THE ENVIRONMENTAL IMPACT OF FLOW REGULATION IN A TROPICAL DELTA.

The case of the Mánamo distributary in the Orinoco Delta, Venezuela

by

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Acknowledgments

Abstract

The regulation of the Mánamo river, one of the major Orinoco distributary channels, has instigated changes in the hydrological and sedimentological regimes of its channel and surrounding wetlands, covering one-third of the Delta area. The dam has altered the hydrodynamics of the Mánamo. While the average flow of its channel was reduced from 10% to 0.5% (200 m^3/s), of the annual discharge of the Orinoco River. The adjacent Macareo distributary, which is not regulated, discharges 11% (4,000 m^3/s) annually. During the seasonal high-water period, the water level in the Macareo rises approximately 7 m, while in the Mánamo is restricted to an periodic oscillation of 0.7 to 1.2 m due mainly to the tidal influence. This flow reduction not only affects the accretion and erosive processes of the banks, due to the decrease of transport of sediments, but also the composition, distribution and diversity of aquatic plants in the region, particularly along the river shores where the species diversity tend to be lower in the regulated river than in the unregulated. The change in the hydrologic dynamic has promoted broad floating meadows to develop in the upper reaches of the Mánamo river creating patches of rafting meadows. The cessation of the annual flooding has allowed an extensive intrusion of saline water from the sea, which only occur during the dry season. This has enabled halophytic species, particularly mangrove communities to expand their distribution upriver and has also forced the migration of part of the Delta inhabitants Creole and Indians, resulting in a modification of the distribution of the forest and marsh ecological communities due to the overexploitation of their subsistence resources. The particular characteristics of the region that have remained mostly undisturbed since the dam construction several decades ago, permit a comparison of 30 years period of the long-term physical and biological characteristics of a regulated (Mánamo) and unaltered (Macareo) distributary.

This thesis investigates these changes and propose a model of the river regulation effects on the ecosystem properties and an equilibrium model of the disturbance and the gain of a new steady state of the ecosystems compartments.

Summary of chapters

The thesis has been divided in chapters. Chapter 1 analyzes the different definitions, theories and methods applied through the thesis development.

Chapter 2 describes the location, main geographical characteristics of the region, the human population, the main studies undertaken, and the magnitude of the environmental impact suffered by the territory. The main divisions of the Delta are a) Upper, Middle and Lower and b) Eastern, Central and Western; then the general physiography, the climate, soils, vegetation and the effects of the dam construction on the physical and chemical characteristics of the river courses are examined.

Chapter 3 focuses on the analysis of the taxonomy of aquatic flora, herbaceous and hardwood communities the organisms more closely influenced by the hydrological changes. The emergent and floating communities, of macrophytes were studied in 23 sites across the entire Delta, including the lentic of the lagoons and marshes and the lotic habitats of streams. A collection of aquatic vascular plants was made and physical and chemical variables were measured. In addition the forest communities were also studied via a series of floristic and structural descriptions.

The principal results identified a total of 174 aquatic macrophyte species, more than 48% of which are new records for the Delta territory. The Canonical Correspondence Analysis used, divided the species and communities into two groups: lentic habitats with a greater species richness and the lotic habitats of the main river courses. It is demonstrated that the hydrological cycle in lagoons and river waters, determine a seasonal variation of the physio-chemical parameters as well as the species composition.

Chapter 4 analyzes the forest communities found in the Middle Delta. These formations have been altered by the anthropogenic influence of the Warao Indians, which were forced to migrate to the area due to the river regulation. The floristic composition, structure and species diversity were analyzed. The main results indicated that the swamp palm communities are the more intense forests used, while the swamp forests support the lower intervention. The characteristics of the forest types are discussed on the basis of the flooding tolerance and species composition and diversity. A species richness increase in the forest communities is discussed in confront to the flooding gradient.

Chapter 5 documents the resulting physico-chemical characteristics of the upper reaches of the Mánamo and the Macareo rivers, established by the water regulation of the former. The physical variables studied comprises the seasonal water level oscillation, current velocity and temperature, while the chemical variables included the dissolved ions content, acidity (pH), dissolved oxygen, and electric conductivity. The results showed no significant difference in the chemical variables of the upper section of the rivers but a clear contrast in the hydrological characteristics of both channels. However other studies demonstrate gradients of salinity along the middle and lower Mánamo.

Chapter 6 relates the aquatic meadows to the geomorphology of the banks. It focuses on the comparison of the floristic composition, species and coverage, within the free-floating and emergent meadows, with geomorphologic features along various stretches of the Mánamo and Macareo rivers. The accumulation of the aquatic plants reported after the damming, is also described as well as the role of changing salinity levels in the control of the dominant floating species. The research methodology covers the determination of topographical profiles and local sedimentary dynamics. The species diversity showed differences along each channel according to the morphology of the river banks. The unregulated river showed a higher diversity than the regulated course.

Chapter 7, focuses on the comparative biomass production of the two dominant species from the regulated Mánamo and the unregulated Macareo river, in order to understand the differences found in the cover and distribution of these species within the Delta region. The analysis was performed by sampling the two community-types throughout the annual hydrological cycle. The total biomass for *E. crassipes* showed higher values in the Mánamo river (mean 909.14 g m^2) than in the Macareo river (mean 661.03 g m^2). Also the leaf biomass production of *Eichhornia crassipes* and *Paspalum. repens* was higher in the Mánamo than in the Macareo river; due to the differing hydrological conditions of the river courses. The creation of a lentic environment in the Mánamo favoured the increased development of these plants. The high flow dynamic of the Macareo prevent the plants to reaching its maximum development.

The analysis distribution of the mangrove communities and the records of its recent history along the lower course of the Mánamo river, reported as consequence of the saline intrusion, is treated in chapter 8. This was evaluated by means of three study sites along the upper, middle and lower river course in a time longitudinal study. The changes in site geomorphology and vegetation were evaluated over three periods, from 1932 to 1992, using

aerial photographs and recent field surveys. Soil and plant samples were taken in the mangrove communities of two sites in a 100 m transects laid out from the shore toward the land. The ion content (Na^+, Cl^-, Mg^{2+}, K^+, and SO_4^{2-}) from the interstitial water and leaves was analysed.

An increase of 600% of halophytic communities (*Rhizophora mangle*) in the Lower Mánamo was observed in the periods after the river closure. The rate of this expansion was 7.8 ha year^{-1} compared to 1 ha year^{-1} prior to the regulation. In the Mánamo river, the depositional processes created new habitats (sand bars) for aquatic and terrestrial vegetation. In the middle and lower course the influence of the tides salinized the soil, enabling mangrove growth. This mainly occurred in the open areas or areas with sparse herbaceous vegetation. The ion content was higher in the site closest to the sea, and also higher in the subsoil compared with the topsoil.

In chapter 9, the distribution of the forest and herbaceous vegetation was studied, in the region of the Pedernales river (Middle Delta). This was analysed from 1930 to 1996, in search of the likely effects of the Mánamo impoundment on the plant communities. Aerial photographs and satellite imagery were used here as well.

The interpretation of the information from aerial photographs spanning a period of 60 years, showed important changes in the distribution and extension of the swamp forests and marshes in the region of the Pedernales river in the Middle Delta. The changes were correlated with internal migrations of Creole and Warao inhabitants. The salinization of the Mánamo river forced the Warao Indians to move south in search of fresh water, thus concentrating them in a reduced area, causing them to overexploit their natural resources.

Chapter 10, consists of a general discussion of the results of the previous chapters. The different wetlands found in the Delta region are discussed at a local and regional scale. A model of the impact of the river regulation is discussed in the basis of the change of the hydrologic regime on the physical and biotic compartments of the Delta area and in the properties of the wetland system. The species diversity and biomass trends are contrasted along salinity gradients of the new estuarine condition of the sub-basin. A model of the disturbances observed and the systems response is proposed.

The main conclusions of the study are the change of the fluvial regime to an estuarine regime:

-The main physical change reported was in the reduction of the seasonal water fluctuation to a tidal regime throughout the year.

-The riparian system suffered a series of successional changes tending to new conditions that include the substitution of meadow species, freshwater to halophyte species and herbaceous to forested communities (mangroves). The general tendency is toward the reduction of species diversity.

-The river regulation promoted forest dynamic processes to occur as a consequence of subsistence overexploitation of resources, modifying the distribution and coverage of the existing communities.

Chapter 1 Introduction

The purpose of this thesis is chiefly to investigate the ecological effects of the construction of a dam across the Mánamo river in the western section of the Orinoco delta in eastern Venezuela. The Orinoco river flows east from the Andes across the central plains of the llanos to discharge its waters through the distributaries of the delta into the tropical North Atlantic Ocean. An ecological comparison of two distributaries, that are locally called caños or canals, lies at the centre of the thesis. These are the Mánamo and the neighbouring Macareo. The Mánamo became a regulated river in 1965 when a barrage was constructed 38 km downstream from its division from the main Orinoco river at the apex of the delta. It flows mainly north to discharge into the Gulf of Paria. The second distributary lies further east towards the centre of the delta and has remained largely unaffected by the regulation of the Mánamo. For the purposes of this study, it may be regarded as being 'natural'.

This study attempts to understand the reasons for the differences in the ecology that may be found between the two river systems and their adjacent 'catchments'. Due to the low elevation of the area above mean sea level, such a study entails a careful analysis of changes to the wetland vegetation that may have occurred as a consequence of regulation. This involves changes to the vegetation most closely associated with the actual river such as the water meadows and floating rafts of vegetation (ch 3) and their biomass (ch 7). It also involves a study of the semi-permanent lagoon areas that are a feature of the inter-riverine or inter-canal areas, along with the surrounding forest margin vegetation along the river levées (ch 6). River regulation has impacted on the nature and distribution of certain distinct ecosystems such as the wetland forests (ch 4) and the mangrove (ch 8). In addition to these ecological impacts, changes in physico-chemical components have occurred and these are chiefly analysed in ch 5 with alteration to the morphology and the hydrological cycle of the basin areas being considered in ch 2. The synthesis of the vegetation dynamics may be seen within the classical framework of succession (ch 9) or placed within the context of other conceptual and impact models, including those that take some account of additional interactions with the human environment (ch 10).

1. 1 Background to the study

The analysis of the ecological and anthropogenic data, collected in the Orinoco Delta involves a number of cognate disciplines, such as limnology, geomorphology, geography, hydrology, plant systematic, plant physiology, and anthropology. These disciplines were used to produce the description and analysis of the wetlands environment. The methods employed to analyse them were, description of vegetation, biomass analysis, numerical

ordination techniques, and remote sensing techniques. The main ecological processes were discussed in terms of the theories of disturbance, succession, competition, and rehabilitation. The river regulations and environmental assessment are also defined as they determined the consequences of the environmental change (Fig. 1.1).

Environmental description

> Wetland definition
> Importance of wetlands
> Wetland conceptual model
> Aquatic plants definition and classification

Anthropogenic intervention

> River regulation effects
> Environmental assessment

Main Ecological processes

> Perturbation and disturbance
> Succession
> Competition
> Rehabilitation

Main study methodology

> Description of vegetation
> Biomass analysis
> Ordination techniques
> Remote sensors techniques

Fig. 1.1. Schematic outline of the chapters.

1.1.1 Wetland definition

Wetlands are areas of low lying land, submerged or periodically inundated by fresh or saline waters (Lincoln et al.,1982). A more precise definition has been proposed by Nilsen and Orcutt (1996): "a region that experiences saturated soil conditions at or above the root zone of most species during at least a month of the growing season". This definition is based on the time required for flooding conditions to affect significantly the metabolism and growth of plants.

Another definition adopted by almost 80 countries and based on conservation principles was proposed by the 'Ramsar Convention on Wetlands of International Importance' whose original statement originated from a desire to embrace all the wetland habitats of migratory water birds:

> "Wetlands are areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters"

(Ramsar Convention, 1971; Scott and Jones, 1995).

1.1.2 Wetland characterisation

Wetlands have a world-wide distribution and although they occupy only 6 %, a small proportion of the world's land surface (Maltby, 1991), they have a large importance in ecosystems processes. Wetland systems have been suggested as possessing many important ecosystem services such as water regulation, water supply, erosion control and sediment retention, soil formation, nutrient cycling, waste treatment, food production and animal refugia among others (Faber and Costanza, 1987; Armentano, 1993; Williams, 1993a; Roggeri, 1995; Nilsen and Orcutt, 1996).

Water related ecosystems can be grouped according to Roggeri (1995), using several criteria such as their hydrological regime, their soil type or vegetation structure. The first criteria may include categories such as, permanently flooded or temporarily flooded wetlands and temporary and permanently waterlogged wetlands. They may be defined as either morphological or ecological units as shown in Table 1.1.

Table 1.1. Wetland typology based in morphological and ecological units (Roggieri, 1995). The wetlands found in the Orinoco Delta are highlighted.

		Wetland typology	
Morphological units	Alluvial lowlands	Fringing floodplains	
		Inner deltas	
		Deltaic floodplains	**Coastal floodplains**
			Fresh- water tidal floodplains
Ecological units	Small valleys		
	Lake shores		
	Depressions		
	Periodically-flooded ecosystems	**Flooded forests**	
		Flooded grasslands	
		Seasonal shallow lakes	
	Swamps and marshes	**Marshes**	
		Herbaceous swamps	
		Peat swamps	
	Permanent Shallow lakes / water bodies	**Shallow lakes**	
	Other shallow water bodies	Oxbow lakes	
		Lagoons	

Delta territories usually constitute wetland environments due to their deposits of fluvial sediments that accumulate in coastal areas at a rate faster than that by which they can be removed by tidal and other currents. In this way low land is formed in close proximity to the sea. Soils are usually heavy impeding the drainage and allowing the presence of stagnant waters. The inland areas are normally flooded and show a vegetation type adapted to waterlogged and saline stresses. They constitute a significant dynamic environment where processes of geomorphic and vegetation succession are constantly changing the vegetation communities, particularly in the outer sections and along the river distributaries.

The vegetation of wetlands may be defined in terms of the regional and local variables such as climate, topography, and geology soils. In turn, these control the formation of the different wetland type - ecosystems, their geographical distribution, and biogeochemical properties (Bedford and Preston, 1988). Wetlands occur in a wide variety of physiographic settings which commonly are topographic depressions, where water might be expected to

accumulate, or lowlands adjacent to river or lakes where periodic overflows from the rivers, seasonal fluctuations, and tide effect, might be expected (Winter, 1988).

Carter (1986), stated that virtually every structural and functional characteristic of a wetland is directly or indirectly determined by hydrological patterns. Hydrology is in its turn controlled by the seasonal climatic cycles and the physiography and vegetation in the watershed. The wetland's hydrologic regimes mostly determine how often, how long and when a wetland soil is flooded and, thereby, influences vegetation and the rates of biogeochemical processes that transform nutrients and pollutants. As Mitsch and Gosselink (2000) stated, "hydrology acts as a limit or a stimulus to species richness, depending of the hydroperiod and physical energies". They also showed that although it is difficult to generalise, many wetlands that sustain long periods of flooding have lower species richness than do less frequently flooded areas.

Geomorphology strongly influences local patterns of water movement. Wetlands found in different geomorphological settings experience different hydro-periods which may be seen as periodic inputs of nutrients and organic matter. For instance, the flood pulse concept proposed by Junk *et al.* (1989) is produced by geomorphological and hydrological conditions. Geomorphological properties as well as soil properties determine the degree to which wetlands are open to transverse exchanges of water, nutrients and pollutants (Bedford and Preston, 1988), such as the river overflow communicating main channels and inner basins. For example if the land depressions receive groundwater discharge, or the ground water level is maintained high by the rivers influence, the surface runoff is added to the groundwater, which commonly results in a permanently flooded wetland (Winter, 1988).

1.1.3 Importance of wetlands

The importance of wetlands can conveniently be considered from the perspective of three hierarchical levels as has been suggested by Mitsch and Gosselink (2000):

1. At the level of human population, wetlands provide nutrients through hunting and fishing or plant products as well as timbering and non-timbering plant materials. For instance the forest products are of chief importance for the subsistence of Creole and Indian people, in the case of the Mánamo river;

2. At the level of ecosystem, wetlands provide services such as control and mitigation of flood, improvement of water quality and aesthetics, the appreciation of the natural ecosystem. Artificial reservoirs also resemble wetlands in some of their functions such as the inundation regulation, facilities for recreation and fishing activities; 3. At the global level,

they may play a significant role in the global cycles of nitrogen, sulphur, methane and carbon dioxide.

Freshwater ecosystems may provide benefits such as nutrient recycling as well as providing aesthetic and cultural benefits for humans (Costanza *et al.*, 1997). The range of goods and services may be divided into two categories:
1. The provision of direct market goods or services such as drinking water, transportation, electricity generation ; and
2. The provision of non-market goods or services which include things like biodiversity, support for terrestrial and estuarine ecosystems, habitats for plant and animal life, and the satisfaction that people derive from knowing that a lake ecosystem or 'the Delta Caños' exist (Wilson and Carpenter, 1999).

The economic valuation of natural ecosystems has become an important tool in the assessment of natural habitats. As Costanza *et al.* (1997) claimed, ecosystem services are not fully 'considered' in commercial markets or adequately quantified in terms comparable with economic services and manufactured capital, they are often given too little weight in policy decisions. The valuation of freshwater ecosystems, in the United States, has been calculated since the 1970's. These studies summarised by Wilson and Carpenter (1999), have used variations of three approaches for a quantitative assessment of economic value:
1. Travel cost methods; 2. Hedonic pricing methods, the valuation of the associated attributes of any good or service; and 3. Contingent valuation methods.

Costanza *et al.* (1997, 1998), have provided data for the current economic value of 17 ecosystems in 16 biomes based on published studies supported by their own calculations. The valuations techniques used in the studies covered by the authors are based, either directly or indirectly, on attempts to estimate the 'willingness-to-pay' of individuals for ecosystem services, such as aquatic sports or fishing. In the case of wetlands that sustain human populations, this must be an estimate of the monetary cost of the wetland products that are directly used or sold to purchase other services or goods. These authors concluded that estuaries and wetlands such as tidal marshes, mangroves communities, swamps and floodplains, are among the world's most valuable ecosystems.

1.1.4 Conceptual model
In practice, the task of the developing science of applied ecology is essentially that of predicting the effects of possible management decisions on plant and animal communities of the ecosystems. Model development was conceived as a way for organising ideas in a

rigorous, quantitative manner, finding out in a process what potentially important data are not available, identifying functional relationships that are insufficiently well understood, and finally, testing our understanding of 'how things work' (Collier et al., 1973).

As Jorgensen (1994) has pointed out, the first of such models was devised as a tool in environmental management using the Streeter-Phelps BOD-DO model, almost 70 years ago. Further development in modelling, took place during the 1970s, including ecological modelling including applications across a wide spectrum of research disciplines, including environmental management.

Complex models have been devised for multiple ecosystem and purposes, particularly in wetlands where they have been used to simulate the fate of environmental variables in river estuaries (Twilley et al., 1998); to simulate the influence of hydrologic regimes on the composition of shoreline plant species (Toner and Keddy, 1997); to assess mangrove forest development along gradients (Ronghua Chen and Twilley, 1998); to examine functions and processes of ecosystems (Bockstael et al., 1995); and to determine the runoff effects on patterns of estuarine community metabolism (Hopkinson Jr. et al., 1995). In summary models have been used in scientific research to reveal ecosystem properties and thereby achieve some results using ecosystem theory. However, we are still far from having the holistic models that we need to solve big problems (Jorgensen, 1994), such as global warming or biodiversity reduction.

Despite the initial optimism, these complex models possessed limitations. An example proposed by Rigler (1982) was that of the predictive modelling of the long-term abundance of species, and the species composition (Jorgensen, 1994) which has proved to have such limitation, even today. On the other hand, models that are more popular in fundamental theoretical ecology tend to be abstract, simple and generic. They do not offer, however, an alternative to the quantitative predictions generated by the complex models and are rarely used for applied purposes (Scheffer and Beets, 1994). Many examples of such "minimalist' models have been proposed (Odum, 1979,1983; Scheffer, 1990).

Landscape Modifications

Tides

Chemistry

Salinity
Nutrients
Sediments
Oxygen
Toxins

Freshwater Discharge

Timing
Velocity
Source

SUN

Productivity
Spatial Heterogeneity
Decomposition
Deposition

Plants/Microbes

Animals

Harvest
Diversity
Migration
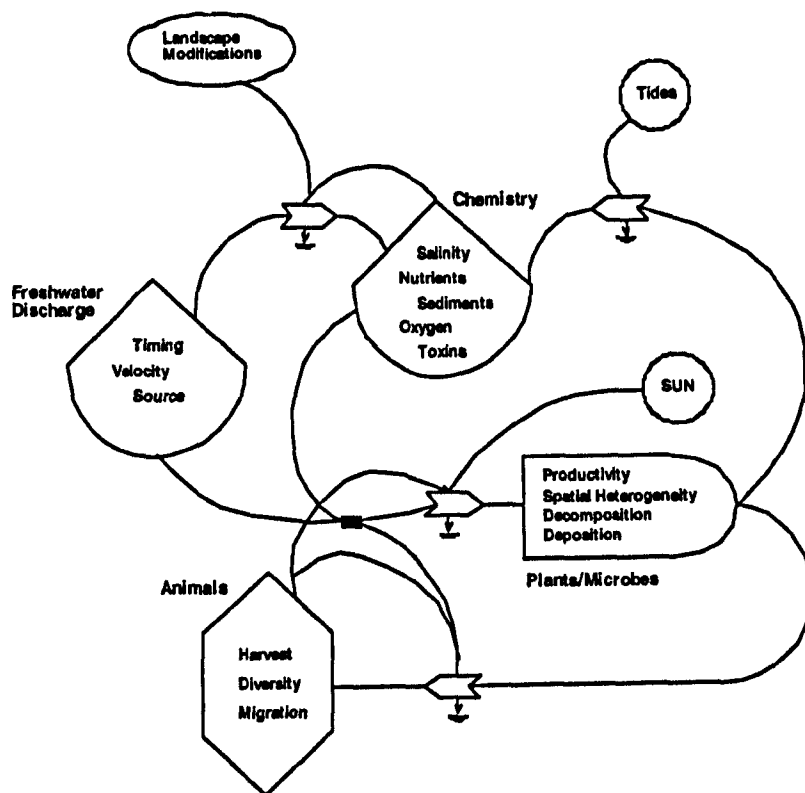
Fig 1.2. Wetland conceptual model of the direct and feedback influences with the source, timing, renewal rate, and velocity of freshwater discharge. The arrows denote the direction of influence as well as the variables involved. The bullet and diamond shapes denote primary and secondary biological functions, respectively. The tank symbol represents both physical and chemical storage within the model. Circles are variables outside the model that influence model structure and function (Adapted from Sklar and Browder, 1998).

A simple conceptual model (Fig. 1.2) was proposed by Sklar and Browder (1998) linking direct and feedback influences associated with the source, timing, renewal rate, and velocity of freshwater discharge to coastal lagoons wetlands and bays: The general influence of freshwater discharge on the three other components chemistry, upper trophic level and lower trophic level is the first aspect to notice in the model. Clearly, watersheds define surface and groundwater flows to estuaries, and these flows have a source, timing, and velocity that can be affected by human alterations in the environment which in turn influence wetland and open-water salinity patterns, nutrients, sediment fertility, bottom topography, dissolved oxygen and concentrations of pollutant. These chemicals, in turn, influence productivity, structure, and behaviour of coastal plant and animal populations (Bedford and Preston, 1988; Sklar and Browder, 1998).

1.1.5 Definition and classification of aquatic plants

Wetlands contain a large proportion of aquatic plants. However there is a general misunderstanding about the nature of aquatic plants, because, due to morphological and physiological adaptations, they may grow in a variety of habitats associated with water bodies such as submerged, floating and rooted to the substrate. However they are also encountered in habitats that do not always have the appearance of water bodies, such as muddy soils, waterlogged soils or even sand or rocky substrates -for example a granite formation may provide a depression where water is retained and aquatic plants develop, some times in elevated position.

There have been many attempts to classify plants according to their life-form; none of these classifications proposed by Sculthorpe (1967) and Hutchinson (1975) have gained widespread acceptance because they contain too many categories, with the consequence that many plants overstep the limits of the categories during their normal development. An example is that of the species *Limnobium laevigatum* which may have an erect habit -mud-phase- when growing in mud soils, and a smaller habit -hydro-phase- with floating leaves when growing in flooded habitats. This variability, particularly noticeable among species growing in habitats with variable hydrologic regimes, such as the Orinoco Delta, makes the identification of macrophytes particularly difficult. The collection of the specimen is usually required for further analysis and comparisons with herbarium vouchers.

According to Cook (1990) vascular aquatic plants as studied in this thesis are interpreted as all Pteridophytina (ferns and ferns allies) and Spermatophytina (seed-bearing plants) whose photosynthetically active parts are permanently or, at least, for several months each year submerged in water or float on the surface of water.

Cook developed the following classification:
1. *Hydrophytes*: plants physiologically bound to water, at least part of the generative cycle takes place in or on the surface of water.
2. *Submerged*: all photosynthetic parts submerged, assumed to be bottom-rooted unless.
3. *Free-swimming*: planktonic, occupying the zone between the bottom and the lower surface of the water (contrast to free-floating).
4. *Haptophytes*: attached to but not penetrating the substrate.
5. *Emergent*: some photosynthetic parts in contact with air, assumed to be bottom-rooted with assimilating parts in air unless.
6. *Free-floating*: floating on the surface, not attached to the substrate.
7. *Floating*: leaves or steams floating but attached to the substrate.

8. *Helophytes*: essentially terrestrial plants whose photosynthetically active parts tolerate long periods submerged or floating.

Fig.1.3 shows the different types of plants found in the Delta wetlands according to the classification of Cook (1990) that has been adopted in this study.

A functional definition, based on flooding tolerance, has been proposed by Nilsen and Orcutt (1996) for plants found in wetlands systems: plants with any mechanism to compensate for flooded conditions whether anatomical, behavioural or physiological are termed 'hydrophyte'. In this sense, these authors distinguish two types of hydrophyte:

1. The 'obligate hydrophyte' which is a plant that must live under flooded conditions to grow and complete its life cycle; and

2. The 'facultative hydrophyte' which is a species that can compensate for flooded conditions but does not require them for their optimal growth and reproduction.

Obligate hydrophytes include most free-floating and submerged plants in river courses, lagoons and permanently flooded marshes and swamps. In contrast emergent species growing in banks and levees of rivers, ponds and temporarily flooded marshes tend to be facultative hydrophytes.
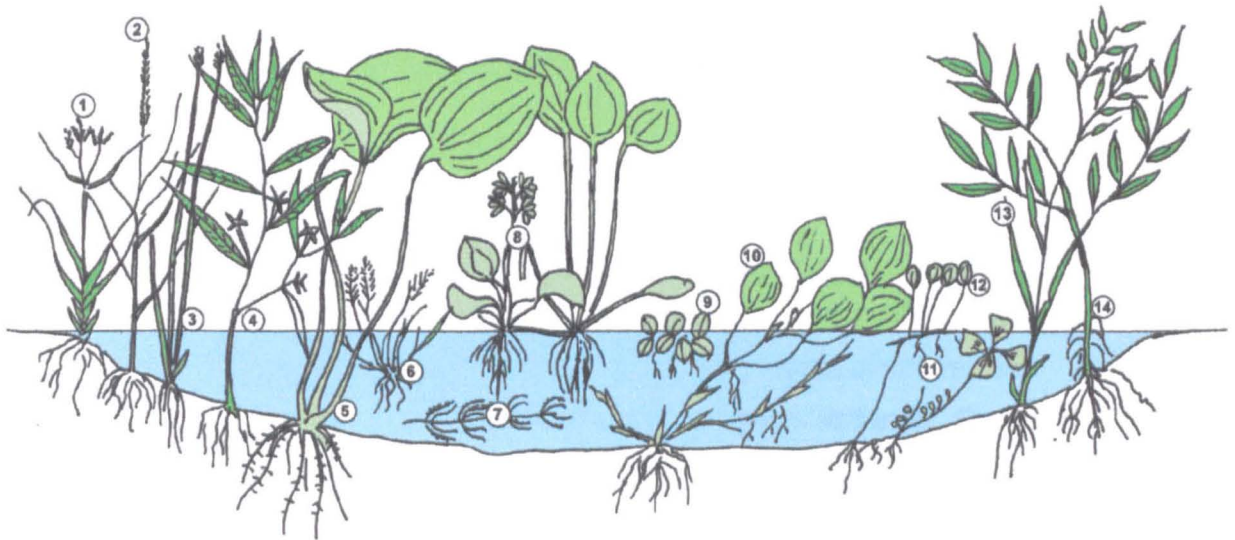
Fig. 1.3. Schematic profile of a typical water body. Plant clasification according to Cook (1990)

1. *Cyperus sp* (H)
2. *Typha dominguensis* (E)
3. *Eleocharis interstincta* (E)
4. *Ludwigia octovalvis* (E)
5. *Limnocharis flava* (E)
6. *Luziola brasiliana* (Ff)
7. *Ceratophyllum demersum* (Fs)
8. *Eichhornia crassipes* (Ff)
9. *Salvinia auriculata* (Ff)
10. *Eichhornia azurea* (F)
11. *Marsilea polycarpa* (F)
12. *Limnobium laevigatum* (F-E)
13. *Oriza rufipogon* (E)
14. *Shenoclea zeilanica* (E)

Ff= Free floating; Fs=Free swimming; H=Hydrophyte; E=Emergent; F= Floating

(Adapted from Velásquez, 1994).

1.1.6 River regulation effects

The project to regulate the Mánamo river and its basin was proposed in order to encourage the development of the western area of the Delta region. The overview assessment showed large tracts of land capable of a high economic productivity that could be realised if the greatest perceived barrier to production that of annual flooding, could be removed (CVG, 1967). Since ancient times people have managed the river courses in order to improve living conditions. Activities such as drainage of land for agriculture practices, regulation of rivers to avoid flooding and the installation of irrigation programs are the most common benefits achieved through river regulation (Petts and Amoros, 1996).

Human actions such as channelization, dredging, groundwater withdrawal, waste management, dam construction, agriculture, mining, and deforestation can alter the timing, volume, and chemistry of freshwater inflows. Of these, dam constructions, channelization and deforestation are likely to have the greatest impact (Hopkinson Jr. *et al.*, 1995). Flood control is considered one of the major disturbances because of the high degree of interrelation between the river course, the upriver watershed and the downstream wetlands. Consequently such disturbance usually produces a sequence of responses that envelop all the related components -from the abiotic features such as landforms, to the biotic such as the vegetation and fauna -and ultimately, the human inhabitants (Roggeri, 1995).

The impacts on rivers and riparian systems downstream from dams have been summarised by Bravard and Petts (1996):

1. Breakdown of longitudinal connectivity (flow of materials and energy along river course or among the river course and its lateral systems) : This impact not only creates a barrier to fish migration but influences their migrating behaviour by changing the flow and water quality regimes.

2. Change in the hydrological regimes: The biological components of running water systems are adapted to the natural fluctuation in unregulated flows.

3. Changes in water thermal regimes and water quality: The flowing waters suffer several physico-chemical changes when slowed down and influenced by decomposing vegetation.

4. Geomorphologic readjustments and transformation of habitats: The geometry of the bed of a river is adjusted to the set of variables comprising the flow and the sediment load.

5. Impacts on aquatic fauna: Impacts of habitat changes are complex but in general river modifications reduce species diversity and increase the abundance of benthos.

6. Impacts on vegetation: The regulation of flow and the reduction in the frequency of flooding causes a general growth of vegetation in the main channel.

One of the most notable dam impact reports was that which investigated the Aswan High Dam (Collier *et al.*, 1973). The dam completed in 1968 was intended, at a single stroke, to modernise the agriculture and encourage the industrialisation of the region. Those were exactly the same reasons for the construction of the Mánamo dam, and as it will be seen in this study, most of the consequences have also been the same.

The specific problems occurring in the area down river of the Aswan dam results primarily from the effects of the dam on the behaviour of the river, the nutrient and silt supply. These may be summarised as:

1. In canals of irrigated areas there is no longer silt deposition during the flood period. A major requirement for use of artificial fertilisers on irrigated land is consequently developing. This need is not paralleled by the increased use of fertilizer, so that the quantity and quality of the harvested crops have been declining in many such affected areas.
2. The flood waters formerly acted to 'flush' the soils of salts, and large areas of irrigated land are experiencing increases in salinity.
3. Finally, the expansion of canal irrigation has increased the incidence of several diseases. In a wider context, the dam influenced negatively the fish harvest, related to the salinity variations in a 600 hundred mile stretch along the coast, because of modified water salinity.

It is interesting to note that in another Delta region, the discharge reduction of the Gorai River, in Bangladesh, induced accelerated sedimentation and increased salinity affecting the agricultural production, the degeneration of freshwater plants, the retrogression of forest types and slowing of the productivity. The quality of the drinking water declined, which probably lead to an increase in diarrhoeal diseases (Mirza Qader, 1998).

The construction of dams throughout South America which affect 5% of its river flow (Bravard and Petts, 1996), increased rapidly during the last three decades. Since 1970 the number of large dams has increased by an average of two new dams every three years (Petts, 1990). Several authors have pointed out the effects of river regulation in South America (Junk and Nunes de Mello, 1987; Bonetto *et al.*, 1988; Neiff, 1996).

Among those examples is worth mentioning the case of the Brazilian Balbina Dam (Fearnside, 1989). The building of this dam shows that the environmental lessons learnt from the impact of the Aswan Dam 20 years ago, were not heeded. In the Balbina project the main biological impact has been on the forest. As the forest vegetation was not removed, the anoxic water condition generated in the waters is likely to cause a deep impact on the fish fauna both

above and below the dam (Fearnside, 1989). In more than one third of the surface the water column will be less than 4 m deep, the very shallow backwaters can be expected to develop a massive emergent and floating vegetation which will lead to significant losses of stored water by evaporation and transpiration.

The negative influence on the social point of view was also very important. The flooding of part of the Waimiri-Atroari tribe's reserve, the Indians which occupied the region since ancient times is the most dramatic of the reservoir's non-monetary costs. In fact as occurred in the Mánamo case, the area flooded caused the disappearance of two villages of the indigenous inhabitants and forced many more to change their habitual life style.

1.1.7 Environmental assessment

The concepts of environmental assessment are closely linked to the concepts of perturbation, disturbance and their consequences, which are discussed in the study (see chapter 10).

As indicated the regulation of the Mánamo river was projected and undertaken in the 1960s and constituted one of the two huge projects of water impoundment realized in the country - the Gury Dam, by 1965 one of the major dams built world-wide, was under construction. At that time the modern concepts of environmental assessment impact were still not common and was therefore not incorporated into the development phases of the project.

Environmental impact assessment (Erickson, 1994), is the process of identifying and evaluating the consequences of human actions on the environment and, when appropriate, mitigating those consequences. These may be described as:
1. Direct impacts, which are changes in environmental components and processes that result immediately from a project-related activity or action.
2. Indirect impacts (sometimes called secondary impacts) which are changes in environment components and dynamics that are consequences of direct impacts. Whereas direct impacts are environmental changes immediately linked to project activities or actions, indirect impacts result from the varied interactions of direct impacts physical, social and environmental components, processes, and conditions that are or may become dynamically linked to those impacts.

In any impact assessment, indirect impacts are likely to be far more numerous than direct impacts and typically account for most of the assessment effort. Cumulative impacts are the

aggregates in direct and indirect impacts resulting from two or more projects in the same area or region (Gosselink *et al.*, 1990; Erickson, 1994).

A similar definition was proposed by Roggeri (1995), who uses the term 'effect' - instead of impact - to include the physical, biological and socio-economic modifications caused by an intervention to the environment. The balance between its beneficial and detrimental effect is defined as the impact of the intervention. The various effects of an intervention can be divided into four categories:

1. Direct effect can be observed during or after the project implementation;
2. Indirect effects are consequences of the direct effects;
3. Secondary effects are the result of projects 'induced' by the original project implemented; and
4. Cumulative effects that are the interacting result of different intervention.

1.1.8 Perturbation and disturbance

The concept of environmental impact should be linked to that of disturbance and rehabilitation. Perturbation and disturbance have been commonly used in a similar manner to describe an unusual change in the properties of communities or ecosystems. These concepts will be linked to the particular responses of the regulated system, in particular the species biomass and diversity.

According to Odum *et al.* (1979), ecological perturbation may be considered as "any deviation or displacement from the nominal state" in structure or function at any level of organisation in the system. The nominal state is the normal operating range, including expected variance. In practice, an ecosystem would be considered to be perturbed if a significant deviation from the nominal (generally some designated control level) has occurred. The authors also pointed out that, in field studies, it is necessary to identify and monitor a nominal system as well as a perturbed system.

A more practical definition has been given by Huston (1994) for 'disturbance'. It is based on the mortality of organisms, and consists in any process or condition external to the natural physiology of living organisms that results in the sudden mortality of biomass in a community on a time scale significantly shorter - several orders of magnitude faster- than that of the accumulation of biomass. Huston distinguished between perturbation and disturbance, where perturbation is a more general term than disturbance, perturbation referring to the displacement of some property of a community or ecosystem, such as the total biomass, reproductive rate or nutrient influx, away from its typical value, which is generally considered

to represent an equilibrium level. Perturbation may be seen as the displacement of one species by others and disturbance as the reduction in biodiversity or in vegetation cover.

In perturbation experiments undertaken in community ecology, Bender *et al.* (1984), distinguished two quite different kinds of perturbations. A 'pulse' perturbation which is a relatively instantaneous alteration of species number, after which the system 'relaxes' back to its previous equilibrium state. A 'press' perturbation which is a sustained alteration of species densities and is maintained until the unperturbed species reach a new equilibrium. These points of view relate the time of the perturbation with its effects. More longer and more severe the perturbation is, the more permanent are its effects.

Glenn-Lewin and Van der Maarel (1992) described three dimensions that determine the dynamic of disturbance:
1. Extent (spatial scale), for instance the processes that follow the felling of one tree in a forest or the fire that destroys entire forest.
2. Return time of a certain disturbance effect.
3. Magnitude, for instance the effect of surface fires against crown fires.

1.1.9 Rehabilitation

The rehabilitation of the Mánamo river and its sub-basin is discussed in some detail in chapter 10 whilst the viability of a partial restoration of the seasonal river regime along with partial recovery of the original biotic and abiotic conditions are investigated.

Gore and Shields (1995) pointed out that the logical goal for developed river systems is the rehabilitation, that is the recovery of some of their ecological functions and values. As Petts and Amoros (1996) stated, in most cases management cannot restore pristine rivers, but the objective is the rehabilitation in order to enhance the ecological diversity of the remaining river corridor.

The scientific premises for river rehabilitation are based on the need to develop models to predict the ecological impacts of human activities, including rehabilitation measures. This requires integration of knowledge from hydrology, geomorphology and ecology, which must be fully integrated to develop applicable models of ecosystem, habitat, community and species responses. The investigation may be undertaken at three levels:
1. *Functional* studies which seek to explain the spatial distribution and interdependence between species, communities and habitat patches.
2. *Historical* and

3. *Palaeoenvironmental* studies, which seek to understand the ways that species, communities and habitats change in response to human impacts and climate change. The objective is to establish the former 'natural' characteristics of the fluvial hydrosystems.

Further insight has been provided into this issue of rehabilitation through the seminal work of Toth *et al*, (1998). More than 20 years of experimental studies have demonstrated the restoration potential and limitations of hydrologic adjustments in the channelised Kissimeee river (Florida US). These authors stressed that managed flooding regimes have been successful at reestablishing wetland vegetation communities and enhancing some associated functional values, including secondary production and faunal utilisation. However deeply degraded ecosystems are not easily rehabilitated.

As Rapport and Whitford (1999) have stated in a study of three disturbed systems, the ecosystems do not 'bounce back' once stress loads are lessened, even with an 'assist' from heroic efforts to restructure the system and create an artificial habitat. The findings of these authors point to three main reasons for the lack of success in such rehabilitation:
1. Damaged systems become more vulnerable to invasion from opportunistic species, which hinder, if not completely block, the re-establishment of the original biotic communities.
2. Disturbances to substrates (such as the soils and sediments of the upper Mánamo), may severely limit the possibilities for re-establishing highly developed biotic communities, which depend on multiple environmental variables and stable substrates.
3. The disruption to nutrient cycling may alter the entire character of the ecosystem, making a return to initial conditions exceedingly difficult to achieve.

1.1.10 Succession and competition
The river impoundment constitutes a large perturbation of a natural system, that has instigated a series of changes in the species composition of the affected communities. The changes that occur, are successional processes because they are marked by a series of stages, which are summarised below. They will be discussed at various points throughout the study and in particular in chapter 10.

Succession in this context, therefore refers to the changes observed in an ecological community following a perturbation that opens up a relatively new habitat (Connell and Slatyer, 1977).

Clements (1904,1916, cited in Begon *et al.*, 1990) proposed that from an initial stage the vegetation grows and matures through a series of seral stages until it reach a state of relatively stable equilibrium in balance with the predominant climate (climatic climax).

Clements defined a series of processes that drive succession:
1. Nudation, the production of an area of bare ground by natural or artificial means (disturbances), from which starts the succession; 2. Migration: the movement of an organism or group from one habitat or location to another, in this case a bare ground; 3. Ecesis, the pioneer stage of dispersal to a new habitat; 4. Competition, the simultaneous demand by two or more organisms or species for an essential common resource that is actually or potentially in limited supply; 5. Reaction, the organisms modification of the habitat that controls the relative ability of the species to establish and survive; 6. Stabilisation: The development of a stable condition of climax.
These processes are still considered valid to the analysis of succession (Picket *et al.*, 1987).

Connell and Slatyer (1977) proposed three theoretical models to explain changes in the composition of communities, the 'facilitation model', the 'tolerance model' and the 'inhibition model'. In all models the earlier species cannot invade and grow when the site is fully occupied by their own or later species. However, models differ in the way later species become established after their propagules arrive. In the facilitation model, the later ones become established and grow only after early ones have suitably modified the conditions. In the tolerance model, later species are successful whether earlier species have preceded them or not; they can become established and grow to maturity in the presence of other species because they can grow at lower levels of resources than earlier species. In these two models the early species are substituted by the late species throug competition. In the inhibition model, later species cannot grow to maturity in the presence of earlier ones. Early species may disappear due to local disturbances such as physical extremes or natural enemies. These models have been criticised because they are not easily distinguishable one from the other and all three might well be important at the same time during a particular successional sequence (Peet, 1992).

More recently Huston and Smith (1987), Huston (1994) criticised the prior succession models arguing that they aggregate many components of competitive ability into a single parameter or environmental condition, usually light or a soil nutrient as nitrogen. They proposed an individual-based model of succession and established a methodology for the study of succession that involves three essential features:
1. The birth, growth, and death of each individual is followed through time.

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2. Each individual is assigned species-specific life history traits of maximum size (height and diameter) maximum age, maximum growth rate, maximum rate of sapling establishment, and shade tolerance.

3. Availability and competition for light are modelled explicitly by calculating the total leaf area above each individual plant and then altering each individual's growth and mortality by its degree of shade tolerance and light availability.

Within fluvial hydrosystems, Amoros and Wade (1996) have listed the following changes or stages in a succession:

1. The herbaceous pioneer stage: The establishment of herbaceous species creates a physical environment suitable for the germination of woody species.

2. The bush and scrub stage: Woody plants with flooding tolerance and generally well adapted to the disturbances caused by river dynamics become established.

3. Tree stage: This stage is marked by the growing of tree species with flood tolerance which cause the raising of the soil surface and the germination of non flood tolerant species.4. The rate of succession: The rate of succession depends on the dynamics of the river. When the overall functioning of the hydrosystem remains stable the life of each stage (seral communities) is prolonged.

5. Complicating the structure of the communities: The establishment of woody species is accompanied by the development of many herbaceous and woody creepers increasing the community heterogeneity.

6. Increase in overall biomass: The great productivity of riparian ecosystems is reflected in a great increase of overall biomass during succession.

The two phases associated with succession are the primary and secondary successions. Primary succession is the formation process of a community that begins on substrates that have never before supported any vegetation. The substrates giving rise to primary succession may emerge from water bodies by silting of lakes, by emergence of a floodplain along a stream, or they may originate from the weathering of rock material (Mueller-Bombois and Ellenberg, 1974).

In cases where the vegetation of an area has been partially or completely removed, but where well-developed soils and seeds and spores remain, the sequence of the re-establishment of species is termed a secondary succession. The local loss of trees as a result of disease, high winds, fire or felling may lead to secondary succession that occurs within the structure of a forest. Successions on newly exposed landforms typically take several hundred of years to run their course. A precisely analogous process occurs among

the sea weeds on recently denuded boulders in the rocky inter-tidal zone of estuaries, and this succession takes less than a decade (Begon *et al.*, 1990).

Other important concepts linked with the succession are autogenic and allogenic succession. Autogenic succession is the succession that occurs on newly exposed landforms and in the absence of gradually changing abiotic influences. That is, the changes are caused by the organisms themselves (Begon *et al.*,1990; Huston, 1994). An autogenic change is, for example, the increase of litter on the forest floor, the creation of a particular microclimate in the forest understorey that modifies conditions and resources, or even the disappearance of a species due to competition interactions or parasitism.

Allogenic succession is, on the other hand, a serial replacements of species as a result of changing external geo-physico-chemical forces (Begon *et al.*, 1990). Environmental fluctuations that occur repeatedly during the lifetime of an organism are unlikly to influence the pattern of succession among species with a long lifespan. In contrast, shifts in environmental conditions that occur over periods as long or longer than the organism's lifespan are likely to result in changes in dominance among those species, that is in succession (Huston, 1994).

The ecological concepts of succession and competition are closely linked, indeed stresses to plants and competition for a given resource has been recognized as a major process in the succession of communities (Clements, 1904, in Gopal and Goel, 1993; Drudy and Nisbeth, 1973; Connell and Slatyer, 1977). Almost every change in species composition or species abundance, is due to a competitive interaction between individuals of the same or different species.

The most common form of competition is the 'exploitative competition' that occurs between two organisms of the same or different species whenever a valuable resource such as space, food, nutrients and light shared by them is in limited supply (Harper, 1977; Gopal and Goel, 1983). In contrast to this, another form is the 'interference competition' which involves denial of success to a resource by one competitor to another (Begon *et al.*, 1990). Allelopathy is another form of competitive interaction well described in aquatic plants, where one of the competing organisms produces chemical substances which on being released in to the environment retard the growth of another species providing it with a competitive advantage against the latter (Gopal and Goel, 1983.; Barrat-Segretarian, 1996)

One of the latest hypotheses linking succession with competition for resources was proposed by Tilman (1985): The resource-ratio hypothesis of succession. According to this hypothesis, limiting resources are reduced by competing populations and then resupplied at some rate characteristic of a particular environment up to a notional maximum level. The limiting resources required by two species A and B define habitats where species A is dominant, habitats where species A and B coexist and habitats where species B is dominant. The transition to each of these stages is gradual along a gradient between the resources R1 and R2, mostly light and nitrogen in the soil. The change in the resource availability, modified by the same species, promotes the succession. The critical assumption of this model is that a superior competitor for one resource is an inferior competitor for another resource (Tilman and Pacala, 1993). The competing species reach a competitive equilibrium at each point along the changing gradient. Thus the model's predictions about changing species composition along a temporal resource gradient are valid only as long as 'the rate of change in resource availability's is slow relative to the rate of competitive displacement'.

The succession and competition hypotheses, mostly generated from research in 'terrestrial' organisms, have been applied to aquatic species in freshwater and marine environments only in recent years (Begon et al., 1990; Gopal and Goel, 1993; Barrat-Segretain, 1996). Light seems to be one of the most important factors regulating macrophyte growth and distribution and therefore it is a prime determinant to explain both inter-and intra species interactions. However non resource variables like water depth may influence the outcome of competition directly or modify the nature and availability of resources (Gopal and Goel, 1993).

Specifically Van der Valk (1981a) proposed a qualitative Gleasonian model of allogenic succession. In this model, succession occurs whenever one or more new species becomes established, when one or more species already present are extirpated, or when both occur simultaneously in a wetland. The extinction of a species from the wetland is due either to all individuals of the species reaching the end of their normal life-span before any new individuals can become established, or to radical shifts in environmental conditions - sustained changes in water level that cannot be tolerated by individuals of the species. It is assumed in this model that interactions among the species (such as competition, allelopathy) will not result in the extinction of any species from the wetland.

1.1.11 Methods of description of vegetation

Vegetation may be defined as an assemblage of plants growing together in a particular location and described in terms of species composition and structure (Kershaw, 1974). The

quantitative study of plant ecology is a diverse discipline, consisting of the related processes of vegetation sampling and description, results, interpretation, and prediction -modelling- of vegetation in space and time (Greig-Smith, 1983). Sampling requires accuracy and selectivity to better describe a representative vegetation unit, usually a plant community or formation, which is an association of individual species populations that have a similar range of environmental tolerances.

The methodology employed (Table 1.2) to describe the effects of the river regulation was largely determined by the objectives of this thesis. These included the documentation of the response of biotic and abiotic parameters to dam construction in the Mánamo river through the spatial and temporal comparisons, of altered and unaltered systems. To achieve this, two approaches were used:

1. The direct comparison of the two rivers and associated communities, supposing that both rivers were similar before the regulation. This methodology is based on four main assumptions: the rivers had a similar annual water discharge from the main Orinoco channel, they flowed over the same substrate types and landform ensembles, they were subjected to similar local rainfall and evaporation regimes. Their connection in the Upper Delta allowed an equal chance for plant species invasion and colonization. This type of study, called a comparative mensurative experiment by Hullbert (1984), has been widely used in this type of study (Nilsson et al., 1991; Battrupp-Pedersen and Riis, 1999).

2. The study of a particular area of the regulated river through the analysis of previous and present environmental conditions, based in historical documents such as aerial photographs and satellite images. This type of approach has recently been termed 'Historical ecology' (Swetnam et al., 1999).

The choice of sites for sampling is an important consideration, often being subjective (non-random) process and involves establishing plots or defining study sites in pre-determined representative areas. It may, however, be completely randomised or partly random, consisting of stratified or systematic sampling; where the sampling is at regular intervals (Kent and Cooker, 1992).

The selection of plot size is one of the main decisions that needs to be taken. Determination of plot size depends on the vegetation community's species-area relationship. This involves establishing the minimum area required to represent community diversity, or the area at which diversity becomes representative of the total community (Mueller-Dombois and Ellemberg, 1974).

For grassy vegetation which resemble the emergent and floating meadows, of the study area, the suggested sizes are 1m x 1m or 2m x 2m (Kent and Coker, 1992). The smaller size (1sq. m) was selected in this study because it represented the minimum area where a maximum number of species could be found. A large number of samples (10) was taken to provide more accurate and statistically more robust data (Greig-Smith, 1983).

To study forest formations, large plots larger than1 ha, have provided useful data to characterise forest structure and composition, and if properly tagged, protected and monitored, they can provide long-term data on the growth, mortality, regeneration and dynamics of forests trees (Dallmeier, 1992, Comiskey et al., 1994). However, given the costs and labour they require to sample and maintain, it is not surprising that these plots are relatively few and spatially scattered. A lower-cost and faster alternative, especially when permanent plots are not required, are tenth ha quadrats (Gentry, 1982). In this study a tenth ha plot was selected due to the field limitation -flooded and muddy substrates- and availability of assistants. In the same amount of time, many smaller plots can be done than a single hectare plot, yielding valuable information about variability (and disturbance effects) in forests sites as well as at a local scale (Primack and Hall, 1992; Clinebell et al., 1995).

In the characterisation and comparison of communities of the herbaceous and forest communities included in the study area, a selection of characters needs to be made. The principal criteria commonly used are :
1. Floristic composition, comprising a simple list of species which are present.
2. Measures of the abundance of the species (Importance value).
3. Growth or life form classifies individuals on the basis of their vegetative morphology. Both terms have similar connotations but 'Life form' is generally used where the classification is believed to have an adaptative significance (such as Raunkiaer's system).
4. Physiognomy refers to the appearance of the stand as a whole and is closely connected with growth form.
5. Spatial patterns of the constituent species.
6. Various constants (in the mathematical sense) and indices derived directly or indirectly (such as the fixed values derived from the form of the species-area-species curve, indices of diversity etc.) from data sets.
7. Biomass and productivity. Each component of community has its particular biomass production per unit of area (productivity).
8. Remote sensors images used to define the boundaries and recognise at meso-scale, the formations, communities and even species.

The methods used in the vegetation description in this study are:

1. Floristic composition: it gives valuable information about a given stand or formation, due to the close relationship between the plant requirements and the habitat's physio-chemical characteristics. Floristic data concern diversity, usually of species although genera and families are also utilised. Also is related to the species richness, which is a simple counting of the number of species on each sample or community.

2. Measure of the abundance of species:

Herbaceous communities

A method which is widely used involves a visual estimate of the plants within a series of adjacent quadrats of increasing areas. The simplest method is to list the species present within an area (species composition) and to indicate a subjective abundance value for each species. One of the most commonly used systems is the DAFOR rating described by Kent and Coker (1992) which involves five classes, Dominant, Abundant, Frequent, Occasional and Rare. A more elaborate subjective rating was developed by Braun-Blanquet (1932) and involves two scales, one combining the estimated number and cover of a species and the second a measure of grouping.

Though devised over sixty years ago, these methods are still valid (Sanderson *et al.*, 2000). They are particularly suitable where the count of individuals is not feasible, such as where many species produce too much biomass (many Poaceae species) or the study area is flooded and the count has to be carried out from semi-remote platforms such as from boats.

Forest communities

A method, for quantitative assessments of abundance, that has become increasingly used in tropical vegetation (Aymard, 1997), is combining two or more measures into a single value. The 'importance value index' (IVI) may produce a more comprehensive estimate of the importance of species in a stand than is available using any one of the measures of abundance. For example, Curtis (1947 in Greig-Smith 1983) combined:

1. The relative frequency, the number of occasions that a given species occurs in a series of samples;
2. The relative density, defined as the number of individuals of a particular species per unit of area. Counts are usually made from a number of quadrats, multiplied by the area under study and divided by the area sampled; and
3. Relative dominance, the basal area for species as percentage of the total basal area (Greig-Smith, 1983; Mueller -Dombois, 1974).

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The latest 'value index' has been employed in this study since it gives a better estimate the importance of species with a large variation of individual numbers and stage development in the plots.

Another Importance value (Iv) was adopted by Dye and Walker (1980) for woody plants, which include the formula $Iv = \Sum_{i=1}^{s} (H_i N_i A_i)$, where H_i means height of height class i, N_i means number of individuals in height class i, and A_i means cross-sectional area of stems in height i. Finally one might use the Importance Cover Index (ICI), which sums the relative density and dominance only, thus excluding the effects of species frequency.

3. Physiognomic description:
Physiognomic measures provide information on the horizontal and vertical structure of the vegetation (spatial patterns and plant layering respectively) and associated features such as relative abundance of different life-forms (Raunkier 1937). The structure of tropical forests is often portrayed using profile diagrams introduced by Davis and Richards (1933-34), prepared on the basis of carefully measurements of variables such as height, girth, and crown diameter, of all the individuals, although their interpretation can only be qualitative in nature (Richards, 1983). Horizontal spatial patterns are easily measured, but vertical structure is harder to assess with the existence of distinct height layers generally established on subjective basis(Richards, 1983).

4. Diversity index:
Various indices have been devised to measure relative diversity of vegetation communities. The most commonly used are the Shannon-Wiener diversity index (H') and Simpson's index of dominance (S). Two aspects of diversity are estimated: those of species richness (number of species) and evenness, or that of equitability, the distribution of relative abundance amongst species (Begon et al., 1990). If two communities possess the same number of species, the more diverse is taken to be the one with the more homogeneous number of individuals per species. Additionally the species diversity is valuable so that a comparison may be made between two communities. The commonest of these indicators are the Sorenson's and Jaccard Coefficient which are generally applied to qualitative data. Both compare the number of species common to the two sites or plots studied and the total number of species common to both samples (Kent and Coker, 1992).

On the other hand diversity can be divided into three main components: alpha, which is diversity of species within the same area; beta, which are differences in species

composition between sample areas; and gamma, a regional scale differences in diversity, a product of the first two (Whittaker, 1973).

5. Biomass and productivity

One distinctive characteristic of any species is its biomass production. The species and, in turn, the communities of aquatic environments respond to the environmental characteristics such as nutrients, light and intensity of grazing (Begon *et al.*,1990). The two dominant aquatic macrophytes *Eichhornia crassipes* and *Paspalum repens* of the Mánamo and Macareo rivers shows a clear difference in their occupation of the river shores which were associated with the biomass production in each river habitat.

Biomass is any quantitative estimate of the total mass of organisms comprising all or part of a population or any other specified unit, or within a given area, at given time (Lincoln *et al.*,1982). This is employed by ecologists, research agriculturists and foresters for a wide range of purposes, such as assessment of crops value, site productivity, grazing potential, regeneration and decomposition (Catchpole and Wheeler, 1992).

Several methods such as: Destructive sampling, planar intercept, weight estimation, relative weight and photo keys, have been devised to sample the biomass production. The destructive method has the advantage of giving an accurate measure of biomass at a particular sampling point. Inaccuracies are therefore only introduced if estimates are made for larger areas (Downing and Anderson, 1985).

