost mono specific dominated by *Leersia hexandra, Paspalum fasciculatum* and *Hymenachne amplexicaulis*. The second class of semiseasonal savanna is derived from the overflow of large rivers. Consequently, the quality of the water is richer in nutrients and the vegetation composition is different with the presence of palms (*Mauritia minor*).

In the flooding savannas of El Frío Biological Station, the soil water availability during the dry period determines three different subtypes of savanna:

- ***Semi-seasonal non-saturated savanna*** (it contains water during the dry period but it is not the saturated type of savanna). The vegetation cover of this subtype is dominated by grasses and sedges. *Leersia hexandra*, *Ipomoea fistulosa* and *Hymenachne amplexicaulis* are the main dominant species.
- ***Semi-seasonal savanna water-saturated*** (soil saturated with water but not flooded). This subtype is dominated by the same species as found in non-saturaed savanna subtype, but in different proportions. Here *Hymenachne amplexicaulis* accounts for a greater proportion of cover than *Leersia hexandra.*
- ***Semi-seasonal savanna flooded***. In this third subtype, the water-level is few centimetres above the soil surface during the dry period, and the dominant species are sedges and aquatic plants.

2.7.4 Forest

The forest vegetation in the Llanos del Orinoco can be classified into four main types which present differences depending on the soil, climate or geology. These types of forest vegetation are: evergreen seasonal forest, semideciduous forest, deciduous forest, and semideciduous gallery forest.

The first class is the evergreen seasonal forest, which is mainly present in the borders of the Llanos the Orinoco. It marks the limit between the Llanos and Guyana and Delta forest at the South and Eastern border and represents the basal forest at the Andes footslope. The seasonality is less intense in relation to the savanna area and the dry period is not larger than 2 months; then the rainfall seasonality has a wider distribution than in savanna areas, and also the total annual rainfall is higher. The flora is very diverse and the species composition at Western area is different from that of the Southern or Eastern areas.

The second class is the deciduous or semideciduous forest, it includes the majority of the large forest areas in the Western side of the Llanos del Orinoco and the main gallery forest in the Western side. The large extension of this kind of forest conform the forest reserve for exploitation in the Caparo and Ticoporo forest.

The third type of forest is represented by the deciduous forest where the foliage responds to the climate seasonality. This class of forest form the patch of forest called “matas” or island forest in the middle of the seasonal savanna.

The fourth type is the semideciduous gallery forest which is a combination of forest elements from the second and third types of forests. This class is present in almost every water course. The area is submitted to periodic inundation and has a slight gradient from the bottom of the watercourse to the high position of the river bank can be observed. The main species relating to this ecosystem are: *Duguetia riberensis, Nectandra pichurini, Chomelia polyantha, Copaifera officinalis* and *Covvoloba obtusifolia* (Castroviejo and López, 1985; Sarmiento *et al,* 1971). Further information about the species composition in the different types of forest is described in Huber (1990), Sarmiento *et al.* (1971), Silva *et al.* (1971), Veillon (1978). A fifth class of forest occurs in flooded areas and it is dominated by a palm which was described above.

Large areas of forest plantation are managed in order to obtain paper pulp. These areas are mainly located in the Eastern and Central region of the Llanos del Orinoco and the principal species used are pine and eucalyptus.

In many cases the transition between forest and savanna is abrupt. This could be due to local changes in soil features or topographic variations. Regarding the explanation on forest – savanna boundaries, Longman and Jeník (1992) explain that the savanna ecosystem is a tropical ecosystem where the photoperiod and temperature have less fluctuation than the temperate zones, and any influence of frost; then rainfall totals and rainfall seasonality play a dominant role in the distribution of forest and savanna vegetation. But not only the rainfall is the determinants of savanna – forest boundaries, when in similar climate conditions the forest and savanna could be occur, then the nutrients is the environmental factor which determine the boundary between savanna and forest (Sarmiento, 1992).

2.8 Fauna

The Llanos del Orinoco has an extraordinary animal diversity which responds to a large variety of habitats, resources and the connectivity among the forest and savanna area, the water reservoirs, and the isolated “matas”. This high diversity is founded on the different zoological groups from the invertebrates until the big mammals including the reptiles, amphibian and birds (Aguilera *et al.*, 2003).

In the group of invertebrates, the arthropods of the savanna grass layer are the most abundant. Spiders, insects and ticks are the most predominant species. They conform a main group of primary consumers species (Gillon, 1983). Little research has been carried out on invertebrates in the Llanos del Orinoco; Bulla (1990) presents the main result on studies of biodiversity of insect in the Venezuelan savanna where he analyzes also the temporal changes derived from the climate seasonality and the effect of fire.

The other functional group of invertebrates is the detritivores and decomposers because they play an important role in the dynamics and fluxes of nutrients into the ecosystem. In the tropical savannas, there are four main taxonomic groups of macrofauna : earthworms, termites, ants and beetles. The latter is mostly represented by larvae (Lavelle, 1983a). From this four groups of macrofauna, earthworms constitute the dominant group in many tropical savanna soils in relation to density (ranging from 234 to 700 ind.m^{-2}), and the biomasses (from 22.3 to 49,0 g fresh weight . m^{-2}) (Lavelle, 1983a).

It is very well known that termites build their nests above the soil or in the trees; these termite mounds are a conspicuous and some time spectacular feature of many savanna landscapes (Josens, 1983). In the Venezuelan savannas, the termite mounds are very frequent, especially on humid savannas. On the other hand, the ant nests have been reported as a precursor of the "matas" generation, because they produce an accumulation of nutrients higher than the around savanna area (Farji-Brenner and Silva, 1995a, 1995b). Both earthworms and termites produce changes in the soil features. They increase the soil fertility and modify its structure (López-Hernández and Ojeda, 1996).

Related to the soil structure, the earthworms produce mounds on the savanna soil which are observed in different humid savannas areas in Venezuela. This earthworm mounds are considered as a principal microrelief feature in the hyperseasonal savanna (López-Hernández and Ojeda, 1996; Monasterio *et al.,* 1971; Sarmiento *et al.,* 1971a, 1971b; Silva *et al.,* 1971). They prevent the packing down of the topsoil. In the Lamto savanna, Lavelle (1983b) found that the volume of transported material above soil surface reaches 30-40 m^3 ha^{-1} yr^{-1}. This corresponds to an equal amount of air belowground level.

The earthworm activities and distribution are related to the environmental conditions. Lavelle (1983a, b) found that the earthworms, in the Lamto savanna, are very dependent on the soil moisture and that in the dry soil, the activities and density of earthworm decrease. In the Neotropical savannas, on the humid savannas (Hyperseasonal savanna), the activities of the earthworms responds not only to the soil moisture but also to the flooded conditions, and during the flood the earthworn produces a earth mound in order to search for aeration.

Related to the vertebrate groups, the most important groups to consider are the amphibians, reptiles, birds and mammals. Into the amphibians group, the Anura order is widely distributed in the tropical savanna (Lamotte, 1983). Frogs constitute a group associated to the water bodies. In savannas, these animals are found close to rivers, lagoons and, during the rainy period, have a large distribution in the flooded areas. The presence of frogs is also frequently associated to the "esteros".

Reptiles are an important animal group in the Llanos del Orinoco because they are represented by big species of crocodiles which are associated to the river, (permanent and intermitent) lagoons and wetlands. There are two main species of crocodiles: Caiman del Orinoco (*Crocodylus intermedius*) and "Baba" (*Caiman crocodilus*). The caiman del Orinoco is larger (4.5 m) than the baba and they are not easily observable in the field. Babas, on the other hand, are 1 and half meters in size and are frequently found in the semiseasonal savanna. Another species which can be observed in the Llanos del Orinoco is the Iguana (*Iguana iguana*).

Birds are an animal group generally abundant and diverse. In Venezuela, the Llanos del Orinoco contains almost all the species reported for Venezuela (Tamisier and Dehorter, 2000). The variety ranges from small to large birds and from sedentary to migrants species. The Llanos represent a variety of habitats and resources for many bird species; they are associated with the transition between savanna and forest, and the water bodies. The bird species groups with larger size are Ciconiiforms (ibis), Charadriiforms, Anseroforms (ducks), Columbiforms (doves), and Galliforms; the three first groups are associated to the water bodies (Pérez and Ojasti, 1996).

The number of Ungulates species (3) in the Llanos is remarkably low compared with the 20-30 species in the African savanna (Ojasti, 1990; Sinclair, 1983; Prins and Olff, 1998). In relation to the fauna size and abundance, the most important species is the Capibara (Brazilian name) or Chigüire (Venezuelan name) *(Hydrochaeris hydrochaeris*) which is comparable to a large ungulate in the African savannas, but belongs to the rodent class. The Chigüire is consumed and exploited by people and it can be used as a wild resource for human use. Another important species are the savanna rabbit (*Sylvilagus floridanus*), the deer (*Odocoileus virginianus*), and large carnivores (American lions and tigers*: Felis spp*) (Ojasti, 1983; Ojasti, 1990; Pérez and Ojasti, 1996). Further information about mammal species, its distribution and ecology in the Llanos del Orinoco is found in Ojasti (1983, 1990).

2.9 Soil

Considering the diversity of soil classes in the seasonal savanna, in America, there are 7 of the 10 soil orders according to the American classification, lacking the Aridisols, Vertisols and Histosols; and the most common class are the Oxisols with a minor proportion of Alfisols and Spodosols (Sarmiento, 1990). Savanna soils have severe physical and chemical constraints due to the waterlogging problems during the wet period or because well drained soils are nutritionally poor and indirectly fragile; then, the seasonal savanna vegetation is a direct result of adverse soil nutrient conditions (Cochrane, 1990). The soils of the Llanos del Orinoco have been developed on a Quaternary sedimentary basin and under very strong climatic conditions, which are the main determinant of the savanna ecosystem and also the driver of the pedological processes (Montgomery and Asked, 1983; Solbrig, 1996). The seasonal savanna is considered a well drained savanna. During the wet season, the capacity of water retention is low and the percolation is fast, maintaining water availability in the soil during this period. During dry period, seasonal savanna easily drained and produce a fast decreasing in the soil water availability and the soil loss the field capacity very fast. It is important to remark that the well drained feature produces a very high leaching of nutrients in the soil; then, the seasonal savanna has low fertility.

2.10 Geology and Geomorphology

From the geology point of view, the Llanos del Orinoco is a large Quaternary deposits on tertiary geosyncline, located among the Andes Cordillera to the West, the Caribbean Cordillera to the North, and the Guiana Shield to the South (Vivas, 1992). The Llanos del Orinoco is composed of quaternary sediments derived mainly from the erosion processes of the Andes and Caribbean mountains during the Pleistocene and Holocene epoch. Four main geological processes have occurred in the Llanos which have determined the four sub-regions described at the beginning of this chapter (Vivas, 1992). The Quaternary sediments accumulated in the geosyncline coul reach 3000 m deep (Vivas, 1992).

The piedmont region presents a geomorphology characterized by alluvial terraces and fans. These geomorphologic units are formed during the Late Pleistocene and the Early Holocene, but some few areas (fans) correspond to the Early and Medium Pleistocene (Acevedo and Silva, 1985; Sarmiento, 1983).

The high plains are sedimentary accumulations older than the other sub-regions which date back to the Late Pliocene (Tertiary period) or Early Pleistocene, there is not data precision about that. These plains correspond to an orogenic process associated to the Caribbean Cordillera in Venezuela called Mesas; the high plains were elevated between 200 and 300 m above sea level, then the name of Mesas (table) (Acevedo and Silva, 1985; Chacón-Moreno, 1991; Sarmiento, 1983; Sarmiento and Monasterio, 1969).

The alluvial overflow plains are located in the large depression of the geosyncline and the relief is still modified by the alluvial processes of the rivers which are coming from the Andes mountains. An accumulation of sediments derived from the overflows of the rivers is the main geomorphological event associated to this sub-region. These overflows produce a topographic catena with difference of high between 3 to 4 meters.

During the Würm glacial period, climatic environment changed in order to create drier conditions, and aeolian morphogenetic processes were developed in the southern part of the Llanos del Orinoco. The main geomorphological characteristic is the presence of dunes and other aeolian deposits.

The main environmental factor which has been acting and modeling the relief of the savanna areas is water. A lot of water courses came transporting sediment from the upper part and depositing this sediments in the large quaternary basin of the Orinoco river. On the other hand, climate and specially the seasonality of the rainy periods is the main force which drives the soil genesis.

2.11 Land use

The use of land in Venezuela occurs in a gradient from strong use in the mountain and central areas to low use in the southern areas, where the ecosystems remains almost in natural conditions. The major proportion of land in the Llanos del Orinoco is covered by native grasslands; the main land use is extensive cattle-raising under low-input management and few areas are used for agriculture, including cultivated pastures. The traditional management in the savannas is related to two main activities: the extensive cattle raising which occurs in almost all the territory of savannas and especially in the seasonal savanna; the low soil fertility and the low quality of grasses conditioning the primary and secondary production, with a low carry capacity from 0.20 to 0.50 animal units per ha. (López-Hernández and Ojeda, 1996; Silva and Moreno, 1993; Thomas *et al.,* 1990).

The non traditional management (intensive production system) in the Orinoco Llanos is developed in different categories, but mainly in intensive agriculture activities and intensive cattle management, other intensive uses are the forest plantation and the management of the flooding savanna.

The first development of intensive agriculture was initiated on a small area on very fertile soil in the western Llanos, but during the last decades the intensive agriculture is carried out on the high lands areas where seasonal savanna are predominant. This agriculture system needs a high use of technology (machines, agrochemical input, pest control, etc.) to compensate the low fertility of the soil. The main crop is corn (*Zea mays*), other important crops are sorghum (*Sorghum bicolor*), beans (*Vigna unguiculata*), soja (*Glycine max*), cotton, and rice (*Oriza sativa*) (López-Hernández and Ojeda, 1996).

Intensive cattle management has been recently introduced in the Llanos and it is mainly associated to a high input of fertilizer to compensate the low soil fertility. The intensive cattle raising is based on the replacement of the native grasses by improved pastures in combination with legumes in order to increase the energetic and nutritional potential of the pasture. Forest plantations were developed in the Eastern Llanos to produce pulp for paper industry; the cultivated species are pine (*Pinus caribae*) and eucalyptus (*Eucaliptus sp*).

Flooded savanna areas in Venezuela have been used for extensive raising of cattle. These areas have a high biomass production (550 to 800 g/m^2) during the rainy period (González Jiménez, cited by Sarmiento, 1983) but it decreases notably during the dry period. Then, the carrying capacity of the flooded savanna is very low (10 to 15 ha/cattle and 4 ha/cattle in the Mantecal area) (Mata *et al,* 1996). During the 1960s, most of the land was composed of *hatos* (properties of more than 10,000 ha) and the government initiated a political project to promote regional development with the introduction and intensification of technology in agricultural activities focused on raising cattle (Sarmiento and Monasterio, 1975). In 1971, the project *Módulos de Apure* started in the Mantecal area. This project involved the construction of dikes to control superficial drainage water through gates. The general idea was to store water for producing grass biomass during the dry period and thus to increase the carrying capacity of the area (López-Hernández and Ojeda, 1996; Sarmiento and Monasterio, 1975).

The meat production in modulated areas was expanded from 15-20 Kg/ha/year with traditional management to 32-50 Kg/ha/year using *Leersia hexandra* (native grass) as main forage (Tejos *et al.,* 1990). One of the principal changes was related to the composition of plant communities and the replacement of natural species in the hyper-seasonal savanna by species adapted to wet environments and with greater palatability, such as *Leersia hexandra* and *Hymenachne amplexicaulis* (López-Hernández and Ojeda, 1996). The *Módulos* have produced an increase in the carrying capacity (reaching 2 ha/cattle) of the savanna with well management to control the level of water (López-Hernández and Ojeda, 1996).

During the last decades the exploration and exploitation of petroleum has be occurred in the savanna areas (especially on the Easter Llanos). The number of exploitation plots is increasing very fast due to the opening market of the petroleum industry. The petroleum exploitation impacts on the savanna ecosystem is not very well known, but one of the most important consequences is the aperture of wells and routes in the natural areas and the fast development of town and cities without planning.

2.12 Overview

After the description of the main aspects of Llanos del Orinoco, a general discussion about the formulation of the hypotheses which deal this thesis is presented (Table 2.1). For that purpose and based on the general scheme of the thesis, a hierarchical structure will be followed.

Llanos del Orinoco can be seen as a large homogeneous savanna area within the Sudamerican continent because conform a climatic homogeneity and vegetation structure which has been mapped at the continental scale (Batista *et al.*, 1997; Hueck and Seibert, 1988; Loveland and Belward, 1997; Loveland *et al.*, 1999; Stone *et al.,* 1994). In this scale the ecological determinants (plant nutrient and moisture availability) are associated to different savanna traits. Plant availability nutrients are mainly determined by the Quaternary sedimentary basin and the frequency of fire occurrence in almost all the area. The plant availability moisture is associated to the rainfall seasonal pattern of the Aw climate.

When the scale is increased to the subcontinental level, different savanna ecosystems can be identified (Fig. 2.2). At this subcontinental scale, the Aw savanna climate presents a gradient in the total annual of rainfall which increases from East to West, keeping similar rainfall seasonality. Besides, the parents materials and the geomorphological dynamics are the distinctive features for the four sub-regions differentiation. Then plant nutrient and moisture availability at this scale will be determined by the association of these factors at different proportions (Table 2.1).

Table 2.1 General framework of the hierarchical structure considered to develop and test methodologies for the definition, characterization, analysis, and modeling of the relationship between the ecological processes and the principal ecological determinants of the savanna ecosystem in a spatial context into the Llanos del Orinoco, Venezuela. For each observation scale, the study and ecological systems are mentioned and the distinctive factors determining the differentiation of the study system are presented.

Scale	**Differentiated system**	**Ecological system**	**Distinctive factors**
Continental	Llanos del Orinoco	Savanna	Aw climate Quaternary sediments Fire
Subcontinental	Piedmont savanna Alluvial overflow plains High plains Aeolian plains	Sub-regions	Geomorphological dynamics Rainfall gradient Parents materials
Regional	Seasonal savanna Hyperseasonal savanna Semiseasonal savanna Gallery forest	Flooding savanna	Geomorphological units Soil water availability Human transformation
Local	Plants species distribution	Flooding savanna (representative area)	Gradients: - soil water availability - relative altitude - flooded condition - nutrients availability

The alluvial savanna plains region presents a fluvial geomorphological dynamics which determines a clear differentiation in the disposition of sediment materials during the overflow processes. Therefore, a topographic catena is the main characteristic in this region. However, in the Northwest part of these alluvial plains, the geomorphological dynamics is associated with the Andean rivers (white waters), which could be supply more nutrients during the overflow; besides, there is an increment in the total annual of rainfall. These two factors could benefit in some areas the growth of forest vegetation instead of herbaceous cover. In contrast, at the Southwest area, the geomorphological dynamics is associated to rivers which are originated on the plains (clear waters), then the charge of sediments and nutrients is much less than the Andean rivers, and the area is flatter than those of the Northwest area. Hence, these two factors could benefit the growth of herbaceous vegetation instead of forest vegetation. The topographic catena conformed on these plains will be dominated by the hyperseasonal savanna, where the rainfall seasonality and the possibility of flood once a year are the main determinants to differentiated this savanna ecosystem. The areas on alluvial overflow plains located to the Northwest side, closer to the Andes mountains, have been replaced by intensive agriculture developed by the use of large irrigation system, while the alluvial plains areas located to the south area have been used for extensive cattle raising.

The high plains present a particular geomorphological structure where soils are well drainage and some lowest areas could be flooded, then the main factor determining the savanna ecosystem type is the availability of soil water. Besides, the soil material is older than in the other regions, which implies that more nutrients are leached and some areas of these high plains present a latosolization soil process; then the high plains are very poor in soil nutrients. The main type of savanna ecosystem will be the seasonal savanna and in some areas where the flood process occurs the main savanna ecosystem will be the hyperseasonal savanna.

Concerning the aeolian plains, the drainage condition is extreme because the soil has great quantities of sand which makes the infiltration process more intensive. Thus the soil water availability is restricted to few months, and the predominant ecosystem is the seasonal savanna with less vegetation cover. Besides, this drainage condition determines that soil could be more oligotrophic.

If these premises about the effect of the ecological determinants on the plant moisture and nutrients availability in the different regional savanna type are true, then the identification and mapping of the Llanos del Orinoco savanna ecosystem could be made on the basis of the indirect association of the climate seasonality and the plant phenology. This aspect is tested using a methodological landscape ecological approach in the next chapter.

At regional scale, the purpose is to analyze the influence of human activities on the ecological determinants of the savanna and its pattern distribution. The selected area is located at the southwest side of the alluvial overflow plains - the flooding savanna - where the geomorphological dynamics determines the topographic catena explained above.

In the flooding savanna, the seasonal availability of soil water determines the variability in the primary production, with the lowest productivity in the dry season; then the capacity to maintain the secondary production of extensive cattle raising is restricted to this season. One of the solutions to this problem is to increase the primary production during this season. In the flooding savanna, the embankment of large areas was constructed to accumulate water during the rainy season and use this water to increase the primary production in the dry period. How these human transformations could modify the flooding savanna landscape and the ecosystems distribution? The assumption is that the dike construction produces severe changes in the soil water availability, then the geomorphological dynamics as the main factor determining the ecological distribution of the savanna ecosystems, is replaced by an assemblage of factors like the flood condition, geomorphological dynamics and embankment characteristics (Table 2.1). The methodological approach and analyses to understand and characterize the role of the human transformation on the flooding savanna are carried out in chapters 4 and 5.

If the distribution of savanna ecosystems in the flooding savanna landscape is influenced mainly by the soil water availability, then how do the plants adapt to this factor? At the local scale others factors like the soil nutrient availability and flood condition could be determining the plants distribution, and also the human transformation can be operating by the dike construction and the water management (Table 2.1). From chapter 6 to 9, the ecological determinants of the plants species distribution are analyzed and modeling into the spatial context in relation the main environmental factors.

CHAPTER 3

Mapping savanna ecosystems of the Llanos del Orinoco using multitemporal NOAA satellite imagery

3. MAPPING SAVANNA ECOSYSTEMS OF THE LLANOS DEL ORINOCO USING MULTITEMPORAL NOAA SATELLITE IMAGERY

3.1 Abstract

Monthly composites of NOAA-AVHRR normalized vegetation index (NDVI) images (June 1992 to October 1993) were used to analyze the phenology of savanna ecosystems in the Llanos del Orinoco region. The objective was to elaborate an ecosystems map of the area based on temporal pattern analysis. Expert knowledge of savannas allowed the selection of representative ecosystems to monitor changes in NDVI. From 54 satellite images, model curves were created for each selected ecosystem. They were analyzed with the objective to characterize and identify each ecosystem. From these temporal patterns and statistical analyses, six satellite images were chosen to carry out a supervised classification using Mahalanobis distance methodological approach. Validation of the map was implemented using ground control points. Differences in phenology between ecosystems are strongly related to the environmental climatic conditions, especially to seasonal rainfall. Therefore the phenology for each ecosystem can be explained based on water availability. A methodological approach, which reveals the phenology of the most important savanna ecosystems in Venezuela, was applied in this work. This study represents an improvement in mapping of ecological processes.

Keywords: vegetation phenology, NDVI, ecological map, supervised classification, Venezuela.

3.2 Introduction

The tropical savanna ecosystem, Llanos del Orinoco, constitutes the major region of northern South America (Sarmiento, 1983, 1990). The phenological variation of the vegetation is related to environmental conditions. These vegetation-environment relationships have been used to classify the savanna ecosystem in the Llanos, which mainly reflects climatic seasonality and geomorphological features (Sarmiento, 1990).

The Llanos del Orinoco area is represented as a homogeneous savanna area as suggested by continental vegetation maps (Batista *et al.*, 1997; Hueck and Seibert, 1988; Loveland and Belward, 1997; Loveland *et al.*, 1999; Stone *et al.,* 1994); however it represents a variety of savanna ecosystems to major scale. Vegetation maps of Venezuela show a variety of taxonomic plant communities, which are related to environmental features similar to climate, geomorphology and soil (Huber and Alarcón, 1988; MARNR, 1983). However some of these maps reflect the spatial features of the vegetation, but do not include the ecological processes associated with ecosystem functioning. I will explore the ecological potential of including phenological information to map the ecosystems of the Llanos of Northern South America.

NOAA-AVHRR images and the normalized difference vegetation index (NDVI) have been used in many studies to understand the relation between the spectral variability of the temporal images and the vegetation vigour or growth rate, and it is useful to determine the production of green vegetation and detect vegetation changes (Batista *et al.,* 1997; Duchemin *et al.,* 1999; Groten, 1993a,b; Hobbs, 1989; Kressler and Steinnocher, 1999; Stone *et al*., 1994). Multitemporal low resolution NOAA-AVHRR NDVI imagery has been used to reveal variations in vegetation phenology of temperate deciduous forest ecosystems (Duchemin *et al.,* 1999), different vegetation types in the USA (Reed *et al.,* 1994), Amazonian forests (Batista *et al.,* 1997), pasture and grass ecosystems (Hill *et al.,* 1999) and continental isogrowth zones (Azzali and Menenti, 1999; Menenti *et al.,* 1991).

Vegetation phenology has been associated with seasonal climatic patterns in temperate vegetation and agriculture areas (Reed *et al.,* 1994). I attempt to relate the phenological patterns of the Llanos del Orinoco vegetation to remotely sensed NDVI time series. The variety of savanna ecosystems in the Llanos del Orinoco is mainly due to the phenological responses of vegetation to environmental conditions (climate, soil nutrients, topography, etc). Its phenological responses have been used to classify the savanna ecosystems (Chacón-Moreno, 1991). One of the classifications of savanna ecosystems is based on hydrological dynamics (Sarmiento, 1984, 1990), in which soil water availability during the year determines ecological characteristics associated with deficit or excess of water in the soil. From the hydrological point of view, a direct association between savanna ecosystems and phenological patterns can be determined (Monasterio and Sarmiento, 1976; Sarmiento, 1984) (See chapter 2).

Knowledge of functioning, ecological processes and the phenology relationship of the main savanna ecosystems will be used to link the multitemporal NOAA-AVHRR NDVI imagery in order to identify phenological patterns of the savanna ecosystems, and to develop a map of the different ecosystems of the Llanos del Orinoco. The main tasks considered in this work are the analysis of multitemporal images to determine seasonal curves of NDVI; a selection, based on statistical considerations, of the images to use in the classification process; a supervised classification to obtain a map displaying a number of ecosystem classes that differ in phenological feature, and an assessment of map accuracy with ground data.

3.3 Methods

3.3.1 Study area

The Llanos del Orinoco is a quaternary basin with an area of about 240,000 km^2. At the regional scale, the Llanos del Orinoco is classified into four main units based on geology, soil, geomorphology and climate (Sarmiento, 1983): The piedmont or footslope savanna; the high plain or tertiary plateau; the alluvial plain or flooding savanna, and the aeolian plains or aeolian savanna.

Further descriptions and maps of the main units is given in Sarmiento (1983) and Acevedo and Silva (1985).

Ecosystem typology for tropical savannas is derived from Sarmiento (1984), where the soil for each ecosystem has different periods of water availability, deficit or excess, and the period of green vegetation may be differentiated in time. **Seasonal savannas** are areas with herb cover, mainly grasses, with two hydrological seasons: a dry season with duration between four to six months, and another ecologically favourable season with availability of water in the soil. The vegetation responds to one long period of stress. **Hyperseasonal savannas** are ecosystems with four different hydrological conditions during the year, a first dry period of approximately two or three months; a second period with availability of water in the soil which lasts one or two months; a third period with excess water in the soil, with a duration of approximately six to seven months, and a fourth ecologically favourable period with a duration of one month. Plants suffer from two different stress conditions; caused by dry soil and by excess of water. **Semiseasonal savannas** are ecosystems with two periods: a favourable one with duration of two to three months, and a long period of approximately nine months with excess water in the soil. Species distribution and response are driven by excess water during a long period. Figure 3.1 presents the main field observations on the relation between seasonality and savanna ecosystems.

Supplementary information on the study area and environmental features were derived from vegetation, geological, topographical, and climatic maps of Venezuela (Huber and Alarcón, 1988; MARNR, 1983), a vegetation map of South America (Hueck and Seibert, 1988), and climate data. Further non-spatial descriptions of the Llanos del Orinoco are presented in Chacón-Moreno (1991).

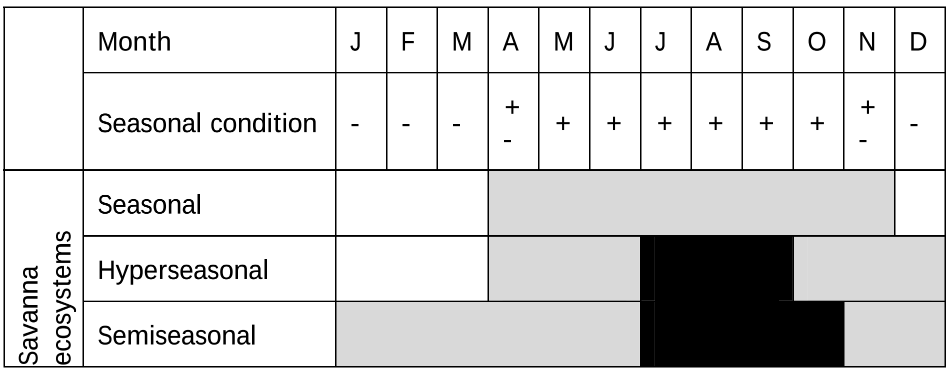


Figure 3.1. Scheme displaying period of rainfall and phenological condition for three savanna ecosystems in the Llanos del Orinoco, Venezuela. Minus and plus signs denote quantity on rainfall. Black = flooded and submergence of vegetation; gray = green vegetation; white = dead/dry vegetation.

3.3.2 Sources of data

The primary data sources for this work were 1-(Km) images of NOAA Advanced Very High Resolution Radiometer (AVHRR). The images were obtained from the global land 1-km data set project, under the proceedings of the International Geosphere Biosphere Programme (Loveland and Belward, 1997; Loveland *et al.,* 1999). The data was collected continuously for 18 consecutive months beginning April 1, 1992, and continuing through September 30, 1993 (54, 10 day image composition). Processing standards for the AVHRR data have been developed for calibration, atmospheric correction, geometric registration, and the production of global 10-day maximum normalized difference vegetation index (NDVI) composites. Further descriptions of image processing for NOAA-AVHRR are detailed in Eidenshink and Faundeen (1998), Los (1998).

3.3.3 Processing of multi-temporal NOAA satellite imagery and sampling areas

The selection of the areas is based on information from previous maps (Huber and Alarcón, 1988; MARNR, 1983) and personal knowledge of the study area. Analysis of multitemporal NDVI-NOAA imagery was carried out to determine phenological patterns of ecosystems into the Llanos del Orinoco Region. The sampling was made considering the major savanna ecosystem types of the Llanos del Orinoco (Table 3.1).

The 10 selected areas are described in Table 3.2. The features of ecosystem, vegetation, climate and soil are derived from Ramia (1959); Sarmiento and Monasterio (1971, 1975); Monasterio *et al.* (1971); Sarmiento *et al.* (1971a, 1971b); Silva *et al.* (1971); Monasterio and Sarmiento (1976); Sarmiento (1983, 1984); and Chacón-Moreno (1991). Using the information derived from S10 (control area), 8 of 54 images were excluded because the cloud cover was too extensive. From the sampled areas, the S3, S4, S5, S6 and S7 were used for the analysis. The other sampled areas, containing information about agriculture use, forest vegetation, and savanna ecosystems outside of Venezuela, were used to compare and complement the information. Each selected area has more than 30 pixels per ecosystem for the 54 NDVI-NOAA images.

The images were processed and displayed using ILWIS 2.2 (ILWIS 1997). The data was processed to obtain the average, maximum and minimum NDVI values, standard deviation and confidence interval for each sampled area, and then the average values for each sampled area were displayed in a graph to have a preliminary green vegetation curve during the time. From this graph values greater than 0, in places like lakes, rivers and sea, were excluded. The graphs resulting from this preliminary analysis are displayed again in order to obtain the definitive NDVI curve along the studied period for each area.

Table 3.1 Distribution of phenological ecosystem types over the four different main geomorphological regional systems. ++ = Major part of the area, + = minor part of the area.

Llanos del Orinoco regions	Savanna ecosystems						
	Gallery forest	Seasonal forest	Seasonal savanna	Hyperseasonal savanna	Semiseasonal savanna	Irrigated agriculture	Rainfed agriculture
Piedmont	+	+	++			+	++
Tertiary plateau	+		++	+		+	+
Alluvial plains	+	+	+	++	++	++	+
Aeolian plains	+		+	++	+		

3.3.4 Statistical analysis of the phenological patterns

Two different approaches were used to select NOAA-NDVI images to run the classification. A visual check of the NOAA-NDVI images resulted in the selection of 17 images following these criteria: a) Images containing the largest number of ecosystems, b) The distribution of the selected images cover the maximum time amplitude, including the two seasons, c) Maximum variability and amplitude in NDVI values for each selected image.

Using a quality index based on the previous criteria, six images were selected for statistical analysis. These six images were analyzed using an ANOVA and posteriori Tukey´s statistical test to recognize differentiation among the ecosystem classes.

3.3.5 NOAA-AVHRR NDVI image classification

Prior to the classification of the selected images, a sub-map of the Llanos del Orinoco area was created for each selected image. The area of these images was obtained using the limits defined in previous vegetation, hydrographical, geology and soil maps.

A supervised classification based on the selection of training pixels was used. A sample set with representative pixels for each ecosystem was created, and used with a map list with the six selected images. Supervised classification is the digital-information extraction technique in which the operator provides training-sites information that the computer uses to assign pixels to categories (Sabins, 1987). We used an alternative variation of the traditional technique, comparing the NDVI values of NOAA-AVHRR NDVI images instead of values of the bands for particular image (Aronoff, 1993).

Table 3.2 Sampling areas selected for the analysis of phenological patterns of savanna ecosystems.

Code	Location name	Ecosystem	Features	Coordinates
S1	Calabozo irrigated rice crop area	Irrigated agriculture	Irrigated crops on extensive area, using irrigation from water reserve. Intensive agriculture. Rice crops. Alluvial overflow subregion, close to high plains subregion.	Lat: 8.45 Lon: -67.50
S2	Orinoco river and Meta river borders	Gallery forest	Rivered and gallery forest occurring along of permanent watercourse (rivers).	Lat: 7.00 Lon: -67.2
S3	Tertiary plateau area I	Seasonal savanna	Savanna parkland on the high plains.	Lat: 8.6 Lon: -67.2
S4	Tertiary plateau area II	Seasonal-Hyperseasonal savanna	Savanna areas with palm and frequently flooded. Located on high plains.	Lat: 8.6 Lon: -67.2
S5	Camaguan Esteros	Semiseasonal savanna	Esteros (semiseasonal savanna) mixed with palm and semiseasonal forest. Located on Alluvial overflow plains.	Lat: 8 Lon: -67
S6	Apure flooding areas between large rivers (Apure and Arauca rivers)	Hyperseasonal and semiseasonal savanna	Savanna areas, which are flooded during 3-4 months per year. Herbaceous vegetation. Located on alluvial overflow plains.	Lat: 7.50 Lon: -69
S7	Piedmont areas (Footslope plains)	Seasonal savanna and disturbed areas	Savanna parkland on low terraces. Disturbed by annual crops and extensive grazing. Located on Andean footslope.	Lat: 8.5 Lon: -70
S8	Colombian Llanos on high plains	Seasonal and Hyperseasonal savanna	High plains close to Meta river	Lat: 4 Lon: -72.5
S9	Guayana rain forest	Tropical rain forest	Different areas on the Bolívar and Amazonas States in Venezuela. Higher values of NDVI	Lat: 5 to 7 Lon: -64 to -67
S10	Control	Water	Areas with water (lakes, sea, rivers)	

Minimum Mahalanobis Distance as a mathematical procedure was used to complete the classification (Bronsveld and Shrestra, 1993; Duda, 1997; ITC, 2001). After the classification process, the map was filtered to eliminate the areas or isolated pixels that produce noise, in order to obtain a map with homogeneous areas.

The final maps were combined with a mask of forest, agriculture, and savannas on Delta Plains, which are ecosystems not considered in the analysis of image classification. These masked ecosystems are derived from the Vegetation Map of Venezuela from Huber and Alarcon (1988).

3.3.6 Validation of the classified ecosystems map

To validate the accuracy of the final ecosystems map, samples set of 76 ground data were collected to confirm ecosystem units. The size of the ground data control was larger than 1 Km^2. A group of 15 data points were collected on the Calabozo area in the Central Llanos of Venezuela on May 2000. Another group of 22 sample points was collected in the Apure flooding savanna area on December 1998. The major group of 39 sample points was collected in the Puerto Ayacucho area, and the Western and Central Llanos area in July and August 2000. This data was collected independently from the information derived in the map. A group of 28 ground data collected, containing unique information about the studied savanna ecosystems, was selected for the analysis. The data was compared to data derived from the ecosystem map of the Llanos del Orinoco and error matrices, Kappa analysis and descriptive technique analysis were used to measure the accuracy of the classification (Congalton, 1991; Congalton *et al.,* 1983; Janssen and van der Wel, 1994).

3.4 Results

3.4.1 Analyses of phenological pattern of savanna ecosystems.

Figure 3.2 shows four phenological patterns from NDVI values, representing the three main savanna ecosystems in relation to the rainfall pattern (bars) obtained from climatic stations in the area. NDVI values for S3 and S4 sampled areas were averaged because they presented similar patterns and 90% of overlaying in the seasonal patterns.

Hyperseasonal and seasonal savannas on tertiary plateau areas displayed the lowest NDVI values. During the 1992 rainy period, the values fluctuated between 0.40 - 0.45. NDVI values decreased from the beginning towards the end of the dry period. However, a peak of increment was observed in March 1993, and then the values reached the lowest point. Between April and June 1993, the NDVI reached medium values; it increases from 0.20 to 0.45 as in the 1992 rainy period.

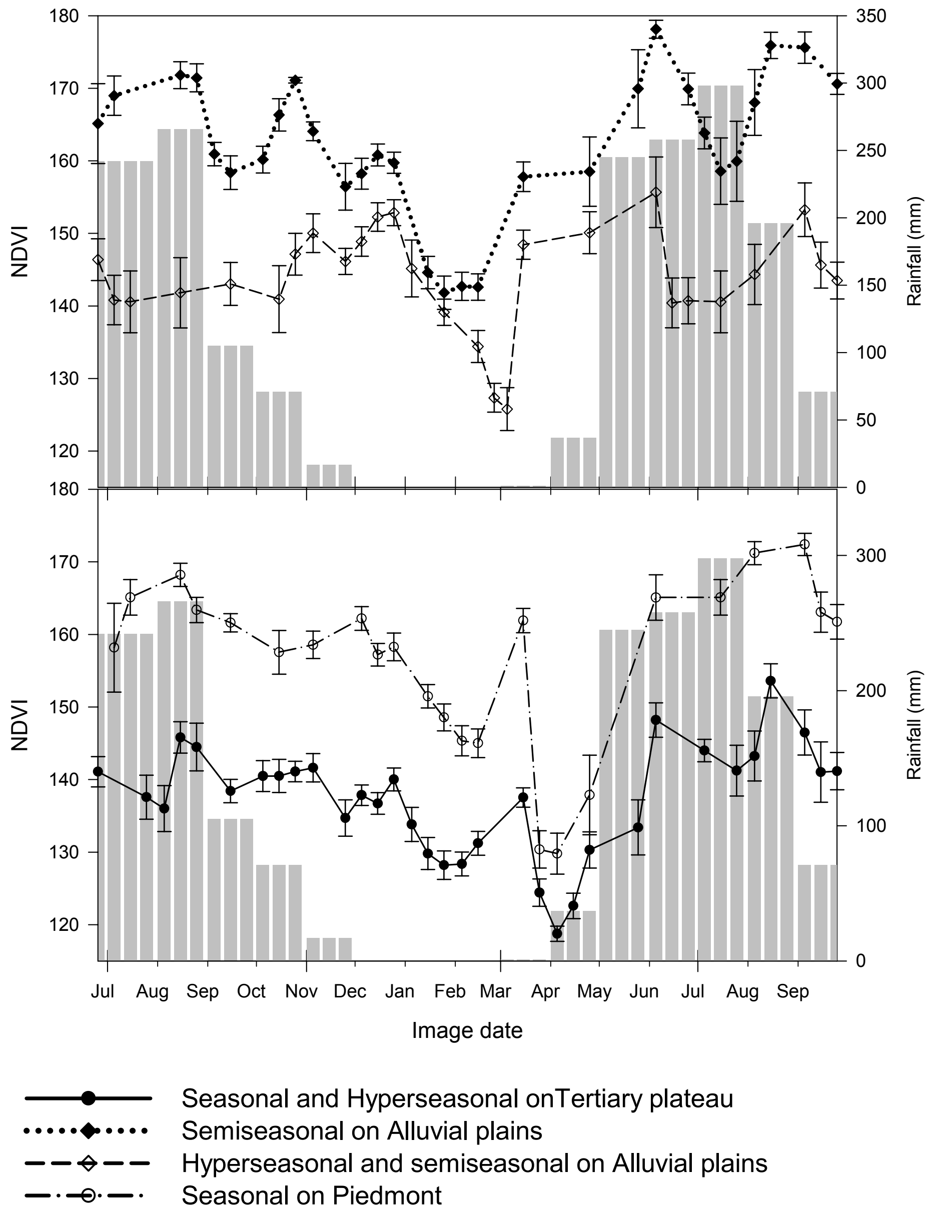


Figure 3.2 Average NDVI values and standard errors for four different savanna ecosystems in the Llanos del Orinoco, Venezuela, between June 1992 and September 1993. Bars indicate the rainfall pattern recorded in San Fernando de Apure, Venezuela.

Semiseasonal savannas areas on alluvial plains showed the highest NDVI values. The pattern was bimodal during the rainy period, with the declination at middle-end of the rainy period, when flooding reached maximum values. During the dry period the NDVI values remained higher (> 0.55) until the middle of the dry period (January 1992). Afterwards, the values decreased to medium values (around 0.45) until the end of dry period. At the beginning of the new rainy period the NDVI again reached higher values.

The pattern for hyperseasonal and semiseasonal savannas on alluvial plains shows a stable curve of medium values (around 0.45) during the first rainy period. However a clearly bimodal pattern was observed in the second rainy period with a large declination of NDVI values during July and August 1993. During the dry period, the NDVI values remained medium until the beginning of January 1992, when they started to decrease, reaching the minimum lowest value at the end of the dry period. At the beginning of the next rainy period the values increased rapidly (March 1993).

A unimodal phenological pattern during the rainy periods for seasonal savannas on the piedmont was observed. Maximum NDVI values were obtained when the maximum rainfall values were reached a month later. The values remained medium-higher (around 0.50) one month after the rainfall stop. After that, the values started to decrease. At the end of the dry period the curve reached a peak and immediately the NDVI values fell to the minimum values. At the beginning of the new rainy period the NDVI values increased faster.

3.4.2 Statistical analysis of the phenological patterns

Based on the visual analysis of the phenological patterns, 18 NOAA-NDVI images were selected for the statistical analysis (Table 3.3). In this table, three criteria were taken into account to qualify the NOAA-NDVI images: a) the number of lines differentiated from visual analysis in figure 3.2 for each image date; b) the number of NOAA-NDVI images considered in those dates (point of image date), and c) the quality index derived from the combination of the two before criteria. Based on these criteria, it was found that the image dates of 12/05/92, 01/25/93 (beginning of the dry season), 11/05/92, 04/25/93 (transition periods), 09/15/92 and 06/05/93 (rainy period), had the best quality to separate the savanna ecosystems. However, this visual selection did not permit an evaluation of the confidence interval.

Table 3.3 NOAA-NDVI images of the savanna ecosystems in the Llanos del Orinoco selected after a visual analysis. Column A represents the number of lines differentiated from visual analysis in figure 3.2 for each image date, column B is the number of NOAA-NDVI images considered in those dates (point of image date), and column C is the quality index derived from the combination of column A and B. (*) are the selected images for statistical analysis.

No	Image date	Seasonal period	A	B	C
9214	8/15/92	Rainy	3	5	Medium (15)
9215	8/25/92	Rainy	3	4	Low (12)
9217	9/15/92	Rainy	4	5	High (20) *
9220	10/15/92	Rainy	4	4	Medium (16)
9221	10/25/92	Rainy	4	3	Low (12)
9222	11/5/92	Transition: Rainy-Dry	5	5	Highest (25) *
9225	12/5/92	Dry	4	5	High (20) *
9227	12/25/92	Dry	5	5	Highest (25)
9303	1/25/93	Dry	5	5	Highest (25) *
9305	2/15/93	Dry	4	5	High (20)
9308	3/15/93	Dry	5	4	High (20)
9310	4/5/93	Dry	5	3	Medium (15)
9312	4/25/93	Transition Dry-Rainy	4	5	High (20) *
9316	6/5/93	Rainy	4	5	High (20) *
9320	7/15/93	Rainy	4	3	Low (12)
9322	8/5/93	Rainy	3	5	Medium (15)
9325	9/5/93	Rainy	4	5	High (20)

Figure 3.3 shows the box plots of NDVI values of the six best images according to the previous analysis, and also considering the distribution of images during the study period. The ecosystems analyzed were grouped in five classes: Seasonal savanna on tertiary plateau (3), seasonal and hyperseasonal savanna on tertiary plateau (4), semiseasonal savanna on alluvial plains (5), semiseasonal and hyperseasonal savanna on alluvial plains (6), and seasonal savanna on Piedmont (7). For all dates the NDVI values for the seasonal (3) and hyperseasonal (4) savannas on tertiary plateau were similar. This observation was clear because the two phenological patterns follow the same way according to Figure 3.3. For each date-plot, three and/or two kinds of value groups can be differentiated, and the dates 12/05/92 and 11/05/92 presented the best differentiation in four groups based on the box separation and low box overlapping.

Tables 3.4a and 3.4b show the results for the ANOVA and Tukey´s test of ecosystem savanna classes associated with Figure 3.3. As was observed before, the seasonal (S3) and hyperseasonal (S4) savanna ecosystems on tertiary plateau never show significant differences in the boxplot figure (Fig. 3.3).

The best image date to differentiated between classes was 11/05/92. On the other hand, a combination of different dates distinguishes all the other ecosystem classes. The semi-seasonal savanna ecosystem (S5) always has the highest separation index from seasonal and hyperseasonal savannas (S3 and S4). Furthermore, this ecosystem class was significantly separated from the hyperseasonal savanna (S6) in three of the images and with seasonal savannas on the piedmont (S7) in the other three image dates.

Results of Table 3.4b confirm the statistical separation into different groups, indicating that the image date from the 5th of November presents the major differentiation between classes. Also Table 3.4b shows that images from April 25th and June 5th permit a significant separation amongst four classes.

3.4.3 Ecosystems map of the Llanos del Orinoco, Venezuela.

Figure 3.4 shows the ecosystems map for the Llanos del Orinoco, which is the result of supervised classification of NOAA-NDVI images.

The **agriculture** unit is defined by the annual agriculture and intensive agricultural areas. The distribution of this unit replaces the seasonal savanna on the piedmont and alluvial plains.

The **forest** unit corresponds to the vegetation type associated to the river or watercourse, planted forest for pulp paper industry, and semiseasonal forest.

The **hyperseasonal savanna** unit is mainly located between the Apure and Arauca rivers, and at the North side of the high plains.

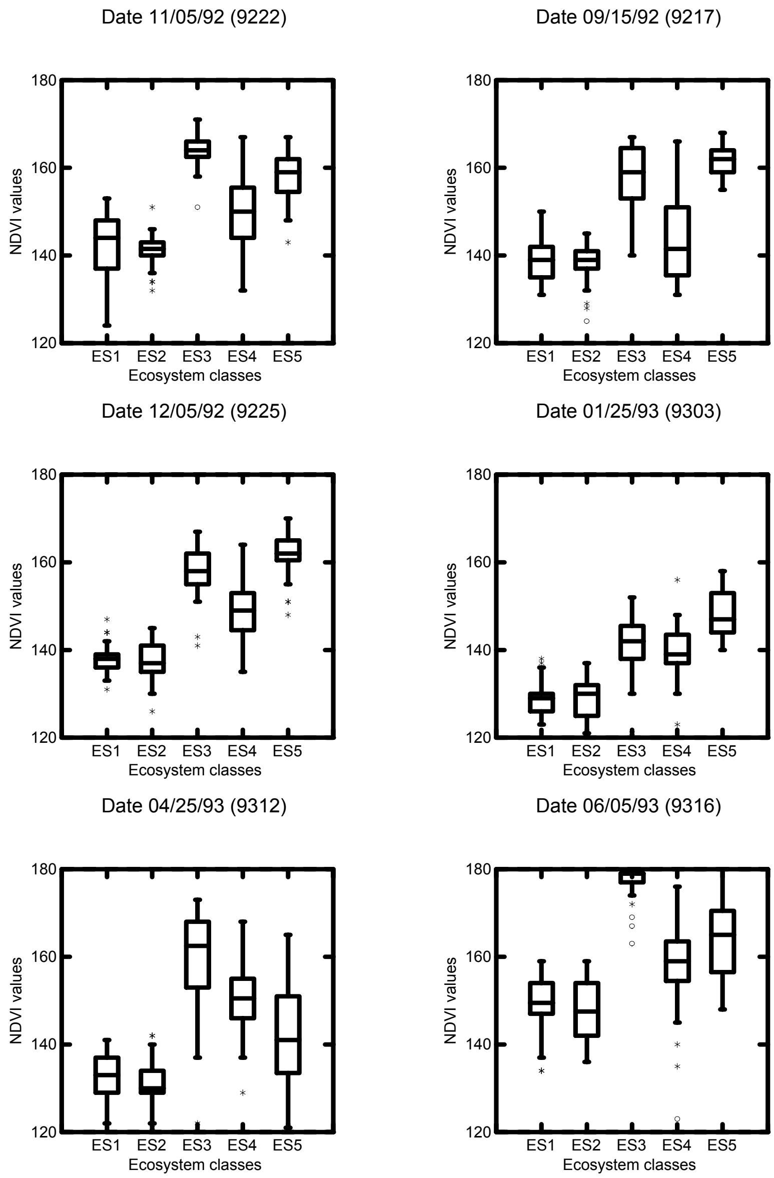


Figure 3.3 Boxplot of NOAA-NDVI values for the six main differentiate dates for the savanna ecosystems classes. 3: Seasonal savanna on Tertiary plateau. 4: Seasonal and hyperseasonal savanna on tertiary plateau. 5: Semiseasonal savanna on alluvial plains. 6: Semiseasonal and hyperseasonal savanna on alluvial plains. 7: Seasonal savanna on piedmont

Table 3.4a Statistical significance of the results from the ANOVA of ecosystem classes for each image date selected. N equals 30 for the five ecosystem classes. Level of significance: n.s. = not significant, * P < 0.05, ** P < 0.01, and *** P < 0.001. S3: Seasonal savanna on tertiary plateau, S4: Seasonal and hyperseasonal savannas on tertiary plateau, S5: Semiseasonal savanna on alluvial plains, S6: Semiseasonal and hyperseasonal savanna on alluvial plains, and S7: Seasonal savanna on piedmont.

Date	S3-S4	S3-S5	S3-S6	S3-S7	S4-S5	S4-S6	S4-S7	S5-S6	S5-S7	S6-S7
9/15/92	n.s.	***	*	***	***	*	***	***	n.s.	***
11/5/92	n.s.	***	***	***	***	***	***	***	***	***
12/5/92	n.s.	***	***	***	***	***	***	***	n.s.	***
1/25/93	n.s.	***	***	***	***	***	***	n.s.	***	***
4/25/93	n.s.	***	***	*	***	***	n.s.	*	***	***
6/5/93	n.s.	***	n.s.	***	***	*	***	***	***	***

The **savanna on Delta plains** unit is an ecosystem located on the overflow plains of the Orinoco delta area. The characteristics of this ecosystem are similar to the semiseasonal savanna, but the location is restrained to the Orinoco delta plains.

The **seasonal and hyperseasonal savanna on tertiary plateau** unit is the larger ecological unit in the Llanos del Orinoco. It is mainly located in or associated with the high plains in the Central and Eastern zone of the area. The seasonal savanna vegetation, with a strata of herbs (mainly grasses) with scattered trees, and the hyperseasonal savanna vegetation, with a main herbs strata, are present and dominant. Poor soils characterize the tertiary plateau.

The **seasonal savanna on piedmont** unit corresponds to the areas located on the footslope of the Cordillera de Los Andes (mountain chain). This unit is very dissected by rivers and the gallery forest, and is often used for agriculture.

The **semiseasonal savanna** unit is located in the lowland area where water flooding is controlled by dikes. The graminoid strata is dominant and trees are absent.

The **semiseasonal savanna with palms** unit is a variation of the semiseasonal savanna with a larger density of palms.

Table 3.4b Homogeneous groups derived from Tukey´s test following ANOVA analysis at significant level of 0.05 of ecosystem classes for each image date selected. S3: Seasonal savanna on tertiary plateau, S4: Seasonal and hyperseasonal savannas on tertiary plateau, S5: Semiseasonal savanna on alluvial plains, S6: Semiseasonal and hyperseasonal savanna on alluvial plains, and S7: Seasonal savanna on piedmont.

Date	**Ecosystem classes**				
	S3	**S4**	**S5**	**S6**	**S7**
9/15/92	**a**	**a**	**c**	**b**	**c**
11/5/92	**a**	**a**	**d**	**b**	**c**
12/5/92	**a**	**a**	**c**	**b**	**c**
1/25/93	**a**	**a**	**b**	**b**	**c**
4/25/93	**a**	**ab**	**d**	**c**	**b**
6/5/93	**ab**	**a**	**d**	**b**	**c**

3.4.4 Field validation of the ecosystems map.

Table 3.5 shows an error matrix comparing the reference data collected in the field and the data derived from the ecosystem map of the Llanos del Orinoco. The user´s accuracy for the hyperseasonal (H), seasonal and hyperseasonal on tertiary plateau (SHM), and seasonal savanna on piedmont (SP) was higher than 75%, and only the semiseasonal savanna ecosystem (Sm) had user´s accuracy below 50%. All producer´s accuracy values were above 60%, which means that the probability of a reference pixel being correctly classified is higher. The overall accuracy was almost 80%. This was confirmed by the value of Kappa analysis which also showed a high (70%) accuracy.

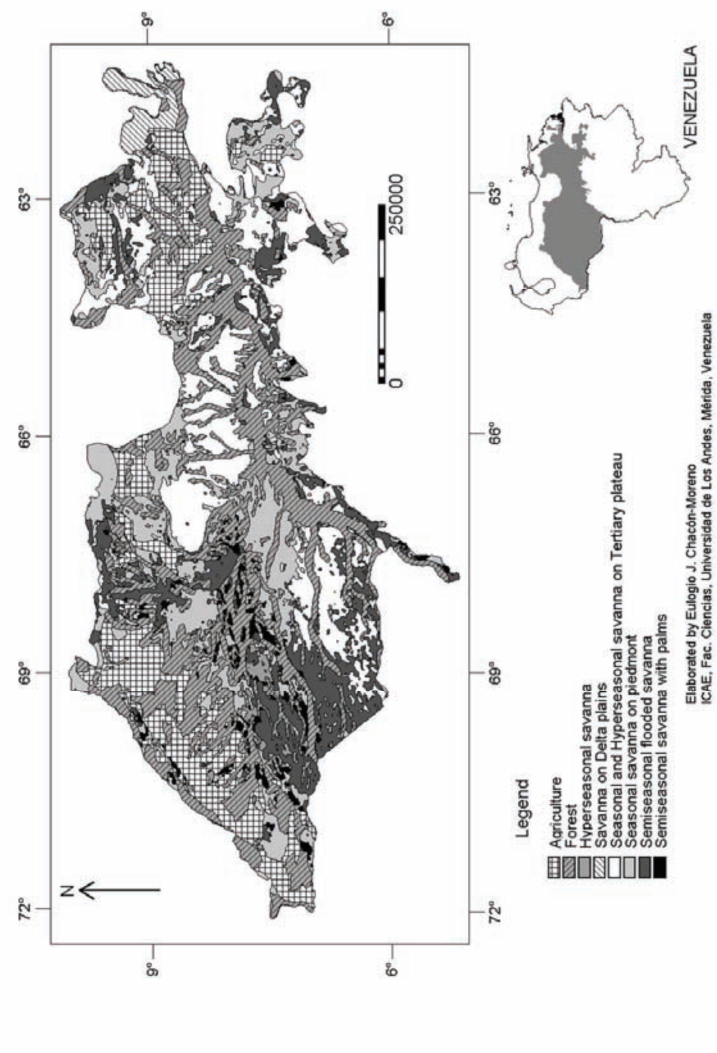


Figure 3.4 Ecosystems map of the Llanos del Orinoco, Venezuela. Derived from supervised classification of NOAA satellite images based on Mahalanobis distance

Table 3.5 Error matrix for the Ecosystems map of Llanos del Orinoco, Venezuela based on supervised classification of NOAA – NDVI images including only the classified savanna classes H: Hyperseasonal savanna, SHM: Seasonal and hyperseasonal savanna on tertiary plateau, SP: Seasonal savanna on piedmont, Sm: Semiseasonal savanna. Kappa analysis was significant.

Reference data

Classified image data

	H	SHM	SP	Sm	Row total
H	3	0	0	1	4
SHM	0	11	0	0	11
SP	0	0	4	0	4
Sm	2	1	2	4	9
Column total	5	12	6	5	28

Producer's accuracy

H	= 3/5 = 60%	
SHM	=11/12 =	92%
SP	= 4/6 = 67%	
Sm	= 4/5 =	80%

User's accuracy

H	= 3/4 =	75%
SHM	=11/11=	100%
SP	= 4/4 =	100%
Sm	= 4/9 =	44%

Overall accuracy 22/28 = 79 %

Kappa value = 0.70

3.5 Discussion and conclusions

Based on analysis of multitemporal NOAA-AVHRR NDVI imagery, phenology of vegetation was determined to better understand the ecology of the main ecosystems of the Llanos del Orinoco. It was analyzed in order to correlate vegetation dynamics with environmental parameters and features. Previous knowledge of ecosystem functioning and the features of the study area was necessary to understand and explain the phenological patterns derived from the remote sensing data.

The phenological patterns presented in Figure 3.2 show a good relation with those expected from Figure 3.1. Most of the changes and line patterns can be explained based on the changes in phenology associated with the climatic seasonality. Seasonal and hyperseasonal savanna ecosystems on tertiary plateau showed lower values during the dry period associated with the senescence of the plant. Another likely explanation is that fire occurs mainly in this kind of savanna, so that the sensor observes ashes and soil. The lowest NDVI values were found on the tertiary plateau on very poor soils, and presumably because reflection from the soil is high and produces low values in the infrared band and high values in the red band.

The phenological patterns of semiseasonal savannas on alluvial plains can be explained by overflows in the area. After the rainfall decreases, the soil maintains field capacity, the vegetation remains green and the values are high. But when field capacity decreases, the vegetation dries up and the NDVI is low. When rainfall begins, the vegetation starts to grow and NDVI becomes high again. The values of NDVI represented a high productivity of grass vegetation, mainly due the C4 metabolism and water availability during whole year.

Hyperseasonal and semiseasonal savanna vegetation remained green (high NDVI values) because there was still water in the soil, but when soil water availability decreased in the dry period (stress by water deficit), the green vegetation started to disappear, then the values of NDVI decreased, too. During the middle of the second rainy period NDVI values decreased, probably because the water level was high and masked the infrared radiation of the green vegetation, then the sensor observed a mixture of water and green vegetation.

The seasonal savanna on the piedmont presented decreasing values of NDVI during the dry period, a phenomena explained by a decrease in water availability. But the isolated peak in NDVI at the beginning of the rainy period could be explained by the permanent crops, as well as the short period of growth at the beginning of the rainy season following dry season fires. The increasing values of NDVI during the rainy period are related to the growth period of savanna vegetation and annual crops in the area.

The patterns of phenological variation for each of the ecosystems show a strong relationship with the environmental features described by Sarmiento (1983, 1990), Sarmiento *et al.* (1971), Silva *et al.* (1971), and Chacón-Moreno (1999), where the annual distribution of rainfall determines conditions of water availability. The patterns also depend on other characteristics such as the geomorphology of the areas where this ecosystem exists.

Using analysis of the multitemporal NOAA-AVHRR NDVI imagery, it was possible to reveal the phenology of the most important ecosystems in the savanna area of Venezuela. This methodology allows a link between the ecological processes with spatial components of the remotely sensed data. The interpretation of the phenological patterns is useful to identify and select a pool of NOAA-AVHRR NDVI images in contrasting periods to produce a map based on the image-supervised classification.

The classification accuracy of the Ecosystems map was good with an overall accuracy of 79%, therefore the classification of the savanna classes derived from the analysis of the phenological patterns of savanna ecosystems was satisfactory. On the other hand, the extension of the agricultural units derived from previous maps indicates that some important changes in land use have been occurring.

Through this chapter the relationship between the climate seasonality and the phenology of the different savanna ecosystems was determined. Here, the climate seasonality is revealed as the main factor determining the savanna ecosystems type, while the soil nutrients availability is not exposed through the phenological dynamics because it is operating to the whole area and every time. The soil nutrients reflect a homogeneous distribution derived from the sedimentary Quaternary basin of the Llanos del Orinoco.

In the next two chapters, we will analyze the changes in the hydrological dynamics derived from the embankment of the flooding savanna, and the main landscape transformation occurred into the flooding savanna. The hydrological dynamic was analyzed at the local level, taken a representative small area of the flooding savanna, and the landscape transformations were studied at the regional level on a large extension about 16000 Km^2.

3.6 Acknowledgements

This work was supported by the Consejo de Desarrollo Científico, Humanístico y Tecnológico (CDCHT), Universidad de Los Andes, Mérida, Venezuela (project C-706-95-01). I would also like to thank the International Institute for Aerospace Survey and Earth Sciences (ITC), The Netherlands for their collaboration in the research. I thank the International Geosphere Biosphere Programme for the use of the global land 1-km NOAA image data set. I appreciate the valuable collaboration of Maryelis Pabón, Daniela and Rebeca Chacón for the assistance during the fieldwork validation. Finally, I would like to thank Dr. R.H.G. Jongman and Dr. Prof. I.S. Zonneveld for helpful comments, and Dr. F. Rada for the review of the manuscript.

CHAPTER 4

Effect of dike construction on water dynamics in the flooding savannas of Venezuela

4. EFFECT OF DIKE CONSTRUCTION ON WATER DYNAMICS IN THE FLOODING SAVANNAS OF VENEZUELA

4.1 Abstract

The flooding savannas of southwest Venezuela or Llanos of Apure are flat landscapes and the annual dynamics of flooding is the key ecological factor controlling ecosystem structure and functioning. In this alluvial overflow plain the hydrological dynamics of the area are largely determined by the topography, which depends on geomorphology and geology. For water management, dikes were built in 1960. The objectives of this study are to develop a methodology to construct a Digital Elevation Model (DEM) for a very flat area, to analyse and evaluate the flooding dynamics of a modulo, which is the unit of water management in the area, and finally to relate the topography with geological features. Therefore field measurements were carried out with real time kinematic geographical positioning system and air photographs as well as radar images are used for further interpretation and modeling. The results were a precise digital elevation model showing distribution of sinks, as well as insight in the process of flooding.

Keywords: Digital Elevation Model, flooding dynamics, tropical savanna, river floodplain, wetland

4.2 Introduction

To carry out the spatial modeling of species distribution into a GIS based model, it is necessary to establish the spatial pattern of the environmental factors associated to the hydrological dynamics, because the ecological responses of the species distribution will be expressed into the spatial context through the environmental variables. In this chapter, the topographical factor is evaluated in relation to the hydrological dynamic of the area based on the elaboration of a Digital Elevation Model.

The flooding savannas of the Southwest of Venezuela or Llanos of Apure, occupy an important extension, approximately 30 000 km², of the Llanos of Venezuela. (Sarmiento and Pinillos, 2001). Contrasting with other savanna areas, in the flat landscapes of this region the annual dynamics of flooding is the key ecological factor controlling ecosystem structure and functioning. Depending on the presence of a flooded period and of its duration three main types of savanna ecosystems can be defined: seasonal, hyperseasonal and semiseasonal (Sarmiento, 1983). The occurrence of these savanna types, their proportion and spatial distribution are very important for biodiversity as they represent different kinds of habitats and offer resources for the fauna in different periods of the year (Rivas *et al.*, 2002; Tamisier and Dehorter, 2000).

The distribution of these three ecosystem types also has a large influence on the extensive cattle breeding in the area, which is the main human activity in the region. Cattle stocking rate and spatial distribution over the year depend on the inundation of the area. The cattle feed on natural pastures and the available fodder over the year is very variable. The bottleneck for cattle breeding is the dry season, when only semiseasonal savanna offers a production of grass and in the other areas grass is dry and often submitted to burning. In order to surpass this shortage during the dry season dikes and small polders (modulos) were built to regulate the water. This measure had its beginnings in the 1960s and state programs, known as the “Modulos de Apure”, were implemented in the 1970s. With the building of modulos the stocking rate could increase from 0.2-0.25 to 0.6-0.75 animal-unit/ha (Betancourt *et al.*, 2001). The dikes have various models, some have floodgates and others are simply earth walls that are broken with excavators when necessary. The dikes are usually placed between two riverbanks in a diagonal way and each modulo can be considered as a separate hydrological unit. The careful planning of the position of the dike is crucial, as it also can lead to the inundation of undesired areas important for cattle grazing during the rainy season (Schargel and Gonzalez, 1972).

Water is the principal factor determining the ecological functioning and land use of these savannas; however, detailed knowledge on the precise relationships between relief and inundation patterns and the effects of the dikes is scarce (Sarmiento and Pinillos, 2001) and the completed study about the species-environment relationships is described in chapters 6 and 7 (Chacón-Moreno *et al.*, 2004; Chacón-Moreno *et al.*, submitted). Also little information is available to perform this kind of analysis. Therefore the first objective of this study was to develop a methodology to construct a Digital Elevation Model (DEM) for a very flat area, where available topographical data are very limited and of poor quality, but at the same time relatively high precision is required because small differences in altitude can have a large influence on the water dynamics. The second objective was to use this DEM, in combinations with fieldwork data and classified radar images to analyse the flooding dynamics of a modulo, which is the unit of water management in the area. A further objective was to evaluate the effect of the dike on the water volume by comparing the current situation with the state before the dike was built by using a hydrological model. And finally the final objective was to relate the topography of the modulo to the different geological epochs in order to examine if geological maps can be used to obtain indicators of the hydrological behaviour in neighbouring areas as height information for these flat ecosystems of Venezuela is not available in the quality or vertical precision adequate for more detailed studies.

The study area is situated in the El Frío Biological Station, an 80,000 ha large farm in the North of the Apure State, described in chapter 6 (Figure 6.1). For water management dikes were built in 1960, surrounding and dividing an area of approximately 5700 ha. In Figure 4.1 the area is shown with the streams and dikes. The central dike, crossing the area in north-southerly direction divides the area in upstream and downstream and has changed the hydrological dynamics of the area. Gallery forest is found along the banks of the main stream and depending on the relative height of the terrain, seasonal, hyperseasonal and semiseasonal savanna occupies the rest of the area. The nearest climatic station is in Mantecal, approximately 25 km west of the study area. The climograph (Figure 4.2) shows that the peak of rain in June and the driest months are from December to March with an average total precipitation of 1590 mm. The monthly mean temperatures are between 25.4°C in July to 28.5°C in March. The soils are sandy on the banks and become loamy at the deepest points in the esteros. The soils are poor in nutrients and base saturation due to leaching and a hard pan can be found in most of the area at around 60 cm depth (Sarmiento and Pinillos, 2001).

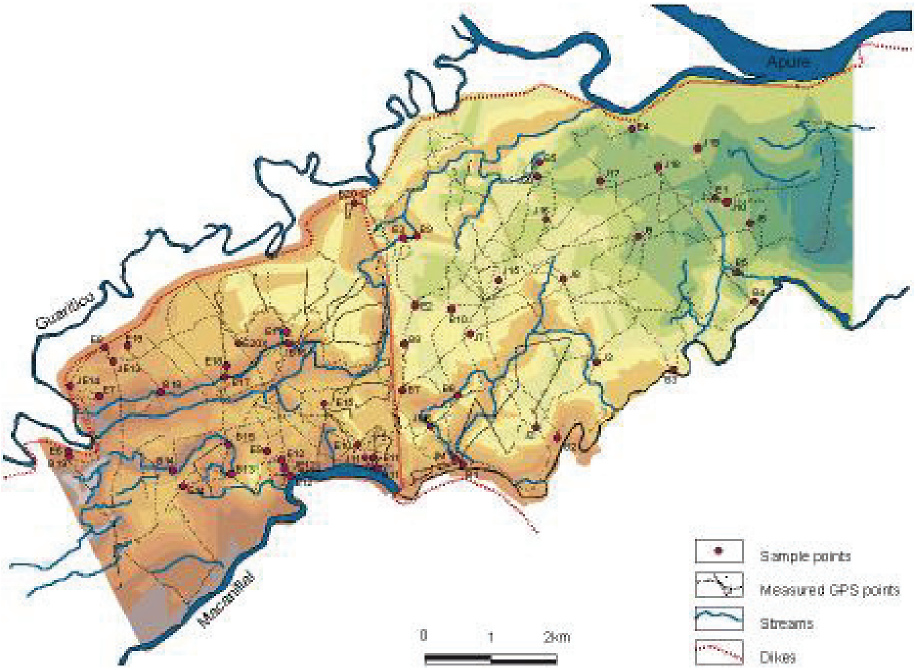


Figure 4.1 Digital elevation model of the Modulo El Frío Biological Station. Brown indicates the highest part of the area, green and blue are the lowest. Sample points (numbered) and GPS points (dotted lines) are indicated

4.3 Methods

4.3.1 Environmental conditions

The hydrological dynamics of the area are largely determined by the topography, which depends on geomorphology and geology. The Llanos of Apure are formed by alluvial overflow plains and in our study area the sediments found correspond to the epochs from upper Holocene to the lower-middle Pleistocene (Figure 4.2: upper Holocene: Q0a, lower Holocene: Q0b, upper Pleistocene: Q1, middle Pleistocene: Q2, lower Pleistocene: Q3). As the older sediments were transported further than the younger ones, Q3 was deposited almost in the entire area and later covered by Q1 and Q2 in a discontinuous form. The sedimentation of Q1-Q0, in contrast to older epochs of sedimentation, conserves their original forms, produced by the fluvial dynamics (natural levees or banks, flat overflow areas and decantation basins) (ECOSA, 1980; Sarmiento and Pinillos, 2001; Vivas, 1992). Although the relief is a fundamental factor for flooding dynamics, the altitudinal differences are very small and tiny variations can have an important effect, consequently the analysis of the water dynamics requires a relatively high precision knowledge of the relief.

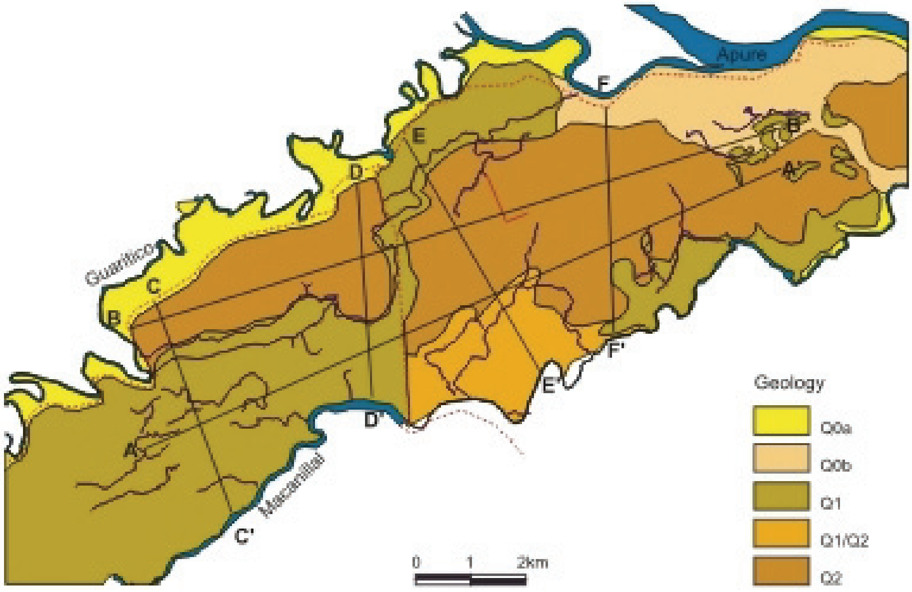


Figure 4.2 Geological map of the study area of El Frío Biological Station. The position of the profiles crossing the geological map are indicated. The types on the geological map are upper Holocene: Q0a, lower Holocene: Q0b, upper Pleistocene: Q1, middle Pleistocene: Q2, lower Pleistocene: Q3 (Pinillos, 1999).

The main water source for the inundation is precipitation and therefore the yearly rainfall and its distribution over the year is another important factor for determining the flooding dynamics. The precipitation pattern is very seasonal, with at least four to five dry months (December to April) when the potential evapotranspiration largely exceeds the precipitation. Only in May water starts to accumulate in the area, when the evapotranspiration falls below the precipitation. After October the evapotranspiration surpasses the rainfall and the inundation begins to diminish. Therefore flooding reflects the precipitation and evaporation patterns (ECOSA, 1980; Sarmiento, 1983).

Another factor that favours flooding in this area is found in the characteristics of the soils. Due to the strong seasonality of the climate the alfisols and ultisols form argillic horizons that are often associated with ferric concretions. These hardpans have almost no hydraulic conductivity (Malagón and Ochoa, 1980; Sarmiento and Pinillos, 2001).

In the flooding savannas water is one of the main factors that determine the ecosystem and its change. During flooding, the level of water and the duration of its presence highly depend on the relative height position of the ecosystem unit. To be able to study the water dynamics in the area and especially to quantify the water content, a Digital Elevation Model (DEM) is needed. As the study area is very flat (overall slope W-E < 0.5%) the height information for the DEM construction has to meet a high vertical accuracy.

4.3.2 igital Elevation Model

For the construction of the DEM various sources for height information were explored. Topographical maps of the area show height information only for a limited number of points, which is not sufficient for the DEM construction. The possibility to construct the DEM from aerial photographs by using photogrammetric methods was tested, but due to the flatness of the study area and the scale of the photographs (1:25000) the obtained results were not satisfactory. As the first two possible data sources were insufficient, field measurements with GPS became necessary. This method of data collection is very time consuming and in order to create a DEM for the area of the modulo of the El Frío Biological Station (57 km^2) a combined method of GPS field measurements and aerial photograph interpretation was developed and applied.

4.3.3 GPS measurements

In March 1998 a three week field campaign was carried out for terrain measurements with real time kinematic Geographical Positioning System (RTK GPS). In the first week a continuous 48-hour measurement was performed to counteract the SA distortion deliberately imposed on the GPS signals by the US Department of Defence. For a single autonomous (single receiver) GPS position the SA effect was in average of ca. 100 metre (2 σ). By logging GPS positions on a fixed point (station) for about 48 hours with a minute interval the SA effect was nearly cancelled out. The mean position expressed in the GPS reference system (WGS84) will show an absolute positional accuracy of about 5 metres (2 σ).

From this ‘point of origin’, baselines were measured to and between four points located in the modulo of the El Frío Biological Station and a single base line to the triangulation vertex in Macanillal place. The terrain description and the XY position in the local (national) UTM grid of this vertex were obtained from Cartografía Nacional de Venezuela, División de Geodesía. Two other triangulation vertices (points) in the area could not be found, probably due to house or dike construction.

All baseline measurements were post-processed in the WGS84 reference system resulting in an adjusted network of reference points. After a datum transformation from WGS84 to the local reference system (Ellipsoid: International 1924/Provisional South American 1956; datum point 'La Canoa') and a subsequent projection/transformation to the local UTM grid these reference points could be used as base stations for the measuring transects. Afterwards all RTK positions were transformed to UTM XY and relative Z (better than 15 cm accuracy).

With the RTK GPS a total of 5500 points were measured. These points contained transects over the entire modulo study area, profiles of selected topographical features such as dikes, riverbeds and their banks, ground control points for the georeferencing of the aerial photographs and sample points for water level measurements.

4.3.4 DEM construction

Transects were driven with a four-wheel drive vehicle measuring X, Y and Z every 50 m. The average distance between transects was 400 m and where accessibility was difficult due to dense bushes and trees a larger separation of transects (maximum distance 700 m) was accepted (Figure 4.1). In the inundated areas driving was impossible and transects had to be measured by foot, but as the dry season was very pronounced in 1997/98 (ENSO effect) only relatively small areas were flooded at the time of the fieldwork. The profiles were located over the entire area and 85 topographical and geomorphologic units (dikes, small rivers beds and their banks) were measured. This information was collected in order to assign height values to streams, dikes and banks digitised from the aerial photograph interpretation.

For the construction of the DEM the linear features such as riverbanks are important, especially as they can function as barriers for superficial runoff. As these features are not always captured in their total extension, when measuring transects over an area, the information has to be obtained from a different source. In the case of the Modulo El Frío Biological Station, the area is too large to measure sufficient transects in an acceptable time period as to be able to extract these linear features directly from the field measurements. For this reason additional information was obtained from orthophotographs, obtained from the aerial photographs (1978, 1:50000), by digitising onscreen the main linear terrain features such as rivers and dikes. By overlaying the measured GPS points, principally the measured profiles, the width and the height of these features were determined. As not all the streams are bordered by banks the ones that are had to be identified and selected. The average width of the banks was 35 m and using this value the streams with banks were buffered and the heights of the banks were automatically assigned, using the height information from the profiles. The heights of the river and streambeds were also extracted and automatically allocated to the stream segments. As for the main dike, the mean altitude was selected for the entire dike. The actual height oscillations are of no importance, because the dike is always so high that it acts as barrier to surface water.

As the measured transects were not very dense and in some areas driving was only possible along the stream banks, notes on all profiles and transects were taken in the field. With help of the notes, problematic points could be identified and eliminated. Another problem was that individual points on banks or in riverbeds lead to an overestimation of these heights, when interpolating the information. For example, if in a transect a point is measured in a riverbed it leads to a depression in the DEM, where no depression exists. The same applies to points on banks, which cause an elevated area in the DEM. These points have to be removed before the DEM is calculated. These problem points are identified by calculating a provisional DEM with all the points and overlaying it with the digitised photo interpretation and the measured points and then eliminated.

Using the corrected GPS points and segments, a Triangulated Irregular Network (TIN) was generated. A TIN is a three-dimensional model of a surface that defines an area as a set of contiguous, non-overlapping triangles, which vary in size and angular proportion. A height value is recorded for each triangle node and the heights between the nodes are interpolated. The advantage of using this method instead of interpolating the points to form a grid is that a TIN can accommodate irregularly distributed data sets and accepts linear as well as point data as input (Burrough and McDonnell, 1998).

The different landforms present in the study area were analysed by comparing the DEM with the geological map (Figure 4.2). Profiles were automatically extracted from the DEM and the geological epoch that was crossed assigned.

4.3.5 Water dynamics

To study the water dynamics ERS2 SAR PRI images of the study area were acquired. The dates of the radar images were the 7th of May 98, corresponding to the transition period between the dry and wet season and the 20th of August 98 for the wet season. The image corresponding to the dry season was not recorded and therefore an ERS-1 SAR PRI image from May 1992 was used. This was possible because in 1992 the months until May were very dry and there was very little flooding. The radar images were processed and classified with ground control areas and flood maps were created for the different seasons (for further information see Jongman *et al.*, submitted).

In order to measure the temporal water level upstream from the dike 10 rulers were installed along the dike, located every 400 m at a distance of about 30 m from the dike. The reading of the water level was needed for interpretation of the modeling results and was carried out with binoculars during the periodical field trips (1997-1999). The exact position and height of the rulers was determined with the RTK GPS. Apart from the data collected with the rulers, additional water level data was collected at different locations and times of the year. 60 fixed sample points were established throughout the area and within the types of ecosystems (Figure 4.1). At these locations the water depth was measured with a tape measure and the position was determined with RTK GPS. Concerning the fieldwork it has to be mentioned that entering the study area during the wet season was sometimes impossible and programmed sampling dates could not always be met.

Using radar images, inundation patterns at different times of the year can be detected, but the amount of accumulated water in the area during the wet season cannot be derived. The DEM offers the possibility to study the hydrology and quantify the collected water. It can also help to interpret the flooding dynamics of an area.

The analysis of the flooding in the Modulo El Frío Biological Station is divided into three parts:

- The flood maps, obtained from the radar images (Jongman *et al.*, submitted), are analysed using the DEM allowing the quantification of the accumulated water in the Modulo.
- The flooded areas and the water volume of the upstream area (from the dike) are calculated for different periods using the DEM.
- Hydrological simulation is used on the field data and to detect the flooding process of the sinks in the area upstream of the dike.

For the detection of the areas of internal drainage the hydrological modeling extension of Arcview was used. Usually for hydrological modeling a DEM free of depressions is required, as small sinks in elevation data are considered, most commonly, to be due to errors in the data. Because of the nature of our study area, the majority of the small sinks are considered to be real. Therefore, the only application of the hydrological model extension that can effectively be used is that of filling the sinks. This process fills each depression in the DEM to the elevation of the lowest overflow taking the flow direction of each cell into consideration and with that the areas of potential flooding are identified. This modeling was carried out on two DEMs, one with the dike and the other without it.

For the calculation of the water volume two approaches were applied. The first was to overlay the DEM with the flood maps created from the radar images and the other was to use water level heights measured in the field and model the inundation. To calculate the volume of the water accumulated in the modulo at the dates of the radar images, the classified radar images were combined with the DEM. New grids were created, showing the DEM only for areas that were classified as flooded in the images. To estimate the water height for the different periods, the borderlines of the inundated areas of each new grid were analysed. As the borderline of a continuously inundated area has the same height all around, the absolute water level heights can be extracted. With these water level heights and the grids showing the DEM only for the inundated areas, the volume of the water flooding the areas, can be calculated. DEM height values are subtracted from the water level height, giving the water depth over each height group of cells. Combined with the area it provides the total water volume. Downstream of the dike, the area was divided into 3 zones, as the inundated areas were not continuous and there is a large difference between the areas close to the dike and the area further downstream. In each zone, the water level was at a different height. Upstream from the dike, one single value for the entire area defined the water level, as the inundated areas were more continuous.

Modeling the inundation was only possible for the area upstream from the dike, as the DEM does not include the entire watershed. The downstream boundary of the DEM acts as an artificial second dike restraining the outflow of the water. The inundation was modelled for the upstream part of the DEM by filling the water level to heights measured in the field. In this newly constructed DEM for the upstream area the central dike was lowered from 72.0 m to 69.89 m, which represents the height 1 cm above the highest point in the terrain.

For the volumetric analysis, the area between the TIN surface and the horizontal plane, formed by the water surface and located at a specified height, is calculated. To model the spatial extension of the flooding, different grids were created with all cells containing the water level height of the specific fieldwork dates. The two height images, the TIN and the water level grid, can be compared. Areas that lie below the water level are separated from the areas above, simulating the flooded area for a specific water level height and giving the volume of the area between the two surfaces.

The comparison of the calculated water volumes with the climatic data of the same year was not possible as this data was not available. Therefore, they were compared with an average year from the data of the climatic station of Mantecal. In the study of ECOSA (1980), the potential and real evapotranspiration is calculated. The potential evapotranspiration is derived from the pan evaporation and the correction factor is 0.8, a factor used for Venezuela (ECOSA, 1980). The real evapotranspiration is calculated with the Budyko method and the estimated retention of water in the soil for the area of Mantecal is 100 mm. Figure 4.3 shows the results of the calculation. To obtain the water remaining in the area, when not taking drainage into account, the real evapotranspiration was subtracted from the precipitation

4.4 Results

4.4.1 The DEM for the modulo of El Frío Biological Station

The Digital Elevation Model of the study area is shown in Figure 4.4. The main slope is in WSW -ENE direction. Over a distance of 12.8 km the height difference between the highest and the lowest area is 3m (66.8 m to 69.8 m). This is equivalent to a general slope of 0.013 º. Apart from the general inclination, the slopes inside the area can be derived from the TIN, resulting in a slope map. Over 65% of the area has slopes below 0.1º and only 3.35% has slopes over 1º. These steeper slopes are found on the dikes and some larger banks.

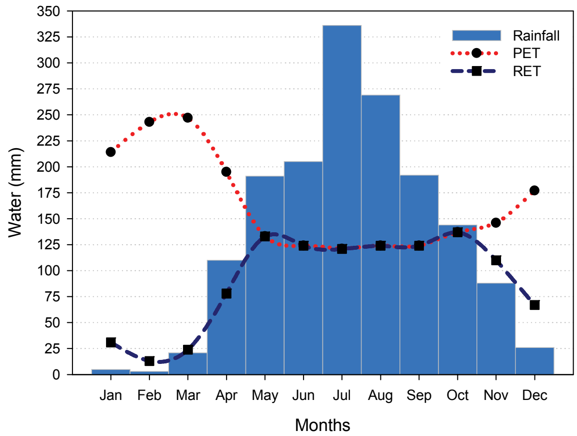


Figure 4.3 Climograph from Mantecal 80 km West from the study area, showing Potencial and Real Evapotranspiration and Precipitation. (taken from ECOSA 1980).

For a visualisation of the topography of the area, six profiles were extracted from the DEM. In Figure 4.4 the position of these profiles is given and Figure 4.2 shows the profile positions on the geological map. Two profiles are situated in the direction of the main slope and four transverse.

In Figure 4.5, it can be observed that profile A-A' crosses several banks. Upstream from the dike the general slope is practically flat whereas downstream the slope is steeper. When comparing both profiles, profile B-B' shows a relative continuous slope over the entire area. The difference between the two profiles can be related to the age of the sediments that are crossed. Comparing the position of the two profiles, profile B-B' lies inside Q1 virtually over the entire area, whereas A-A' crosses Q2 upstream from the dike. In general the higher banks are found in Q1. This can be observed more clearly in the profiles, which lie vertical to the main slope (Figure 4.5). The main difference between the two epochs in our area is that the older sedimentation forms have been subject to fluvial and Aeolian erosion for a longer period, erasing the natural levees and filling the basins.