The size and number of the sampling quadrats are important in order to gain an accurate estimation of the biomass. Downing and Anderson (1985), tested the accuracy of a series of 5 sizes of quadrats from 0.01 to 1 m^2 in herbaceous vegetation and all five yielded equivalent biomass estimates. This range included over 90% of the sample sizes employed in the published literature, with over 70% of quadrats falling between 0.2 and 0.25 m^2. A larger number of samples gave a better estimate allowing for appropriate statistical analysis. However, several limitations on extensive surveys may exist such as the availability of technicians and laboratory facilities.

6. Remote sensings: The comparison of the environment prior to the dam construction in the Mánamo river required the analysis of historical data. In addition mainly old aerial photographs provided a clear picture of aspects of the environment such as vegetation types, river morphology, sediments distribution (sand bars) and even social aspects such as villages distribution and land use.

The knowledge of environmental history is of prime importance to understand how wetlands have functioned. Such information also provides insights into how to manage, conserve and restore natural resources. Historical studies usually involve the documentation of the causes and effects of past natural events, including disturbances such as floods and fires, and human actions on ecosystems structures and functions (Wissmar and Beschta, 1998).

Aerial photographs, radar and satellite images are the most common tools used and have been employed in studies of riparian restoration (Wissmar and Beschta, 1998), effects of dams on wetland communities (Pautou *et al.*, 1992), natural changes in vegetation patterns (Civco *et al.*, 1986; Jean and Bouchard, 1991) and definition of sensitive areas for massive industrial developments (Gómez and Medina, 1998) among others. Aerial photographs have also been used to describe and map vegetation formations as a tool for rapid environmental assessments (RAP's). This is where aircraft flights are used to define at large scales the precise contours of the vegetation communities as well to select sites for ground studies (Sobrevila and Bath, 1992; Conservation International, 1994, 1997).

1.1.12 Ordination techniques

Formal statistical techniques have been devised to allow a more objective approach to community description. One such technique is ordination. Ordination allows communities to be represented in graphical form so that communities that are most similar in both species composition and relative abundance will appear closest together. Communities which differ greatly in their relative species diversity, or which possess quite different species, are located further apart (Begon *et al.*, 1990).

Ordination orders vegetation data along the most important continuous environmental gradients -associated with axes-, with each point being related according to their relative similarity and their position in relation to the axes identified. Ordination may be either direct, in which environmental data, with known influence, orders the vegetation data, or indirect, in which intrinsic variation within the vegetation data is assumed to reflect environmental influences.

Two of the more recent ordination techniques widely used (since the 1980's) are the Detrended Correspondence Analysis and the Canonical Correspondence Analysis (Kent and Coker, 1992).

Detrended Correspondence Analysis (DCA), which runs using the FORTRAN program
DECORANA, is a powerful and widely employed tool that carries out an indirect ordination of
the data. DCA is derived from Correspondence Analysis (CA), but gives better results since it
eliminates the 'arch effect' and 'axis compression effect' (Hill, 1979). The arch effect occurs
when the sample scores of the second ordination axis are shown as a Quadratic function of
the sample scores on the first axis (Ter Braak, 1987-1992).

DCA as an indirect ordination method is best used to perform the analysis on the species data
alone first, and then environmental ordination is made by superimposing environmental data
on the ordination plots and looking for patterns and correlations. CCA, in contrast,
incorporates the correlation and regression between floristic data and environmental factors
within the ordination analysis itself (Kent and Coker, 1992).

DCA and CCA uses eigenvalues (the proportion of the total variance accounted for by the
correspondent principle component) to represent the proportion of data variation explained by
any axis, and re-scales the axes using units of standard deviation of species turnover.
Potential problems with the ordination include the existence of outliers (extreme data points),
and discontinuities (gaps in the data distribution along the axes) (Kent and Coker,1992).

The Correspondence analysis has been applied in many investigations. In particular the
relationships between vegetation and their environments has proved to be particularly fruitful
(Ali and Soltan, 1996; Colonnello 1996; Colonnello *et al.*, 1992); Khedr and El-Demershad,
1997).

Table 1.2 summarises the main methodology aspects utilised in the vegetation description
within this thesis.

Table 1.2. Main methodology utilised

Methodology utilised	N° of sites	Sites distribution	Size of site	N° of plots/ site	Size of plots	Plot distribution	Physio-chemical analysis and plant analysis	Indices/Mesurements Numerical ordination	Remote sensors employed
Floristic inventory/ Herbaceous communities. Environmental data (Chapter 3)	23	Non-random	Varied	10 plots	1 sq m	Random	E. conductivity pH, transparency, DO, ions(P, K).	DAFOR (cover) Shannon's (diversity) Sorenson's (similarity) CCA	
Forest communities (Chapter 4)	9	Non-random	0,1 ha (10x100 m)	10 plots	100 sq m	Systematic	Species composition, community structure, flooding intensity, anthropogenic intervention.	Importance Value Relative Freq., dens and cover.. Shannon's (diversity) Sorenson's (similarity)	
Meadows comparison (Chapter 6)	13	Non-random	Varied	10 plots/ belt	1sq m	Random	Species composition, species cover, water depth, sediment type.	DAFOR (cover) Shannon's (diversity) Sorenson's (similarity)	
Comparative Biomass production. (Chapter 7)	2	Non-random		5 plots	0,5 sq m	Random	Plant samples E. conductivity, pH, transparency, DO, temperature.	Plant biomass	
Mangrove colonisation (Chapter 8)	3	Non-random Non-random	0,1 ha (10x100 m)	1 plot (0,1ha)	100 sq m	Systematic	Species composition, plant ions (Na, K, Mg) interstitial water ions (Na,Mg, Cl, SO4	Species cover, communities and sand bars surface	Aerial photos (1932-1996)
Successional community dynamic (Chapter 9)	1	Non-random	9856 ha			Systematic	Species composition, flooding intensity.	Communities area	Aerial photos (1932-1996)

1. 2 Research background

During the 1980s, La Salle Foundation of Natural Sciences together with other institutions initiated a systematic study of the Orinoco, Venezuela's main river. In particular, La Salle Foundation undertook studies in the Lower Orinoco and its floodplain in the limnology research centre in Ciudad Guayana city (see Fig. 2.1).

In the mean time a series of anthropological studies were being undertaken in the Orinoco Delta, focusing on the Warao Indians (Heinen, 1987) and the effects of the Mánamo regulation on the indigenous and Creole inhabitants (Escalante, 1993). The report from Escalante (1993) and several documents, movies and newspaper articles based in interviews with inhabitants, was used to investigate the significant impact of damming the Mánamo on the environment.

Additionally since the 1980's an ambitious program has been established to develop economically the river corridor along the Orinoco's main tributary. This flows down from the Andes foothills, into the Apure River to its confluence with the Orinoco and thence to the Delta. The plans under consideration include the impoundment of the Orinoco waters and that of other large rivers such as the Caroní (the Caruachi dam in the Caroní River between Ciudad Guayana and Ciudad Bolivar, is almost complete) and Caura, by the construction of several lowhead dams (MARNR, 1983). These dams are located in the middle section of the river. The knowledge gained of the consequences of regulating the Mánamo river should be used to avoid negative environmental impacts in these new river impoundment schemes. In particular another large project is proposed involving the diversion of the Orinoco water at the delta apex, downriver from the town of Barrancas (see Fig. 2.2). The objective of this scheme is the deepening of the navigation channel to the Ocean (IRNR(USB)-Ecology and Environment, 1999), but the new barrage will modify the sediment deposition and the spawning areas for fish resources in the region, among other effects.

However many wetland sites (including designated protected areas) along the central coast of the country have been considerably modified by human activities and are currently facing growing land use pressures. Many others such as the 'Ciénaga de Aguas blancas y Aguas Negras', in Zulia State lack any comprehensive floristic studies. Urgent action is required from the scientific community to address the poor state of current knowledge of both fresh-water and estuarine wetlands, including inventories and the mapping of individual sites.

In particular, the general floristic knowledge of species and communities, was extremely poor in the Delta region prior to the current study since almost 50% of the species recorded have

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proved to be new records to the territory. The comparison of regulated systems with unregulated systems, in particular the Mánamo and the Macareo rivers, could not have been carried out without a substantial improvement in the quality of the data base.

1.3 Study aims and objectives

Main aims:

The present research encompasses two approaches to the study of the aquatic vegetation in the region of the Orinoco River Delta:

1. The description of the species and communities through an extensive field survey leading to a correlation with environmental parameters; and
2. The documentation of the response in biotic and abiotic systems to dam construction in the Mánamo river. This to be carried out by means of spatial and temporal comparisons, of both altered and unaltered systems.

Hypothesis:

The regulation of the Mánamo river produced significant changes in the river hydrology affecting the properties of the Delta sub-basin ecosystem, its habitats and communities, and creating differences with the non impounded region.

Specific objectives and desired outcomes

1. To describe the structure, species composition and ecological parameters, physico-chemical characteristics, of the aquatic herbaceous and forested plant communities of the Orinoco Delta.

2. To characterise the aquatic plants of the floating and emergent meadows in terms of their species diversity, biomass and habitat along the banks of the Mánamo and Macareo rivers.

3. To document the increase in the downstream distribution of the mangrove communities resulting from changes in hydraulic dynamics after the construction of the Mánamo dam, and to relate the present distribution of mangrove and non-halophytic aquatic communities to the increase of the estuarine condition of the river basin.

4. To document the changes in the wetland forest communities caused by the damming of the Mánamo river.

5. To model the functioning of the regulated system in term of the biodiversity and biomass.

6. To model the successional response of the wetland ecosystem components to the disturbance created by the river regulation.

Chapter 2 Area and site description

The Orinoco Delta is one of the largest wetlands in South America, and one of the best conserved ecosystems in the world. The isolation and the unsuitability for agriculture of the existing soils have prevented the exploitation of the area so that a major part of its biological diversity in terms of species and communities remain largely unaltered. However, one major dam structure has caused an ecological disturbance, modifying the 'pristine' state of the ecology, thereby altering the vegetation of large areas.

2.1 General features

It is worth presenting a general overview of this region in order to understand the importance of a tropical Delta such as that at the mouth of the Orinoco River. The Delta distributaries discharge the waters of the Orinoco into the North Atlantic Ocean which are derived from a catchment of circa 1.1 million sq. km, of which two thirds lie in Venezuela and one third in Colombia (Fig 2.1). The main sources of the Orinoco are located in Amazonas State, in southwestern Venezuela on the Guayana Shield. The principal tributaries of the Orinoco are the Caroní, Caura, Ventuari and Parguaza rivers from the south side and from the north, the Guaviare, Vichada, Tomo, Meta, Cinaruco, Capanaparo, Arauca and Apure rivers (Colonnello, 1990a; Lundberg, 1998).

The environment of the Orinoco Delta possesses the following characteristics, that are not shared by most of the other large rivers Deltas of the world:
1. The main Delta distributary, the Río Grande river, flows along the southern edge of the Delta fan, against the emerging Guayana Shield;
2. The Delta lacks saline lagoons; and
3. The Delta is partly influenced by the ocean (PDVSA, 1992).
In addition, it possesses a barrage on one of its main distributaries.

2.1.1 Human settlement of the Delta

The human population of the Orinoco Delta comprises the aboriginal Warao who first settled the region between 7,000 and 9,000 years ago (Wilbert, 1996) and the 'Creole'
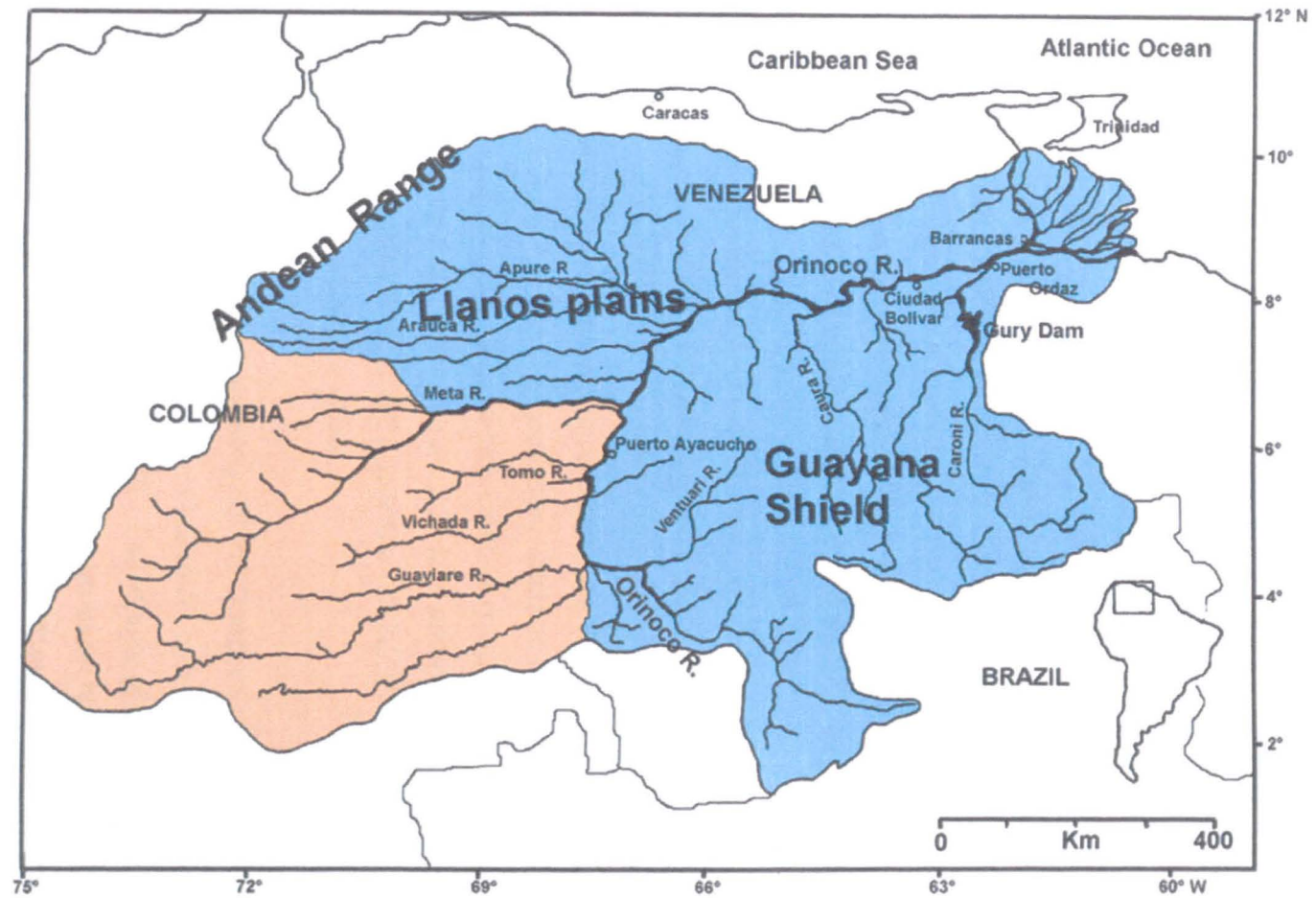
Fig. 2.1. The Orinoco river Basin. Main tributaries, from the Andes Range and the Guayana Shield.

people, locally called 'Criollos', who migrated into the area in the 18th century, mainly from the Island of Margarita (Venezuela) in the Caribbean (Fig 2.2) (Salazar-Quijada, 1990). The Criollos practiced sedentary agriculture, including the cultivation of coffee and rice. They founded settlements such as Pedernales, Capure, Curiapo, La Horqueta and Tucupita. On the other hand the Warao Indians maintained a subsistence economy based on the palm communities dominated by the 'moriche' tree (*Mauritia flexuosa*) called 'morichales', from the 'temiche' palm (*Manikaria saccifera*) forming the 'temichales' communities, and subsistence fisheries (Wilbert, 1994-1996).

2.1.2 Ecosystems of the Delta

The Orinoco River Delta (Fig 2.3) is a complex of little known ecosystems that comprise both aquatic and semi aquatic habitats. Until the decade of the 1970s, the region remained relatively isolated from more developed parts of Venezuela due to the lack of roads. Until recently many wetland areas in the tropics have escaped the impact of human occupancy because of their remoteness or unsuitability for agriculture (Armentano, 1993).

This vast territory of approximately 40,000 sq. km, just over half of which is dominated by aquatic habitats, is interconnected by thousands of channels ranging from small anastomosing streams and rivulets through to very wide rivers of over several hundred meters wide, locally called 'Caños'. The most important river is the Río Grande (discharging circa 84 % of the Orinoco waters) which flows eastwards, whereas all the other major rivers, Caño Sacupana, Caño Araguao, Caño Araguabisi, Caño Guiniquina, Caño Araguaito, Caño Mariusa, Caño Macareo (discharging circa 11%), flow predominantly in a north-easterly direction. The most westerly river. the Caño Mánamo, currently discharges only 0.5% of the total waters and flows in northerly direction.

There is a dearth of research into the ecology of the Orinoco Delta region. Of the few available vegetation studies, probably the first botanical collections were conducted by H.H. Rusby and W.R. Squires in 1896 (Dorr, 1995). The reports of the botanical communities of the Orinoco Delta and specifically of the Mánamo sub-basin have been provided by Delascio (1975), Danielo (1976), Pannier (1979) and Huber and Alarcón (1988). Other authors mention few species and communities (Kahn and Mejia,1990; Armentano, 1993).
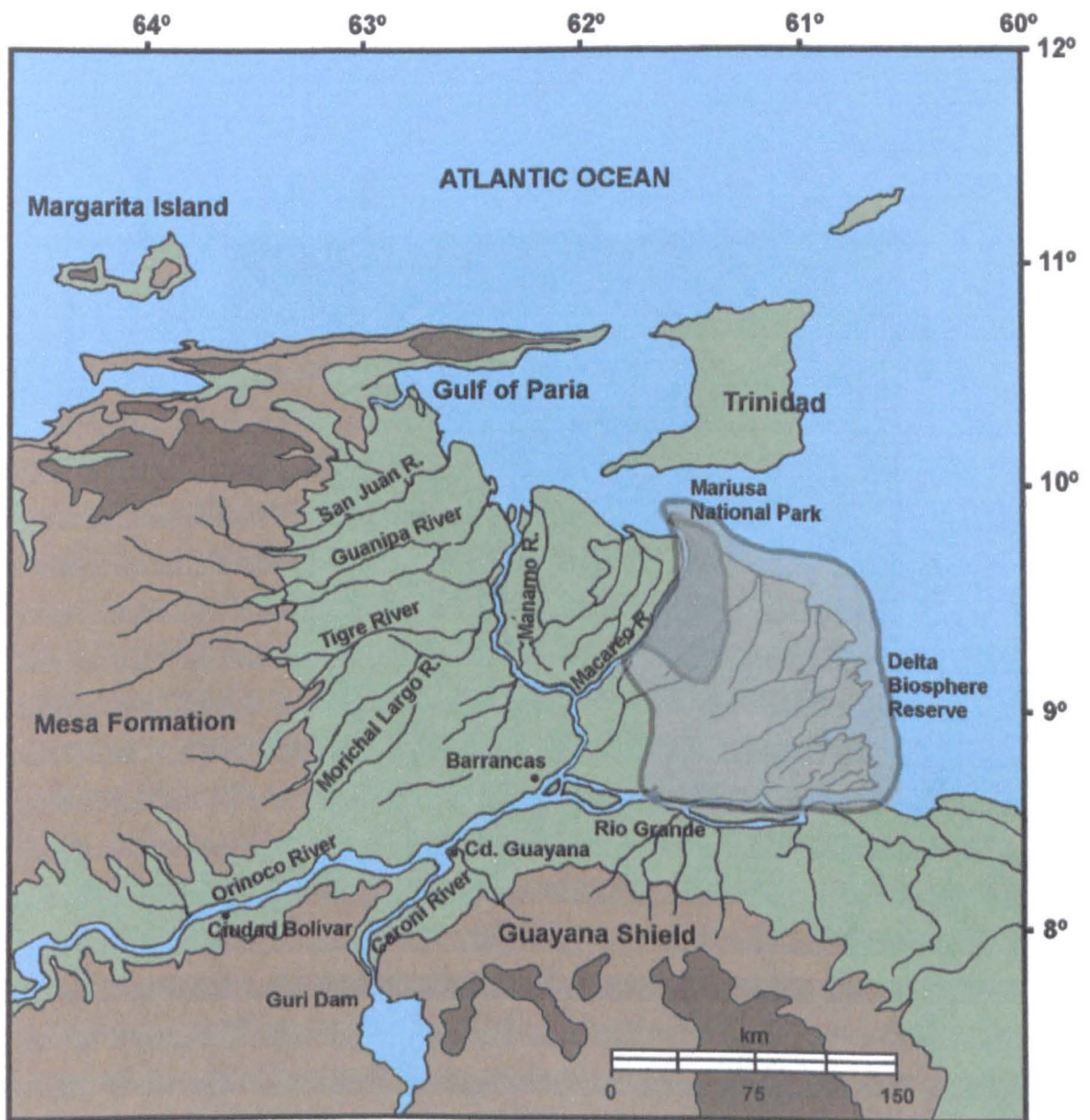
Fig. 2.2. North eastern region of Venezuela. The Orinoco Delta, regional physiography and the two areas under special protection, the "Mariusa National Park" and the "Delta Biosphere Reserve".
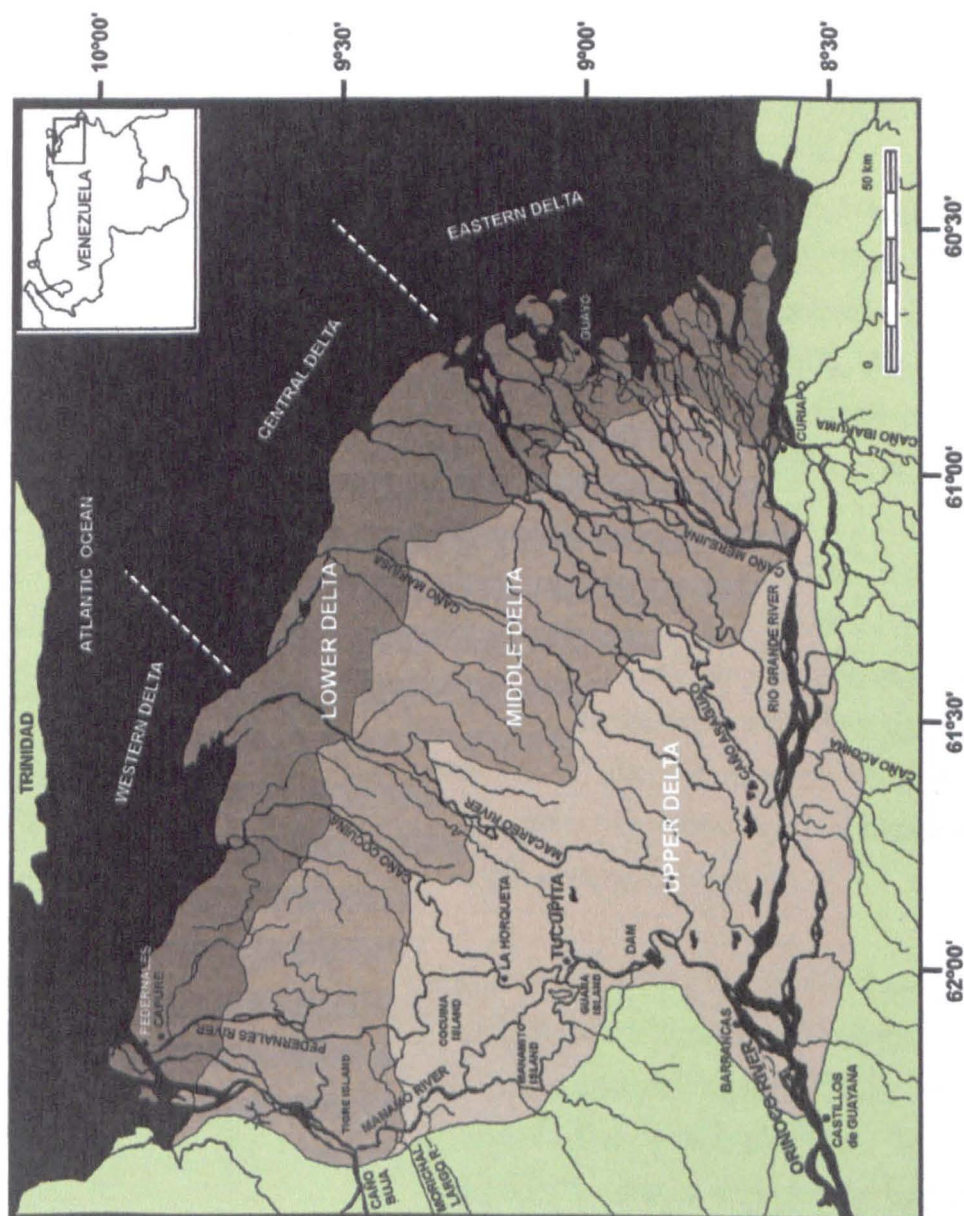
Fig. 2.3. The Delta region. Main divisions and distributaries.

Only the work of CVG-Tecmín (1991), provides a survey in any detail of the floristic composition and the vegetation structure.

The aquatic vegetation, in particular, has been analysed by Colonnello *et al.* (1993) and Colonnello (1996). Previous studies concerning ecological aspects of this vegetation are scarce, and include CVG-Tecmín (1991) and Colonnello (1998a). Nevertheless, similar environments have been studied in the Amazon Basin (Junk, 1970, 1986; Junk and Howard-Williams,1984) and in the Paraná River System (Burkart, 1957; Franceschi and Prado, 1989; Neiff, 1990b).

In contrast, the physical aspects of the region have received more attention, in large part as a consequence of the exploitations of oil reserves that has occurred recently. The sediment types, the morphology of the landscapes and their relationship with the terrestrial vegetation in the deltaic region have been previously discussed by Van der Voorde (1962), Vila (1964), Van Andel (1967) and Danielo (1976). In addition, the fluvial and sedimentary dynamics of the Mánamo and Macareo distributaries have been touched upon by Pfefferkorn *et al.* (1988).

Human impacts on wetlands in South America have increased in recent times - a result of a rapid increase in the human population alongside the growth in labour demand for newly established industries (Junk, 1995). The 'pristine' nature of the Delta changed with the damming of the Mánamo river as did various industrial and semi-industrial developments such as lumbering, particularly of mangrove trees, extraction of palm hearts (Pannier, 1986) along with large cattle and buffalo ranches. In addition, tourism has intensified over recent years with the construction of various lodges with overnight accommodation.

The most recent and extensive industrial development started in 1997 and was associated with the renewed activity of the petroleum industry in the area located between the mouths of the Mánamo and the Mariusa rivers a territory of 25,000 square km (see Fig 2.3). Within the next 15-20 years the entire region is expected to be affected by oil exploitation. Extensive studies of environmental impact have been undertaken in order to minimise the negative effects of seismic exploration and extraction of the oil by international companies such as British Petroleum, AMOCO and the Louisiana land Company (Infrawing & Asociados, 1997; Natura SA, 1998; Geohidra Consultores, 1998; Delta Centro Operating Company, 1999). However there is a general concern about the possible effects of oil spills on the environment of the Delta such as have occurred elsewhere in the Niger Delta where a total of approximately 2300 m^3 of oil is accidentally discharged annually (Moffat and Lindén, 1995).

The impoundment of the Mánamo channel remains the major alteration to the ecology suffered by the Delta, because of the extent of the affected area and the diversity of ecosystems located within that zone. In Venezuela, it is second only exceed by the 'Guri dam' on the Caroní river which impounds waters that cover about 3,500 sq km (Fig 2.2).

Documents and reports on the environmental impacts generated by the Mánamo regulation are not available from the archives of the responsible agencies. A few basic reports were produced on the impact of dam closure upon the agriculture and soils (Buróz and Guevara, 1976; COPLANARH, 1979). Only recently, a description of the biotic and abiotic features of the Delta before and after damming has been obtained through a series of interviews with older inhabitants of the region (Escalante, 1993). With the recent revival of the petroleum oil industry and the new environmental and conservation approaches of the National Environmental Ministry (Ministerio del Ambiente y de los Recursos Naturales Renovables (MARNR)) there is a growing interest in the Mánamo regulation. In turn, this has led to several workshops and seminars (Colonnello, 1998a) being held. At an international level, the case has been discussed at several meetings and conferences (Colonnello, 1998b; Colonnello, 1998c; Colonnello and Yánez, 1999).

The impact of the barrage has centred on the Upper Delta and the Mánamo sub-basin, so that large tracts of the Delta remain unaffected, especially in the north and east of the Delta fan. These require greater protection and more research. The importance of this huge natural territory has been recognised in the designation of large areas under special protection by the MARNR, comprising the Mariusa National Park (265,000 ha) and the Orinoco Delta Biosphere Reserve (876,500 ha) (MARNR, 1992) (see Fig 2.2). Moreover, the Delta region encompasses 77% of the wetland habitats (for birds and wildlife) across the entire country (Lentino and Bruni, 1994). It has been included as part of the 'Basin of the deltaic platform' in the regional conservation strategy by IUCN (Rodriguez Altamiranda, 1999). Despite the timely studies conducted within the protected areas by private environmental organisations (Colonnello, 1997), economic resources have been lacking to promote study and conservation programs to cover the whole region.

2.2 General physiography
The Delta Region constitutes a fluvial/marine floodplain whose sediments have been transported principally by the Orinoco River and, to a lesser degree, by the San Juan and other rivers that drain the high plains of the 'Mesa formation' to the west (Fig 2.2). These

sediments were then mixed with local organic material and deposited over marine clays, rich in sulphate material dating back to the Holocene period (Van-Andel, 1967; MARNR, 1982a). Fig 2.4 shows a schematic profile across the Delta region. The fluviatile material, particularly the sand is deposited along the river banks in the Upper Delta, a process that has created the high levees along the rivers. In a transect across the Lower Delta the levees become lower and the few deposits of peat found in the depressions of the Upper Delta become thicker as the effects of the flooding increase. Oligotrophic and acidic peat deposits up to 6 m, have been reported in the Mariusa river (see map on Fig 2.3) (MARNR, 1979).

The underlying cat-clay or sulphidic sediments, have caused the formation of sulphate acid soils as a consequence of the river regulation (see section 2.3). Currently the main sediments transported to the Delta fan are brought by the Orinoco River, which transports an average 100 million tons of sediments each year (Pérez Hernández and López, 1998).

The region (Fig 2.3) may be divided according to the hydrology, drainage, sediments distribution, vegetation and climate in three natural regions (MARNR, 1979; Canales, 1985):
1.The Upper Delta, between 7 to 2.4 meters above sea level;
2. The Middle Delta between 2.5 to 1 m a.s.l. and
1.   The Lower Delta between 1 to -1 m a.s.l.
This division is useful to locate main types of soils, hydrology regimes and vegetation communities, however, lacks of detailed topographic measurements and thus of precise boundaries.

From a geographical point of view, we may also distinguish three sub-regions:
1. The Eastern Delta from the Rio Grande to the Caño Araguao, where the network of channels is most complex.
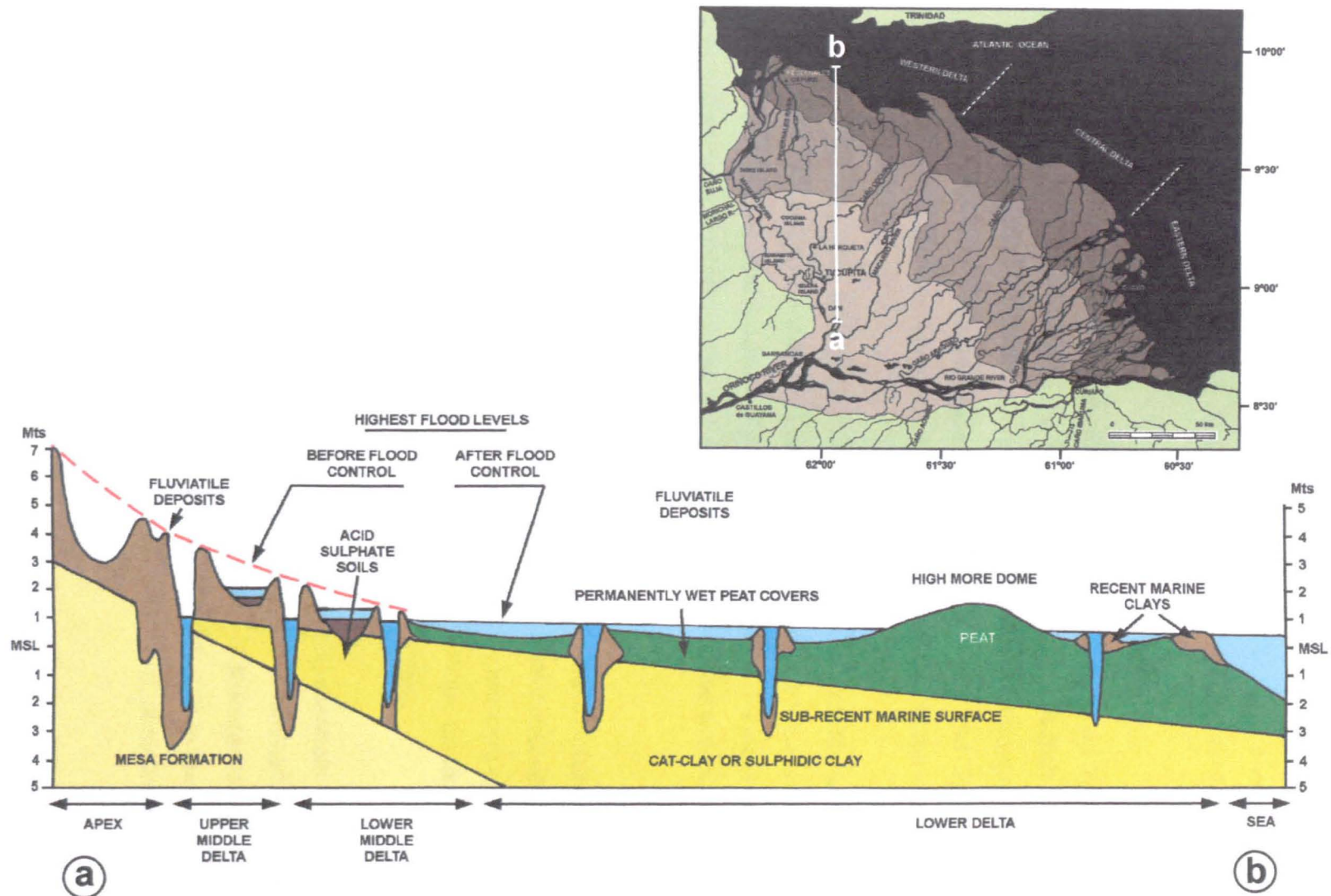
Fig. 2.4. Schematic profile of the Delta region. Main topography, substrates and underlaying sediments. Adapted from H-Dost (1971).

2. The Central Delta, the area between the Caño Araguao and the Caño Macareo, consisting of a great expanse of swampland without functional tributaries because the few connections with the Orinoco water occur through the Caño La Tortuga and Caño Macareo, when they reach their maximum water level.

3. The Western Delta, between the Caño Macareo and the Caño Mánamo, encompassing the Mánamo sub-basin. After the damming several connections with the main Orinoco River were either closed or suffered from siltation.

The Upper Delta consists of an accumulation of fluvial sediments transported by the Orinoco River. Islands with high surrounding levees are characteristic of this area which is seasonally flooded for relatively short periods by the local rains and river incursions through the levees. The largest islands are the Islas Tucupita, Macareo, Cocuina, Manamito and Guara (Fig. 2.3). The drainage is medium to poor and very poor, particularly in the centre of the internal basins.

The Middle Delta comprises wide flatlands in the central part of the deltaic fan whilst the soils are of fluvial-marine origin. The topography is very flat with slopes of 0-1 % and the drainage is, in general, very poor. The land is seasonally flooded for periods of 6-9 months mainly by the rivers as well as by local rainstorms as well as the height of the tides which impedes the drainage of the land.

The Lower Delta comprises the coastal belt which is permanently flooded because of incursions from the rivers aided by the diurnal cycle of tides. The tidal influence is very strong during the dry season, when the water discharge of the rivers is low, reaching as far as the Upper Delta. During the rainy season however, the increase of the water discharge annuls the influence of the tide and the tidal system switches to a fluvial system.

Every portion of land in the Delta constitutes an island surrounded by channels. In a typical profile shown in Fig. 2.5, the main morphological forms of the land are summarised. These include levees and depressions; soils types along a cross section of Macareo island (according to Van der Voorde, 1962) as well as typical vegetation, forests in the levees, grading to herbaceous and scrubby vegetation toward the depressions, sometimes with temporary or permanent lagoons in the lower depressions.

GALLERY FOREST (GF)

SWAMP PALM forest (SPF)
(Morichales)
Variable cover

SWAMP FOREST (SF)

MARSHES (M)
Variable cover of palms(M-P)

AQUATIC VEGETATION

High tide

Low tide

Undecomposed
peat, flooded
throughout year

Unripened clay soils
increasing layer of
organic matter, flooded
throughout the year

Half ripened,
heavy clay soils
flooded throughout
year

Basins

Ripened, ligh to heavy
clay soils, flooded
drying out seasonally

Overwash sediments
sandy along ckeclets
Clayey, mixed between
active and passive
streamlets.
Seasonally flooded

LEVEES
Sandy sediments
permanently dry

Channel

Fig. 2.5. Schematic profile of the Delta inter-riverine terrain, morphology, main vegetation communities and soil types.

The difference of altitude between levees and depressions is circa. 1.2 m in the Upper Delta (van der Voorde 1962). This difference diminishes in the general direction of the Lower Delta. For example, along the Pedernales river entering the Middle Delta (see boundary in map of Fig 2.3), the differences are almost imperceptible. This topographical gradient from the Upper to the Lower Delta largely determines the type of forest communities of the river banks and inter-riverine terrain (see chapter 4).

The Orinoco River built up its Delta through the normal processes (Van der Voorde 1962); levees surrounding larger or smaller basins areas being formed alongside the river courses. This process has led to a general differentiation in the texture of the sediments which are lighter in texture on the levees and heavier in the basin areas. At high river water level, from July to August (see section 5.3.1), more bedload is transported owing to the increase in transport capacity resulting from the increase in velocity (see section 5.3.6). The heavier sandy particles are then deposited alongside the river course. The lighter particles (silt and clay fractions) are transported over the levees into the basin area where they may be deposited (Van der Voorde, 1962).

2.3 Climate

The Delta region lies well within the tropical climate zone characterised by a low variability in temperature throughout the year. The amount of precipitation and its abundance across the deltaic plains determines the nature of the meso-climates. In addition temperatures are similar across the delta since there are few topographical differences within the territory or in the neighbouring areas. The period of maximum rainfall, coincides with the poleward movement of the inter-tropical convergence zone across Venezuela enhancing precipitation in the Delta (MARNR, 1979).

According CVG-Tecmín (1991) and Huber (1995), the Delta region shows two main climatic types (Fig 2.6):
1. Macrothermic Ombrophylous climate which is dominant in the outer section of the region, consisting in a short dry season from December to February, but without water deficit. In the rainy season precipitation may reach 2,798 mm on the coast.
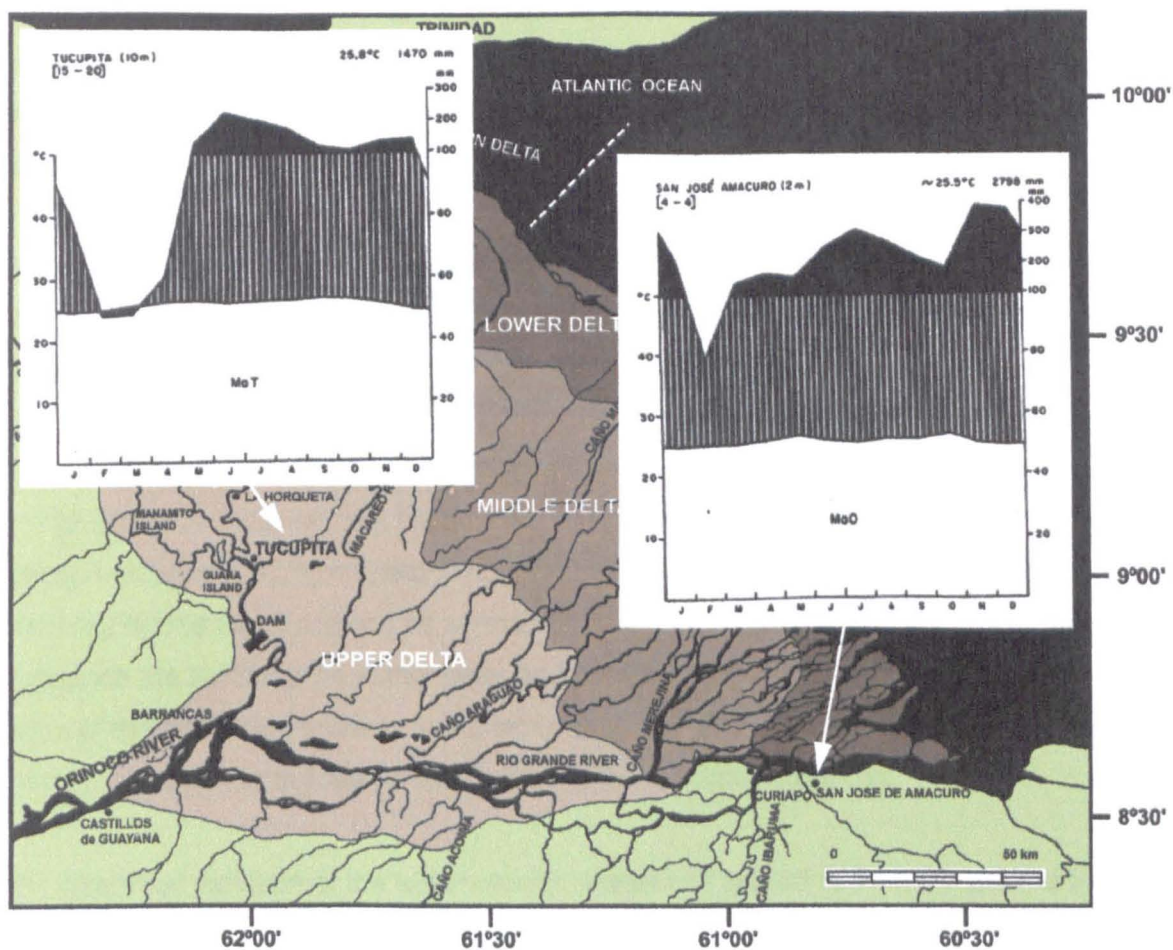
Fig. 2.6. Climatic diagram of Tucupita and San José de Amacuro.

Climatic diagrams from the Venezuelan Guayana, following the conventions of Walter (1979). Top line, left, is the locality of the climatic station, followed in parentheses by the height above sea level; to the right is the mean annual temperature and the mean annual precipitation. On the second line, in brackets, the first number is the number of full years of observation for temperature, the second for precipitation. The lower line on the diagram is the mean monthly temperature, whereas the upper and more variable line is the mean monthly precipitation. Dotted line is the estimated mean temperature when records are lacking. Black= periods of high precipitation (> 100 mm per month); striped= relatively humid season; checkered= period of relative drought. MaO= macrothermic ombrophilous climate; MaT= macrothermic tropophilous climate.

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Mean temperature is approximately 25.5 °C. This area is strongly influenced by the moisture-laden trade winds that constantly blow off the nearby North Atlantic Ocean.

2. Macrothermic Tropophylous climate, encompassing the inner Delta region. This area has an annual rainfall of between 1,500 and 1,800 mm with a marked dry season of up to 4 months from December to March. This is associated with a short period of water deficit in the soils when the mean annual temperature rises to 25.8 °C. The trade winds remain a dominant influence on evaporative losses, especially during the dry season.

The precipitation can be very irregular, fluctuating year by year as well as locally. As seen above it varies from 1,500 mm year^{-1} in the Upper Delta to more than 2,000 mm year^{-1} in the Lower Delta where the wet season lasts from May to November.

Winds vary in strength from the dry to the wet season, mean values in the Upper Delta reach 8.4 km h^{-1} (2.3 m/s) in April, and 5.6 km h^{-1} in July. Mean values at 0.65 m above ground show similar values in the Upper Delta (Tucupita) and Lower Delta (Pedernales), but with a higher velocity during the dry period as seen in table 2.1. The pattern and velocity of the winds influence the temperature in the water bodies of the region (see section 5.4.4), and the distribution of the free-floating plants in the lagoons and rivers (see section 6.3.1.3), among other ecological factors in the region such as the plant evapotranspiration.

Table 2.1 Seasonal variation of the wind velocity, measured at 0.65 m from the ground (mean values in km h^{-1})(Geohidra Consultores, 1998).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Tucupita	1.6	2.2	2.3	2.1	2.1	1.7	1.5	1.2	1.3	1.3	1.4	1.2
Pedernales	1.9	2	1.7	2.6	2.3	2.2	1.6	1.2	1.1	1.2	1.1	1.3

Precipitation constitutes the major climatic factor in the Delta area, because it precedes the pulse of flood-water in the main channels - contributing to the replenishment of the lagoons and lowlands across the whole of the Delta. Figure 2.7, shows the precipitation for Tucupita (Upper Delta) and Guiniquina (Lower Delta) stations (Monente and Wiscovitch, 1993), exhibiting the two peaks in rainfall, in June and in December alongside the hydrograph of the main channel of the Orinoco River. It shows that the maximum discharge occurs two months later than the maximum peak in precipitation.
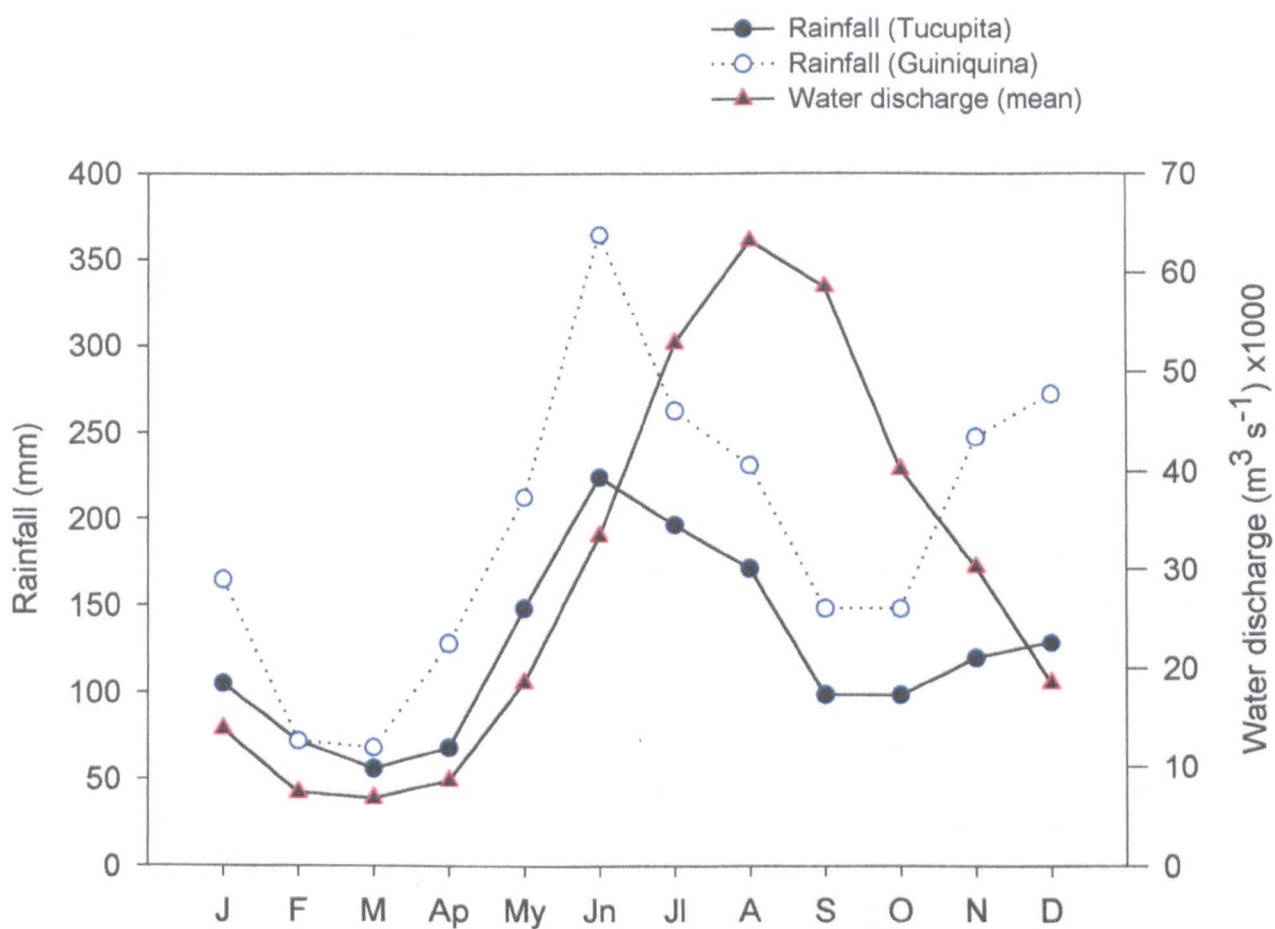
Fig. 2.7. Precipitation of the Tucupita and Guiniquina stations and mean water discharge for the main channels (Monente and Wiscovitch, 1993).

Due to the heavy soils in the depressions between the levees of the islands the downward percolation is negligible (see section 2.3). This causes the water level to rise, promoting the formation of lagoons, that reach capacity in July-August when the water from the main river overflows the levees. The influence of the rainfall is especially important in the Upper and Middle Delta where it helps define the chemical characteristics of the waters by diluting the runoff from the higher (see a complete discussion in section 2.5).

The intense rainfall, the evapotranspiration and the soil characteristics also determined the productive activities of the local inhabitants because they affect the crops development by reducing their growing season, as well as the grazing period for cattle (MARNR, 1979).

Table 2.2 shows the water balance for the Upper Delta region, based in the temperature and rainfall data for the period 1968 to 1983. The annual evapotranspiration is generally lower than the precipitation, particularly during the months of June to August and November-December, thus promoting the flooding of the land.

Table 2.2 Water balance for the Upper Delta region (Adapted from MARNR, 1988).

	Temperature °C	Rainfall (P)mm	Evaporation (E)mm	Evapotranpiration (ETP)mm	Difference (P-PET)mm	Surplus mm	Deficit mm
Apr	26.2	63	63	44	19	19	0
May	26.3	122.4	122.4	85.15	37.25	37.25	0
Jun	25.7	212.4	107.8	75.06	137.34	137.34	0
Jul	26	186.3	113.4	78.9	107.4	107.4	0
Aug	26.4	153.9	126.7	88.16	65.74	65.74	0
Sep	26.7	111.6	135.8	99.46	12.14	12.14	0
Oct	26.6	93.6	134.4	93.49	0.11	0.11	0
Nov	25.9	121.5	111.3	77.49	44.01	44.01	0
Dec	25	122.4	103.6	72.15	50.25	50.25	0
Jan	24.8	78.3	114.8	79.91	-1.61	0	-1.61
Feb	25.5	40.5	68	47.48	-7.2	0	-7.2
Mar	25.5	44.1	44.1	30.92	13.18	13.8	0
Totals		1350	1245.3	872.2			

2.4 Soils

Soils are predominantly hydromorphic and even where high local heterogeneity exists, they are dominated by a few main groups. Soils types in the Upper Delta are mostly Fluvaquents, Sulfaquents and Hydraquents, and in the Middle and Lower Delta Tropofibrist and Hydraquent types. In general the soils are heavy, poorly drained, highly acidity and of low fertility (COPLANARH, 1979).

A detailed analysis of the soils along a gradient from the levees to the depression of the Delta island in the Upper Delta (see Fig 2.5) has been presented by Van der Voorde (1962) across Macareo Island. The results are shown in table 2.3. The levees (sample S1), which are always dry, are composed of humic, very fine, sandy loam in the uppermost layers of the soil profile changing to a very fine sand, which shows mottling in the lowest zone (90cm). In a transect towards the depression of the island, the flooding increases (circa 50-80 cm) and the soils, sample S3 and sample S4, become a granular peaty clay on the surface (0-20 cm) and an ageing silty clay at the base (50-90 cm). In the lower part of the transect, in the centre of the island, the flooding is deeper at 110 cm, and the soils become immature dark, brown to black, and clayey peat in the soil surface (0-20 cm) and immature silty clay to clayey wood peat.

The profiles, as described here are not homogeneous as they reflect the accretion events under which they were formed (Van der Voorde 1962). When the waters invade the inland areas, overflowing the levees, small streams or creeks scour out the levees -sometimes utilising former small stream channels. Sand previously deposited there is entrained by these active streamlets and transported into the basins. Due to a reduction in velocity of the flow, this sand is deposited as a secondary over-wash sediment along the streams. The silt and clay particles will be dispersed by these streams, thereby in addition forming small basins areas within the over-wash sediments. The result is a very complex pattern of sedimentation behind the river levees, resulting in lighter and heavier textures in the soils profiles. These complex patterns may well influence the biotic heterogeneity that is to be found in the Middle Delta (as it will be discussed in chapter 9).

The soil acidity varies as well, increasing from the levees to the depressions. In the levees the pH values were very similar 5.1 and 5.2 pH with a slight decrease toward the base of the soil profile, to 5.8 pH. Towards the centre of the depressions, acidity increased. The lower pH values were recorded in the immature clay soils (4.2-4.0 pH). The presence of underlying sulphidic clays covered by riverine sediments as in the case of the Orinoco Delta, is one of the ingredients to produce sulphate acid soils (as described in section 2.7.2).

In the Lower Delta, even though many analyses have probably been carried out by the petroleum companies, results of such sampling have not been made public. The few known data sets from the Jarina and Pepeina sites (see Fig 4.1 for location), indicate a similar pattern to that seen in the Upper Delta, where the levees have a lower proportion of sandy sediments, indicating a similar formation process to that described above. The sediments in

the depressions are acidic with pH values of 5-6 at the surface and less than 5, in the bottom of the soil profile (Delta Centro Operating Company, 1999).

S	W. depth (cm)	0-10 cm	10-20 cm	20-30 cm	40-50	50-90 cm
1	0	Humic very fine sandy loam	Humic very fine sandy mottled	Humic very fine sandy mottled	Very fine sand mottled	Very fine sand mottled
2	0	Slightly humic loose very fine loamy sand	Loose very fine sand	Loose very fine sand	Very fine sandy clay loam	Very fine sandy clay loam mottled
3	45	Black granular peaty clay	Silty clay very fine mottling, slightly sticky	Silty clay very fine mottling, slightly sticky	Silt loam mottled	Silt clay loam mottled
4	80-120	Half-ripened clayey peat granular	Half-ripened clayey peat granular	Half-ripened to nearly unripened silty clay mottled	Half-ripened to nearly unripened silty clay mottled	Half-ripened silty clay motless along roots
5	125	Unripened brown and black slightly clayey peat	Unripened brown and black slightly clayey peat	Unripened brown and black slightly clayey peat	Unripened silty clay, some humus in layers	Unripened silty clay, some humus in layers
6	110	Black and grey unripened clayey peat	Black and grey unripened clayey peat	Unripened wood peat	Unripened wood peat	Unripened wood peat

Table 2.3. Successive development of sediments in the Macareo island. S: samples; 1: Levee of the Caño Mánamo; 2: Overwash levee under cocoa trees; 3: Over-wash soils east of Caño Manamo, under cocoa trees; 4: Behind levee of Caño Tucupita; 5: Marsh near Caño Macareito; 6: Swamp forest

2.5 Vegetation

2.5.1 General remarks

The vegetation in the region follows a general pattern revealed in the profiles shown in Fig. 2.8. These profiles corresponding to community types according to the vegetation map presented by Infrawing & Asociados (1996). This shows herbaceous communities and relicts of semi-deciduous forests to be dominant in the Upper Delta, forests dominated by palm trees in the Middle Delta, and evergreen forests and palm communities more common in the Lower Delta.

The Upper Delta is predominantly covered by a medium density mixed deciduous/evergreen non flooded forest of moderate height (20-25 m), much of it the result of anthropogenic disturbance as well as transformed pasture-lands (CVG-Tecmín, 1991; Huber, 1995). This vegetation has been classified as 'Tropophylous Evergreen Forests' by Beard (1955) and as 'Upper Delta Forests' by Danielo (1976). The seasonally flooded marshes located in the depressions, correspond to the 'Swamp with Floating Plants' proposed by Beard (1955).

The Middle Delta mostly comprises low to medium, seasonally flooded, swamp forests and swamp palm forests (Morichales), occasionally with treeless marshes in the central portions of the terrain which are flooded throughout the year (Fig 2.5) (Huber, 1995)

The Lower Delta is dominated by low evergreen permanently-flooded swamp forests, defined as 'Lower Delta Swamp Forest' (Danielo,1976) and 'Bosques de Cienága' that is Swamp forests (Veillón, 1977). Large areas are covered by marshes composed mainly of grasses and sedges, which were defined as 'Marshes with floating plants' and 'Marshes with Giant Herbaceous Plants' (Beard,1955). A belt of variable width composed of different species of mangroves is found in the coastal zone (Pannier, 1979; Huber and Alarcón, 1988; CVG-Tecmín, 1991; Huber, 1995). T

In the upper and middle Delta, the flora is composed purely of freshwater species. In the Upper Delta the forest dominant species are *Ceiba pentandra* (Bombacaceae), *Ocotea* sp (Lauraceae), *Mora excelsa* (Caesalpinaceae), *Erythrina* sp (Fabaceae), *Tabebuia capitata*

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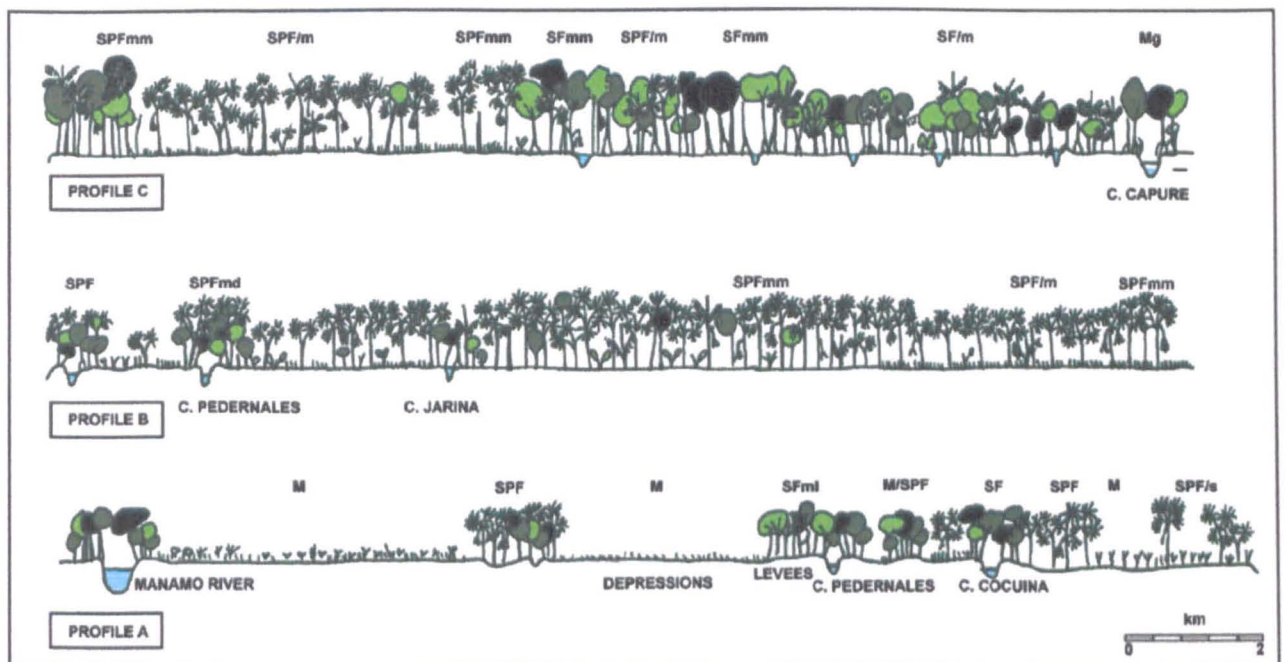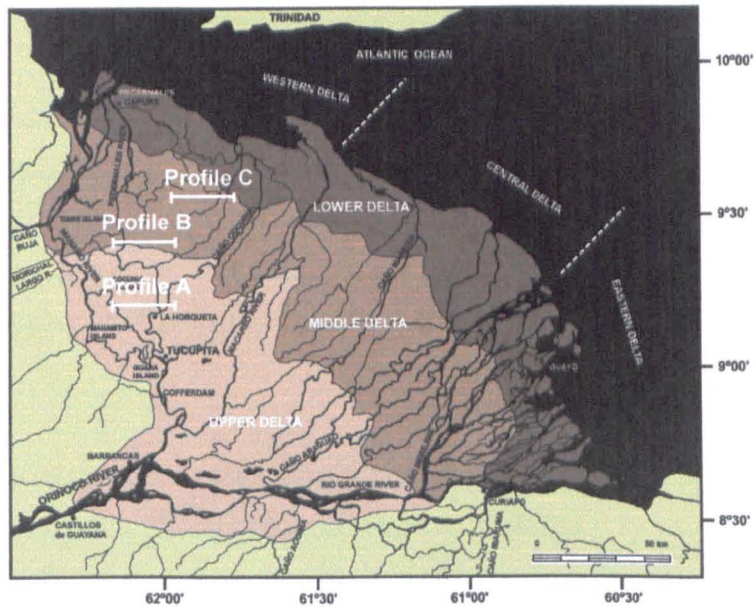
Fig. 2.8. Schematic profiles of the vegetation communities in the Upper Delta (profile A); Middle Delta (profile B); and Lower Delta (profile C). Key for symbols in section 9.3.1

(Bignoniaceae), *Spondias mombin* (Anacardiaceae), *Triplaris surinamensis* (Polygalaceae), *Gustavia augusta* (Lecythidaceae) and *Licania densiflora* (Chrysobalanaceae) (CVG-Tecmín, 1991; Huber,1995).

In the Middle Delta the commonest trees species are *Symphonia globulifera* (Clusiaceae), *Virola surinamensis* (Myristicaceae), *Carapa guianensis* (Meliaceae), *Pterocarpus officinalis* (Fabaceae), *Mora excelsa* (Caesalpinaceae), *Pachira aquatica* (Bombacaceae). Palm trees such as *Mauritia flexuosa, Euterpe oleraceae, Manicaria saccifera* and *Bactris* sp. (Arecaceae) are also dominant. (CVG-Tecmín, 1991; Huber, 1995) (see detailed descriptions in chapter 4).

In the Lower Delta few tree species are widely distributed, *Pterocarpus officinalis, Symphonia globulifera, Euterpe oleraceae*, and *Tabebuia insignis* and *T. fluviatilis*.

Estuarine species are distributed along the coastal belt and upriver almost as far as there is tidal influence. Large colonies of dense mangrove forests form the outermost vegetation type, growing along the extensive shoreline. According to Pannier and Fraino de Pannier (1989) mangroves cover approximately 4,600 sq. km of the outer Delta. These medium-sized tree species are composed of just a few species, *Rhizophora mangle* in waters with higher salinity, *Avicennia schaueriana* and *Laguncularia racemosa* found in more brackish waters (Huber, 1995). However as it will be seen in chapter 8, *R. mangle* may occupy also river shores with low salinity sediments due to its ecological adaptation to low salinity levels of up to 6 $^{o}/_{oo}$ (Pannier and Rabinovich, 1976). This species may grow as well along the shore because it has a high tolerance to tidal oceanic conditions (Nilsen and Orcutt, 1996), even if the plants are smaller in size. Other halophyte macrophytes are extending their distribution upriver as a consequence of the river regulation. This is particularly true of mangroves and aquatic macrophytes, as will be discussed in chapters 6 and 8.

Species such as *Eichhornia crassipes, Echinochloa polystachya, Paspalum fasciculatum* and *Paspalum repens* occur in the river fringe vegetation, forming meadows of floating and emergent species, which are among the most important and abundant aquatic macrophytes in large tropical rivers (Junk, 1970; Neiff, 1986). In the inland marshes, Poaceae species such as *Leersia hexandra*, Cyperaceae such as *Oxicarium cubensis* and Onagraceae species such as *Ludwigia* spp. are encountered.

The eco-community term 'floating and emergent meadow' is widely used in this study in accordance to the meaning given by Junk (1970-1973) to the floating vegetation, composed

by the emergent (rooted) and floating species communities along the rivers banks in the Amazon Basin.

2.5.2 Plant communities

Two detailed reports and maps of the Delta communities has been prepared by Canales (1985) and CVG-Tecmín (1991). Canales (1985) focuses his study on the natural resources of the region as well as the exploitation systems and their actual and potential management though species and communities are not described in detail. CVG-Tecmín, (1991) on the other hand, classifies all the communities on the basis of their structural characteristics, but stresses only those species having economic value as timber.

Table 2.4, shows the distribution of plant communities, according CVG-Tecmín (1991). The study includes 14,900 sq. km (1,490,000 ha), from 8° 58' N to the coast (see Fig 2.3), that represent approximately 67% of the alluvial region. The eastern half, from the 61° 50' E to the coast, has a macrothermic tropophylous climate and the remainder a macrothermic ombrophylous climate (Fig 2.6). The forest types that account for 46 % of the total alluvial vegetation, include six different community types (not shown in Table 2.4). Swamp forests of low height and medium density in the Lower Delta occupy 30%, whilst the percentage for mangroves is 7.5% of the area -being particularly well distributed in the coastal belt. A mixture of forest species, including eight more structural types, account for the 11.3% of the forested.

The herbaceous vegetation (38.4%), includes many associations with isolated trees (and palms), clusters of trees and patches of swamp forests or swamp palm forests (see chapter 9). The classification also divides the formations where the forest dominates, into the dominant herbaceous vegetation and vice-versa. The dominant communities (Table 2.4 and Fig. 2.8) are the medium and dense swamp forests with marshes (1.81%) in the Middle and Lower Delta; the marshes with isolated trees and swamp forest (1.52%) in the Middle Delta as well; and the drought marshes with clusters of trees of the Upper Delta (0.84%), produced due to the Mánamo river regulation.

An important community area is listed as the marshes with isolated, clustered palm trees and palm forests (morichales), that occupy large areas (18.9% of the total area surveyed) of the Middle and Lower Delta (see section 4.3.1). Another important area, some 168,722 ha (11.3%) has been classified as mixed communities of forests and marshes with anthropogenic influence, mostly in the Upper Delta in the regulated Mánamo sub-Basin. A discussion of anthropogenic influence on vegetation communities dynamic is presented in chapter 9.

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The mentioned distribution coincides with the general pattern presented in Fig 2.8, the swamp forests occupying the Middle and specially the Lower Delta region. Human occupation of the land mainly inhabiting the Upper Delta is closely related to the intensity of the disturbance and the distribution of the communities types. Other large deltas intensively occupied and developed have already lost their lowland forest cover derived to savanna with small areas of intact forest remaining (Moffat and Lindén, 1995)

Table 2.4. Herbaceous and forest formations of the Orinoco Delta (CVG-Tecmín, 1991).

Formation	Community type	Area (ha)	%
Wooden	Forests	444,429.80	29.83
	Mangroves	111,130.87	7.45
	Mixed forests	168,956.70	11.32
	Sub-total	725,017.29	46.63
Herbaceous	Marshes with trees and forest patches	97,774.14	6.56
	Forests with marshes	67,493.80	4.52
	Marshes with trees and large forests	41,618.30	2.79
	Marshes with forests patches	12,568.83	0.84
	Marshes with trees and Swamp palm forests	282,479.49	18.95
	Forests with anthropogenic intervention	168,722.40	11.32
	Sub-total	572,883.52	38.42
Water bodies		9,522,50	6.39
Total		1,490,900.00	100

2.6 The hydrological cycle

The beginning of the wet season, as shown in Fig 2.6 and Fig. 2.7, occurs two months before the peak flow in the Orinoco and has important effects on the lakes and lagoons of the Upper Delta. The regional rainfall and runoff is a potentially significant water input for lagoons and

marshes (Hamilton and Lewis, 1990a). The water input to a particular water body, its source and volume, can directly modify and change chemical and physical properties such as nutrient availability, degree of substrate anoxia, soil salinity, sediment properties and pH. Except in nutrient-poor bogs, water input is the major source of nutrients to wetlands; water outflows often remove biotic and abiotic materials from wetlands as well (Mitsch and Gosselink, 2000).

Figure 2.9 is a schematic representation of the series of hydrodynamic processes to which the bodies of water (particularly temporary lagoons and ponds) of the Upper Delta, are subjected. The components involved, precipitation, evapotranspiration, surface inflow, surface outflow and groundwater flows. These are the general components of any wetland water budget (Mitsch and Gosselink, 2000) and determine the hydro-period of the water body. The ponds described in the Delta region fit the general model of coastal marshes (Mitsch and Gosselink, 2000), with a surface inflow, runoff and flooding through neighbouring streams, surface outflows, precipitation and evapotranspiration. In some areas of the Upper Delta, due to the relatively good drainage, the groundwater inflow and outflow may be included. In the Lower Delta the tidal inflow and outflow is also a relevant component, because the influence of the ocean tides is much higher than fresh water from rainfall as will be discussed in section 2.7.2. An example of the water budget for a floodplain lagoon in the Lower Orinoco River was presented by Hamilton and Lewis (1987)(Table 2.5). The authors included the input from the main river, from the associated lagoon, from the runoff and from rainfall. Whilst output to the main river, to the associated lagoon and via evaporational losses. The lagoon showed a net storage of 0.6 x10^{6}m^3
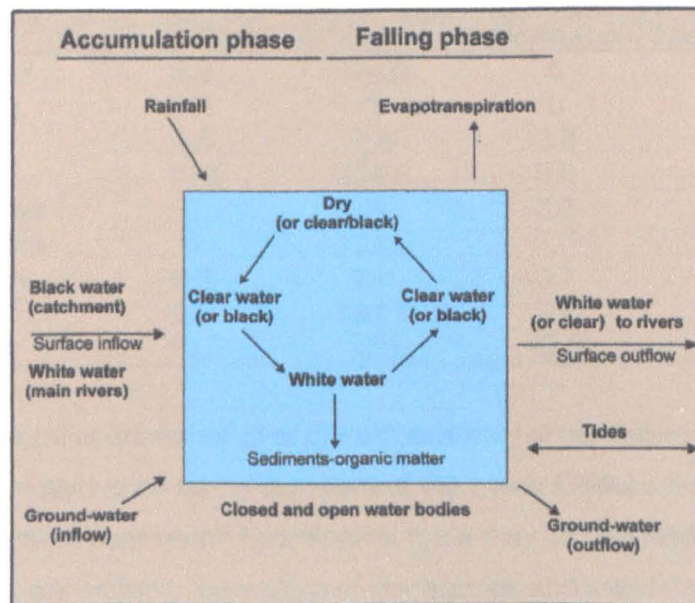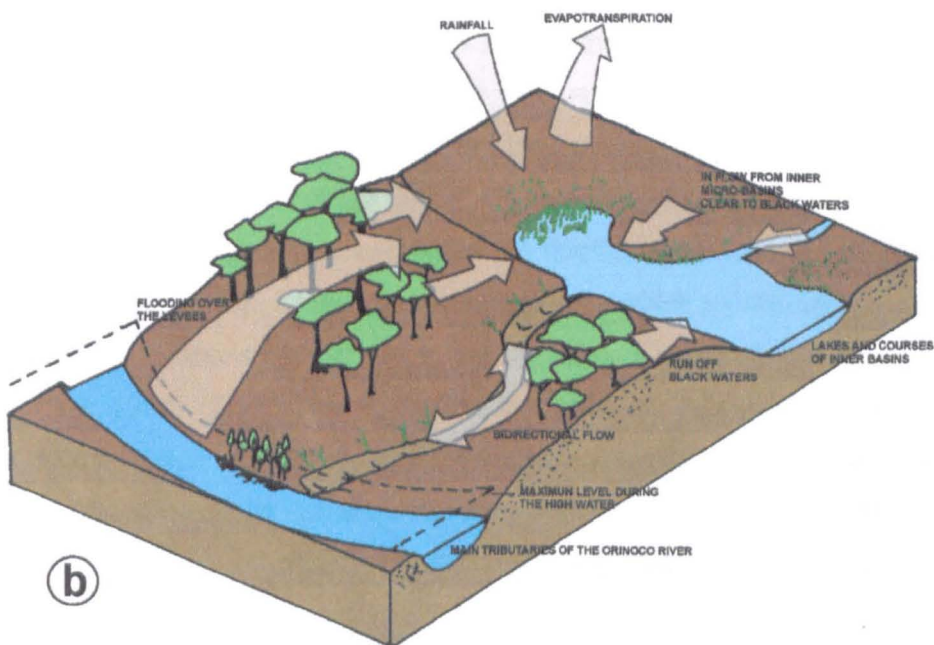
Fig. 2.9. Schematic diagram (2.9a) and profile (2.9b) of the hydrologic cycle in the Delta region. In the Lower Delta-over flow is due to tidal accion.

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Table 2 5 Water budget ($0.6\ 10^6 m^3$) for Lake Tineo (Adapted from Hamilton and Lewis, 1987).

	Filling	Through flow	Drainage	Isolation
Inflow. River	8.8	155.8	0	0
Inflow. Piña	1.5	0	0	0
Rainfall	0.5	2.4	0.8	0.5
Total gain	10.8	158.2	0.8	0.5
Outflow. river	0	0	5.3	0
Outflow. Piña	0	158.9		0
Evaporation	0.3	2.4	0.7	2.1
Total Loss	0.3	161.3	0.6	2.1
Net storage	10.5	-3.1	-5.2	-1.6

The physical and chemical characteristics of the lagoons may show strong seasonal fluctuations. This has proved to be so for the lakes of the Lower Orinoco floodplains (Hamilton and Lewis, 1987). A typical year-round hydrological cycle may be described as follows: Towards the end of the dry season, the waters of the lagoons and rivers reach their lowest level. Many of the lagoons become dry. As the rains begin, preceding the rise in river levels(Fig 2.7), the depressions rapidly fill with water due to the low permeability of the soils (Fig. 2.9a). In most of the lagoons and marshes, the surface waters contain a high level of organic matter, produced by the runoff through the litter of the woody or herbaceous vegetation (Hamilton and Lewis,1987), often resulting in waters that are black, acidic and poor in nutrients. When the level of the main rivers reach their maximum between July and August (Fig 2.7), as a consequence of the onset of the wet season in the headwaters of the Orinoco River basin, waters with a high sediment load enter the floodplain via small channels or by overflowing the levees (Fig. 2.9b). The waters then, become white waters (Fig. 2.9a), basic in pH and with high levels of cations and anions similar to values found in the Orinoco waters (Lewis and Saunders, 1990). Due to the sediment deposition, and chemical processes, such as nutrient and organic matter incorporation and release, the waters become transparent. The isolation phase begins with the subsequent fall of the water, along with the receding of river levels, and evaporation. The waters may first becoming black before eventually drying out altogether (Fig. 2.9a).

Towards the end of the wet season, the process of sedimentation of organic particles, depletion of nitrate, growth of phytoplankton and depletion of dissolved oxygen (Hamilton and Lewis,1987) changes the surface waters back to a clear state. As the waters recede from the plain and evaporates from the lagoons and marshes, the condition of the remaining water changes due to the concentration of sediments, the increasing daytime temperatures and diminishing oxygen supply in the water.

A clear example of such a transformation of the physico-chemistry of the waters was presented by Hamilton and Lewis (1990a), in a study of five water bodies which showed a period of 'chemical divergence' during the isolation phase. Each of the lagoons showed somewhat different effects whilst maintaining a similar pattern with respect to the concentration of the principal ions in the stagnant water as well as the pH. The authors attributed the differences between lagoons to the morphological differences between the water-bodies, regulating the evaporation with the re-suspension of sediments. The physico-chemical characteristics of one of these water bodies are shown in Table 2.6 contrasting the two phases, inundation and isolation. Nutrient concentrations varied substantially while consistent seasonal variations were clearly visible for some variables, in particular the concentration of total particulates was always an order of magnitude higher at isolation phase than during the inundation phase.

Table 2.6. Contrasting physico-chemical variables for the Lake Tineo in the Orinoco floodplain. TSP: Total suspended phosphorus (Adapted from Hamilton and Lewis, 1990a).

Phase	Isolation			Inundation		
	April-May			July-November		
Dates	Apr-84	Apr-85	Apr-88	Jul-84	July-86	Jul-88
Ca^{2+} (mg l^{-1})	2,45	2,52	1,52	3	2,77	2,75
Mg^{2+} (mg l^{-1})	0,81	0,92	0,5	0,73	0,83	0,8
Na^+ (mg l^{-1})	3,47	3,56	1,76	1,18	1,09	1,35
K^+ (mg l^{-1})	1,03	1,59	1,33	0,77	0,91	0,1
Cl^- (mg l^{-1})	4,62	2,82	2,21	0,69	0,49	1,02
pH	6,7	7,2	5,7	6,6	6,3	6,6
Conductivity $\mu S\ cm^{-1}$	37,9	33	27,3	29,1	26,7	28,5
TSP (mg l^{-1})		36	49	17	19	

Similar processes are described in lagoons seasonally flooded by the Metica River system in the Colombian Orinoquia (Galvis et al., 1989).

2.6.1 Variability of water quality

Data collected throughout the study period (Table 2.7) shows the values of several water-bodies of contrasting characteristics, for the low water (December-April) and high water (May-November) periods. Changes in the pH levels are observed, particularly in the channels that flow from Imataca (Acoimito and Ibaruma), which are more acidic in the rainy period due to the influence of the organic matter transported by the channels. Transparency changed dramatically in Lag. Ataguía from 150 cm in September of 1993, when the lagoons were at

their highest levels (Macareo waters) to 18 cm in April of 1995, when the evaporative processes increased the concentration of suspended material in the waters. In most of the water bodies the levels of dissolved oxygen in the surface and depth increased from November at high water level to April at very low water level.

Table 2.7. Physico-chemical data of different habitats in the Delta region in contrasting seasons. L. Alam. = L. Alamilla; L. Ata. = L. Ataguia; L. Clav. = L. Clavellina; C. Ibar. =C. Ibaruma; C. Acoi. = C. Acoimito; C. Pede. = C. Pedernales; C. Flo.= C. Florida. H= High water (Sept. 1993) period; L= Low water period (April. 1995).

Variables	L. Alam.	L. Ata.	L. Clav.	C. Ibar.	C. Acoi.	C. Pede.	C.Flo.	Period
pH	5.3	5	6	4	5.4	6	6	H
	4.6	5.6	7.4	4.6	6.2	6.8	5.7	L
Cond (μScm^{-1})	38	34	160	35	34	200	28	H
	40	25	175	40	50	350	55	L
DO. Sur. (mg l^{-1})	6.8	1.6	2.1	1.1	1	1.6	0.4	H
	5.5	5.8	5.8	3.9	6.4	7	0.5	L
DO. Depth (mg l^{-1})	0.6	0.2	-	0.2	0.8	0.4	-	H
	5.2	5.4	-	2.4	5.8	6.4	-	L
Trans. (cm)	12	150	60	45	65	15	25	H
	-	18	83	55	63	108	-	L

Another interesting case of dramatic variations in the water quality is shown by the Cuberima and Mariusa channels (see Fig 2.3). During their exploration, in early July 1996, the local guides explained to us that the channels 'just became breathless', implying that they contained no fish. This temporary phenomenon also described for thye Amazon basin (Calheiros et al, 2000), is due to the reduction of the oxygen levels in the waters of the basin as a consequence of the high concentrations of organic matter which is washed from the upper and middle basin of the Mariusa channel at the beginning of each rainy season in July. Towards the end of the same month, the arrival of white waters via La Tortuga channel may be witnessed. These come from the Araguaito channel (white waters) to the south and via Caño La Playa, whose waters come from the Macareo to the north as witnesses in this study. The variables of the two types of waters in the channel 'Caño La Tortuga', at the moment when they transfer to the Mariusa basin, are as follow

Variable:	pH	Electrical conductivity ($\mu S\ cm^{-1}$)	OD (mg l^{-1})	Transparency (cm)
White waters	5,4	34	5,1	15
Black waters	5,2	50	0,1	35

Physico-chemical characteristics such as dissolved oxygen and transparency, of the waters are determinants of the prevailing composition and diversity of the aquatic flora as demonstrated in section 3.4.2. The Mánamo river regulation influenced the hydro-regime of its entire basin and in turn the water characteristics influencing the species composition and dominance (see chapter 3 and 6)

2.7 The damming of the Mánamo river and its influence on the environment
2.7.1 The Mánamo river
Until its regulation, the Mánamo river was one of the major branches of the system of distributary channels constituting the Orinoco Delta -discharging 10% of the total water carried by the Orinoco. Beginning at the confluence with the Macareo river it flowed for 195 km downstream to Pedernales, a coastal town in the Gulf of Paria (Fig. 2.3). According to topographic and geomorphologic criteria of the drainage basin (Canales, 1985; Van Andel, 1967), the Mánamo river can be divided (as was the case with the Delta) into the upper, middle and lower section. However due to the poor topographic and morphological data, the boundaries between these are unclear. Two sections are easily recognisable: the upper, encompassing the course between its origin and 120 km downstream, whose margins are characterised by old levees and high banks; and the lower section beginning at Isla de Tigre (120 km downstream) down to the sea. This section is characterised by lowlands flooded twice a day by the large tidal range of the Gulf of Paria of up to 2.5 m (Herrera et al., 1981; Natura SA, 1998). Intensity of flooding is also affected by heavy seasonal rainfall. It is the middle section that is difficult to define because of the scarcity of field measurements.

2.7.2 The regulation of the Mánamo river
The construction of a dam across the Mánamo river (Plate 2.1) and the 172 km of additional cofferdams in 1965 (see also Fig 2.10 b), designed to regulate its waters, represented the first large scale intervention in the Delta. Officially the purpose for its construction was to develop the agricultural potential of the area (CVG, 1972).

This regulation influenced the catchment area consisting of some 9,000 sq. km of the Western Delta. However the Central Delta and even the Eastern Delta some 13,000 sq. km, were also influenced, due to the increase of the water levels during the flow peaks in the middle of the rainy periods.

The consequences of the dam construction were reflected in dramatic changes in the hydrological regime (see Chapter 5) of the Mánamo, whose seasonal flooding regime has been eliminated. Before the regulation, the mean percentage discharge of the Mánamo and

the adjacent Macareo which branches away from it a few kilometres before the dam, were 10 and 6%, respectively, of the Orinoco River total discharge according to Tams (1956). The Wallingford Hydraulic Research Station, on the other hand used the following data to construct the hydraulic model of the closure of Caño Mánamo and Macareo: Mánamo 11.4% and Macareo 7.9% (Wallingford, 1969). Today however, the Mánamo discharges through the sluices only 0.5%, approximately 200 m^3 s^{-1}, whilst the Macareo has increased to 11% while the other distributaries of the Orinoco, chiefly the Rio Grande river, increased their discharge from 84 to 88 % to accommodate the excess of flow due to the natural restrictions on flow in the Macareo river(Table 2.8) (Funindez-USB, 1999).

Table 2.8 Water discharge of the Rio Grande, Mánamo and Macareo rivers (Funinvez-USB, 1999)

	% of Water discharge	
	Prior to regulation	Posterior to regulation
Rio Grande river	84	88
Mánamo river	10	0.5
Macareo river	6	11

Plate 2.2 shows the Mánamo and Macareo rivers at the site where the Macareo branch off from the Brazo Macareo. Prior to the dam construction the river bed of the Mánamo currently much reduced by sedimentation, was almost 1,000 m wider than that of the Macareo (250 m), however the banks of the Macareo are almost 2 times the height of the Mánamo (see section 6.3.1). On the other hand the difference in water discharge may be partly compensated by the increase of water velocity along the channel. In years of exceptional rains, however, the Macareo overflows its banks due to the increased water discharge even in the Upper Delta close to his union with the Mánamo, as has been documented during this study. The inhabitants of the Macareo river shores claim the lost of their crops and houses as a consequence of the unusual levels which are commonly reached after the Mánamo damming.
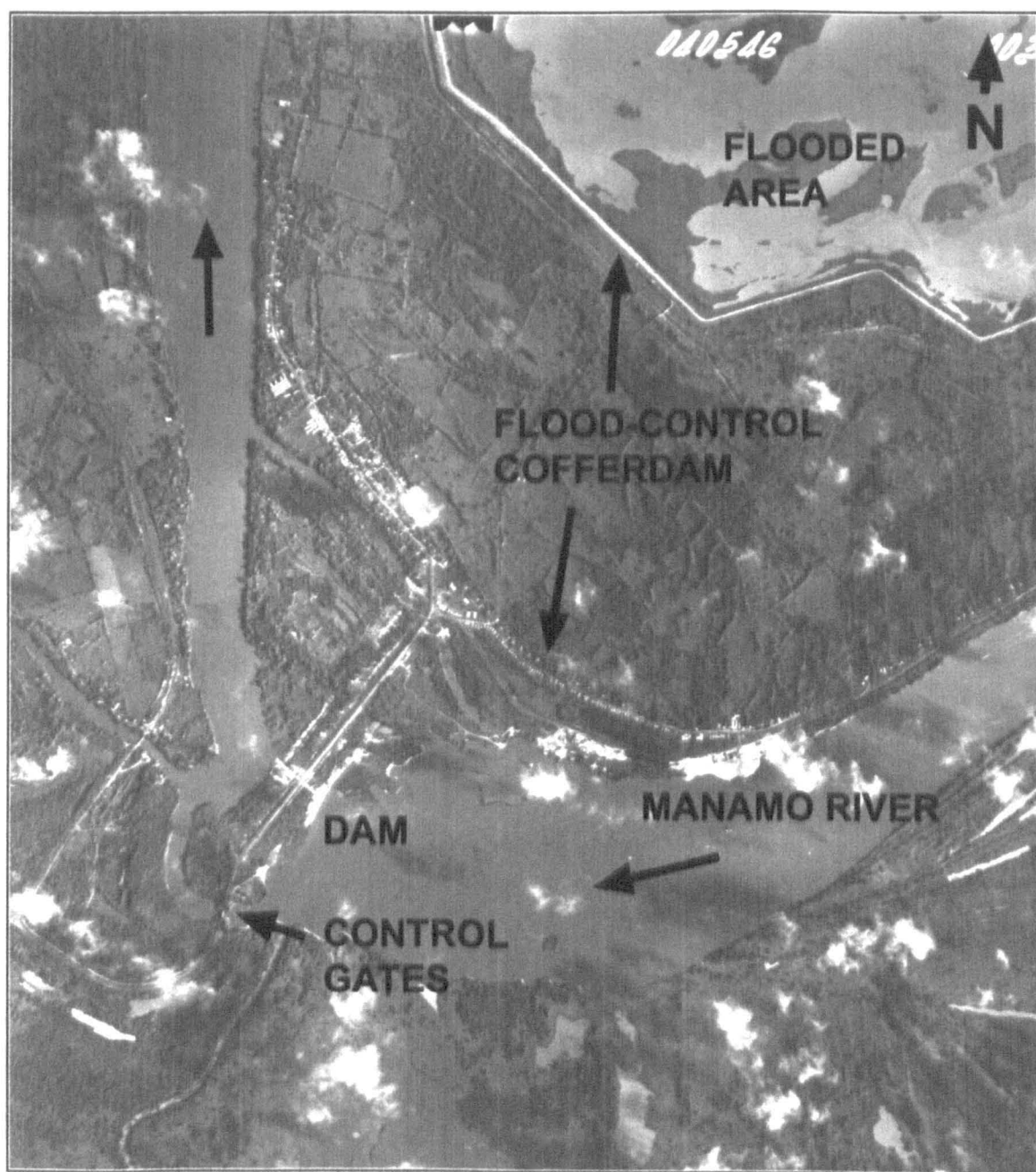
Plate 2.1. The dam in the Mánamo river. In this picture taken in the high water period, are noticeable the additional cofferdam built to protect the area from flooding

The result of the Mánamo river regulation was the transformation of a typical fluvial unregulated system into one that is now mostly estuarine, that is, influenced chiefly by a tidal system. Table 2.9. indicates the approximate water balance for the Mánamo river. Today the major part of the water flowing into the present Mánamo (and in turn into its sub-basin) comes from the sluices that discharge a mean of 200 $m^3 s^{-1}$. Other inputs are from the tributaries of the west shore of the Mánamo - the river Morichal Largo and El Tigre (Fig 2.3) with contributions of about 100 $m^3 s^{-1}$ (Buroz and Guevara, 1976; Funindez-USB, 1999) and from the regional precipitation, with an estimated contribution to the water of 0.07 x $10^9 m^3 yr^{-1}$. The ratios of water input /resident waters (in the river bed), indicate that the Mánamo requires an annual input of 5.3 times the existing water volume.

Table 2.9 Estimated water balance of the Mánamo river after the river regulation based on rainfall and evapotranspiration, data in Table 2.2).

	water input $10^9 m^3 yr^{-1}$	Ratio water input/ resident	Water output $10^9 m^3 yr^{-1}$	Ratio water output/ resident
Main channel	6.3	3.3/1	6.3	3.3/1
West-shore tributaries	3.2	1.9/1	3.2	1.9/1
Rainfall	0.21	0.13/1		
Evapotranspitarion			0.14	0.1/1
Water resident in channel	1.6		1.6	
Totals	11.31		11.24	

The main changes in the hydrology of the principal water courses of the Mánamo sub-basin and water discharge, before and after dam construction, are indicated in Fig. 2.10. The arrows indicate the direction of water flow, according to field observations. Prior to the regulation (Fig 2.10a) the Mánamo discharged an average of circa 3,600 $m^3 s^1$ into its basin. It should be noted that discharge during the dry period was considered negligible compared with the tidal effect. This included the Tucupita and Cocuina rivers as well as the main river. The latter two distributaries were important because they provided good quality irrigation water that flooded agricultural areas, and maintained the water-table in the inter-riverine terrain (see blue arrows in Fig 2.10a).

The regulation of the Mánamo led to the surplus water being drained from the inter-riverine terrain leading to a semi-permanent fall in the water-table of several metres.

After the dam construction (Fig. 2.10b), about 95 % of the Mánamo discharge was diverted into the Macareo and other distributaries whose discharge has risen to an average of 35,000 $m^3 s^1$ as determined by Funindez-USB (1999).

The discharge values shown in red in Fig. 2.10b, are due to water movement caused by the tides (red arrows). The chief drainage connections between the Mánamo river and its basin have been disrupted due to the obstruction of the Tucupita and Cocuina rivers (Fig. 2.10b). Currently the ratio of freshwater to brackish tidal waters in these tributaries is dependent on the rains. The ratio shows an increase from 1:11 in the town of La Horqueta (the Cocuina channel), to 1:17 in the lower section of the Pedernales river. This highlights the effects of the water availability within the basin (Delta Centro Operating Company, 1998). Currently (2000) also, the connection between the Pedernales and the Cocuina in the town of La Horqueta is also obstructed. The flow during low tide period is severely impeded by the debris in the shallow channel.
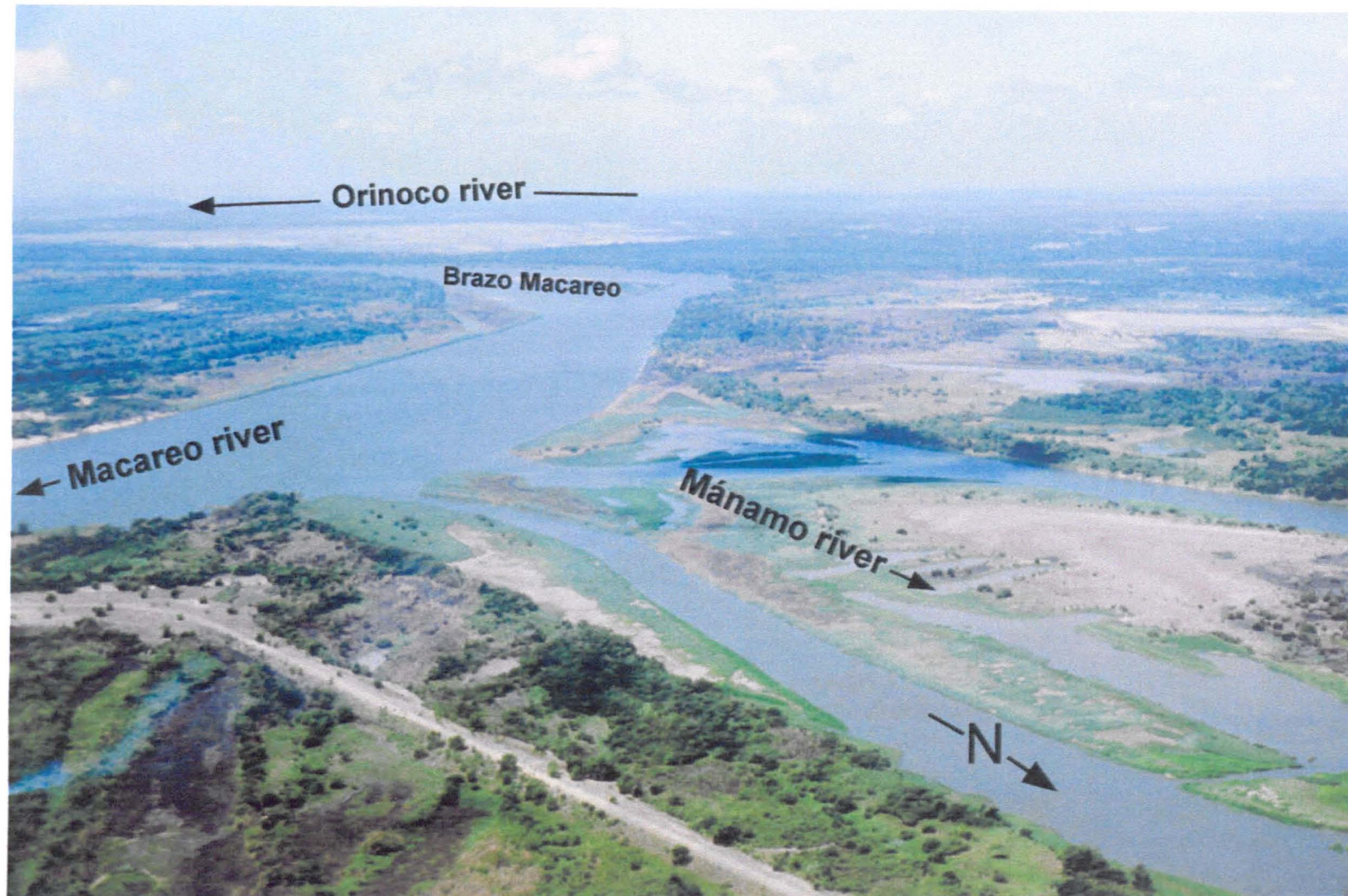
Plate 2.2 Mánamo and Macareo rivers. In the background flows the Orinoco river, not visible in the image. In the Mánamo are noticeable the sand bars covered with aquatic meadows, formed as a result of the dam construction.
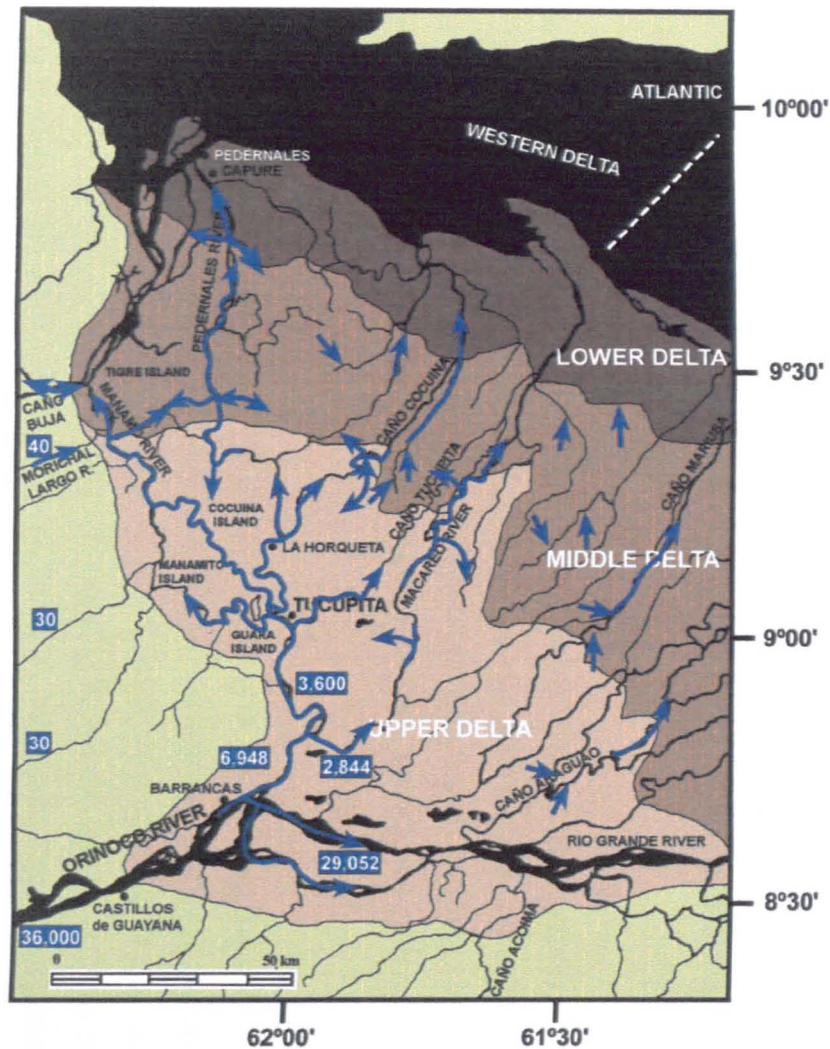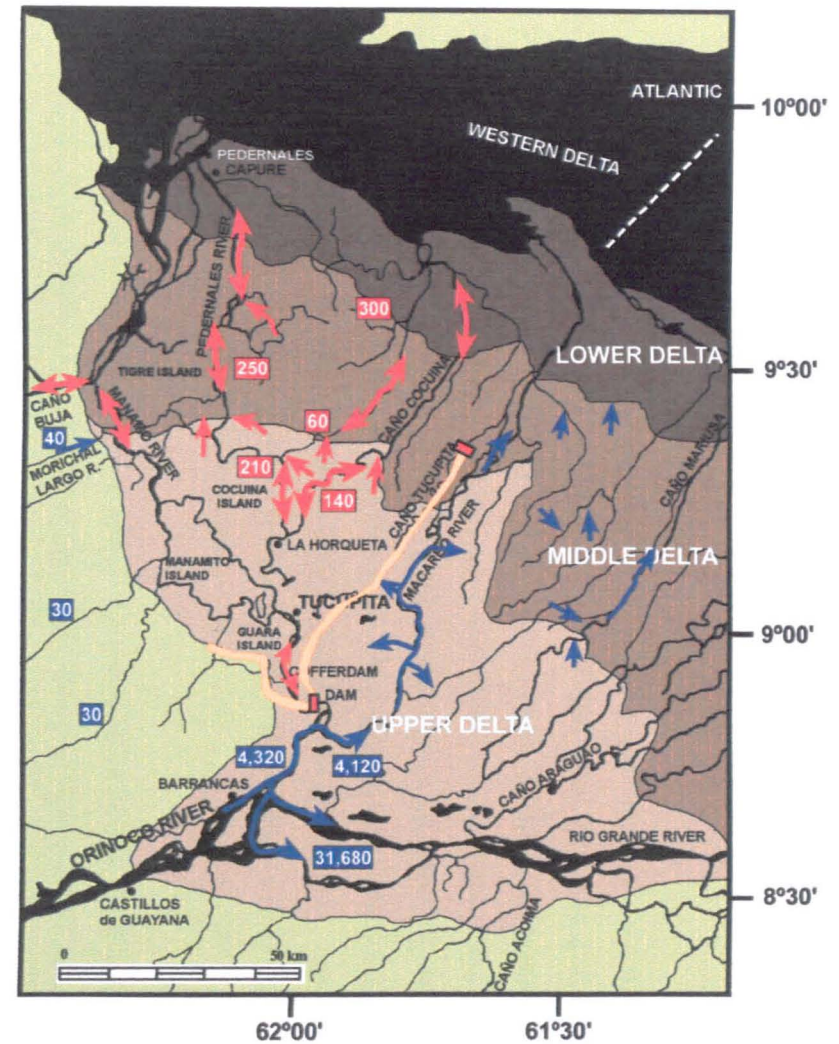
Fig. 2.10. Chief hydrologic changes produced by the dam.
a: Prior to the river regulation.
b: After the river regulation. Note the disconnection of the Cocuina and Tucupita channels.
Discharge data from: Delta Centro Operating Company, 1998.

Coffer-dam
300 Discharge (m³ s⁻¹) Regulated tidal water
300 Discharge (m³ s⁻¹) Unregulated Orinoco Water

The tidal regime is now a dominant influence throughout the year with the only positive runoff from the inter-riverine terrain to the main channels occurring when the local precipitation exceeds the evaporative losses which have been estimated to be 0.07 10^9 m^3 yr^{-1})(see section 2.3). A net runoff throughout the regulated basin would be achieved with a local precipitation of 1500 to 1800 mm y^{-1}.

The greatest biotic impact of regulation on the vegetation was along shores and banks of the principal rivers in the Mánamo sub-basin: Cocuina, Pedernales, Tucupita and Capure, and in the inland depressions (seasonally to permanently flooded). As a consequence, emergent and free-floating aquatic plants, including macrophytes and tree communities such as the mangroves or palms (which are also considered aquatic) were affected. Species diversity was reduced due to the disturbance that changed the habitat characteristics allowing the colonisation of aggressive species, better adapted to the new conditions. Successional processes initiated as a consequence of the new hydrologic regimes promoted fast species and communities replacements even inland.

Both the reduction in flow and in erosion with a consequent increase in sedimentation allowed banks to emerge from below the former water level. Several 'low season' islands in the main channel of the river also increased in size, becoming semi-permanent. They have been colonised mainly by aquatic emergent species initiating a primary succession. After thirty years the more elevated areas of the islands were covered by a dry forest up to 15 meters high characterised by deciduous species (as seen in Plate 7.1). The increase of area may reach 30 % of the island surface (see ch 8).

The change in the land-forms and the currents, has led to the disappearance from the shores of the upper main river course of some species such as *Echinochloa polystachya* and *Eichhornia azurea*. These were adapted to cope with significant changes in water level. Colonisation by *Montrichardia arborescens* along the river shores was also noted by Colonnello, (1998a).

As a result of the water diversion, the estuarine regime of the Mánamo sub-basin has been extended upriver. Although there have been no extensive water salinity measurements along the Mánamo river, reports of conductivity, sodium and chloride gradients have been given by Paolini *et al.*, (1983), and Olivares and Colonnello, (2000) (see chapter 5). The change of salinity has been observed by the local inhabitants from Boca de Tigre Island and even from locations upstream (see location in Fig 2.3) where there are reports that the Mánamo water becomes salty during the dry season..

It is possible that global warming may enhance the invasion of saline water into the Lower Mánamo through rising sea-levels. This could lead to the inundation of wetlands and lands close to sea level and increased salinity of estuaries (Boucher 1999). This somewhat remote scenario has been attracting the attention of the scientific community during the 1990s as evidenced in recent studies undertaken within in the 'Wider Caribbean Region' (Parkinson *et al.*, 1994).

Similar analysis in West Africa, comparing the expected sea level rise with the accretion promoted by the littoral mangrove has been undertaken in the Niger River Delta by Mofat and Lindén (1995). The Niger Delta is located at the same latitude as the Orinoco Delta and shares with it some common characteristics such as the flatness of the outermost region, a wetland surface area of about 20,000 sq. km, and a similar area occupied by freshwater swamp forest of about 11,000 sq. km. Flooding due to the sea water rise by the year 2100, is estimated conservatively at 2,700 sq. km by for 0.4 mm yr^{-1}, and 18,000 sq. km for a medium case scenario of 1 mm yr^{-1}.

In addition the inland soils of the Orinoco Delta have been affected also by river regulation. Indirect effects include, drains being excavated in the Upper Delta to protect the area from the flooding caused by the seasonal rains. The areas where the main agricultural development was projected were the islands surrounding the apex of the Delta -Guara, Cocuina and Manamito island. In fact Guara Island was totally drained (23,000 ha) by means of an extensive network of ditches. Also Cocuina island was partially drained some 44% (8,600 ha). Perhaps because the adverse results were already becoming clear, the drainage of the Manamito island was modified, so that only 8.7 % (1,800 ha) was drained by 1980 (CVG, 1980).

Although soil surveys were undertaken on Manamito Island and in the north of Cocuina Island, many areas were drained without an adequate soil survey being carried out (MARNR, 1979). As a result, with the drying out of the land, sulphide was produced from the iron and sulphur contained in the underlying marine clays (Dost, 1971), causing a chemical reaction leading to sulphate acid soils. As Van der Kevie (1972) has stressed "In the formation of potentially acid sulphate soils, it is not only the concentration of sulphides that is important, it is also the content of neutralizing components (which are restricted in the Delta region) that will prevent a strong acidification after oxidation of the sulphides upon drainage".

The result was the acidification of the fluvial soils to levels as low as 2.5 pH (COPLANARH, 1979). Reports have yet to be published on the exact extent and magnitude of the resulting acidification of the soils.

As well as the consequent impoverishment of the land under cultivation, the species composition of the islands mentioned above has also changed. They were covered by grasses such as *Paspalum fasciculatum* and *Hymenachne* spp (CVG, 1970) which today have partially disappeared. They are supplanted by Cyperaceae species such as *Cyperus giganteus*, *Eleocharis mutata* and *Eleocharis diffusus*. These aspects will be further explored in section 10.4.1.

A summary of the changes occurred in the Delta region as a consequence of the Mánamo damming is presented in section 10.3.1.

Chapter 3   The aquatic plant communities and their environment

One of the most important environmental aspect of the Delta territory is the complex network of water courses and the inland water bodies which are covered by a profusion of aquatic vegetation. The primary task of the study was to investigate the effects of river regulation on the Mánamo river, a distributary of the Orinoco. In order to achieve this task, it was necessary to establish an adequate knowledge of the aquatic plants, the macrophytes and their communities along the rivers. It was also important to construct an ecology of the inland plant communities, both wetlands and forests, which have remained largely unknown until the1990s (see chapter 4).

3.1 Aims

The aims of this section of the study may therefore summarised as follow:

- To carry-out a systematic collection of the aquatic macrophytes of the Orinoco Delta, followed by the detailed identification of species and communities.

- To analyse the herbaceous communities with respect to species composition and diversity, and to establish the relationship with the ecological parameters of the aquatic habitats.

This type of investigation would allow the formulation of a research hypothesis that would incorporate both classifications and ecological characterisation. A working hypothesis would therefore be that the plant species in the Delta occur in associations that can be largely determined from a group of environmental, physical and chemical parameters.

3.2 Methods

This section explores the methods that must be employed in order to establish relationships between the plant communities of the Delta and their ecological environment. It involves the choice of sampling sites, the methods of collection and the appropriate analysis techniques.

3.2.1 Sampling: Site location

The sampling sites, the geographical coordinates of which are provided in Appendix 1, were selected after a series of reconnaissance visits combined with the analysis of aerial photographs and radar images. They included representative samples of each habitat type covering the different types of wetlands present in most of the territory of the Orinoco Delta, 10 semi-permanent and permanent lagoon margins and 13 small to large river edges. A random method of selecting sites was not adopted in this study as the objective was to

characterize the different communities by their respective physical and chemical variables. Each site was defined by the particular topographic and lithological characteristics of that part of the river basin that they drain (Vásquez & Wilbert, 1992; Colonnello, 1993).

3.2.2 Methods: Data collection and analysis

The emergent, free-floating and submerged macrophytes (as defined by Cook, 1990) were systematically recorded at 23 sites (Fig. 3.1), during the high water seasons, between Sept. 1993 and Sept, 1995. Assemblages of plants, were collected preserved and then deposited in the herbarium of La Salle Natural History Museum (**CAR**) and in the National Herbarium of Venezuela (**VEN**). For the identification of specimens Stodola (1967), Fassett (1975), Cook (1990), Gortz-Van Rijn (1990) and Velásquez (1994) were consulted.

At each designated site, ten quadrat plots of 1 sq. m were randomly selected within an homogeneous vegetation zone. However such a random distribution was difficult to achieve because the depth of water at some of the sites impeded free access. The access by boat was sometimes difficult because of the high density of plant communities. Most of the sites consisted of a mixed formation of different plant types: free swimming, emergent, free-floating, floating and submerged species, according to the Cook (1990) classification.

Vegetation cover was recorded during the survey and assigned a DAFOR rating (Kent and Coker, 1992). This method, has been successfully employed in wetlands communities studies such as ditches and channels (Colonnello *et al.*, 1992).
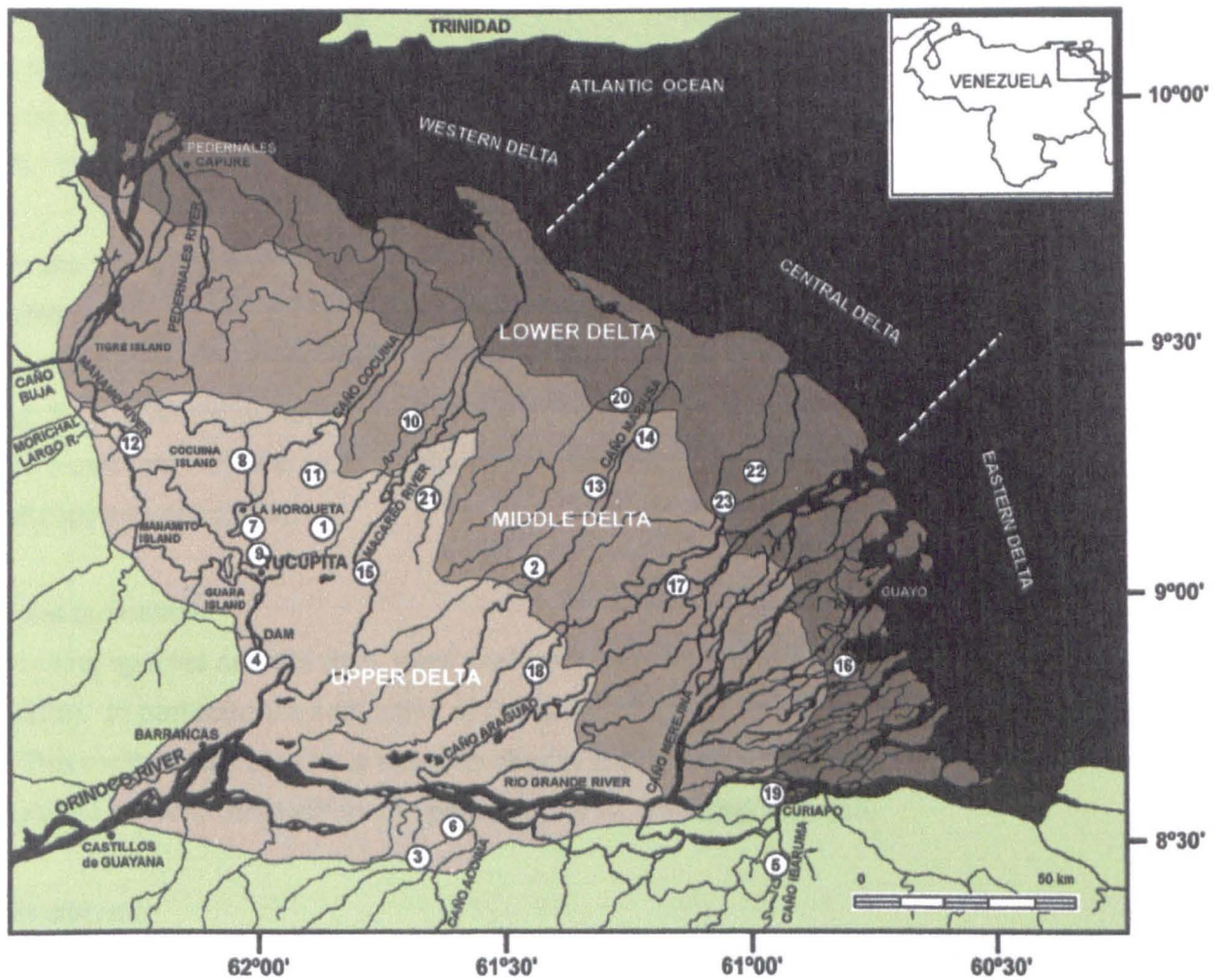
Fig. 3.1. Study sites of aquatic communities in the Delta region.

1. L. Terraplen
2. L. Travesia
3. L. Alamilla
4. L. Ataguía
5. C. Ibaruma
6. C. Acoimito
7. L. Clavellinas
8. C. Pedernales
9. La Florida
10. C. Tucupita
11. Los Guires
12. C. Mánamo

13. C. Mariusa
14. Isla Mariusa
15. C. Macareo
16. B. Merejina
17. C. Coboina
18. A Araguao
19. Curiapo
20. C. Cuberima
21. C. Guapoa
22. C Guiniquina
23. P. Jarahuaja

Each type of vegetation to be surveyed was categorised,. For each category of vegetation a DAFOR rating was assigned to allow further analysis of diversity, and numerical ordination. The cover range of each DAFOR scale was therefore as follows:

Dominant = 70-100 %; Abundant = 30-70 %; Frequent = 10-30 %; Occasional = 3-10 %; Rare = 0-3 %. The mean value of cover for each species in the ten plots was then calculated.

At each site the following variables were measured: water depth, colour, transparency (Secchi disc), electrical conductivity, dissolved oxygen (DO on surface and at 2 m depth) and flow rate (where appropriate). These variables are important in the characterization of aquatic habitats (Wetzel, 1981). Water samples were refrigerated and sent for laboratory analyses to determine calcium, magnesium, potassium, iron, phosphorus, and pH (for detailed methodology see chapter 5).

Numerical ordination:

The resulting species and site data, were analysed using the CANOCO package (Ter Braak, 1987-1992). In particular the subroutine of Canonical Correspondence Analysis (CCA) was used. This method was chosen to examine directly the association between patterns of macrophytes species composition and patterns of environmental variation.