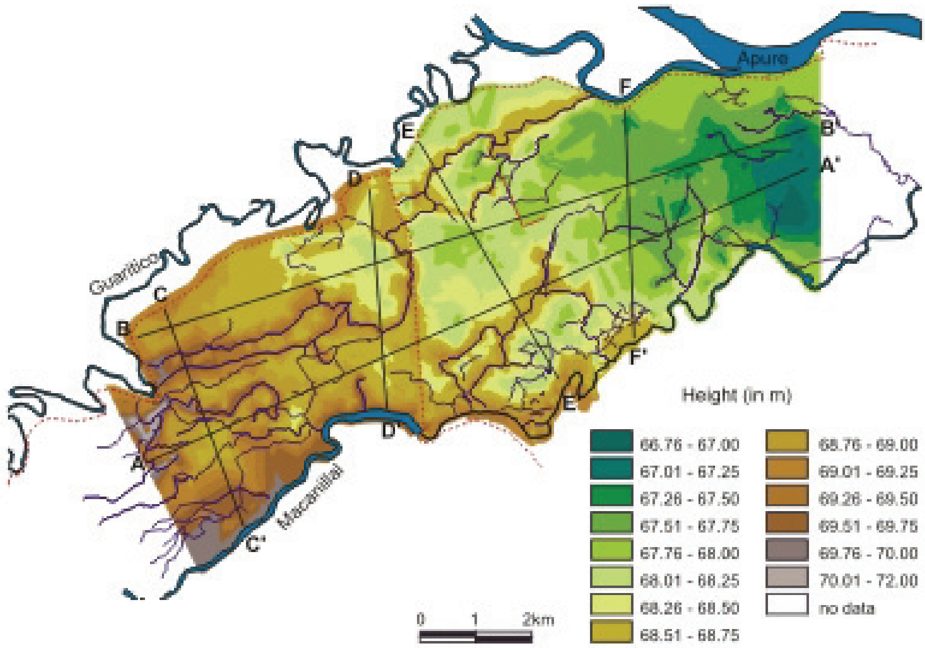
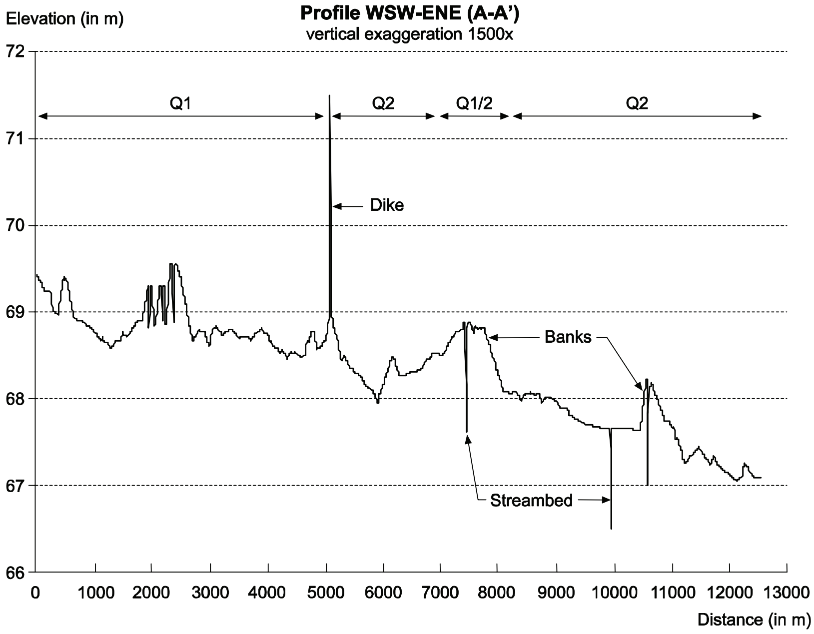


Figure 4.4 Digital Elevation Model of the study area of El Frío Biological Station. The position of the profiles crossing the DEM are indicated.

The comparison between the different profiles, vertical to the main slope, show that the terrain level of Q1 is slightly higher than Q2 as in profile D-D' (Figure 4.6). In Profile C-C' this is not the case, because the profile crosses a sink in Q1, which can also be recognised in the DEM. Profile F-F' shows that when no banks are crossed, there is also a slope in northern direction. The degree of the slope is relatively high because of the influence of the bank of the Mancanillal. The comparison between the DEM and the geological map shows the relationship between the age of sedimentation and the topography.

4.4.2 Flooding dynamics in the Modulo El Frío Biological Station

The map showing the sinks in the area is presented in Figure 4.7a. It can be observed that a large basin exists upstream from the dike covering almost the entire area. Downstream from the dike, sinks can also be found, but they are smaller and do not cover the a large part of the area. In Figure 4.7b the sinks are shown for the area if the dikes (central and lateral) did not exists, simulating the situation before it was built. Here it can be observed that without the dikes, the upstream area is similar to the downstream area at present time with sinks scattered over the area but not dominating.



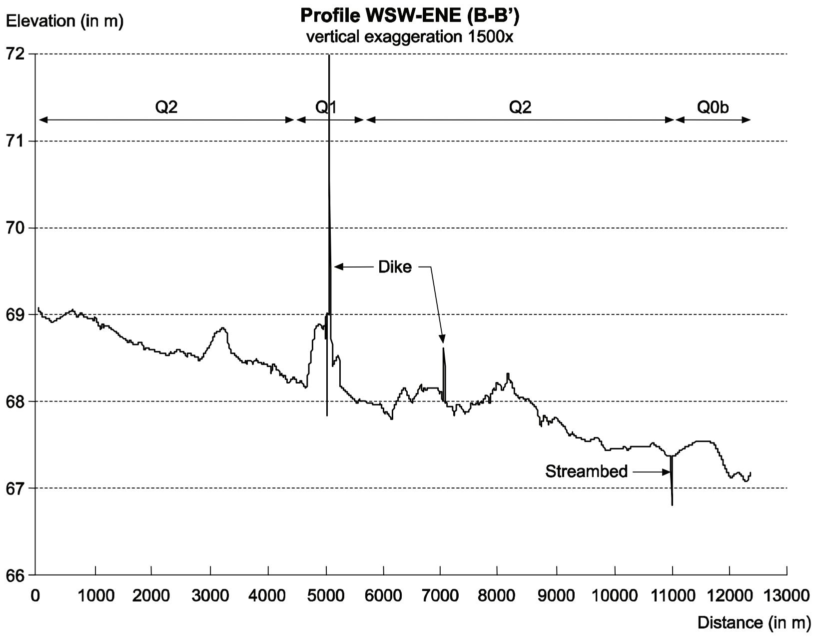


Figure 4.5 Profiles in direction of the main slope in the area and the epoch of the sedimentation of the area that is crossed. The profiles are placed in a right angle to the main dike. For the interpretation of the geological layers see Figure 5b

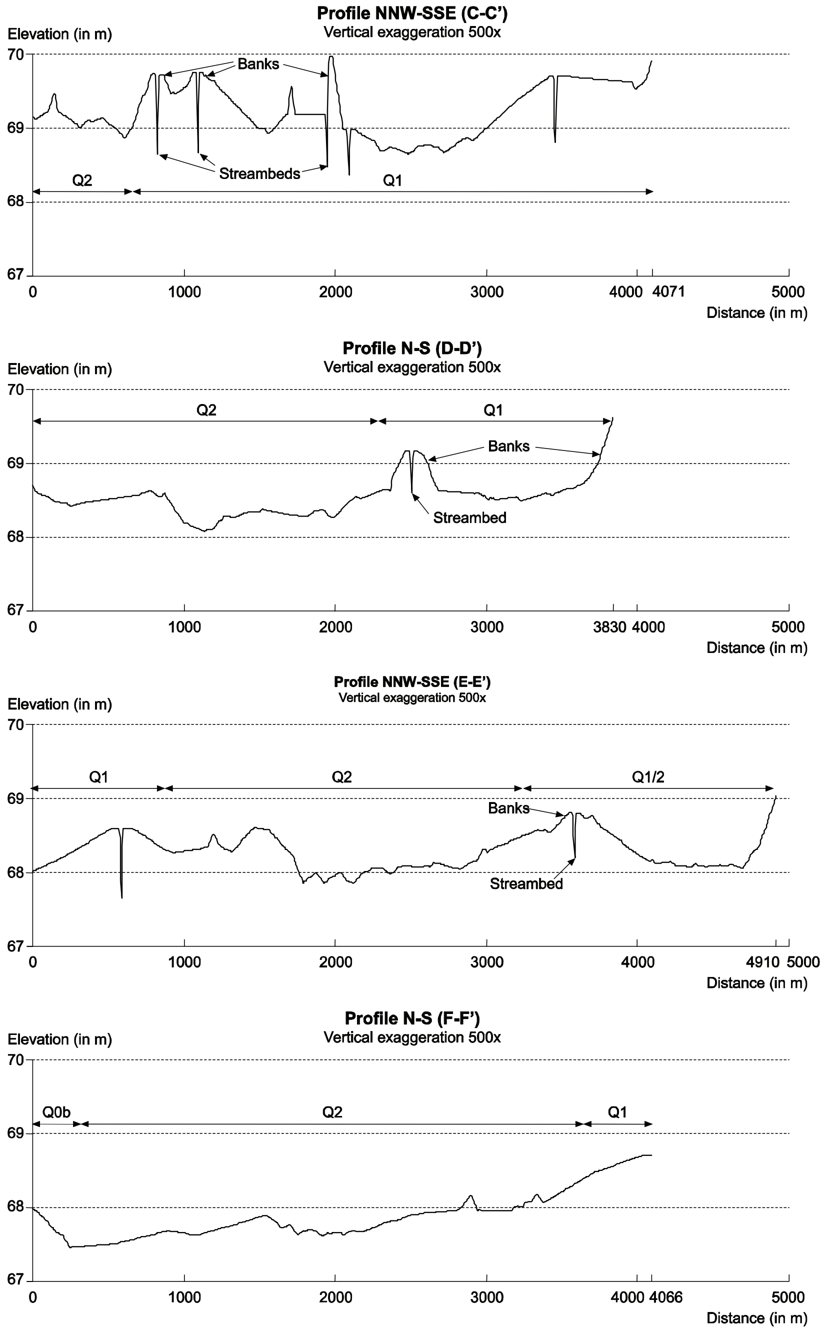


Figure 4.6 Profiles vertical to the main slope in the area. The profiles are placed parallel to the main dike. For the interpretation of the geological layers see Figure 7.3b

To compare the situation before the dike construction to the current situation, the amount of water, which would be held in the polder area (modulo) if all sinks were filled to their minimum overflow level, was calculated for both DEMs. Without the dikes 2.27 x 10^6 m^3 of water are collected in the area and with the dike 8.86 x 10^6 m^3, almost four times as much. The values given are for the entire area.

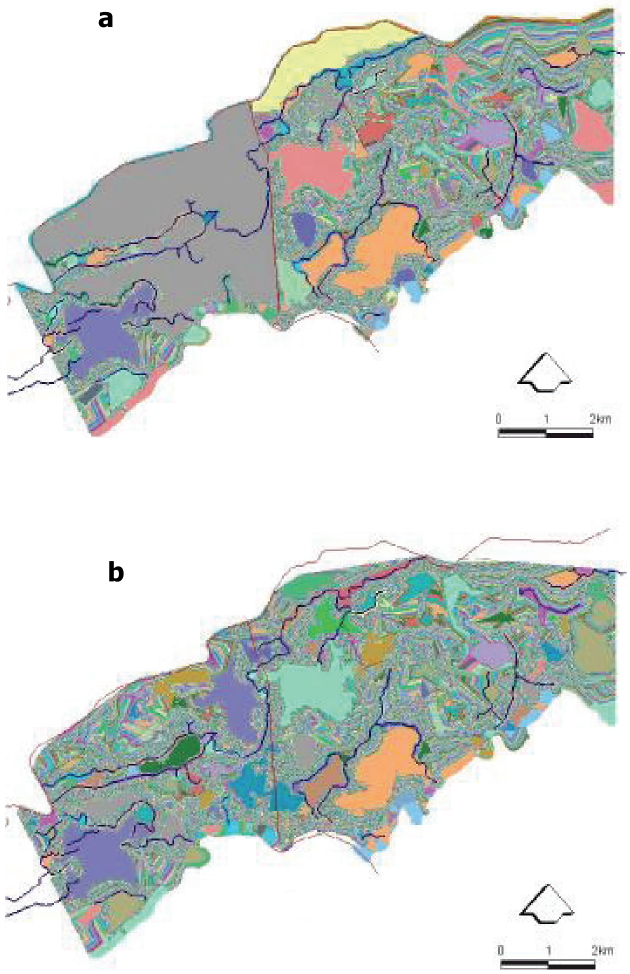


Figure 4.7 Filled sinks of the DEM with the dike (a) and without the dike (b). The larger areas of one colour are the sinks filled to the level of the lowest overflow. The main dike and streams are indicated. Each surface of one colour delineates one area of internal drainage, which has been filled to its lowest overflow. The mingled areas are without sinks.

The progressive filling of the area upstream from the dike cannot be observed in Figure 4.7a. With the reduction of lowest overflow level, the filling of the new

DEM the inundation increases at different levels. The result can be observed in the Figure 4.8. The legend values indicate the water level height that fills the respective area. The continuous areas show the progressive filling or emptying of the basins. When interpreting the map it has to be taken into consideration that the sinks are filled with by precipitation and sinks that are at different height levels can be flooded at the same time.

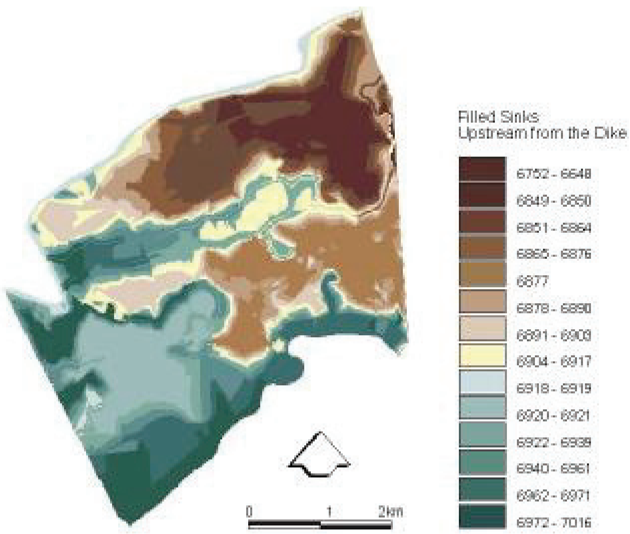


Figure 4.8 Filled sinks of the DEM upstream from the dike. For this DEM the dike height was lowered to reduce the lowest overflow level. With this modification the sink sizes are reduced. The height values are given in cm.

4.4.3 Water volumes extracted from the radar image classification and the DEM

The quantification of the water, flooding the modulo area at different times of the year is shown in Table 4.1. The values were calculated by combining the DEM with the classified radar maps. As the areas upstream and downstream from the dike have different sizes, the average water height over the terrain was calculated for comparison.

In the transition season, the water level height is only 11 cm higher than in the dry season. As the area is so flat only small changes in the water level height can cause the flooding of large areas. The difference of the water level height between the transition and wet season is almost 60 cm and the water volume is more than tripled. Again the effect of the dike can be clearly observed.

At the end of the dry season the area downstream of the dike has no superficial water and upstream there is also little superficial water. Upstream the inundation was decreased to only some small areas. In the transition period between the dry and the wet season the superficial water began to collect in some downstream areas, whilst upstream large zones were flooded. In the wet season the majority of the modulo was inundated, leaving only small areas without superficial water.

Table 4.1 Water volume of the flooded areas obtain from the classified radar images and the DEM. The water level heights were extracted from the DEM and the water depth is calculated as if the water were distributed uniformly over the area

	Dry season		Transition		Wet season	
Area relative to the dike	Up-stream	Down-stream	Up-stream	Down-stream	Up-stream	Down-stream
Water volume (in 1000 m^3)	166	0	2 674	767	10 579	7 376
Water depth: (m^3/m^2)	0.01	0.00	0.12	0.02	0.49	0.21

To be able to control if the calculated volumes are in a possible range, theoretical water volumes were calculated using the hydrological balance for "Mantecal" (ECOSA, 1980) (Figure 4.3). Even though the precipitation in the study area is variable, general tendencies can be extracted from the data of an average year. From April the water level for each month was calculated and multiplied with the polder area (modulo). For the calculation, a totally dry area at the end of the dry season was presupposed. The comparison of the calculations downstream from the dike shows that all water volumes from the climatic data are much higher. In the wet season the water volume derived form the radar classification was 7.38 x 10^6 m^3 and from the climate calculations it was 18.7 x 10^6 m^3, almost 2.5 times as much. This indicates that without the dike the runoff is probably relatively high and the estimation from climatic data without runoff is not valid. On the other hand the comparison of the water volumes upstream from the dike shows that the general tendency from the dry to the wet season is similar in both cases.

4.4.4 Modeling of the inundation

As was shown above, the modeling of the flooding, downstream from the dike is not possible, as the DEM does not cover the entire watershed and the outflow out of the area is unknown. Therefore the modeling of the inundation was performed only for the upstream area.

To model the inundation, the absolute water level heights obtained from fieldwork and the DEM upstream from the dike were used. In Figure 4.9 the process of the flooding of the DEM from the dry to the wet season is shown for the year 1998. As no field data exists for August 1998, the water level height of July 1997 was used for period of the largest extension of inundation.

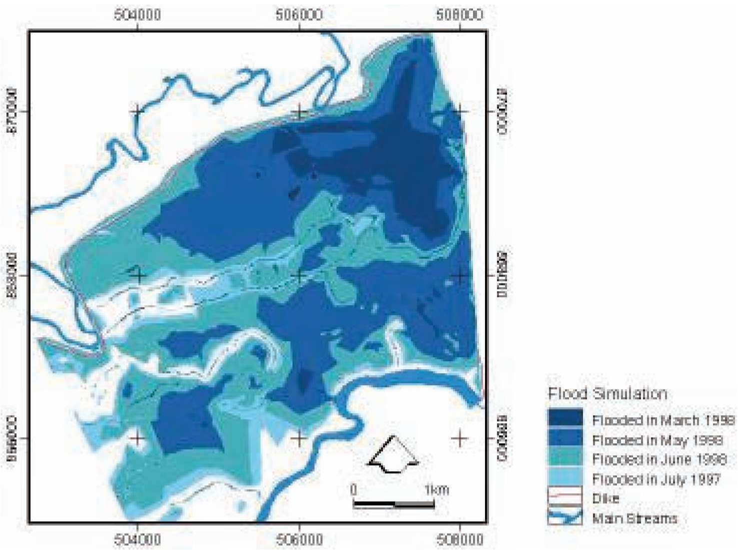


Figure 4.9 Simulation of the flooding with the DEM based on the water level heights measured in the field

In Figure 4.10 the calculated water volumes for the different periods can be observed and compared to the volumes obtained from the radar images and the climatic data. The increase of water volume taken from radar is very similar to the volume extracted from the modeling and also the data acquired from an average year show a similar tendency in the increase to the maximum inundation. Only the diminution of the water at the end of the year is very different between the fieldwork and the climate calculation.

4.5 Discussion

The hydrological dynamics of the flooding savannas of Apure situated in the Southern Venezuelan Llanos appear to depend mainly on the presence of natural sinks or basins. The landscape of the area, including the presence of these sinks, originates from successive depositional events that took place during the Middle Pleistocene and Holocene period (Q_3-Q_0) (Sarmiento and Pinillos, 2001). The erosion of the sediments that was more or less prolonged depending on their age produced a progressive homogenisation and levelling of the landscape. Also the very active current alluvial dynamics is dissecting the landscape and depositing new sediments. Due to the virtual absence of slope in the area and the widespread presence of a hardpan or plinthitic horizon that is highly impermeable in the soil profile, drainage is strongly limited and significant amounts of water tend to accumulate in the natural sinks from where they are progressively lost to the atmosphere by evapotranspiration. The capacity of the system to store water depends on the size of these natural sinks, which are formed and delimited by the levees of the fluvial system (active and former rivers and streams).

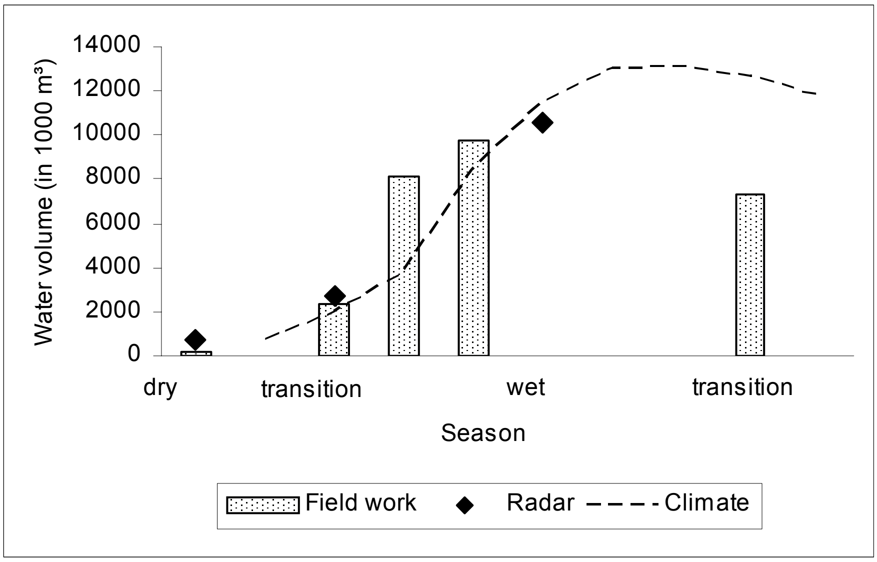


Figure 4.10 Comparison of the water volume calculated with the different methods: From radar image classification, from the field work and from climatic data of an average year.

In the area an intricate network of levees can be observed, forming natural dikes and sinks of different sizes and capacities to store water. A few centimetres of difference in the height of a levee can produce large differences in the size of the sink, due to the very low slope of the area. Using the DEM the relationships between the heights of the levees, the size of the sinks and the depositional epoch of sedimentation can be clearly observed. On older sediments (Q_2 in the area), where erosive processes have been active over a longer period of time, the landscape is more homogeneous, the levees are lower and consequently the size of the sinks and their capacity to store water are reduced compared to the younger sediments (Q_0 and Q_1) where bigger sinks are formed and more water can be stored. Consequently on younger sediments larger areas are flooded and the water level is higher. On these younger sediments semiseasonal savannas predominate because extended areas remained flooded or with a high soil moisture all the year round. On older sediments fewer areas are flooded and the water level is lower, consequently hyperseasonal or seasonal savannas predominate. The relationships between the geological epoch and the predominant ecological type of savanna have been previously observed by Sarmiento and Pinillos (2001), but our results clarify the effect of the depositional epoch on the hydrological regime, explaining the different capacities to store water in terms of the characteristic of the sinks. Hudson and Colditz (2003) also find in the Pánuco basin in Mexico that although floodplains are often portrayed as homogenous (flat) surfaces subject to flooding, that the duration of flooding varies due to the geomorphic complexity of large alluvial valleys and not all surfaces are inundated.

The main effect of the dikes on the hydrology is that natural sinks are enlarged or new sinks are created, increasing the amount of water that can be retained considerably. The main ecological consequence is that the relative proportions of the different types of savanna ecosystems change, decreasing the extension of the hyperseasonal savanna and increasing the semiseasonal savannas. In the next chapter 5 (Chacón-Moreno, 2001) it is show that between 1960 and 1988 semi-seasonal savannas increased their extension by 4.6 times due to the construction of dikes. An interesting aspect is that dikes are not creating new types of environments but changing the proportion of the existing ones. From an ecological point of view this is important because the creation of new habitats can promote the invasion of foreign species while the extension of an existing ecosystem would not produce this effect. However the spatial pattern and temporal offer of resources are modified by the dikes and the global ecological effect on wild fauna and ecosystem functioning can be important and have to be evaluated. From an agronomical point of view the primary productivity of the area increases, as the semiseasonal savannas are the more productive (Bulla, 1980; Sarmiento, 1984).

The upstream volume of water retained by the dike in the study area is very large. According to the results of flooding modeling with and without the dike based on DEM the volume increases by a factor of almost 4 in relation to what would be retained without the dike. This large volume of retained water increases the evapotranspiration in relation to superficial drainage and this change between the two main outputs of water from the ecosystem probably affects the regional hydrological balance.

The dikes also have an effect on the temporal flooding dynamics, causing the upstream area to flood earlier. Also the flooding period is extended during the dry season, despite the very high evaporative demand during this season, due to the increase in the water level height. The evapotranspiration during the dry season can be as high as 8 mm day^{-1} (ECOSA, 1980), so an approximate level of one meter of water is needed to maintain the inundation over the four months of the dry season.

The positive effect of the dike on water retention in the upstream area is accompanied by a negative effect downstream. As the drainage from upstream is cut off, sinks in this part of the modulo are only filled with rainwater and consequently the area close to the dike dries out faster than in the natural situation.

The consequences of the dike for the land use are multiple. On the one hand the inundation lasts longer, providing water when downstream areas are already dry and enabling the cattle to pasture these areas, but on the other hand the inundation can reach far upstream. This could cause a lack of available land for grazing at the peak of the wet season, as banks that formerly were used by the cattle in the wet season are now flooded. This disadvantage is reduced if the dikes have floodgates, as is the practise in other parts of the flooding savannas of Apure. Also the areas downstream can be used for grazing when the upstream areas are already flooded.

Comparison of the results of flood modeling on the basis of fieldwork data and the radar classification shows that these methods arrive at comparable values. The values derived from the climatic data (water balance method) also show that predicted volumes of water are roughly similar to the water estimated by the other methods for the period from the dry to the wet season. Nevertheless a direct comparison is not possible because the climatic data for the years of the study are not available and when using the mean values the strong annual fluctuations in precipitation in the study area have to be considered. Comparing the results of the water balance to the others methods for the end of the rainy season the differences are more pronounced (more water is predicted by the water balance method) and this is probable not due only to the climatic variations between years. The hypothesis is that runoff plays a more important roll after the sinks in the area are filled and in the water balance method runoff and drainage were neglected.

The modeling of the flooding dynamics shows that a detailed DEM could provide the possibility to model the effects of a dike before its construction. Different scenarios can be calculated for dry and wet years and various possible positions and height of the dikes can be tested. This could help to decide on the impact of a dike and if acceptable on the best location. Also the maximum height of overflow can be determined so that the flooding does not exceed the desired zones. The desired flooded zones would have to be defined, so maintain enough pasture in the dry season as well as in the wet season. If the inundating areas are too large there would be a shortage of grassing areas in the wet season and if it were too small the shortage would be in the dry season.

From a methodological point of view, the results show that when a detailed DEM exists, the water dynamics in an area can be modelled with relatively little fieldwork. The requirements are that the DEM covers the entire watershed and that the data has sufficient vertical and horizontal accuracy. This is also one of the biggest problems, when working in very flat areas, because often contour lines and height points are not very dense in the available topographic maps (Marks and Bates, 2000). Although a DEM can also be created with digital photogrammetry techniques (Baily *et al.*, 2003; Lane *et al.*, 2000), the required accuracy is frequently not met by the data. This is especially the case, when working in countries where very little topographical data and large-scale aerial photographs are available as is often the case within humid tropical areas (Hudson and Colditz, 2003). Therefore the developed method using aerial photograph interpretation and a geological map in combination with GPS measurements could be an alternative for these environments. The results have shown that although the DEM is not an "exact" reproduction of the topography of the area, it allows the modeling of the flooding dynamics and the results resemble those obtained from the radar image classification.

The construction of the DEM allows the clarification of the relationship between the epochs of sedimentation and the relief forms as was discussed before. These relationships could be used to deduce important aspects of the relief of other zones by extrapolating the relative height information from the profiles. This information could be combined with the data from a geological map and aerial photograph interpretations and the overall slope of an area could be extracted from available maps. This method would not give detailed information on the relief, but it would help identify the barriers, such as levees, for superficial runoff. Nevertheless the possibility of extrapolation needs to be explored further, but it could prove interesting for an area, where DEMs with the precision and scale of our study are difficult if not impossible to find.

We presented the analysis of the hydrological dynamics in a representative area of the flooding savanna. In the next chapter we analyzed the processes of landscape transformation derived from the embankment in the flooding savanna, where the construction of dikes had occurred in an enormous extension of more than 16,000 km^2. In that chapter, the change to regional scale is appropriated because through that and the availability of remote sensing data, we had a complete vision of the transformation. In the next chapters we used the knowledge derived from this chapter in order to explain the ecological aspects considered in this Thesis: ecosystems replacement in Chapter 5, species-environment relationship in Chapter 6, species responses in Chapter 7, and the spatial distribution of the species in Chapters 8 and 9.

4.6 Acknowledgements

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CHAPTER 5

Landscape change by embankment of the Llanos del Orinoco flooding savanna: a land unit approach

5. LANDSCAPE CHANGE BY EMBANKMENT OF THE *LLANOS DEL ORINOCO* FLOODING SAVANNA: A LAND UNIT APPROACH

5.1 Abstract

This work presents an analysis and description of the landscape changes derived from the construction of dikes to control inundation in the flooding savanna of the *Llanos del Orinoco* in Venezuela. Elaboration of the landscape ecological maps was based on a land unit approach. This allowed the land (ecological) units to be defined and described as ecosystems by linking the main ecological processes associated with the savanna ecosystems to the remotely sensed features. Based on this approach, two landscape ecological maps were produced from two different spatial data sources: aerial photographs for the 1960 map and Landsat TM for the 1988 map. These landscape ecological maps contain the same land units as the ecological ecosystems defined by Sarmiento (1983), where ecological processes are related to water dynamics. An important change process occurred during the period between 1960 and 1988, with dike construction producing a large impact on water management. The dikes and the water management change the size and distribution of the main land units (ecosystems). These changes are mainly represented by the replacement of the hyperseasonal savanna unit, which in 1960 occupied more than 45% of the area, by semiseasonal savanna units, representing more than 50% of the total area in 1988. Almost all the changes observed in the landscape ecological map are derived from dike construction. The accumulation of water upstream from the dikes and the drainage pattern downstream determine to a large extent the distribution of the ecological classes in the 1988 landscape ecological map. The changes derived from water management not only produce economic benefits, with an increment in secondary production, but also lead to changes (increment/decrement) in the number and abundance of animal habitats, which could affect habitat conservation, and modify many ecological processes as well as the stability of the natural ecosystem.

5.2 Introduction

The flooding savanna is a large extension of savanna ecosystem into Llanos del Orinoco, which were described in chapter 2 and analyzed in chapter 3. In the previous chapter, the water dynamics of the flooding savanna derived from the effect of dike construction was analyzed, and in this chapter, the main landscape transformation of flooding savanna will be analyzed.

Important ecological processes such as plant succession, biodiversity, foraging patterns, predator-prey interactions, dispersal, nutrient dynamics, and the spread of disturbance all have remarkable spatial components, and the relationships between spatial patterns and many ecological processes can be analyzed throughout the developments in landscape ecology (Turner and

Gardner, 1990). Perception of the landscape can be considered from many points of view, depending on the observation scale as in the Australian 'land system concept' or with emphasis on the vertical (topological) or horizontal (chorological) structure and relations of the landscape (Zonneveld, 1989, 1995, 1998). According to the chorological view, the landscape can be defined as a heterogeneous land area composed of a cluster of interacting ecosystems that are considered as the landscape elements. The relationships between the structure, function and change of these landscape ecological maps are examined (Turner and Gardner, 1990; Forman and Godron, 1986). On the other hand, to understand the ecological processes of the flooding savanna ecosystems, it is necessary to know, and interpret the relationships between structure, function and change within the landscape into the spatial context and dynamics. For this task, a chorological view of the flooding savanna is used, based on the concept of landscape as ecosystem (Zonneveld, 1989, 1995, 1998). The survey and characterization of the landscape into the different ecosystems of the flooding savanna area units, defined according to the ecological processes, are therefore fundamental to understanding the complexity of the whole system.

Implementation of water management system (project *Módulos de Apure* refered in Chapter 2 and Chapter 3) favoured an increase in cattle production, aquatic fauna and terrestrial fauna in the wetland region (Pinowski and Morales, 1981, cited by Pérez and Ojasti, 1996; Tejos *et al,* 1990). However, the prolonged retention of water has led to the mosaic of gallery forest, seasonal savanna and hyperseasonal savanna being replaced by large areas of semiseasonal savanna, with consequent habitat loss in the ecotones (Ojasti, 1978, cited by Pérez and Ojasti, 1996).

In order to analyze the relationships between the spatial patterns and dynamics of the landscape and the ecological processes of the ecosystem, a method to define and recognize the ecological units or land units as ecosystem types was developed, being defined according to the function and vertical structure of each one. If I can identify the ecosystem through a combination of spatial features related to the function, structure and ecological processes of the ecosystem, I can then create an ecological map as a basis from which to embark on an analysis of the landscape.

This study includes two approach types: (1) the basic theory about the ecosystem and all its inherent processes, and (2) the spatial dimension of the ecosystem as land unit. The basic idea of this work is to link, by means of remote sensing analysis, the spatial dimension of the landscape element with the ecosystem processes.

The study area was submitted to a management process that produced a landscape change. Consequently, many of the original ecosystems have changed in size, altering the landscape matrix. However, the management process used was mainly geared to increasing a single ecosystem of the area, *ie*, semiseasonal savanna ecosystem, in order to produce large quantities of forage for cattle raising. The increment in the semiseasonal savanna has therefore led to a reduction in other areas such as the hyperseasonal and seasonal savannas.

The main objective of this chapter is to analyze the influence dike construction on the ecological determinants of the savanna, through the modification of the soil water availability. For that purpose a landscape ecological map of the flooding savanna area at regional level is produced using remote sensing techniques to link data on the main functional ecosystem features with the spatial dimension. Besides, a landscape ecological map of the area before the landscape transformation is produced, in order to study the process of change.

The specific tasks or research activities were to:

- define landscape ecological units, based on the ecosystem types of the area and the definition of savanna ecosystems described by Sarmiento (1983, 1990)
- select features linking the ecological processes with structure, using remote sensing data. The main ecosystem types of the study area have different species compositions, and I therefore expected these differences to be reflected in the remote sensing data. Then a principal research question was: To what extent is the functioning classification used for ecosystem types related to the spectral classification derived from remote sensing?
- elaborate the current landscape ecological map through Landsat TM image classification, using the ecosystem definition of flooding savannas, and combine the spectral result from the classification with previous surveys
- elaborate a landscape ecological map of the area prior to management change, through aerial photo interpretation using the ecosystem definition of flooding savannas
- analyze the landscape ecological changes derived from the land use change.

5.3 Ecological map and ecological unit (land unit) concept

To describe ecological processes in a spatial context, a map unit has to represent the structure and function of the landscape element. Therefore, the landscape can be interpreted as being composed of landscape elements (Forman and Godron, 1986). These landscape elements allow the description of not only the structure but also the associated ecological processes. In terms of landscape ecology, the land unit represents the landscape element where the ecological processes can be spatially analyzed (Forman, 1995; Forman and Godron, 1986; Turner and Gardner, 1990; Zonneveld, 1989, 1995, 1998).

The land unit as an ecological spatial unit includes (in the legend) the vertical structure of the ecosystem and the main features related to the ecological processes, such as the internal flux among the components, responses to environmental conditions, and balance of energy and mass (Zonneveld, 1995). The ecosystem structure can be linked to the ecological processes. For example, canopy structure determines the distribution of light and water from the top of the canopy to the soil; soil texture can contribute to determining water storage in the soil; and topographic position can also contribute to establishing the water balance and species.

In the study area, the main environmental factor determining species distribution is hydrologic dynamics, which in turn is controlled by other environmental factors such as geomorphology, soil type, seasonality and land management. The ecosystems derived from these environmental conditions respond by showing different ecological processes. Sarmiento (1983, 1990) defined these ecosystems and described the main associated ecological processes. The spatial definition of the land unit can be expressed as the link and combination of the ecological processes with the ecosystem structure and environmental features.

A landscape ecological map can be defined as the graphical representation of the pattern distribution of land units. However, these land units can be expressed in two different ways. First, the landscape ecological map can be defined as the sum of the layers, forming the ecosystem's structure, ie, the overlay of soil, vegetation, animal, water, geology, geomorphology and other spatial information (Figure 5.1a). Attribute information about the ecological processes, together with non-spatial information, can complement this spatial information.

In the second definition of the landscape ecological map, land units are described as the integration of the structure and the ecological processes within and between the land units. In this approach, the land unit can be delineated based either on attributes related to one or more components of the ecosystem structure, or on environmental features that determine ecological processes (Figure 5.1b). In this integrated approach, complementary information can be used.

In the integrated approach, some of the ecological processes related to the ecosystem can be mapped through the relationship between these processes and the spectral response of remotely sensed information. With this approach the ecological processes related to dynamics (temporal dimension) such as phenology, growth and production, the movement of species, and ecological changes can be analyzed. In this work, the integrated approach was used to generate ecological maps based on the previous definitions of ecosystem, ecological processes and environmental variables.

5.4 Methods

5.4.1 Study area

The study area, a large part of the flooding savanna in Venezuela, is located between two large rivers, the Apure and the Arauca, and covers about 16,000 km^2 (Figure 5.2). The drainage pattern of the area is formed by several periodic rivers that flow in the direction south-west to north-east, parallel to the Apure and Arauca rivers. The vegetation is a herbaceous cover with narrow corridors of gallery forest along the rivers and watercourses.

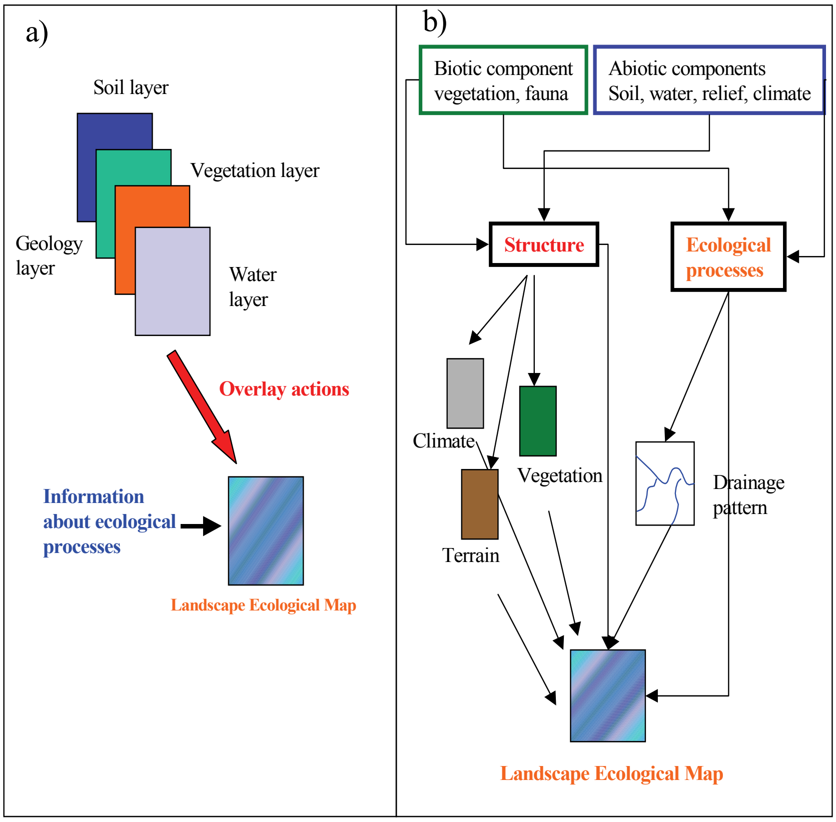

Figure 5.1 Representative schemes of two different approaches to define and elaborate landscape ecological maps (LANDSCAPE ECOLOGICAL MAPs): (a) overlay procedure to obtain ecological map from thematical maps; (b) integrated procedure relating ecological processes to landscape structure.

The geomorphological units derived from the river dynamics (banks, intermediate shallow and seasonal swamps, see Chapter 2) present different soil features. The banks are the natural levees along the borders of the streams and main rivers, with sandy soils predominant from alluvial deposits. The intermediate shallow are the larger areas, where silty alluvium predominates. The seasonal swamp corresponds to the lowest part of the catena, with a predominance of clay texture. These geomorphological features produce a differentiation in the distribution and accumulation of water in the soil during the year. This differentiation coupled with water dynamics leads to the distribution of species.

Four principal ecosystems are present in the flooding savannas:

1. gallery forest, which occurs on the banks and forms narrow strips along the rivers;
2. seasonal savanna, which also occurs on the banks;
3. hyperseasonal savanna (the most widespread ecosystem in this low region), which occupies the wide silty extensions between successive banks; and
4. semiseasonal savanna, which occupies the lowest lands, which remain under water (1 m or more) during the rainy season and slowly dry out through the dry season.

5.4.2 Data sources

Two different data sources were used to elaborate the ecological maps. For the current landscape ecological map, the primary data source was a Landsat TM image of January 1988 (middle of dry period; spatial resolution 30 x 30 m; covering a width of 185 km), which covered the whole study area in the Llanos del Orinoco. Topographic maps were used to geo-reference the image and complement the spatial information. To produce the landscape ecological map of the area before dike construction, 268 aerial photographs (January 1960; scale 1:60,000) were interpreted.

Descriptions of the vegetation communities and other ecosystem features were obtained from the species and environment parameters sampled in 58 sites in El Frío Biological Station (Chapter 6) and earlier species lists and surveys (Castroviejo and López, 1985; Monasterio *et al.*, 1971; Ramia, 1959; Sarmiento, 1983; Sarmiento *et al.,* 1971a, 1971b; Silva *et al*., 1971).

5.4.3 Data processing

All the image processing, digitising and spatial analyses were carried out using a geographical information system (ILWIS: Integrated Land and Water Information System). The Landsat TM image did not present any radiometric problems, and the geo-referencing was based on topographic maps of the area. The image was processed to obtain a false-colour composite (FCC), following the standard procedure. Based on the FCC and the definition and analysis of land units, a supervised image classification was made. This was filtered to eliminate the smallest pixel clusters and noise. After concluding the image processing, resampling was carried out to correct the geographical distortion of the rastered objects. All these procedures were based on the methods and techniques of image processing and GIS described in Aronoff (1993), ITC (2001), Meijerink *et al.* (1994) and Sabins (1987).

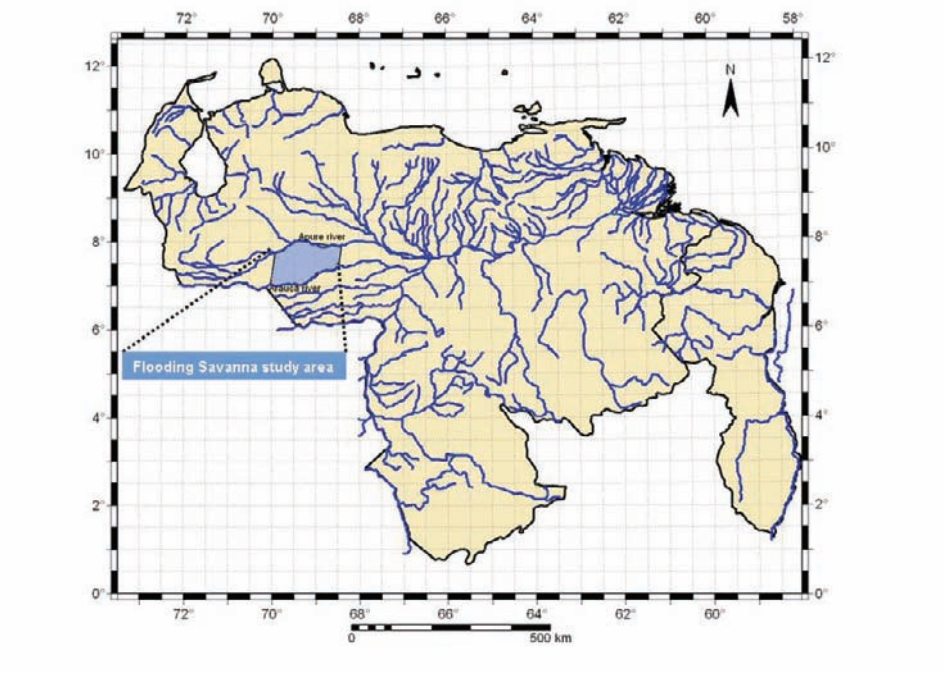

Figure 5.2 Geographical location of the flooding savanna area in Venezuela. Apure and Arauca rivers are indicated.

As for the aerial photographs, these were interpreted following the standard procedures that are well described and summarized by Zonneveld (1988) and Zonneveld (1995). The interpretation of the 268 photographs produced a map, which was digitized using ILWIS. The interpretation was based on the integrated approach, combining the features of terrain, vegetation and water dynamics from the land unit definition.

Although the origins and types of remote sensing information were very different, definition of the land units followed the same criteria, and in some aspects the results can be compared. However, the information about the size and number of units is not comparable. Using GIS, the spatial information was analyzed to obtain the final landscape ecological maps, and the spatial information about land unit pattern distribution (size, area, number) was also analyzed.

The accuracy of the maps was checked by field sampling in El Frío Biological Station. For the current map, areas with dikes were used to confirm the ecological units. The accuracy of the 1960 landscape ecological map was checked against field areas that had not been submitted to management. Some marginal areas in the north of the 1960 landscape ecological map could not be included or compared with the landscape ecological map derived from the Landsat TM image because some aerial photographs were missing.

5.5 Results and discussion

5.5.1 Land unit and ecosystem link

Using the integrated approach, structure and dynamics were combined with remote sensing data in order to produce maps. Although the land units defined for the two landscape ecological maps were the same, the method of delineating the units was different for each map. Linking ecosystem structure and ecological processes with remote sensing patterns from two different sources is a problem. First of all, the structure and ecological processes of each ecosystem had to be defined and described. Then, the structure parameters or ecological conditions that could be described through remote sensing parameters were selected. Finally, this key was used to interpret the photographs or process the image.

Sarmiento (1983, 1990) described the components and main ecological processes of the three savanna ecosystems and the gallery forest. Table 5.1 presents the main features of each ecosystem and the links with the remote sensing data. Using the parameters described in this table and the description of the ecological processes, the land units could be defined and delineated to elaborate the landscape ecological maps.

The criteria for defining land units were based on particular aspects of the features presented in Table 5.1. Some structure features were clearly associated with remote sensing features, but other criteria had to be used to define land units presenting similar structure features that could not be differentiated in the remote sensing data. The different criteria associated with the environmental conditions or particular ecological processes were then used to complement the delineation.

Vegetation as a structure criterion allows the differentiation between forest and herb cover; then the gallery forest can be defined from the texture and red color in the aerial photographs and satellite images, respectively. Next, the herbaceous vegetation communities (savanna ecosystems) could be differentiated based on environmental features such as the topographic position exposed in the aerial photographs (Skidmore, 1990).

Table 5.1 Main features of the structure, ecological processes and environmental parameters associated with the four principal ecosystems in the flooding savanna area in Venezuela. Also key to main characteristics in the remote sensing data (aerial photographs and satellite image) associated with each ecosystem and such ecological processes and structure as presented

Ecosystem	Main structural components	Main ecological processes	Environmental parameters	Associated remote sensing features
Gallery forest	Tree vegetation, high tree density	Semiseasonal and evergreen phenological state; water dependency; large radical system	River levee, watercourse, sandy soils	Photos: coarse texture, dark tones, high topographic position Image: FCC red color
Seasonal savanna (banco)	Herbs (grasses and non-grasses) and shrubs	Seasonal phenological state associated with seasonal climate; one stress period with soil water deficit (3 months); fire presence; little vegetation cover in the dry period	River levee and higher topographic areas; no flooded areas; sandy soils	Photos: fine-smooth texture, light tones, higher position Image: brown and white areas during dry period
Hyperseasonal savanna (bajío)	Herbs (grasses and non-grasses) and few shrubs; earthworm mounds; large areas between watercourses	Marked seasonal phenology; two stress periods: one for soil water deficit and one for soil water excess; fire presence	Approximately four flooded months; intermediate topographic position; silty soils	Photos: light grey tones, fine texture, intermediate position, large and homogeneous areas Image: greenish-brown color in dry period
Semiseasonal savanna (estero)	Grasses and sedge cover, no shrubs; little species diversity; homogeneous areas; smooth relief; lowest topographic position	No soil water deficit during the year; flooded stress during four months; physiological responses to the flooding; high productivity for grazing	Lowest topographic position; soil water availability during the dry seasonal period; all areas flooded during rainy period; presence of flooding gradient; clay soils	Photos: medium grey tones, smooth texture, some areas with heterogeneous drainage pattern; some areas with mirror reflection; can differentiate two or three types Image: red-orange light colour (non-flooding areas in dry period); red-brown dark colour (flooding areas in dry period)

Through topographic position, we can define levees, the intermediate position and the lowest position. For image data, the ecological conditions relate to the phenological state, and production during the dry period can be used to differentiate the ecosystems. During the dry season the savanna is not green, and part of the soil is not covered by vegetation; these areas reflect as dry soil (cyan color).

The hyperseasonal savanna retains water in the soil during the dry period, and the vegetation is not completely dry, so the image color is different from that of the seasonal or semiseasonal ecosystem.

As regards the semiseasonal savanna, soil water availability during the dry period enables the vegetation to grow at a high rate (including the (C4) vegetation type with a high metabolic rate), which can be differentiated in the image by a red-orange color. However, the areas of the semiseasonal ecosystem that remain inundated can be differentiated by the dark color or mirror reflection in the water. All these features relating to vegetation phenology and production are ecological processes.

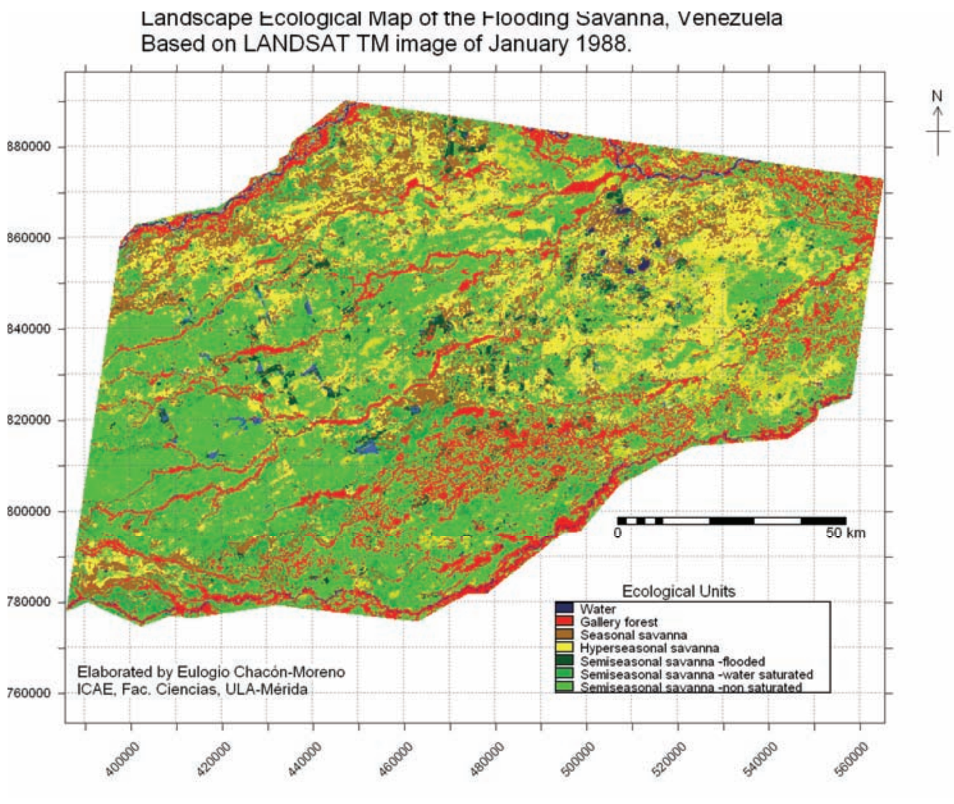

Figure 5.3 Current Flooding Savanna Landscape Ecological Map, Venezuela.

5.5.2 Landscape Ecological Maps (LEMs)

Figures 5.3 and 5.4 present the landscape ecological maps and the land units legend were previous described in chapter 2.

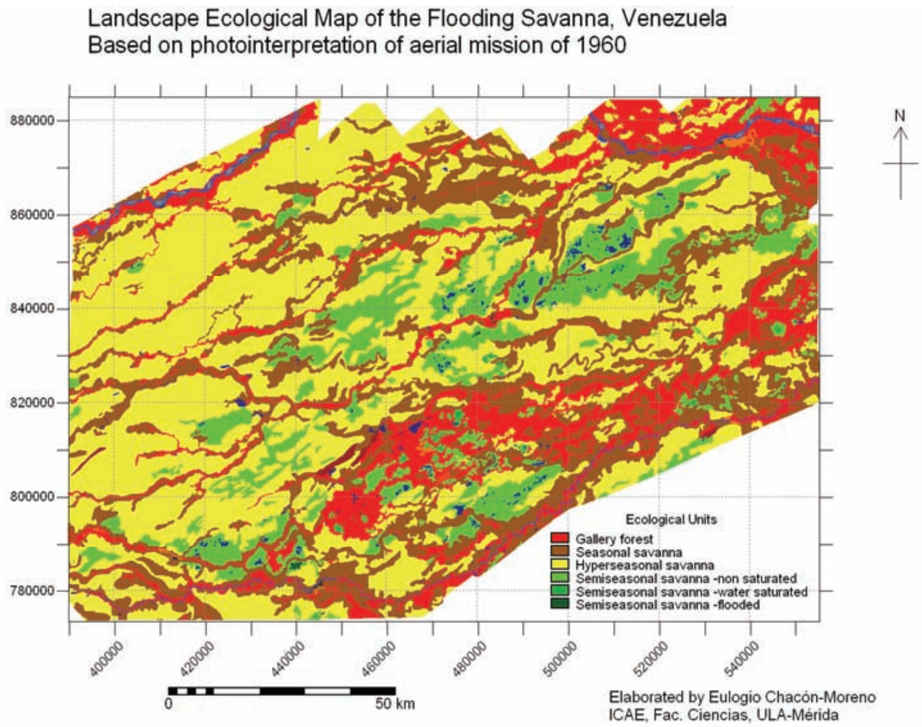

Figure 5.4 Flooding Savanna Landscape Ecological Map before dike construction, Venezuela.

5.5.3 Landscape change analysis

The information derived from the 1960 and 1988 landscape ecological maps of the flooding savanna was analyzed to compare the spatial parameters relating to the number of polygons per land unit in each map, the total area per map, and the rate of change for each ecological unit between 1960 and 1988.

As the original data sources for the two ecological maps were different, only certain aspects were comparable. For example, the total areas represented by each ecological class in both maps could be compared, whereas the numbers of polygons or patches per unit could not. Photo interpretation for the 1960 landscape ecological map generated continuous and homogeneous areas with few patches, and the scale or spatial resolution (1:60,000) gave an interpretation resolution of around 36 ha. However, the Landsat image gave a spatial resolution of approximately 0.09 ha, with the landscape derived from image processing thus showing smaller patches or polygons.

To carry out the change analysis, we used the total area common to both maps as the reference total area. In Figure 5.5, the total area and the area percentage per ecological class are presented for the two maps.

Figure 5.5a shows the distribution of areas per class for the 1960 landscape ecological map. Almost half the total area is covered by the hyperseasonal savanna class (*ie*, the characteristic units for flooding savanna), because it is related to the two seasonal climatic periods. Seasonal savanna is the second class in respect to cover percentage, with more than 26%; gallery forest and semiseasonal savanna non-saturated cover around 12% each. We can see that the class with water availability during the year, and no stress caused by hydric deficit, represents a limited area. The other classes of semiseasonal savanna have a cover percentage of less than 1%.

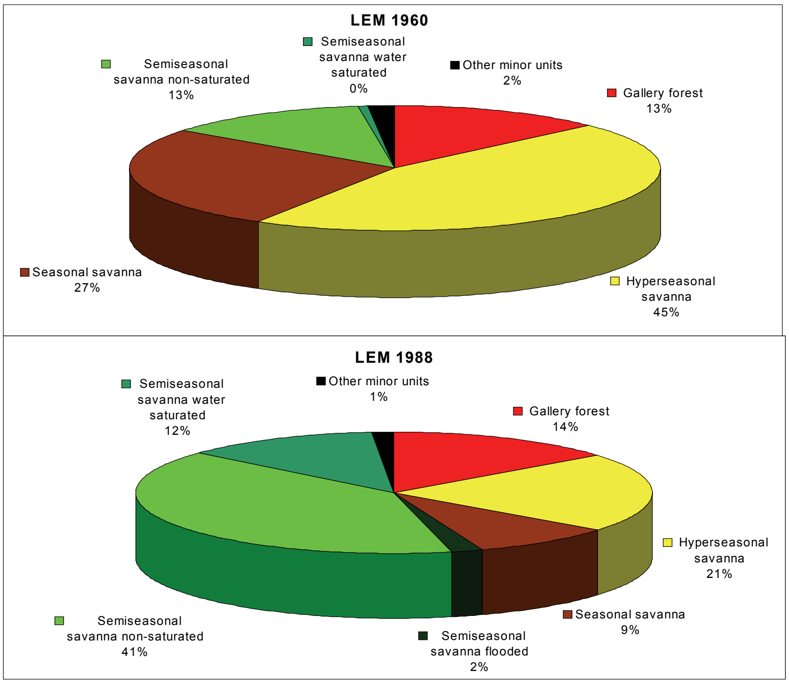

Figure 5.5 Percentage of area per ecological classes of the Landscape Ecological Maps of the Flooding Savanna in 1960 (a) and 1988 (b).

Figure 5.5b shows the percentage cover distribution of ecological classes in the 1988 landscape ecological map. The changes in cover distribution have been considerable as a consequence of dike construction, which led to a greater accumulation of water during the dry period and the continuous availability of water in some areas throughout the year. The biggest part of the area is covered by semiseasonal non-saturated savanna, representing more than 40%. The other semiseasonal savanna classes presented in 1960 now cover less than 1% of the all, with 12% and 2% for the water-saturated and flooded semiseasonal classes, respectively. On the other hand, the area of the predominant class in 1960, the hyperseasonal savanna, has decreased from almost half the total area to 21.17%. The proportion of seasonal savanna has also decreased, although gallery forest accounts for around the same area as in 1960. An important observation is that the semiseasonal savanna classes in 1988 represents more than 54% of the total area, which is the result of the water accumulation attributable to the dikes.

In the 1960 landscape ecological map, the four main land units (gallery forest, hyperseasonal savanna, seasonal savanna and semiseasonal savanna) represented more than 97% of the total area. To understand the process of change between 1960 and 1988, a diagram is presented for each of the ecological classes mentioned, showing the percentage and area of change. In each diagram, arrows indicate the direction of change. The full arrow shows the main change.

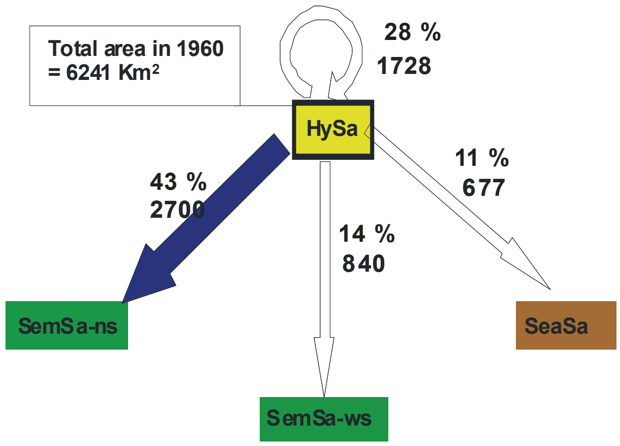

Figure 5.6 Change of hyperseasonal class in 1960 landscape ecological map to other classes in 1988 landscape ecological map (HySa: hyperseasonal savanna; SemSa-ns: semiseasonal savanna non-saturated; SemSa-ws: semiseasonal savanna water-saturated; SeaSa: seasonal savanna).

The first diagram (Figure 5.6) shows the percentage and area of change for the hyperseasonal savanna class in relation to the other main classes in the 1988 landscape ecological map. The hyperseasonal savanna class is the land unit covering an area of more than 45% in the 1960 landscape ecological map. The increase in water-level, as a result of repressing and managing water during the dry season, accounts for the change in the soil wetness conditions; therefore, the plant communities have changed and the hyperseasonal savanna ecosystem has turned into semiseasonal savanna. The main change is to semiseasonal non-saturated savanna.

Because the increase in water-level, the areas closer to the up-stream of dikes have turned from hyperseasonal savanna into semiseasonal water-saturated savanna. The soil wetness conditions change to non-flooded areas at any period of the year; therefore the soil conditions permits the establishment of the seasonal savanna ecosystem.

Figure 5.7 shows the diagram of landscape ecological change from seasonal savanna in the 1960 landscape ecological map, to other ecological classes in the 1988 landscape ecological map. In this figure, seasonal savanna changes mainly to non-saturated semiseasonal savanna (as observed in Figure 5.6). However, the percentage of change is not larger than 40%. Another important change is from seasonal to hyperseasonal savanna. This can be observed in lower areas where water conditions change from water availability during the wet period into flood conditions, hence establishing the hyperseasonal savanna ecosystem. Important is the change from seasonal savanna to new areas under the gallery forest ecosystem (more than 16% of the seasonal savanna transformed into forest).

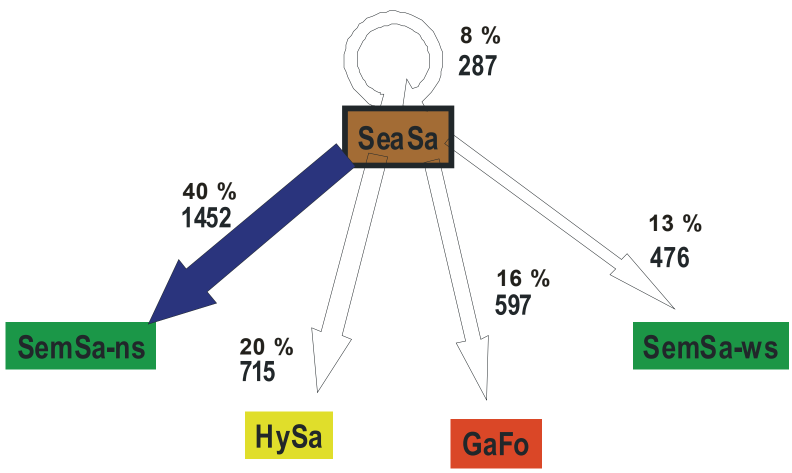

Figure 5.7 Change of seasonal savanna class in 1960 landscape ecological map to other classes in 1988 landscape ecological map (HySa: hyperseasonal savanna; SemSa-ns: semiseasonal savanna non-saturated; SemSa-ws: semiseasonal savanna water-saturated; SeaSa: seasonal savanna; GaFo: gallery forest)

The dike construction produced conditions of water availability throughout the year, but without flooding and the decrease in water and consequent dry conditions down stream, so has created favourable environmental conditions for forests (Van Os, 2000). The figure also shows that an important percentage of seasonal savanna has changed to water-saturated semiseasonal savanna. This could be because these higher areas are closer to the dike up-stream, where water accumulation is high and thus larger areas could be covered by water.

Figure 5.8 shows the transformation of the gallery forest ecological class into other classes in the 1988 landscape ecological map. This figure illustrates a different mechanism of change (Figure 5.7). Gallery forest do remains largely unchanged as dike construction does not affect forest conditions. However, 26 % of the preliminary gallery forest in 1960 changed to non-flooded semiseasonal savanna, and another 12% of the gallery forest changed to other classes. It is possible that the areas of gallery forest closer to the dikes and in specific zones up-stream were inundated because of the dike construction, and that this made the forest vegetation disappear from these areas. It is the inverse of the phenomenon that occurred down stream, where the hydric conditions contributed to the establishment of forests.

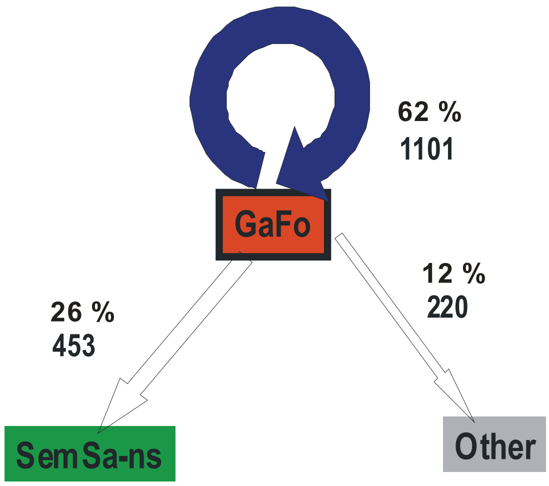

Figure 5.8 Change of gallery forest class in 1960 landscape ecological map to other classes in 1988 landscape ecological map (SemSa-ns: semiseasonal savanna non-saturated; GaFo: gallery forest).

Figure 5.9 shows the process of change from the semiseasonal non-saturated savanna ecological unit of 1960 to the 1988 ecological classes. The first observation is that almost half (46%) of the non-saturated semiseasonal savanna class does not change. However, change does occur in two directions: for 13% to wetter areas as the water-saturated semiseasonal savanna class, but also to drier areas as hyperseasonal and seasonal savannas. In the first case, the change to wet areas occurred because the level of water increased through the dike construction; in the second case, the change could be because some areas became drier when the dike interrupted the water flow to these areas. As a consequence of the dike construction, the percentage of change to drier areas in relation to the total area is 4%, which is lower in relation to the change from drier areas (hyperseasonal and seasonal savanna) to wet areas (semiseasonal savannas).

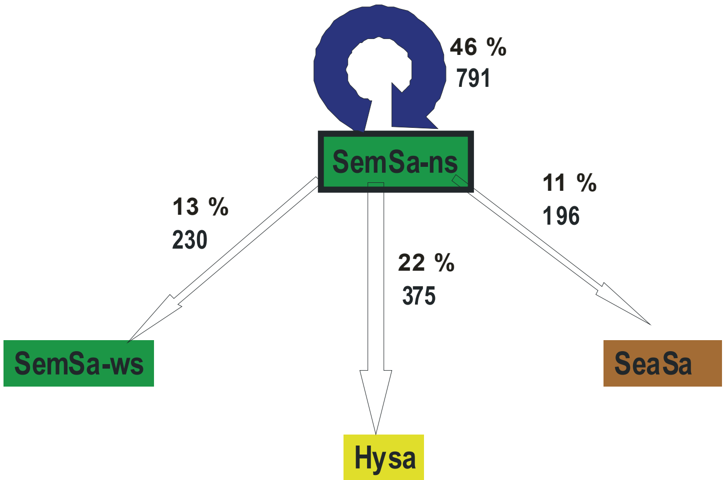

Figure 5.9 Change of semiseasonal savanna class non-saturated in 1960 landscape ecological map (HySa: hyperseasonal savanna; SemSa-ns: semiseasonal savanna non saturated; SemSa-ws: semiseasonal savanna water saturated, SeaSa: seasonal savanna

In a general comparison about cover percentage, between the two landscape ecological maps, the 1988 (current) map presents a landscape ecological unit distribution where the semiseasonal savanna ecosystems, cover the majority of the area, while hyperseasonal savanna is the second in respect to percentage of area covered. On the other hand, the 1960 landscape ecological map presents a distribution of ecological units, where the hyperseasonal savanna and seasonal savanna together cover more than 70% (45% and 26%, respectively).

When the two landscape ecological maps are compared in relation to the direction of change, we find that the main change observed is from the hyperseasonal savanna and seasonal savanna classes to the non-saturated semiseasonal savanna. This is because of the accumulation of water during the dry period caused by the dike construction. An important change can be observed from hyperseasonal savanna in the direction of seasonal savanna, as a product of the drainage in the areas downstream of the dike, where the soil water conditions have become drier.

5.6 Conclusions

Based on the land unit concept, an approach was developed to link the ecological processes associated with the main ecological ecosystems and the spatial definition and distribution of these ecological units. Ecological processes such as soil wetness conditions and vegetation responses to these conditions were used to define and associate remote sensing features in order to identify, for two different dates, those land units where an important water management process had produced great changes in the study area.

The technique used to produce the 1988 landscape ecological map was a simple supervised classification of Landsat TM, where the spectral features were related to ecological processes, *eg,* the productivity represented in the green vegetation and the tone derived by water accumulation (inundation). Elaboration of the landscape ecological map of 1960 was based on the interpretation of aerial photographs, and photo characteristics were linked to ecological processes associated with vegetation growth and the inundation of certain areas.

From the conceptual point of view, the definition and characterization of the land (ecological) units linked to the remote sensing features with ecological processes, was a key for understanding transformation changes in the flooding savanna. With this approach, changes in a landscape can be compared using different mechanisms of spatial data capture, because the focal points of description are the ecological processes and not the physical features, which can be very different in relation to the data sources.

The remote sensing features related to water conditions were the most important used to define and characterise the ecological units. These remote sensing features were also related to the pattern of vegetation growth, *ie*, greenness to separate hyperseasonal savanna from semiseasonal savanna, and texture to separate forest vegetation from other vegetation types.

From the point of view of grass production and forage utilization, the change (from a less productive ecosystem or one with a stress period caused by dry soil conditions during the dry period, to an ecosystem with a continuous period of growth because water is continuously available throughout the year) favours secondary production, as represented by cattle and wild life.

The flooding savanna in Venezuela is an area used mainly for extensive cattle raising, where the water-deficit conditions owing to seasonality determine the carrying capacity of the landscape to support the primary production of forage. The embankment of the landscape contributes to increase the carrying capacity for forage production; consequently, the number of animals (cattle) supported by the landscape is increased too. Also, the landscape change and the growth of the semiseasonal savanna ecosystem contribute to the increase in number and size of animal habitats, especially for wild species such as large numbers of birds, crocodiles, big mammals (*chigüire*) and many others. However, the landscape change also leads to a reduction in the area of other ecosystems, *eg,* the hyperseasonal savanna, which can in turn lead to a reduction in habitats for animals such as the deer (*Venado caramerudo)*, ant-eater (*Oso palmero*) and American lion (*Puma*), as well as a reduction in the numbers of plant species and vegetation types associated with this savanna ecosystem. It is difficult to conclude that the changes benefit habitat conservation because many other vegetation species and wild life could disappear; also many ecological processes are changed and the stability of the natural ecosystem could be modified.

The two landscape ecological maps resulting from the integrated approach represent two completely different stages. One stage represents almost-natural conditions, where the dynamics of the ecosystems are not greatly modified by human actions (represented by extensive grazing). The second stage represents a landscape ecological unit distribution derived from intensive water management, where the ecological conditions, especially those related to duration of flooding, have been changed by dike construction. These two maps can be compared in terms of area per ecological class but not in terms of patch numbers per class.

This study, from the spatial point of view, will not only allow the ecological processes associated with each ecosystem or land unit to be integrated in a general model, but also allow the changes in species distribution and abundance derived from the landscape change to be described. With this model of species distribution and abundance associated with the land units described in the maps, we can predict the rate of change and also monitor the influence of the embankment on the associated ecological processes.

It is clear that the embankment produces an important change in the hydrological balance of the region. From the economic point of view, the dike construction to control water contributes to increase the primary production during the dry period; however, it produces severe changes in the soil water availability. The replacement of the hyperseasonal savannas by the seasonal savannas produces that plants adapt for a long time to the flood conditions, rather than plants adapt to the extreme dry conditions without soil water. Therefore, a plant stress caused by soil water deficit is replaced by a stress caused by soil water excess. Because both plant communities associated to the hyperseasonal and semiseasonal savanna ecosystems are present, the plant species are easily replaced in responses to the new hydrological conditions.

With the embankment, the large areas of hyperseasonal savanna developed on the flooding plains in the intermediate topographical position have been replaced by semiseasonal savanna ecosystem on the same geomorphological unit. It is clear that in these areas with a new semiseasonal savanna ecosystem, the functioning of the ecosystem is similar to the areas where the semiseasonal savanna is developed on the lowest topographic position. Therefore, the geomorphological dynamics as the main factor determining the ecological distribution of the savanna ecosystems, is replaced by an assemblage of factors, such as flood conditions, geomorphological dynamics and embankment characteristics. But, how do these plants communities respond to the changes of the hydrological condition? In the following chapters, a detailed description, analysis and modeling of the plant species distribution will be developed for a representative area of the flooding savanna, which was affected by the embankment. Again, the observation scale change in order to detail the ecological aspect in a representative area of the flooding savanna, then much of the analysis and conclusions derived from the local scale, could be applied to the regional scale.

5.7 Acknowledgements

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CHAPTER 6

Direct and indirect vegetation-environment relationships in the flooding savanna of Venezuela

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

6.1 Abstract

The direct and indirect response of vegetation to environmental factors is analyzed in this work. Canonical Correspondence Analysis (CCA), direct gradient analysis technique and Path Analysis, as well as indirect statistical technique, were used to evaluate and understand the response of the vegetation from a flooding savanna in the El Frío Biological Station 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 the lowest indirect correlation values with the 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.

6.2 Introduction

In the previous chapter, the landscape transformation of the flooding savanna by embankment was analyzed. One of the results of this transformation is the replacement of drier ecosystems by wetter ecosystems. This replacement implies the displacement of the plant species. In this chapter, the plants species distribution along changing hydrological gradient derived from the embankment is studied.

Patterns in plant species composition reflect the response of the vegetation to environmental conditions (Jongman *et al.*, 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, because the climatic condition through the rainfall has been leaching the soil (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 climate determines regional and continental patterns (Skidmore, 2002), the local soil features such as topography, parent 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, 1976b; van Coller *et al*., 2000).

The patterns of species distribution in seasonal neotropical savannas are mainly associated with gradients of soil moisture (Huston, 1994; Silva and Sarmiento, 1976a, 1976b). 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, 1976b) found that soil textures in 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 the highest areas located on river bank, which never flood, and are dominated by *Paspalum chaffanjonii* Maury, *Axonopus purpusii* (Mex.) Chase, and *Sporobolus indicus* (L.) R.Br., to the lowest topographical positions, which are flooded for longest periods, and dominated by *Hymenachne amplexicaulis* (Rudge) Ness and *Leersia hexandra* Swartz. The intermediate positions, flooded for short periods, are dominated by *Panicum laxum* Swartz, *Paspalum chaffanjonii* and *Leersia hexandra* (Medina and Motta, 1990). These zones occur 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. Cattle are associated with the medium to high topographic positions, where grazing could be an important factor for the plant species distribution.

It has been reported that hydrology is a main factor determining species composition in flooding savannas (Castroviejo and López, 1985; Silva and Sarmiento, 1976a, 1976b; Tejos *et al.*, 1990) as well as 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 increase 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 (López-Hernandez *et al.,* 1994), however there are no analyses of the relationship between species composition and environmental factors using ordination techniques. In addition, there is no evidence of how plant species composition is distributed along the environmental gradient. Even if hydrological factors control the species distribution, how are other environmental factors associated to soil fertility related to species distribution?

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

6.3 Study site

The study was carried out in a 5000 ha area on the El Frío Biological Station in the flooding savannas of the Llanos del Orinoco, Venezuela (Figure 6.1). 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 Biological Station , 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). Detailed description of Llanos del Orinoco is presented in Chapter 2 and in Chapters 4 and 5, the hydrological dynamics and the regional changes in ecosystems and vegetation following to the construction of the dikes is described.

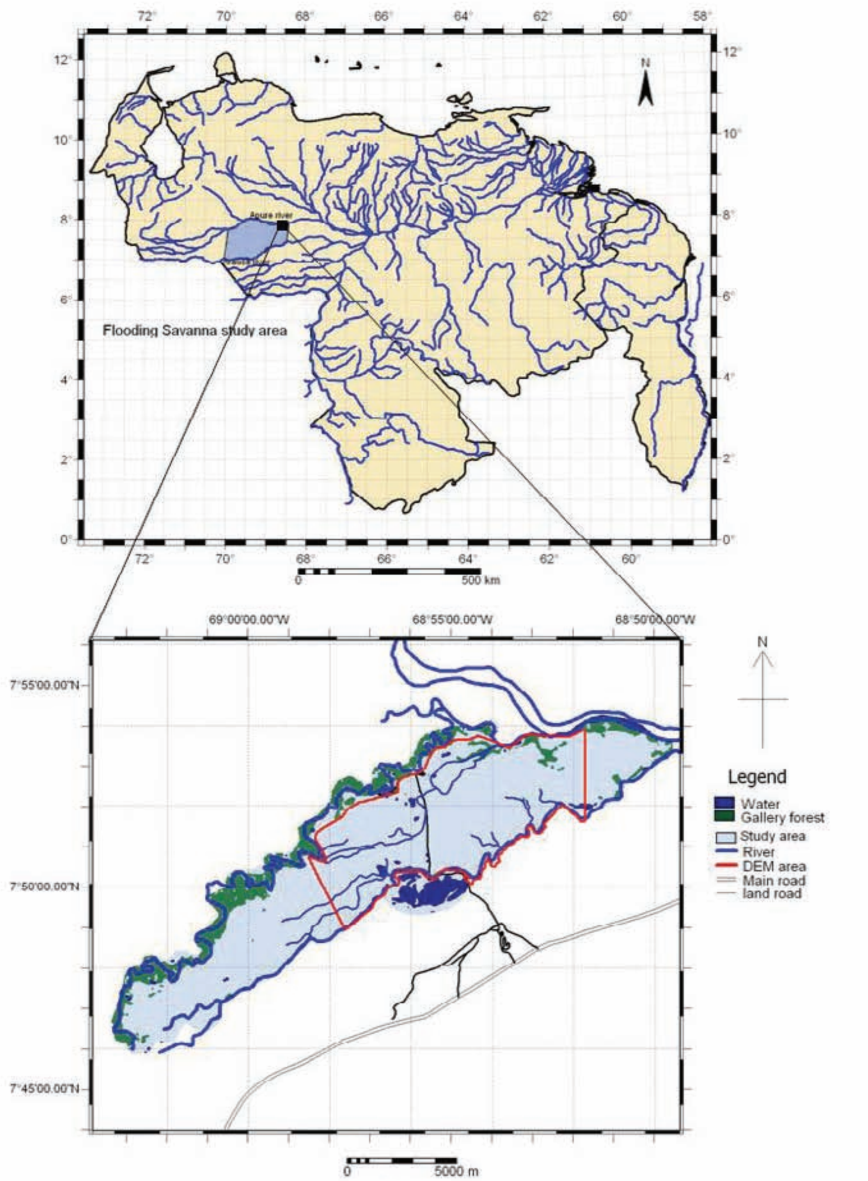


Figure 6.1 Geographical location of the study area in the flooded savanna of El Frío Biological Station, Venezuela.

6.4 Methods

6.4.1 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 and 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/m2), 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).*

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 including: 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.*, 2006). The position of each site in relation to the dike (upstream or downstream) was determined (See Fig. 6.1). Flooding condition derived from flood duration map based on radar images classification was determined (Jongman *et al.,* submitted).

6.4.2 Data analysis

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, 1986, 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; this approach 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. 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 not strongly related physical environmental factors to the ordination axis, path analysis models were used (Legendre and Legendre, 1998; Sokal and Rohlf, 1995).

6.5 Results

6.5.1 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 *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%.

6.5.2 Gradient analysis (CCA).

In the CCA for vegetation cover data (Fig. 6.2) we observed a site distribution mainly associated with 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 contains the wetter semiseasonal savanna site, while the second group is composed mainly of hyperseasonal savanna sites and some seasonal savanna sites. The third group is dominated by seasonal savanna sites and the fourth group 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 to higher water contents as well as flooded conditions. 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, 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 the extreme left with *Axonopus purpusii* and *Sporobolus indicus* (L.) R.Br. The species *I. fistulosa, M. pigra* and *H. spinosa* are associated to the second group of sites, while the other five species *P. laxum*, *P. chaffanjonii, Sida sp., H. lappacea, D. ciliata*, are more related to the third and fourth groups of sites.

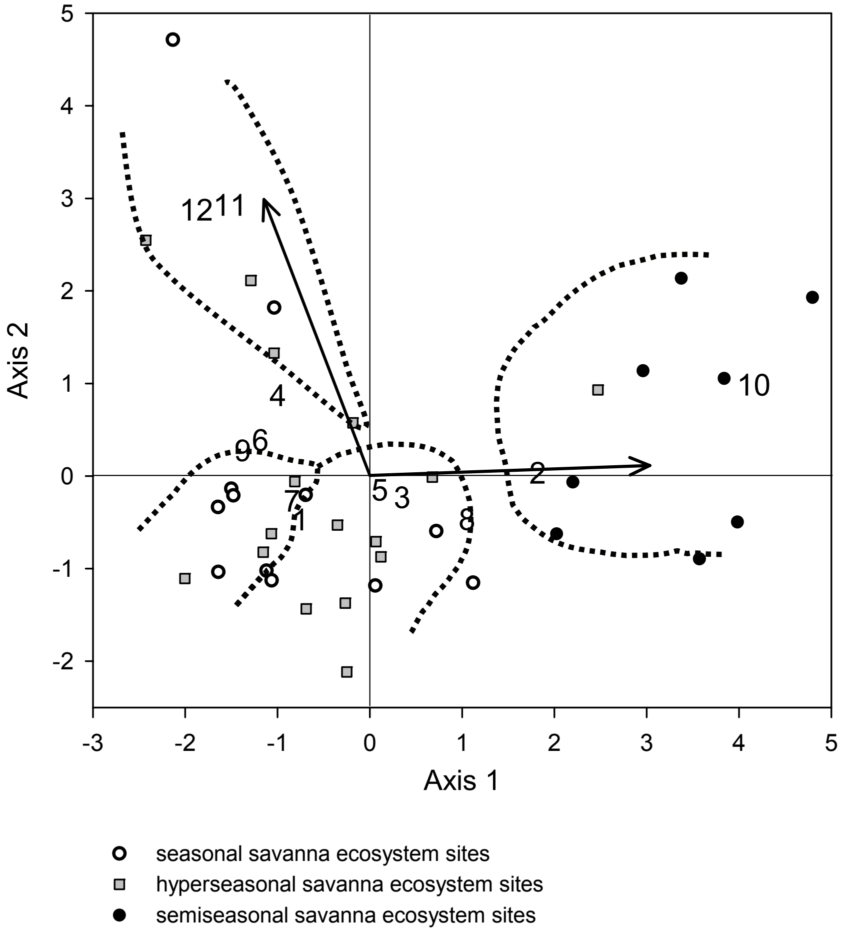


Figure 6.2 Biplot of sites and most dominant species according to Canonical Correspondence Analysis of cover vegetation data of the El Frío Biological Station, in the flooded savanna area of Llanos del Orinoco, Venezuela. Symbols represent the savanna ecosystems in the area. Arrows show the significant 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.

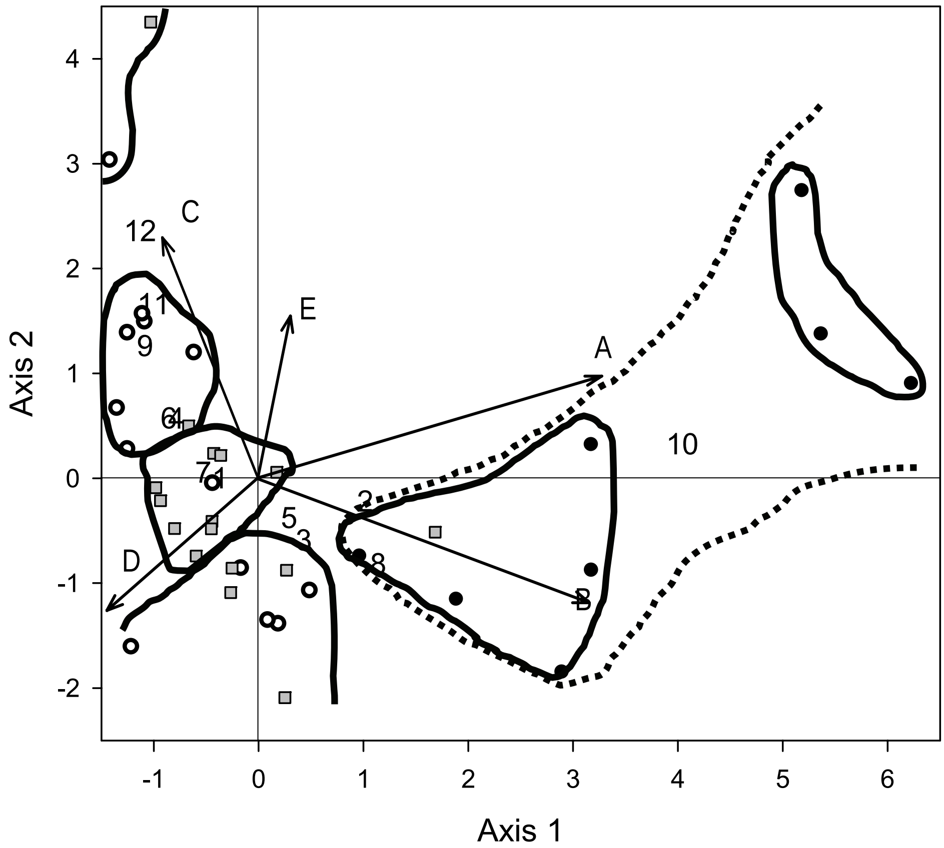
This analysis allows a clear differentiation of the semiseasonal savanna sites which are represented by *H. amplexicaulis* and *L. hexandra*, and correlated with the wettest environmental gradient.

Using CCA for the frequency vegetation data (Fig. 6.3), the sites had a similar distribution pattern for the CCA for cover data; however the differentiation between the classified ecosystems was more evident. The first ordination axis is mainly related to relative soil water content and depth of flood which are hydrological variables.

Four groups can be separated presenting more differentiation on the second ordination axis than the first. One of these group of sites is mainly composed of seasonal and hyperseasonal savanna and is associated to non-grazing areas, while two other groups of sites, mainly composed by seasonal savanna sites, are associated to medium and elevated grazing intensity. 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 6.3 followed a similar pattern as in Figure 6.2; however, *D. ciliate* is associated with grazing intensity and *H. spinosa* is associated with semiseasonal savanna sites. Ordination analysis of frequency vegetation data shows a better definition 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.

Table 6.1 shows the cumulative percentage variance of the species composition data explained by the four CCA axes. The first four axes of the CCA, dominated by the 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 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. 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.



o seasonal savanna ecosystem sites
▫ hyperseasonal savanna ecosystem sites
● semiseasonal savanna ecosystem sites

Figure 6.3 Biplot of sites and most frequents species according to Canonical Correspondence Analysis of frequency vegetation data of the El Frío Biological Station, in the flooded 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 6.1 Cumulative percentage variance explained by the four principal ordination axes of Canonical Correspondence Analyses (CCA) (frequency and cover) of the El Frío Biological Station, 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)

Table 6.2 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 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, relative soil water content and soil water saturation-class. 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.