Species diversity

Floristic diversity was estimated by both number of species (species richness) and diversity indices, that express species richness combined with their relative abundance.

The species diversity of the different sites was assessed using the Shannon-Wiener index (H'). This index was used due to the relatively simple structure of the community. In such cases the samples included all the species at the site. On the other hand in Shannon's index, the species are standarised to proportions, in contrast to the McIntosh index (Kent and Cooker, 1992).

Shannon-Wiener index was calculated using the formula:
$$H' = - \sum_{i=1}^{S} P_i \ln_e P_i \qquad \text{(Eq 3.1)}$$
where S is the number of species and P_i is the proportion of individuals of the i th species.

Equitability was calculated with the formula:
$$J' = H/Hmax = H/\ln_e S \qquad \text{(Eq 3.2)}$$

Similarity indices.

It is often advantageous to make comparisons among samples taken at different sites, because species usually develop in different ways placing variable demands in their habitat. (Wolda, 1981). Thus a numerical difference in species between two or more sites may be important. These differences are tested by indices that evaluate the presence or absence of species in two samples and the species common to both, as Sorensen's Index.

The Sorenson's Coefficient of Community (S_s) index was chosen in preference to the Jaccard method because its suitability for both quantitative and qualitative data. It also gives weight to species that are common to multiple plots rather than to those that only occur in either sample (Kent and Coker, 1992). Similarity was calculated and the results presented as a matrix, using qualitative (presence/absence) species data.

Sorenson's Coefficient of Community S_s is calculated with the formula:

$$S_s = \frac{2a}{2a+b+c} \qquad \text{(Eq 3.3)}$$

Where a is the number of species common to both sites,

b is the number of species in the site 1 and

c the number of species on site 2.

3.2.3 Site descriptors

Initial physical and floristic descriptions are provided in Appendix 5 for each of the study sites. A preliminary characterization of the waters was made based on the physical characteristics of transparency and colour (according to Sioli, 1965). The following types were identified:

1. White waters are those relatively rich in sediments (and nutrients), of low transparency with neutral to slightly acidic pH values;

2. Black waters, that derived their colour from the high concentration of dissolved carbon (Lewis and Saunders, 1990). They are typically extremely poor in suspended sediments (and nutrients), of high transparency and acidity;

3. Clear waters are those with characteristics between the above-mentioned categories, constituting a transitional stage between white and black water.

Sites were also divided into two categories, lentic habitats and lotic habitats. The lentic habitats were characterised in this study, basically, by showing:

1. Slow current velocities up to 10 cm s^{-1};

2. Low rate of water rise during inundation (by flooding or rain events); and

3. Long periods of relatively stagnant water conditions.

3.3 Results

3.3.1 Floristic composition of aquatic plants.

More than 200 macrophytes species were collected, including free-floating, emergent and submerged. Up to now, 174 species have been identified and are shown in Appendix 2. Mánamo

The families with the most species (Table 3.1) were: Poaceae with 33 species, the dominant genera are *Panicum* and *Paspalum*, the majority of which are floating and emergent plants; Cyperaceae with 24 species, *Cyperus* and *Eleocharis* being the dominant genera; Papilionaceae with 12 species and Alismataceae, Rubiaceae and Onagraceae with 7 species.

Due to the scarcity of botanical collections from the Delta region of the Orinoco, an identification key of the Poaceae species was prepared to facilitate this task. This is presented in Appendix 3. The description of the species and the illustrations are shown in Appendix 4. The extensive survey undertaken revealed a new record for the flora of the Delta and the Venezuela territory, the Poaceae *Spartina alterniflora* Loisel. This species is widely distributed in North and South America and was collected in the Mánamo mouth growing in muddy and saline beaches (Colonnello, in press).

Table 3.1. Number of species by family.

FAMILY	# SP	%
Poaceae	33	13.64
Cyperaceae	24	9.92
Papilonaceae	12	4.96
Alismataceae	7	2.89
Rubiaceae	7	2.89
Onagraceae	7	2.89
Arecaceae	6	2.48
Pontederiaceae	5	2.07
Euphorbiaceae	5	2.07
Asteraceae	5	2.07
Lemnaceae	5	2.07
Scrophulariaceae	5	2.07
Polipodiaceae	4	1.65
Guttiferae	4	1.65
Malvaceae	4	1.65
Marantaceae	4	1.65
Mimosaceae	4	1.65
Moraceae	4	1.65
Lythraceae	3	1.24

Musaceae	3	1.24
Araceae	3	1.24
Caesalpiniaceae	3	1.24
Convolvulaceae	3	1.24
Verbenaceae	3	1.24
Others		30.57

3.3.2 The herbaceous communities and their environment

In order to analyse the diversity and distribution of the species across the sites according to their physico-chemical variables, the data were analysed using a variety of routines of Canonical Ordination Analysis (Ter Braak ,1987-1992). As a first attempt to study both groups together produced no clear result the data were divided (1) into species belonging to floating meadows, that occur mostly on the water surface and (2) those belonging to emergent meadows. The latter are capable of surviving for long periods on non inundated soils such as obligate hydrophytes and facultative hydrophytes (according to the definition of Nilsen and Orcutt 1996)

The species belonging to floating meadows and those belonging to emergent meadows and their cover are shown in Appendix 6. The physico-chemical data are shown on Table 3.2.

Variables/Sites	Lag. Terr aplén	Lag. Trav esia	Lag. Alam illa	Lag. Atag uía	Lag. Clav ellinas	C. Guini quina	P. Jara huaja	C. Mari usa	Isla Mari usa	C. Ibaru ma	C. Acoi mito	C. Gu apo a	C. Cube rima	C. Pede rmale	C. Flori da	C. Tuc upit	Cie. Gui res	Maca reo	Curia po	Barra Mere jina	Mán amo	C. Cob oina	Alto Arag uao
pH	5	5	5.3	5	6	5	3	5	5	4	5.4	5	5	6	6	6	6	6	6.3	5.9	6.3	5.5	6.1
Cond ($\mu S\ cm^{-1}$)	40	30	38	34	160	73	92	50	38	35	34	37	160	200	280	280	260	31	22	35	41	29	15.5
OD.sup.($mg\ l^{-1}$)	1.6	0.4	6.8	1.6	2.1	3.8	1.2	0.3	0.4	1.1	1	0.2	1.5	1.6	0.4	0.2	0.4	6.6	5.5	8.6	7	6.8	7.2
OD.fondo ($mg\ l^{-1}$)	0.2	0	0.6	0.2		2.3	0.2		0.2	0.2	0.8	0.1	0.3	0.4				5.4	3.6	6.7	6.8		6
Transp. (cm)	100	95	120	150	60	50	25	20	40	45	65	100	22	15	25	40	20	10	8	25	25	10	25
HPO_4^{2-} ($mg\ l^{-1}$)	0.75	0.69		0.3	0.04	0.44	1.65	0.47	0.47	0.22			0.28	0.01	0.54			0.94	1.1	1.1	0.31	1	5.2
$Fe^{2+,3+}$ ($mg\ l^{-1}$)	0.4	0.4	0.66	0.25	0.7	0.95	1	0.4	0.6	0.6	0.24	0.3	0.6	5.4	5.6		3.4	0.5			0.8	0.7	0.2
Mg^{2+} ($mg\ l^{-1}$)	1	0.3	0.2	0.8	7.5	0.8	0.2	0.4	0.5	0.2	0.1	0.8	0.5	7.5	10		7.5	0.3	7.95	2.2	0.3	0.4	0.5
Ca^{2+} ($mg\ l^{-1}$)	2.1	1	0.61	2.1	1.6	2.26	0.43	1.5	1	0.52	0.57	1.7	1	2.8	9		2.6	1.37	1.56	1.8	1.35	1.42	2.24
K^+ ($mg\ l^{-1}$)		0.7				0.85	0.5	1	0.7	0.7			0.7					0.6	0.74	0.53	1.7	0.6	1.2

Table 3.2. Physico-chemistry variables of the study sites.

3.3.3 The floating communities

The relationships between the species within the sites and the sites similarity, within the floating communities are discussed below in terms of the species diversity, site similarity and numerical ordination.

Species diversity

The results from the analysis of species distribution using the relative frequency and constancy and of diversity using Shannon's index in the sites, are shown in Fig. 3.2, a and b (respectively).

The commonest species observed at the sites (Fig. 3.2a) were *Eichhornia crassipes* (17 sites), *Salvinia auriculata* (17 sites), *Paspalum repens* (14 sites) and *Eichhornia azurea* (14 sites), accounting for the 74, 74, 61 and 61 % (respectively) of the sites investigated. Four species, *Phyllanthus fluitans*, *Utricularia hydrocarpa*, *Sagittaria latifolia* and *Heteranthera reniformis*, were recorded in only one site.

The sites with higher diversity indices (Fig. 3.2 b) were lagoons such as Lag. Alamilla, Lag. Ataguía, Lag. Terraplén (sites 3, 4 and 1; Fig. 3.1) and minor rivers and distributaries such as the Caño Ibaruma and Caño Acoimito (sites 5 and 6, Fig. 3.1). In contrast, the sites with lower species diversity were large distributaries such as the Macareo, Alto Araguao, Mánamo and Caño Pedernales. Habitats such as Ciénaga Los Guires a highly contaminated site and Pozo Jarahuaja a pond with low acidity also showed low diversities.

Site similarity

The results from the analysis of site similarities using Sorenson's Coefficient of Community (Ss), are presented in Table 3.3 a and b. The sites matrix has been constructed sorting the sites by their species diversity order (see previous section) and divided (for practical purposes) into the two groups of sites having the higher similarities (on the opposite sides of the matrix). A full matrix is presented in Appendix 7.

The relatively high similarity values link the sites of lentic habitats (Table 3.3 a), such as the lagoons Lag. Alamilla, Lag. Ataguía, Lag. Travesía, Lag. Terraplén and Lag. Clavellinas,

Fig. 3.2. Floating species, a)constancy and frequency, and b) diversity and equitability.
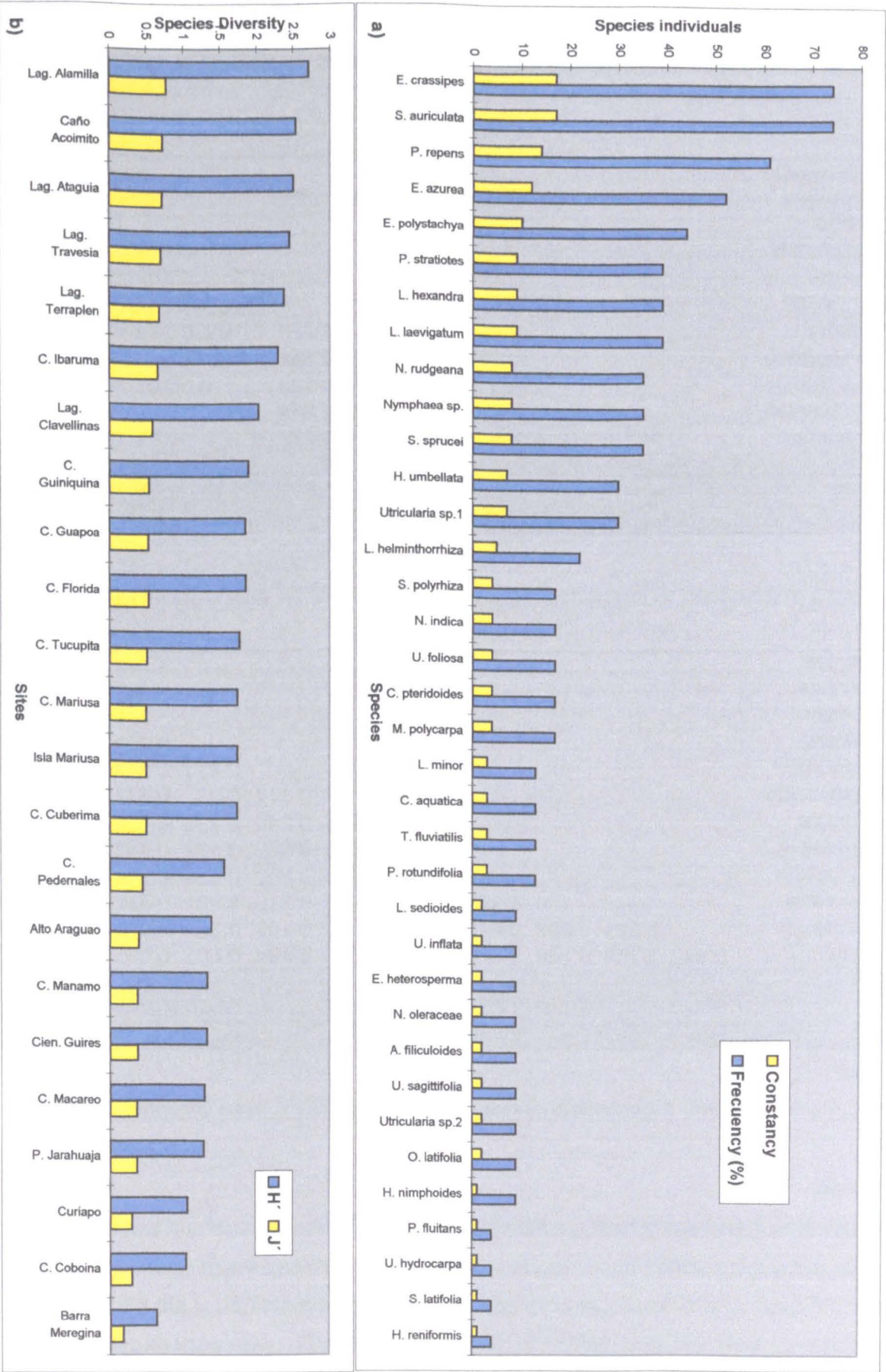
also the two streams Caño Acoimito and Caño Ibaruma. The other group of high similarities was found between the lotic habitats (Table 3.3 b) of the large rivers such as Mánamo, Macareo, Caño Coboina and Barra Merejina, the latest site is located in the lower section of the Caño Merejina one of the largest distributaries of the Río Grande (see Fig. 3.1). The higher similarity values link the species of the neighbouring rivers, the Mánamo and the Macareo.

Table 3.3 a. Sorenson´s Coefficient of Community Similarity for lentic habitats. Higher values in bold.

	Lag. Acoi	Lag. Atagu	Lag. Trave	Lag. Terra	C. Ibaru	Lag. Clavel	C. Guini	C. Guap	C. Florid	C. Tucup	C. Mariu
Lag. Alamilla	**0.415**	0.286	**0.364**	0.216	0.182	0.25	0.154	0.207	0.087	0.087	0.222
Lag. Acoimito		**0.367**	**0.356**	0.286	0.3	0.222	0.148	0.25	0.286	0.258	0.214
Lag. Ataguía			**0.383**	**0.4**	0.2	0.313	2.58	0.276	0.267	0.276	
Lag. Travesía				0.242	**0.368**	0.285	0.276	0.345	0.285	0.24	
Lag. Terraplén				0.278	**0.489**	0.323	**0.353**	0.231	0.222	0.231	
C. Ibaruma					**0.462**	0.345	0.333	0.333	0.296	0.308	
Lag. Clavellina						0.111	0.32	0.211	0.2	0.4	
C. Guiniquina							0.211	**0.381**	0.3	0.133	
C. Guapoa								**0.364**	0.211	0.3	
C. Florida									**0.381**	0.143	
C. Tucupita										0.133	
C. Mariusa											

Table 3.3 b. Sorenson´s Coefficient of Community Similarity for lotic habitats Higher values in bold.

	C. Cubei	C. Peder	Alto Aragu	C. Mána	Cien Guire	C. Macar	P. Jarah	Curia po	C. Coboi	B. Mereg
Isla Mariusa	0.348	0.316	0.333	0.333	0	**0.471**	0.154	0.267	**0.381**	**0.375**
C. Cuberima		0.125	0.316	**0.381**	0	**0.364**	0	0.25	0.333	0.267
C. Pedernales			0.267	**0.353**	0.154	0.333	0	0.286	0.333	**0.4**
Alto Araguao				**0.444**	0.167	**0.421**	0.182	0.308	**0.421**	0.333
Mánamo					0	**0.625**	0.167	0.308	**0.421**	0.333
Cie. Guires						0	0.182	0	0	0
Macareo							0.2	0.285	**0.455**	**0.4**
P. Jarahuaja								0.333	0.167	0.222
Curiapo									0.286	0.222
C. Coboina										**0.4**
B. Meregina										

The results of applying the similarity index between the two major groups of lentic and lotic habitats, were analysed . No clear division emerged as some sites such as Caño Acoimito

and Ibaruma, located in the southern section of the Río Grande river, are river courses of apparently lotic environments characterised by clear to black waters. These showed unusual links with lagoon and lentic environments of white to clear waters associated with the Upper Delta.

Numerical ordination

Table 3.4 shows that the environmental variables are moderately well related to the first four species axes of the CCA , explaining the 36 % of the variance of axis 1, 34 % of axis 2, 21 % of axis 3 and 20 % of axis 4. However, the species-environment correlation showed high values.

Table 3.4. Eigenvalues and species-environment - correlations coefficients for the four axes.

	Axis			
	1	2	3	4
Eigenvalues	.3634	.3359	.2199	.2049
R (Spe.-Env.)	.9443	.9151	.8700	.9533

Despite the reasonable correlations found, the interpretation of the axes (Table 3.5) is unambiguous. The first axis is mainly defined by electrical conductivity and to a lesser degree by water transparency, the second, by dissolved oxygen (in depth) and potassium content. This is also true for the third axis. The fourth axis is defined by the pH.

Table 3.5. Delta vegetation data: intraset correlation of environmental variables with axis.

	Axis			
	1	2	3	4
Variables				
pH	.3203	.1651	.2359	-.5159
Cond.	.6965	-.0882	-.1554	.0755
DO(surf.)	-.3157	.3107	-.0459	-.2993
DO(depth)	-.1079	.4895	.0883	-.2821
Transp.	-.3907	-.4051	-.2255	-.0623
HPO_4^{2-}	-.0535	.2874	.2319	-.0761
$Fe^{2+,3+}$	.2453	.0901	-.0965	.0971
Mg^{2+}	.3349	-.1839	.0919	-.2074
Ca^{2+}	.1836	.1922	-.0245	-.0253
K^+	-.0421	.4963	.4226	-.0356

Figure 3.3 shows the ordination diagram regarding the three environmental variables with the highest correlation and the associated sites and species. The results of the Canonical Correspondence Analysis (CCA) showed a clear separation of two main groups, based on the environmental variables: electrical conductivity, water transparency, dissolved oxygen (DO) and potassium content.

The first group are sites characterised by communities with the greatest number of species (up to 17) that occur in lentic habitats. The representative sites of this 1st group are: Caño Ibaruma, Caño Acoimito, Lag. Terraplén, Lag. Alamilla, Lag. Ataguía and Lag. Travesía. The physical and chemical characteristics of these waters reveal low to medium pH values (3.8-4.9), medium conductivity (35-100 $\mu S\ cm^{-1}$), very low DO at 2 m depth (0.1-1.6 mg l^{-1}), high transparency (50-150 cm) and low calcium and phosphorus levels (Table 3.2).

As expected, due to the unstable river environment, the second group of sites contained communities with relatively fewer species (up to 10) than were represented in the first group. Their habitats tend to be straight, wide channels with low sinuosity, high current speed and low transparency. This reduces the establishment of free-floating and submerged plants. Only a few emergent species grow on the shallow banks. A higher species diversity may be found on active sedimentation bars in the middle stretches of these large rivers (see chapter 6).

Sites representing this second group are: Barra Meregina, Caño Araguao (upper reaches), Macareo (medium-upper reaches), Mánamo (upper reaches), Curiapo (Río Grande main channel).
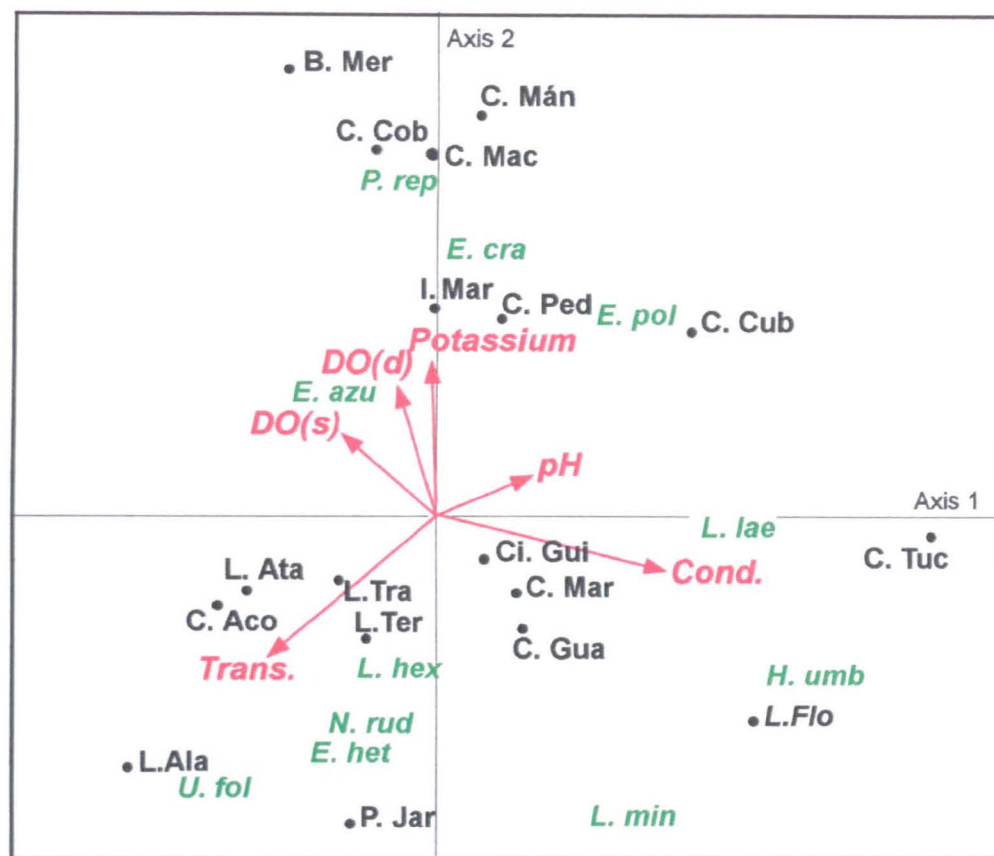
Fig. 3.3. Floating meadows data: CCA ordination diagram. Site samples: L. Alamilla, P.jarahuaja, C. Acoimito, L. Ataguía, L. Travesia, L. terraplén, C. baruma,Ci.Guires,C.Mariusa, C. Guapoa, L. Florida, C. Tucupita, Isla Mariusa, C. Pedernales, C. Cuberima, C. Macareo, C. Coboina, C. Mánamo, B. Merejina. Species: U. foliosa, E. heterosperma,N. rudgeana, L. hexandra, H. umbellata, L. laevigatum, E. azurea, E. crassipes, E. polystachya, P. repens, Lemna minor.

The water quality analysis at these sites shows higher pH values (5.3-6.6) than the first group , lower conductivity (10-35 µS cm⁻¹), very low transparency (8-50 cm), high DO at depth (2.6-6.7 mg l⁻¹) and higher values of calcium and phosphorus (Table 3.2). All these factors are partially influenced by the suspended sediments of the local waters, which are variable according to the season of sampling (see section 2.5).

The third group of sites contain an heterogeneous type of habitats, a marsh, Ciénaga Los Guires and three minor distributaries, Caño La Florida, Caño Cuberima and Caño Tucupita. These sites shows high conductivity values (160 to 280 µS cm⁻¹), low transparency of the waters (15-40 cm), medium pH values (5-6) and very low to low DO values in the surface (0-1.6 mg l⁻¹) (Table 3.2).

3.3.4 The emergent communities

The relationships between the intra and inter site similarity within the communities of emergent species are discussed below in terms of the species diversity, site similarities and numerical ordination.

Species diversity

The results from the analysis of species distribution using relative frequency and constancy; and diversity using Shannon's index in the sites are shown in Fig. 3.4, a and b (respectively).

The commonest species observed in the sites, with the higher frequency values (Fig. 3.4a), are the Onagraceae *Ludwigia octovalvis* (16 sites), the Cyperaceae *Oxicarium cubense* (15 sites), the Araceae *Montrichardia arborescens* (14 sites) and the Poaceae *Hymenachne amplexicaulis* (12 sites), recorded in 69, 65, 61 and 52 % of the sites investigated. Twenty species were recorded in only one site (not showed in Fig. 3.4 a, see Appendix 6).

The species diversity in the sites is shown in Fig. 3.4 b. The sites with higher diversity index are lagoons such as Lag. Alamilla and Lag. Ataguía (sites 3 and 4, see Fig. 3.1) but most are, minor rivers and distributaries, the Caño Acoimito, Caño Ibaruma and Caño Guapoa (sites 6, 5 and 21). In contrast the sites with lower species diversity are, as in the floating species, lotic habitats, large distributaries such as the Caño Macareo, Alto Araguao, Caño Guiniquina and Caño Pedernales.
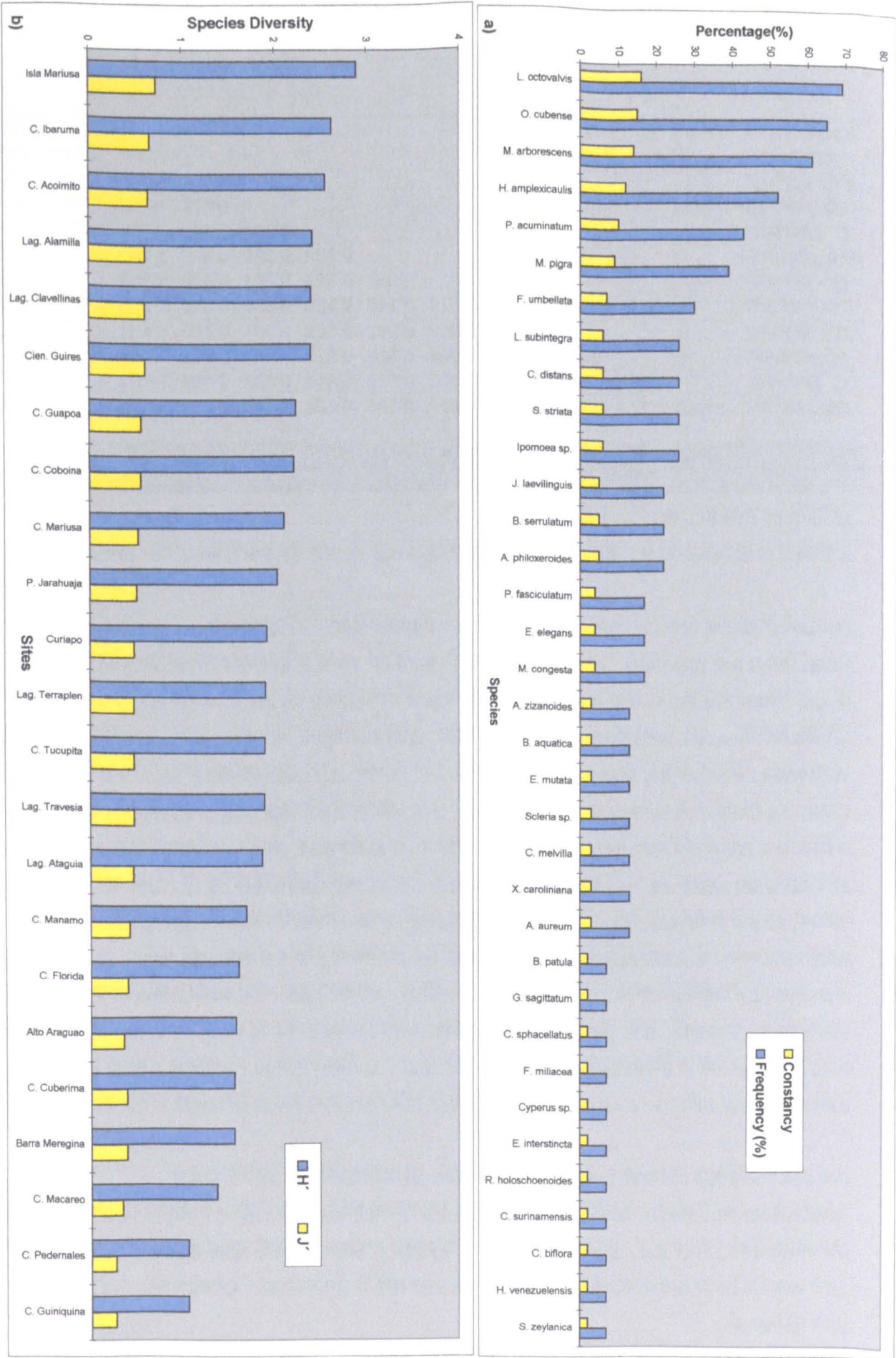
Fig. 3.4. Emergent species, a) constancy and frequency, and b) diversity and equitability.

Site similarity

The results from the analysis of site similarities using Sorenson´s Coefficient of Community, are presented in Table 3.6. The site matrix has been constructed sorting the sites by their species diversity order (see previous section). For practical purposes only a portion of the matrix, with the higher coefficients is shown. A full matrix is presented in Appendix 8.

The sites with higher similarity values are the lagoons and lentic habitats such as Lag. Terraplén and Lag. Travesía (see sites 4 and 2 in Fig. 3.1). These sites are closely linked to river courses of reduced currents, that allows the development of meadows of emergent plants, or streams with standing waters such as the Caño Tucupita. Among the lotic sites there is a high similarity index between the Mánamo river and Caño Pedernales (sites 8 and 12) which are relatively close, 40 km (see Fig. 3.1). The highest values were obtained among the Caño Guiniquina and Isla Mariusa (sites 14 and 22) both located in the Lower Delta (Fig. 3.1). The communities of the regulated Mánamo and the unregulated Macareo showed a very low value of 0.154 (see the full matrix of Similarity shown in Appendix 8). This result contrasts with the high similarity index observed between the community of floating species. The difference is due to the different morphology of the river channels and banks. The Macareo site with high, steep banks, is located in the upper stretch of the river (Fig. 3.1), and is colonised by tall emergent species. On the other hand the Mánamo site is located in its lower course with low banks, mostly colonised by floating species (see section 6.5 and 6.6 for a more detailed discussion).

Table 3.6. Sorenson´s Coefficient of Community Similarity for emergent species habitats. Higher values in bold.

	C. Ibaru	C. Acoim	Lag. Alamil	Cien. Guire	C. Coboi	Lag. Terra	C. Tucup	Lag. Trave	Lag Atagui	Mána mo	Alto Aragu	C. Peder	C. Guiniq
Isla Manusa	**0,340**	0,273	0,318	0,286	**0,391**	0,242	0,194	0,242	0,138	0,267	0,250	0,160	**0,910**
C. Ibarama		0,372	**0,359**	**0,400**	0,303	0,286	0,231	0,333	0,231	0,261	0,240	0,200	0,118
C. Acoimito			0,381	0,316	0,250	0,276	0,276	**0,364**	0,323	0,250	0,231	0,190	0,222
Lag. Alamilla				0,294	0,313	**0,387**	0,296	**0,387**	0,296	0,273	0,250	0,211	0
Cien. Guires					0,214	0,240	0,296	0,296	0,240	0,273	0,250	0,211	0,125
C. Caboina						0,320	0,261	0,261	0,190	0,300	0,200	0,235	0
Lag.Terraplén							**0,364**	**0,364**	0,300	0,267	0,235	0,167	0
C. Tucupita								**0,364**	0,300	0,267	0,133	0,167	0
Lag. Travesía									**0,417**	0,267	**0,381**	0,167	0
Lag Ataguía										0,154	0,316	0	0
Mánamo											0,286	**0,364**	0
Alto Araguao												0,182	0

Numerical ordination

The Correspondence analysis did not produced any particular association between the environmental variables and the sites as it did with floating species, probably due to the environmental variables used and sediment homogeneity (see discussion below).

3.4 Discussion

3.4.1 Floristic composition of aquatic plants

When compared with the aquatic vegetation of other wetlands of South America (Table 3.7), the Orinoco river Delta shows a greater floristic diversity. The previous inventories of the region by Delascio (1975), Danielo (1976), Canales (1985) and CVG-Tecmín (1991) only recognised some 80 species. Such reports do not show comprehensive lists of species of selected communities, but only a general description. This might be expected since the reports by Canales (1985) and CVG-Tecmín (1991), as has already been pointed out in section 2.4, are oriented more towards the exploitation of natural resources (such as timber production) than macrophytic composition. So this accounts for the number of species reported previously being much lower than in the current study.

Based on work of Venezuelan aquatic plants prepared by Velásquez (1994), the present survey has increased the documented aquatic flora of the region by more than 48 % (Colonnello et al., 1993). It represents approximately 50 % of the herbaceous and scrubby species associated with aquatic habitats in the country. The increase in the number of species registered is a clear indication of the poor floristic knowledge of the region, which should have a particularly important species richness because it functions as a sink for the species of all the Orinoco watershed. Only the species with particular ecological niche requirements such as those found associated with waterfalls, or other specialised habitats of the Guayana shield, are not found within the Delta environments.

Table 3.7. Species richness in aquatic habitats in South America

Habitat	Species richness	Source
Orinoco floodplain lagoon	20	Sánchez and Vásquez (1986)
Peruvian Amazony lagoon	21	León and Encarnación (1993)
River basins of Surinam	71	Werkhoven and Peeters (1993)
Amazon River	68	Junk (1990)

The Paraná River Delta	87	Lahitte *et al.* (1997)
Paraná River Basin	113	Neiff (1986).
Delta region	360	Velásquez (1994)
	100	Colonnello (1993)
	174	Colonnello (This study)

The Orinoco Delta species common to the four South-American wetland systems are shown in Appendix 9.

The community similarities, calculated with the Sorenson´s index presented below, indicate that the species of the Orinoco Delta are more closely related to those of Amazon river, mainly because of the geographical proximity and the morphological similarity of the river basin with the Orinoco. Other factors include the area of the drainage basins, drainage over similar lithology from the Andes range, and a large floodplain associated with the main channel (Rosales *et al.*, 1999). The Paraná floodplain in southern Brazil even if sharing similar hydrologic regimes to that of the Orinoco (Neiff, 1990 b), is governed by a more temperate climate leading to a different assemblage of species. The Surinam wetlands (Werkhoven, 1993) show fewer similarities to that of the Orinoco, despite their geographical proximity. This is probably because of physiographic differences, such as a smaller river basin draining from the highly eroded mountains of the Guayana Shield and with a much lower water contribution from the alluvial plains, such as are present in the Orinoco. This leads to lower habitat heterogeneity.

Sorenson´s index

Amazon floodplain	Paraná floodplain	Paraná Delta	Surinam wetlands
0.324	0.145	0.109	0.136

The species which are common to all the regions are *Eichhornia crassipes*, *Eichhornia azurea*, *Pontederia rotundifolia* and *Pistia stratiotes*. With the exception of *P. rotundifolia*, these species are considered to be among the 12 most notorious aquatic invaders. *Eichhornia* species shows vegetative reproduction, *E, azurea* by chance fragmentation and *E. crassipes* by daughter rosettes that form rapidly in brittle stolons (Haynes, 1988). The analysis of the genus composition, would produce closer similarities. However, further quantitative or floristic comparisons are not valid due to the different criteria adopted by the authors in relation to the 'aquatic status' of each species. It must also be

remembered that the inventories are still far from being complete. At least this is certainly the case in the Orinoco Delta.

3.4.2 Species diversity and sites ordination
3.4.2.1 The floating communities

The species diversity index at each site is related to the physical and chemical characteristics of their habitats. The sites of lentic habitats such as lagoons that showed the higher index of species diversity, are almost identical to those selected using the ordination analysis. Such sites are associated with low to medium pH values, medium electrical conductivity, very low dissolved oxygen and high water transparency.

This first group of sites contains a variety of habitats, ranging from black water channels with very sinuous courses such as Caño Ibaruma and Acoimito, to lagoons located in the Upper and Middle Delta replenished by the rainfall and the white water from rivers during the rainy season. Caño Acoimito is a small channel that is seasonally flooded by the Orinoco River, forming a large flooded area. In the wet season it is a lentic habitat, establishing its link to the lagoons. In the lakes (large lagoons that may be semi-permanent or become dry for few months) the lack of strong currents promotes the rapid deposition of sediments. This creates the habitats on which submerged plants such as *Cabomba aquatica* and *Utricularia* ssp., and floating plants such as *Nymphoides indica*, *Neptunia oleracea*, *Limnobium laevigatum*, *Nymphaea rudgeana*, *Ludwigia helminthorriza* and *L. sedioides* can develop with numerous species of grasses and sedges, such as *Leersia hexandra* and *Oxicarium cubense*. For discussion of the hydrological cycle associate to the lagoons, see section 2.5.

Other types of clear-black waters assemblages are those found in small ponds of 'morichales' (palm communities), whose vegetation cover is predominantly herbaceous. In the middle of the herbaceous swamps of the Lower Delta, dystrophic pools such as the Pozo Jarahuaja (site 22 in Fig. 3.1) are also found. They are characterised by a depth gradient, marked by a peripheral sedge zone and central water-lily zone. This distribution is common to the water bodies where the depth defines the occurrence of emergent and floating species, as reported in other tropical (Zutchi and Gopal, 1990) and subtropical wetlands (Schalles and Shure, 1989). Species diversity is moderate in this site.

The sites of Caño Ibaruma, Caño Acoimito and the associated, Lag. Alamilla, show the highest species diversity index among the lentic habitats. These sites combine the influence of two particular types of waters, the black waters from the Imataca foothills which dominate

during dry period and the white waters from the Orinoco that flood the region during the rainy season. For example In Caño Acoimito the conductance varied from 34 to 50 μS cm^{-1} and the dissolved oxygen from 1 to 6.4 mg l^{-1}. In Lag. Alamilla the dissolved oxygen at 2 m depth varied too from 0.6 to 5.2 mg l^{-1}, and the pH varied from 5.3 to 4.6. The heterogeneity of habitats (temporal heterogeneity as discussed by Tilman and Pacala, 1993) allows the occurrence of species such as the Pontederiaceae *Eichhornia heterosperma* and the Lentibulariaceae *Utricularia hydrocarpa* which are only found in these waters.

The first group of sites, particularly the lagoons, with a relatively high number of species may be compared with those grouped as the 'functional units VI and VII' (Neiff, 1986) in the Paraná system. These are ponds flooded only by exceptional floods and wetlands that are subject to several months of inundation each year. They may also be similar to the 'plants-habitat associations' of 'lake shores' or 'habitats with minor water-level variations', proposed by Junk (1986) in the floodplain of the Amazon River.

A low value of species diversity index has been registered at the second group of sites, produced by the numerical ordination which is associated with the lotic habitats along the shores of large distributaries. The environmental variables associated with these sites are low conductivity values, very low to low water transparency and high DO at depth. The species that can produce extensive communities along the banks are emergent plants which are adapted to this particular environment, e.g. *Paspalum repens*, *E. polystachya* and *E. azurea*, and which have long floating stems. As Junk (1986) stressed with reference to the Amazon river, large rivers such the Amazon are unsuitable habitats for aquatic plants, because their water depth varies from a few metres to 75 m. Other factors include strong current velocities of up to 11 km h^{-1}, strong wave action, high erosive and depositional capacities. High suspended sediment load (circa 150 mg l^{-1}) may further destabilise communities. These conditions are comparable to those found in the main Orinoco distributaries (see chapter 5 and 6).

The few species encountered, such as free floating species *E. crassipes* and *Salvinia auriculata*, develop in sheltered areas. During major flooding events most of them are removed by the current. This rafting process will be discussed in more detail In section 6.3.3). Such is the case in the main distributary channels of the Orinoco river: the Río Grande, Caño Merejina, Caño Araguao, Macareo and Mánamo. This was also the case in those channels with a high daily tidal oscillation such as Caño Pedernales and Caño Guiniquina.

The second group of sites, which include a low number of species are homologous to those grouped as the 'functional unit II' according to Neiff (1986) in the Paraná system. These are environments of low to moderate flows along river margins, swamps and wash-ways that flow only at times of high river water levels. In the Amazon floodplain they would be similar to the 'plant-associations', as proposed by Junk (1986), of the 'main river channel', at least during the low water period and also to the 'river shores' where perennial aquatic and terrestrial grasses are established.

The physico-chemical characteristics of the above mentioned habitats (in both groups) are similar to those reported by Junk (1983) and Junk and Howard-Williams (1984) for the different aquatic environments of the Amazon Basin. The first of these authors postulated that the water courses of the black waters did not support a great floristic richness or biomass of aquatic plants. However, several sites of the Delta exhibit high species diversity, such as the Caño Ibaruma, Río Acoimito and Caño Guapoa corresponding to black or clear waters with acidic conditions and a low nutrient concentration. Similar results were obtained by Furch and Junk (1980) in the extremely poor quality waters of the 'Parecis-Formation' in the Amazon Basin. In the same study the authors found no correlation between the species composition and the chemical characteristics of a range of 45 creeks and rivers in Amazonia. However, the water samples were analysed several months after their collection and cannot therefore be considered reliable.

The third group produced by the numerical ordination includes some sites like the marshes of Ciénaga Los Guires. Also included are the very polluted water-courses near areas of high population density such as Caño Tucupita and some areas of Caño Cocuina (La Florida site). These had extremely high values of electric conductivity (max. 280 μS cm^{-1}), no dissolved oxygen and restricted water current.

The species diversity of these sites is moderate, with a mean H'= 1.8 (Fig. 3.2 b). This is because the sites combine slow flowing or standing waters and high nutrients with high conductivity and too low dissolved oxygen levels. These conditions lead to extensive populations of certain species such as *E. crassipes*, *P. stratiotes* and *Hydrocotyle umbellata* which constitute a serious weed problem. Those courses were active channels before the Mánamo regulation. The floating meadows were seasonally washed out to the sea, however, today are totally covered by aquatic weeds and constitute a waste disposal area in the surroundings of the city of Tucupita (the Caños Tucupita and Cocuina).

3.4.2.2 Emergent species communities

In general, there were fewer relationships among the sites of the emergent species than among those of the floating meadows. The numerical ordination (CCA) could not distinguish clearly among them. It may be because the emergent species are present in many different types of sites. On the other hand the environmental data collected in this study were chiefly of water parameters. Other variables such as substrate composition, for instance, which could partially explain the results, could not be examined on each of the study sites. An investigation on the site morphology and substrate types in relation with species composition in presented in chapter 6.

In contrast to this study, Khedr and El-Demershad (1997) in a study of aquatic plants in the Nile Delta, reported a clear separation of the species, in terms of plant habit, emergent, floating and submerged vegetation. The environmental data for their sites that produced better correlations between the three groups were, shading, canal width, and electrical conductivity. These authors studied aquatic habitats of similar characteristics, drainage canals from 4 to 28 m in width, with some clear differences.

The geology underlying a watershed also has a major influence on the chemical and physical characteristics of its river channels, and hence on macrophyte colonization (Fox, 1992). The sediments deposited in most of the study sites are derived from the main Orinoco river channel, whose dissolved and particulate minerals even if collected in two different watersheds, the Andean range and the Guayana Shield, are well mixed. This is because the last main contributor, the Caroní river, joins the main channel some 70 km upstream from the apex of the Delta. On the other hand the correlation of macrophytes with nutrient (particularly phosphorus and nitrogen) concentrations is complicated by the ability of many species to obtain minerals either by foliar uptake from the water or from the substratum via their roots (Fox, 1992).

Van Andel (1967) suggests that the sediments should have the same grain size, at least in the lentic habitats close to the river shore where emergent plants are established, as was observed in the middle-lower stretches of the Mánamo and Macareo rivers (see section 6.5.2). Baattrup-Pedersen and Riis (1999), found that the species occurrence in the regulated and unregulated stream reaches in Denmark where the main physical and chemical characteristics were similar, was correlated with the substrate type, which was the only significant difference between the two types of river courses.

The higher species diversity found in sites of lentic habitats, such as lagoons and standing or low moving water habitats (Fig. 3.4b), may be explained in a similar way to that of the floating meadows. This is because the plants are continuously modifying their substrate, particularly adding autochthonous nutrients by decomposition and retaining sediments by accretion along with other materials, depending on the local environmental conditions, which lead to habitat diversity. Along the large river banks, the dynamics of the water flow impedes those processes. The similarities according to the Sorenson's Community Coefficient were higher among lentic sites than among the lotic sites (Table 3.6). The highest values were obtained in Isla Mariusa and Caño Guiniquina, both sites constituted a sheltered habitat, protected from currents and other disturbances. The very low similarity between the Mánamo and Macareo sites, support the view that differences in species diversity found in an extensive survey of these rivers is of fundamental importance. This aspect will be further analysed in chapter 6.

As occurred with the floating communities, an exception to the substrate homogeneity may be the sites of Lag. Alamilla, the Caño Acoimito and Caño Ibaruma, located in the foothills of the Imataca Range to the south side of the Orinoco main channel. In this area, the substrates comprises sediments transported by mountain streams, partially mixed with white waters due to the seasonal flooding of the Orinoco river. As a consequence the sediments should maintain some local characteristics that explain the high similarity values that link these sites (Table 3.3). Notably species such as the Onagraceae *Ludwigia torulosa* and the Poaceae *Paspalum writii* as well as the Poaceae species *Panicum pilosum* and *Panicum scabridum* seem to be restricted to these sites.

3.5 Final remarks

Species diversity is a clear indicator of the ecological constraints affecting a particular site. Restrictive environmental condition such as strong currents (high variable hydrodynamic regimes) and low dissolved oxygen and conductivity highlight the competition processes among the species and individuals, limiting the diversity and favouring the abundance of certain species. Higher diversity in lentic habitats may be explained by the models of spatial and temporal heterogeneity discussed by Tilman and Pacala (1993). According to these models, several species may coexist in conditions where there may be a trade-off between their abilities to compete for the available resources such as light and nutrients(spatial heterogeneity). Their coexistence may also be seen as adaptation to changing seasonal factors (temporal heterogeneity).

Such successional processes may occur in the lentic environments of the lagoons (Table 3.8), either in the dry or in the wet zone. The gentle slope of the sites, which are basically depressions (see section 2.1) with an irregular micro-topography, show numerous soil microhabitats, because the aquatic plants (and the terrestrial plants and animals, when dry) modify the soils, creating an environmental mosaic. These conditions (spatial heterogeneity) have allowed the establishment of several floating and emergent species with different requirements of resources such as access to nutrients, light, and particular soil condition. Towards the end of the rainy season the characteristics of the waters of the lagoons such as light (that increases) or dissolved oxygen (that decreases) may change, leading to temporal heterogeneity (see section 2.6, Fig. 2.9). Many species that were formerly dominant may be excluded or become less dominant. In this case the species composition may change but diversity may be conserved.

In the lotic environments (Table 3.8) the spatial heterogeneity is reduced because few species should compete in conditions imposed by the seasonal changes in the hydrological regime.

The variation in composition, diversity and cover of the aquatic flora could be explained by the physico-chemical processes that cyclicly occur in the water bodies of the region (see section 2.6). Changing hydrological conditions can directly modify the chemical and physical properties such as nutrient availability, degree of substrate anoxia, soil salinity, sediment properties and pH as exposed by Mitsch and Gosselink (2000). For example Lag. Ataguía site whose floristic cover, in 1994, was dominated by several species of grasses (contained in the site description) changed subsequently to an almost absolute dominance of *Neptunia oleracea* as documented in the1995 field survey. During the water rising and receding phases, the species communities change in structure and composition following the changes in transparency, from 150 to 18 and 36 cm; pH, from 5 to 5.6; conductivity from 34 to 25 μS cm^{-1}; dissolved oxygen from 1.6 to 5.8 mg l^{-1}. Such dynamic changes within the aquatic plant communities have been widely reported, for example in Paraná do Xiborena along a connecting channel between the Río Negro and Solimões (Junk, 1973), and in several shallow water bodies on the Indian subcontinent (Zutshi and Gopal, 1990).

Due to the large territorial area encompassed by the previous study based on a limited number of samples it was not feasible to relate the effects of the river regulation, on the site species diversity and composition. In particular the seasonal and tidal regimes are constantly changing the environmental conditions of the habitats as seen in section 2.6. Despite these provisos, a detailed

comparison of the regulated Mánamo and the unregulated Macareo river is presented, in chapter 6.

If there is no clear signal regarding the impact of regulation on aquatic plants, the forest formations may present a different picture. The next chapter focuses attention on the inland forest formations of the Mánamo sub-basin. This completes the vegetation overview of the Delta environment.

Table 3.8. Main differences between the aquatic environments investigated.

	Aquatic environments (Sites) Floating meadows			Emergent meadows
	Lentic habitats	*Lotic habitats*	*Polluted habitats*	
CCA ordination	First group	Second group	Third group	No division
Electric conductivity	High	Low	Very high	-
Potassium content	Low	High	Low	-
Dissolved oxygen	Low	High	Very Low	-
Transparency	High	Low	-	-
Current hydrodynamic	Low	Very high	Standing waters	All types
Water type assoc.	Clear to black	Mostly white	Clear to black	All types
Species diversity	High	Low	Low-intermediate	High
Spatial heterogeneity	High	Low	Low	Low
Sites similarity	High	High		Very high
Characteristic species	*U.foliosa*	*P. repens*	*P.stratiotes*	*L. octovalvis*
	L. hexandra	*E. polystachya*	*H. umbellata*	*O. cubense*
	N. rudgeana	*E. crassipes*	*L.laevigatum*	*M. arborescens*
	S. auriculata	*E. azurea*		*P. acuminatum*

Chapter 4 Water-Associated Forest Communities

From an aerial perspective the extensive forest communities of the Delta constitute one of the more striking and seemingly undisturbed features on the landscape. However, upon closer scrutiny many forest communities show varying degrees of human intervention, particularly in those areas surrounding village sites where species diversity and vegetation community structure has been notably modified.

As part of the research project, forest communities were studied in the region of the Pedernales and Cocuina rivers that constitute part of the sub-basin fed by the regulated Mánamo river (see Fig. 4.1). Comparisons may then be made between disturbed sites that are due to human migration caused by the regulation of this particular channel and the former distribution of these communities (see chapter 9). Site selection was made following an exploratory expedition that included the survey of forest ecological communities that have undergone various modifications due to human impact.

4.1 Aims

- To analyse the wetland forest communities in terms of species composition and principal ecological parameters.

4.2 Methods

Since a complete identification of all existing species was not feasible due to the scarce knowledge of the regional flora, the community analysis was based on structural and physiognomic characteristics that were then compared with the available data on habitat characteristics. Budgetary restraints to perform the necessary laboratory analyses restricted the number of samples that could be processed to provide the necessary environmental data.

4.2.1 Site location

The 9 sites were studied during 1995 and 1996. They are located at the following co-ordinates (see Fig. 4.1):
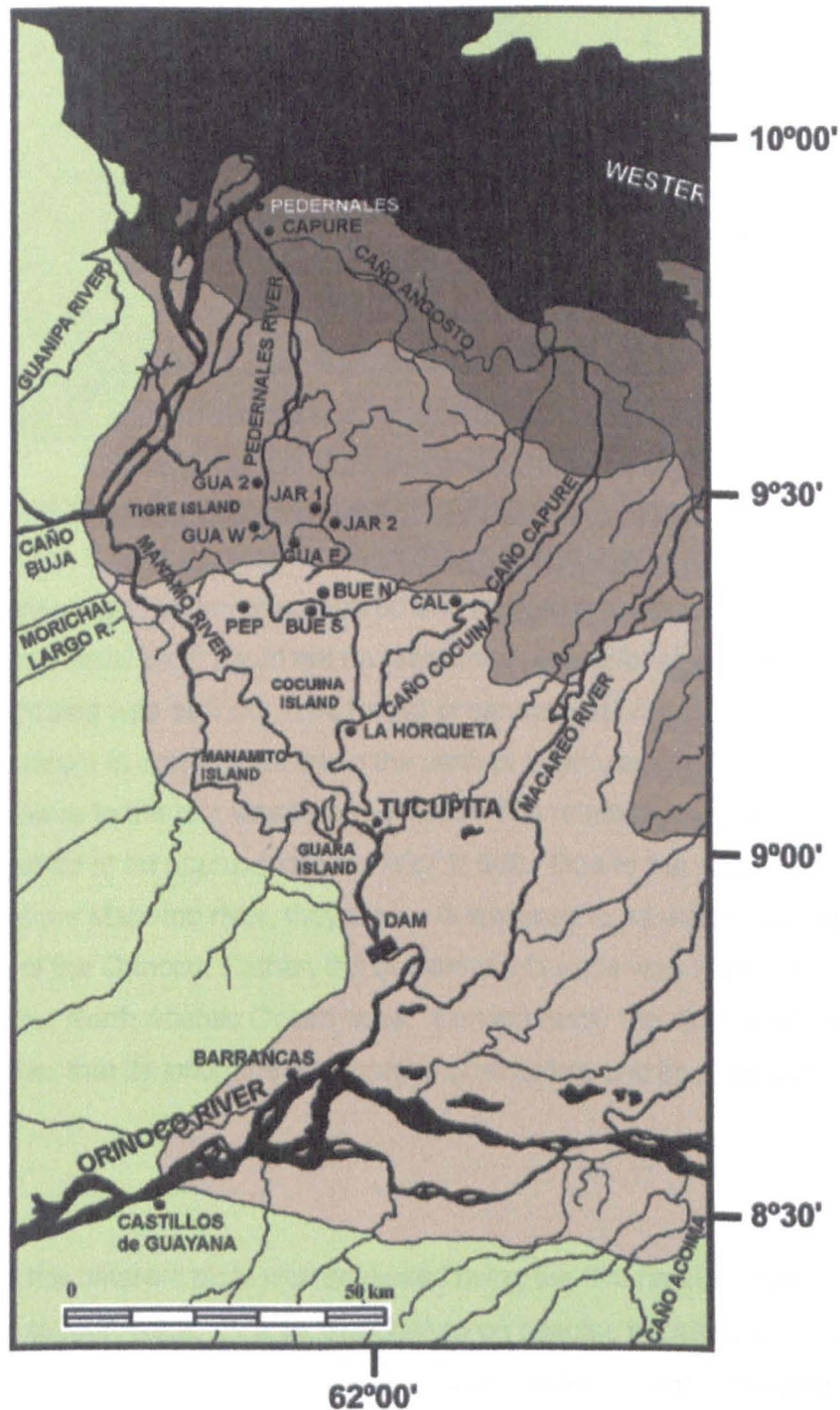
Fig. 4.1. Study sites of forests communities. PEP=
Pepeina; BUE S= Buenaventura south; BUE N=
Buenaventura north; GUA E= Guacajara east; GUA
W= Guacajara West; GUA 2= Guacajara 2; JAR 1=
Jarina 1; JAR 2= Jarina 2; CAL= Calentura.

Guacajara east	(09° 26' 28" N and 62° 12' 17" W);
Calentura	(09° 20' 33" N and 62° 00' 20" W);
Pepeina	(09° 21' 30" N and 62° 10' 07" W);
Buenaventura south	(09° 24' 05" N and 62° 09' 12" W);
Guacajara west	(09° 26' 27" N and 62° 12' 38" W);
Guacajara 2	(09° 27' 39" N and 62° 11' 28" W);
Buenaventura north	(09° 24' 34" N and 62° 08' 11" W);
Jarina 2:	(09° 27' 39" N and 62° 08' 22" W); and
Jarina 1	(09° 27' 30" N and 62° 09 42" W).

4.2.2. Data collection and analysis

For each plot of 10 x 100 m (0.1 ha), all plants higher than 2 m in height, whose diameter at breast height (1.3m) exceeded 5 cm, were measured and identified at the species level. In those cases where an individual plant could not be identified in the field, a sample was collected or a morphospecies was defined. The height of canopy was measured using a clinometer and tape measure in order to ascertain the vertical structure of the vegetation. The position of each tree relative to the plot was also recorded. The resulting data were then used to construct detailed profiles at an approximate scale of 1: 500. Due to the sites being located in the regulated basin of the Mánamo river, they were not exposed to seasonal oscillations caused by the flooding of the Orinoco. Rather, the dominant influence was the diurnal fluctuations caused by the North Atlantic Ocean tides. Consequently the diurnal tidal cycle of flooding was measured so that its influence on community structure and species composition could be investigated.

4.2.3. Species diversity:

Species diversity within the different plots was assessed using the Shannon´s Index. It was applied as described in section 3.2.2. This index is based on species frequencies involving non-parametric measures and is applicable to any community independent of species abundance distribution (Lande, 1996). It was selected because the proportion or dominance of each species (IVI value) was considered instead of the number of individuals when Simpson´s Index is used (Magurran, 1989). Other indices that were used included:

Similarity indices:

Sorenson's Coefficient of Community (S_s) similarity was calculated as in section 3.2.2.

Importance Value Index:

The absolute density, frequency (within subplot areas of 10x10m) and dominance (basal area) of individuals of each species was calculated for each plot.

The importance Value Index (IVI) (Mueller-Dombois and Ellemberg, 1974) of each species within each plot was calculated by summing its relative density, frequency and dominance, in order to give a maximum score of 300 for each plot.

Disturbance level:

The disturbance level on each site was determined on the basis of qualitative estimations of the number of fallen trees, evidence of fire, and interviews with local inhabitants.