Table 6.2 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 Biological Station, 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 cm)	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 cm)	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

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.

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.

6.5.3 Environmental correlations

Table 6.3 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. 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.

Table 6.4 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 6.2. 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 6.2).

6.6 Discussion

Hydrological gradient was the first and most important factor determining the distribution of species in the flooding savanna, whereas grazing intensity was an independent factor related to the second ordination axis. Besides, the analysis of the conditional effects shows that only these two factors presented statistical significant relations, which explained a high percentage of the variance. Other factors, mainly associated with hydrological conditions, were particularly significant in explaining the relation of plant distribution in the ordination analysis; moreover, when all types of environmental variables were included, the variance explained increased. This suggests that some of the spatial data could contribute to the explanation of species composition.

Table 6.3 Correlation matrix between environmental factors of a flooded 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 %(0-20cm)					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 cont (%)																	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

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* which are responding to the hydrological gradient, and the response model follows a unimodal pattern. 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).

Table 6.4 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		

Along of the first diagram axis, which corresponds to a hydrological gradient, the separation of semiseasonal savanna sites is very clear, however the seasonal and hyperseasonal savanna sites did not present a clear boundary. This could be due because there is a several species that are present in both types of savanna: seasonal and hyperseasonal, and the border between the two ecosystems is fuzzy; but the semiseasonal savanna present an association of species which are not present in the hyperseasonal savanna, then the border between these ecosystems is more clear in the field.

Differences between the cover and frequency analyses could be explained because dominant species like *P. laxum*, and *L. hexandra*, presented a wide distribution along the gradients, and could be found with low cover in other ecosystems or transitional areas. Consequently, 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. In contrast, 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).

The semiseasonal savanna ecosystems are mainly derived as a consequence of the dike construction, and many areas present a similar geomorphology (Sarmiento and Pinillos, 2001), then the hyperseasonal and semiseasonal savanna ecosystems are situated on the same geomorphological pattern. Besides, 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 as a consequence of the dike construction shows sediments accumulation dynamics different than the original semiseasonal savanna. This savanna type derived from dike construction does not have enough time to generate or modify the soil, then presents soil features similar to the hyperseasonal savanna from it was derived.

These two facts - the similar geomorphology for both hyperseasonal and semiseasonal savanna ecosystems, and the non formation of new soil type – together with the lack of nutrients, suggest and could explain the non correlation or low correlation between the environmental factors associated to the soil physical properties with the ordination axes.

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 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 longer than the relatively higher areas.

On the other hand, the presence of a 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 note that water remaining 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 seasonal savanna areas of Venezuela, outside of the flooding savannas, different and opposing results were presented by Silva and Sarmiento (1976a, b); they 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 that study.

The second ordination axis 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* (non palatables species). Therefore, this second ordination axes is in fact dividing the preferred areas from grazing from those overgrazing areas. It is important to note that this ordination axis, associated to the grazing intensity, is the main land use in the whole area, and also the principal savanna ecosystem used for grazing is the hyperseasonal savanna (Chapter 2). 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 *et al.*, 1996).

At regional scale the plant-available moisture and plant-available nutrients are considered the two main determinants of tropical savannas (Sarmiento, 1984, 1996; Solbrig *et al.*, 1996), while 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, while the plant-availability nutrients is masked by the flooding condition.

The hydrological dynamics is the main factor affected by the embankment (Chapter 5) and also it is the principal environmental factor that determines the plants species distribution. In the next chapter, the specific plant responses to the main environmental factors will be analyzed through the use of Gaussian logistic models.

6.7 Acknowledgements

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CHAPTER 7

Plant species distribution in environmnental gradients of flooding savannas, Venezuela

7. PLANT SPECIES DISTRIBUTION IN ENVIRONMNENTAL GRADIENTS OF FLOODING SAVANNAS, VENEZUELA

7.1 Abstract

A Gaussian logistic model is used to evaluate the response of vegetation data of the flooding savanna to environmental factors. The vegetation data collected contain information about the species presence/absence, frequency and cover percentage for 57 sampling units (sites). Environmental variables were collected for each site in the field and from other spatial data. Using Gaussian logit curves, the presence/absence, frequency and cover percentage for the most important species were analyzed with respect to the two main environmental variables that are derived from ordination analyses which were developed in the previous chapter. The result is that *L. hexandra* and *P. laxum*, which are the most abundant species, occupy different positions in the environmental gradients. The relative soil water content and relative altitude environmental variables are complementary and have a strong relation to the hydrological dynamics in the flooding savanna. These results complement the information of the previous chapter and afirm the final ecological model of the plant species distribution along the main environmental gradients in the flooding savanna.

Keywords: Gaussian Logistic Model, Generalizad Linear Model; grazing intensity; Llanos del Orinoco, Venezuela; Relative soil water content; topography.

7.2 Introduction

The description and understanding of the environmental factors as determinants of the species distribution was analyzed in chapter 6. In the present chapter, the modeling of the species responses into those environmental gradients was studied. The hydrological gradient derived mainly from the soil storage capacity, relative altitude (topography) and the rainfall seasonality is the main factor on which the species distribution was analyzed.

The flooding savannas on alluvial overflow plains occupy a vast depression in the southern part of the Llanos del Orinoco in Venezuela. They are mainly used for extensive cattle grazing. In these savannas, the ecological processes are associated with the hydrological dynamics, which, in turn, is associated to the topography. These are the main environmental factors determining a hydrological gradient from areas that, during the wet period, remain dry or non-flooding to areas which, during the dry period, remain flooding or with available water in the soil. This environmental gradient determines the plant species composition in the flooding savanna (Chacón-Moreno *et al.*, 2004) (Chapter 6).

Large parts of flooding savannas (approximately 16,000 km^2) were managed by construction of dikes. These dikes control the superficial drainage water through gates in order to store water for producing grass biomass during the dry period and thus increase the carrying capacity of the area (López-Hernández and Ojeda, 1996; Sarmiento and Monasterio, 1975; Chapter 2 and 5). As a consequence of the dike construction, changes in landscape had been observed and analysed (Chacón-Moreno, 2001; Chapter 5). These landscape transformations implied the change in composition of plant communities and the replacement of natural species in the hyperseasonal savanna by species adapted to wet environments and with greater palatability, such as *Leersia hexandra* and *Hymenachne amplexicaulis* (Chacón-Moreno, 2001; Chacón-Moreno *et al.*, 2004; López-Hernández and Ojeda, 1996; Chapter 6). However, the prolonged retention of water is the cause by which the mosaic of gallery forest, seasonal savanna and hyperseasonal savanna have been replaced by large areas of semi-seasonal savanna, with consequent habitat loss in the ecotones (Chacón-Moreno, 2001; Ojasti, 1978 cited by Pérez and Ojasti, 1996; Chapter 5).

These changes have produced a replacement of the hyperseasonal and seasonal savanna plant species communities by the almost mono-specific plant communities associated to semiseasonal savannas. Therefore, large areas covered by wetlands species such as *Leersia hexandra* and *Hymenachne amplexicaulis* have increased their dominance in the wetter areas where, before dike construction, hyperseasonal plant species, such as *Panicum laxum* and *Paspalum chaffanjonii* were present. The distribution analysis of dominant species associated with the flooding savanna ecosystems is important to model and understand how landscape changes could affect the diversity and abundance of the plant species in that ecosystem. Besides, planning and water management policies could be modified in order to maintain conservation areas for animal habitats and increase the extensive cattle production.

The objective of this work is the application of a Generalized Linear Model (GLM) through the method of Gaussian Logistic Regression in order to study the response of the more abundant and frequent species of the flooding savanna in relation to the relative altitude, grazing intensity and relative soil water content environmental variables.

The three main environmental factors were selected according to the results observed in the vegetation-environment relationship of the flooding savanna described in Chapter 6 (Chacón-Moreno *et al.*, 2004). We found that for frequency and cover vegetation data the first ordination axis was mainly related to relative soil water content, and this variable was highly correlated with relative altitude in catena. Both variables determined the hydrological dynamics of the flooding savanna. Besides, the second ordination axis was associated with grazing intensity.

Several statistical approaches can be used to model the response of the species to different environmental factors. In the present work, the regression method is used to explore the vegetation-environment relationships based on the observations of species and environmental variables at different sites (Ter Braak and Looman, 1995). Unimodal models, like those used in ordination methods, were used to represent the response of the species to environmental variables. Unimodal response models for one environmental variable can be obtained by adding a quadratic term (χ_i^2), but this quadratic model can predict negative values, whereas species abundance are always zero or positive. Therefore, a solution to this problem is solved by the Gaussian response curve, in which the logarithm of species abundance is a quadratic in the environmental variable (Ter Braak and Looman, 1995; Ter Braak and Prentice, 1988). The logistic regression or logit regression is a special case of the Generalized Linear Model (GLM), where the parameters are estimated by the maximum likelihood principle (Smilauer, 1992; Ter Braak, 1986; Ter Braak and Looman, 1995; Ter Braak and Prentice, 1988).

7.3 Methods

7.3.1 Study area and data sampling

The study was carried out in a 5000 ha area on the El Frío Biological Station in the flooding savannas of the Llanos del Orinoco, Venezuela (Chapter 6, Figure 6.1). A complete description of the study area is made in Chapter 2, 4, 5 and 6, and Castroviejo & López (1985); Pereira da Silva & Sarmiento (1997); Pinillos (1999); Chacón-Moreno (2001); Chacón-Moreno *et al.* (2004).

7.3.2 Vegetation and environmental data

A field data collection for plant species and environmental variables was carried out in the study area. Fifty seven sites of 100 m^2 (10m x 10m) according to a stratified random sampling design were selected. Further description of the methodological approach for that collection and treatment of the data is described in Chapter 6 (Chacón-Moreno *et al.*, 2004). A slope correction of digital elevation model (Chapter 4, Smith *et al.*, 2006) was used to create a gradient of relative altitude in catena (cm).

The vegetation and environmental data collected were split into two groups. The first group of data contains all the vegetation data and the environmental variables that do not change during the year, such as the physical soil features (57 sites). The second group of data includes all vegetation and environmental data collected from November to December 1997 (37 sites) which is the largest sampling period that contain a complete data set of relative soil water content.

The vegetation data collected were processed in order to obtain the matrixes for frequency and cover data of species *versus* the two sites groups. The selection of the environmental data was made based on the previous results of ordination analyses described in chapter 6 (Chacón-Moreno *et al.*, 2004). For the two groups of data, the following environmental factors were selected: Relative altitude in catena and grazing intensity for all data (57 sites), and relative soil water content and intensity of grazing for the second group of samples (37 sites).

7.3.3 Data analyses

Using General Linear Model (GLM) for presence/absence data, the presence probability model of a species related to an environmental parameter or variable can be calculated using the Gaussian logit curves as the predictor model (Ter Braak and Looman, 1995). For abundance data, with many zero values and the assumption that the abundance data follow a Poisson distribution, the Gaussian curve can thus be fitted by carrying out a log-linear regression (Ter Braak and Looman, 1995; Ter Braak, 1995). The proceedings to create the Generalized Linear Model are presented in CanoDraw software (Smilauer, 1992).

Three kinds of analysis were carried out for each group of data previously mentioned. The first type of analysis corresponds with the presence-absence vegetation data, the second type is related to the frequency vegetation data, and the third type is carried out with cover vegetation data. Therefore, a total number of six types of analysis were made (Table 7.1).

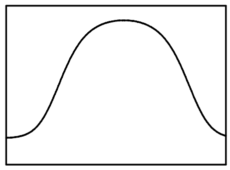
Table 7.1 Vegetation and environmental type of data used in Gaussian logistic analyses.

Analysis	**Vegetation data**	**Environmental data**	**Group of data**
GAU01	Present/absence	Relative altitude from DEM. Intensity of grazing	57 sites
GAU02		Relative soil water content. Intensity of grazing	37 sites
GAU03	Frequency	Relative altitude from DEM. Intensity of grazing	57 sites
GAU04		Relative soil water content. Intensity of grazing	37 sites
GAU05	Cover	Relative altitude from DEM. Intensity of grazing	57 sites
GAU06		Relative soil water content. Intensity of grazing	37 sites

The predictor model used for presence/absence data is the “logit” predictor (equation 1) where P= linear predictor. In equation 1, the quadratic term is normalized for presence/absence data which contain binomial data (1 or 0). The linear model predictor used for species distribution based on frequency or cover data is expressed in equation 2. In this equation the quadratic term is not normalized. b_0, b_1 and b_2 are the coefficients of the Gaussian Logit Model.

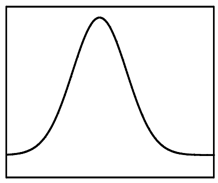
Equation 1:

$$P = \frac{e^{(b_0 + b_1\chi + b_2\chi^2)}}{1 + e^{(b_0 + b_1\chi + b_2\chi^2)}}$$



Equation 2:

$$P = e^{(b_0 + b_1\chi + b_2\chi^2)}$$



Then, the final equation solutions for the model of species probability, and frequency and cover distribution are presented in equations 3 and 4. In these equations the quadratic term is modified including ecological terms as *tolerance* and *optimum* (Ter Braak and Prentice 1988; Ter Braak and Looman 1995).

Equation 3

$$\gamma = \frac{ae^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}}{1 + ae^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}}$$

Equation 4

$$\gamma = ae^{-0.5\left[\frac{(\chi - \mu)^2}{t^2}\right]}$$

Where ***y*** is the probability (equation 3) and abundance (relative frequency) or the percentage of cover (equation 4) estimated by the model, ***x*** is the environmental value, μ is the species' optimum, ***t*** is the tolerance, and ***a*** being a coefficient related to the height of the peak. Ecological definitions of this parameter are described in Ter Braak and Prentice (1988), and Ter Braak and Looman (1995). The relation between equations 1, 2 and 3, 4 and a further description of the statistical methods and proceedings to analyze the data are found in Jongman *et al.* (1995), Smilauer (1992), Ter Braak (1996), and Ter Braak and Smilauer (1998).

7.4 Results

7.4.1 Selected species

Table 7.2 presents the list of the species with most frequent and cover values for each savanna ecosystem of El Frío Biological Station. *L. hexandra, P. laxum* and *I. fistulosa* are the most common species found for the whole area. However, for each particular ecosystem class, the species dominance changes; in the seasonal savanna, *P. laxum* is the most frequent species observed and *L. hexandra* shows lower values than those for the whole area, while *P. chaffanjonii* shows an important value of frequency (0.79). In the hyperseasonal savanna ecosystem class, the frequency values are similar to those showed for the whole area. In the semiseasonal savanna ecosystem class, *L. hexandra* predominates over other species and *H. amplexicaulis* and *E. interstincta* present important high values of frequency, over 0.45.

For cover data, the results are similar to those of frequency data, where *P. laxum* and *L. hexandra* present the major cover values with dominance for the total list over 25%, while the other species do not reach the 10%.

Based on table 7.2, the following six most frequent species were selected to make the presence/absence and frequency analyses: *Leersia hexandra, Panicum laxum, Ipomoea fistulosa, Paspalum chaffanjonii, Hymenachne amplexicaulis* and *Eleocharis interstincta.* A total of seven species were selected for cover analyses: *Panicum laxum, Leersia hexandra, Paspalum chaffanjonii, Axonopus purpusii, Ipomoea fistulosa, Hymenachne amplexicaulis* and *Eleocharis interstincta*.

7.4.2 Presence-absence data analyses

Annex 6.1 presents the significant results of estimated values for the Gaussian logit model of the most frequent species for GAU01 and GAU02. Figure 7.1 shows the species probability model according to presence-absence data of 57 and 37 sites. For the 57 site data group, the presence-absence model was calculated in relation to relative altitude in catena (Fig. 7.1a) and grazing intensity (Fig. 7.1b). For the 37 site data group, the presence-absence model was determined in relation to the relative soil water content (Fig. 7.1c) and grazing intensity (Fig. 7.1d).

Table 7.2 Species list showing the most frequent and cover values for each savanna ecosystem and the total of collected species in the flooding savanna of El Frío Biological Station. Frequency and cover values are in brackets.

Major frequency	**Major cover**
From the whole area: *Leersia hexandra* Swartz (0.81) *Panicum laxum* Swartz (0.72) *Ipomoea fistulosa* Mart. Ex Choisy (0.52)	**From the whole area:** *Panicum laxum* Swartz (32.3%) *Leersia hexandra* Swartz (26.1%) *Paspalum chaffanjonii* Maury (5.0%) *Hymenachne amplexicaulis* (Rudge) Nees (2.5%)
From seasonal savanna *Panicum laxum* Swartz (0.94) *Paspalum chaffanjonii* Maury (0.79) *Leersia hexandra* Swartz (0.68)	**From seasonal savanna** *Panicum laxum* Swartz (43.0%) *Leersia hexandra* Swartz (14.2%) *Paspalum chaffanjonii* Maury (9.0%) *Axonopus purpusii* (Mez) Chase (5.0%)
From hyperseasonal savanna *Panicum laxum* Swartz (0.90) *Leersia hexandra* Swartz (0.80) *Ipomoea fistulosa* Mart. Ex Choisy (0.70)	**From hyperseasonal savanna** *Panicum laxum* Swartz (48.1%) *Leersia hexandra* Swartz (15.1%) *Paspalum chaffanjonii* Maury (5.8%) *Ipomoea fistulosa* Mart. Ex Choisy (1.3%)
From semiseasonal savanna *Leersia hexandra* Swartz (0.94) *Hymenachne amplexicaulis* (Rudge) Nees (0.74) *Eleocharis interstincta* (Vahl) Roem. & Schult. (0.47)	**From semiseasonal savanna** *Leersia hexandra* Swartz (49.6%) *Hymenachne amplexicaulis* (Rudge) Nees (7.4%) *Eleocharis interstincta* (Vahl) Roem. & Schult. (6.8%) *Panicum laxum* Swartz (4.8%)

Figure 7.1a shows a clear division between the two groups of species. At the lowest topographical position, *H. amplexicaulis* and *E. interstincta* have the highest probability; however, when the relative altitude increases above 1.5 m, the probability of them decreases immediately to 0. *L. hexandra* remains with the highest probability values until 2.0 m, when it begins to decrease to minimum values at 3 m. On the other hand *P. laxum* and *P. chaffanjonii* present the highest probability values at the highest topographic position (2-3 m), nevertheless, the probability decreases when the altitude is lower than 1.5 m. The model represents a clear niche separation among the species.

In figure 7.1c, the patterns of species distribution along the relative soil water content variable show a bell form for all the species, except *P. laxum* which has the highest probability at the lowest water relative content value. *L. hexandra* and *I. fistulosa* present similar patterns and amplitude at the medium-high values of relative soil water content (optimum between 15 and 30 %). Conversely, *P. chaffanjonii* was restricted to a narrow range of relative soil water content (5-13%), and *H. amplexicaulis* was restricted to the highest range of relative soil water content (> 25%).

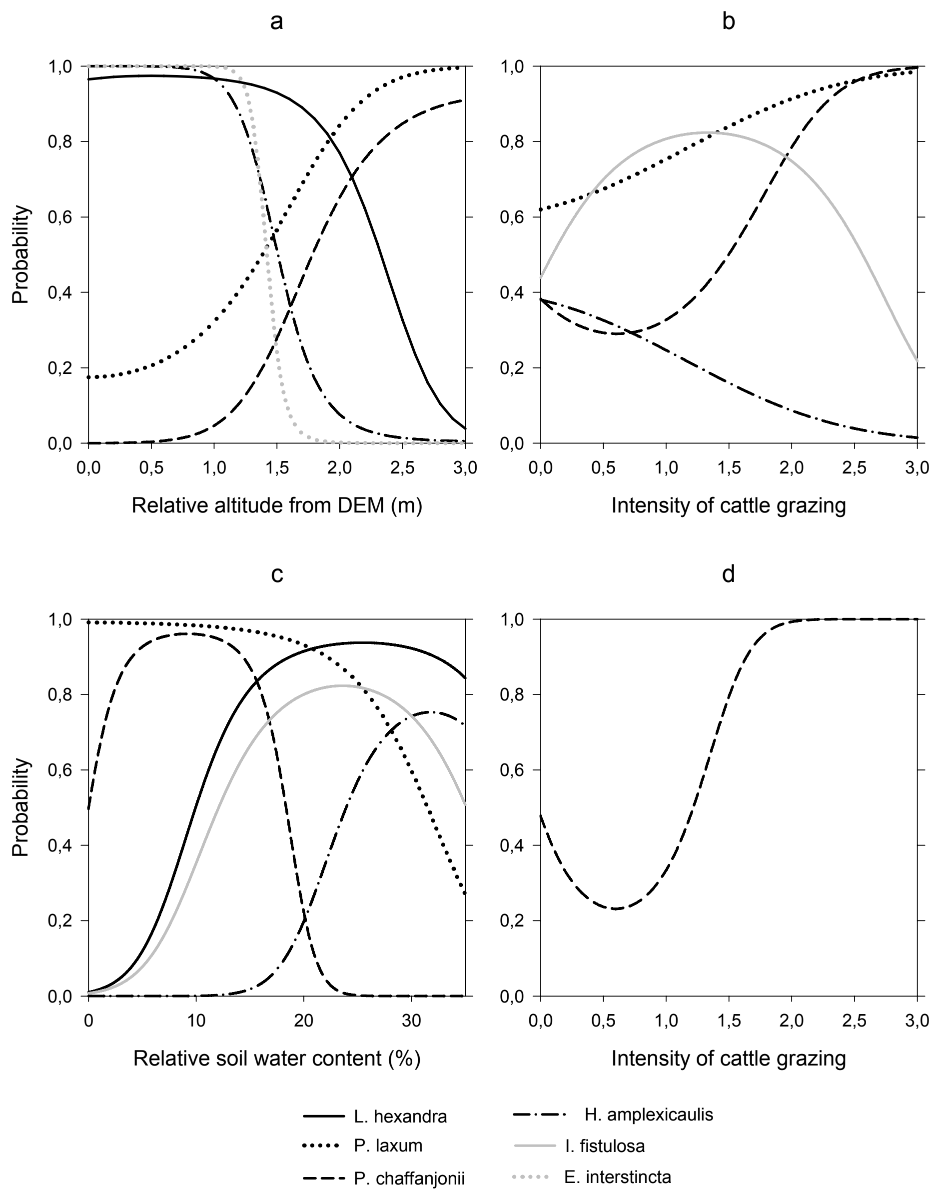


Figure 7.2 Species probability model according to presence/absence data in relation to the following environmental variables: a) relative altitude in catena derived from DEM for 57 sites; b) grazing intensity for 57 sites, c) relative soil water content for 37 sites, and d) grazing intensity for 37 sites.

In figure 7.1b, *I. fistulosa* presents a bell distribution in relation to grazing intensity whith the highest probability values at the middle of the gradient. *P. laxum* increased the probability from 60 to 100% when the intensity gradient increased, but *H. amplexicaulis* decreased the probability from 40 to 0% when the grazing intensity increased. It is interesting to observe in figures 7.1b and 7.1d that *P. chaffanjonii* presented a special pattern with medium probability values at the lowest grazing intensity values, low probability values at the medium-low grazing intensity values and high probability values at highest grazing intensity values. Only *P. chaffanjonii* had significant analysis in relation to grazing intensity with 37 sites.

7.4.3 Frequency data analyzes

Annex 7.2 presents the significant results of estimated values for Gaussian logit model of the most frequent species for GAU03 and GAU04. Figure 7.2 shows the species frequency model according to frequency data of 57 sites in relation to relative altitude in catena derived from DEM (Fig. 7.2a) and grazing intensity (Fig. 7.2b). For the 37 site data group, the model for frequency was calculated in relation to relative soil water content (Fig. 7.2c) and grazing intensity (Fig. 7.2d).

In figure 7.2a, *H. amplexicaulis*, *L. hexandra* and *P. laxum* present a pattern distribution with optimums above 90% of frequency. *H. amplexicaulis* is located at low relative altitude and narrow distribution whereas *P. laxum* is located at high relative altitude. *L. hexandra* exhibits a wide distribution along the topographical gradient ranging from 0.5 m to 2 m with relative frequency above 40%. *I. fistulosa* presents a narrow distribution and the lowest frequency values (> 50%) as well as *P. chaffanjonii* with a distribution located at the highest altitude.

Figure 7.2b presents a similar pattern of species distribution as figure 7.1b. *I. fistulosa* increased at intermediate grazing intensity while *H. amplexicaulis* decreased its frequency when the grazing intensity increased, and *P. chaffanjonii* increased the frequency values when the grazing intensity was high. Also, similar pattern of species distribution is observed in figure 7.2d for *H. amplexicaulis* and *P. chaffanjonii*.

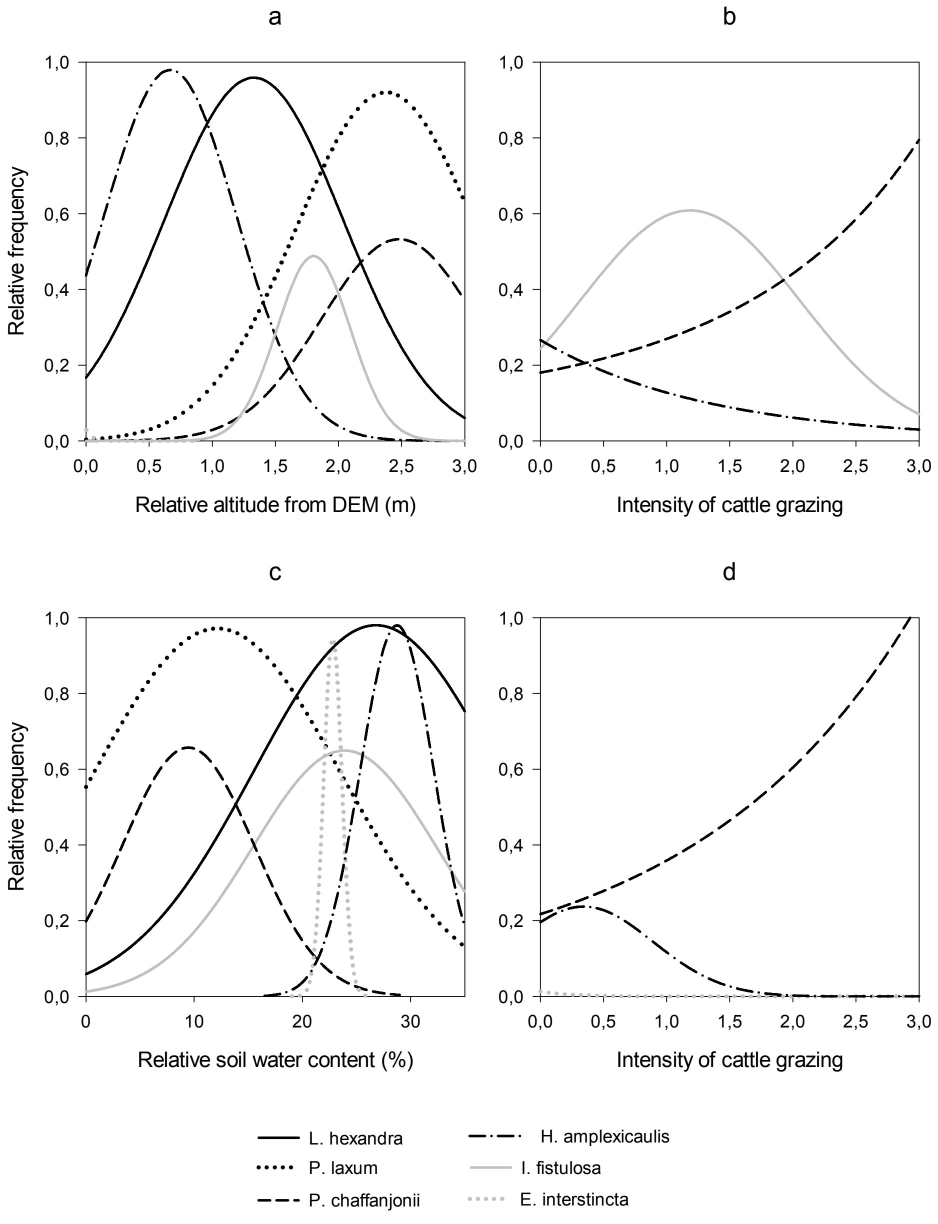


Figure 7.3 Species frequency model according to frequency data in relation to the following environmental variables: a) relative altitude in catena derived from DEM for 57 sites; b) grazing intensity for 57 sites, c) relative soil water content for 37 sites, and d) grazing intensity for 37 sites.

7.4.4 Cover data analyzes

Annex 7.3 presents the significant results of estimated values for Gaussian logit model of the most abundant species for GAU05 and GAU06. Figure 7.3 shows the species cover model according to the cover data of the 57 sites in relation to relative altitude (Fig. 7.3a) and grazing intensity (Fig. 7.3b). Figure 7.3c and 7.3d shows the species cover model according to the cover data of the 37 sites in relation to relative soil water content and grazing intensity.

In figure 7.3a, only *P. laxum* and *L. hexandra* present cover values above 40% and a wide distribution; moreover, these species occupy different niche or position into the gradient, *P. laxum* grows on areas above 1m high whereas *L. hexandra* grows on areas under 2m high. On the other hand, *E. interstincta* presents a narrow distribution on low areas with a comparative high cover value around 20%. *P. chaffanjonii*, *H. amplexicaulis* and *I. fistulosa* present cover values under 5%.

The cover percentage observed in figure 7.3b is very low for all the species, however, *L. hexandra* and *A. purpusii* showed a small increment in the cover percentage when the grazing intensity increased.

The percentage of cover vegetation of *P. laxum* was the largest with respect to the relative soil water content showed in figure 7.3c, reaching 60% of cover and ranging between 20 and 60% for water content between 0 and 22 %. Besides *L. hexandra* presented a maximum cover of 50 % with a wide range distribution along the gradient on the wet side. These two species occupy the whole gradient with maximum covers and overlapping. *P. chaffanjonii* and *H. amplexicaulis* presented cover values above 8%, and they were restricted to dry and wet areas respectively, without any overlapping between them.

In figure 7.3d, the expected cover response of the vegetation is present for the intensity of grazing environmental gradient. Only *P. Chaffanjonii* presented high cover values when the intensity of grazing was increased, and *L. Hexandra* responds to medium-lower values of grazing with higher cover values (40 %). *A. purpusii* presented relative high values of cover percentage at the maximum grazing intensity. The other species presented the lowest cover values.

7.5 Discussion

Hydrological dynamics in the system studied is associated to the rainfall seasonality. This rainfall seasonality, combined with the topography establish the flood duration in the area. Therefore, the hydrological dynamics of the flooding savanna establish two important stresses, the soil water deficit during the dry period, mainly associated to seasonal and hyperseasonal savannas, and the flood condition with excess of soil water and anaerobiosis, mainly related to hyperseasonal and semiseasonal savannas. Plant species are adapted to these stresses, and their distribution, for many species, is restricted to a very short part of the gradient where only one type of stress is presented.

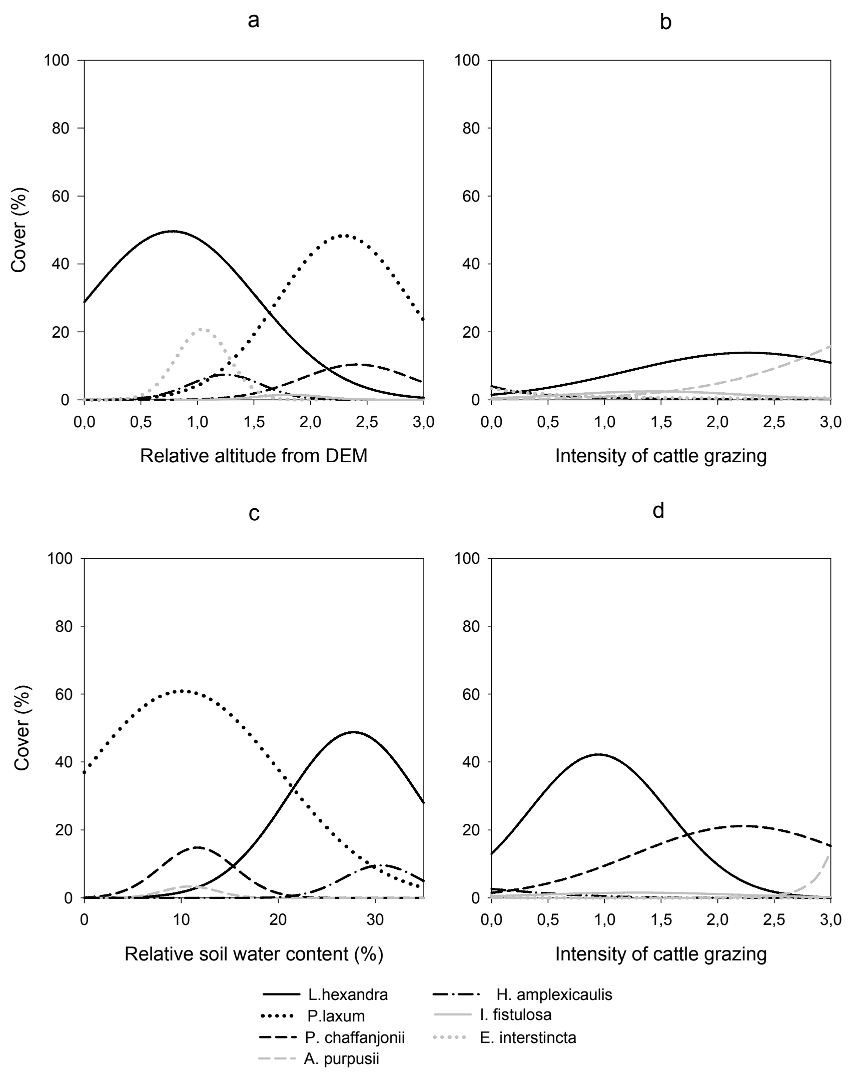


Figure 7.4 Models of species cover according to cover data in relation to the following environmental variables: a) relative altitude in catena derived from DEM for 57 sites; b) grazing intensity for 57 sites, c) relative soil water content for 37 sites, and d) grazing intensity for 37 sites.

These hydrological dynamics in the flooding savanna of Llanos del Orinoco presents a wide range of conditions, which have a strong relation to topographic features. Seasonal savannas which occupy river banks and never get flooded, have a very low quantity of soil water during the dry period. On the other hand, semiseasonal savannas have permanent soil water availability even during the dry period. This dynamics associated to the geomorphological characteristics produce a long hydrological gradient on which the plant species are distributed.

The Gaussian model used reflects the ecological responses of the species into the long hydrological gradient. The model reflects the principal ecological parameters as the species amplitude or tolerance, and the species optimum which is the gradient value where the species reach their maximum values.

Three groups of species may be differentiated from the type of adaptable responses to the soil water availability showed in the graphs and also derived from the analysis described in the chapter 6. The first group contains those species which present a wide range of distribution (large tolerance) and high frequency and cover values as the optimum for each species. This group is represented by *P. laxum* and *L. hexandra* which are adapted to a soil water deficit during the dry period and the flood condition during part of the rainy period.

The second group of species contains species with a very narrow tolerance and high frequency and cover values in the optimum of each species. These species are very well adapted to the flood condition in a specific range of soil water content. This group is represented by species like *H. amplexicaulis* and *E. interstincta* which are typical semiseasonal savanna species.

The third group has species, such as *P. chaffanjonii* and *I. fistulosa* which have a large range of distribution on the gradient, but they are not dominant, presenting medium-low frequency and cover values in the species optimum.

These results complement the information of the previous chapters, and allow us to build an ecological model about plant species distribution in the flooding savanna. The Gaussian models of species distribution developed in this chapter will be used as the equation for the elaboration of a spatial plant species model.

The information analyzed in this chapter and chapter 6 represents the ecological response of the species vegetation in the environmental gradients. Combining that information and the spatial pattern of the hydrological dynamics associated to the Digital Elevation Model developed and analyzed in the chapter 4, spatial models of species distribution are developed in the next chapters.

CHAPTER 8

Prediction of plant species distribution resulting from changes in hydrological processes in a Venezuelan flooding savanna

8. PREDICTION OF PLANT SPECIES DISTRIBUTION RESULTING FROM CHANGES IN HYDROLOGICAL PROCESSES IN A VENEZUELAN FLOODING SAVANNA.

8.1 Abstract

This study presents the main results of the analysis and integration of ecological processes and spatial explicit by models into an ecological-spatial model in order to understand, evaluate and predict the distribution of dominant plant species in a changing flooding savanna landscape effected by the embankment in the Llanos del Orinoco, Venezuela. For ecological input data, we used the ecological analysis and results derived from chapters 5 and 6, where the relationship between plant species and environmental factors was determined, and where these responses were analyzed using Gaussian logistic models. These ecological responses are integrated into a spatial model using the spatial variable determined in chapter 7. Maps of plant species distribution of the dominant species were elaborated based on the ecological integration between Gaussian responses and the Digital Elevation Model as environmental variable. Plant species community gradually changes and the dominant species have a strong relation to subtle environmental changes. *L. hexandra* and *P. laxum* are in a complementary relation because they do not present niche overlapping, whereas *E. intersticnta* and *P. chaffanjonii* are dominant in very reduced areas with medium-low frequency and cover values. The application of this model is very important to find out and predict changes in species diversity in the flooding savanna derived from the landscape transformation.

8.2 Introduction

A very dynamic process of ecosystem transformation has been occurring in the Venezuelan savannas. Particularly, in the flooding savannas of Southern Venezuela, that transformation involves changes in the hydrological dynamics of the area. In 1971, the project *Módulos de Apure* started in the Mantecal area. This project was based on dike construction to control the superficial water drainage through sluices. The general idea was to store water in order to produce grass biomass during the dry period and, thus, increase the resource capacity of the area (López-Hernández and Ojeda, 1996; Sarmiento and Monasterio, 1975). One of the main changes is related to the composition and distribution of savanna ecosystems is described in chapter 4 (Chacón-Moreno, 2001), and the replacement of savanna species adapted to hydrological deficit by species adapted to wet environments with greater palatability (López-Hernández and Ojeda, 1996).

Due to the large extension of these flooding savannas and their importance as habitats for a very rich fauna, it is fundamental to evaluate the changes in plant distribution caused by the dike construction. The species distribution responds to several environmental conditions described in chapter 5; then, when the environmental conditions or the different environmental factors change in different ways in the gradient, the distribution of species could change too. On the other hand, the species are a durable entity in time which responds to environmental factors and competition relations with other species. Therefore, mapping plant species distribution will allow us understand how the species are related among them and to the environment in a spatial context.

Most research about species distribution is focused on animal species because it is necessary to know their occurrence in order to implement conservation strategies. Much research is based on the mapping of animal habitats and the inference of the localization of the animal (Atkinson, 1985; Crosby, 1994; Dettmers and Bart, 1999; Mauro, 1999; Skidmore and Gauld, 1996; Tamisier and Dehorter, 2000). Knowledge about the plant species distribution will be useful to understand the ecosystem dynamics in a spatial context, and how the environmental conditions can determine the change in the composition and abundance of species; then, it is possible to model the resource capacity of different areas according to the species composition as well as an understanding of the animal species distribution in this kind of environment.

In landscape ecology, the use of modeling has become an important tool in order to understand and analyze the relationship between the spatial heterogeneity and the ecological resources (Goodchild, 1994; Turner *et al.,* 2001). Two different general modeling approaches could be used. The first approach is the direct analysis of the ecological processes into the spatial context without deep knowledge of the environmental factors, through autocorrelation techniques or surface pattern methods (interpolation, variograms and kriging), which have a important geostatistic component (Fortin, 1999; van Horssen *et al.*, 1999).

In the second approach, the ecological processes are analyzed in relation to the environmental factors; then, these relations are associated to the spatial heterogeneity and distribution of those environmental factors (Austin *et al.*, 1994; Goodchild, 1994; Guisan, *et al.,* 1998; Guisan and Zimmermann, 2000; Neilson, 1995; Skidmore, 1989; van de Rijt *et al.,* 1996; Zimmermann and Kienast, 1999). This approach uses the ecological knowledge about the processes and dynamics of the species, populations, communities or ecosystems, and the spatial patterns of the environment.

Models are useful tools for analysing and evaluating plant species distribution in a spatial context. They allow the exploration and analysis of the ecological processes in the changing scenarios generated by the natural dynamics in the environment or induced by human changes such as the global climatic changes (Aber *et al.,* 2001; Bachelet *et al.,* 2001; Hansen *et al.,* 2001; Malcolm *et al.,* 2002; Neilson and Marks, 1994; Neilson and Drapek, 1998).

In this study the development and application of ecological models in a spatial context are presented in order to determine the plant species distribution in a changing flooding savanna landscape of the Llanos del Orinoco in Venezuela. This objective is achieved by combining two methodological phases. In the first phase, the relationships between the environmental factors and the plant species composition of flooding savanna are established using ecological vegetation analysis through ordination techniques. Results and methodologies are described and analyzed in chapters 5 and 6 (Chacón-Moreno, 2001; Chacón-Moreno *et al.,* 2004). In the second phase, spatial information was used to determine the environmental distribution pattern of the main factor -hydrological gradient-, using the results of Digital Elevation Model (DEM) of the study area (Chapter 7, Smith *et al.,* 2006) and, the correlation between DEM with relative soil water content derived from the field data. The results are integrated and analyzed into Geographic Information Systems (GIS).

8.3 Study area

The study was carried out in the flooding savannas of the Llanos del Orinoco, Apure state, Venezuela, specifically on an area about 10,000 ha at the El Frío Biological Station. This area is boarded by tributaries of the Apure river; the landscape is very flat (3 m height difference over 12 km) and during the rainy season, between April and November, large areas are flooded. During the dry season most of the area dries out completely and at the end fires are common. For a further description and location of the study area, see chapters 2, 4 and 6 (Figure 6.1).

Four main ecosystems are predominant on the area (Picture 8.1), three of these correspond to savanna ecosystems differentiated by soil water availability during the year and the seasonal pattern of phenology: Seasonal, hyperseasonal and semiseasonal savannas described in chapter 2 (Chacón-Moreno, 2004; Sarmiento, 1984, 1990) and the gallery forest associated to water courses.

Extensive grazing is the most common land use activity in the area. An earthen dike was built to manage and storage water during the rainy period and supply water in the dry period in order to maintain forage availability, increasing the productivity of cattle. Besides, this kind of construction and management has been generating landscape changes, which were described in chapter 5. One of those changes is the replacement of hyperseasonal savanna by the semiseasonal savanna in which a reduction of the area of the former goes from 45 to 21% (Chacón-Moreno, 2001).

Picture 8.1 A Semiseasonal Savanna ecosystem during rainy season in the first plane and Gallery Forest in the second plane Scarlet ibis flying on the flooded area (up). Seasonal and Hyperseasonal Savanna ecosystems during dry season. Flying ducks are observed on the small water pot (below).

Three geomorphological units originated from the river dynamics (figure 8.1). They are: bancos, bajíos, and esteros. *Bancos* are natural levees along the edge of streams and main rivers where sandy soils predominate as well as seasonal savanna ecosystems. *Bajíos* are extended areas with medium topographic relative altitude, where soils are of silty texture. On this kind of unit, the hyperseasonal savanna ecosystem is dominant. The third unit is *estero*s which is the lowest unit of the topographic catena with a predominance of clay. Semiseasonal savanna and swamp ecosystems predominate on this unit. These geomorphological units are highly influenced by the water distribution and soil humidity during the year and, consequently, the spatial distribution of the plant species and ecosystems are associated to them. Because of the construction of dikes, large areas of the medium topographic unit *bajío* are almost permanently flooded; then, there is predominance of semiseasonal savanna ecosystem. A detailed description and analysis of the patterns and geomorphological processes in the flooding savanna are presented in Sarmiento and Pinillos (2001).

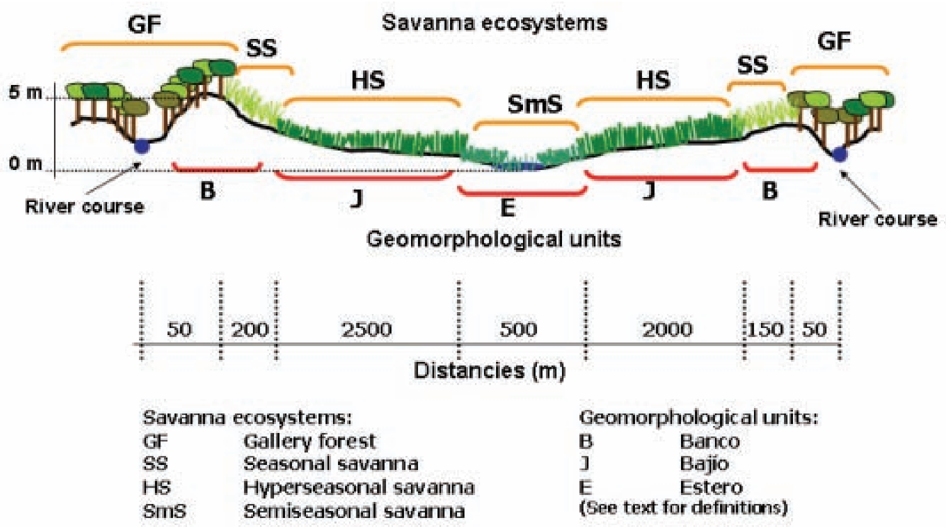


Figure 8.5 Idealized profile showing the ecosystem distribution in the study area in relation to the topographical gradient on the geomorphological units. Approximately distances between different units and relative altitude are showed.

Previous studies about the ecology, soil and geomorphology of the study area have been presented by Castroviejo and López (1985), Pereira da Silva and Sarmiento (1997), Pinillos (1999), Sarmiento and Pinillos (2001); Sarmiento *at al.* 2004; Chacón-Moreno *et al.,* (2004). Chacón-Moreno (2001) described the regional changes in ecosystems and vegetation following the construction of dikes.

8.4 Methods

The methodological approach used in this study has three phases: Ecological analysis of species distribution, spatial explicit model of environmental dynamics, and the integration of the species distribution in a spatial model.

8.4.1 Ecological analysis of species distribution

The direct and indirect response of vegetation to environmental factors was analysed using canonical correspondence analysis (CCA) as a direct gradient analysis technique and path analysis as indirect statistical technique. The collected vegetation data contained information on plant species presence/absence, frequency and cover of 57 sampling sites. For each of these sites, environmental and management characteristics were recorded, whereas relative soil water content was recorded only in 37 sample sites. Apart from the field data, additional information from maps created from remote sensing data (radar and Landsat images) was incorporated in the analysis. Detailed description of the results and analysis were presented in chapter 6 (Chacón-Moreno *et al.,* 2004).

After the main environmental factors were determined, the distribution of the most abundant plant species in relation to the three main environmental variables were analyzed using a Gaussian logistic model as Generalized linear model (GLM). The results of these analyses represent the main ecological inputs for the final integration model. The main results and analysis are described in chapter 7. See figure 8.2 with the methodological scheme.

8.4.2 Spatially explicit model of hydrological dynamics

To determine and understand the topography of the savanna ecosystems, a Digital Elevation Model (DEM) was created from 5500 points measured with real time kinematic GPS (precision <15 cm) and additional information taken from aerial photograph interpretation. The altitudes of the DEM were normalised by eliminating the general slope to obtain relative heights. As the general slope is very flat, internal relative height differences are more important for the hydrological dynamics. A complete description and analysis of this dynamics are presented in chapter 4 (Smith *et al.,* 2006).

A modification of the Digital Elevation Model (DEM) described in chapter 4 (Smith *et al.,* 2006) was made in order to obtain a raster map where the values of altitude or elevation are related to a virtual plane. The result of this modification is the Relative altitude model (Figure 8.3) where each point in the area is related to an inclination plane described by a simple equation, taking the maximum elevation point at the beginning of the slop and the minimum elevation point at the end of it (Figure 8.4). This simple model was made because the area presents a large plane with a small slope which is derived from the natural course of the rivers from West to East in the Apure-Arauca basin. This plane shows a change in the elevation following the topographic sequence between the rivers which border the study area (Guaritico and Macanillal rivers). All the new values for the Relative altitude model are calculated using a simple equation (Figure 8.4).

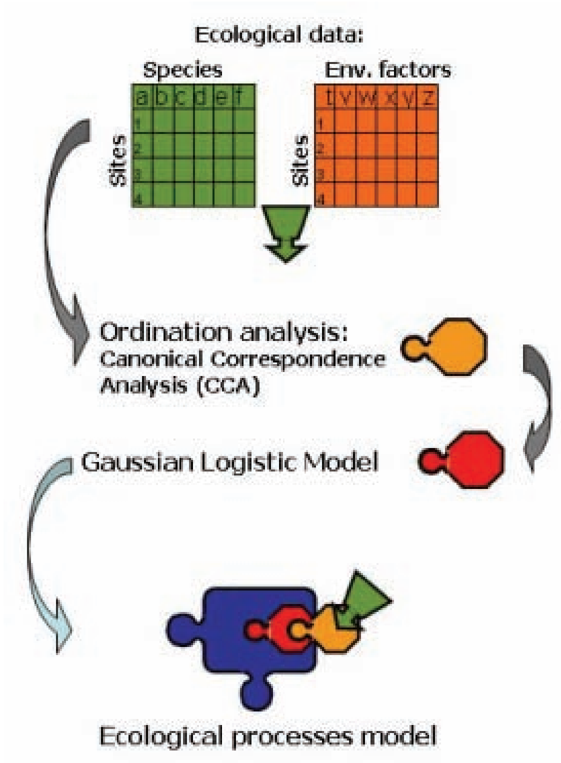


Figure 8.2 Scheme of the methodological approach for the Ecological analysis of species distribution. Integration of species and environmental data into the ecological analysis (ordination and Gaussian models) is indicated in order to produce a model of ecological processes.

Using regression analysis between Relative altitude model and the relative soil water content based on data collected in the field (Chapter 4), the hydrology-topography relationship was established (see table 6.3) and raster maps of the relative soil water content (RSWC) were made. The regression coefficients derived from the regression analysis were used to calculate the relative soil water content for each pixel or cell of the relative altitude model raster map. In the regression analysis, we also made two additional analyses considering the field data with and without the influence of the dike (Figure 8.3).

8.4.3 Ecological and spatial integrated model of species distribution

The spatial distribution of the plant species was obtained by integrating the main results of the ecological analysis and plant species distribution models with the spatial models. The spatial model for the topographical gradient is represented by the relative altitude model and the spatial model of the hydrological soil condition is represented by the relative soil water content model (Chapter 6). The integration of ecological and spatial models was developed using a GIS.

The species distribution was modeled by integrating the relative altitude model and relative soil water content maps with the Gaussian regression model of the species into a Geographical Information System (ILWIS). The highest coefficient regression between relative soil water content and the relative altitude was used. Models of species distribution were made considering different hydrological scenarios. Maps of present/absence, frequency and cover of the main species were constructed. See methodological scheme in figure 8.5.

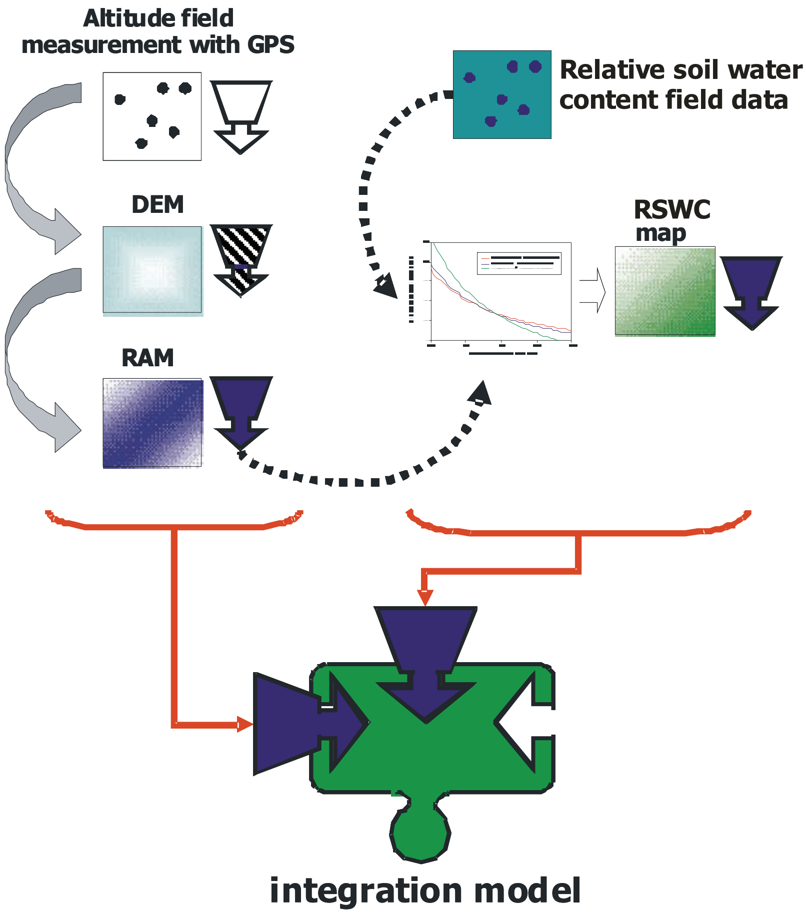


Figure 8.3 Scheme of the production of the spatially explicit integrated model. Digital Elevation Model (DEM) derived from GPS measurements, and relative altitude model (RAM) derived from DEM. Relative soil water content (RSWC) map derived from regression between relative soil water content field data and relative altitude model.

8.4.4 Validation of the species distribution models

To validate the accuracy of the final species distribution models, a new sample set of 43 ground data was collected to confirm species presence/absence, frequency and cover. The size of the sampled ground data control was a square of 10 x 10 m. This data were independently collected from the information for that of in the map; however, due the different collecting dates and the difference in personnel involved, they are only valid for presence /absence data. The data were compared to species distribution maps and error matrices; Kappa analysis and descriptive technique analysis were used to measure the accuracy of the models (Congalton, 1991; Congalton *et al.,* 1983; Janssen and van der Wel, 1994).

Calculation model of the relative elevation:

The diagram shows a representation of the slope in the area and the relation with the real situation (blue line) where the hmax and hmin are the maximun and minimum elevation, dmax is the length of the gradient, dx is the distance from the point of maximun elevation, and y is the elevation value in the model.
The relative elevation is the difference between y and the real elevation derived from field measurement.

$$y = d_{max} + ((h_{min} - h_{max}) \div d_{max}) \times d_x$$

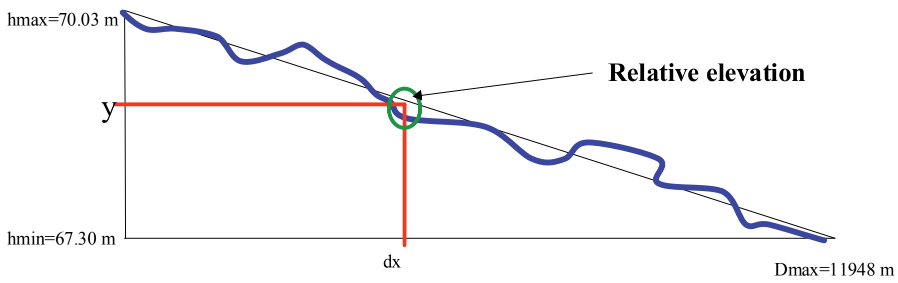


Figure 8.4 Representative diagram of slope calculation from the Digital Elevation Model (DEM) described by Smith *et al*. (2006), in order to obtain a raster map values of relative altitude.

8.5 Results

8.5.1 Selected species

From table 7.2 (Chapter 7) the following species with most frequent and cover values for each savanna ecosystem of El Frío Biological Station were selected: *Leersia hexandra, Panicum laxum* , *Paspalum chaffanjonii, H. amplexicaulis* and *E. interstincta*.

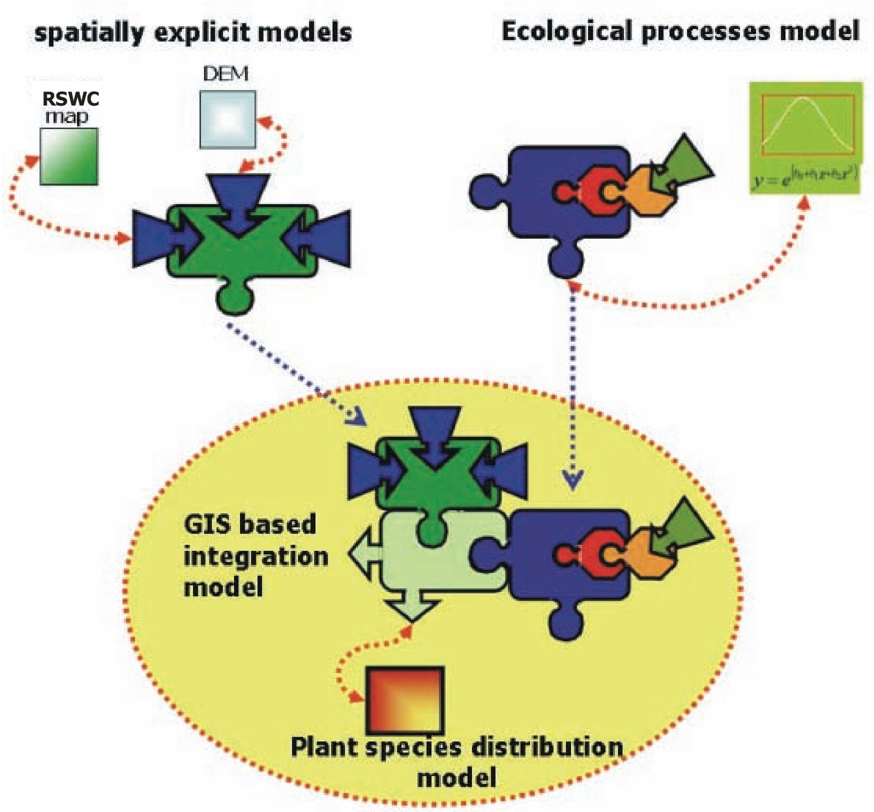


Figure 8.5 Methodological scheme of the ecological and spatial plant species distribution. The ecological process models and spatially explicit models are integrated using a GIS

8.5.2 Spatial model of relative altitude from DEM

Figure 8.6 shows the relative altitude model derived from DEM for the study area (Smith *et al.*, 2006) (the equation is explained in figure 8.4). This model shows that the depth areas are mainly located upstream the dike and associated to the Macanillal river at the south-west side. Higher zones are associated to the small banks of the small rivers inside the area and the highest area is associated to the Guaritico river bank in the confluence with the Apure River at the north-east side. Despite of the fact that the area presents an inclination from higher areas in the north-east side to lower areas in the south-west side, a pattern of low patch on a relative flat area with narrow banks areas associated to small water courses is predominant.

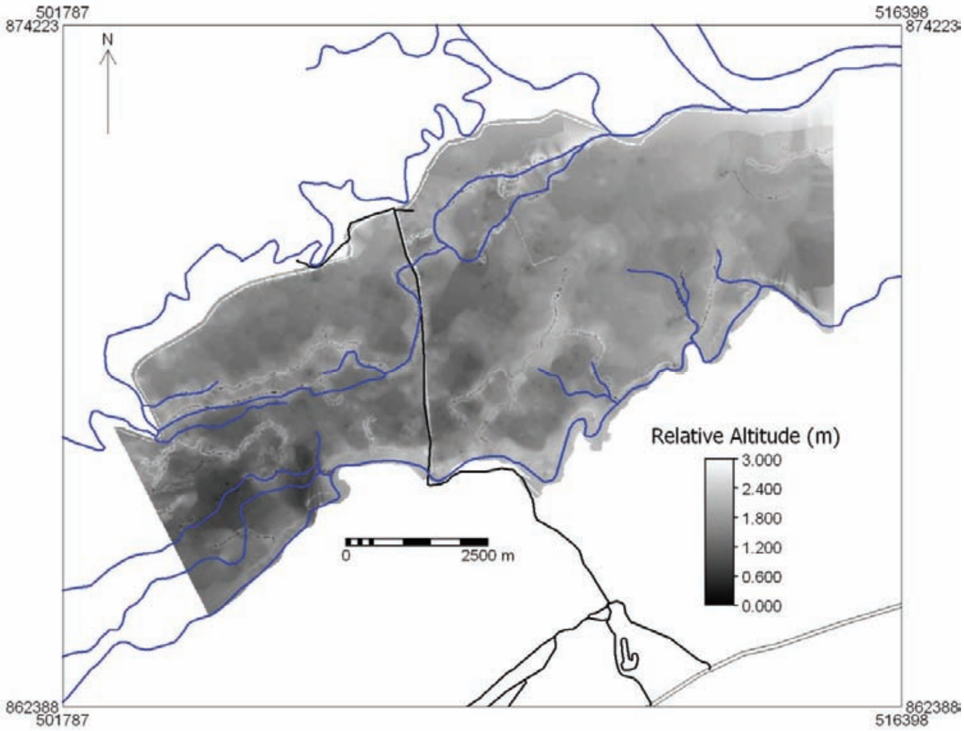


Figure 8.6 Relative altitude model (RAM) of the studied area of El Frío Biological Station, in the flooding savanna, Venezuela, derived from DEM (Smith *et al.,* 2006, and slope equation described in figure 5).

8.5.3 Ecological and spatial model of species distribution based on relative altitude model

Figure 8.7 presents the frequency distribution model of the most common species in relation to the relative altitude in the catena. It is clear that the major frequency values of *L. hexandra* (> 0.75) are associated to the lowest areas in the west side (upstream of the dike); however, higher frequency values are observed at the middle of the study area close to the east side of the dike. Medium frequency values for *L.hexandra* are observed in the rest of rest of the study area. High frequency values of *P. laxum* are mainly distributed to the highest areas in the East (downstream from dike), but medium-low values are observed on the up-stream dike area (west).

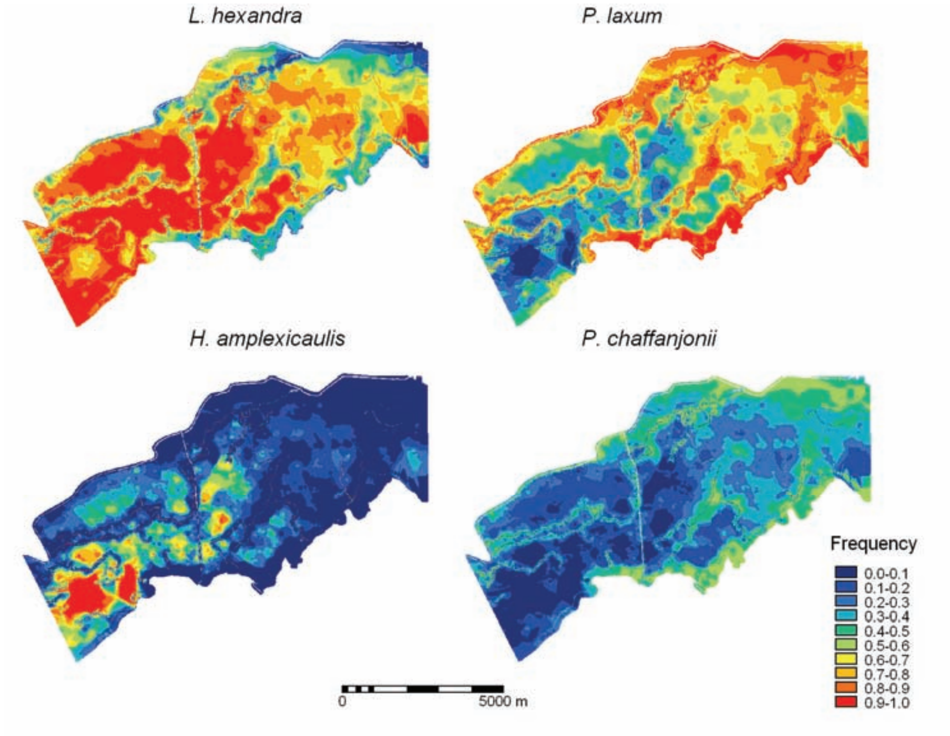


Figure 8.7 Model of species distribution of *P. laxum, L. hexandra, H. amplexicaulis* and *P. chaffanjonii* for frequency data based on Relative altitude model in the flooding savanna of El Frío Biological Station, Venezuela.

H. amplexicaulis presents a similar distribution to *L. hexandra*, but the frequency values are lower, except for the deepness zones in the west side where the frequency values reach over 0.70. *H. amplexicaulis* is absent in areas associated to higher zones in the east. *P. chaffanjonii* presents lower frequency values and distribution similar to *P. laxum*; however, this species is almost present in all the area, except in the lowest part of the west side.

In figure 8.8, the coverage model for the most important species is presented in relation to relative altitude model. *P. laxum* presents the maximum cover with values above 15% for almost the whole area, but the cover values decreased less than 5% in the depths zones. *L. hexandra* presents the highest cover in areas upstream from the dike, medium cover values (10-25%) downstream from the dike and values < 5% in the highest areas on the river banks.

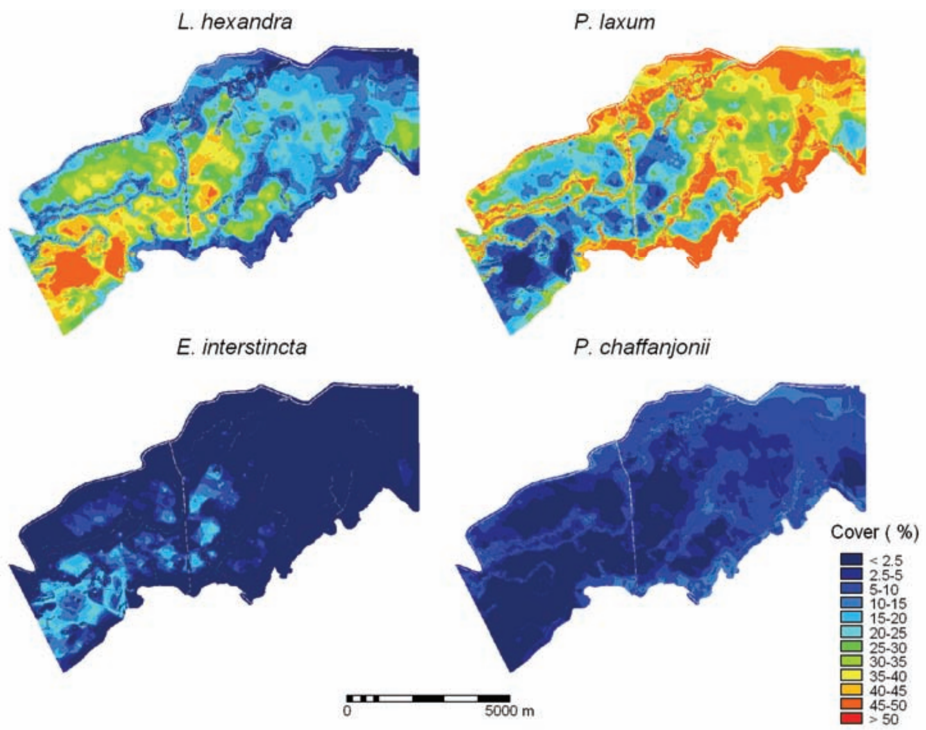


Figure 8.8 Model of species distribution of *P. laxum, L. hexandra, E. interstincta* and *P. chaffanjonii* for cover data based on Relative altitude model in the flooding savanna of El Frío Biological Station, Venezuela.

On the other hand, *E. interstincta* and *P. chaffanjonii* present the lowest cover values (>5%). *E. interstincta* shows medium values in the deeper zones, while *P. chaffanjonii* is only confined to the river bank zones where it presents medium cover values.

8.5.4 Species distribution model validation

Table 8.1 presents the results of accuracy level and Kappa values derived from the error matrix analysis by comparing the result of species distribution models with the ground data collected.

The values of producer accuracy obtained for the 5 studied species are high when presence/absence data are considered, while producer accuracy values for frequency data are higher for *L. hexandra*, and *P. laxum*, and higher for cover data of *P. chaffanjonii* and *E. interstincta*. In contrast, the user accuracy presents low to intermediate values for present/absence, frequency and cover data. Overall accuracy for *L. hexandra*, *P. laxum*, and *E. interstincta* was around 55 % and lower for *P. chaffanjonii* and *H. amplexicaulis*. The Kappa values are very low for all data analysis.

Table 8.1 Accuracy level and Kappa value derived from the analysis of error matrix of species distribution models versus independent ground collected data. For frequency data, the species frequency was considered valid if the frequency value in the model was higher than 0.5, and for cover data, the species cover data were considered valid if the cover value in the model was higher than 25% and higher of 10%. For *H. amplexicaulis* there are data only for frequency (0.5 and 0.25), and for E. *interstincta* there are data only for cover (25% and 10%). NA = non applicable.

Species	Data type	Accuracy level			Kappa value
		Producer	User	Overall	
Leersia hexandra	Presence/absence	100	53	53	0
	Frequency	91	57	58	0.12
	Cover 25%	35	73	58	0.19
	Cover 10%	91	58	60	0.17
Panicum laxum	Presence/absence	100	60	60	0
	Frequency	77	57	51	-12
	Cover 25%	73	58	51	-0.1
	Cover 10%	96	60	58	-0.05
Paspalum chaffanjonii	Presence/absence	100	23	23	0
	Frequency	20	67	79	0.22
	Cover 25%	70	22	35	-0.03
	Cover 10%	100	24	26	0.01
Hymenachne amplexicaulis	Presence/absence	100	19	21	0.01
	Frequency (0.5)	0	0	67	-0.19
	Frequency (0.25)	25	25	72	0.08
Eleocharis interstincta	Presence/absence	83	20	51	0.13
	Cover 25%	0	NA	86	0
	Cover 10%	50	33	79	0.28

8.5.5 Ecological and spatial model of species distribution based on hydrological gradient

Figure 8.9 presents the regression models between the relative altitude derived from DEM and the relative soil water content considering all points, down-stream and up-stream points. The regression model for data collected up-stream presents a major slope due to the water accumulation by the dike effect. On the other hand, the model for down-stream data presents lower relative soil water contents at the lowest relative altitude.

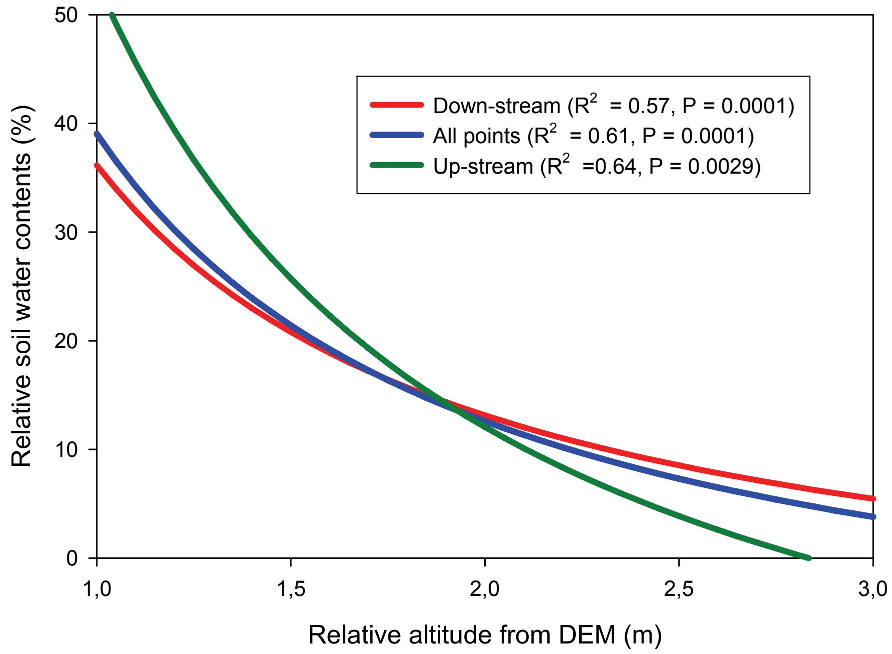


Figure 8.9 Regression curves between relative altitude model values derived from DEM (Smith *et al.* 2006) and Relative soil water content values measure in the studied area of flooding savanna of El Frío Biological Station, Venezuela. Three set of values were considered: all field observations, down stream of dike observations, and up-stream observations. Regression coefficients and significance values are indicated.

Figure 8.10 shows the cover distribution of the two most important species: *L. hexandra* and *P. laxum* in relation to the spatial hydrological gradients. Three hydrological conditions were modeled; first, the actual conditions where the dike controls the water distribution determining an accumulation of it in the west side (upstream from the dike) and a deficit in the east side (downstream from the dike). The two species show a clear niche differentiation. *P. laxum* presents major coverage downstream, where the hydrological conditions are drier than upstream.

The second situation presents a hydrological condition without the dike and has a more uniform water distribution, leaving the upstream area less wet. In this situation, *L. hexandra* shows a cover reduction and *P. laxum* increases its cover, especially upstream.

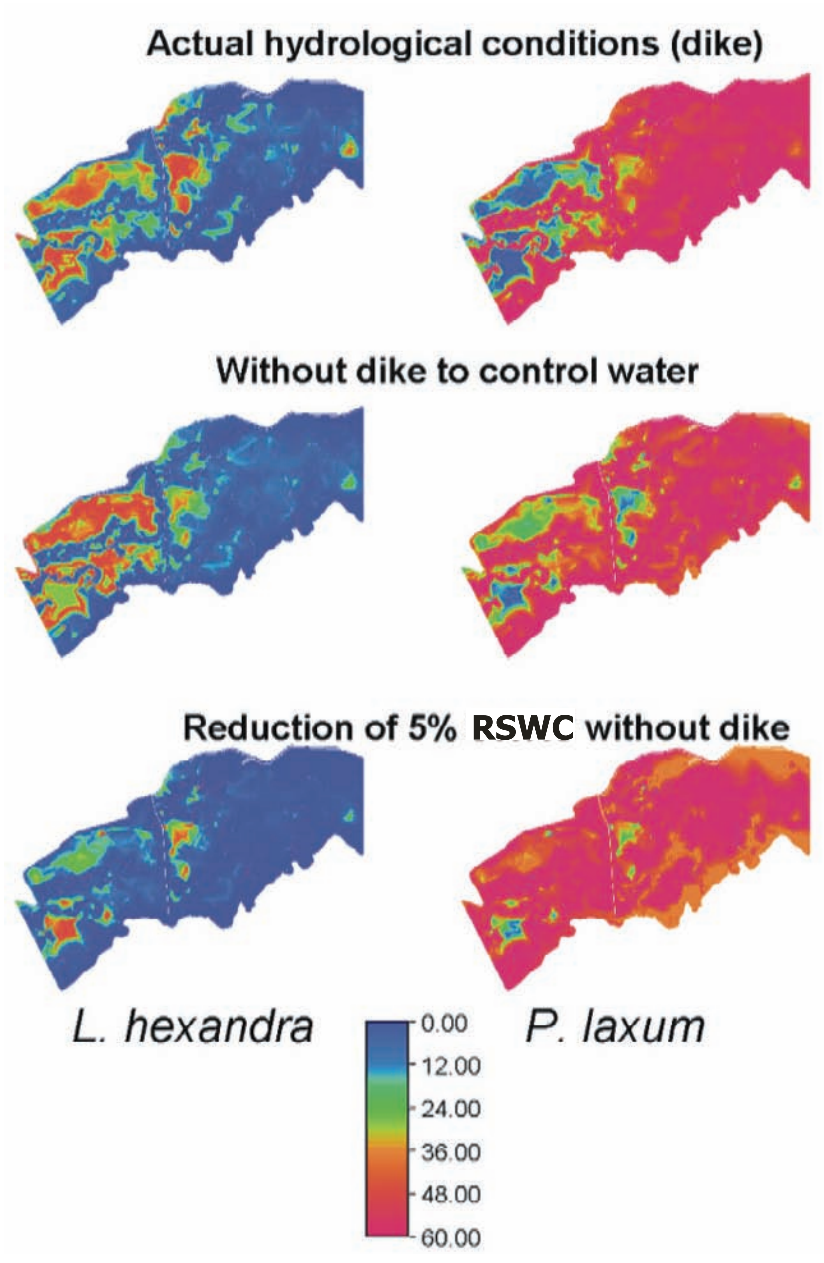


Figure 8.10 Distribution model of *P. laxum* and *L. hexandra* for cover data based on Relative soil water content (RSWC) for three different hydrological conditions: actual hydrological conditions, without dike effect or control, and reduction of 5% of relative soil water content for the flooding savanna of El Frío Biological Station, Venezuela.

The third situation shows a reduction of the relative soil water content of 5% where an almost absolute dominance of *P. laxum* and an important decrease of *L. hexandra* are observed. The areas where *L. hexandra* presents higher cover values are reduced to three sinks with the lowest depth.

8.6 Discussion

The landscape of flooding savanna is practically flat and the relative altitude differences are very low (not larger than 3 meters); however, direct observation shows that the species community gradually changes and the dominant species have a strong relation to the small environmental gradients determined in chapter 5.

The dominance of *P. laxum* and *L. hexandra* over the other species was remarkable when the cover values were considered; nevertheless, the frequency values are more related to the species importance because cover parameter changes drastically during the year due the climate conditions and phenological growing phase, whereas frequency is a vegetation parameter depending not on the extension or green quantity, but on the presence and number of plants, which do not present much variation as the cover parameter. Therefore, the other frequent species like *H. amplexicaulis* in the semiseasonal savanna or *P. chaffanjonii* in the seasonal savanna have a great importance to characterize these ecosystem classes.

When the natural slope was deleted from the digital elevation model, the relative altitude model showed an inverse slope direction, presenting the highest altitudes in the west side associated to the Apure river bank, which is the largest river in the area. Besides, river banks of Apure and Guaritico determine higher altitudes than the Macanillal river bank located at South where the deepest sink is found. The presence of lower areas in the West side and the accumulation of water by the embankment determine a very wet environment where water in the soil can remain during a long period of time.

The frequency distribution model of plant species based on the relative altitude model confirms the associations among the species and the hydrological conditions derived from the water availability and the flooding conditions expressed in the relative altitude model. *L. hexandra* is a species associated to medium-high values of soil water content, and the model presents a distribution associated to lower relative altitude values, but does not present higher frequency values in the deepest areas. On the other hand, *P. laxum* occupies those medium-high areas associated to hyperseasonal savanna condition. *H. amplexicaulis* is distributed mainly to the deeper areas, where the water accumulation is larger, while *P. chaffanjonii* presents a strong relation to the river and the water course banks areas, where the flooded condition is not frequent or is absent during the year.

Plant species distribution model for cover data confirm the dominance of the four species considered in the study. *L. hexandra* and *P. laxum* are in a complementary relation to the cover areas without niche overlapping.

The higher producer accuracy values of plant species distribution model mean that the selection criterion and significance considered in the analysis are good. On the other hand, the lowest Kappa values are explained because the models overestimate the species distribution and there are few places in the models where the species are not present. Moreover, the number and selection of the sampled ground data control were not suitable, leaving some key areas without sampling.

Strong and significant regression is presented between relative altitude model and relative soil water content, which confirm that the relative altitude is the main environmental variable determining the soil water availability (Chapter 6). Also, the regression between relative altitude model and relative soil water content allows the possibility to estimate the relative soil water content in conditions dissociated to the dike effect, and even simulate the plant species distribution with different hydrological conditions.

The plant species distribution for frequency data in relation to relative soil water content of *P. laxum* and *L. hexandra* is similar to the distribution in relation to relative altitude model; however, the reduction of the dike effect causes drier conditions upstream. These conditions create favorable areas where the frequency values of *P.laxum* increase whereas the frequency values for *L. hexandra* decrease. These effects are amplified with a reduction of 5% of relative soil water content. *P. laxum* is a dominant species associated to the hyperseasonal savanna, where the drier and flooded soil conditions occur every year. Then, when the simulation is directed to diminish the relative soil water content, the frequency values increase because the conditions are similar to the hyperseasonal savanna. This result shows the transformation derived from the embankment where the dominant species like *P. laxum,* in the hyperseasonal savanna, and *L. hexandra,* in the semiseasonal savanna, could displace to give origin to the landscape change described and analyzed in chapter 4.

The results obtained from the ecological models confirm that the water duration in the soil over the year is the principal environmental factor that leads to plant species distribution in the flooding savannas and determines the ecological responses of the ecosystems. Furthermore, it is important that the plant distribution follows a gradual change where the main species do not overlap. Distribution and separation of dominant species along the gradient show a clear niche separation.

The ecological model developed to understand ecosystem functioning must be incorporated into the new ecological-spatial model as a conceptual basis. Consequently, a definition, determination and understanding of the environmental dynamics through spatially explicit models allow relating the species and plant communities to spatial patterns of different environmental factors.

A relevant feature obtained from these models was the possibility to monitor the changes in species distribution derived from changes in the relative soil water content. Therefore, the distribution (cover and frequency) of the main plant species could be determined if changes in the hydrological balance are introduced and the plant communities and habitats could be quantified in order to understand the impact of ecosystem changes in diversity of the flooding savanna.

Finally, the application of this model could be useful to predict new changes in the plant species composition if hydrological conditions are modified; besides, it represents a technique for the conservation planning and development in equilibrium with the environmental conditions and needs. The innovation of the model mentioned above resides in that it will allow relating ecological aspects to a spatial dimension. This relation is possible with the integration of methodological approaches and conceptual models.

The next chapter improves the plant species distribution models by the combination of more than one environmental variable associated to the environmental gradients founded in the flooding savanna. In this case multiple Gaussian regression models for binomial and frequency data are used.

8.7 Acknowledgements

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CHAPTER 9

Plant species distribution in the Venezuelan Flooding Savanna using models of multiple spatial variables

9. PLANT SPECIES DISTRIBUTION IN THE VENEZUELAN FLOODING SAVANNA USING MODELS OF MULTIPLE SPATIAL VARIABLES

9.1 Abstract

This study presents the main results of the analysis and integration of ecological processes and responses in combination with several spatial variables into an ecological-spatial model. This model will allow understanding, evaluation, and prediction of the distribution of dominant plant species in a changing flooding savanna landscape caused by the embankment in the Llanos del Orinoco, Venezuela. The ecological processes were analyzed using ordination and regression techniques to determine the effect of the environmental factors on the species distribution. The spatial explicit variables used to elaborate the model correspond to the main factors associated to the flooding savanna using the results of the analysis of radar image temporal sequences; Landsat image interpretation; field data of soil water content, and digital elevation model. Single and multiple Gaussian regressions were used to evaluate the significance of the spatial variables with the species data of *P. laxum* and *L. hexandra* (presence/absence, frequency and cover), and determine the parameters of the multiple Gaussian regressions equations. Spatial ecological models of the species probability, frequency and cover were elaborated using a maximum of four spatial variables. The models using multiple spatial variables presented better accuracy than those which used a single variable. Besides, the models confirm a clear dominance of species in separated niche along the gradient. Application of ecological integrated model of several spatial variables could be useful to analyze possible changes in the plant species composition on local, regional or global change.

9.2 Introduction

Flooding savanna is a large extension of land which has been transformed by the embankment of many areas to supply water during the dry season and increase its productivity (López-Hernández and Ojeda, 1996). The main effect of the embankment was the reduction of the hyperseasonal savanna ecosystems and the increase of the semiseasonal savanna ecosystems, which was described and explained in chapter 5 (Chacón-Moreno, 2001). This transformation causes possible changes in the habitat and in the plant species abundance and distribution. How can we evaluate the responses of the species to this transformation?

First of all, the species-environment relationship has to be determined in order to measure and understand how the environmental factors affect the plant distribution. To answer the above question we analyzed and determined the main environmental factors affecting the plant distribution in the flooding savanna in chapter 6, and in chapter 7 we described the responses of individual species along a gradient of the environmental factors.

With the description of the plant species distribution in relation to the gradient factors, as ecological responses, we need to integrate these responses into a spatial context; then, in chapter 4, we determined one of the most important variables, which is the topographical variation and the principal factor which leads the hydrological dynamics. With this spatial variable and its relation with the soil water, the dominant species distribution models were elaborated.

In this study, the development of the plant species distribution models derived from the multiple integration of spatial variables in a changing flooding savanna landscape of the Llanos del Orinoco in Venezuela is carried out. This is achieved by studying and selecting the significant combination of spatial variables using multiple Gaussian regressions to calculate the equation parameters to be integrated into a Geographical Information System (GIS) (Chacón-Moreno *et al.*, submitted; Guisan and Zimmermann, 2000). The spatial information is derived from different sources: a) RADAR image analyses of temporal sequences to obtain the flood duration model (Smith *et al.*, 2006); b) a relative altitude model derived from a Digital Elevation Model (DEM) of the study area described and analyzed in Chapter 4 (Smith *et al.,* 2006) ; c) Landscape Ecological Maps of the study area obtained from a LANDSAT image interpretation and aerial photo interpretation described in Chapter 5 (Chacón-Moreno, 2001), and d) a Relative Soil Water Content model (RSWC) elaborated from the regression between relative altitude model and field data of soil water content, explained in Chapter 8 (Chacón-Moreno *et al.*, submitted).

This chapter represents an integrated approach of the main results given in the previous chapters into the spatial context of flooding savanna. This approach represents a contribution to express the ecological processes of the specific area or ecosystems into the spatial context, understanding and analyzing the ecological issues.

With the inclusion of spatial variables such as the flood duration, landscape ecological maps or relative altitude model, we can establish future scenarios of plants, ecosystems and habitat distributions linked to global and local climatic changes, as well as predict possible effects on the biodiversity of the flooding savanna.

9.3 Study area

The study was carried out in the flooding savannas of the Llanos del Orinoco, Apure state, Venezuela, specifically in an area about 10000 ha at the El Frío Biological Station. This area is delimited by tributaries of the Apure River. It is a very flat area which submerges during the rainy season (between April and November) and, during the dry season; the most of this area dries out completely (from December to March). Fires are common at the end of the dry period. The principal features and processes of the area have been described in previous chapters. Chapter 8 describes the spatial arrangement of the four predominant ecosystems on the area (Chapter 8, Picture 8.1 and Figure 8.1), three of these ecosystems — seasonal, hyperseasonal and semiseasonal savannas — are differentiated from each other by the soil water availability during the year and the seasonal pattern of phenology described in Chapter 2 (Chacón-Moreno, 2004; Sarmiento, 1984, 1990) and the fourth ecosystem gallery forest is associated with water courses. A description of the ecology, soil and geomorphology of the study area has been presented by Castroviejo and López (1985), Pereira da Silva and Sarmiento (1997), Pinillos (1999), Sarmiento and Pinillos (2001); Sarmiento *at al.* 2004; Chacón-Moreno *et al.,* (submitted). Chacón-Moreno (2001) described the regional changes in ecosystems and vegetation following the construction of dikes.