4.3 Results

4.3.1 Site descriptions

The detailed description of each site, including its general physical characteristics, species composition, and community structure is presented in Appendix 10.

4.3.2 Forest types

The vegetation of the studied sites may be divided into three basic formations (Table 4.1): Swamp palm forests, Gallery forests, and Swamp forests. Table 4.1 presents the total number of species, trunks, palm species individuals, degree of flooding, as well as the degree of disturbance.

Table 4.1. Formation type, total number of species, trunks, palm species individuals, degree of flooding, degree of disturbance (H: height, M: medium, L: low), diversity index (H') and equity (J') of the studied sites.

Site	Formation type	Trunks N°	Species N°	*Mauritia flexuosa*	*Euterpe oleracea*	Manicaria *saccifera*	Flooding depth(cm)	D	H'	J'
				IVI	IVI	IVI				
Guacajara east	SPF-GF	120	7	75.2	65.3	-	20-40	H	1.38	0.71
Calentura	SPF	163	13	100.5	9.9*	-	20-40	H	1.44	0.56
Pepeina	SPF	501	22	137.7	41.7	-	50-70	L	1.63	0.52
Buenaventura south	SPF	312	29	65	61	-	15-35	L	2.11	0.62
Buenaventura north	GF	461	36	-	34.5	1.5	0-0	H	2.57	0.71
Guacajara west	GF	314	26	32.5	87.2	4.6	0-20	H	2.17	0.66
Guacajara 2	GF	444	34	45.4	49.1	-	0-20	M	2.64	0.75
Jarina 2	GF-SF	532	52	-	78	22	0-0	N	2.58	0.65
Jarina 1	SF	609	41	-	56	23	0-10	N	3.02	0.81

As represented in Fig. 2.8, the general distribution of vegetation types in the Delta, shows a pattern of increased dominance of forests toward the Lower Delta. In the middle of this zonation, most of the communities are dominated by dense swamp palm forests.

4.3.2.1 Swamp palm forests

This community type is dominated by palms, chiefly *Mauritia flexuosa* and *Euterpe oleraceae* and occurs on permanently flooded and organic soils occupying depressed areas. These sites included Guacajara east (Fig. 4.2), Calentura (Fig. 4.3), Pepeina (Fig. 4.4), and Buenaventura south (Fig. 4.5 and are subject to major flooding events up to a depth of 70 cm.

In all of these sites, the dominant species higher than 2 m are *Erythrina fusca (Bucare de agua)*, *Mauritia flexuosa* (Moriche palm), *Euterpe oleracea* (Manaca palm), *Virola surinamensis* (Cuajo), *Annona* sp., *Symphonia globulifera* (Peramancillo), *Carapa guianensis (Carapo)*, *Ficus* spp (Higuero), *Pterocarpus officinalis (Sangrito)*, *Tabebuia insignis* (Apamato), *Cecropia peltata* (Yagrumo) and *Macrolobium bifolium* (Leguminosae) (see species list in Appendix 11). These account for 60-70% of the total IVI value. The survey by C V G.-Tecmín (1991) includes these communities within the type Hb/B8-1Pdll termed marshes with forests. This ecological group has a maximum height of 20 m, a similar species composition and. They suggest that many patches that show a richer species composition and structure, are relics of a former extensive forest.

The permanent standing water at these sites is an ideal environment for several species of aquatic macrophytes. These include both emergent plants such as *Montrichardia arborescens*, *Costus arabicus* and *Urospatha sagittifolia*, as well as free-floating species such as *Wolfiella lingulata*, *Lemna perspusilla*, *Azolla filiculoides* and *Salvinia auriculata* (see species list in Appendix 11). *M. arborescens* is the most common and may become dominant when the understorey or the canopy is cleared, because it is sensitive to any increase in PAR (photosynthetically active radiation).
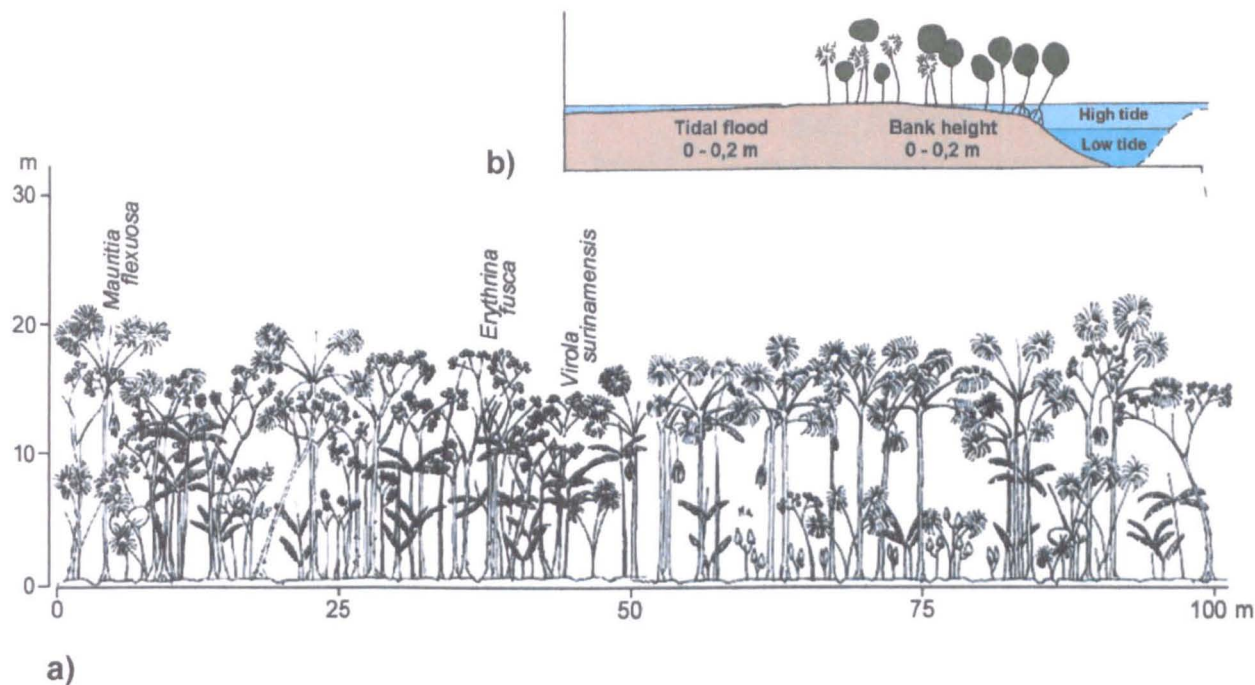
Fig. 4.2. Schematic profile of Guacajara east site. a) Vegetation and b) physiography.
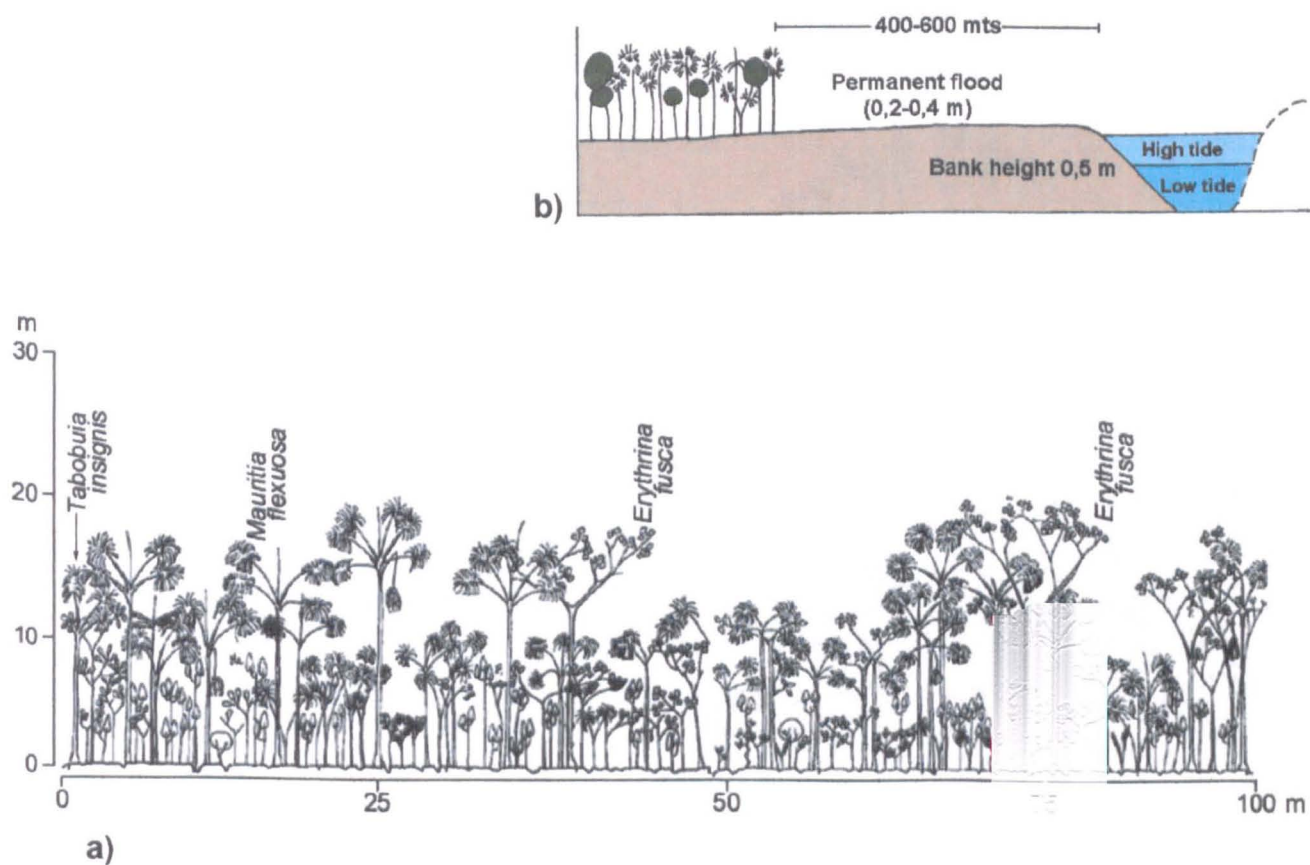
Fig. 4.3. Schematic profile of Calentura site. a) Vegetation and b) physiography.
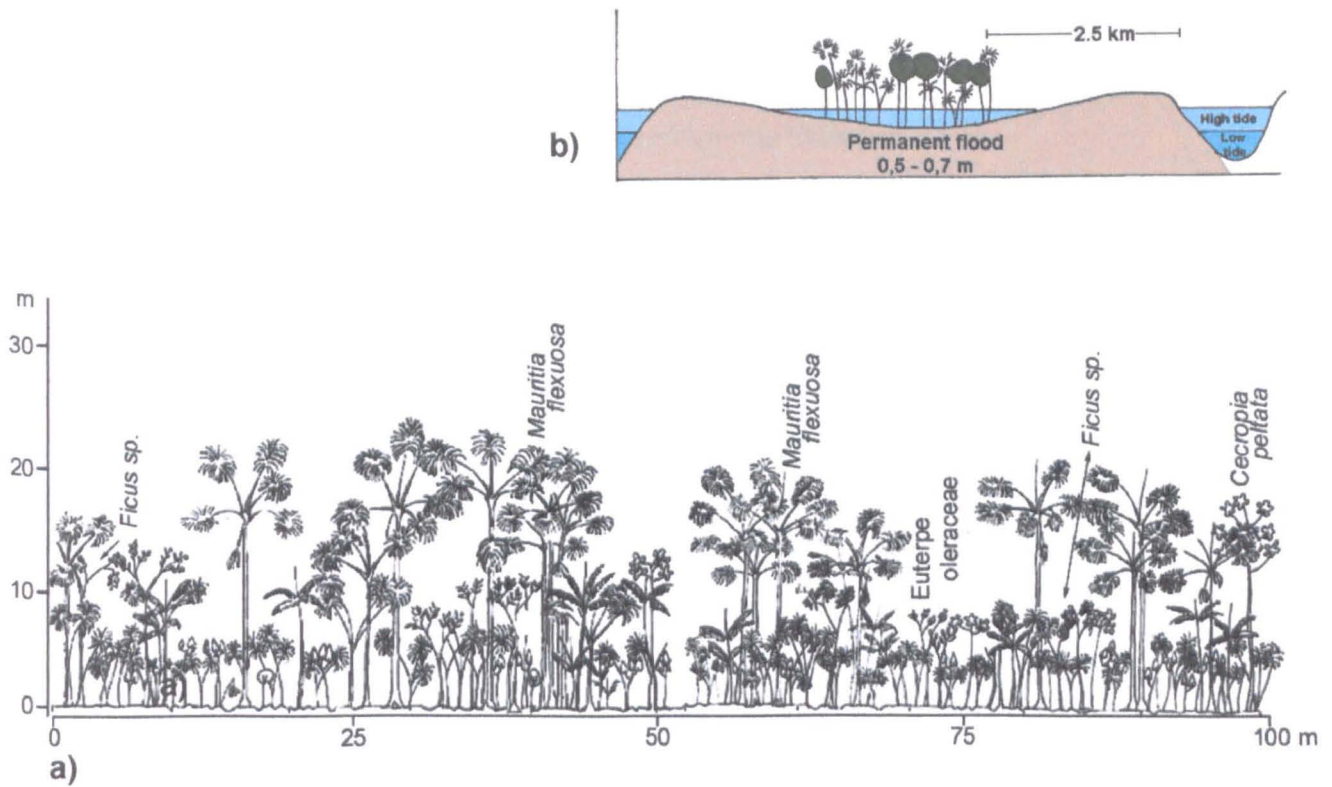
Fig. 4.4. Schematic profile of Pepeina site. a) Vegetation and b) physiography.
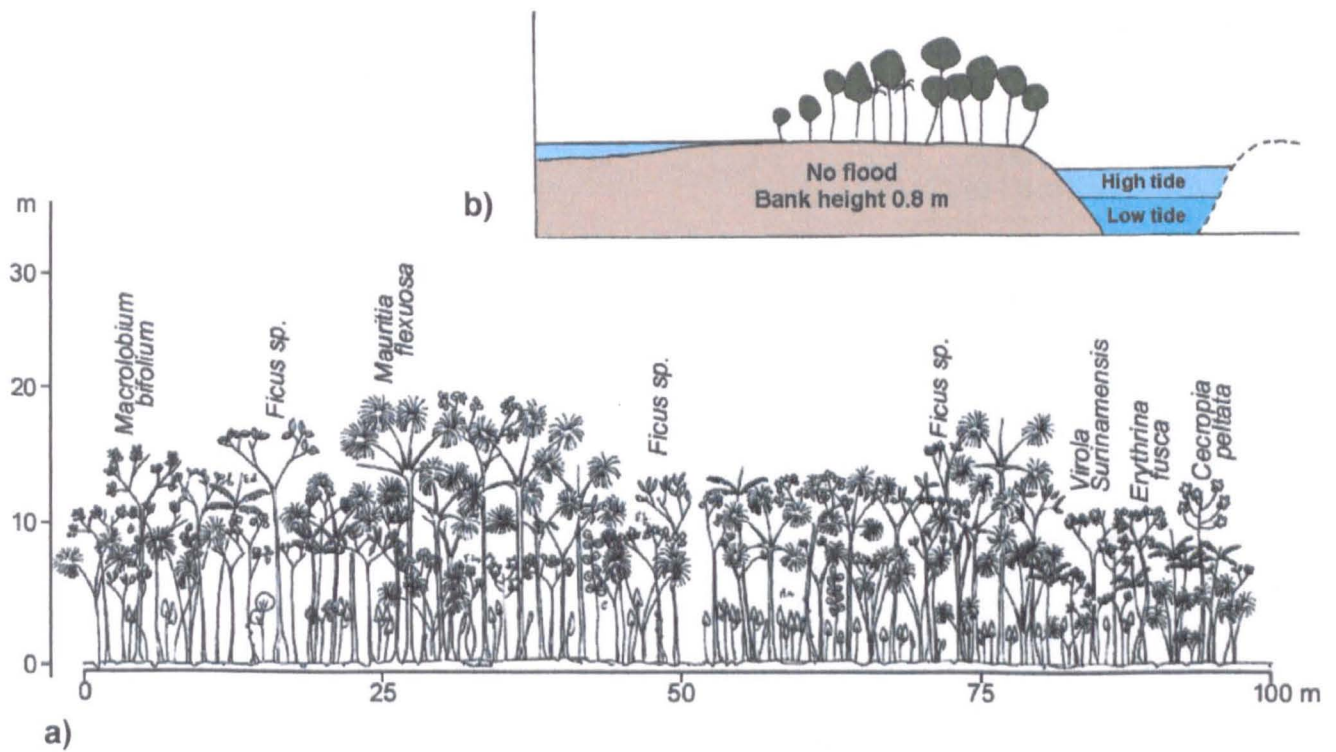
Fig. 4.5. Schematic of Burenaventura south site. a) Vegetation and b) physiography.

When the trunks of the vegetation at these sites are divided according to height classes (Fig. 4.11), several differences become apparent. Guacajara east shows a similar distribution of trunks in each size class; in the Calentura site 90% of the trunks fall into the lowest class (2-5 m); the Pepeina site shows a steadily decreasing distribution; and Buenaventura south shows a low number of trunks in the lowest class.

The vegetation structure of these plots (Table 4.2) consists of a medium height formation where the individuals do not attain heights higher than 20-25 m and where *Mauritia* and *Erythrina* individuals form the upper strata (as in Guacajara east and Calentura sites). The middle strata height range (10 m -18 m) is composed of *Virola surinamensis, Euterpe oleraceae, Symphonia globulifera* and *Ficus* sp., *Annona* sp. *Euterpe oleraceae* and *Mauritia flexuosa* dominate the lower level range (between 2 m and 10 m). González *et al.*(1983), describe swamp palm forest communities of three strata of 24 m in height, and communities of simpler structure, of two strata, which are up to 20m in high.

Table 4.2. Vertical structure (Upper, Middle and Lower strata) and main species composition of the sites corresponding to the swamp palm forest.

Site/ Heith range	Upper strata (m)	Middle strata (m)	Lower strata (m)	Herbaceous/ saplings (m)
Guacajara east	*Erythina - Mauritia* (20 - 25 m)	*Virola Erythryna Symphonia* (10 - 15 m)	*Euterpe -Annona* (2 - 10 m)	*Costus - Montrichardia* *Urosphata - Wolfiella Salvinia - Azolla* (0 - 6 m)
Calentura	*Erythina - Mauritia* (18 - 25 m)	*Mauritia - Ficus* *Euterpe - Cecropia Pterocarpus* (10 - 18 m)	*Mauritia - Tabebuia* *Ficus* (2 - 8 m)	*Montrichardia - Costus Wolfiella - Lemna* *Salvinia - Azolla Panicum* (0-6 m)
Pepeina	*Mauritia* (15 - 18 m)	*Euterpe-Virola* *Ficus* (10 - 15 m)	*Euterpe - Cecropia Mauritia* (2 - 8 m)	*Montrichardia - Costus Echinodorus - Lemna Wolfiella* (0 - 4 m)
Buenaventura south	*Mauritia - Ficus* (15 - 20 m)	*Erytrina - Virola Ficus - Clusia* *Tabebuia* (10 - 15 m)	*Annona - Ficus Coccoloba - Casearia* (2 - 10 m)	

4.3.2.2 Gallery forests

Three gallery forest communities were investigated in the Lower Delta along the Pedernales river: Buenaventura north (Fig. 4.6) located on a non flooded bank, Guacajara west (Fig. 4.7) and Guacajara 2 (Fig. 4.8), both located downstream and flooded by the ocean tides.

In these sites the number of species tends to be greater than those of the swamp palm forest (Table 4.1). The dominant species higher than 2 m (see species list in Appendix 11) are: *Euterpe oleracea, Mauritia flexuosa, Symphonia globulifera, Virola surinamensis, Cecropia peltata, Rhizophora mangle* (Red mangrove), *Virola surinamensis* (Cuajo), *Calophyllum brasiliense* (Cachicamo), *Casearia silvestris, Bactris* sp., *Gynerium sagittatum, Cecropia* sp., *Couroupita guayanensis, Nectandra* sp and *Genipa americana.* The herbaceous layer (see species list in Appendix 11) comprises emergent species, capable of surviving the alternating dry-wet conditions. Here there are no floating species. *Acrostichium aureum*, a fern that may reach 3-4 m in height, is a halophytic species growing on the ecotone between the mangrove belt and the fresh-water species (Medina *et al.*,1990).

The trunk height class distribution of these sites (Fig. 4.11) shows an homogeneous pattern where the highest number of individuals falls into the lowest size class (2-5 cm) while the number among the larger classes decreases steadily. The vegetation of the three plots represents a medium size formation up to 25 m tall and emergent trees that attain heights of up to 40 m. Typically, one may distinguish three strata and an herbaceous layer among the communities (Table 4.3). The upper level (up to 25 m in height) is composed of such species as *Symphonia globulifera, Mauritia flexuosa* and *Hernandia guianensis.* In the Buenaventura north site the trees are taller, reaching up to 35 m (such as *Couroupita guianensis* and *Symphonia globulifera*). This phenomenon is attributed to the high permeability allowed by the sandy texture of the soils, that predominate in these levees (Infrawing & Asociados, 1997). The second layer range (10 m -15 m), is characterised by *Euterpe oleraceae, Virola surinamensis* and *Erythrina fusca.* These species are less important here than in the swamp palm forest. The third stratum (2 m - 10 m) is dominated by the lower species such as *Annona* sp, *Cecropia peltata, Myrcia* sp. and *Casearia silvestris*, and the saplings of taller species.
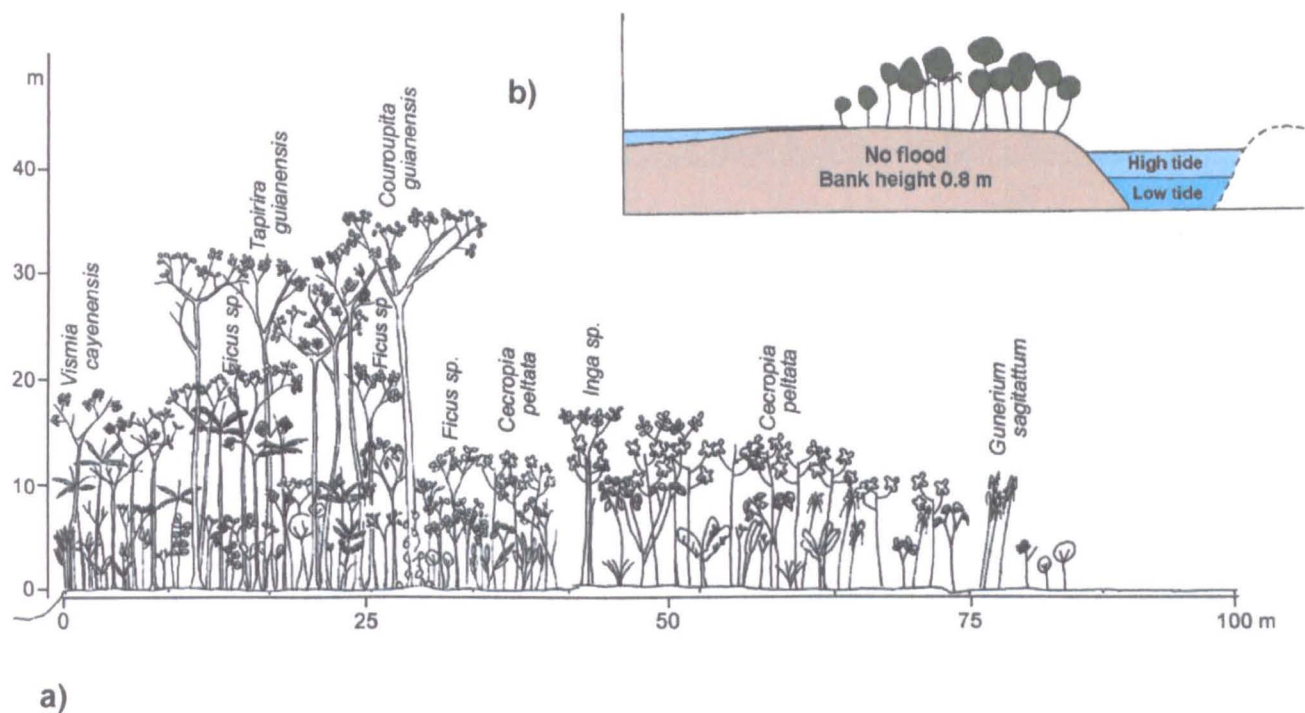
Fig. 4.6. Schematic profile of Buenaventura north site. a) Vegetation and b)physiography.
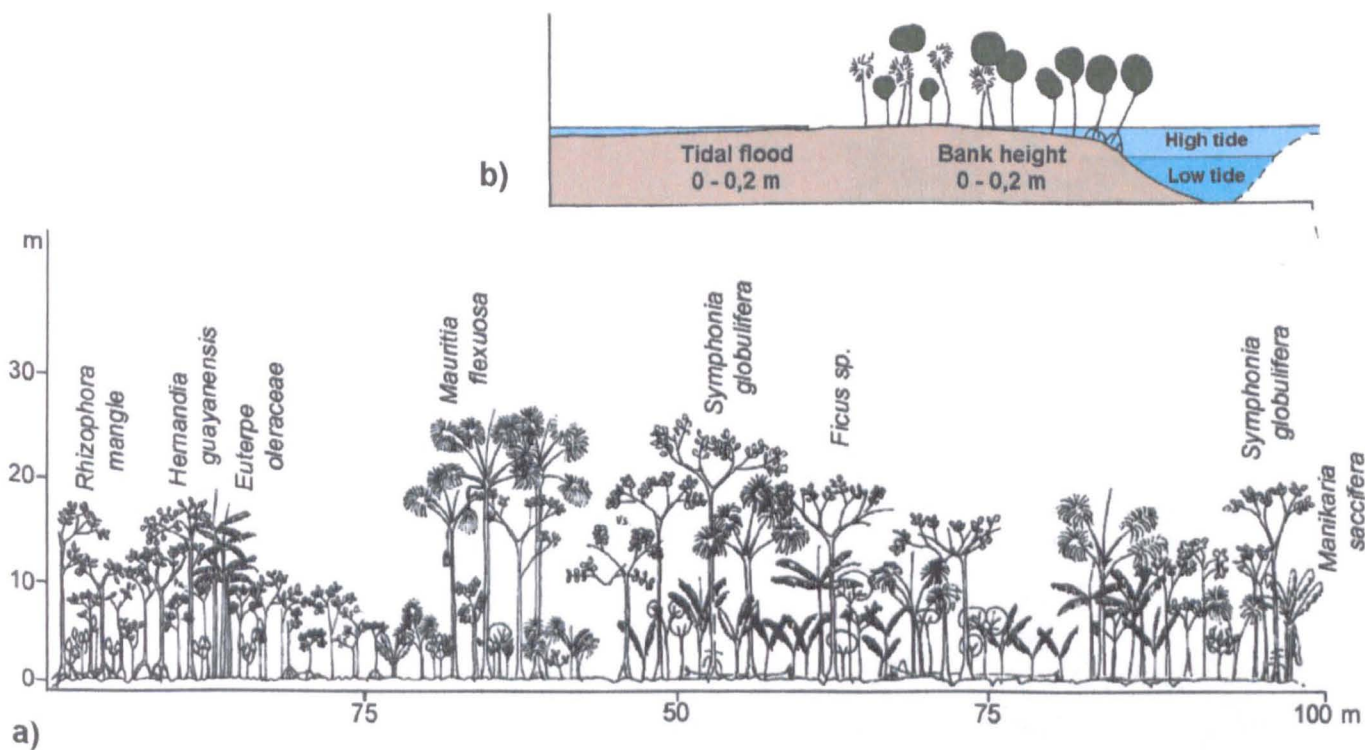
Fig. 4.7. Schematic profile of Guacajara west site. a) Vegetation and b) physiography.
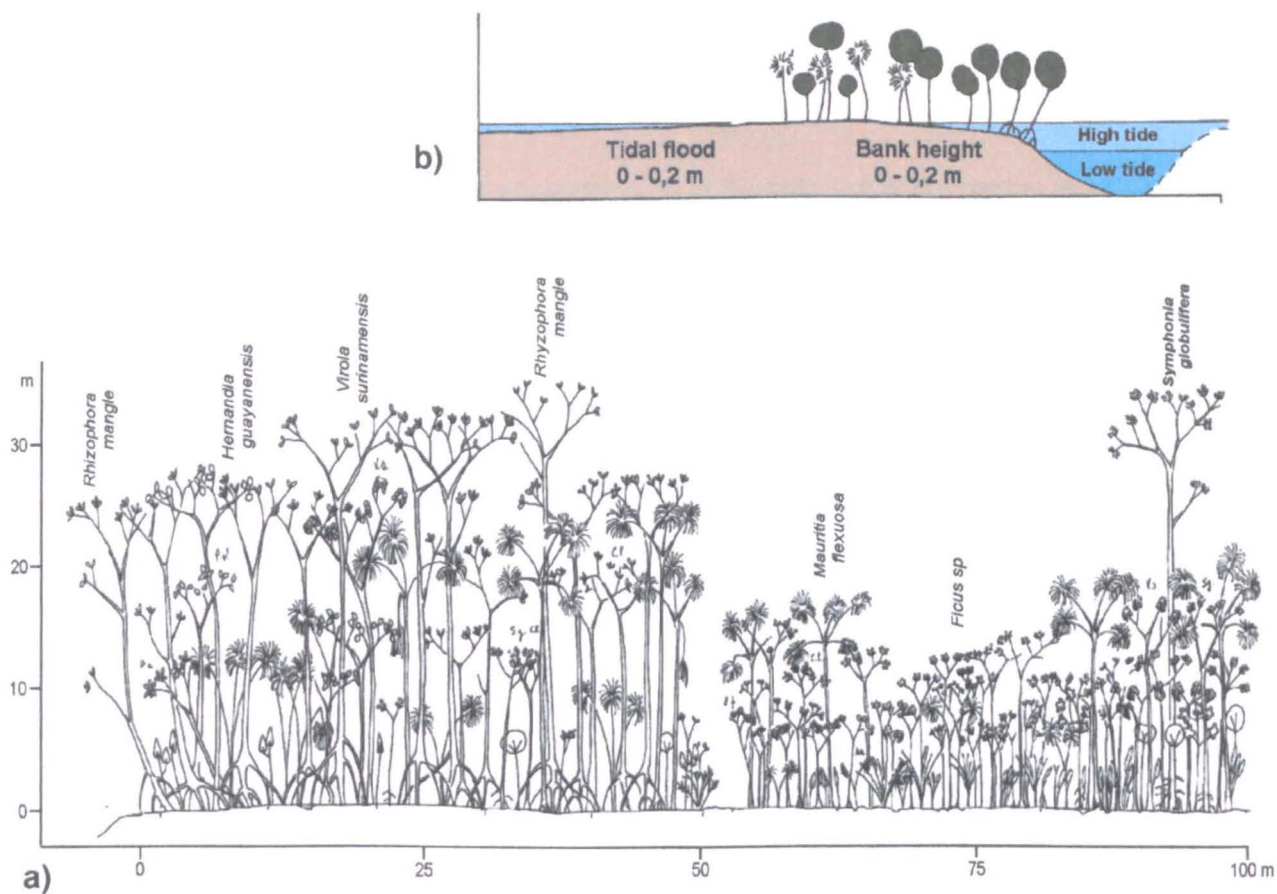
Fig. 4.8. Schematic profile of Guacajara 2 site. a) Vegetation and b) physiography
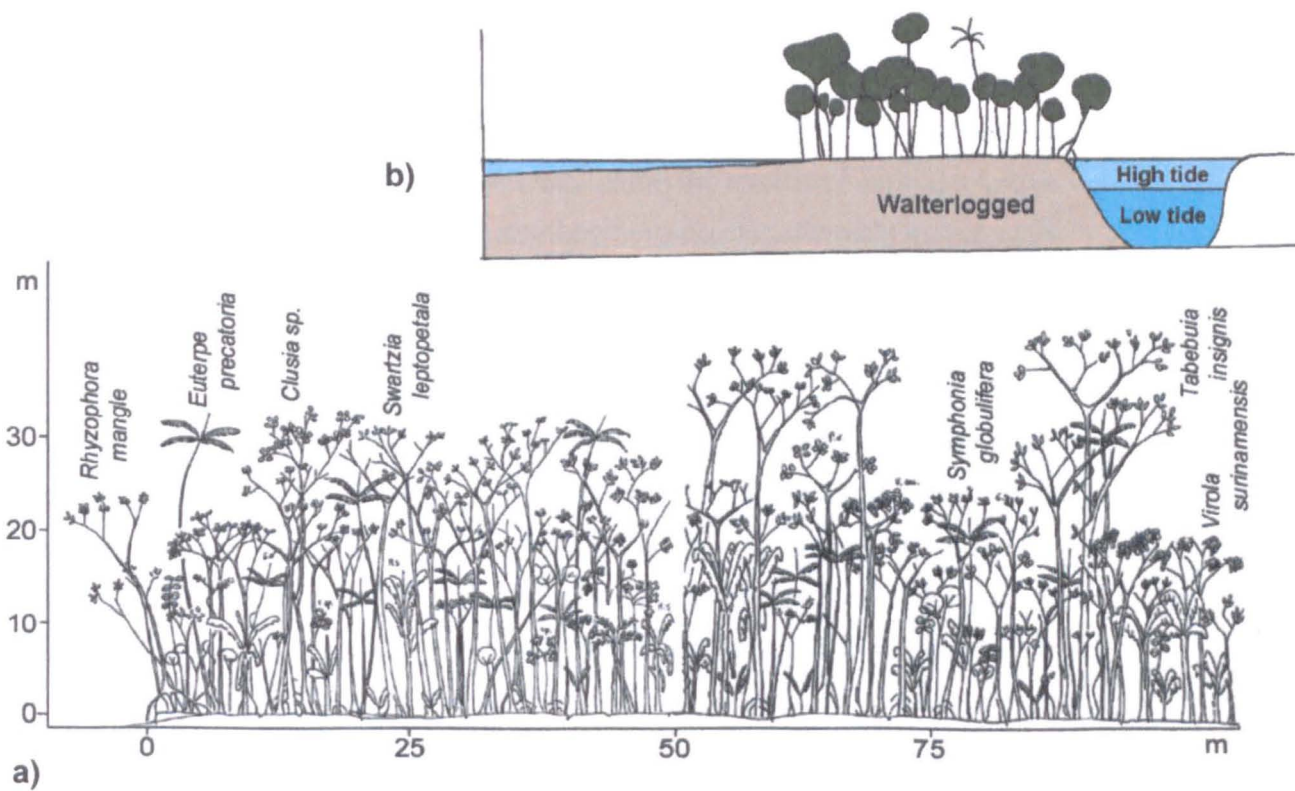
Fig. 4.9. Schematic profile of Jarina 2 site. a) Vegetation and b) physiography.

Table 4.3. Vertical structure (Upper, Middle and Lower strata) and main species composition of the sites corresponding to the gallery forest.

Site/ Heith range	Upper strata (m)	Middle strata (m)	Lower strata (m)	Herbaceous/ saplings (m)
Buenaventura **north**	Couroupita - Spondias Genipa (30 - 35 m)	Euterpe - Virola Manicaria 10 - 15 m)	Cecropia Casearia - Hura Euterpe - Piper (2 - 8 m)	Montrichardia - Costus Piper - Calathea Ferns (0 - 6 m)
Guacajara **west**	Mauritia (18 - 25 m)	Rhizophora -Euterpe Virola - Mauritia (10 - 15 m)	Manicaria - Euterpe Cecropia (2 - 10 m)	Costus - Heliconia Acrostichium (0 - 2 m)
Guacajara 2	Symphonia - Rhizophora (emergent up 35 m) Hernandia - Symphonia Callophyllum (15 - 25 m)	Rhizophora Virola - Erytrina Mauritia (10 - 15 m)	Myrcia - Annona Ficus - Cecropia Pterocarpus (2 - 8 m)	Calathea - Montrichardia Urosphata Acrostichium (2 - 6 m)

4.3.2.3 Swamp forests

Two swamp forest communities have been described: Jarina 2 (Fig. 4.9) and Jarina 1 (Fig. 4.10). They are located in the Lower Delta along the shores of Jarina; a 'black water" channel (with high content of dissolved carbon) flooded diurnally through the influence of the tides (see discussion in section 2.5).

In these sites the dominant species taller than 2 m (see species list and IVI in Appendix 11) are: *Euterpe oleracea, Carapa guianensis, Manicaria saccifera* (Temiche palm), *Symphonia globulifera, Pterocarpus* sp., *Virola surinamensis, Hernandia guianensis, Protium* sp (Currucay), *Vitex orinocensis, Virola surinamensis,* and *Macrolobium bifolium.* The palm *E. oleraceae* has been reported as a dominant species in waterlogged formation in the Ecuatorian Amazony where it constitutes 62% of the formations, that are known locally as 'naidizales'.

Due to the dominance of this species and its active reproduction *E. oleraceae,* has been considered as a helophyte, pioneer species in the Orinoco Delta swamp forests (Finol, 1993). However this pioneer characteristic has not been observed in this study as none of the marshes visited showed solitary individuals or even clusters of this palm.

The herbaceous layer (see species list in Appendix 11) is dominated by *Ischnosiphon obliquus* (Tirita) a species not present in the palm communities nor in the gallery forests. It belongs to the Maranthaceae and utilised by the Warao Indians to fabricate tools and baskets. Many saplings of the tallest trees were represented here.

The height size class distribution of these sites (Fig. 4.11) demonstrates a higher number of trunks in the category of 5 m - 10 m, than in the smaller size class. The number of trunks in the next classes decreases steadily.

The structure of the swamp forests shows three strata of trees (Table 4.4). The upper level (20 m - 30 m) is composed of *Pterocarpus* sp, *Pachira aquatica* and *Euterpe precatoria*. A stratum of emergent trees up to 40 m tall, mainly *Protium* species, and isolated individuals of *E. precatoria* individuals are also encountered. In the intermediate level (10 m - 20 m) *Euterpe oleraceae*, *Campsiandra laurifolia*, *Carapa guianensis*, *Inga* sp, are found among other species. The lower stratum contains smaller species such as *Sterculia pruriens*, *Pentaclethra* sp., *Tabebuia insignis* and *Erythrina fusca* that range from approximately 2 m - 10 m. The swamp forest described by González *et al.* (1983), have also three layers of plants but with heights up to 20 m. There are several common species such as *Protium* spp and *Calophyllum lucidum* but includes *Mauritia flexuosa*, which in the Delta is characteristic of more flooded habitats.
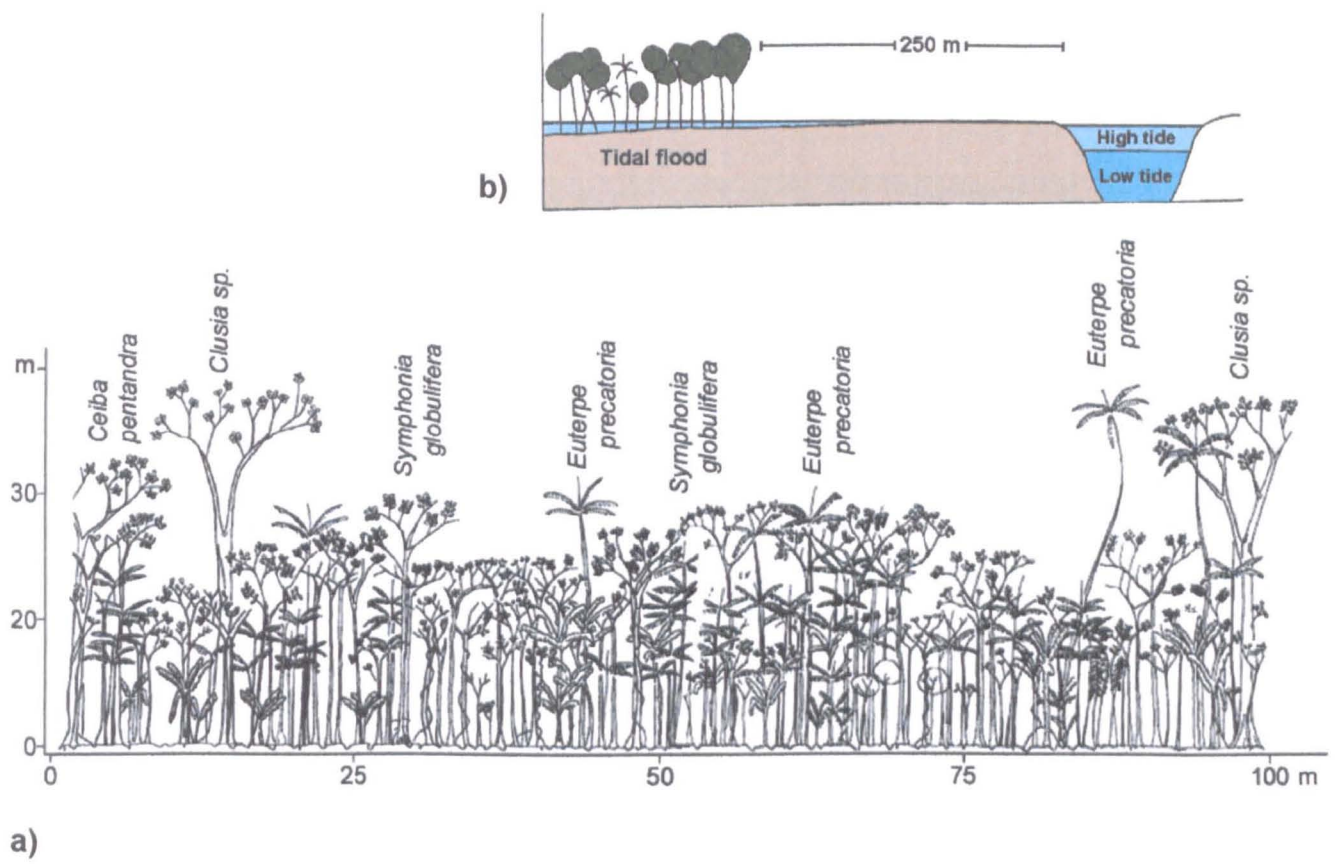
Fig. 4.10. Schematic profile of Jarina 1 site. a) Vegetation and b) physiography.

Table 4.4. Vertical structure (Upper, Middle and Lower strata) and main species composition of the sites corresponding to the swamp forest.

Site/ Heith range	Upper strata (m)	Middle strata (m)	Lower strata (m)	Herbaceous/ saplings (m)
Jarina 2	*Protium insignis* (emergent up 40 m) *Protium sp* *Pterocarpus-Pachira* *Euterpe precatoria* (20 - 30 m)	*Euterpe-Virola* *Campsiandra* *Carapa* *Symphonia* *Manicaria* (10 - 20 m)	*Euterpe-Inga* *Sterculia* *Pentaclethra* (2 - 10 m)	*Ischnosiphon-Costus* *Protium* *Euterpe-Heliconia* (0 - 10 m)
Jarina 1	*E. precatoria-Clusia* *Ceiba* (emergent up 40 m) *Macrolobium* *Protium-Sterculia* *Sterculia-Virola* (15 - 25 m)	*Vitex-Manikaria* *Inga-Manilkara* *Virola* (10 - 15 m)	*Nectandra* *Protium* *Tabebuia* (2 - 10 m)	*Ischnosiphon-Costus* *Protium* *Heliconia-Annona* (0 - 10 m)

Plot similarity

The results from the analysis of plot similarities using Sorenson's Coefficient of Community (S_s), are presented in Table 4.5.

The values of similarity between the studied sites are relatively low. However, there is a clear relationship between sites. In the swamp palm forests, the higher values are between the sites of Calentura and Pepeina, and Guacajara east and Buenaventura south. The higher links among the gallery forest sites are between Guacajara west and Guacajara 2. Similarity with Buenaventura north site is low. The two swamp forest sites also show high values, while the links with the other communities are generally low. Medium values are found between the gallery forest sites of Guacajara west and Guacajara 2.

Table 4.5. Sorenson's Coefficient of Community Similarity for all sites.

	Gua.east	Calen.	Pepei.	Bue.south	Bue.norh	Gua. west	Gua. 2	Jarina2	Jarina 1
Guacajara east		0,375	0,256	0,217	0,122	0,233	0,255	0,169	0,143
Calentura			0,34	0,323	0,169	0,361	0,338	0,198	0,229
Pepeina				0,282	0,237	0,314	0,282	0,196	0,222
Buena.south					0,253	0,267	0,241	0,243	0,239
Buena.north						0,205	0,186	0,228	0,252
Guacajara west							0,333	0,25	0,28
Guacajara 2								0,271	0,257
Jarina 2									0,309
Jarina 1									

4.4 Discussion

The communities of forest vegetation presented here are distinguished by their species composition and coverage. Each formation showed a particular tolerance to flooding which, in turn, was related to its adaptation to the soil characteristics and drainage. Periodic flooding, poor soil aeration, heavy rainfall throughout the year, and a low atmospheric vapour pressure deficit are believed to be the chief physical factors leading to the development of floodplain forests. These may exhibit many of the characteristics, typical of lowland rain forests and floodplain wetlands (Frangi and Lugo, 1985).

4.4.1 Swamp palm forest

The most common tree species of this community is the palm *Mauritia flexuosa*. This species forms dense groves, not only along the coastal regions of tropical South America (the Amazon river estuary), but also in the interior (Klinge *et al.,* 1990), as seen in the Lower Ucayali river valley (Kahn and Mejia, 1990). The second species of importance is *Euterpe oleracea*. It is the most common palm found in waterlogged soils (Kahn and de Granville, 1992). In heavily flooded areas, *Euterpe precatoria* and *Manicaria saccifera*, which are less well adapted to wet conditions, are scarce or entirely absent. González *et al.,* (1983), in a study of swamp palm forests (morichales) in the high plains of the Mesa Formation (see Fig 2.2) east to the Delta region, reports importance values (IVI), for *Mauritia flexuosa* that account for 15 to 49 % of the community results - comparable with the Delta region. In contrast *Euterpe oleraceae*, was relatively unimportant in those communities.
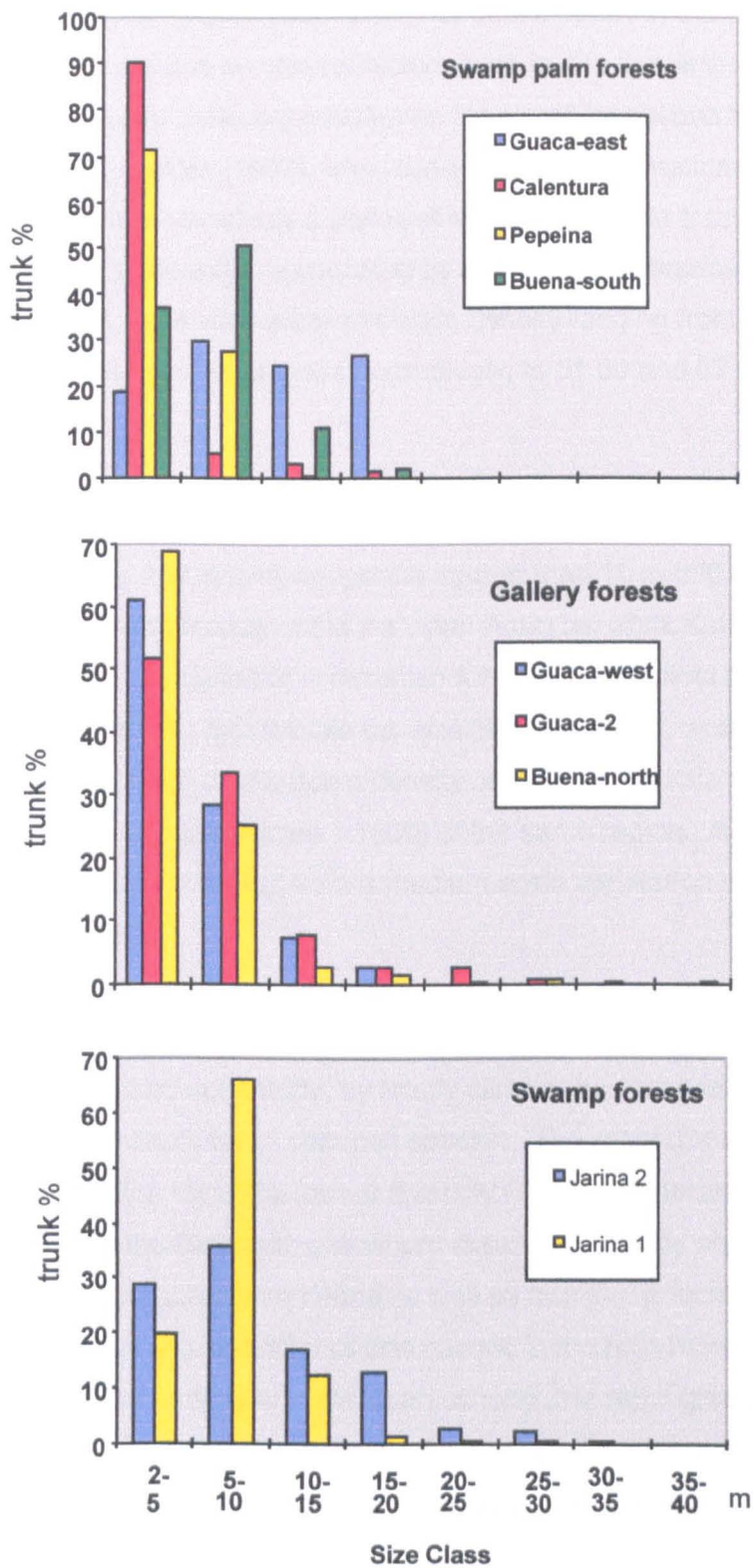
Fig. 4.11. Percentage of trunks and trunk height range for the three forest types.

The density of the moriche palm groves (also known as 'morichales') in the swamp palm forests varies and seems to depend on several factors such as the flooding conditions and soil characteristics. The influence of these parameters on the forest formations is still not well understood. According to González (1987), who studied the palm formations in the Upper Llanos of Venezuela, these may constitute a series of seres or possible transitional stages from a sparse distribution (low density) represented by herbaceous marshes to high density palm groves (see chapter 9). The sites show a relative density ranging from 20.0 and 18.27 in Guacajara east and Buenaventura south sites respectively, to 51.09 and 57.06 in Pepeina and Calentura sites respectively.

There is little literature that discusses the density of moriche groves. Kahn and de Granville (1992) report 170 to 207 individuals per ha (higher than 10 m tall) in the seasonal and permanent swamp forests of the Peruvian Amazon, while Kahn *et al.* (1993) report 230 individuals per ha in the Amazonian forests. In our plots the maximum density was 180 individuals per ha that fall into the size class of >10 m, while the total number of trunks (all size classes) may reach a density of 2590 individuals per ha. In counts made from aerial photographs (scale 1:1600) of the same region, values of up to 400 individuals per ha, were documented from a medium scale vegetation survey (Infrawing & Asociados, 1997).

Among the swamp palm communities, the degree of disturbance suffered by each site determined species diversity and equitability, by totally eliminating some rare species or reducing the number of the individuals of common species. The most disturbed sites (Guacajara east and Calentura) show the lowest diversity (7 and 13 species respectively). Particularly in the Calentura site where even the normally abundant *E. oleracea* was affected by harvesting palm hearts as well as burning, a technique used to facilitate hunting activities. Another indicator of disturbance is the high number of thin trunks, between 2 and 5 cm in width due to the open canopy ,the rapid growth and proliferation of the herbaceous species *Montrichardia arborescens* that reaches heights of up to 8 m. If incorporated into the calculations, the results from the Calentura site would show an IVI of 169 (Appendix 11).

4.4.2 The gallery forests
Gallery forests have generally been defined as formations extending along riverbanks. Their species composition and canopy structure depends on the specific flooding regime and soil characteristics. Typically, they are striking features of most savanna landscapes, especially in the Llanos of Venezuela and Colombia where they form belts

between 100 and several hundred metres in width along the waterways (Roggeri, 1995). In the Delta this particular term is used because the formation is well defined and immediately distinguishable from the surrounding vegetation. The community width is variable depending on the levee development, which in turn depends on the hydrological regime and the sedimentation process. In the Upper Delta the levees are much wider than in the Lower Delta. In the particular sector of the Pedernales river investigated, varied from about. 100 m, in Buenaventura north site to a narrow band, that is hardly discernible at the Guacajara 2 site

The Buenaventura north site is located on a narrow strip of non-flooded levees in the Upper Delta where the soils are clayey to sandy, neutral pH and showing a relatively good drainage in the A1 horizon. The selected plot represent an area along the river bank that underwent intense management during 1950s and 1960s (Fig. 4.6), but was abandoned in 1975 following the regulation of the Mánamo river (see chapter 9). The plantations of bananas, pineapple, and cacao were left unattended, and only the coconut palms and coffee bushes have survived among the regenerating forest and the herbaceous formations. Interspersed among the partially secondary vegetation of the plot are remnant coconut (*Cocos nucifera*), coffee (*Theobroma cacao*), and pineapple (*Ananas* spp.) plants.

The dominant species of this site (*Casearia silvestris, Bactris* sp, *Inga* sp., *Virola surinamensis, Spondias mombin, Hura crepitans* and *Genipa americana*) are quite different from those of the other communities and *Mauritia flexuosa* is noticeably absent due to the dry conditions of this particular site.

As one travels down river towards the Middle Delta, the levees gradually disappear and the banks may be temporarily flooded for 8-12 hours a day due to the influence of the ocean tides. The soils become silty, organic, acidic and poorly drained (CVG-Tecmín, 1991). The forest physiognomy and species composition constitute a kind of mixture between the swamp palm forest and the gallery forest. At the Guacajara west and Guacajara 2 sites (see profiles on Figs. 4.7, 4.8), species such as *Pterocarpus officinalis* and *Symphonia globulifera* dominate because they can tolerate the water-logged conditions. Other species, such as *Inga* sp. are less tolerant to water saturated soils and are therefore limited to the drier areas (CVG-Tecmin, 1991). Due to the intrusion of brackish waters caused by the regulation of the Mánamo fluvial subsystem, mangrove trees (*Rhizophora mangle*) have colonised the river banks inland to the location of Pepelna. A similar phenomenon is witnessed on the Mánamo river itself (see chapter 8).

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The gallery forests included in this study are more diverse than the swamp palm forests, both in terms of species composition and the complexity of the canopy and understorey. Among the three sites studied, the Buenaventura north site (which is not influenced by flooding) showed higher values for tree trunks and species number. However, due to anthropogenic intervention, the plant diversity is similar to that of the other gallery forest sites (Table 4.1).

The moriche (*M. flexuosa*) and Manaca palms (*E. oleracea*) are still present in the forest structure but are much less prominent here than in the swamp palm forests (see table 4.1). Here they are gradually replaced by the temiche palm, *Manicaria saccifera*. The Guacajara west site shows a reduced number of species due to the high degree of disturbance caused by the Warao inhabitants (see chapter 9).

4.4.3 The swamp forests

This type of forest is located towards the lower Delta where the topography becomes very shallow and, particularly along the smaller channels, the differences between the levees and the lower areas are scarcely perceptible. The soils are mostly organic, very acidic (pH up to 3.2, Infrawing & Asociados, 1997) and there is no water drainage. Although soils are not deeply flooded, they remain waterlogged most of the year and are inundated by the daily tides. Klinge *et al.* (1990) classify this kind of wetland forests as 'Tidal forests', flooded diurnally by fluvial waters that become 'backed-up' by the incoming tides.

A clear demonstration of the influence of flooding on species composition and vegetation structure can be seen on the two plots of the Jarina sites (Fig. 4.9, 4.10). The Jarina 2 site is located along the banks of the Jarina river where the soils are dryer than on the Jarina 1 site, which is located 200 m inland in a more depressed area, and under a stronger tidal effect with daily 12 hour periods of flooding. The tree species richness is higher in the less frequently flooded site of Jarina 2 (52 species) than in the more frequently flooded site at Jarina 1 (41 species). Plant diversity however, is higher in Jarina 1 (H'= 3.02) than in Jarina 2 (H'=2.58). In fact, the equity is lower in Jarina 2 (0.65) than in Jarina 1 (0.81) because of the many species represented by only few individuals. Several authors have stressed the negative correlation of species diversity with water level and the duration of flooding in large tropical river floodplains (Colonnello, 1990b; Valle Ferreira and Stohlgreen, 1999).

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Both of these sites show a similar floristic composition, at least in regard to the most common species, *Euterpe oleracea, Manicaria saccifera, Virola surinamensis* and *Symphonia globulifera*. These represent a common plant association in the swamp forests of the Venezuelan high plains (González *et al.*, 1983) and Amazonian ecosystem (Kahn and de Granville, 1992). However, they differ with respect to the dominance of other species. There are 29 species such as *Protium* sp, *Sterculia pruriens, Casearia silvestris* and *Manilkara nitida* that are represented by only one to four individuals which results in a relative density of 0.188 to 0.75. The appearance of a new palm species, *Euterpe precatoria*, that was not present in the other formations, here constitutes a component of the canopy (the upper level strata).