9.4 Methods

The methodological approach used in this study has two phases: Ecological analysis of species distribution using Gaussian regressions (single and multiple) and the integration of the species distribution (probability, frequency and cover) in a spatial model of multiple variables.

9.4.1 Spatial variables

Four spatial variables were considered in the study: the relative altitude model the relative soil water content (RSWC), Landscape Ecological Maps of the study area, and the Flood Duration Model. The methodological scheme, showing the proceedings and integration of the spatial variables into a spatially explicit model, is presented in figure 9.1

The first variable is the relative altitude model developed and described in Chapter 8 (Chacón-Moreno, *et al.*, submitted) which is derived from the Digital Elevation Model of the study area (DEM) explained in Chapter 4 (Smith *et al.,* 2006). Based on the regression between relative altitude model and field observations of the relative soil water content, a map was made (RSWC) which corresponds to the second spatial variable. A complete description of this map is presented in Chapter 8 (Chacón-Moreno, *et al.*, submitted).

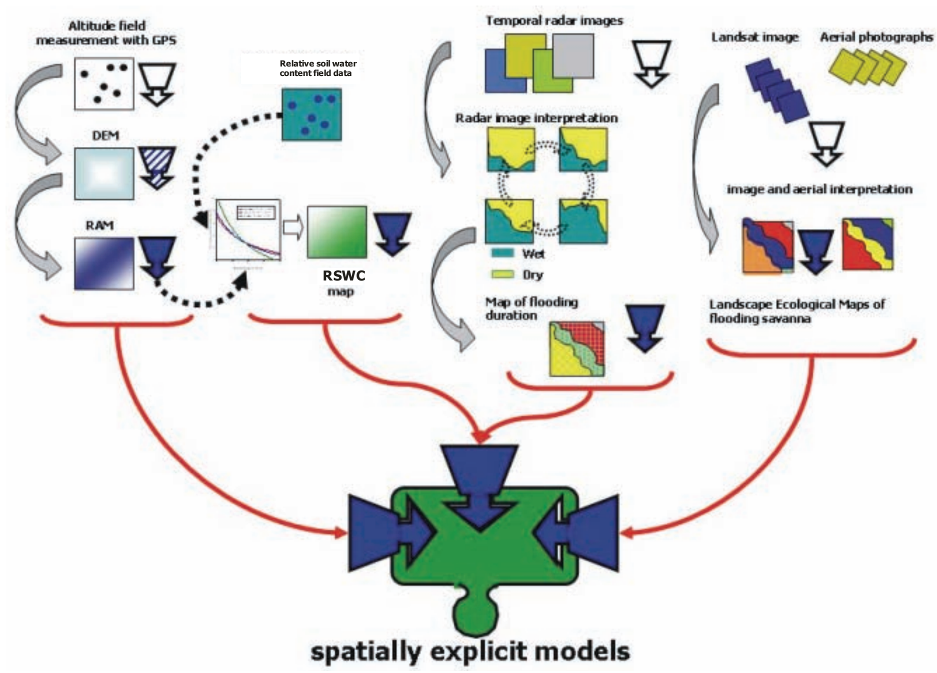


Figure 9.1 Scheme of the development of the spatially explicit model. Digital Elevation Model (DEM) derived from GPS measurements, RSWC derived from DEM and field data, Flood Duration Map (MFD) derived from interpretation of temporal radar images and Ecological Landscape Maps derived from aerial photographs and Landsat image interpretation.

The third spatial variable is the Landscape Ecological Map of the study area, which was elaborated from Landsat TM image classification, for the period after dike construction (1988). A retrospective Landscape Ecological Map for the period before dike construction (1960) was created from aerial photograph interpretation. The methodological description of the Landscape Ecological Maps was defined in Chapters 3 and 5 (Chacón-Moreno, 2001, 2004).

The fourth spatial variable is a Flood Duration Model. To understand the flood dynamics over the year, a flood duration model was constructed from four temporal radar images (ERS2 SAR PRI). These images were interpreted using fieldwork observations and vegetation dynamics to distinguish flooded from non-flooded areas and, by combining the results of the 4 scenes, a flood duration map was obtained (Smith *et al.,* 2006).

The Landscape Ecological Map of 1988 and the Flood Duration Model derived from the radar interpretation mentioned above were codified (Table 9.1). The Landscape Ecological Map was codified following a gradient of flooding in relation to the Ecological Units described in Chapter 2 and 6 whereas the Flood Duration Model was codified in a gradient from the minimum period of time in which an area is flooded to the maximum period of time in which the area is flooded. This last period corresponds to the areas flooded in dry season.

Table 9.1 Codification of the Ecological Units from the Landscape Ecological Map of 1988 with values following the hydrological gradient of each unit and codification of the flooded condition unit derived from the Flood Duration Model following a gradient from minimum to maximum flooded condition.

Ecological Unit	EU Code	Flooded condition	FC code
Seasonal savanna	1	Not flooded	1
Hyperseasonal savanna	2	Flooded wet season	2
Semiseasonal savanna non flooded	3	Flooded dry-wet season	3
Semiseasonal savanna flooded	4	Flooded wet-dry season	4
		Flooded dry season	5

9.4.2 Ecological species distribution related to multiple variables

Data of presence/absence, frequency and cover for the main plant species were obtained from 57 fieldwork sites. Complete descriptions about sampling, compilation, analysis and results are presented in Chapters 6, 7 and 8 (Chacón-Moreno *et al.,* 2004, submitted). From the variable maps developed earlier, values were obtained for each sample site in order to contrast them with the species variables data from the field (presence/absence, frequency and cover) using regression analyses. Single Gaussian regressions analyses were made for each spatial variable for presence/absence, frequency and cover data in order to determine the significant level of the equation parameters and select the best significant analyses.

The multiple Gaussian regressions for two, three and four spatial variables are described in the equations 9.1 and 9.2. The spatial variables are denoted by: x = relative soil water content (RSWC), y = relative altitude model (RAM), z = Landscape Ecological Map (LEM), and v = Flood Duration Map (FDM) ; x_0, y_0, z_0 and v_0 represent the optimum of the species fitness and *b, c, d* and *e* represent the tolerance of the species (Chapter 7), and *a* represent the magnitude of the initial parameter related to the curve top.

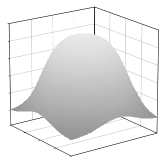
Equation 9.1 Presence/absence data, the figure is an idealized model for two variables

2 variables

$$\gamma = \frac{ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)\right]}}{1 + ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)\right]}}$$

3 variables

$$\gamma = \frac{ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)\right]}}{1 + ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)\right]}}$$



4 variables

$$\gamma = \frac{ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)+\left(\frac{(v-v_0)^2}{e^2}\right)\right]}}{1 + ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)+\left(\frac{(v-v_0)^2}{e^2}\right)\right]}}$$

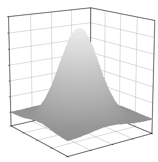
Equation 9.2 Frequency for cover data. The figure is an idealized model for two variables

2 variables

$$\gamma = ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)\right]}$$

3 variables

$$\gamma = ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)\right]}$$



4 variables

$$\gamma = ae^{\left[-0.5\left(\frac{(x-x_0)^2}{b^2}\right)+\left(\frac{(y-y_0)^2}{c^2}\right)+\left(\frac{(z-z_0)^2}{d^2}\right)+\left(\frac{(v-v_0)^2}{e^2}\right)\right]}$$

9.4.3 Multiple spatial distribution model of species

Based on the results obtained from the single and multiple regressions for each type of data and for *P. laxum* and *L. hexandra*, the equations parameters were selected and integrated into a Geographical Information System (GIS). The variables x, y, z and v used in the regressions were replaced by the maps of RSWC, relative altitude model, Landscape Ecological Map and Flood Duration Model, respectively, in order to obtain the probability, frequency and cover distribution model of *P. laxum* and *L. hexandra*. The annex 9.1 presents the parameters selected for the model construction. A schematic representation of the integration of ecological responses and spatial variables is presented in figure 9.2.

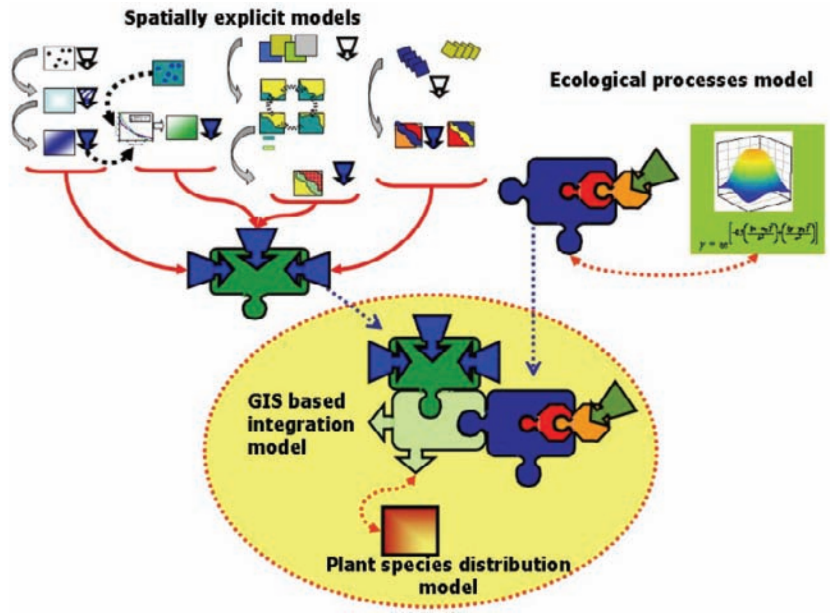


Figure 9.2 Methodological scheme of the ecological and spatial plant species distribution. The ecological process models and spatially explicit models are integrated using a GIS

9.4.4 Validation of the species distribution models

The methodological approach to validate the species distribution model was described in Chapter 8. Further descriptions of the statistical analyses are explained in Congalton *et al.* (1983), Congalton (1991) and Janssen and van der Wel (1994).

9.5 Results

9.5.1 Landscape Ecological Maps of flooding savanna of El Frío Biological Station

Figure 9.3 presents the Landscape Ecological Maps of flooding savanna of El Frío Biological Station derived from aerial photo interpretation of the area before dike construction (1969) and LANDSAT image classification of the area after the dike construction (1988).
The description of the Landscape Ecological Units is presented in chapters 2 and 5. The maps present the distribution of the savanna ecosystem found between the Guaritico River which is associated with the gallery forest to the Northwest side, and Macanillal River as the border in the Southeast side (Chapter 6, Figure 6.1), the lagoon in both maps is a reference point. These

rivers flow parallel for many kilometres from open savanna in the Southwest to flow into the Apure river in the Northeast extreme in the maps. In the Landscape Ecological Map of 1988, we can observe how the constructions of dikes retain water which leads to changes in the vegetation in relation to the map of 1960. One of the main changes is the replacement of the hyperseasonal savanna by the semiseasonal savanna. A schematic profile of the maps from Guaritico to Macanillal describing the ecological units is presented in figure 8.1 (Chapter 8).

9.5.2 Flood duration model

Figure 9.4 presents the flooding areas for different time periods during the year in the El Frío Biological Station area. The flooded areas for each seasonal and transitional period are indicated. The smaller areas correspond to those which remain flooded after the end of dry period. The main areas where water remains for longer periods of time is associated to the dikes. At the upstream side (west) of the dike, water accumulates and terrain remains flooded for a long time. At the downstream side of the dike (east), some important areas close to it remain flooded for a long period because there is a continuous flow of water though the dike sluices.

Dry areas are associated to the natural levees or banks of the Guaritico-Apure rivers at the North side, and Macanillal River at the South side; these areas also have a major extension on the downstream side of dike, where the natural water flux from the open savanna is blocked.

9.5.3 Ecological and spatial model from multiple variables

Table 9.2 presents the summary of the significant values of the parameters and R^2 values for the single regressions among the species data of presence/absence, frequency and cover *versus* the spatial variables.

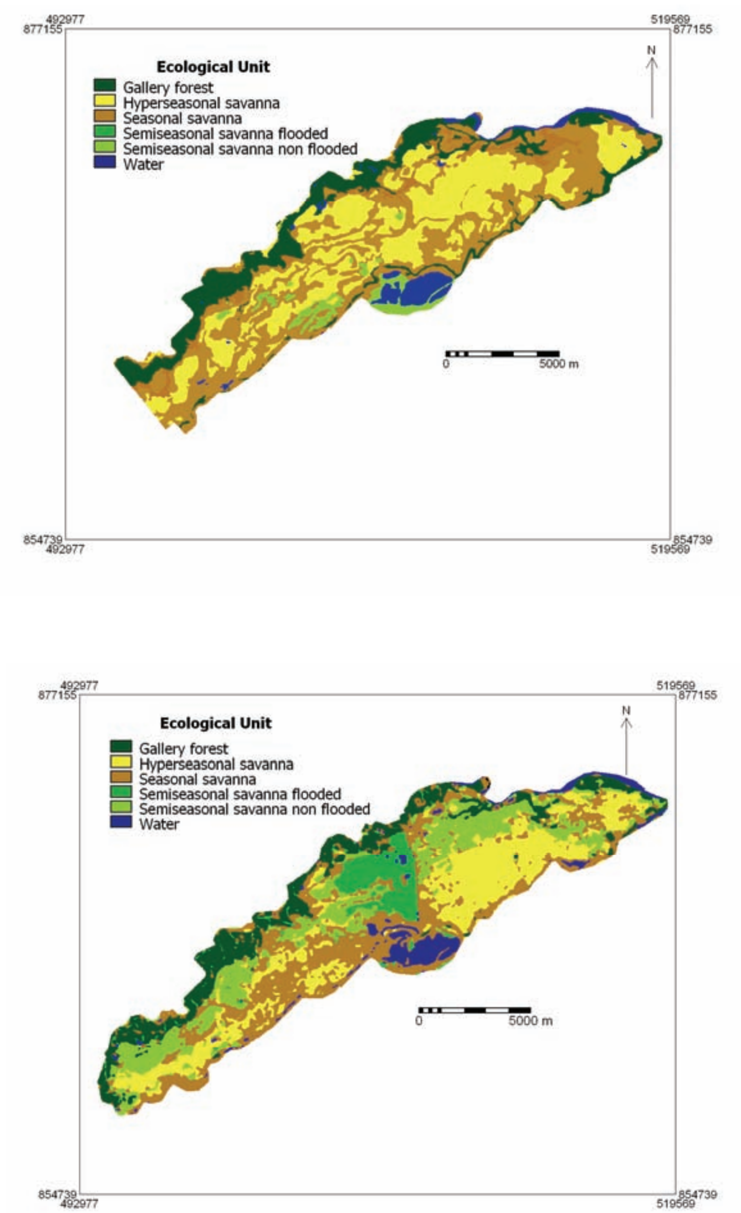


Figure 9.3 Landscape Ecological Maps of flooding savanna of El Frío Biological Station elaborated using: aerial photo interpretation of the area before the dike construction (1960)(up); LANDSAT image classification of the area after dike construction (1988)(below).

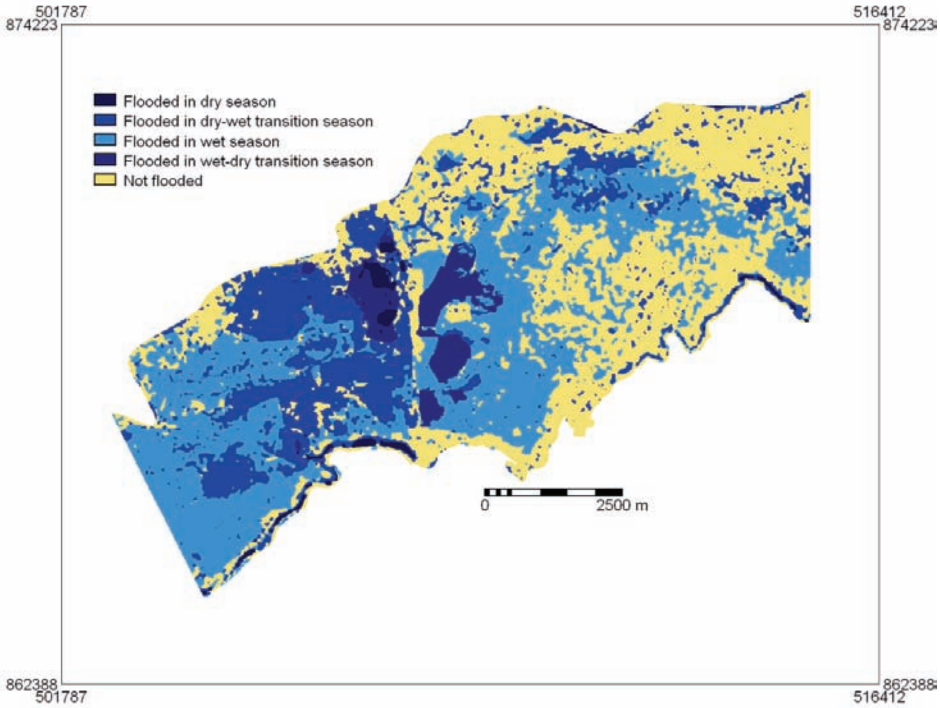


Figure 9.4 Flood duration model of the El Frío Biological Station area, Venezuela (From Smith *et al.* in press).

For *P. laxum* and presence/absence data, one multiple regression (Reg 1) with two variables were selected including RSWC and Landscape Ecological Map variables for 57 sites; nevertheless, the P value for a, b and X_0 of RSWC in single regression are not significant. For frequency and cover data, the combination of variables with major quantity of significant variables and major R^2 values was considering 57 sites and including all spatial variables (Reg 2 and Reg 3). Single regressions for *P. laxum* presence/absence data with 37 sites did not showed significant values, and for frequency and cover data only RSWC presented significant P value of the total analysis.

For *L. hexandra* present/absence data, it is observed that three analyses out of eight are significant, but as neither of the parameters are significant, multiple regressions for these data could not be calculated (Table 9.2). For the frequency data, three of the spatial variables show significant values of P for all the parameters and for the complete analyses; besides, they are better expressed in the data with 57 sites. The relative soil water content variable and Flood Duration Model variable, both with 57 sites, present the best significant regression parameters for cover data of *L. hexandra.*

Table 9.2 Values of R^2 for single regressions of each spatial variable: relative soil water content (RSWC), relative altitude model (RAM), landscape ecological map (LEM) and flood duration model (FDM), with presence/absence, frequency and cover data of *P. laxum* and *L. hexandra*. R^2 = regression coefficient; P_t = statistical significance for the total analysis; P_a, P_b and P_{x0} = statistical significance for the equation parameters a, b and x_0 respectively. ns = P not significant, *** = P < 0.0001, ** = P < 0.001 and * = P < 0.05.

Panicum laxum

Spatial variable and sites number	Type of data														
	P/A					Frequency					Cover				
	R2	Pt	Pa	Pb	Px0	R2	Pt	Pa	Pb	Px0	R2	Pt	Pa	Pb	Px0
RSWC 57 sites	0.4	***	ns	ns	ns	0.6	***	***	***	***	0.4	**	***	*	ns
RAM 57 sites	0.1	ns	ns	ns	ns	0.2	*	***	ns	***	0.1	*	***	*	***
LEM 57 sites	0.3	**	ns	*	***	0.2	**	***	***	***	0.3	**	***	***	***
FDM 57 sites	0	ns	*	*	***	0.2	*	***	**	***	0.2	*	***	*	***
RSWC 37 sites	0.8	***	ns	*	ns	0.7	***	***	***	***	0.4	**	***	*	ns
RAM 37 sites	0.1	ns	ns	ns	ns	0.1	ns	**	ns	*	0.1	ns	***	ns	***
LEM 37 sites	0	ns	ns	ns	ns	0.1	ns	***	*	***	0.1	ns	***	*	***
FDM 37 sites	0	ns	ns	ns	ns	0.1	ns	***	ns	ns	0.1	ns	***	ns	ns

Spatial variable and sites number	Leersia hexandra														
	P/A					Frequency					Cover				
	R2	Pt	Pa	Pb	Px0	R2	Pt	Pa	Pb	Px0	R2	Pt	Pa	Pb	Px0
RSWC 57 sites	0.3	*	ns	ns	ns	0.4	**	***	**	***	0.6	***	*	***	***
RAM 57 sites	0.2	*	ns	ns	ns	0.3	***	***	**	***	0.2	*	ns	ns	ns
Landscape Ecological Map 57 sites	0	ns	ns	ns	ns	0	ns	ns	ns	ns	0.2	*	ns	ns	ns
FDM 57 sites	0.1	ns	ns	ns	ns	0.2	*	***	*	***	0.1	*	***	*	***
RSWC 37 sites	0.3	*	ns	ns	ns	0.4	**	***	**	***	0.7	***	*	***	***
RAM 37 sites	0.2	ns	ns	ns	ns	0.3	*	***	*	***	0.1	ns	ns	ns	ns
Landscape Ecological Map 37 sites	0	ns	ns	ns	ns	0	ns	ns	ns	ns	0.2	*	ns	ns	ns
FDM 37 sites	0.1	ns	ns	ns	ns	0.1	ns	***	*	**	0	ns	ns	ns	ns

From these analyses, the following set of data, variables and conditions were selected: Reg1 = P. laxum presence/absence data, 37 sites, 2 spatial variables; Reg2 = P. laxum frequency data, 37 sites, 4 spatial variables; Reg3 = P. laxum cover data, 57 sites, 4 spatial variables; Reg4 = L. hexandra frequency data, 57 sites, 3 spatial variables; Reg5 = L. hexandra cover data, 37 sites, 2 spatial variables.

Figure 9.5 presents the spatial distribution model of *P. laxum* for presence/absence data, frequency and cover data. Related to presence/absence data, the model predicts that *P. laxum* occurs in almost all the areas; however, there are some places close to the deep areas in the southwest side where the species have the lowest probability of occurrence. For the frequency data, the situation is similar than for presence/absence data, but the higher frequency values are found in the downstream side of the dike (east side), reaching a frequency above 0.50 in almost all this side. For cover values, the highest percentage values are located in the east side, and the low percentage values in the depression and temporarily more inundated areas.

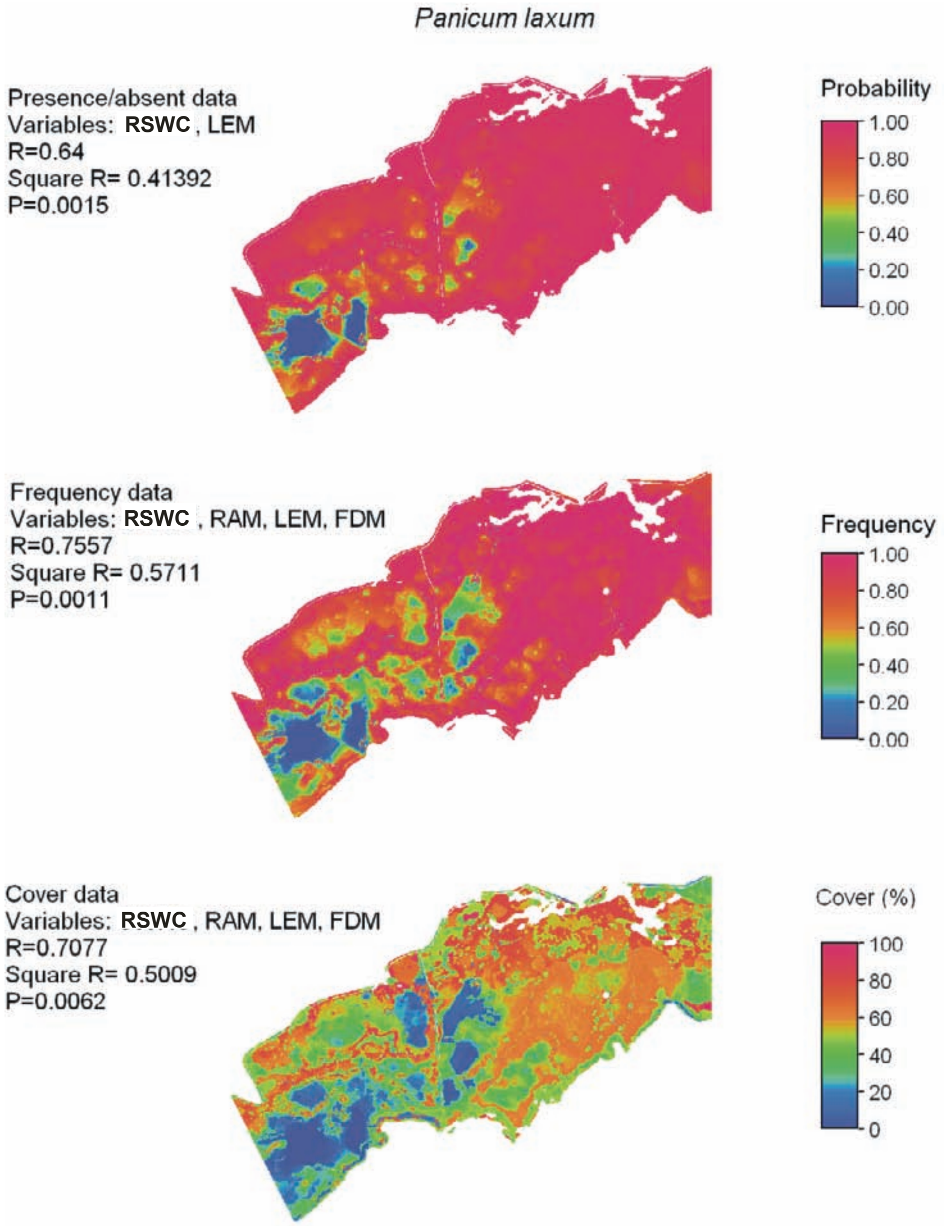


Figure 9.5 Model of spatial distribution of P. laxum for presence/absence, frequency and cover data, in the El Frío Biological Station area, Venezuela. Spatial variables, regression and correlation coefficients and statistical P value are indicated.

The model for frequency presented the highest regression coefficient (R^2=0.57) in relation to the presence/absence data and cover distribution models (Fig. 9.5); moreover, it includes the four environmental variables. We observe that the pattern distribution for frequency and cover distribution are similar, and the major frequency and cover values are inversely associated to the lowest areas; conversely, present/absence model is most associated to the lower areas.

Figure 9.6 presents the model distribution of *L. hexandra* for frequency and cover data. *L. hexandra* presents higher frequency values in deep and flooding zones, particularly to the west side (up-stream of dike). The lowest frequency values are associated to river banks and gallery forest of Guaritico-Apure and Macanillal in the east side, and the deepest areas (Chapter 8, Figure 8.6) in the southeast of the map. The highest values of cover of *L. hexandra* are present in the flooded and flooding areas. Comparing the distribution of *L. hexandra* for frequency and cover, we observe that, even though, this species is present in a large proportion of the area, it is only dominants in specific areas which are deep, but not in deepest ones.

Comparing the distribution models of *P. laxum* and *L. hexandra* for frequency values, we observe that these species occupy similar sites for almost the whole areas, and especially do not occur in the extremes of the environmental gradients. Nevertheless, when cover data are compared, these species occupies different niche. Besides, the areas with deepest relative altitude values, and flooded in dry-wet transition season, in the south-east side are not dominated by either of these two species.

9.5.4 Species distribution model validation

In table 9.3, we observe that the producer accuracy values were the highest (> 70%) for almost all analyses, while medium-high values (between 50 and 70%) were obtained for the user accuracy analyses. For overall accuracy, the values were medium-high about 63%. However, the Kappa values are very low for all the analyses, but *L. hexandra* shows the highest Kappa value between the two species for cover data.

9.6 Discussion

The Landscape Ecological Maps of flooding savanna of El Frío Biological Station confirm the result obtained in Chapter 4 about the landscape changes caused by the embankment, where the hyperseasonal savanna ecosystem has been replaced by semiseasonal savanna ecosystems. The replacement is mainly the result of hydrological dynamics, with new wet areas instead of drier areas, and the consequent change in vegetation composition and the new spatial arrangement of the plant species. Besides, this hydrological condition and vegetation change cause transformations in the animal species habitat and its distribution. There is a reduction of the habitat area for some animal species including deer, anteater, and the American lion, but offers increasing habitat area for other animal species as capibara, caiman, and many birds' species. For the Landscape Ecological Map of 1988, the semiseasonal savanna area not only increased upstream of the dike (west side), but also down stream of the dike because water is supplied through sluices.

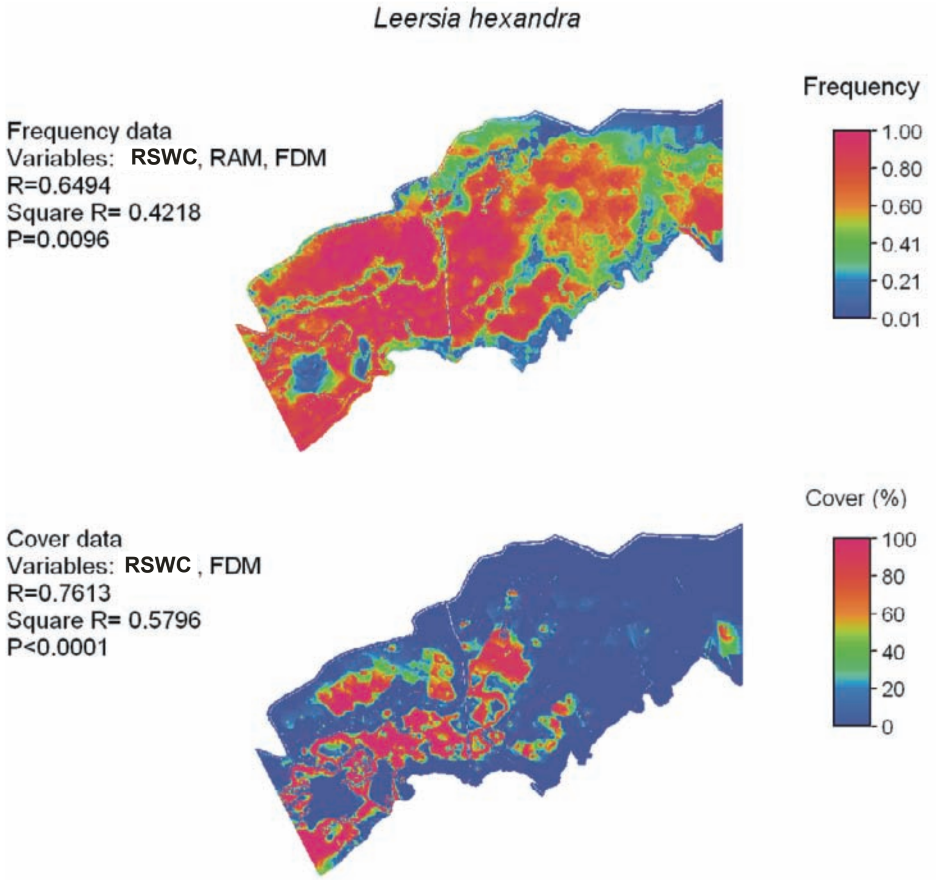


Figure 9.6 Model of spatial distribution of *L. hexandra* for frequency and cover data, in the El Frío Biological Station area, Venezuela. Spatial variables, regression and correlation coefficients and statistical P value are indicated.

This embankment modified the hydrological dynamics, including the annual water accumulation. The flood duration model derived from the radar image interpretation represents the yearly water accumulation. This model shows, in the downstream side of the dike that the expected dry condition is attenuated by the water availability generated by the discharge from the embankment, which creates a wet condition in the surrounded area. It is clear that the embankment effect is larger than the rainfall effect because the up-stream areas present flooded conditions derived from those effects, and the transition periods show large extension of flooded areas. This hydrological dynamic up-stream of dike is associated not only with the embankment, but also with the soil characteristics, such as the clay layer (Chapter 6, Sarmiento *et al*., 2004, Smith *et al*., 2006) which hinders the infiltration of water to the deepest soil layer and the areas are flooded for a long time.

Table 9.3 Accuracy level and Kappa value derived from the analysis of error matrix of species distribution models versus independent ground collected data. For Presence/absence, the data were considered directly. For frequency data, the species frequency was considered valid if the frequency value in the model was larger than 0.5. For cover data, the value was considered valid if it was present in the model, or was larger than 25% and 5%.

Species	Data type	Accuracy level			Kappa value
		Producer	User	Overall	
Leersia hexandra	Presence/absence	100	53	53	0
	Frequency	83	63	65	0.28
	Cover	70	70	67	0.35
	Cover 25%	30	100	63	0.29
	Cover 5%	43	83	65	0.32
Panicum laxum	Presence/absence	100	60	60	0
	Frequency	92	59	56	-0.09
	Cover	100	60	60	0
	Cover 25%	88	59	56	-0.07

Moreover, the construction of the dike has allowed the development of similar geomorphology and hydrological conditions observed along the gallery forest. Consequently, the gallery forest species have established on the dike creating a new forest corridor (van Os, 2000) which, in turn, generates new habitats for animals.

The statistical preliminary test of single regression shows that for frequency and cover data of both species, a large number of analyses were significant, but the selection of the best regression was made based on the best regression coefficient. However, for presence/absence data of *L. hexandra*, the results were less significant.

The general pattern distribution of *P. laxum* is similar to that observed in chapter 8 for the single model based on the relative altitude model and RSWC. The species shows a strong association to the medium-dryer areas, especially those located down stream of dike. Nevertheless, there are some areas located to the northeast side of the map, which increased the presence, frequency and

cover of *P. laxum*, compared with the single model presented in Chapter 8. Besides, the model with multiple spatial variables for cover data is more precise and the definition of areas with dominance of the species is clearer.
L. hexandra shows different results in relation to the pattern of distribution, if frequency or cover data are considered. For frequency data, *L. hexandra* presents a wide distribution with medium-higher values. However, for cover data, the dominance of this species is restricted to few zones. *L. hexandra* is dominant in those zones which correspond to the medium-high soil water content and those where water remains for longer periods of time and is not permanent flooded. It is clear that L. *hexandra* occurs frequently in many areas, but it is dominant in very restricted conditions. The plant model distribution of *P. laxum* and *L. hexandra* confirms a clear dominance of species in separated niches along the gradient.

The accuracy of the validation analysis from the error matrix indicates the quality of the multiple integration. The multiple integration model has better validation results than those found for single distribution model described in Chapter 8. The inclusion of more significant variables into the model distribution enhances the result and accuracy of the model.

The relative altitude model allowed modeling the species distribution into the topography and hydrological gradients; however, the understanding of the temporal hydrological dynamics and the changes derived from the dike construction were only possible through the interpretation and analyses of the flood duration map and the ecological landscape maps which show the ecosystem changes.

The application of an ecological predictor (Chapter 7) combined with a maximum of four spatial variables (Chapter 4 and 8) allows obtain the spatial distribution of the main dominant species in the flooding savanna in relation to the principal environmental gradients that are affecting the plant species distribution (Chapter 6). The methodological processes based on GIS-model permits integrate the ecological and spatial aspects.

Models for plant and animal species distribution could be developed by different ways. When the integration of spatial variables is based on GIS, the way to formulate the model implies the use of a model predictor (Austin, *et al*., 1994; Dettmers and Bart, 1999; Guisan *et al*., 1998; Venterink and Wassen, 1997; Zimmermann and Kienast, 1999). This model predictor presents the ecological responses associated to the environmental variables, which generally represent a gradient. Also, the ecological responses could be modelled using GIS directly from the data collected, without an ecological analysis (Debinski *et al*., 1999; van Horssen *et al*., 1999).

Application of an ecological integrated model of several spatial variables could be useful to analyze possible changes in the plant species composition into local, regional or global changes. Models of vegetation and plant species distribution based on the hydrological features have been developed in climatic change scenarios where the integration of environmental factors in the spatial context is related to the ecological responses (Bachelet *et al.*, 2001; Daly *et al.*, 2000; Neilson, 1995; Neilson and Marks, 1994). The flooding savanna could be affected by other changes and transformations, as the climate change, which could involve the hydrological dynamics and the plant species distribution; therefore, the application of an ecological integrated model will be useful to understand and predict possible ecological changes in the flooding savanna.

9.7 Acknowledgements

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CHAPTER 10

Synthesis

10. SYNTHESIS

10.1 Introduction

The main objective of this thesis was to determine the importance of the ecological determinants of the savanna ecosystem at different observation scales in the Llanos del Orinoco, and the effect of human transformation on these ecological determinants. It was assumed that the ecological determinants of the savanna ecosystems play an important role at different intensities and at diverse observational scales, and that some of them could be masked by the landscape transformation due to human influence. At the beginning of this thesis, several assumptions related to the pattern distribution of the savanna type, the effect of the human transformation and the distribution of plant species were made. At the subcontinental level, the pattern distribution of the main savanna ecosystem of the Llanos del Orinoco was analyzed and it was found that the rainfall seasonality pattern was the ecological determinant in order to discriminate the ecosystem types. At the regional scale, the landscape changes derived from the embankment were analyzed, and it was found that those changes mainly associated to the flooding condition, mask the geomorphological influence. It is known that the patterns in plant species composition reflect the response of the vegetation to environmental conditions (Jongman *et al.*, 1995; ter Braak, 1987, 1996; Whittaker, 1967), then in the last chapters of this work, the focus was on the study and modeling of the spatial distribution of the plants species in relation to the main ecological determinants together with the effect of changes in the hydrological condition. It was found that the hydrological gradient is the principal determinant factor of the plant spatial distribution, and that the soil nutrients do not have any correlation with that distribution. Besides, the plant distribution followed a clear niche differentiation between the dominant species associated to the savanna ecosystems. The methodological approach was based on the analysis of the savanna landscape through the use and application of ecological tools: Landscape Ecology concepts, vegetation analysis and modeling to understand the processes into the spatial context.

10.2 Llanos del Orinoco and their transformation

Llanos del Orinoco constitutes one of the largest tropical savanna ecosystems located at the Northern part of South America and represents a typical neotropical savanna where the climate and soil are the main determinants of this ecosystem (Sarmiento, 1983, 1984; Solbrig *et al.*, 1996). This region has been submitted to processes of intense transformation, such as agriculture and cattle raising, producing a change in the number and size of natural areas, thereby affecting their biodiversity (Silva and Moreno, 1993). There is no clear evidence what the consequences of those transformations are, nor the effective species distribution and biodiversity and the functioning of the ecosystem.

The change and transformation processes of Llanos del Orinoco ecosystems produce important changes in the species composition and distribution. These changes include the displacement, disappearance as well as the appearance of species. Such changes are related to environmental factors. The characterization of the pattern distribution of these environmental factors contributes, in the spatial context, to explain the possible changes in the species distribution.

The Llanos del Orinoco can be divided according to the age of parent material, landform and soil into four principal sub-regions: piedmont, high plains, alluvial overflow plains and aeolian plains (Chacón-Moreno, 1991; MARNR, 1985; Sarmiento, 1983). Within these sub-regions, savanna is the predominant ecosystem. This ecosystem is defined as a tropical formation where the grass stratum is continuous and dominant. Occasionally, savannas could be interrupted by trees or shrubs, where fires are frequent and the growing patterns are associated to the climate seasonality (Bourliere and Hadley, 1983). In general, the Neotropical savanna presents a higher annual rainfall than African or Australian savannas, with a marked seasonality (Aw climate class), low soil nutrient content and frequent fires (Huntley and Walker, 1982; Sarmiento, 1984).

This tropical savanna ecosystem can be divided into four major categories from an ecological point of view: Tropical Seasonal savanna, Tropical Hyperseasonal Savanna, Tropical Semiseasonal Savanna, and Swampland (Sarmiento, 1983; Sarmiento, 1990). Seasonal savannas (SS) are the areas with one dry season and another season ecologically favorable with soil water availability. Hyperseasonal savanna (HS) is the ecosystem with four different hydric periods during the year: a first dry period which lasts approximately two or three months, a second period with soil water availability which lasts one or two months, a third period with excess of water in the soil, with a duration about 6 to 7 months, and a fourth ecologically favorable period with a duration of one month. Semiseasonal savanna (SS) is the ecosystem with two periods: a favorable period with duration of two or three months and a long period with excess of water in the soil of approximately 9 months.

Moreover, apart from the predominant savanna ecosystems, forest ecosystem are present in the areas where the climate and soil conditions are relatively enhanced and important gallery forest ecosystem is associated to the main water courses. Llanos del Orinoco has an extraordinary animal diversity which responds to a large variety of habitats, the connection between the forest and savanna areas, the water reservoirs, and the isolated forest patches (matas).

10.3 Ecosystem map of Llanos del Orinoco

At a sub-continental scale, the savanna ecosystem distribution of Llanos del Orinoco was determined. Based on the analysis of multitemporal NOAA-AVHRR NDVI imagery, the phenology of vegetation was determined to understand better the ecology of the main ecosystems of the Llanos del Orinoco. The methodological approach included determination of seasonal curves of NDVI; supervised classification to obtain a map displaying a number of ecosystem classes that differ in phenological feature, and an assessment of map accuracy with ground data. A previous knowledge of ecosystem functioning and the features of the study area was necessary to understand and explain the phenological patterns derived from the remote sensing data. The patterns of phenological variation for each of the ecosystems show a strong relationship with the environmental features described by Sarmiento (1983, 1990), Sarmiento *et al.* (1971), Silva *et al.* (1971), and Chacón-Moreno (1999), where the annual distribution of rainfall determines conditions of water availability. The patterns also depend on other characteristics such as the geomorphology of the areas where this ecosystem exists. This methodological approach allows us to establish a link between the ecological processes and the spatial components of the remotely sensed data.

The Llanos del Orinoco represents a typical neotropical savanna where the climate, soil and fire are the main determinants of this ecosystem (Sarmiento, 1983, 1984; Solbrig *et al.*, 1992, 1996; Silva 1987). In the Llanos del Orinoco ecosystem map, the seasonal availability of rainfall was almost the unique criteria to determine the image classification of the savanna ecosystem. However, knowledge of the fire occurrence associated to the phenological pattern was an important key factor to identify the savanna ecosystem. On the other hand, nutrients do not have much influence as a discriminable criterion at this scale. Here, the fire is a factor which occurs frequently in the seasonal and hyperseasonal savanna ecosystems, but it is almost absent in the semiseasonal savanna ecosystem, whereas the low nutrients availability is a general condition for all savanna ecosystems. Therefore, we can assert that, at the subcontinetal scale, the main criteria to differentiate savanna ecosystems classes are the soil water availability and fire.

10.4 The flooding savanna changes

Within Llanos del Orinoco, an important large sub-region corresponds to the flooding savanna (16000 Km^2). This savanna was analyzed evaluating the changes derived from the embankment of the hyperseasonal savanna in order to increase the carrying capacity of savanna for secondary production. The methodological approach used here is based on the knowledge and interpretation of the relationships among structure, function and change within the landscape. For this task, a chorological view of the flooded savanna is used based on the concept of landscape as an assemblage of ecosystems (Zonneveld, 1989, 1995, 1998). A method was developed to define and recognize the ecological units or land units as ecosystem types according to the function and vertical structure of each one. Thus, an ecological map was created to analyze the landscape changes.

The ecological processes were described based on the map unit concept, which represents the structure and function of the landscape elements (Forman, 1995; Forman and Godron, 1986; Turner and Gardner, 1990; Zonneveld, 1989, 1995, 1998). A landscape ecological map was defined as the integration of the structure and the ecological processes within and between the land units. In this approach, the land units were delineated based on attributes related to one or more components of the ecosystem structure. In the integrated approach, some of the ecological processes related to the ecosystem can be mapped through the correlation of these processes with the spectral response of remotely sensed information.