Figure 4.11 shows the tree size classes of the trunks higher than 2 m. The size class from 5 m -10 m is the dominant category in both sites. The Jarina 2 site on the river bank has a denser lower stratum (2 m - 5 m) and less individuals in the 5 m -10 m category. None the less it has a higher number of individuals in the higher classes, with emergent trees reaching up to 35 m. Consequently the physiognomy of the two plots is different; the trees in Jarina 2 are both taller and larger than those in Jarina 1. The distribution of the trunks and species in both sites may be explained on the basis of their tolerance to the flooding and possibly to the somewhat brackish water. The salinity or sodium concentration in these waters has not been measured but the halophytic species *Rhizophora*, grows in the river edge as an indication of some saline influence. Although there are fewer individuals representing each species, the Jarina 2 supports more species than the Jarina 1 site because it demonstrates less restrictive environmental conditions.

In the areas more susceptible to flooding the species show anatomical and morphological adaptations such as adventitious roots (*Symphonia globulifera*) and lenticel hyperthrophy (*Casearia silvestris*); structures that are known to avoid anaerobiosis (Gill, 1970; Arteca, 1997). Similar adaptations have been reported to explain the distribution of plants in habitats with differential flood conditions along the Orinoco (Colonnello, 1990b) and on the Amazon floodplain (Rosales *et al.*, 1999).

Plot height class distribution

The differences found according to height classes distribution (Fig. 4.11) are due to the disturbances in the forest communities, in particular in the swamp palm forests. In the Guacajara east site, only seven species higher than 2 m were recorded, indicating a high

level of intervention. Likewise, the large number of small individuals present on the Calentura site is due to recent fires that cleared the canopy. In addition, the remaining size classes are composed of only a few trunks, allowing for the growth of heliophillous species.

Within the gallery forests, the tree individuals on these plots shows a reverse J shape, or negative exponential distribution characteristic of most tropical forests, despite the severe disturbance found on Buenaventura north and Guacajara west. The pattern shown by the swamp forest sites indicates a low number of juvenile individuals that can be related with the high number of trunks on plot, 532 and 609 respectively. In contrast with the other sites, where light was not a limiting resource, the competition for light and nutrients may be restricting the seedlings of new plants, particularly in the Jarina 1 site which is located in a more flooded position, inland from the levee of the channel. Campbell *et al.*, (1980) reported a similar pattern in a 'varzea' forest (seasonally flooded) and a 'terra firme' (dry) forests in Amazonia.

Similarity values in between the sites (Table 4.5) do not show strong links because the presence of many species such as *Euterpe oleraceae*, *Annona* sp., *Symphonia globulifera*, *Cecropia peltata*, *Psidium* sp and two species of *Ficus*. which are common to all the flooded environments and even to the waterlogged sites of Jarina. The data, however, suggest strong similarities between the more altered swamp palm forests sites of Guacajara east and Calentura; the plots with lower species diversity (Table 4.1). The later two sites are linked to the gallery forest sites such as Guacajara west by high intervention and with Guacajara 2 of medium intervention (Table 4.1).

The Gallery forests sites of Guacajara west and Guacajara 2 are also closely linked because their locations along the Pedernales riverbanks are under tidal influence. However they differ from Buenaventura north site which is located on a high levee, and therefore not susceptible to flooding. This plot is more closely associated with the Jarina sites that are also free from flooding.

4.5 Final remarks

Flooding is the chief ecological constraint on the forest vegetation in the area under investigation. The soil environment becomes depleted of oxygen due to its consumption by roots, soil biota and aerobic micro-organisms. Atmospheric oxygen diffuses so slowly into the dense, wet and flooded soils, that it can drop to a few percent or disappear completely in a few hours (Larcher, 1995). Flooded forest species seem to be distributed

according to their tolerance to the anaerobic conditions. This is suggested in the analysis of the species Importance Value Index (IVI) along the sites flooding gradient as shown by the distribution of six of the dominant species (Fig. 4.12). *Mauritia flexuosa* offers a clearer pattern in the Pepeina site; increasing its importance as the flooding reaches its maximum (longer and deeper conditions). *Erythrina fusca* shows a similar behaviour even though, surprisingly, it was not recorded in the Pepeina site. *Euterpe oleraceae*, the second species in importance in all the sites and *V. surinamensis*, reveal a wider ecological adaptation; growing from deep sites to non flooded (or waterlogged) habitats such as the Buenaventura north site. *S. globulifera* can grow in a flooding range from short and shallow floods (0 cm -10 cm) as in the Jarina 1 Site. It was not found on the levees of Jarina 2, where waterlogged soils dominate even though a flooding event is rare. *Manicaria saccifera* prefers the dry habitat or the relatively low and brief flood events. In the Buenaventura north site as a consequence only a few plants were found. Finol (1981), found that a similar relationship existed among the dominance of *M. saccifera* and the flooding intensity in the Delta area south of the Río Grande. In that site, *E. oleraceae* was found to have a higher IVI, 42 % of the total, in deep flooded soils while *M. saccifera* showed higher importance in the driest sites, 22 to 43 % of the total.

The severe ecological conditions imposed by flooding or waterlogging produce increased competition which results in a highly-specialised wetland flora with a lower diversity (Dumont *et al.*, 1990). Givnish (1999) summarised several ecological gradients that condition the species richness in tropical forests: the numbers tend to increase with precipitation, forest stature, soil fertility, rate of canopy turnover and time since the last catastrophic disturbance, and tend to decrease with seasonality, latitude, altitude and diameter at breast height. Data from this study suggest that the increase of the species richness is associated with the gradient decrease of flooding and of increasing dryness. Fig. 4.13, shows species richness values set against a hypothetical gradient from flooded to non flooded habitats, from temperate and tropical regions (Table 4.6). The term 'Permanent flood' refers to flooded habitats exhibiting a fluctuating water level. Seasonal floodings refers to a habitat that undergoes deep flooding for several months within a year whilst waterlogged or tidal areas indicate permanently or almost permanently wet conditions or with daily short term flooding. Non-flooded area indicates a permanently dry or shortly waterlogged habitat. Despite the differences in the area and shape of the sampling plots, which yield different numbers of species (Laurance *et al.*, 1997), the flooded habitats show lower species richness that the non flooded sites. This also holds true for the Delta region, as observed in the Middle Delta area and in the Río Grande

area in the Lower Delta (Finol, 1981). A species richness within a 0.1 ha or similar, shows a positive correlation with the increase of the flooding intensity.

In a similar fashion, Dumont *et at.*, (1990.), Klinge *et al.*(1990) and del Valle (1996) concluded from their analysis of the Amazon basin forests, that their floristic inventories clearly demonstrated that species richness is higher in upland than in wetland forests. There is a general tendency towards a decrease in plant diversity under more demanding environmental conditions- that is, from swamp forest to gallery forests to swamp palm forest. This was stressed by Armentano (1993) for the freshwater swamp forests of northern South-America. In the Fig. 4.13, the species diversity of the Buenaventura north site (BuN, in the graph) should have contained, prior to its disturbance, a higher number of species; probably 60 to 70.

All the studied sites have been affected by human intervention, from the very marked alteration in the swamp palm forests, the felling of large trees at the Guacajara east and Guacajara west sites and fires at the Calentura site. Disturbances clearly diminish the species diversity (Cochrane and Schultze, 1999), compared with the almost undisturbed swamp forests where only fruits and palm leaves are harvested. Species diversity is consequently influenced by these disturbances as noted in Table 4.1 as well as by flooding influence (Fig. 4.12).
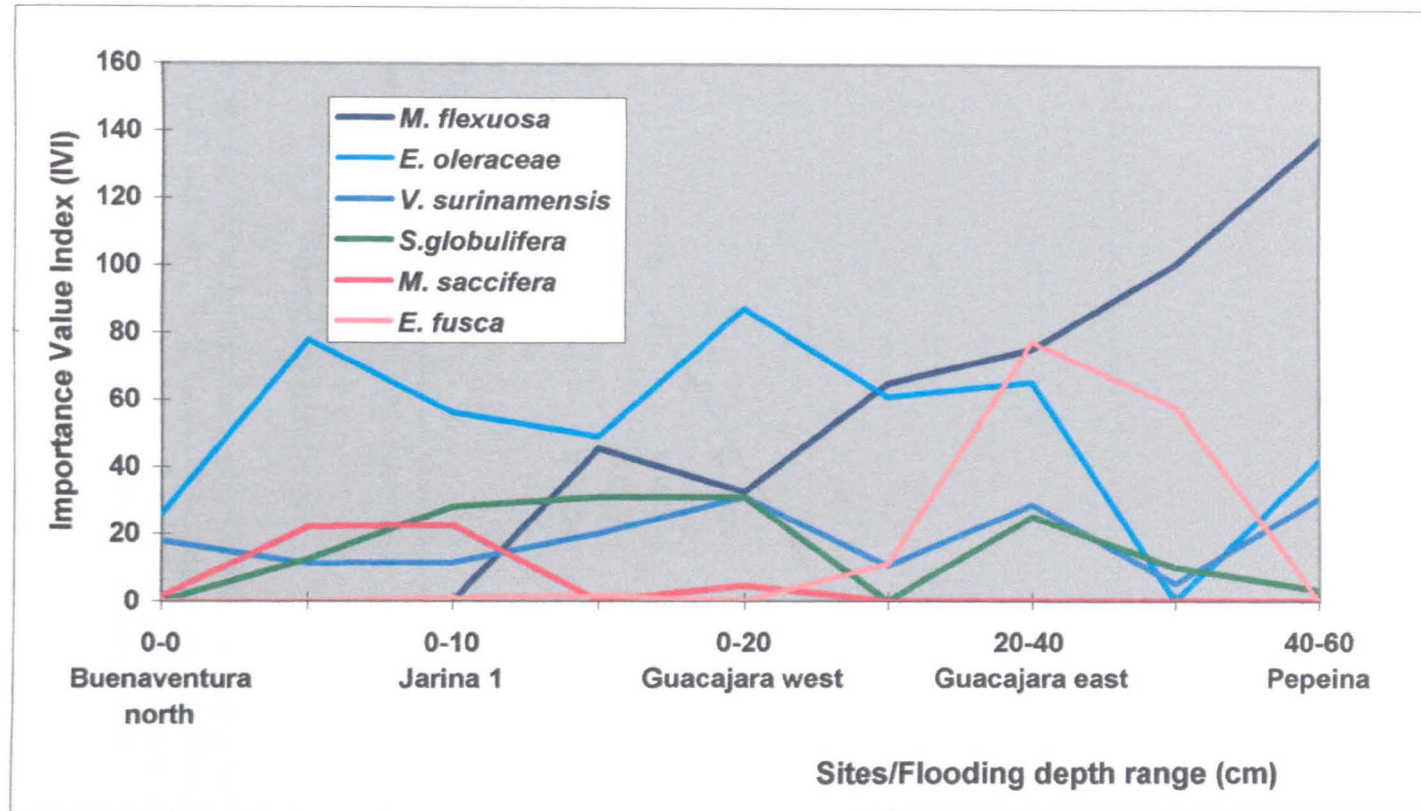
Fig. 4.12. Distribution of six dominant species along the sites flooding gradient.
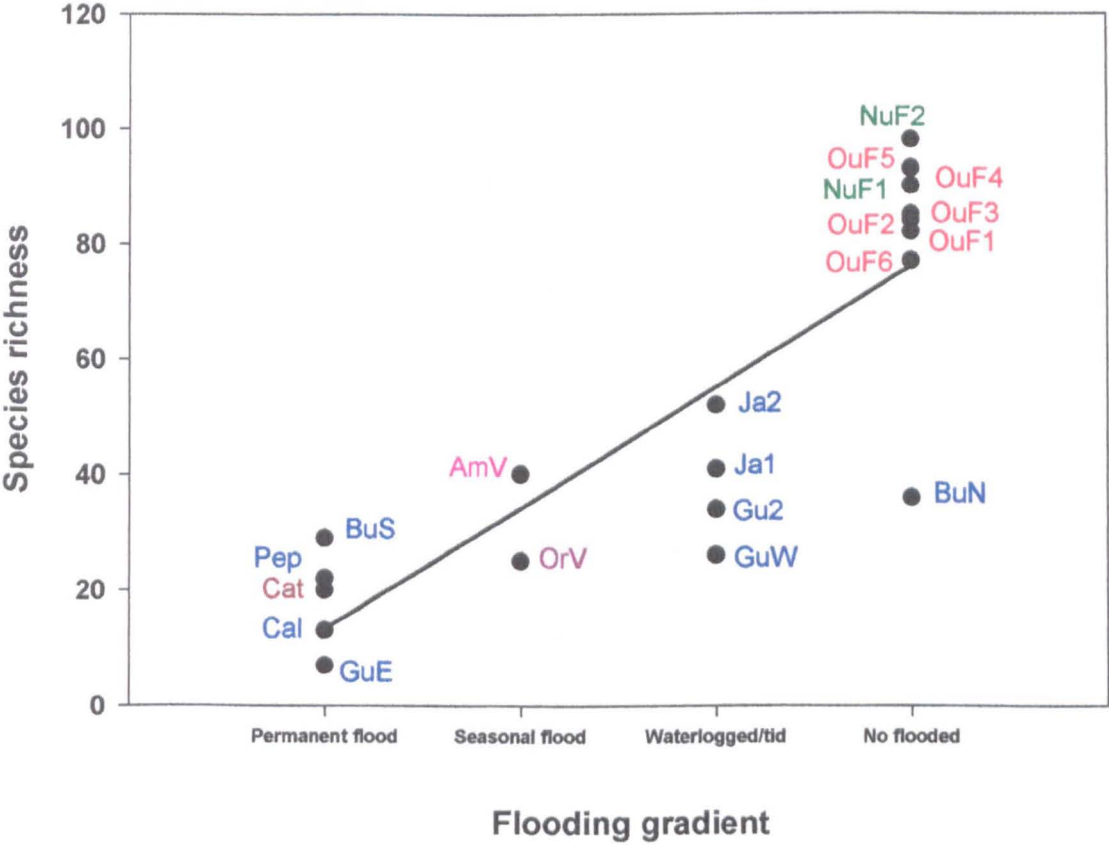
Fig. 4.13. Relation of the trees richness and flooding condition in several forest communities. BuS, Pep, Cal, GuE, Ja2, Ja1, Gu2, GuW, BuN: this study; Cat:Mississippi floodplain swamps; OrV: Orinoco floodplain rebalses; AmV: Amazonian floodplain várzea; OuE: Orinoco floodplain dry forests; NuF: Tropical upland forests.

The observed disturbances are the result of a series of anthropogenic alterations that have taken place over a period of at least 60 years. They have caused extensive successional, natural and man-promoted changes in the vegetation (see chapter 9). The more recent of these disturbances, witnessed in the structure and composition of forest communities, have been caused by the overexploitation of natural resources in the Middle Delta region. This may be considered as an indirect impact of the regulation of the Mánamo river upon the neighbouring ecological environment.

Table 4.6. Woody plant species richness vs. a gradient from flooded conditions to non flooded, upland, forests.

Habitat	Simbol	Richness	Source
Orinoco Delta (0.1ha)	BuS,PeP,Cal,Ja2, Ja1,Gu2,GuW,BuN	Table 4.1	This study
Mississippi floodplain 'swamps' (0.03 ha)	Cat	20_a	Devall (1990)
Orinoco floodplain 'rebalses' (0.2 ha)	Or	25_b	Colonnello (1990b)
Amazonian floodplain 'varzea' (0.5 ha)	Am	40_a	Campbell *et al.* (1986)
Orinoco upland-forest (6x0.1 ha)	OuF	$85\text{-}84\text{-}82\text{-}77\text{-}90\text{-}93_c$	Aymard (1997)
Tropical upland-forest (0.1 ha)	NuF	$98\text{-}85_c$	Gentry (1993)

a = dbh >10 cm; b = dbh > 5 cm; c = dbh > 2.5 cm

Chapter 5 Physico-chemical and hydrological variables of the Mánamo and Macareo rivers

It has been established in preceding chapters that river regulation is one of the major disturbances to wetlands, affecting ecosystem functions including nutrient cycling, primary productivity and a variety of ecosystem components, such as the hydrologic cycle, and the composition of vegetation and faunal communities. There are extensive effects downstream from the dam but there are also effects upstream, in the 'impounded reservoir' section. The chief effects are on the hydrological regimes which in turn modify or influence many other aspects such as regional physiography, and water chemistry.

The Mánamo river impoundment affected about 8,000 sq. km and to date, there were no detailed physico-chemical data, comparing this river and its sub-basin with a non regulated system thus this study seeks to rectify this deficiency.

5.1 Aims

- To document and compare the physical and chemical characteristics of the Mánamo regulated system, with a natural system - the Macareo river.

The research hypothesis is that the dam construction caused changes in the hydrology and physio-chemistry of the Mánamo waters and its system.

5.2 Methods

Sampling strategy for water quality

The period of active sampling was designated to coincide with the time of the rising levels and associated increase in input of nutrients. River regulation led to a diminution of the water flow and sediment load in the Mánamo. This knowledge is particularly important in tropical rivers where the seasonal rainy period is associated with a proportional increase in the erosive processes within the watershed and also to an increase in the nutrients transported by such rivers.

The water quality sampling programme and measurements of variables, was then arranged as follows: five samples during the period of rising river water levels from April to the beginning of August (1994), two samples during the maximum high water or flood stage from 15 of August to end of September (1994) and three samples during the period when levels were receding from October to January. One more sample was taken in April 1995, at the beginning of the next cycle of water level increase (Table 5.1).

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The sampling sites are shown in Fig. 5.1. They were selected at 20 km intervals in order to minimise the influence of other water courses and local rains as well as material transport, on the water quality variables. Samples were always taken in the middle of the channel at the water surface. While dissolved oxygen and temperature measurements, were taken at the water surface and at 1.5 m in depth.

Table 5.1. Distribution of the samples along the increasing and falling water periods of the rivers.

	Increasing water					Falling water							
	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Day of sample collection	25	16	5 & 19	10	1 & 14	27	24		12	1			10
	1994									**1995**			

5.2.1 Hydrology (water level)

Data on the seasonal variations in water level in the Macareo river were obtained from the Department of Agriculture (Departamento de Infraestructura Agrícola) of Corporación Venezolana de Guayana from the Station No 17, located 100 m upriver from the Mánamo Dam. The gauge is located in the unregulated section of the river and the data is used as a proxy set simulating the fluctuations in the unregulated Macareo river. This was because no discharge data was available for the Macareo. The resulting values were checked against the low and high water values observed at the town of Boca de Macareo located along the Macareo river bank one kilometre downriver from its branching from the Mánamo (see Plate 2.1). The Boca field measurement indicated a similar maximum and minimum value for the period 1990-2000 as that of the 20 years records from gauge N° 17.

This data was normally collected daily but not continuously. Given the limitations of collecting such a data set, a monthly hydrograph was prepared for the period of January
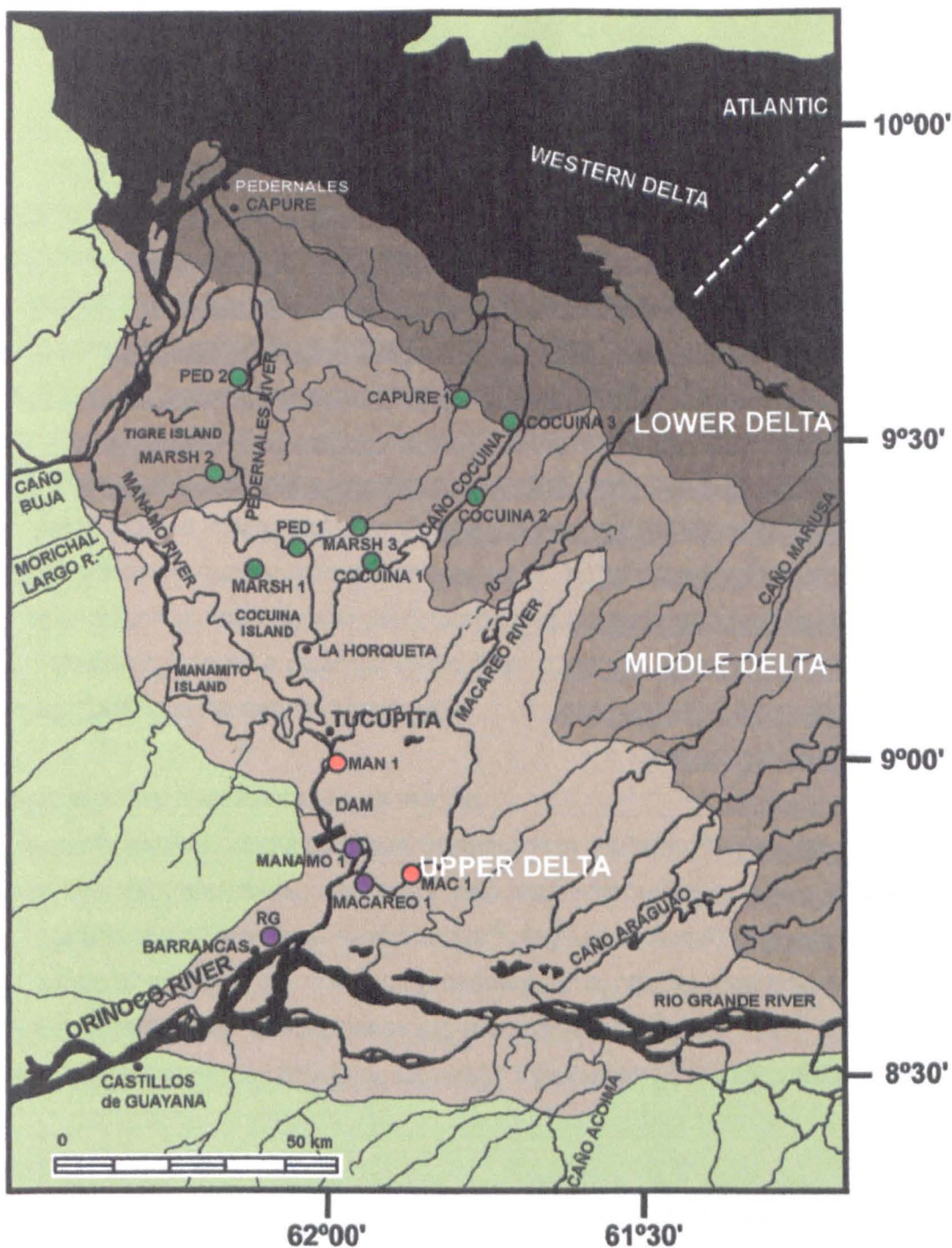
Fig. 5.1. Sampling sites of physico-chemical data:

○ MAN1 and MAC1 (This study)

● PED1= Pedernales 1; PED2= Pedernales 2; Cocuina 1= C. Cocuina 1;
Cocuina 2=C.Cocuina 2; Cocuina 3= C.Cocuina 3; Marsh 1; Marsh 2;
Marsh 3 (INFRAWING & ASOCIADOS, 1997).

● RG= Río Grande; Macareo 1; Macareo 1: 2 sites (IRNR (USB) Ecology
and Environment, 1999).

1994 to June and for a period of 20 years from 1970 to 1990 to validate the 'normality' of the water regime during the study period.

A graph of the daily rate of water level variation was also prepared for the period April 27 to September 28 to correlate the results of biomass production from the aquatic meadows (see chapter 7). Additional data was collected by the author during the high water period from June to August (1994) and from September to November (1994), in an irregular cycle of 10-15 days, using a measuring scale located in a tower standing in the Macareo shore close to the Boca de Macareo town. Data concerning the Mánamo river was obtained directly from a graduated staff fixed to the channel bank close to the dam (see plate 2.2).

5.2.2 Cations, phosphorus and nitrogen

Water samples were collected in polyethylene bottles and kept refrigerated for subsequent laboratory analysis, which was performed within 5 hours of collection. Due to the restrictions on the number of samples that could be analysed, each 'sample' was prepared from three bottles of 1 litre from several places around the boat and mixed in the lab to obtain a single composite sample. Each sample was analysed twice.

The techniques used for each element were as follows:

1. PO_4^{3-}: Samples were filtered using a 'Millipore' membrane of 0.45 µm, acid digested (H_2SO_4-HNO_3 concentrated) and measured through colorimetry methodology (APHA., 1985).
2. Samples for analysis of total dissolved elements, Ca^{2+}, Mg^{2+}, Na^+, and K^+ samples were filtered, using a 'Millipore' membrane of 0.45 µm, and analysed on 'atomic absorption spectrophotometer', model Varian, AA-30, according to the methodology of APHA(1985).
3. Total nitrogen was determined by EPA procedure 351.3 (colorimetry) (APHA, 1985).

5.2.3 pH and electric conductivity

The pH and electric conductivity were measured in the lab from water samples at a temperature of 25 °C, using a pH-metre Corning 3D and a conductimeter La Motte DA-1.

5.2.4 Temperature and Dissolved Oxygen (DO)

The temperature and dissolved oxygen (DO) were measured in situ with an Oxygenometer ISI 51-B at the surface and at 1.5 m depth . Measurements were always taken between 9 to 10 am local time in the Macareo river and between 2 and 3 pm in the Mánamo river.

All data were analysed to identify any significant differences using the 't paired' (at 95.5 % of confidence) and Kolmogorov-Smirnov tests (Abacus Concepts, StatView, 1992).

5.2.5 Transport of sediments and transparency

Total suspended sediments were separated from 250 ml sub-samples, taken from a water sample of 1 litre, which was collected in several steps along a transect in the centre of the channel, at 30 to 40 cm depth. Sediments were obtained by filtration, using a Millipore membrane of 0.45 µm. The sediment was measured by the difference in weight of the membrane before and after filtration.

The transparency was measured with a Secchi disc, following the method proposed by Roldán Pérez (1992).

5.2.6 Current velocity

The current velocity, measured along the banks and in transect sections of the Mánamo and Macareo channels, was determined through the use of a 'General Oceanics' meter and a 'Garmin' GPS (model 75). Both pieces of equipment were used in the same site to confirm the readings obtained. Additionally measurements were taken in other areas of the rivers course to relate current velocity with geomorphology processes and the data obtained in chapters 6, 7 and 8.

5.3 Results

5.3.1 Hydrology (water level oscillation)

The comparison of the regulated system with the natural system hydrology was considered fundamental since it was anticipated that there would be a high correlation in the physico-chemical and biological variables when compared with the discharge regimes of the two rivers (de Cabo *et al*, 1999).

The hydrograph of the regulated and unregulated sections of the Mánamo and Macareo rivers are shown in Fig. 5.2a. The Macareo river (the unregulated section of the Mánamo), as expected, shows a clear fluctuation of increasing (and then falling) water level up to 7.35 m.
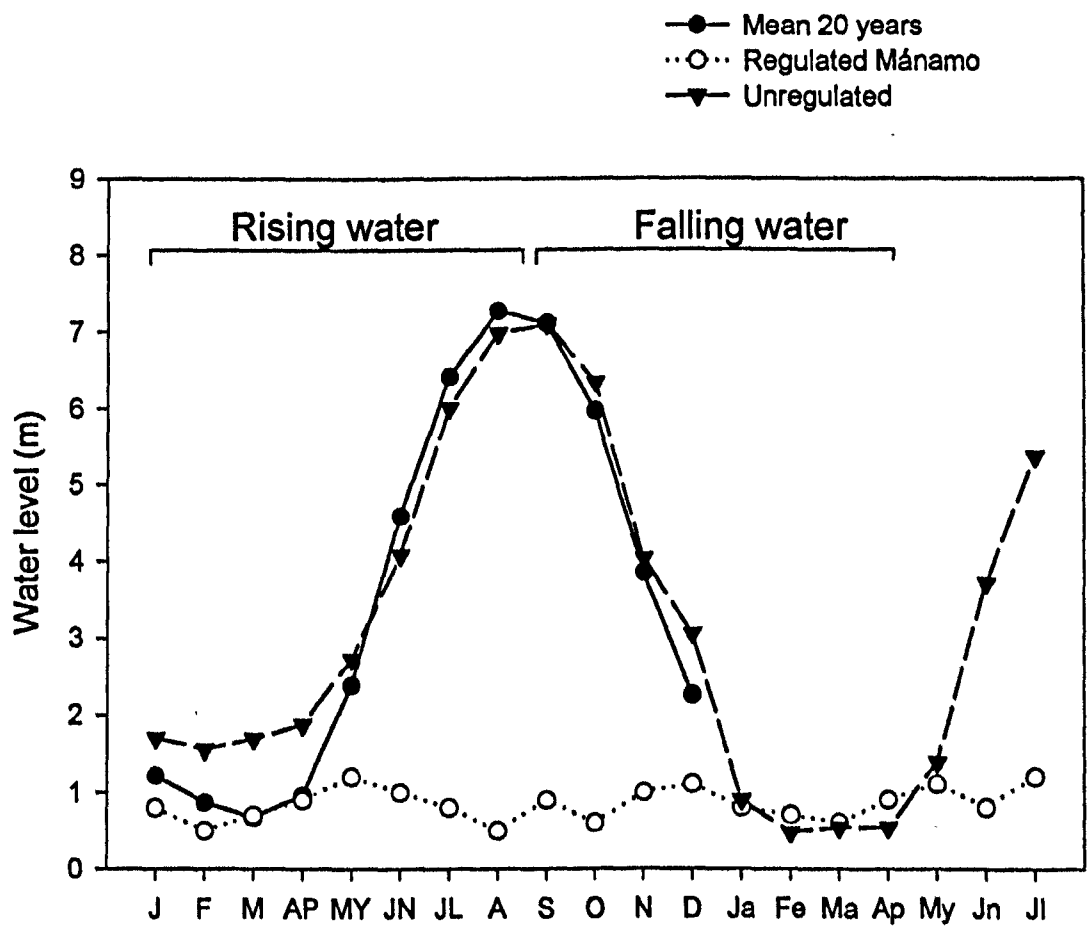
Fig. 5.2 a. Hydrograph of the regulated and unregulated Mánamo river.
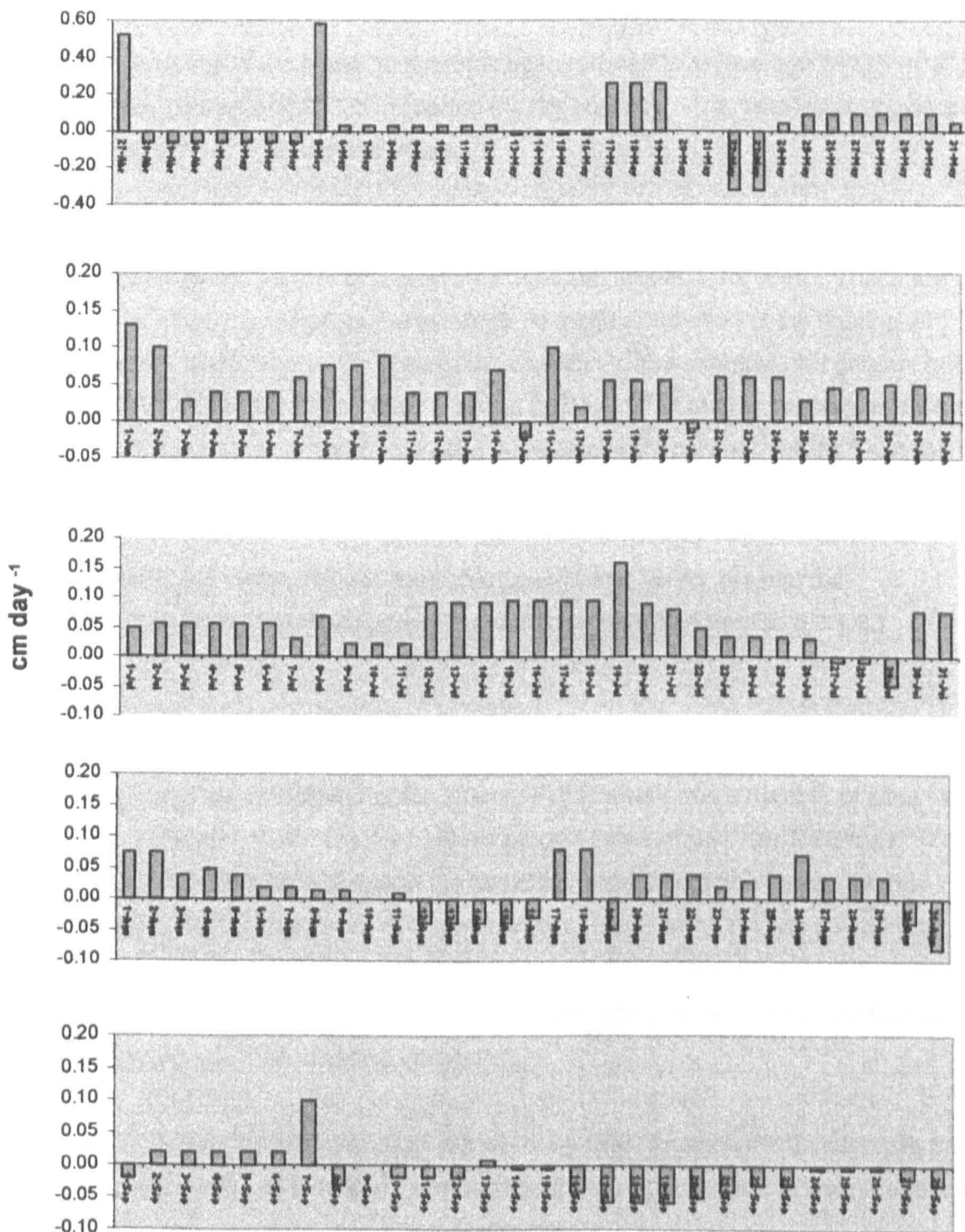
Fig. 5.2b. Daily variation of the water level in the unregulated Mánamo
and Macareo rivers (increasing water stage April-September 1994).
Note the differences in the 'y' axis in the first graph.

High waters were generally recorded between June and October. There is a low water period between the receding phase and the subsequent rise in water levels. This hydrograph is representative since it is similar to the long-term hydrograph (20 years).

The regulated discharge of the Mánamo river has been reduced to an average of 175 m^3 s^{-1}(150 m^3 s^{-1} during the rainy season and 200 $m^3 s^{-1}$ during the dry season). The water level shows a daily oscillation of only 0.7-1.2 m due to tidal effects.

The increase of the water level in the unregulated Macareo river, during June to September (Fig. 5.2 b), shows several periods of accelerated rises and falls in water levels. These are important 'events' since they regulate the establishment and distribution of the floating and emergent meadows along the riparian zones (see chapter 7). For example, the general rate of increase in level was about 1.2 cm day^{-1} from the 24th to 31th of May increasing to 13 cm day^{-1} on the 1st of June. The variation was even more significant between the 12th and the 18th of August when the rate of fall of circa 4 cm day^{-1} was reversed to a rise of 8 cm day^{-1}. The rising water phase started on May 24th and the falling phase commenced on September 8th. The water dynamic, high velocities and swift changes in water levels, prevent the establishment of extensive meadows across the river channels (see section 6.3.1.3.).

5.3.2 Cations, phosphorus and nitrogen

Results for Na$^+$, K$^+$, Mg^{2+}, Ca^{2+}, PO$_4$$^{3-}$ and N are shown in Figs. 5.3 to 5.5.

The Na$^+$ was sampled as an indicator of the influence of sea water on a number of sites along the Mánamo and Macareo river. The Na$^+$ values ranged between 0.97 and 2.68 mg l^{-1} (Fig. 5.3a) and showed little difference between the two channels although the values for the Mánamo are slightly higher than those of the Macareo, at least during the rising water stage, but this difference is not statistically significant (t-test, P= 0.09). In fact the two curves have a high correlation score (r^2 =0.93) maybe because the dominating influence from the Orinoco water has a damping effect on any local variation.

It might be expected that the penetration of salt water up river would be most noticeable on the Mánamo during the dry season when seaward discharge was very low or even negative. However this was not observed in the upper river section.
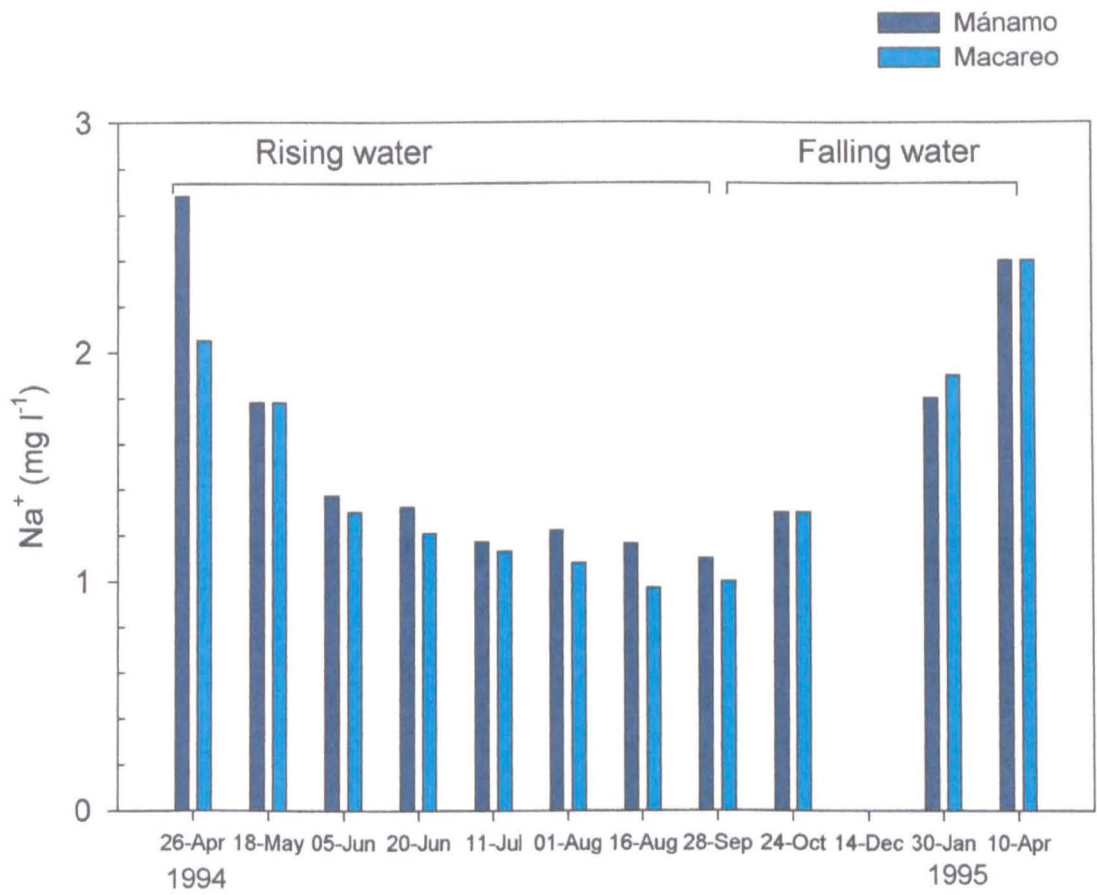
Fig. 5.3 a. Seasonal variation of sodium.
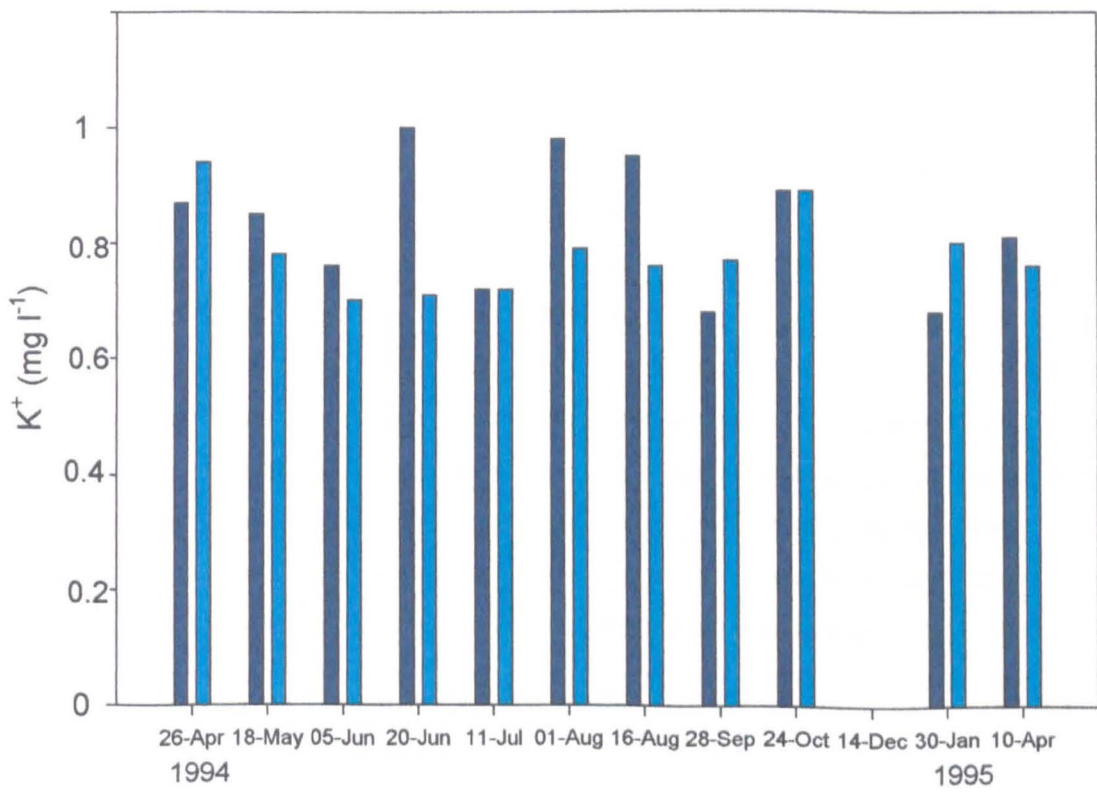
Fig. 5.3 b. Seasonal variation of potassium.

The values of K^+ obtained for the Mánamo and Macareo vary between 0.65 and 1.2 mg l^{-1} (Fig. 5.3b), are not statistically different (t-test, P=0.239) and not well correlated between the channels (r^2 = 0.09). Probably, local influence, such as runoff could have affected the data.

The values of Ca^{2+} obtained (Fig. 5.4a) in the waters of the Mánamo are statistically similar to those measured in the Macareo river (t-test, P= 0.103). There is some weak correlation between both graphs (r^2 = 0.48). The data for the samples in the two meadows shows no significant differences (t-test, 0.116<P<0.483).

The Ca^{2+} levels show an inverse relationship to the hydrological cycle in both rivers. The Macareo, in the period of low waters in January through to February, shows the highest concentrations (3.5 mg l^{-1}) and in the high water period of August - September, it reached the lowest values (1.92 mg l^{-1}). This is because of the dilution effect, caused by the increase in discharge of the rivers due to the seasonal increase in catchment rainfall.

The Mg^{2+} values obtained (Fig. 5.4b) in the waters of the Mánamo ranging from 0.5 to 1.2 mg l^{-1} are significantly higher than those of the Macareo river (t-test, P: 0.032), there is also a strong correlation between both sites (r^2 = 0.91).

The values of total nitrogen (Fig. 5.5a), including nitrites, nitrates and ammonium, that were obtained from the open waters, range between 0.2 and 2.3 mg l^{-1} and are not statistically different for the two channels (t-test, P=0.103). The data for both channels are, in general, poorly correlated (r^2= 0.56). Nevertheless there are two clear trends, firstly a random component during the increasing water stage, and secondly, diminishing concentrations during the low water season. The latter is possibly related to the decline of water turbulence during the receding period, when the water current velocity and the wind are lower (see sections 5.3.6 and 2.3).

Phosphorus, PO_4^{3-}, values in the Mánamo and Macareo channels (Fig. 5.5b) range between 0 and 0.118 mg l^{-1}. The former value should be attributed to any laboratory equipment malfuntion. There was a maximum in the month of June and minimum in August and September, the general tendency being a reduction during the low water period. The results showed no statistical difference between the two courses (t-test, P=0.690) and were poorly
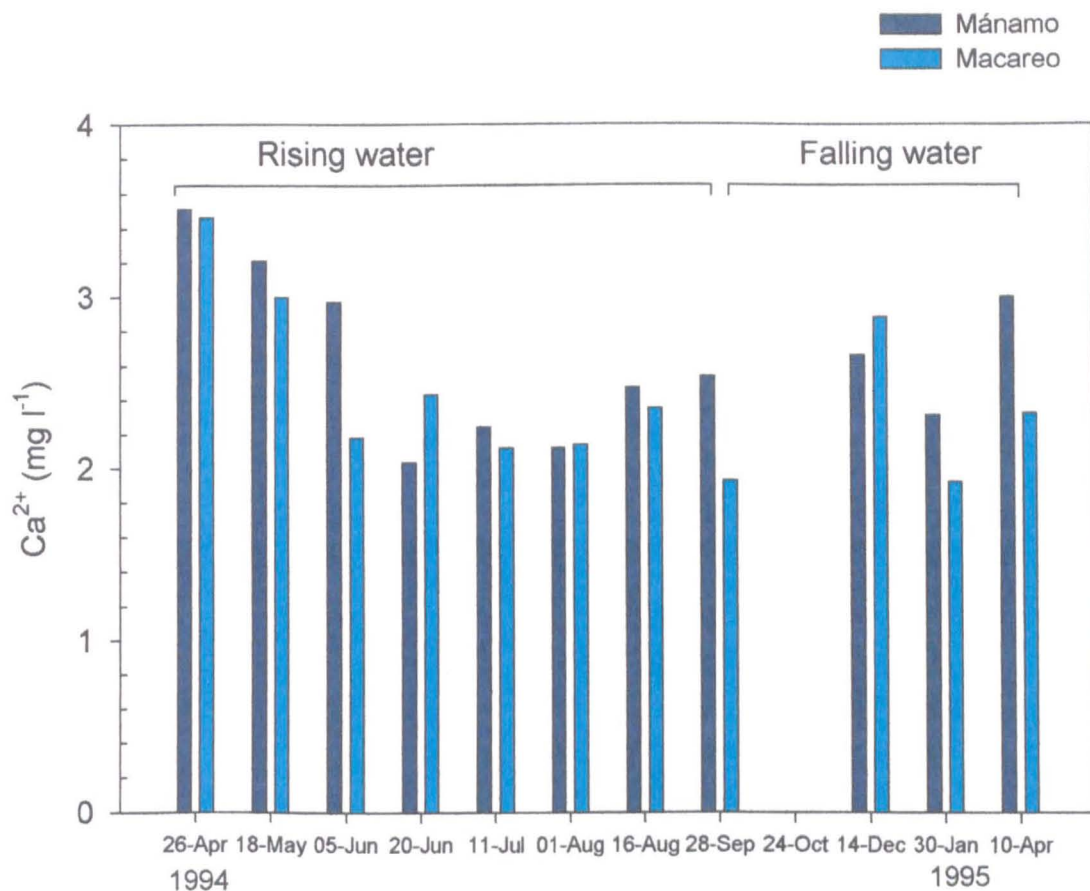
Fig. 5. 4 a. Seasonal variation of calcium.
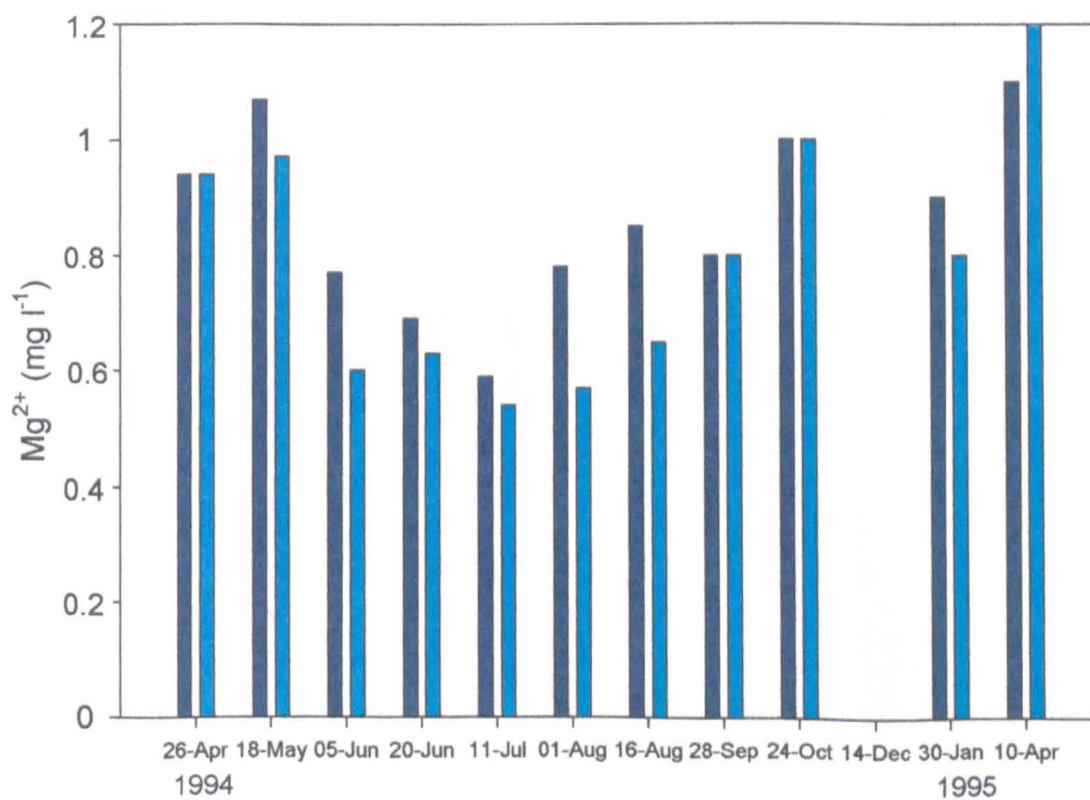
Fig. 5. 4 b. Seasonal variation of magnesium.
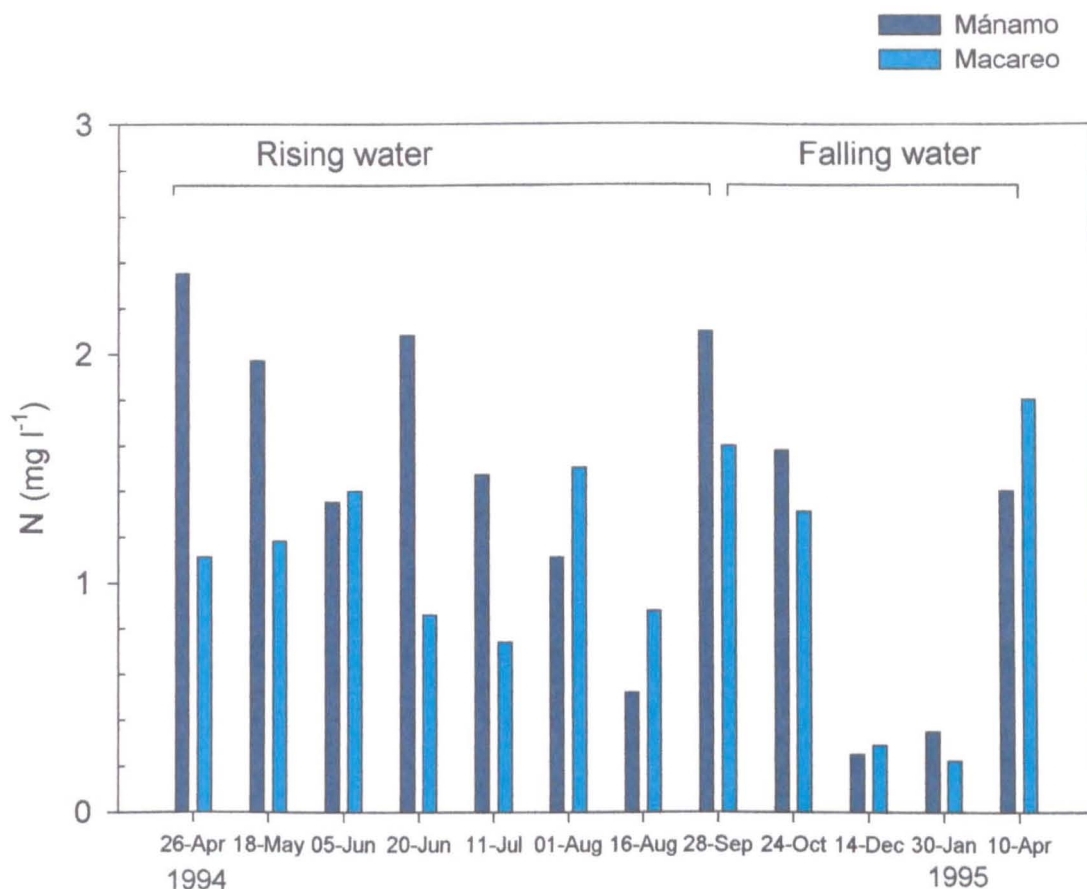
Fig. 5.5 a. Seasonal variation of nitrogen.
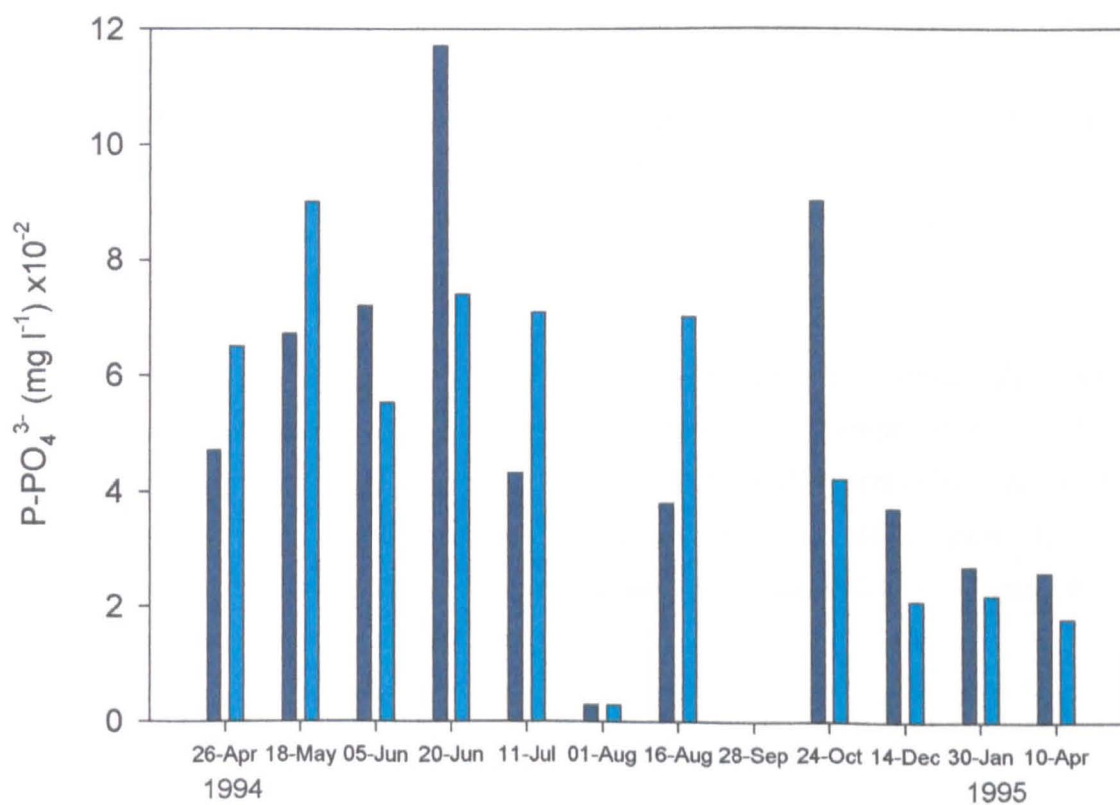
Fig. 5.5 b. Seasonal variation of phosphorus (phosphate).

correlated (r^2 = 0.68). The inverse relationship is due, as in the case of the others elements, to the dilution effect.

5.3.3 Electrical conductivity and pH

The comparative values of our study (Fig. 5.6a) range between 32 and 63 μS cm^{-1} in the water samples of the Mánamo and Macareo rivers; they show no significant differences (t-test, P= 0.067) and a positive correlation of the curve tendencies (r^2 = 0.85) indicating a similar pattern of variation during the year. However during the height of the flood period the conductivity values from the Mánamo river were apparently higher than those of the Macareo, from June to the first week of August.

Results of the pH (Fig. 5.6b) from the Macareo and Mánamo rivers shows no significant differences (t-test, P=0.891) and a high correlation (r^2 =0.97).

5.3.4 Dissolved oxygen and temperature

The values for dissolved oxygen measured in the Mánamo and Macareo rivers (Fig. 5.7a) that range from 4.80 to 7.75 mg l^{-1}, showed no significant differences (t-test, 0.27<P< 0.80) at either the water surface or at depth. The results for each channel exhibited a high correlation (0.70<r^2 <0.85). During the period of increasing water the values were higher in the Mánamo than in the Macareo. These results are unexpected because the Macareo shows a higher turbulence than in the Mánamo river. This should lead to higher values of dissolved oxygen in the former river course. On the other hand Junk (1973) reported dissolved oxygen levels significantly higher at sunset than at sunrise in the open water of a floodplain lake, because of the assimilatory activity of the phytoplankton. These results coincide with our observation of higher values in the afternoon (Mánamo) than in the morning (Macareo).

The surface water temperature of the two channels are shown in Figure 5.7b and oscillate between 27 and 32 °C. The waters in the Mánamo river were generally higher in temperature, by 0.5 to 2°C, than in the Macareo, during the months of June to November. According Fox (1992), some species with a worldwide distribution such as *Phragmites australis, Lemna minor*, do not appear to have any special temperature requirements. Temperature differences are too small to affect tropical species distribution as in the case of *Eichhornia. crassipes.*
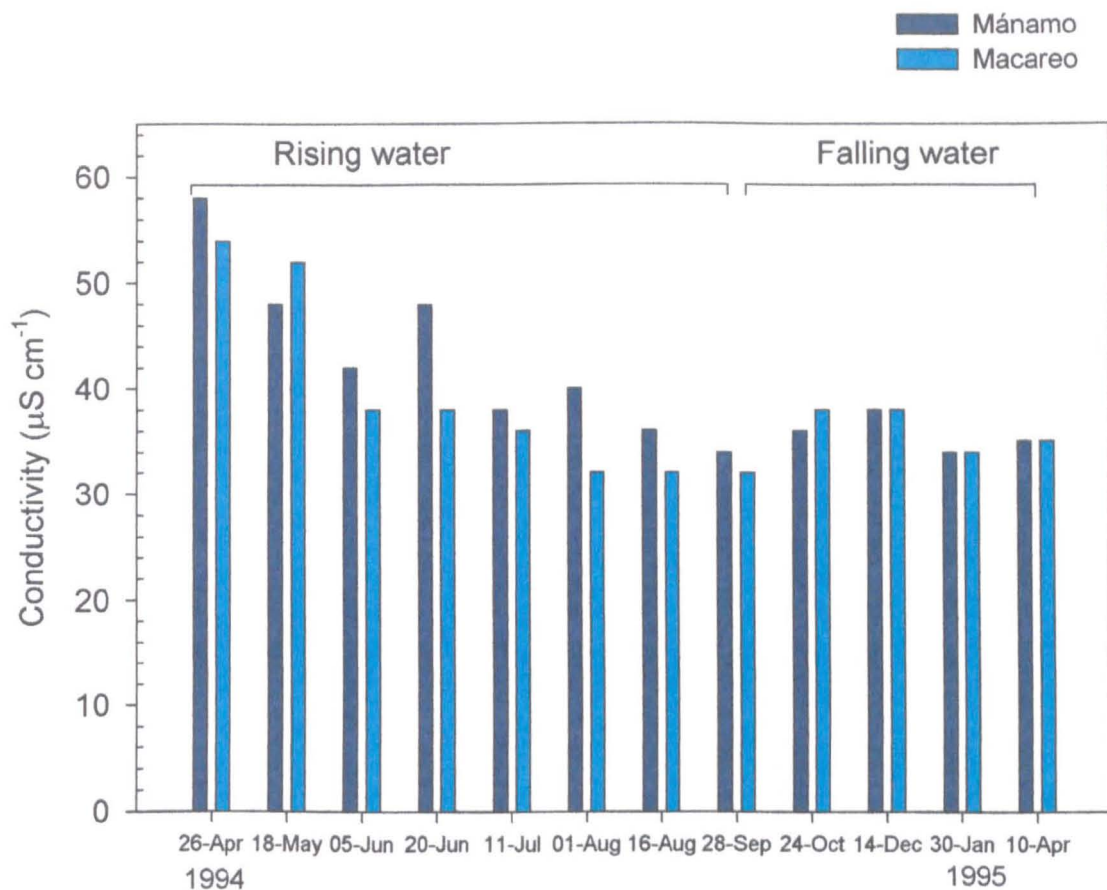
Fig. 5.6 a. Seasonal variation of the electrical conductivity.
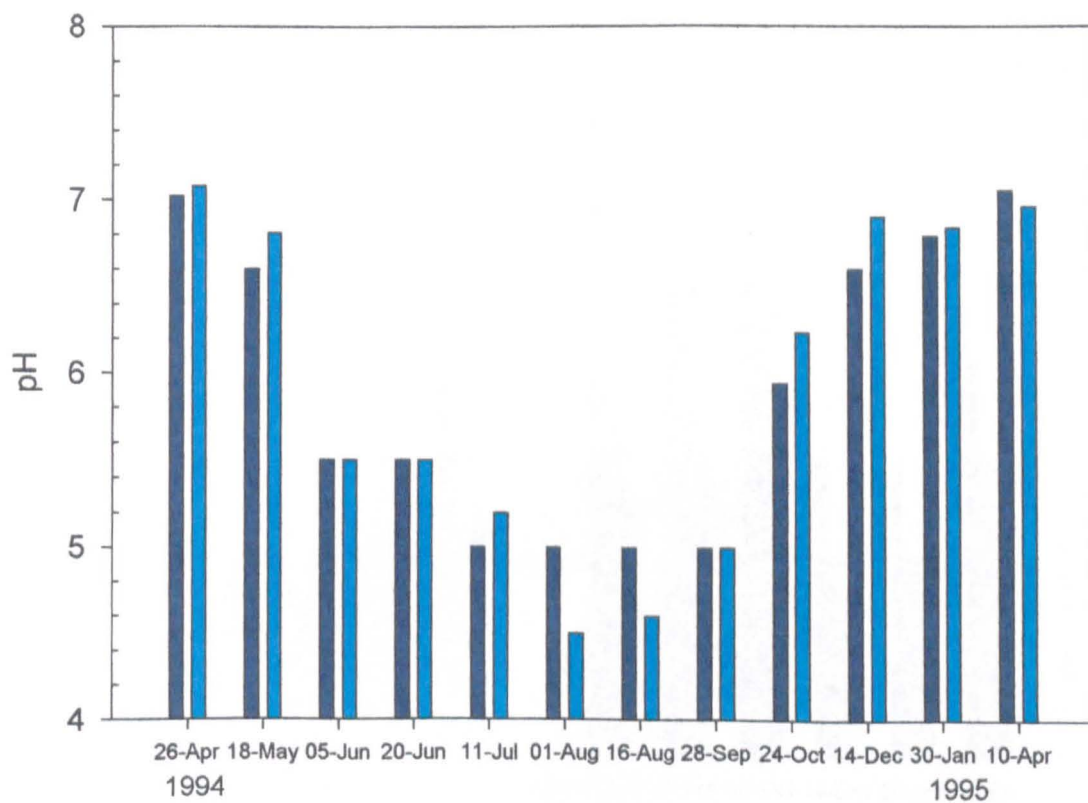
Fig. 5.6 b. Seasonal variation of the pH.
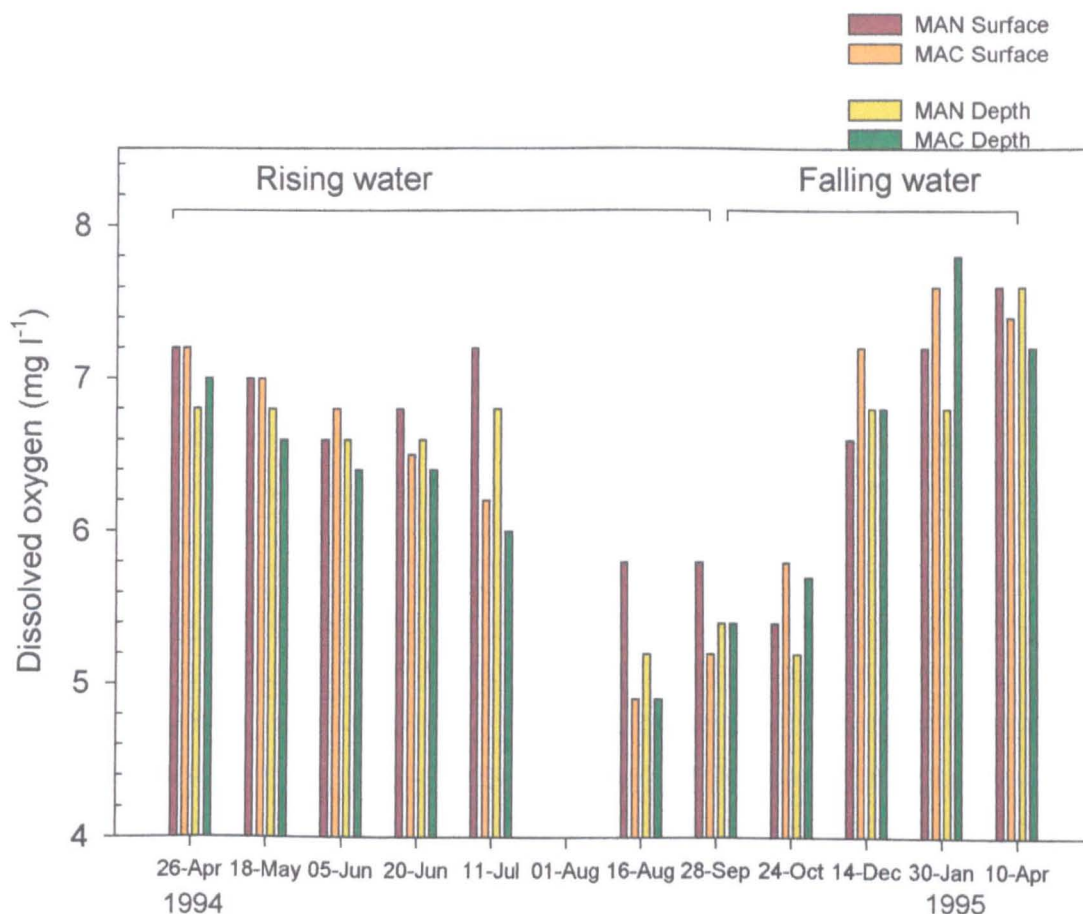
Fig. 5.7 a. Seasonal variation of the dissolved oxygen (DO).
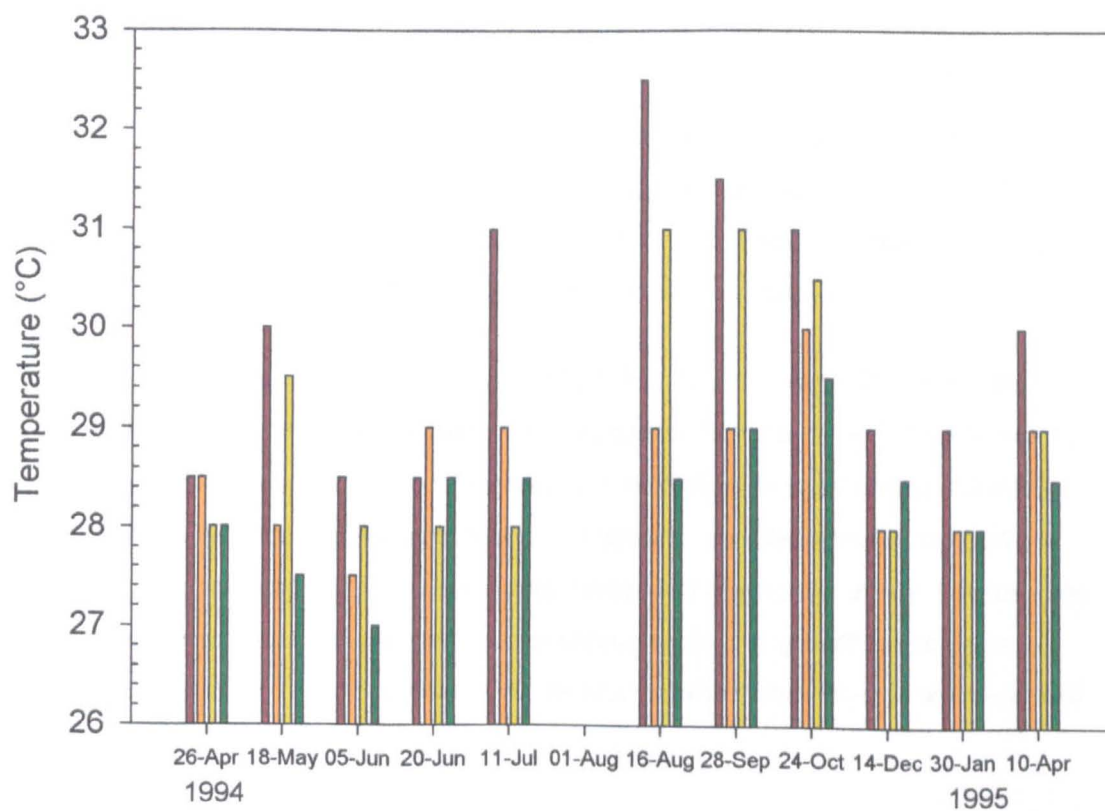
Fig. 5.7 b. Seasonal variation of water temperature.

5.3.5 Sediment transport and water-transparency

The construction of upstream dams with the subsequent sedimentation in the reservoirs decreases the supply of sediments to the lower stretches of the rivers (Barrow, 1987; Moffat and Lindén, 1995), Fig. 5.6).

Therefore it was expected there would be a reduction in the sediments in the Mánamo in contrast with the Macareo. The mean amount of sediment obtained (Fig. 5.8a) in the Mánamo was 7.25 mg l^{-1} and in the Macareo river 22.85 mg l^{-1}. The curve shows two peaks, the first one at the 5th of June in the Mánamo river (21. mg l^{-1}) and the 20th of June in the Macareo river (38. mg l^{-1}), and the second around December 12th.

The water-transparency for both rivers is shown in Figure 5.8b. The minimum values (10 cm), were recorded during the rising water in both rivers, the Mánamo always showing higher values. The maximum value of 145 cm was recorded during the lowest water period in the Mánamo. This was to be expected due to the negative correlation between the sediments transported and the water transparency in water bodies.

5.3.6 Current velocity

The current velocity of the Mánamo and Macareo rivers along their shores is shown in Fig. 5.9. The flow velocity measured along the river banks of the Macareo river showed higher values than in the Mánamo, reaching peaks of 55 cm s^{-1} and 75 cm s^{-1}, during June and July when the water level reached its highest level (Fig. 5.2b). The Mánamo showed very little change in velocities ranging from standing waters to 8 cm s^{-1}, because of the regulated flow. The maximum values, 155 cm s^{-1}, were obtained in the middle course of the upper Macareo, during maximum discharge in July 1994, where the water course was rather narrow (circa 300 m in width). In the Mánamo, up to 75 cm s^{-1} was recorded in the centre of the channel in the upper stretch where velocity increase was due to elevation produced by the dam.

Current velocities are related to the water discharge (Fig 5.2a). Higher currents velocities(in both rivers) occurred during period of high water level increase and determine the establishment of the riverine plant communities. In the Macareo river the uprooting of the floating meadows along the river shores is associated to the fast rise of the waters, as discussed in section 6.3.1.3. and with the falling of portions of the banks as witnessed during the study. On the other hand in the Mánamo the meadows are constantly expanding while the growth conditions are optimal close to the river shore. They are dislodged, however, when velocities in the centre of the river bed, reaches approximately 75 cm s^{-1}.
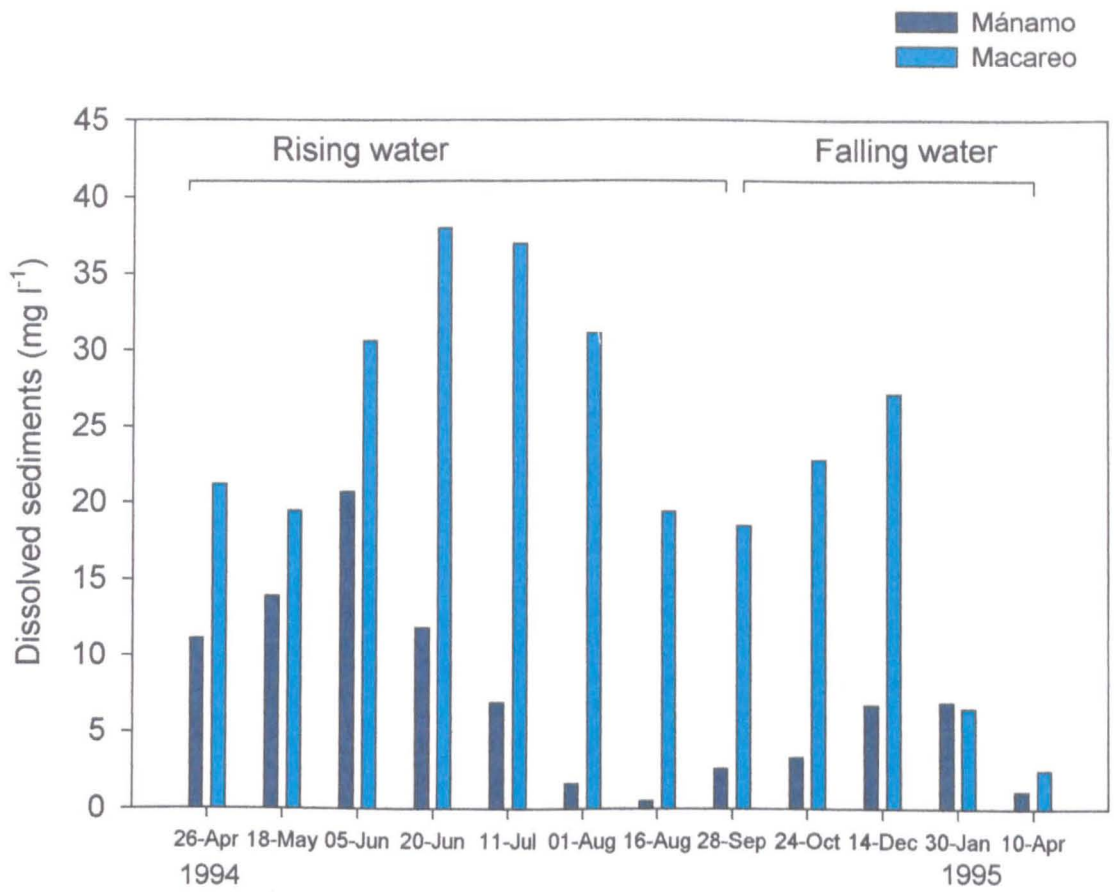
Fig. 5.8 a. Seasonal variation of dissolved sediments.
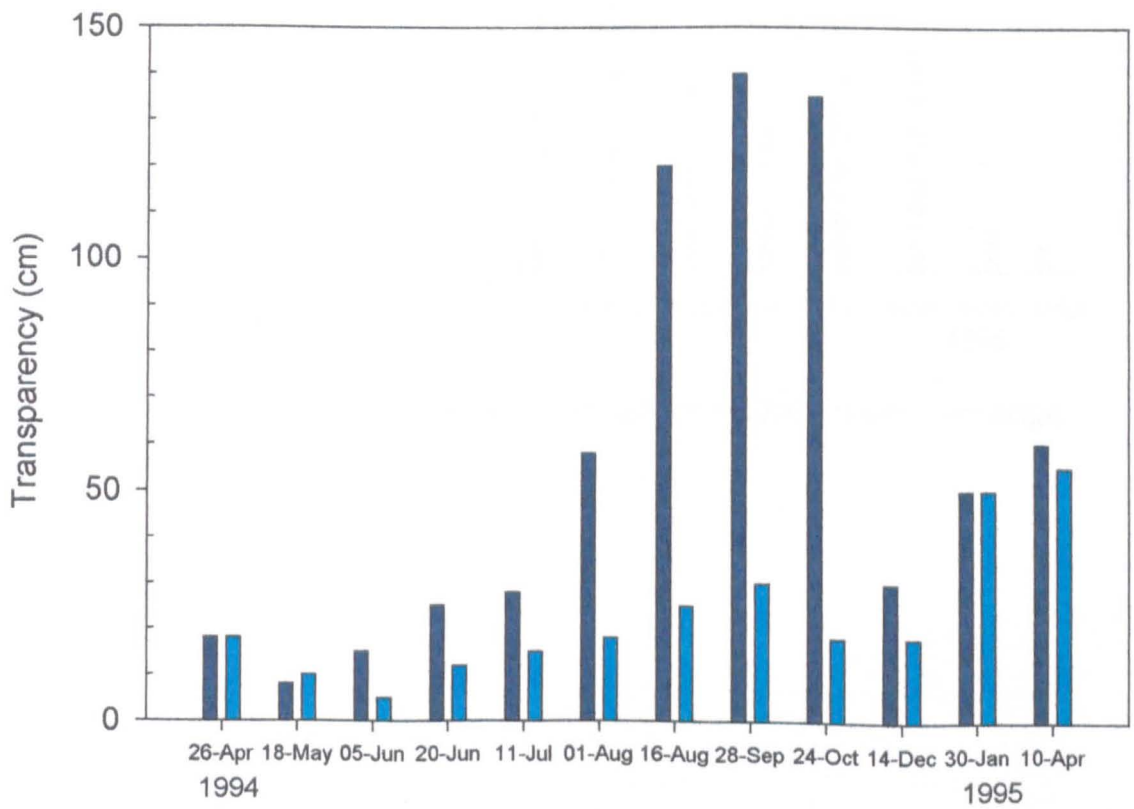
Fig. 5.8 b. Seasonal variation of transparency.
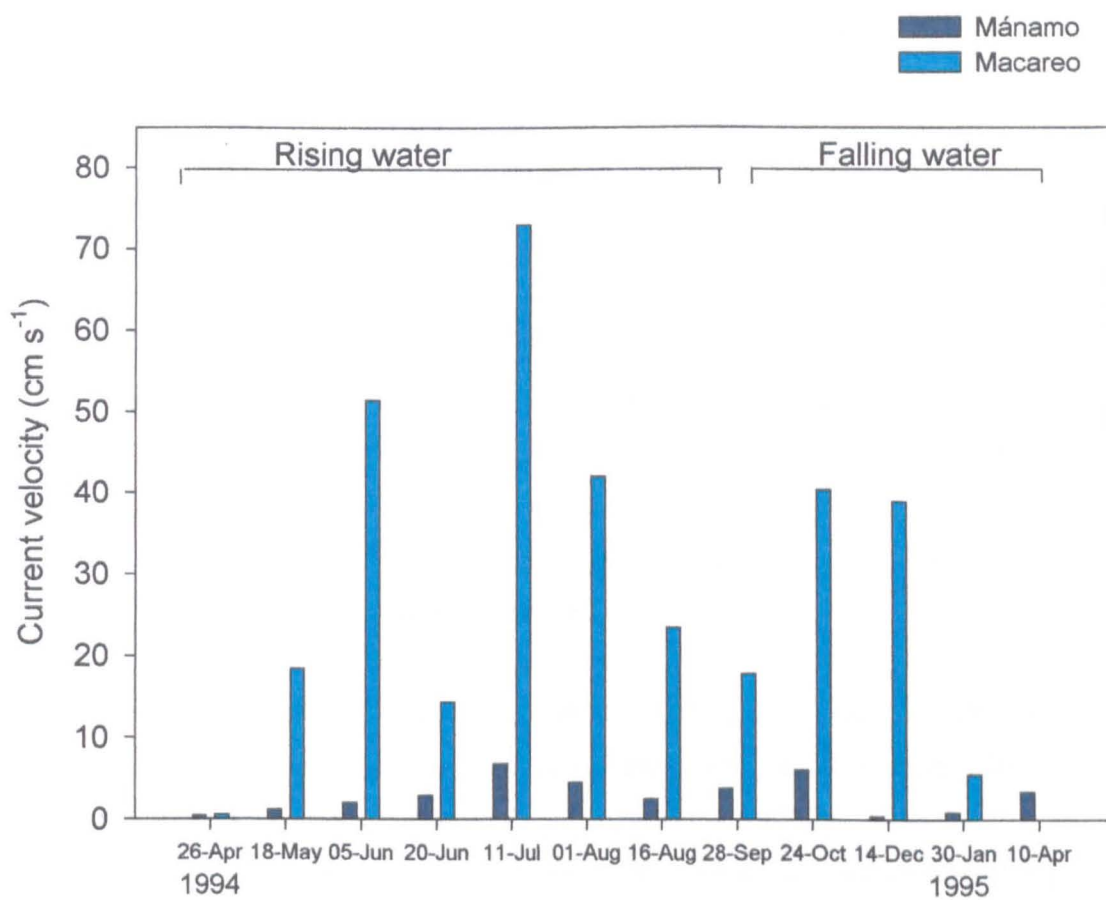
Fig. 5.9. Seasonal variation of current velocity in the river edge.

5.4 Discussion

The chemical and physical characteristics of the river waters are a result primarily of the lithology of their catchment basins. In tropical rivers the chemical composition of the river waters is mostly determined by the chemistry of the surface rocks and to a lesser extent, the activity of erosive processes (Stallard *et al.*, 1991). From a tectonic perspective there are three important structural provinces within the Orinoco River basin (see Fig. 2.1). These are:

1 The Guayana Shield which is located along the southern margin of the basin and in the south-eastern one-third of the basin;

2 the fold and thrust terrain of the Andes and the Caribbean coastal ranges (the Cordillera de la Costa) located along the western and northern margins of the basin; and

3 the Llanos, a region of alluvial plains within the foreland basin that is located between the shield and the mountain belts (Stallard *et al.*,1991).

Rainfall distribution in the three provinces of the watershed is also characterised by their local climatological characteristics (Colonnello, 1990a).

The drainage into most large rivers like the Orinoco, is varied, and frequently includes runoff from highly erosive uplands or alluvial plains as well as runoff from plateaus dominated by crystalline rock and covered by vegetation. It may therefore be expected that the Orinoco waters should result in a range of concentrations of dissolved and suspended materials that reflect the contrast in watershed components, the Andes and Llanos on one hand and the Guayana Shield on the other (Lewis and Saunders, 1990).

The dissolved load in rivers that drain the mountain belt is enriched in Na^+ relative to K^+, and Ca^{2+} relative to Mg^{2+}. These enrichments are indicative of partly weathered material. The sand and fine grained sediments contain abundant primary mineral material. Dissolved $Si(OH)_4$ is depleted relative to K^+, Na^+, and Cl^- as an indication that 2:1 clays may be forming during weathering. In contrast, in river basins of the Guayana Shield, chemical weathering is far more intense, as indicated by the lack of soluble cations in the solid load and the proportion that soluble cations in the dissolved load are near bedrock proportions (Stallard *et al.*, 1991).

In this sense the cation properties transported downstream by a river may be indicative of the origin of its sediments (Lewis and Saunders, 1990.; Moss, 1993). In rivers such as the Caura and Caroní draining the eroded landforms of the Guayana Shield (see Fig. 2.1), the mono-valent cation Na^+ is of much greater importance ($Na^+ > Ca^{2+} > Mg^{2+} > K^+$) than in the waters draining from the north of the Orinoco such as in the Apure river ($Ca^{2+} > Mg^{2+} > Na^+ > K^+$). Similarly, Yánez (1997), in a detailed study of the sediment weathering the Guayana Shield,

demonstrated the dominance of the cations Mg^{2+} and Na^+ on the dissolved fraction of the drained waters. As will be observed, the Delta water bodies located close to the sea and in the regulated sub-basin show a dominance of Na^+, while in the remnant inland waters the dominant ion is Ca^{2+}.

5.4.1 Hydrology (water level)

The hydroperiod of the hydrograph defines the rise and fall of a wetland's surface and subsurface water. It characterises each type of wetland and the constancy of each pattern from year to year, ensuring a reasonable stability for that wetland (Mitsch and Gosselink, 2000). The hydrograph shown by the Mánamo and Macareo rivers (Fig. 5.2a) is associated with the seasonal variation of the rainfall in the Orinoco basin (Vásquez and Wilbert, 1992; Colonnello, 1990a, 1993). High waters are generally registered between June and October. The waters contributing to the Orinoco discharge have two main origins. From the Andean and Llanos regions, where the rainfall shows a clear bimodal pattern with a higher values of about 2,800 mm yr^{-1}, and from the Guayana Shield, where rainfall shows a more homogeneous distribution throughout the year and the mean precipitation reach 3,500 mm yr^{-1} (Colonnello, 1990a; Weibezahn,1990).

The total discharge is highest in the main section of the Orinoco, for instance at Ciudad Bolívar (see Fig. 2.2), about 200 km upriver from the Delta apex, it reaches a range in height of about 12 m, and diminishes towards the Lower Delta. Similar wide ranges are evident in other South American rivers, namely up to14 m in the Amazon River in Manaus (Junk 1970; Day and Davies. 1986), about 6 m in the Paraná and Paraguay Rivers in Pto. Bermejo (Neiff, 1990a), and about 7 m in lowland valleys of the Magdalena River (García Lozano and Dister, 1990).

The periods of accelerated rising and falling of the Macareo river have a direct effect on the plant communities established at the river banks. Such changes in water level may aid the dislodging of free-floating plants from the riverside water meadows such as *Eichhornia crassipes*, *Pistia stratiotes* and *Salvinia auriculata* and even uprooting the communities of *Paspalum repens* and *Eichhornia azurea* (see section 6.3.1.3). Such phenomena are also common in the Amazon River system (Junk, 1986).

In contrast to the Macareo, the hydrograph of the Mánamo river, after the dam construction, is mainly influenced by the tidal regime of the ocean. The present regime, influences the transport of materials and dissolved elements such as the floating plants and the pollutants produced by the Tucupita city, the villages, and the production activities such as farms

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established along the river banks. The residence time of waste waters, for instance has not been determined, but may last several days or weeks. This may pose health problems for the river-shore inhabitants that utilise the waters for washing and personal cleaning. The water volume and in turn the positive movement toward the river mouth is only influenced in the upper section by the reduced discharge through the dam (200 $m^3 s^{-1}$), the local rains and the consequent runoff. As seen in previous chapters (section 2.3) the evaporation is high and only a small part of this input remains. In the middle sector, few streams add water (100 $m^3 s^{-1}$) to the main channel, reducing the intrusion of the saline wedge from the ocean (see differences in ionic composition among the rainy and dry period in Table 5.5). The isolation from the main hydrological pattern of the Orinoco River has therefore led to a number of changes in the chemical, physical components and in the biota of the Mánamo which are detailed in chapters six through to nine.

Mitsch and Gosselink (2000) summarised the general changes in the hydrology in wetland ecosystems. The effects primarily influence the chemical and physical components of the wetlands, which in turn, affect the biotic components of the ecosystem. The biotic components, have a feedback effect on hydrology.

Four main principles may be identified regarding the importance of hydrology
1. Hydrology leads to a unique vegetation composition but can limit or enhance species richness.
2. Primary productivity and other ecosystem functions in wetlands are often enhanced by flowing conditions and a pulsing hydroperiod often depressed by stagnant conditions.
3. Accumulation of organic material in wetlands is controlled by hydrology through its influence on primary productivity, decomposition and export of particulate organic matter.
4. Nutrient cycling and nutrient availability are both significantly influenced by hydrologic conditions.

The hydrological changes produced by river diversion or channelization may alter the nutrient distribution leading to eutrophication or nutrient deprivation (Sklar and Browder, 1998). Likewise hydrological changes are likely to affect the distribution and diversity of vegetation and fauna (Greening and Gerritsen, 1987) through the modification of the aquatic habitats along river shores and inter-riverine areas. The change in soil moisture within a floodplain, downstream from a dam, is a determining factor for plant populations (Bravard and Petts, 1996). In the same fashion the flooding of terrestrial units in winter and early spring favours the plant productivity by recharging the water resources of the soils and the stock of nutrients before the spring resumption of growth (Amoros *et al.*, 1996)

The reduction of water level (discharge) closed the connections between Mánamo's main channel and the inter-riverine wetland communities. Four large courses were affected (see section 2.5), the Cocuina, Pedernales, Tucupita and Capure rivers (see Fig. 2.10b), along with many other minor tributaries. This periodic linkage and severing of small channels with the main channel flow also affected nutrient supply As Amoros *et al.* (1996) stressed that when abandoned channels are connected to a river at times of high water level, the organisms that are unable to maintain their position (plankton, some macroinvertebrates, alevins and juvenile stages of fish), may be carried away by current, providing a food resource for organisms in the main river as proposed by 'flood pulse concept' (Junk *et al.*, 1989).

5.4.2 Cations, phosphorus and nitrogen

The biomass production on aquatic systems which includes benthic to macrophytic organisms is related most directly to freshwater inputs of nutrients carried by rivers (Sklar and Browder, 1998). A flood pulse is particularly important in the tropical rivers, because it is associated with an important seasonal input of dissolved and particulate nutrients, and with particular conditions of dissolved oxygen, electrical conductivity, pH and sediments, after a receding period (Junk *et al.*, 1989).

The most relevant ionic elements determining the chemical characteristics of water courses are as noted above Na^+, K^+, Ca^{2+} and Mg^{2+}. Sodium and potassium are not limiting elements for productivity in aquatic environments. In river systems potassium is normally found at lower concentrations than sodium (Esteves, 1988).

Figure 5.3a indicates a reduction in the Na^+ concentration during the rising water stage, probably as a result of dilution by the increase of the water discharge in the Macareo river. This contrasting pattern seen also in the results of Mg^{2+} and Ca^{2+} is commonly found during high water period. Despite the input of new sediments and nutrients from weathering, the water volume largely exceeded the particulate and dissolved materials. Likewise Weibezahn (1990) found a significantly negative correlation (99.9 %) of the Na^+, K^+, Mg^{2+} and Ca^{2+} concentrations with the water discharge of the Middle Orinoco Main channel, throughout the year. In concordance with the Orinoco results, consistent reductions of dissolved oxygen, nitrates, sulphates and increases in conductivity, bicarbonates and calcium, were reported, in low water in the Lower Paraná river Delta in Argentina-Uruguay (de Cabo, *et al.*,1999).

The Na^+ values are higher than those reported in the upper reaches of the Orinoco River (max. 1.3 mg l^{-1}) where only clear waters are found (Weibezahn, 1990). However they

increase as a result of the input of the white waters from the Apure River, due to the important contribution of this ion in the Andean sector of the watershed. In Barrancas the Na^+ is much higher (Table 5.2) as reported Lewis and Saunders (1990). The values for Mánamo are similar to those reported near Tucupita city (a few km downriver) by Paolini *et al.* (1983) in a previous preliminary study of the two water courses.

The values of potassium for the Mánamo and Macareo rivers are comparable to measurements at the Delta apex (Table 5.2). The variation obtained (Fig. 5.3b), throughout the year, from 0.6 to 1.2 mg l^{-1}, is similar to that reported from the Orinoco main channel (Sánchez, 1990; Lewis and Saunders, 1990). The fluctuations are wider in the rising water stage probably due to local input through runoff. Likewise. the higher values observed in the Mánamo than in the Macareo from August through September might be associated to leaching of decomposing macrophytes as proposed by Furch (1984).

Table 5.2. Mean concentration of main cations, nitrogen and phosphorus, in the Orinoco main stem (Barrancas) and three major tributaries (discharge-weighted) (Lewis and Saunders, 1990), and the Mánamo and Macareo rivers (this study).

Rivers	Apure	Caura	Caroni	Orinoco (Barrancas)	Mánamo	Macareo
Cations	mg l^{-1}	mg l^{-1}	mg l^{-1}	mg l^{-1}	mg l^{-1}	mg l^{-1}
Ca^{2+}	16.2	0.6	0.5	2.6	2.4	2.4
Mg^{2+}	3	0.2	0.2	1.5	0.86	0.79
Na^+	2.3	1.2	0.7	1.5	1.57	1.47
K^+	2.2	0.6	0.4	0.7	0.92	0.78
N	0.9	0.4	0.3	0.46	1.32	1.01
P	0.18	0.018	0.011	0.065	0.054	0.046

Calcium constitute the most abundant mineral elements in freshwater. It is essential to the development of aquatic flora (algae and macrophytes) and fauna (fish and mollusc) and represents about 48 % of all the cations present in the water (Roldán Pérez, 1962). The main sources in the Orinoco watershed are the Andean range and the open plains of the Llanos mainly through the Meta River (flowing from the Colombian Andes) and the Apure River (Fig. 2.1). The higher percentage (67 %) of the major cations of the Apure waters is due to the Ca^{2+} (Lewis and Saunders, 1990).

The values and trends shown by the Ca^{2+} (Fig. 5.4a) are common throughout the course of the Orinoco (Weibezahn, 1990; Lewis and Saunders, 1990. and Sánchez, 1990) and in the Mánamo and Macareo river (Paolini *et al.*,1983; Monente and Colonnello,1997). The Ca^{2+}

values show higher fluctuations during the falling water stage in the Macareo, than in the Mánamo.

Magnesium is the second most important element in inland waters, as it constitutes the nucleus of the chlorophyll molecule. It mainly originates from silicates (Roldán Pérez, 1992). The main source to the Orinoco system is from the Guayana Shield where it is a main ionic component of the water dissolved fraction (Yánes, 1997). The values reported in this study (Fig. 5.4b) diminish during the rising water stage, increasing again with the receding waters, and reaching their maximum in the driest period of the year. Their behaviour throughout the study period is similar to that observed by Weibezahn (1990), although his values are much higher, because the samples were collected in water coming from the Guayana Shield, upriver from the confluence of the Orinoco with the Meta River (see Fig. 2.1). The Delta values range from 0.5 to 1.2 mg l^{-1}, which are similar to those reported in the lower Orinoco (Lewis and Saunders, 1990) near Barrancas (mean of 0.7 mg l^{-1}) (Table 5. 2), and in the Delta by Paolini *et al.* (1983).

A study of sodium, chloride and sulphate concentration in the Mánamo river conducted by Olivares and Colonnello (2000) revealed an increase of these ions in a transect from Tucupita to the mouth of the river (see Table 5.5). Most sampling places had Na^+ concentrations corresponding to freshwater values, however a constant increase of this cation is observed along the transect constituting a clear gradient from freshwater to saline waters. Values are higher during the low water period than during the rising water stage due to the lower input to the river system from the rains and tributaries, allowing the intrusion of the saline wedge from the Ocean. The same gradient was observed in the Mánamo sub-basin. The localities of Pedernales 2, and Capure located close to the sea showed higher concentrations than further inland localities, such as Cocuina 1 and Pedernales 1 (see map 5.1 for sampling location).

Table 5.3. Water physico-chemical variables of several water courses and marshes in the Mánamo sub-basin (Adapted from Infrawing & Asociados, 1997)

	Tem. °C	Tran. cm	Con. µS/cm	DO mg/l	Na^+ mg/l	K^+ mg/l	Mg^{2+} mg/l	Ca^{2+} mg/l	Cl^- mg/l	P mg/l	NO_3^{-2} mg/l	pH µg/l
C. Pedernales 1	29	40	230	-	18.8	2.5	8.5	2.5	4.49	145.4	267	6.9
C. Pedernales 2	2.9	75	33.5	-	34.5	2.4	10.3	1.6	83.49	75.35	127,5	6.39
C. Cocuina 1	30	40	18.5	0.25	18.8	2.3	6.3	2.5	34.9	140.7	58,7	6.6
C. Cocuina 2	27	30	390	0.05	13.6	2.3	5.1	1.5	39.45	108	23,6	6
C Cocuina 3	27.3	75	33	0.25	1.6	2.1	1.5	1.2	4.5	49.6	7,23	6.04
(depth= 6 m)			440									
C. Capure	27.3	-	550	-	71.5	2.6	18	2	158.4	98.7	36,25	6.09

Marsh 1	-	-	-	-	44.16	2.3	9.1	2.4	102.4	278.6	6,76	5.2
Marsh 2	-	-	-	-	10.11	2.1	3.7	1.5	4.2	187.5	6,76	5.4
Marsh 3	-	-	-	-	11	2.3	6.9	1.3	29.9	264.6	7,23	6.0

Nitrogen and phosphorus are main components of metabolism in aquatic organisms, due to their role in the construction of proteins and production of biomass, storage of energy and the formation of the cell membrane (Wetzel 1981, Esteves 1988). Natural dissolved inorganic nitrogen concentrations may be restrictive to the growth of aquatic plants in sub-tropical lakes and lagoons (Carignan et al., 1994). Phosphorus, compared with the other nutritional and structural elements of living matter, is the less abundant and normally acts as a factor limiting the biological productivity of water bodies (Wetzel, 1981; Reddy et al., 1999).

The values of nitrogen recorded in this study (Fig. 5.5a) are, in general, higher than those reported

1. for the Orinoco River (mean 0.46 mg I^{-1}) by Lewis and Saunders (1990) (Table 5.2),
2. for the Delta region (mean: 0.56 mg I^{-1}) (from 1992-93 field campain) by Monente and Colonnello (1997),
3. for 46 streams of the Amazon Basin (0.4-0.65 mg I^{-1}) by Furch and Junk (1980) and
4. In several water bodies in the Paraná river system, where only temporary lagoons reached the highest values found in the Mánamo and Macareo rivers (Thomaz et al., 1997).

The values of PO_4^{3-} measured (Fig. 5.5b) are similar to those reported for the Orinoco main stream (0.065 mg I^{-1}) by Lewis and Saunders (1990), the Orinoco Delta (mean 0.167 mg I^{-1}) by Monente and Colonnello (1997), the Amazonian waters (0.105 mg I^{-1}) by Furch (1984) and in several water bodies in the Paraná River system (Thomaz et al.,1997).

The marked oscillations of both elements phosphorus and nitrogen and the high concentrations of the nitrogen may be explained, in the case of the Mánamo, by the enrichment of the reservoir created in the river stretch before the dam. In the shore banks of this areas are establish two towns. In addition the water pollution (carried upriver by the tidal influence) of the Tucupita city, located few Km downriver from the sampling site (see Fig. 5.1). The distance between the release into the river and the sampling site did not lead to any mixing of the waters.

In the case of the Macareo the water washes organic and inorganic detritus from the banks. This effect is particularly evident during the rising water period when the river floods the

densely vegetated (*Paspalum fasciculatum* stand) banks. During the falling period, however, the values are similar and shows a steady decrease with the water level.

The main nutrients, phosphorus and nitrogen. in the Mánamo sub-basin (Table 5.3) showed variable values. Phosphorus values, measured as total P, in localities closer to the sea are lower than in the inland sites due to the intrusion of saline waters. Nitrogen is represented as nitrates, of the Orinoco watershed (Wibezahn, 1990). The values show an increase close to the inhabited areas, suggesting anthropogenic inputs into the rivers (Infrawing & Asociados, 1997).

Summarising the relation of the cations measured from the Mánamo and Macareo (Ca^{2+} > Na^+> $Mg^{2+} \geq K^+$) are similar to those obtained at Barrancas at the apex of the Delta (Fig. 5.1) (Ca^{2+} > $Na^+ \geq Mg^{2+}$ > K^+) by Lewis and Saunders (1990). These relationships are typical of runoff from the Andean and Llanos catchment. The major contribution of Na^+ in the Delta waters may be due in part to the atmospheric transport of NaCl in precipitation systems originating to the east over the nearby Atlantic. The ocean is known to be an important source of ions in the Guayana region, particularly Na^+, Cl^- and Mg^{2+} (Yánes, 1997). In a study of the concentrations of the aerosol species collected from large clouds drops in coastal California (Collett et al, 1994; cited in Seinfeld and Pandis In general in the Mánamo sub-basin, the relation of dominance was Na^+> Mg^{2+} > K^+ > Ca^{2+} in almost all the sampling localities, differing from the main Orinoco waters and Macareo and Mánamo upriver from the dam. This evidence indicates the isolation conditions within the regulated basin.

The analysis of the sites studied in chapter 3 (Table 3.3), even if not complete because the Na^+ was not analysed, indicate a similar influence. The Mg^{2+} dominates over Ca^{2+} in the sites such as Lag. Clavellina, La Florida and Cien. Los Guires which are located in the Mánamo sub-basin. In contrast, the Ca^{2+} dominates over the Mg^{2+}, in sites such as Lag. Ataguía, Lag, Alamilla, Alto Araguao and Caño Macareo, in the unregulated region of the Delta. This situation was reversed in sites such as Curiapo, Barra Merejina and Caño Ibaruma which are located relatively close to the sea, and therefore under the influence of the marine environment. An interesting observation was obtained from Lag. Terraplén which showed a Ca^{2+} dominance on the upstream unregulated side of the Mánamo cofferdam and Mg^{2+} dominance on the downstream regulated side of the Mánamo.

5.4.3 Electrical conductivity and pH

Electrical conductivity may be used as an indication of the ion content in water environments which in turn reflect the ionic composition due to chemical weathering, atmospheric

contributions and anthropogenic influence (Yánes, 1997). In this sense waters with higher ion concentration will show higher conductivity than oligotrophic waters (Roldán Pérez 1992; Esteves, 1988). The data from the individual cations Ca^{2+}, Na^+, K^+ and Mg^{2+} investigated (Figs. 5.3-5.4) showed a similar trend, associated to the dilution effect as the discharge increased in the rainy period. The contribution of several ions not investigated, such as carbonates (CO_3^{2-}),

sulphates (SO_4^{2-}) and chlorides (Cl^-), which form a major proportion (56.15%) of the total ionic components (Roldan Pérez, 1992) could explain some of the observed results.

Conductivity values (Fig. 5.6a) obtained during the low water period are higher than those recorded by Paolini *et al.* (1983) and IRNR(USB)-Ecology and Environment (1999) (see table 5.4) in the Delta and also by Weibezahn (1990) in the Upper Orinoco main stream. However they are similar to those reported by Junk (1973) in several aquatic environments, lagoons and river channels, in the Amazon Basin. Decreasing values are associated with an increase of water discharge, which has been reported to occur (Weibezahn, 1990; Junk, 1973.). This is as a result of several factors, such as the bank effect, the runoff of organic matter from the river banks, associated with the rainy period and the subsequent dilution effect caused by the raising water levels. However no further increase is noted during the dry period.

The pH in the Mánamo and Macareo (Fig. 5.6b) follows a similar pattern, showing a clear negative correlation with the hydrological cycle. This pattern has been also reported for the main channel of the Orinoco River (Weibezahn, 1990). The low values observed during the high water period may be explained by the contribution of the water from the Guayana Shield that shows very low values up to 4.7 pH (Yánes, 1997).

Table 5.4. Physico-chemistry data from Mánamo river (upriver from the dam), Macareo river and Río Grande (Barrancas) in the main Orinoco river (see location in Fig. 5.1) (Adapted from IRNR(USB)-Ecology and Environment, 1999). DO: Dissolved Oxygen

Locality		Trans. cm	Cond. $\mu S\ cm^{-1}$	DO $mg\ l^{-1}$	pH
Macareo	Sep-99	0.3	22.7	4.7	5.1
Macareo	Sep-99	0.3	24	4.5	6.6
Mánamo	Sep-99	1.05	23.5	4.7	5.1
Río Grande	Sep-99	-	23.4	-	-

Conductivity and pH in the inter-riverine terrain of the regulated Mánamo sub-basin are variable. Conductivity showed higher values in the localities closest to the sea or measured during the high tide period, the Capure, Cocuina 2, 3 and Pedernales 2 , as described in Table 5.3 (Infrawing & Asociados, 1997). The isolation from the waters of the main rivers determine a permanent high conductivity condition in these regions. The lower pH values were observed in the localities Cocuina 3 and the marshes. The observed values ought to be influenced by the high concentration of organic acids (fulvic and humic) dissolved in the stagnant waters. In addition the waters and soils lacks of carbonates determining a low buffer capacity on the acidity variations (Infrawing & Asociados, 1997)

5.4.4 Dissolved oxygen and temperature

The pattern of DO obtained in the Mánamo and Macareo (Fig. 5.7a), where higher values occurred during the period of increasing water, was also reported for the Orinoco main channel (Sánchez, 1990). This pattern is associated with the active decomposition of organic matter transported by the currents when entering the floodplains from the main channel and when the river waters recede. This results in a drop in the dissolved oxygen, from about 7 mg l^{-1} to 5.5 mg l^{-1} as observed between August and October.

Several factors interact in these unstable environments in which the oxygen availability is seasonally modified. Aquatic plants, which are abundant in the Mánamo river may increase the oxygen consumption due to decomposition, from roots (Junk,1973; Jedicke et al., 1989). However in unregulated systems the oxygen availability is restored during the next flooding phase. In contrast, in the regulated area of the Mánamo sub-basin, where the seasonal pulse (which includes nutrients and high levels of dissolved oxygen among other components) has been suppressed, the local decomposition rapidly consumes the available oxygen, creating permanent anoxic waters conditions. This would explain the values as low as 0.05 mg l^{-1} observed in the extensive wetlands, rivers and marshes (Table 5.3). When these anoxic waters are transported to the rivers through runoff created by the local rains, they lead to a reduction in the diversity and biomass of the aquatic biota. This was observed in the water courses of the region such as that of the Cocuina river (Infrawing & Asociados, 1997). A similar effect was noted in the Lower Paraná river Delta, where water exchange, instigated by floods from marshy environments, caused the decrease of dissolved oxygen, nitrates, sulphates and an increase in phosphates, conductivity, calcium and magnesium in the main course (de Cabo et al., 1999).

The higher values of temperature recorded in the Mánamo river (Fig. 5.7b) compared with the Macareo, may be explained with reference to the time when sampling took place. The unregulated Macareo was sampled earlier in the day than the Mánamo. Junk (1973) reported an increase of the temperature at the surface on the floodplain lakes of the Amazonas River during the day as a result of the increasing solar radiation in the early afternoon. The differences observed among the surface and the depth measurements in both rivers are, as well, mainly due to the higher radiation expected at the surface than at depth. The differences observed between the Mánamo and the Macareo particularly during the high water period (up to 3 °C) may be due to the lack of turbulence in the Mánamo waters. The turbulence, which is partly due to the strong currents and partly due to wind action, constantly removes the thin hottest layer of air above the water surface, resulting in a more effective cooling of the water surface and upper layer of the water column. As Rosemberg (1974) observed when turbulence is restricted the aerial resistance increases and the temperature gradients are intensified. According to Junk (1973), the wind plays an important role in the temperature stratification observed in the water bodies of the Amazon River floodplain.

5.4.5 Sediment loading and water-transparency
The waters contributing to the Orinoco from the Andean and Llanos regions are the source of most sediments transported by the river. These regions are Tertiary formations and are undergoing active erosion due to the intense rainfall deforestation. The sediment contribution from the Guayana Shield, even if showing a more intense precipitation is almost negligible due to the densely vegetated cover (Stallard, 1991; Yánez, 1997).

The amounts of sediment obtained from the Macareo water samples (Fig. 5.8a) were three times greater than the amount obtained from the Mánamo river. This result was expected due to the intense sedimentation that occurs at the junction of both rivers, few kilometres upstream from the dam, an area that behaves as a reservoir In this area the sand bars created since the river regulation (an approximate amount of 414 million tonnes) are covered by emergent species as is seen in Plate 2.1. This input of sediments is associated with the rainfall peaks (in July-August and November-December) showen in the Orinoco Basin (Colonnello, 1990a). The pattern is also related to the local precipitation (see Fig. 2.5, 2.6) that causes erosion along the river shores. The reduction on the concentration of total dissolved sediments observed in the Mánamo river, may be seen in all its sub-basin. Values ranging from 0.003 mg l^{-1} to 0.01 mg l^{-1}, contrasting with a mean of 7.75 mg l^{-1}. registered in the Mánamo, were

found in second order channels and in first order channels (Infrawing & Asociados, 1997).

The mean value of the sediments transported by the Macareo was about 14 million tons yr^{-1}, while the Mánamo transported just 0.16 million tons yr^{-1}. These values are within the estimations of 100-150 million tonnes yr^{-1}, given by different authors, for the total discharge of sediments of the Orinoco River (Meade *et al.*, 1983; Monente, 1993). The Mánamo deposits an estimate 13.8 millions tonnes of sediment annually, upstream from the barrage. The reduction in flood peaks can suppress or greatly reduce the load and alter the transport capacity of rivers. This results in a series of morphological adjustments, usually characterised by a reduction in a channel capacity and the spread of the riparian woodland onto the new floodplain, as pointed out by Bravard and Petts (1996). In the Stiegler's Gore Project, Mwalyosi (1998) reported that 25 millions tonnes of riverine sediments are expected to be trapped by the impoundment to be constructed on the Rufiji River in Tanzania, every year. The rivers may degrade their beds downstream from a barrage. Maximum scouring usually occurs immediately down-stream from the dam, as reported in the upper river section of the Mánamo river (in chapter 8), and is progressively attenuated further down-stream (Bravard and Petts *op. cit.*). Additionally, reduction of the timing and intensity of flooding accelerate the infilling of shallow channels.

The results of the water-transparency (Fig. 5.8b) show, as expected, that the transparency is related to the sediments carried by each channel (Fig. 5.8a). The Mánamo showed higher values during the high water period, from June to October, than the Macareo. In the lowest water period, from January to April of 1995, when bedload transport is minimal in the Orinoco main channel (January to April), the values are similar. IRNR(USB)-Ecology and Environment (1999), reported the same differences in samples of Macareo and Mánamo upriver from the dam. The water transparency determines the species diversity in lagoon and lentic habitats. The sites studied in chapter 3, with high water transparency , supported several submerged species such as *Utricularia* spp and *Cabomba* spp, not present in sites with low transparency.

5.4.6 Current velocity

The differences observed in the current velocities, measured along the river shore, (Fig. 5.9), are related to the periodic variation in the water level (Fig. 5.2a). In the Macareo, they were associated with the Orinoco seasonal water discharge and with the two peaks in the local rainfall (Fig. 2.7). They are difficult to discern in the Mánamo.

Day and Davies (1986), summarise current velocity data of the Amazon River from several authors. The values normally vary between 50 and 100 cm s^{-1} at low water, however there is a report of 300 m s^{-1} during floods. These values are comparable with the results obtained in this study. The maximum velocity recorded in the Macareo river may attain 140 cm s^{-1}, as measured during the high water period in the middle of the channel and in the upper river section. But the water discharge and magnitude of the Amazon River is many times higher. The implications for vegetation of high current velocity has been explored by Junk (1984) who stressed that large rivers banks are not a suitable environment for plant establishment, due to the high current velocities and large water level oscillations, among other factors.

Current velocity is also an important factor determining the transport of sediments and debris downstream. It is also fundamental in understanding the dynamic of the riparian vegetation, as it controls the establishment and composition of the meadows of floating and emergent species along the river shores (see chapter 6), and even the biomass production of the river system (see section 7.4.3). Sedell *et al.* (1989) have demonstrated that the speed of flood water over a plain (for example) also has a major influence on the nutrient dynamics. Rapid passage of a flood through a valley slope gradient with a moderately steep gradient gives rise to rapid recycling and the productivity of the system is higher than that in areas which are
permanently flooded or which are covered with stagnant waters.

5.5 Final remarks

As discussed in previous sections large tropical rivers are subject to wide annual fluctuation in water throughout the year as a result of the dominating influence of the seasonal rainy period. Anthropogenic factors may also play a part, such as poor land management in the catchment area, promoting intense soil erosion. As a result the rivers transport huge amounts of sediments, for example the Amazon River 900 millions tonnes yr^{-1}, (Day and Davies, 1986); the Orinoco 100 million tonnes yr^{-1} (Monente, 1993); the Uruguay River 17 million tonnes yr^{-1} (Di Persia and Neiff, 1986). As a consequence, the water's chemical and physical characteristics may vary considerably throughout the year (Weibezahn, 1990; Sánchez 1990; Lewis and Saunders ,1990).

In general, results showed no major differences between the chemistry of the water quality between the regulated and unregulated rivers in their upper reaches. The results obtained in this study probably reflect the environment of the sample sites where local factors outweigh

the more general controls on water quality. Greater differences were anticipated considering the totally different hydrodynamic conditions along with the observed explosion in floating macrophytic growth. In contrast along the middle and lower sections of the Mánamo, the water chemistry did change as shown in the data presented by Paolini *et al* (1983), Monente and Colonnello (1997) and Olivares and Colonnello (2000).

An attempt has made to complete the survey of water chemistry along the middle and lower stretches of the Mánamo by Olivares and Colonnello (2000). Partial results for sodium, chloride and sulphate are shown in Table 5.5. These data demonstrate a progressive increase of the sodium, chloride and sulphate anions in the Mánamo river water, especially in the zone close to the river mouth -due to the tidal influence and the intrusion of the saline wedge (see also chapter 6 and 7) . As a result of the suppression of the seasonal flooding, the salt water intrusion is more intense during the dry season, e.g. January, when the only non saline-water supply is by the dam with about 200 m^3 s^{-1}, and through the few tributaries from the left bank (50-100 m^3 s^{-1}). The data showed by Infrawing & Asociados (1997), indicated similar variation of water salinity as a clear indication of the effects of the damming of the river.

Limited physico-chemistry data are available from the unregulated region of the Delta as a result of three surveys due to Paolini *et al*. (1983), Infrawing & Asociados (1997) and Monente and Colonnello (1997). These preliminary studies suggest that the water regulation created a different water environment in the middle and lower stretches Mánamo river, when compared with other channels in the Delta.

Table 5.5. Location of the sites, including 'MAN meadows' where sodium concentration was evaluated in the river water. Salinity was calculated as follow: Salinity (g l^{-1})=1.8065 Chloride (g l^{-1}). Values given are means ± SE of seven samples collected at each site (high and low water, August and January respectively). Chloride and sulphate in river water sampled during the low water phase (January). (Adapted from Olivares and Colonnello, 2000).