The dike construction to control water and increase the primary production during the dry period produces severe changes in the soil water availability. Then the geomorphological dynamics as the main factor determining the ecological distribution of the savanna ecosystems is replaced by some interrelated factors. The flood condition generated by embankment characteristics becomes the main factor which determines the soil hydrological condition, through large extensions of flooded areas during long time.

The embankment of the flooding savanna drastically changed the landscape pattern in terms of the size and proportion of the land unit (savanna ecosystem). The main change was observed for the hyperseasonal savanna ecosystem with a cover percentage of 45% in 1960 to less than 22% in 1988; while semiseasonal savanna ecosystem increased the cover from 13% in 1969 to 40% in 1988. These changes are derived from the water accumulation during the dry period by the dike effect, creating wetter hydrological conditions.

The increase of cover for the semiseasonal savanna ecosystem represents an increment in the forage availability for secondary production. Consequently, the flooding savannas can now support not only increased cattle raising, but also an increment of abundance for some species including capybara, birds, and amphibious. The landscape changes also lead to a reduction in the area of other ecosystems, for example, the hyper-seasonal savanna, which can, in turn, lead to a reduction in habitats for animals. It is difficult to conclude that the changes benefit the habitat conservation because many other vegetation species and wildlife could disappear; besides, many ecological processes are changed and the stability of the natural ecosystem could be modified.

One important result derived from the comparison between the two landscapes ecological maps described in chapter 5, was the establishment of change percentage among the different ecological classes and the direction of this change. Therefore, a state and transitional model or pathway model (Keane *et al.*, 2004) to describe the changes of the successional states when a disturbance (dike construction) modifies the hydrological dynamics of the landscape was developed (Fig. 10.1).

The state and transition model for the successional vegetation states and the transitions derived from the hydrological disturbance originated for the dike construction (Fig. 10.1) present five vegetation states which correspond with the main savanna ecosystems described in chapter 5: seasonal savanna (SS), gallery forest (GF), hyperseasonal savanna (HS), semiseasonal savanna non saturated (SmS ns), and semiseasonal savanna water saturated (SmS ws).

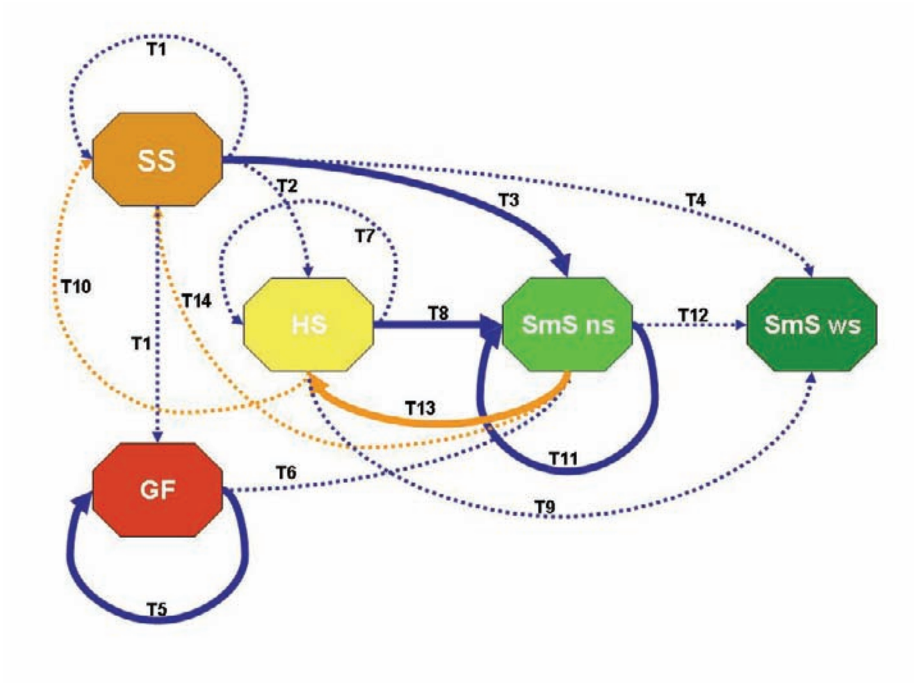

Figure 10.1 State and transitional model for the flooding savanna landscape derived from the hydrological change for dike construction. Each state represents the savanna ecosystem classes (octagonal figure): seasonal savanna (SS), gallery forest (GF), hyperseasonal savanna (HS), semiseasonal savanna non saturated (SmS ns), and semiseasonal savanna water saturated (SmS ws). Transitions (T1 to T14) are represented by arrows. Blue lines correspond with the change derived from flooded increase, and orange lines derived from flooded decrease. Unbroken lines represent the major changes and the broken lines the minor changes.

Based on the percentage of change between the units described in chapter 5, transitions between the states were established. Two types of transition can be described: the first transition type corresponds to an increase in the flooded condition by the accumulation of water up-stream of the dikes (blue arrows); the second type of transition corresponds to a decrease in the flooded condition derived from drainage in the surrounding areas near the downstream side of the dikes (orange arrows). In the model, the major transitions are represented by unbroken lines and the minor transitions by broken lines. The main transition corresponds to the change from seasonal and hyperseasonal savanna to semiseasonal savanna (T3 and T8), while gallery forest and semiseasonal savanna non-saturated states do not change when the disturbance occurs (T5 and T11). However, an important transition occurs from non-saturated semiseasonal savanna to the hyperseasonal savanna in areas down stream from dike where drainage takes place (T13).

The gallery forest state did not present any change in another directions, while the most affected sates were the seasonal and hyperseasonal savanna. However, due to the type of disturbance, which produced an immediate hydrological change, the transition from the seasonal savanna to the semiseasonal savanna through the hyperseasonal savanna is not observable with a high percentage of change (T2). Several minor self-transitions correspond with the displacement of the state to new areas, which are occupied by other ecosystems (state). The semiseasonal savanna water saturated is the state that increased its area by the contributions from other three savanna ecosystems (states) through the transitions T4, T9 and T12. This state does not present displacement or transition in direction to other state. The creation of this state and transition model will make clear the understanding and improve the species distribution model described from chapters 6 to 9.

10.5 Species-environment relationship in the flooding savanna

If the distribution of savanna ecosystems in the flooding savanna landscape is mainly influenced by the soil water availability, then how do plants respond to this factor? Are there any other factors like the soil nutrient availability and flood condition influencing the plant species distribution? In chapter 4 and 5, the replacement of savanna ecosystems was observed, however no new ecosystem was derived from this transformation. Then, the plants communities which integrate the savanna ecosystems are being displaced by the effect of the new hydrological condition.

In this plant community displacement, the species associated to the hyperseasonal savanna ecosystem, which without the influence of transformation is occupying the medium topographical position (bajío), are moving, in some cases, towards the high topographical position which are now flooded. Whereas, in the case of the semiseasonal savanna ecosystems, the species associated to this ecosystem move and occupy the new flooded space which could be, from the geomorphological point of view, a deep topographical position or a medium topographical position (bajío). The movement of the species either towards the lowest or the medium topographical position, the plant community of the semiseasonal savanna presents similar characteristics. This fact is a preliminary evidence that the soil water availability and the flooding condition have a remarkable influence on plants distribution and they are masking the nutrients influence.

Therefore, at the local scale, into the flooding savanna, the flooding condition could mask the nutrients availability and change the equilibrium between plant available moisture and plant available nutrients. If this assumption is accepted, then, how can plants be replaced in relation to the water availability change? To answer this question, in chapter 6 and 7 the ecological determinants of the plants species distribution were analyzed.

Multivariate gradient analysis, path analysis and Gaussian logistic regression techniques were used to determine and understand the species-environment relationship in a representative area of the flooding savanna in the El Frío Biological Station (Chapters 6 and 7). Thirty seven sites were sampled according to a stratified random sampling design were species list, frequency and cover were quantified. Furthermore, a large number of environmental variables associated with hydrological conditions, soil features, topographical, geomorphological characteristics, use, and remotely sensed and mapped variables, were determined for each sampled area.

We found a total of 213 plant species, the most frequent and cover recorded species were *Leersia hexandra* (81% of the plots), *Panicum laxum* (72%), *Ipomoea fistulosa* (52%), *Paspalum chaffanjonii* (48%), and *Mimosa pigra* (47%).

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. The responses follow unimodal patterns. 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 boundary.

No significant direct relations were found between physical soil properties and the ordination gradient. Path analysis revealed that the relative soil water content was significantly correlated to 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 determines mainly the distribution of species in the flooding savanna. 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). In the flooding savanna ecosystems, we found that the main factor, which determines species composition, was the relative soil water content related to the topographic position (Chapter 6).

Based on the previous determination of the main environmental factors associated to the plant species distribution, application of Generalized Linear Model (GLM) through the method of Gaussian logistic regression was used to study the response of the most abundant and frequent species. The model reflects the principal ecological parameters of the species distribution along the gradient: the tolerance, which is the gradient amplitude in where the species can develop, and the optimum, which is the gradient value where the species have the best fitness.

The Gaussian curves obtained for the main species shows the same pattern using frequency or cover data, and three clear groups of species are derived from the analysis. The first group contains those species which present a wide range of distribution (large tolerance) and high frequency and cover values as the optimum for each species. Representative species of this group are *P. laxum* and *L. hexandra*, which are the dominant species in the study area. Also this species represent the two large savanna ecosystems: *P. laxum* is associated to the hyperseasonal savanna and *L. hexandra* is associated to the semiseasonal savanna. It is clear that this two species with this characteristic distribution can adapt themselves to the transformation because of its wide tolerance which enables them to occupy new hydrological conditions when a transformation occurs, and also adapt themselves to the yearly variation of the flooded condition. In this case, the plant species distribution reveals the realized niche (Guisan and Thuiller, 2005) and this distribution reflects the response of the species to limiting or eco-physiology factors (soil water excess and deficit), disturbance factors (the fluctuations of the flooded conditions by natural or human causes), and the resources (soil water availability) (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005).

The second group of species contains those with a very narrow tolerance and high frequency and cover values in the optimum of each species. These species are very well adapted to the flood condition in a specific range of soil water content. Representative species of this group are *H. amplexicaulis* and *E. interstincta*. They present morphological characteristics in order to adapt to flooded condition as the aerenchyma for *E. interstincta* and the floating capacity of *H. amplexicaulis* in relation to the water level. The narrow distribution of these species with high frequency value at the optimum reflect a specialization of the species to the flooded condition. However these two species are separated along the gradient without any overlapping between them. The realized niche of theses species is mainly affected by eco-physiological factors (Guisan and Zimmermann, 2000; Guisan and Thuiller, 2005) like the soil water excess where the species are responding by the morphological adaptations.

The third group has species which have a large range of distribution on the gradient, but they are not dominant, presenting medium-low frequency and cover values in the species optimum. *I. fistulosa* and *P. chaffanjonii* are two representative species of this group, these species, as in the first group, present a wide distribution along the gradient with the possibility to adapt to soil water availability fluctuations by natural or human influence, however its dominance could be limited by competition with other species, and even the cattle grazing.

The two environmental variables analyzed are complementary, because they have a strong relationship to the hydrological dynamics of the flooding savanna, and the species distribution pattern is similar when using either of the variables. The final result is an **Ecological Model** where the main dominant species show a clear niche separation along the environmental gradients (Chapter 7).

10.6 Ecological – spatial models of species distribution

The species distribution models (SDMs) are based on the quantifying species – environment relationship, and they have derived from non-spatial statistical quantification of species-environment relationship to the spatially explicit statistical and empirical modeling of species distribution (Guisan and Thuiller, 2005). In this work, the formulation of the species distribution model followed three conceptualized phases: model formulation, model calibration, and model evaluation (Guisan and Zimmermann, 2000). To obtain the species distribution into spatially explicit empirical models, it was necessary to integrate two concepts developed in the present work: the **ecological model** or conceptual framework (Guisan and Zimmermann, 2000), which corresponds to the model formulation, describes the species distribution responses into environmental gradients of flooding savanna, and the determination of **spatial pattern** of the main environmental gradients. Chapter 4 and 5 present and analyze the landscape changes, making emphasis on the ecosystems replacement derived from the hydrological dynamic modifications. The hydrological dynamics is associated to the topographical variation studied with the Digital Elevation Model (DEM), which is used as the main spatial variable for the ecological – spatial models of species distribution. Chapters 6 and 7 described and analyzed the ecological responses and chapters 8 and 9 present the integration in ecological-spatial models which are representing the final model including the calibration and evaluation.

Based on precision measurement of altitude in the study area, and combining information derived from Radar imagery, we obtained a Digital Elevation Model (DEM). This DEM shows a clear separation of the study area by the dike, and a lot of banks and sinks distributed in the whole zone. The consequences of the dike construction for the land use are multiple. On the one hand, the inundation lasts longer, providing water when downstream areas are already dry and enabling the cattle to pasture these areas, but on the other hand the inundation can reach far upstream. This could cause a lack of available land for grazing at the peak of the wet season, as banks that formerly were used by the cattle in the wet season are now flooded. This disadvantage is reduced if the dikes have sluices as in other parts of the flooding savannas of Apure. Also the areas downstream can be used for grazing when the upstream areas are already flooded.

Comparison of the results of flood modeling on the basis of fieldwork data and the radar classification shows that these methods reach comparable values. The values derived from the climatic data (water balance method) also show that predicted volumes of water are roughly similar to the water estimated by the other methods for the period from the dry to the wet season (Chapter 4).

From the DEM and field data about relative soil water content, we obtained the pattern distribution of these two variables for the study area of El Frío Biological Station. Based on these spatial variables and the ecological responses of the main dominant species obtained in chapter 7, we determined and analyzed the spatial pattern distribution of dominant plant species in the flooding savanna (Chapter 8). Plant species distribution models show a clear niches separation along the gradient.

The species distribution models made possible to monitor the changes in species distribution derived from changes in the relative soil water content. The application of these models could be useful to predict new changes in the plant species composition if hydrological conditions are modified, and represents a technique for modeling in change scenarios. These models allow ecological aspects to be related to the spatial dimension through the integration of methodological approaches and conceptual models.

The species are responding to more than one environmental factor. In chapter 9, we summarized the concepts and methodological approach developed in the previous chapters, in order to obtain a species distribution model of dominant species based on multiple spatial environmental variables. The spatial environmental variables considered in the analysis were the RAM, SWRC, the landscape ecological maps derived from Landsat image interpretation, and the flood duration model derived from radar image interpretation. The inclusion of more spatial variables in the analysis increased the regression coefficient value, and the evaluation of model accuracy is better.

10.7 SDMs into the changing flooding savanna ecosystems

The ecological determinants of savanna and the effect of the human transformation on these determinants at different observation scales into the Llanos del Orinoco have been analyzed. Those observation scales include two of the main organization levels in ecology: the savanna **ecosystem** and the plant **species**. In the case of the ecosystem level, the relationship between the ecological processes as the phenological productivity of savanna and the determination of ecosystem types was carried out. In the case of the species level, models of species distribution were created based on the determination of the relationship between species and environmental factors. In both organization levels, the hydrological processes associated to environmental factors (geomorphology processes, climate seasonality, geology, human transformation) were the principal determinants for such spatial distribution. However, these two levels could be joined into one approach using the state and transitional model developed before. In this approach the spatial distribution of the representative flooding savanna species are the main component of the state and the two gradients associated to the species distribution are the transition directions of the model.

In a first step, a new version of the state and transitional model for flooding savanna is presented to describe the possible different states of the flooding savanna as a function of the soil water availability and topographic gradient (Figure 10.2). In this model the original savanna ecosystems derived from the natural conditions are situated in a line from the highest geomorphological position and low soil water availability to the lowest topographical position and permanently flooded condition. When the hydrological conditions are modified by the embankment, the main changes are represented in this model by the transition from the seasonal and hyperseasonal savanna to the semiseasonal savanna, but on the geomorphological unit associated to the original savanna ecosystem.

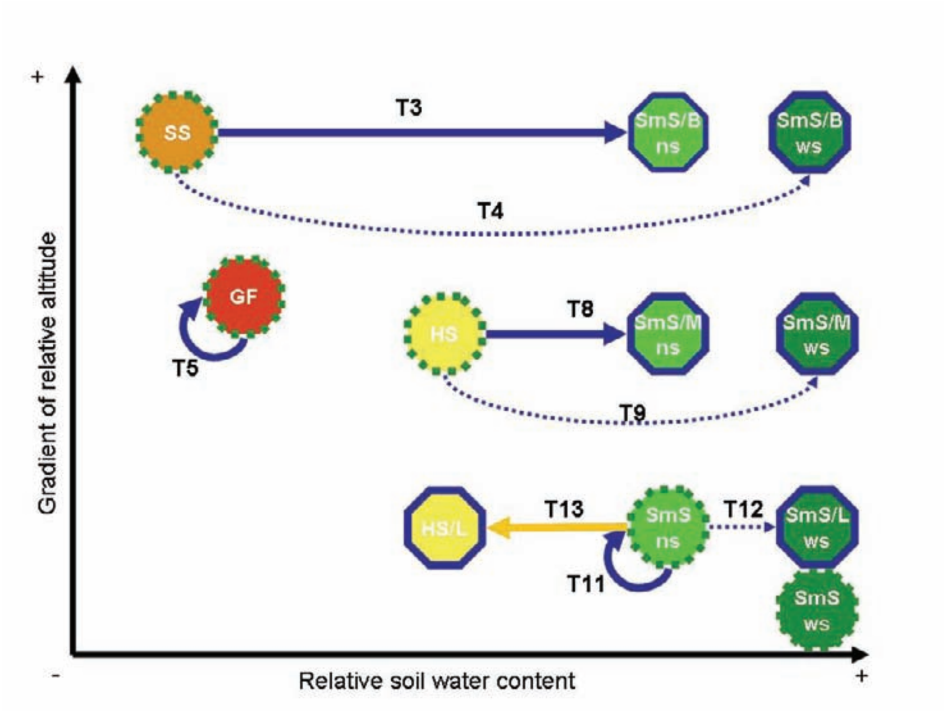

Figure 10.2 State and transitional model for the flooding savanna landscape derived from the hydrological change for dike construction including the hydrological and topographical gradients. The original states correspond with the savanna ecosystem classes (octagonal figure with the dashed border): seasonal savanna (SS), gallery forest (GF), hyperseasonal savanna (HS), semiseasonal savanna non saturated (SmS ns), and semiseasonal savanna water saturated (SmS ws). The new states derived from the change on different original geomorphological unit are indicated with the octagonal figure with the blue border. Transitions are represented by arrows, and the numbers correspond to the transitions described in figure 10.1. Blue lines correspond with the change derived from flooded increase, and orange lines derived from flooded decrease. Unbroken lines represent the major changes and broken lines the minor changes.

In the case of the seasonal savanna (SS), the transition (T3) occurred to the semiseasonal savanna on bank position (SmS/B ns), and from the hyperseasonal savanna (HS), the transition (T8) occurred to the semiseasonal savanna on medium topographical position (SmS/M ns). This means that in the new state the hydrological conditions determine the ecosystem function, but the soil properties and the geomorphological condition remain as in the initial state. However, the savanna ecosystem is responding to the hydrological dynamics as it was stated in the previous chapters, then the new state on previous topographical position (SmS/B ns and SmS/M ns) present, in relation to the ecosystem function, similar characteristics than the semiseasonal savanna ecosystem. The transitions T4, T9 and T12 are observed from the semiseasonal savanna water saturated (SmS ws) towards the semiseasonal savanna ecosystem on different topographical positions (SmS/B ws, SmS/M ns, and SmS/L ns), but the percentage of change in the transition is lower than for semiseasonal savanna non saturated (SmS ns).

One important transition (T13) occurred from the semiseasonal savanna non saturated (SmS ns) to the hyperseasonal savanna, but on low topographical position (HS/L). This state corresponds with areas down stream of dikes, where drainage occurred during the dry period.

The different states could be associated to the distribution of the main species using the information described in chapter 7. Based on table 7.2, in which the most frequency values for the principal species in each savanna ecosystem are presented, and considering the curve shapes and amplitude for frequency values of the main savanna species in the figure 7.2a and 7.2c, the frequency limits of the species to integrate the state were determined. In the case of the seasonal savanna, there is a dominance of *P. laxum*, and *P. chaffanjonii* present higher frequency values than *L. hexandra*. In the case of hyperseasonal savanna there is a codominance between *P. laxum* and *L. hexandra*; whereas the semiseasonal savanna the importance of *P. laxum* is low, and the codominance is between *L. hexandra* and *H. amplexicaulis*. With this information as criteria, the limits for frequency values of each state or savanna ecosystem were determined using the overlapping, crossing and optimum of the species frequency curves of figures 7.2a and 7.2b. The frequency limits for the state are summarized in table 10.1.

Table 10.1 Frequency limit values established for the main flooding savanna species distribution in each savanna ecosystem of the El Frío Biological Station derived from the analysis of figures 7.2a and 7.2b.

	Species name			
Ecosystem / State	**P. laxum**	**P. chaffanjonii**	**L. hexandra**	**H. amplexicaulis**
Seasonal savanna	> 0.59	> 0.30	< 0.49	NA
Hyperseasonal savanna	> 0.43	< 0.49	> 0.49	< 0.43
Semiseasonal savanna ns	< 0.50	NA	> 0.49	> 0.30
Semiseasonal savanna ws	NA	NA	< 0.60	> 0.20

The information of table 10.1 was used to combine the information derived from species distribution models described in chapters 8 and 9. The frequency single model for *P. chaffanjonii* and *H. amplexicaulis* and the multiple variables models for frequency data of *P. laxum* and *L. hexandra* were used. GIS-based model of the ecosystem distribution (Fig. 10.3) with the information from the species distribution models for frequency data was created combining the species models under the criteria explained before.

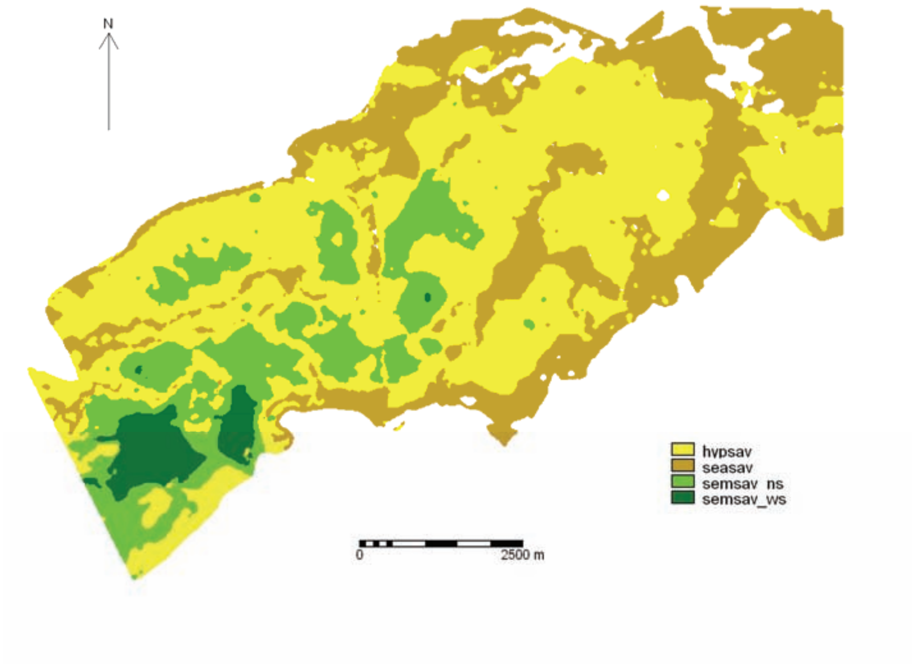

Figure 10.3 Spatial model of savanna ecosystem states derived from integration of spatial distribution models of the most important plant species for the flooding savanna landscape of El Frío Biological Station. Ecosystems: seasonal savanna (seasav), hyperseasonal savanna (hypsva), semiseasonal savnna non-saturated (semsav_ns) and semiseasonal savanna water saturated (semsav_ws).

This model of ecosystem distribution presents the distribution of the savanna ecosystem type based on the individual distribution of each plant species. In this model, the distribution of the savanna ecosystem shows a concordance with the landscape ecological map presented in figure 9.3b; however, the semiseasonal savanna ecosystem is underestimated in this model. On the other hand, the spatial patterns of the seasonal and hyperseasonal savanna present a good match with the pattern distribution in figure 9.3b. In both maps (Figures 9.3b and 10.3), the patterns distribution of the savanna ecosystem have a reasonable criteria and analysis to be considered valid, but both present some differences in the pattern distribution, especially about the location of the semiseasonal savanna respect to the dike.

The landscape ecological map of figure 9.3b could represent an intermediate pattern distribution, where the state for the semiseasonal savanna ecosystem has not reached its total area of the pattern distribution showed in figure 10.3. This assumption is based on two facts: the long period which ranges from the time the Landsat image was taken (1988) and the date of vegetation sample collection (1997), in which the flooded condition could change. The second fact is that the flooding conditions change from year to year and this depends on the rainfall and the management of the sluices in the dike.

The map derived from the remote sensing analysis represents not only the features of the vegetation, but also the flooded conditions through the reflection pattern, whereas the model derived from the species distribution represents the plant assemblages better as well as the responses to the ecological factors determining its distribution.

The model presented in figure 10.3 could be considered as the summary of the ecological responses of each plant species to the hydrological condition (figure 10.2). This model of state or savanna ecosystem shows the direction of the transition when the hydrological condition is transformed by the embankment.

10.8 General conclusion

The savanna ecological determinants were considered in this work through the description, analysis and modeling of ecological processes observed in Llanos del Orinoco at three integrated spatial scales, where landscape changes and transformations are evaluated under the Landscape Ecology approach. The main tools incorporated into the Landscape Ecology approach permit the complement and integration of ecological analysis, processes and responses with the environmental spatial pattern resultant from climate seasonality, remote sensing analysis and GIS-based models.

In savanna vegetation, climate and soil are mainly responsible for plant species distribution. Climate is the principal influential factor 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). In the Llanos del Orinoco savanna ecosystem, the availability of water is a variable dependent on the rainfall seasonality and drainage patterns. Whereas climate determines regional and continental patterns (Skidmore, 2002), the local soil features such as topography, parent material and age determine the drainage patterns.

At the regional scale and focused on the flooding savanna, the soil water availability is changed by the human influence. At the local scale, into the flooding savanna, the plant available moisture – plant available nutrient equilibrium could be addressed to mask the nutrients availability by the flooding condition.

The savanna ecosystem transformation derived from the dike construction can be conceptualized in a state and transition model. Through this state and transition model and based on the plants species distribution models, a new model of savanna ecosystems distribution was elaborated, integrating two different ecological level.

The application of these methodological approaches could be useful to analyze the changes in the savanna landscape into the Global Climatic Change and Global Change scenarios. Moreover, through these approaches we can establish bases for conservation and development planning in the savanna region.

The landscape transformation in the Llanos del Orinoco is mainly associated to the agriculture advance on the natural savannas; therefore the method applied in chapter 3 could allow monitoring the changes in the landscape through the analysis of the phenological pattern. Besides, Global Climatic Change and Global Change can be affect the pattern distribution of the environmental gradients in the savanna, specially for the flooding savanna, where the hydrological dynamic is the main factor driving the species distribution. The application of the methodological approaches presented in this work, which taking into account the ecological responses of the vegetation to the environmental factors, could be applied in changing scenarios, where the environmental factors are modified and the vegetation responses can be simulated using the knowledge of the ecological processes determined in this work.

The GIS-based methodological approach and the previous determination of the ecological processes associated to the environmental factors can be used to determine key areas for habitat conservation and predict the possible repercussions by the increment of the agriculture use and landscape transformation.

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12. ANNEXES

Annex 7.1

GAU01 Estimated values for Gaussian logit model of the most frequent species according to presence-absence data of El Frío Biological Station using relative altitude derived from DEM (REALDEM) and intensity of the cattle grazing (INTGRA) as environmental factors. 57 sites and 6 species are considered, only the significant analyses are presented. Freedom degree 54.

Term	Estimated values for REALDEM				
	L. hexandra	P. laxum	P. chaffanjonii	H. amplexicaulis	E. interstincta
b_0	3.329	3.741	-8.62	12.42	33.64
SE b_0	0.33563	0.29477	0.26495	0.29477	0.36324
b_1	1.177	-6.684	6.573	-10.61	-32.56
SE b_1	10.069	7.9521	9.2919	15.089	54.746
b_2	-1.119	2.847	-0.9754	1.576	6.25
SE b_2	2.6263	2.4842	2.5231	4.3861	17.404
Deviance	47.54	58.35	66.9	46.23	19.58
Optimum of the specie μ	0.5254		3.369		
Tolerance of the specie t	0.668		0.716		
P value	0.0125	0.0183	0.0112	0.0000	0.0000

Term	Estimated values for INTGRA			
	P. laxum	P. chaffanjonii	H. amplexicaulis	I. fistulosa
b_0	0.4887	-0.4772	-0.4887	-0.247
SE b_0	0.29477	0.26495	0.29477	0.26527
b_1	0.3218	-1.373	-0.3218	2.692
SE b_1	1.3934	1.4776	1.3934	1.0379
b_2	0.3058	1.129	-0.3058	-1.012
SE b_2	0.69926	0.77192	0.69926	0.40017
Deviance	61.29	66.27	61.29	70.84
Optimum of the specie μ			0.5262	
Tolerance of the specie t			1.28	
P value	0.0689	0.0087	0.0689	0.0552

GAU02 Estimated values for Gaussian logit model of the most frequent species according to presence-absence data of El Frío Biological Station using relative soil water content (SWRC) and intensity of the cattle grazing (INTGRA) as environmental factors. 37 sites and 6 species are considered, only the significance analyses are presented. Freedom degree 34.

Term	**Estimated values for SWRC**					
	L. hexandra	P. laxum	P. chaffanjonii	H. amplexicaulis	E. interstincta	I. fistulosa
b_0	-4.582	4.746	-0.01426	-17.15	-2.00 EXP 6	-4.922
SE b_0	0.37019	0.446	0.33184	0.39935	0.72699	0.33184
b_1	0.5725	-0.03083	0.7007	1.149	54.69	0.5475
SE b_1	0.29255	0.5951	0.88131	1.24	3.79 EXP -7	0.26223
b_2	-0.01124	-0.003804	-0.03812	-0.01807	1816	-0.0116
SE b_2	0.006959	0.012545	0.031014	0.023807	0.000023	0.005973
Deviance	34.11	19.39	19.28	19.17	8.997	44.05
Optimum of the specie μ	25.47	4.052	9.191	31.79		23.61
Tolerance of the specie t	6.67	11.5	3.62	5.26		6.56
P value	0.0182	0.0001	0.0000	0.0000	0.0001	0.0942

Term	*Estimated values for INTGRA*
	P. chaffanjonii
b_0	-0.08701
SE b_0	0.33184
b_1	-3.733
SE b_1	2.4591
b_2	3.126
SE b_2	1.8573
Deviance	39.67
Optimum of the specie μ	
Tolerance of the specie t	
P value	0.0159

Annex 7.2

GAU03 Estimated values for Gaussian logit model of the most frequent species according to frequency data of El Frío Biological Station using Relative altitude derived from DEM (REALDEM) and intensity of the cattle grazing (INTGRA) as environmental factors. 57 sites and 6 species are considered, only the significance analyses are presented. Freedom degree 54.

Term	**Estimated values for REALDEM**					
	L. hexandra	P. laxum	P. chaffanjonii	H. amplexicaulis	E. interstincta	I. fistulosa
b_0	-1.792	-5.594	-8.819	-0.6988	-3.534	-19.98
SE b_0	0.15598	0.16644	0.24618	0.30289	0.44281	0.23905
b_1	2.634	4.637	6.603	2.42	8.207	21.36
SE b_1	3.5185	4.6954	7.8453	6.2229	12.631	12.3
b_2	-0.9909	-0.9754	-1.331	-1.812	-4845	-5.921
SE b_2	1.0345	1.2317	1.9999	2.1994	5.1377	3.42
Deviance	17.8	22.93	23.96	18.51	9.348	23.24
Optimum of the specie μ	1.329	2.377	2.48	0.668	0.847	1.803
Tolerance of the specie t	0.71	0.716	0.613	0.525	0.321	0.291
P value	0.0067	0.0064	0.0092	0.0000	0.0000	0.0037

Term	**Estimated values for INTGRA**		
	I. fistulosa	P. chaffanjonii	H. amplexicaulis
b_0	-1.416	-1.714	-1.323
SE b_0	0.23905	0.24618	0.30289
b_1	1.552	0.3558	-0.7398
SE b_1	0.82208	0.76111	1.4362
b_2	-0.6549	0.04633	0.003326
SE b_2	0.36858	0.25672	0.64416
Deviance	24.66	23.28	27.03
Optimum of the specie μ	1.185	-	-
Tolerance of the specie t	0.874	-	-
P value	0.0184	0.0042	0.0467

GAU04 Estimated values for Gaussian logit model of the most frequent species according to frequency data of El Frío Biological Station using Relative altitude derived from DEM (REALDEM) and intensity of the cattle grazing (INTGRA) as environmental factors. 37 sites and 6 species are considered, only the significance analyses are presented. Freedom degree 34.

Term	**Estimated values for SWRC**					
	P. laxum	E. interstincta	L. hexandra	I. fistulosa	P. chaffanjonii	H. amplexicaulis
b_0	-0.593	-306.7	-2.79	-4.383	-1.621	-35.04
SE b_0	0.19245	1.8257	0.20943	0.27951	0.28284	0.43853
b_1	0.09296	32.7	0.2092	0.3306	0.254	2.456
SE b_1	0.12214	1.45 exp -8	0.15559	0.21518	0.37398	3.8097
b_2	-0.00383	-0.717	-0.003903	-0.006916	-0.01343	-0.04272
SE b_2	0.003221	3.68 exp-10	0.0034162	0.0047243	0.01466	0.070152
Deviance	6.531	5.075	13.77	14.64	8.505	5.054
Optimum of the specie μ	12.14	22.81	26.8	23.9	9.452	28.75
Tolerance of the specie t	11.4	0.835	11.3	8.5	6.1	3.42
P value	0.0000	0.0000	0.0141	0.0400	0.0000	0.0000

Term	*Estimated values for INTGRA*		
	E. interstincta	P. chaffanjonii	H. amplexicaulis
b_0	-4.34	-1.527	-1.631
SE b_0	1.8257	0.28284	0.43853
b_1	-4.073	0.4917	1.125
SE b_1	15.768	0.87026	3.6325
b_2	0.03605	0.01002	-1.643
SE b_2	0.021724	0.29721	2.9088
Deviance	1.499	14.36	14.62
Optimum of the specie μ		24.54	0.3423
Tolerance of the specie t		7.06	0.552
P value	0.0518	0.0253	0.0558

Annex 7.3

GAU05 Estimated values for Gaussian logit model of more abundant species according to cover data of El Frío Biological Station using Relative altitude derived from DEM (REALDEM) and intensity of the cattle grazing (INTGRA) as environmental factors. 57 sites and 7 species are considered, only the significance analyses are presented. Freedom degree 54.

Term	**Estimated values for REALDEM**					
	P. laxum	L. hexandra	P. chaffanjonii	H. amplexicaulis	E. interstincta	I. fistulosa
b_0	-3.801	3.358	-9.666	-5.611	-7.168	-20.39
SE b_0	0.023467	0.025819	0.058981	0.083423	0.088302	0.13793
b_1	6.692	1.402	9.953	12.2	19.5	22.93
SE b_1	0.73452	0.51605	2.1729	2.7299	3.4634	7.3577
b_2	-1.458	-0.8991	-2.063	-4.889	-9.317	-6.325
SE b_2	0.1904	0.16165	0.54239	0.91156	1.4056	2.0409
Deviance	1740	1372	732	413.5	258.2	89.78
Optimum of the specie μ	2.295	0.7795	2.412	1.247	1.046	1.813
Tolerance of the specie t	0.586	0.746	0.492	0.32	0.232	0.281
P value	0.0073	0.0005	0.0148	0.0003	0.0000	0.0083

Term	**Estimated values for INTGRA**				
	P. chaffanjonii	H. amplexicaulis	E. interstincta	A. purpusii	I. fistulosa
b_0	0.3861	1.384	1.203	-2.174	-0.8375
SE b_0	0.058981	0.083423	0.088302	0.086257	0.13793
b_1	1.982	-2.302	-1.67	2.324	2.42
SE b_1	0.19099	0.64646	0.48299	0.48019	0.45741
b_2	-0.4379	0.4046	0.3537	-0.2264	-0.8379
SE b_2	0.061368	0.28844	0.19474	0.11988	0.19425
Deviance	619.7	461.1	538.4	217.4	76.26
Optimum of the specie μ	2.263			5.133	1.444
Tolerance of the specie t	1.07			1.49	0.772
P value	0.0002	0.0061	0.0803	0.0000	0.0001

GAU06 Estimated values for Gaussian logit model of the more abundant species according to cover data of El Frío Biological Station using relative soil water content (SWRC) and intensity of the cattle grazing (INTGRA) as environmental factors. 37 sites and 7 species are considered, only the significance analyses are presented. Freedom degree 34.

Term	*Estimated values for SWRC*				
	P. laxum	L. hexandra	P. chaffanjonii	A. purpusii	H. amplexicaulis
b_0	3.61	-4.349	-1.956	-6.704	-28.97
SE b_0	0.025571	0.040895	0.064577	0.15523	0.12549
b_1	0.09857	0.5929	0.7968	1.452	2.042
SE b_1	0.017581	0.05061	0.12338	0.46391	1.6827
b_2	-0.004871	-0.01067	-0.03413	-0.06652	-0.03338
SE b_2	0.00051017	0.0010191	0.0047812	0.01986	0.031031
Deviance	685.3	495.3	452.6	180.3	110.2
Optimum of the specie μ	10.12	27.78	11.67	10.91	30.58
Tolerance of the specie t	10.1	6.84	3.83	2.74	3.87
P value	0.0000	0.0000	0.0009	0.0076	0.0000

Term	*Estimated values for INTGRA*					
	L. hexandra	P. chaffanjonii	H. amplexicaulis	I. fistulosa	A. purpusii	E. interstincta
b_0	2.558	0.3938	0.9659	-0.6585	-4.808	-0.4545
SE b_0	0.040895	0.064577	0.12549	0.19281	0.15523	0.26171
b_1	2.503	2.39	-1.06	1.685	-1.668	-11.14
SE b_1	0.16448	0.21919	1.2975	0.64107	3.1101	30.673
b_2	-1.322	-0.5374	-0.5907	-0.6511	1.381	2.763
SE b_2	0.095407	0.06852	0.86956	0.2785	0.89469	11.463
Deviance	708.3	424.2	238.1	37.13	40.02	90.36
Optimum of the specie μ	0.9463	2.224	0.8969	1,294		
Tolerance of the specie t	0.615	0.965	0.92	0.876		
P value	0.0027	0.0003	0.0573	0.0493	0.0000	0.0881

Annex 9.1

Parameters estimated for the best Regressions coefficients obtained for multiple regressions of spatial variables RSWC, relative altitude model, Landscape Ecological Map and Flood Duration Model with presence/absence, frequency and cover data of *P. laxum* and *L. hexandra*. Description and definition of the parameters is made in the text. Reg_1 = *P. laxum* presence/absence data, 37 sites, 2 spatial variables; Reg_2 = *P. laxum* frequency data, 37 sites, 4 spatial variables; Reg_3 = *P. laxum* cover data, 57 sites, 4 spatial variables; Reg_4 = *L. hexandra* frequency data, 57 sites, 3 spatial variables; Reg_5 = *L. hexandra* cover data, 37 sites, 2 spatial variables.

Parameters	Reg_1	Reg_2	Reg_3	Reg_4	Reg_5
R	0.6434	0.7557	0.7077	0.64949864	0.76134075
R^2	0.4139	0.5711	0.50085	0.42184848	0.57963973
P	0.0015	0.0011	0.0062	0.0096	< 0.0001
Power	0.05: 0.99	0.05: 0.99	0.05: 0.99	0.05: 0.99	0.05: 0.99
a	23.9548	1.1104	862.6391	1.8928	206.4549
b	12.0663	13.1912	16.8246	18.1482	3.7544
c		-408111.5863	1.7140	0.4540	
d	256825.8108	3.5048	5.0251		
e		4.1855	1.8685	11.0120	5.1781
x_0	0.9773	10.4772	-7.0993	31.7946	27.0376
y_0		-147688.0515	-0.8213	1.5321	
z_0	9861.8052	2.6748	7.9781		
v_0		2.1943	1.3870	13.5451	-2.5339

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Researcher. Project: "Impacto de la intervención humana sobre la biodiversidad en cuencas de la vertiente norte de Los Andes venezolanos. BIOANDES – CONICIT. Coordinator: Dra. Michele Ataroff. 1999-2002.

Researcher. Project: "Estrategias agroforestales para la conservación de la biodiversidad y la recuperación de áreas degradadas en el sector norte de la Reserva Forestal Sipapo, Edo. Amazonas (SAF/Amazonas). CONICIT 97003188. Coordinator: Dr. Eduardo Escalante. 1999-2002.

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Experience as academic supervisor

Co-Supervisor: Assesment of the distribution of rare species in different habitats in the savannas of Venezuela. Jan Fehse. Grade Thesis of Biology, University of Amsterdam, The Netherlands. March-July 1995.

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With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 22 credits (= 32 ECTS = 22 weeks of activities)

Review of Literature (3 credits)
- Llanos del Orinoco, Venezuela (1995)
- Landscape ecology and spatial-ecological modeling (1998)

Writing of Project Proposal (3 credits)
- Ecology diversity and land use relationship in the Orinoco Savannas. Landscape ecological approach. ITC, Enschede, The Netherlands (1995)

Post-Graduate Courses (4 credits)
- Rural and land ecology survey (1993)
- Advances in NOAA and radar imagery interpretation and analysis (1996)

Deficiency, Refresh, Brush-up and General courses (6 credits)
- Remote sensing and GIS (1994)
- Field work module for landscape ecology (1994)
- Workshop on dendrochronology, ecology and environmental variability (2005)

PhD Discussion Groups (3 credits)
- Landscape ecology discussion group at Institute of Environmental and Ecology Sciences (ICAE), University of Los Andes, Venezuela (2003-2006)

PE&RC Annual Meetings, Seminars and Introduction Days (3 credits)
- Discussion meetings on radar interpretation for water monitoring. ITC (1996)
- Seminar on times series analysis of NOAA-NDVI imagery ITC (1996)
- Discussion meeting on landscape ecology. Department of Ecology, University Complutense, Madrid, Spain (2000)

International Symposia, Workshops and Conferences (9 credits)
- Encontro sobre sensoriamento remote aplicado no pantanal (1995)
- Workshop on planning INCO project on flooding savannas (1996)
- Workshop on flooding savannah. INCO project (1998)
- IV Venezuelan conference of ecology (2001)
- 17th Annual symposium of the IALE- US (2002)

- V Venezuelan conference of ecology (2003)
- VI Venezuelan conference of ecology (2005)

Laboratory Training and Working Visits (6 credits)
- Vegetation, agro-ecology, terrain and soil survey course (1993)
- Discussion and planning research on ecological bases of flooded tropical ecosystems (1998)
- Laboratory and working visits ITC, The Netherlands (2001)