Meadow	Lat. Lon.	Na$^+$ in river water (mmol m^{-3}) Aug.　Jan.		Chloride (mmol m^{-3})	Sulphate (mmol m^{-3})
Tucupita	9°03′35″ N 62°03′38″ W	55 ± 0	44 ± 1	33 ± 1	27 ± 0
Mánamo -MAN 2	9°09′56″ N 62°09′37″ W	79 ± 1	45 ± 1	40 ± 2	29 ± 2
Junction	9°22′19″ N 62°19′47″ W	107±2	53 ± 1	46 ± 1	34 ± 0
Morichal Largo	9°25′46″ N 62°26′04″ W	212±4	190±7	257 ± 8	34 ± 2
Morichal Mouth	9°26′34″ N 62°24′13″ W	126 ± 2	113 ± 2	-	-
Boca de Tigre-MAN 3	9°30′42″ N 62°26′13″ W	145±2	122±2	-	-
Güina Morena-MAN 4	9°38′45″ N 62°22′29″ W	208±2	430±13	703 ± 1	55 ± 1
Bagre Island-MAN 5	9°48′14″ N 62°18′58″W	866±3	59828 ± 1904	53307 ± 205	2738 ± 15
Pedernales	9°55′32″ N 62°18′18″ W	31692 ± 381	114707± 6307	128903 ± 394	6557 ± 227
Muelle-MAN 6	9°58′06″ N 62°15′33″ W	47712 ± 536	211350 ± 5673	134804 ± 188	14194 ± 32

Chapter 6 River morphology and vegetation

Large changes in the river hydrology, such as that experienced by the Mánamo due to the dam construction, have substantial consequences for riverine vegetation. For the Mánamo, the hydrological isolation affected the main characteristics of the waters (see chapter 5) in terms of:

1. Flooding influence, from several months to a permanently dry condition, of many areas along the banks and in the inter-riverine terrain;

2. Water quality, which included the general increase of electrical conductivity, due to the increase of organic acids, reduction of dissolved oxygen available for metabolic and decomposition processes, inversion of the chemical composition, dominance of anions and cations, with predominance of sodium due to the increased salinization; and

3. Decrease of the sediment input modifying the patterns of accretion and erosion along the river edges and in the inter-riverine regions, where the sedimentological evolution is suppressed.

The principal biotic components of the system affected are the plants, herbaceous and forested communities established along the river edges. The influence is mainly due to the hydrologic changes in the upper river stretches and due to water quality changes in the middle and lower river sections.

6.1 Aims

• To compare the floristic composition and coverage within the floating and emergent meadows along various stretches of the Mánamo and Macareo tributaries.

• Relate the species diversity of the meadows with the physical and morphological characteristics of the river banks.

• To correlate the floristic composition of two meadows on the middle course of the Mánamo and Macareo rivers with the sediment characteristics.

The research hypothesis in this section is that the changes in the hydrologic patterns, and sediment transport, caused by the damming of the Mánamo river produced changes in the river shore morphology and consequently in the species composition and floral diversity.

6.2 Methods

6.2.1 Study sites

The study sites (Fig. 6.1) were selected after a detailed analysis of the morphological features of every river, using radar images (scale 1:250.000).

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Plate 6.1. Floating rafts gathered in the middle course of the Mánamo river.

In the Mánamo (MAN):

MAN 1	(09° 01' 13" N and 62° 03' 49" W);
MAN 2	(09° 03' 35" N and 62° 03' 38" W);
MAN 3	(09° 31' 45" N and 62° 26' 70" W);
MAN 4	(09° 38' 34" N and 62° 22' 84" W);
MAN 5	(09° 47' 35" N and 62° 18' 45" W); and
MAN 6	(09° 57' 05" N and 62° 18' 20" W).

In the Macareo (MAC) the following sites were selected:

MAC 1	(08° 49' 52" N and 62° 00' 16" W);
MAC 2	(08° 55' 26" N and 61° 51' 46" W);
MAC 3	(09° 11' 47" N and 61° 47' 57" W);
MAC 4	(09° 15' 33" N and 61° 46' 44" W);
MAC 5	(09° 23' 50" N and 61° 40' 30" W);
MAC 6	(09° 34' 45" N and 61° 35' 08" W); and
MAC 7	(09° 39' 34" N and 61° 30' 48" W).

These meadow sites are representative of different sectors of the river. Each site was visited during July 1995 where a schematic representation of each site was prepared.

6.2.2 Vegetation data collection and analysis

The vegetation in the meadows, was analysed in a 10 m wide swathe with a maximum 100 metre to the bank, or as wide as the meadow, at right angles to the river bank. In each meadow 10 quadrats of a square metre were randomly selected. Species cover was recorded during the survey as in section 3.3.2. Species diversity of the different plots was assessed using the Shannon-Wiener index (H'), and the Equitability (J') as described in section 3.2.2. This index was applied because it evaluates the proportion of the individuals in the sample and considers that all the species are represented in the samples and the plots are randomly distributed, as described by Magurran (1989).

Species were collected preserved, identified and deposited in the herbarium of the Museo de Historia Natural La Salle (CAR) and the Venezuelan National Herbarium (VEN). A general table with site location and description, species composition and comments was prepared (Appendix 12 and 13).

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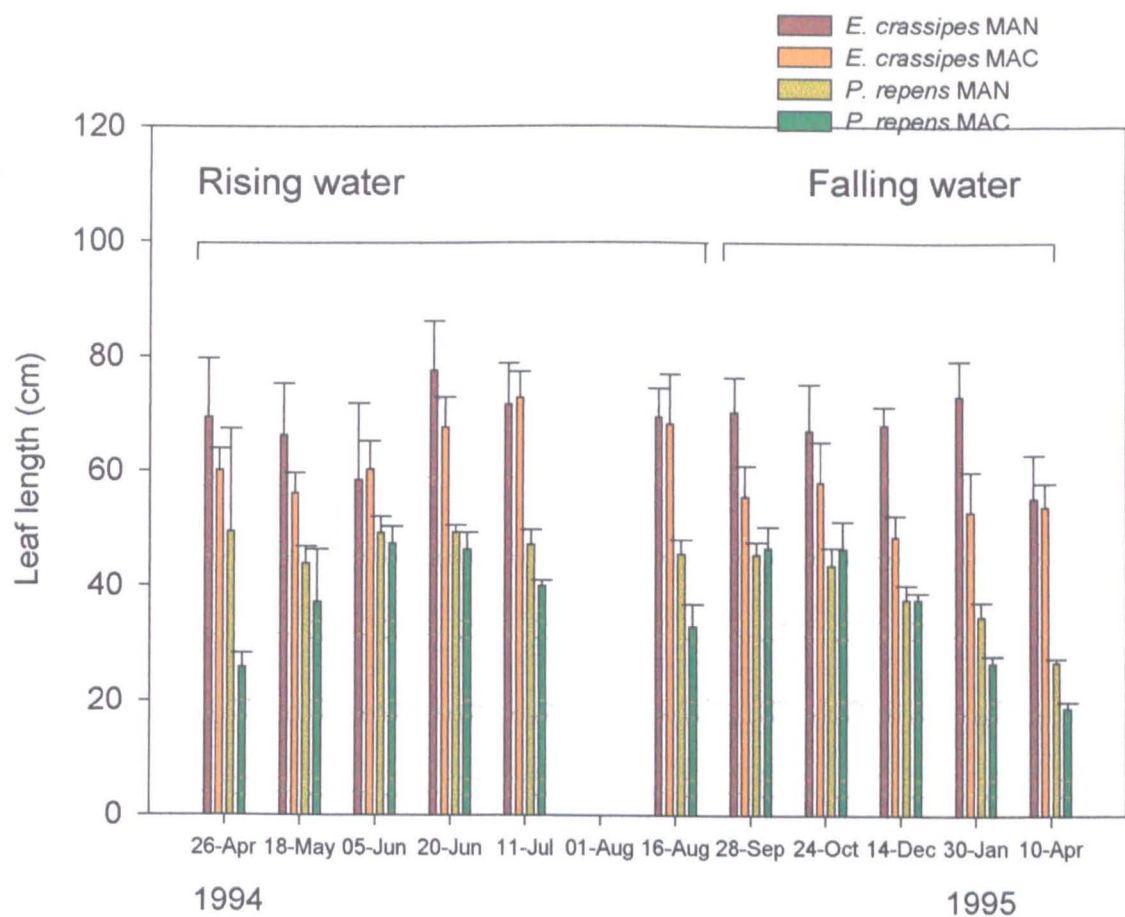
Fig. 7.3 a. Seasonal variation of leaf length
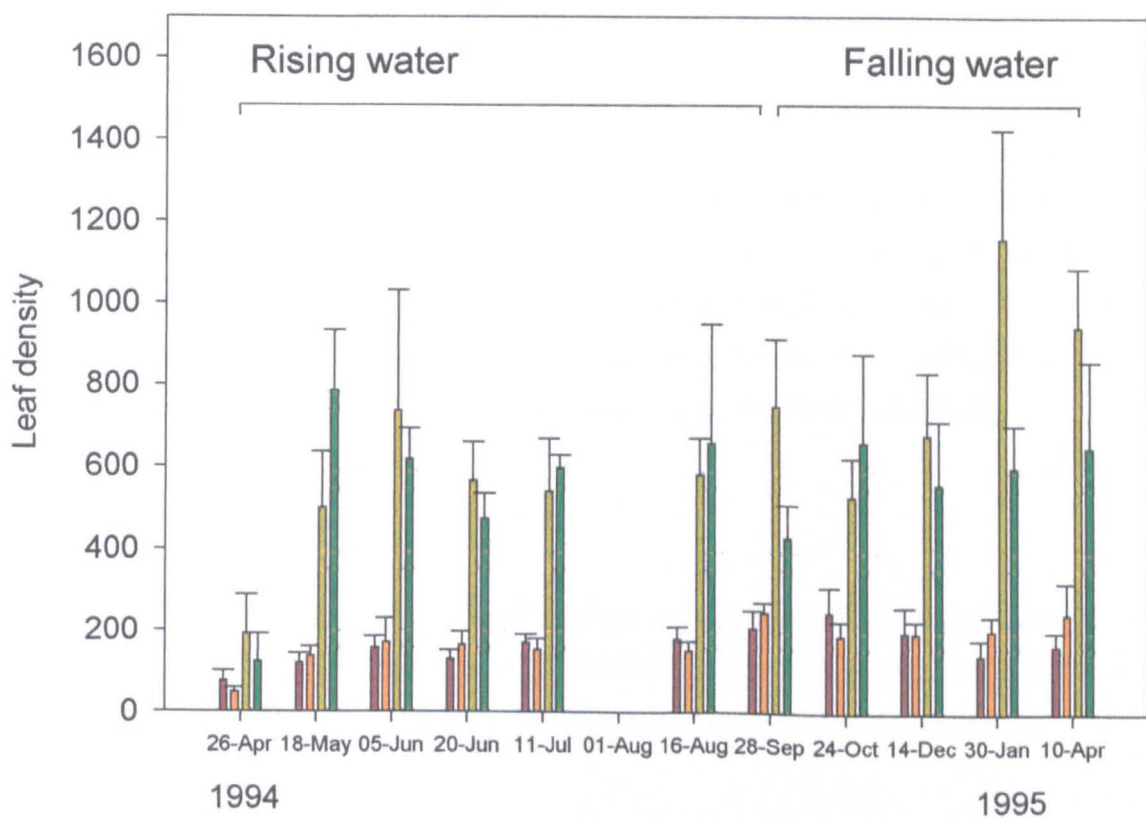
Fig. 7.3 b. Seasonal variation of leaf density

6.2.3 Topographical profiles and species coverage

In order to establish the relationships between the topography and the species composition, a topographical profile in the meadows of the Mánamo and Macareo banks was surveyed. Measurements were taken every metre, in a transect of 100 m length perpendicular to the shore during high tide, using a graduated pole. They included the band of aquatic plants, plus a variable extension up to 20 m of open waters. Sites investigated were meadows of MAN 1, 2 and 3 and MAC 1, 4 and 5. The cover of each plant species was estimated every 10 m in 10 plots of 1 sq. m along the transect. Due to the permanent flooding, and muddy substrates, the use of a more technical device such as an optical level, was not suitable.

The selection of the sites was assessed through the analysis of time-series of aerial photographs (scale 1:25.000). The sites included river sections that were undergoing active change, in the Mánamo river such as the expansion of sand bars and in the Macareo river the lateral translation of the river bed. The latter was estimated at 1.5 metres a year, in the period from 1932 to 1996 (G. Colonnello, unpublished data)

6.2.4 Sediment sampling

Sediment samples were analysed in order to
1. Correlate the species composition and diversity with the sediment composition and
2. Compare the sediment composition in between the two rivers in their lower courses.

During low tide periods, samples of sediments were taken from sites MAN 3 and 4 in the regulated river and from sites MAC 4 and 5, located in the unregulated river section that was undergoing active morphological change. Samples were taken as an integrated sample between 0-60 cm and between 60 and 100 cm. A core-sample was used in the middle of each meadow and a 'Horse' dredge at the edge of the meadow. Samples were taken at intervals of 10 m, including a 20 m stretch of open water. They were stored in plastic bags for laboratory analysis.

6.2.5 Analysis of the sediment fine fraction

The procedure followed here was to pre-treat with sodium-pyrophosphate for a period of 24 hours, then dry the samples at 80°C for 48 hours. The analysis was carried out using the hydrometer method (Emery, 1938). The samples were then screened using the 'Tyler' column at intervals of '1 phi' to determine the macrogranulometry (Krumbein, 1936; Wenworth, 1936). To determine sediment texture the Sheppard triangle was employed (Sheppard, 1954). Range and relation parameters were determined using the Folk and Ward (1957) criteria and interpretations were made according to Alvarez (1987).

6.3. Results and discussion

6.3.1 Species composition and river morphology

In Appendix 12 and 13 are shown the species composition and coverage and the river morphology registered in the Mánamo and Macareo meadows.

6.3.1.1 The Mánamo river and its vegetation

As has been explained both the Mánamo river and the Macareo river, originate in the Upper Delta area, with the free flowing Macareo branching away from the main course of the eastward flowing Orinoco not many kilometres from the head of the Delta town of Barrancas (see Fig. 6.1). However the course of the Mánamo has been obstructed by the dam built a few kilometres downstream after its separation from the Macareo river.

Along its uppermost section, downstream of the dam, the levée of the bank measures between 3-4 meters in height. Its maintenance was impeded with the damming of the Mánamo. The vegetation associated with the lower part of the banks of this stretch are small meadows of no more than 500 m², whose principal species are *Paspalum repens*, a floating Poaceae with inflated stems, and *Eichhornia crassipes*, a floating Pontederiaceae that forms dense growths due to the interlacing of the individuals through the production of stolons. Another part consist of emergent plants such as the semi-herbaceous *Montrichardia arborescens*, that colonise the banks forming mono-dominant communities and, on occasions, represent the first component of the *Montrichardia-Paspalum-Eichhornia* community.

In the middle of the river are various islands (Plate 7.1) with gently sloping banks upon which develop extensive meadows that are more complex than the communities described above. *E. crassipes*, *Sacciolepis striata* and *P. repens* are found on the shores, while other emergent plants, *Sesbania exasperata*, *Urena lobata* and *Mimosa pigra*, form an ecotone with the dry forest and emerge at water level on a substrate (30 to 50 cm in depth) composed of roots and semi-decomposed organic material. The ecotone is located at the highest level of the sandy bank adjacent to the semi-deciduous forest. In this transitional formation, aquatic species such as *Tonina fluviatilis*, *Borreria scabiosoides* and the emergent (sometimes showing a floating eco-phase) *Hymenachne amplexicaulis*, are established (MAN 1, Appendix 12). In this river section, there also exist extensive areas of shoreline with shallow waters that are covered by populations of the Cyperaceae, *Eleocharis elegans* and *Cyperus articulatus*.

In the intermediate stretch of the Manamito Island (Fig. 6.1) the only communities of aquatic plants found are small meadows of *Paspalum-Eichhornia* and narrow belts of *Montrichardia* at

site MAN 2 (see Appendix 12). Beyond the rejoining of the Mánamo with the Manamito, approximately in the Middle Delta, the levées measure between 1 to 1.5 m in height.

The Lower Delta has been defined for the purposes of this study (see section 2.1), as that zone where the bank levées are no longer present, enabling the permanent inundation of whole of the area. Flood depth varies according to the influence of the ocean tides at the estuary of the Mánamo, which keeps the soils permanently saturated. The physiographic change created by flooding is reflected in the existence of meadows of considerable dimensions, 3 to 8 hectares in extent, inside the bends of the meanders (MAN 3 and 4). Successive conditions include the reappearance of shallow banks, with lentic environments in the main channel or on the islands, thereby facilitating the colonisation of emergent and floating species such as *Eichhornia crassipes, Paspalum repens, Ludwigia octovalvis* and *Polygonum acuminatum.*

From the Tigre Island which lies at the junction of the Mánamo with Caño Buja (Fig. 6.1), down river to the mouth, the meadows are no longer to be found along the river margins so that the halophytic communities of mangroves (*Rhizophora mangle*) become dominant replacing the meadows of emergent species and the evergreen flooded forest (see chapter 8 for a detailed analysis). Only a few small meadows are found on cleared areas of the banks, possibly a result of anthropogenic intervention (isolated Indian huts are found). The emergent plants present are *Crenea maritima*, a halophytic species and the Poaceae *Echinochloa colona* (MAN 5 Appendix 12). These environments with high salinity and high tidal fluctuations (up to 2.4 m. Herrera *et al*, 1981) also permit the anchoring of free-floating species (a few damaged plants of *E. crassipes* and *P. repens* are found).

The meadows of freshwater species are no longer encountered at some 50 km from the river mouth of the Mánamo except for one lowermost meadow which was registered near the town of Pedernales in the mouth of the river (Site MAN 6, Appendix 12). This meadow consisted of three halophytic species: two Poaceae *Spartina alterniflora* and *Sporobolus virginicus* and an emergent Apocynaceae *Rabdadenia biflora* (see also Appendix 12). In the following winter seasons (1996-1998) there was no trace of them, the community was affected by the active shore accretion and erosion.

In the Lower section of Mánamo river, the distribution of the dominant species of the aquatic meadows, *E. crassipes* and *P. repens* are limited by the salinity of the waters particularly during the dry season. The highest salinity increase along this gradient was obtained at Bagre Island (9° 48') (Olivares and Colonnello, 2000) close to the meadow site MAN 5 (see

section 5.5, Table 5.2). The Pontederiaceae may even be found anchored downstream from the site MAN 5, but such communities show severe leaf damage due to sodium uptake from the saline water. Due to the low tolerance of the Poaceae for salt conditions, this species disappears from this section of the river altogether.

6.3.1.2 The Macareo river

As might be expected in the early discussion in this chapter, the unregulated course of the Macareo, flowing through the Central and Eastern Delta zones, emulates the hydraulic regime of the Orinoco river characterised by an annual oscillation between high water (June to October) and low water (November to April).

The stretch of the river within the Upper Delta is characterised by long and straight sections with levées measuring between 7 to 9 m in height, flooded only at peak discharge, sometimes overtopping the levées. The slopes of the levees are steep, varying from 45 to 75 degrees, and when the water level drops, their surfaces are colonised by emergent species such as *Eclipta prostrata*, *Ludwigia octovalvis* and *Eleocharis elegans*. On the slopes of the levées *Echinochloa polystachya* grows whilst toward the top *Paspalum fasciculatum* is founded since it can tolerate longer periods of drought (MAC 1, see also Appendix 13). *P. fasciculatum* of erect stems predominates during the dry season, *E. polystachya* of floating stems occupy the greater area during the flood season.

The species comprising the floating meadows in this sector are *E. crassipes* which forms populations anchored to decaying tree trunks along the river margins of the meadows, *P. repens*, with roots penetrating the base of the levées, and *E. polystachya* and *P. fasciculatum* alternating at the top of the river bank (site MAC 2, Appendix 13). The species composition and dominance in the banks is determined by the water level oscillation, the water tolerance and the adaptation to the rising level and increasing currents. Junk (1970) defines this plant association found in the 'várzea' region of the Middle Amazonas as *Paspalo-Echinochloetum*.

In the Upper Delta section of the Macareo, the power of the currents mobilises the water-borne communities of *E. crassipes* downriver. This 'rafting' is also partly the result of waves produced by squalls associated with rain storms as well as those produced by river craft. The species *Paspalum repens* and *Echinochloa polystachya* are subsequently uprooted as the current's velocity increases significantly beyond a critical threshold value. In the middle of the channel the maximum velocity measured was 150 cm s^{-1}, while along the edges of the meadows it was about 75 cm s^{-1}. Such velocities are sufficient to up-root those rooted

species with floating stems. *Paspalum fasciculatum*, in contrast remains firmly rooted providing stability to the top of the banks (Junk, 1970).

Some lentic micro environments, such as embayments of between 100 to 600 meters width and 3000 m length (Pfefferkorn *et al.*, 1988), formed by water erosion permit the complete maintenance of habitat diversity and vegetation zonation in the upper river sections even during high water periods. Only major floods may disturb the areas.

Whilst the velocities of the river current remain moderate at the river edges, about 40 cm s^{-1} (as seen in Fig. 5.9, the current velocity in the Macareo river shore varies from almost zero to 75 cm s^{-1}) and the rise of the water level is slow, populations of *P. repens* and *E. polystachya* (floating plants), maintain their position in situ along the levées because they can elongate their stems sufficiently fast enough to maintain their existence. On the other hand, *P. fasciculatum* does not have such a capacity to elongate its stem system, but still remains firmly anchored to the substrates even when completely submerged by the water. In this section of the Macareo river, the levées are also colonized by *Gynerium sagittatum* a giant Poaceae (MAC 3, Appendix 13). According to Junk (1970; 1990), the vegetation communities along the banks of the Amazon river show similar distributions patterns and physiological adaptations.

As the topographical gradient between the Upper and Lower Delta becomes less, the levées diminish to the point where they are no longer discernible. On entering the Lower Delta, the river course begins to meander and the stream velocity diminishes to maximum speeds of 128 cm s^{-1} along the edges of the river. The plant species distribution remains the same as in site MAC 3, although *P. fasciculatum* unable to support an almost permanent flooding, can be replaced by *E. polystachya*. In addition *E. azurea* appears and becomes one of the dominant species along the borders of the meadows.

In the lowermost river section, the Macareo once again has straight and long sections. The meadows that are close to the Nabasanuca channel mouth (see site 6, Fig. 6.1) are dominated by *Cyperus giganteum*, a tall Cyperaceae associated with sandy and flooded levées as well as *P. repens* at site MAC 6, (Appendix 13). In the ecotone where the meadows meets the forest, extensive populations of *P. fasciculatum* occur. Simultaneously the mangroves become establish along the gentle slope of the river edges. Closer to the river mouth, the meadows almost disappear, and the entire shore complex is covered by the halophytic community of *Rhizophora*. The last meadow is located some 24 km from the open

sea and is composed of *Paspalum repens* at its external edge and *Montrichardia arborescens* (MAC 7, Appendix 13). This marks the end of the river section under consideration.

6.3.1.3 The floating rafts of the Mánamo

As the Mánamo river flows through the Middle and the Lower reaches of the Delta, important ensembles of free-floating plants (Plate 6.1) appear whose movement is influenced by tidal motion. They may aggregate to form larger meadows that become large enough to be recognized as important floating community units. These interact with the other meadows of emergent and floating plants, as parts become dissociated and are incorporated into the communities along the banks. These free-floating islands, which range from isolated plants to patches of tens of square meters, are uprooted from the extensive meadows of the Upper Delta and other minor tributaries of the Mánamo river (Buja, Morichal Largo, Uracoa) in which they originate.

Experiments conducted by Petrell and Bagnall (1991) to determine the behaviour of *Eichhornia crassipes* mats under towing conditions, showed that at velocities exceeding 40 cm s^{-1} the plants lose stability 'rolling under' the mat, which destroys their structure. These observations suggest the mechanisms that are responsible for the separation of the floating rafts of vegetation from the meadows as they drift into the main channel. The current velocities presented in section 5.3.6, for both channels far exceed this threshold value of 40 cm s^{-1}.

E. crassipes and *P. repens* are the commonest constituent species of the communities, whilst sometimes *Salvinia auriculata*, *S. sprucei* and *Pistia stratiotes* are also present. The duration of time that these plants reside in the main channel and their subsequent movements have not been fully investigated, but preliminary observations reveal a complicated pattern influenced by the factors already identified - the tidal and seasonal currents and the squalls from storms. Most of the rafts never reach the open waters of the ocean as they eventually move driven by the predominant north to north-east winds, along the left Mánamo river shore, forming extensive floating meadows inside the Buja channel (Fig. 6.1) while other parts, virtually disappear in the region of Isla de Tigre Island (between sites MAN 5 and MAN 6).

The floating meadows that are not washed out to sea create a serious weed problem in the river. The modification of the river current regime of shallow flowing tributaries, from dynamic to lentic water habitats due to the river regulation favours the developing of extensive communities of *Eichhornia crassipes* and *Pistia stratiotes*. These obstruct the courses and

cause the filling of the river channels. This is an observed phenomenon that occurs in many similar situations throughout the world as exemplified by Moffat and Lindén (1995) in the Niger River as well as in the Amazon Basin, where the impoundment created by the building dams generate suitable conditions such as shallow waters, emerging woody debry and enriched water habitats, for the establishment of aquatic macrophytes (Barrow, 1987; Pedrozo and Bonetto, 1989; and Bonetto et al, 1989).

Variables floods, high turbidities and unstable sediments preclude the development of extensive macrophyte beds in non regulated distributaries of the large rivers. These natural control mechanisms have been well documented from large rivers such as the Amazon river (Junk, 1970) and the Murray river in the Australian Continent (Walker, 1992). In regulated systems such as the Mánamo sub-basin, the drifting rafts are predominantly controlled by the existence of salinity wedge, as proposed by Olivares and Colonnello (2000). *Eichhornia crassipes* plants found near the river mouth have shorter leaves and lower mass as consequence of the salinity (Fig. 6.2). Plants on Bagre Island (corresponding to MAN 6) and Pedernales close to site MAN 7, had 33% and 45% of dead leaves respectively, with a sodium concentration in the water of 0.87 and 31.7 mol m^{-3}, which correspond to salinity values of 1.3 and 0.05 g l^{-1}.

The effect of high levels of sodium chloride, on aquatic species is to produce leaf necrosis, reducing of the biomass production and the growth rates. For tropical species such as *Pistia stratiotes* and *Eichhornia crassipes* , Haller *et al.* (1974) reported toxic salinity values of 1.6 and 2.5 g l^{-1} respectively, in greenhouse conditions. In temperate species such as *Potamogeton* spp and *Ranunculus circinatus*, van der Brink and van der Velde (1993), reported negative effects at salinity levels of 7 mmol l^{-1} Chloride (0.2 g l^{-1}) in artificial ponds.
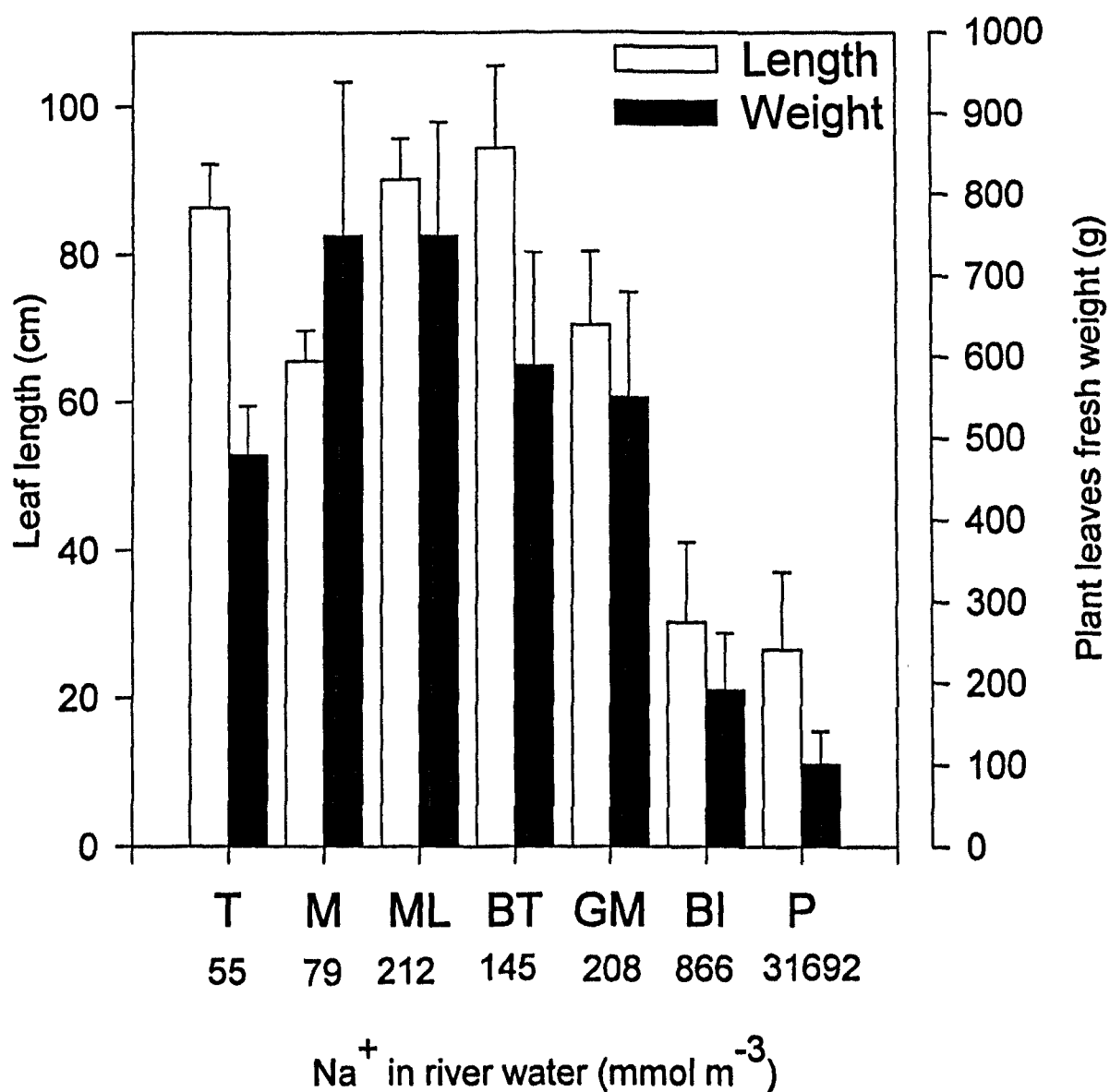
Fig. 6.2. Leaf length and total leaves fresh weight of *E.crassipes* during the high water period inTucupita (T), Mánamo (M), Morichal Mouth (MM), Boca de Tigre (BT), Güina Morena (GM), Bagre Island (BI) and Pedernales (P). Adapted from Olivares and Colonnello (2000).

Table 6.1. Sites location, including 'MAN meadows' where sodium concentration was evaluated in the river water. Salinity was calculated as follow: Salinity $(g\ l^{-1})$=1.8065 Chloride (g^{-1}). Values given are means ± SE of seven samples collected at each site. The presence (+) or absence (-) of *E. crassipes* and *P. repens* is indicated in each case. Distance (Km) from the river mouth is indicated (Modified from Olivares and Colonnello, 2000).

Meadow	Salinity $(g\ l^{-1})$		E. crassipes		P. repens		Km
	Aug.	Jan.	Aug.	Jan.	Aug.	Jan.	
Tucupita	$3\ 10^{-3}$	$2\ 10^{-3}$	+	+	+	+	153
Mánamo -MAN 2	$5\ 10^{-3}$	$3\ 10^{-3}$	+	+	+	+	128
Junction	$6\ 10^{-3}$	$3\ 10^{-3}$	+	+	+	+	103
Morichal Largo	$18\ 10^{-3}$	$16\ 10^{-3}$	+	+	+	+	88
Morichal Mouth	$7\ 10^{-3}$	$6\ 10^{-3}$	+	+	+	+	86
Boca de Tigre-MAN 3	$8\ 10^{-3}$	$7\ 10^{-3}$	+	+	+	+	60
Güina Morena-MAN 4	$22\ 10^{-3}$	$45\ 10^{-3}$	+	+	+	+	50
Bagre Island-MAN 5	$49\ 10^{-3}$	3.41	+	-	-	-	30
Pedernales	1.30	8.26	+	-	-	-	9
Muelle-MAN 6	1.95	8.63	+	-	-	-	7

The contribution of these rafts of biotic communities to the river ecosystem should be further investigated because they retain a substantial amount of particulate matter, especially in the *E. crassipes* roots. They also support a diversity of faunal communities such as the invertebrates associated with plant roots (Poi de Neiff *et al.*, 1994). They also occasionally provide a habitat for vertebrates such as birds and frogs that nest inside the floating mats. These mobile communities contribute to the species diffusion and interbreeding. The plants themselves when mobilised by the waves or salinity effects, contribute to the enrichment of nutrient and particulate elements within the riverine environment. In the space of a few weeks most of the plant material may be incorporated into the system. For example Junk and Furch (1991) reported high rates of decomposition that could reach 80 to 90% of the original mass within a month in a tropical wetlands environments such as that of the Amazonas floodplain. These authors also suggested an accumulation of organic material, in permanently wet habitats as a consequence of the plants decomposition. In the Mánamo case, this may accelerate the processes of eutrophication due to the volume of aquatic plants incorporated to the system. On the other hand, the floating rafts increase the degree of connectivity along the different section of the river course. This has been proposed for the riparian corridor, which is

viewed by some researchers as a major vector component, propagating matter, energy and organisms (Tabacchi *et al.*, 1998).

6.3.2 Meadow species diversity comparison

Despite the magnitude of the river courses, only some 40 species listed below (Table 6.2) of the approximately 160 aquatic macrophytes recorded in the Delta region are present in the meadows along either the Mánamo and Macareo rivers. The number may vary from one year to another because the meadow and the river edges are in an unstable state due to the changes in flow dynamic and sediment flux, as was observed in the site MAN 6.

Of all the species, 26 were found along the Mánamo margins and 26 along the Macareo banks, indicating that there were no major differences in species richness between the two rivers. Moreover the same number of species,14 (table 6.2) were found exclusively in each channel during the study period. The species that showed the greatest adaptations to salinity -*Crenea maritima, Spartina alterniflora, Rabdadenia biflora* and *Sporobolus virginicus* were present only in the lower section of the Mánamo. this was due to the particular conditions of salinity 1.95 and 8.63 g l^{-1} at high and low water respectively, of the waters as seen in Table 6.1. The plant species that are able to complete their life cycles in an environment with between 0.5 and 6 % salt content on a dry basis are called halophytes (Nilsen and Orcutt, 1996). On the other hand *C. maritima* clearly showed a greater degree of tolerance for freshwater environments, since it was found also in a few localities upriver, where salinity values up to 45 10^{-3} g l^{-1} (Table 6.1).

Unexpectedly, some emergent species such as *Paspalum fasciculatum, Gynerium sagittatum, Cyperus giganteus* and *Panicum elefanthipes* are almost absent from the Mánamo river banks and others such as the floating plants *Echinochloa polystachya* and *Eichhornia azurea* are scarce. The differences in the occurrence of the emergent species may be explained by:
1. The modification of the habitat of these species;
2. The colonization of sandy ridges along the middle course by the invading forest vegetation; and
3. The absence of seasonal flooding.
These reasons, however, do not elucidate the limited occupancy of the floating species.

Table 6. 2. Species recorded in the Mánamo (MAN) and Macareo (MAC) meadows.

Mánamo and Macareo meadows	Species exclusive to	
	Mánamo meadows	Macareo
Borreria scabiosoides	X	
Costus arabicus		X
Crinum erubescens	X	
Crenea maritima	X	
Cyperus giganteus		X
Cyperus odoratus		X
Echinochloa polystachya		
Echinochloa colona	X	
Echinodorus sp.	X	
Eichhornia azurea		
Eichhornia crassipes		
Eclipta postrata		X
Eleocharis elegans		X
Gynerium sagittatum		X
Hibiscus striatus		X
Hymenachne amplexicaulis		
Heliconia sp.	X	
Ludwigia helminthorrhiza		
L. octovalvis		
Ludwigia sp 1		X
Mimosa pigra		
Mikania congesta		
Montrichardia arborescens		
Nimphaea connardii	X	
Oxicarium cubensis		X
Panicum elefanthipes	X	
Paspalum fasciculatum		X
Paspalum repens		
Pistia stratiotes		X
Polygonum acuminatum		
Sacciolepis striata	X	
Salvinia auriculata		
Salvinia sprucey	X	
Sesbania exasperata	X	
Sphenoclea zeylanica		X
Tessaria integrifolia		X
Tonina fluviatilis	X	
Sporobolus virginicus	X	
Spartina alterniflora	X	
Rabdadenia biflora	X	

Despite that same number of species was recorded in each channel the diversity index calculated (Table 6.3), showed differences in the meadows along each channel and between the two rivers. The index indicated a generally higher diversity along the Macareo river than along the Mánamo. For instance Site 4, shows the same species richness - 10 - in both rivers but the Shannon´s index indicated H´=1.54 for Mánamo and H´= 2.19 for Macareo, because of the higher equitability of the species distribution in the meadows.

Table 6.3. Species richness, diversity and equity of the meadows of the Mánamo (MAN) and Macareo (MAC) rivers. H´=Shannon´s index; and J= Equitability.

	MAN			MAC		
	N° Species	H´	J	N° Species	H´	J
Meadow						
1	11	1.92	0.5	6	1.1	0.3
2	4	1.38	0.36	13	1.68	0.44
3	8	1.66	0.43	5	1.09	0.28
4	10	1.54	0.4	10	2.19	0.57
5	4	0.77	0.2	12	2.07	0.57
6	3	1.09	0.29	9	1.95	0.51
7	-	-	-	3	0.74	0.19

The more diverse sites are those associated with zones of sedimentation, where a number of microhabitats showing different flooding conditions are available. In the upper section of the Mánamo, the diversity value H´=1.92 (Shannon´s index) is higher than that of the Macareo H´=1.1. In this section of both rivers the steepness of the Mánamo banks at site MAN 1, are less 5-10 % than along the Macareo 45-75 % at site MAC 1, and the water fluctuation is lower too, about 7 m vs. about 1 m, potentially allowing the establishment of more species (see schematic profile in Fig. 6.3). In the dry period in the Macareo several species, small bushes and herbs (see Appendix 12-13), were found to colonize the slopes, however, during the water rising period the levées are mostly flooded and only the resistant species survived, the tallest Poaceae *Paspalum fasciculatum*, established in the top of the levées survive. This macrophyte, the dominant species found in the upper Macareo section, usually forms thick stands (dominant sere) occupying all the banks, effectively preventing colonization by other species.
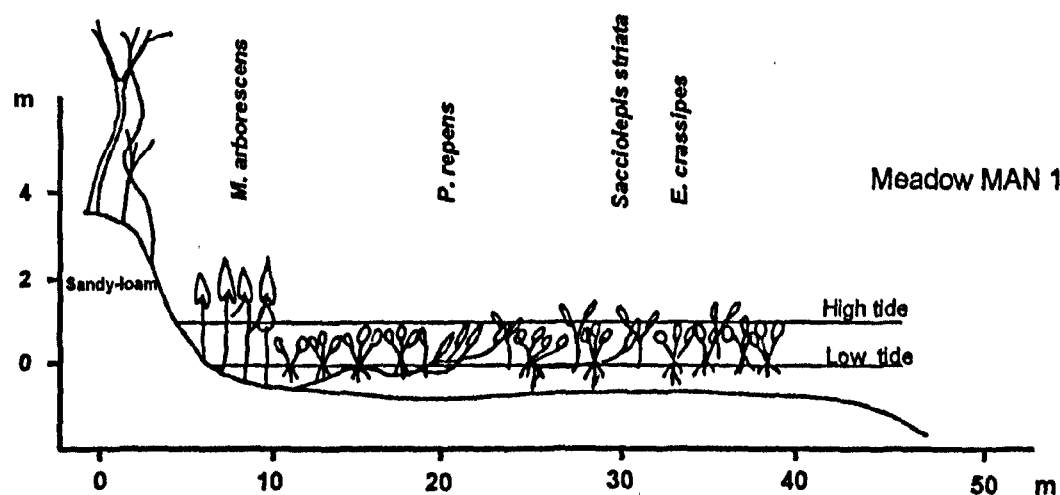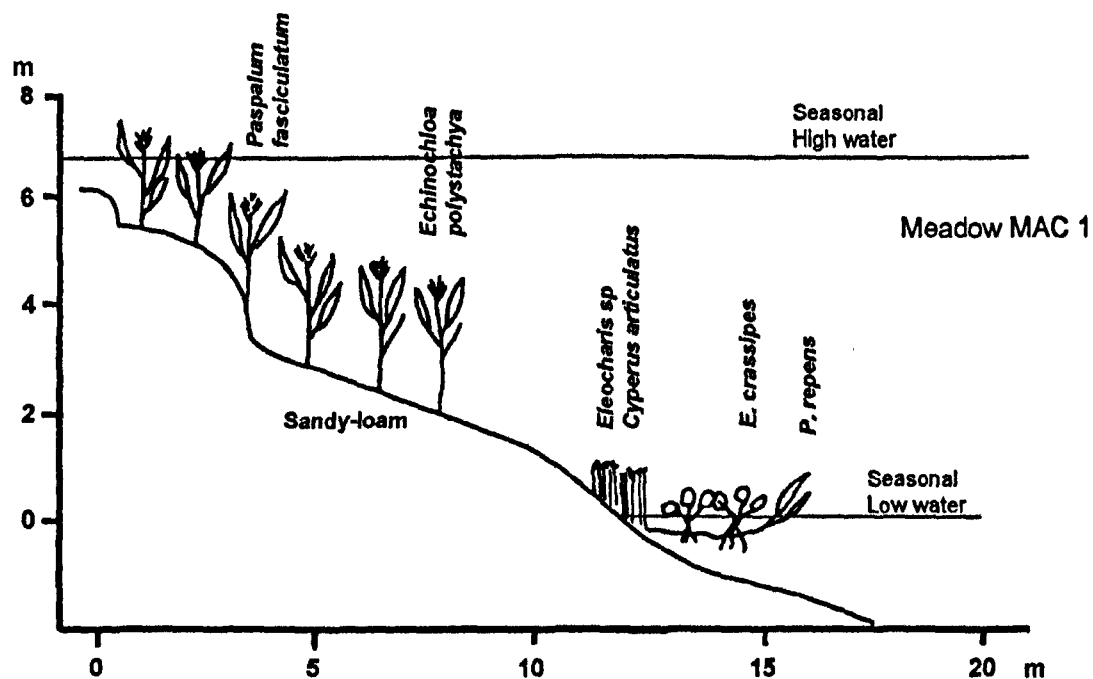
Fig. 6.3. Schematic profiles of sites MAN 1 and MAC 1.

Down stream, in the Mánamo river, site MAN 2, the species diversity diminishes as shown in Shannon's index, from H'=1.92 to H'=1.38 (Table 6.3) due to the disappearance of the shallow areas of silt-clay. These are replaced by steep banks of sand-clayey material where a poor biotic ensemble, mostly composed of floating macrophytes, is established. On the other hand, in the Macareo river in sites MAC 2 and MAC 3, the reduction of the bank slope and height, allowed the establishment of emergent species thus increasing the plant diversity.

In the Middle and Lower river sections the height of the banks diminish to the point where they are no longer in evidence. Large bars of sand and silty-clay are deposited along some river stretches. Conversely, the river beds are wider and river meandering creates suitable conditions for plant colonisation. This is due to lowest water velocities (currents up to 25 cm s^{-1}), mainly in the depositional zones, and reduced seasonal variations in water level up to 1.5 m in October (see section 5.3.6). This therefore enables the establishment of emergent and floating macrophytes.

Those areas, sites MAN 3 and MAN 4 (see schematic profile in Fig. 6.4), in the Mánamo river and sites MAC 4 and 5 (see schematic profile in Fig. 6.5) in the Macareo river show the higher species diversity H'= 1.66 and 2.19 in the Mánamo and Macareo respectively (Table 6.3). The soils are composed of silt-clay and are similar within the two channels due to the similar hydrodynamic conditions. Species composition is different probably due to the regulated river discharge that promotes a more homogeneous substrate in the Mánamo meadows (fewer habitats), in terms of the microtopography, than in the Macareo (see section 6.5.1). This environmental variable could not be measured.

These results coincide with the species diversity values found in the sites analysed in chapter 3, where lentic habitats showed higher diversity than lotic habitats. The large sand bars created in the middle and lower sections of large rivers resemble the lagoons physico-chemistry environment described in section 3.3.4.

Towards the river mouth of both rivers, lower species richness, and diversity values of H'=0.77 and H'=1.09 are found in sites MAN 5 and 6 and H'= 0.74 in MAC 7 (Table 6.3). In this river sector of the Mánamo, the higher tidal range, reaching 2.1 m in the Parla Gulf (Herrera, 1981) and higher salinity (see section 5.5) limit the extent of freshwater species colonization.

The diversity of species in site MAN 5 is at its lowest level, however, the establishment of halophytic species in site MAN 6 produces a subsequent increase in the
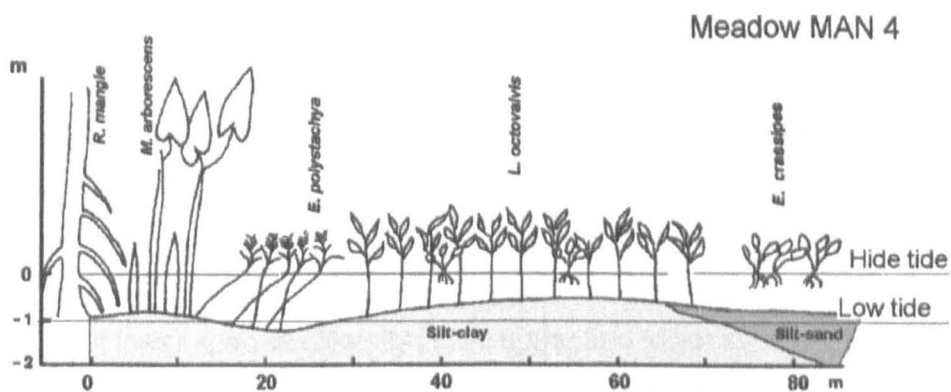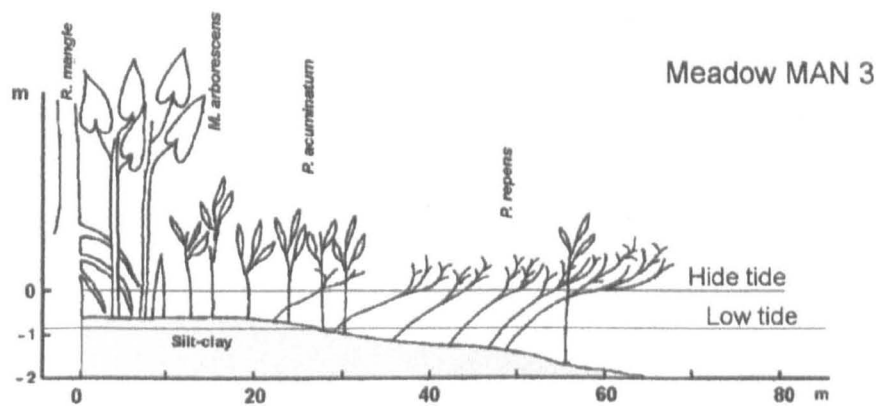
Fig. 6.4. Schematic profiles of sites MAN 3 and MAN 4.

diversity of this type of macrophyte. In the unregulated Macareo river, characterised by large seasonal pulses of freshwater, there is no suitable habitat for the creation of complex halophytic communities such as were found in the Mánamo.

Nilsson et al.(1991) compared two rivers in northern Sweden which before the complete regulation of one of them, had almost identical physical, chemical and biotic characteristics. After 30 yrs of the regulation, the chief differences between these two rivers were as follows:

1. The water discharge is much higher in the unregulated river;
2. The higher species richness was recorded in natural sites, and in regulated sites with remnants of pre-regulation river margin vegetation than in regulated sites; and
3. The lower-per site species richness (diversity index are not shown) and percentage cover of vegetation was observed in regulated rivers rather than in unregulated rivers.

Likewise Baattrup and Riis (1999) reported that the macrophyte coverage was similar in seven rivers, regulated in the mid 1900s and seven unregulated streams of Denmark, but species richness and Shannon diversity were higher in the unregulated courses. The diversity values were correlated with the higher heterogeneity of the substratum. Similarly the analysis of species richness contrasting natural channels, of different width order, with constructed channels of similar width order in Canadian marshes, showed significantly greater number of species in the natural water courses than in the artificial ones (Sanderson et al., 2000).

A higher invertebrate species diversity has been also widely reported in unregulated streams than in regulated ones as exeplified by the reports of Greenwood et al,(1995) in the River Trent and by Boon (1988).

The general pattern of lower species diversity in the upper and lower section of a river and a higher values in the intermediate sections is observed in the Macareo river (Table 6.3) has been also been reported in several studies (Nilsson et al., 1989; Tabacchi et al., 1998) and support the intermediate disturbance hypothesis proposed by Connell (1978) and Lubchenco (1978). They stressed that the highest species diversity is found in the intermediate sectors along disturbance gradients. As was observed by Tabacchi et al. (1998), maximum species richness has been reported, in most cases, in the middle course of the rivers where intermediate hydrological disturbances occur and, as a consequence, where maximum habitat diversity can be found. If we consider the seasonal flooding as a disturbance, the Macareo river, for example, shows in its upper reaches, (sites MAC 1 and MAC 2), large oscillations of water level and discharge. In contrast in the lower stretches, site MAC 7, the river fluctuations and current variation are minimal. It is in the middle stretches, sites MAC 4 and MAC 5, however, where the disturbances are intermediate. The fluctuation of the

environmental condition has been discussed by Tilman and Pacala (1993) as one of the forces that reduce species diversity by increasing the extinction rate of rare species. Locally in the Macareo upper sections, the large fluctuation of the water level can determine the maintenance of a low diversity based on dense populations of species such as *Paspalum fasciculatum* and *Echinochloa polystachya*. Species that colonize these banks (dynamic environments) with few individuals have a high chance of been uprooted by the currents.

In the Upper Mánamo where the dam restriction produced the largest change, the river regulation allowed a high species diversity (Table 6.3), creating extensive sand bars with an intermediate level of disturbance, the tidal water fluctuation. Towards the middle and lower river sections the species diversity follows the pattern of the Macareo river, but in general with lower values.

The reduction of the species diversity along the river banks as a consequence of the river regulation may be seen also in the mangrove colonization along the lower Mánamo river (see chapter 8). After river regulation the halophyte community occupied the sandy bars, previously covered by emergent and floating aquatic species (data from historical aerial photographs), similar to meadows MAN 3 and MAN 4. The species richness, and the diversity, diminished, because the mangrove community comprises a single dominant species (*Rhizophora mangle*). The ecotone of the community may contain, however, other fresh water or halophyte species (see section 8.3.2).

The reduction of the diversity from several species of aquatic plants to a tree community of a single species (mangrove community), is associated with the biomass increase which is evident when the physiognomy of the communities in particular sites is compared prior to, and after the river regulation. In the upper stretches of the Mánamo river, a similar process occurred when the seasonal flooding of the banks was reduced to a small daily oscillation. The exposed sand bars, previously occupied by several species as in the upper Macareo river banks, were colonized by extensive meadows composed of *Eichhornia crassipes, Sacciolepis striata* or *Paspalum repens* which excluded other species. Some more species may be found but they are restricted to the ecotone of the adjacent forest. That process supposes a diversity reduction and a biomass increase.

Huston (1994) refers to the case of aquatic systems where the addition of nutrients can lead to great increase of algal productivity and a corresponding decrease in algae diversity. This is also true for terrestrial systems where the addition of fertilisers to herbaceous plant communities often results in a reduction of the species diversity (Grime, 1979; Silvertown, 1980). This is the case in the Upper Mánamo - the resource suddenly becomes available,
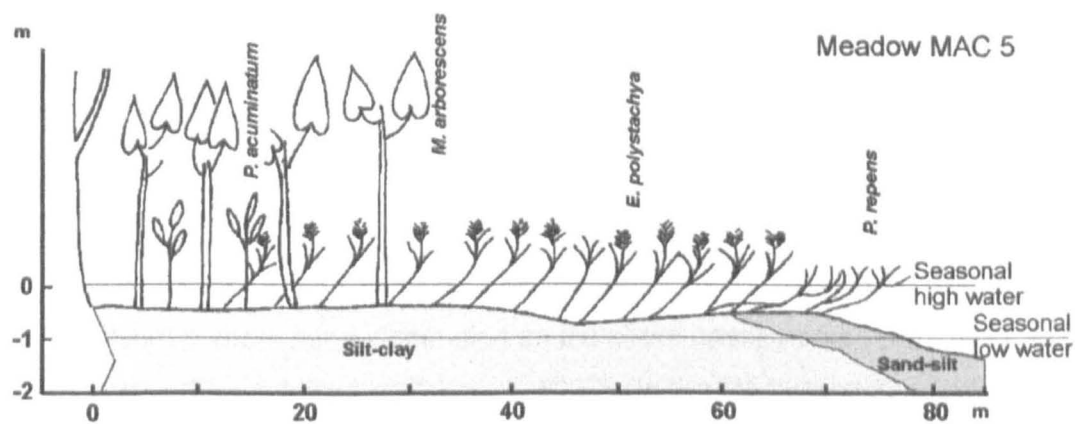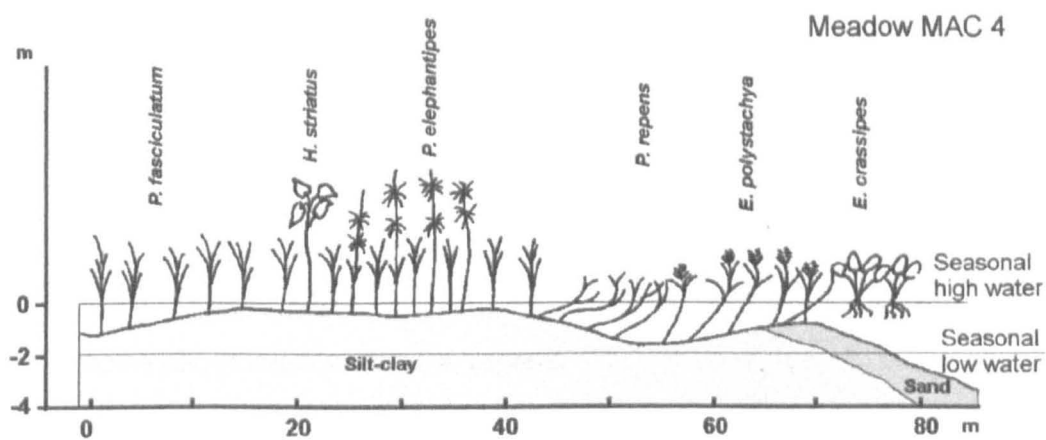
Fig. 6.5. Schematic profile of sites MAC 4 and MAC 5.

following the river isolation, where the shallow and non-vegetated sandbars are rich in nutrients. In these areas some species could competitively exclude others.

The species that were growing along the steep banks of the upper Mánamo before the regulation should have short reproductive periods to be able to produce seeds before the next flooding event. Huston (1994) observes that frequent disturbances favour species that reproduce at smaller size, while infrequent disturbances favour species that reproduce at larger size and produce offspring with a high probability of survival. When the flooding was suppressed in the Mánamo the species of the banks should have very rapidly invaded the slopes. However, their place was occupied by species with an even shorter reproductive rate (vegetative reproduction equivalent to short reproductive periods) and higher productivity such as *Eichhornia crassipes*. Henry *et al.*(1996), proposed that the first species to re-establish in the river banks after a flood disturbance should be able to produce turions, as *E. crassipes* does, or other non-subterranean vegetative organs.

6.3.3 Relations of the vegetation, topography and sedimentary textures

6.3.3.1 Species distribution in the profiles

Species distribution in the profiles, is related to the maximum depth attained during the high water season. The vegetation of the river ecotone is conceptually represented as being spread-out in concentric zones parallel to the shore line (see Plate. 7.1 of the meadows in the upper Mánamo river), reflecting the biological types adapted to gradients (Segal, 1971), of increasing humidity or flooding conditions from the river shore to inland.

In the Upper Delta the bank slopes (Fig. 6.3) and the fluctuations in water level determine the sequence of species along the gradients from the edge of the meadows to further inland. The water level fluctuations may have a different effect on the creation or the loss of various microhabitats within the shore zone, depending on the shore configuration, plant cover and detritus accumulation (Pieczynska and Zalewski, 1997). In the Macareo only a few meadows of free floating or emergent plants may be established and the slopes are occupied by emergent plants. Occasionally, one species *Paspalum fasciculatum* dominates the stand. In the shallow sand bars of the Mánamo, from a depth of 1.2 to 0.6 m, the outer edge is dominated by *E. crassipes*, and towards the shore by *P. repens* and *S. striata*. In the shallower, almost dry, inland areas other communities of emergent herbaceous and scrubby plants are found.

In the Middle Mánamo, sites MAN 3 and MAN 4 (Fig. 6.4), the only free-floating species, *E. crassipes*, occupies the outer vegetation belt as its presence depends on the strength of the

rooted anchoring. The next species encountered is *P. repens*, with floating stems intertwined at their base, which occurs up to a maximum depth of 2 m. The length of the stems of this species are controlled by mechanical damage caused by waves generated by the wind and boats. Along side it can be found several erect-stem, emergent species such as *Polygonum acuminatum* and *Ludwigia* spp, limited to depths between 0.9 and 1 m. Higher up, these species reach dense cover between 0.9 and 0.7 m. In the Lower Delta, the ecotone is composed of stands of *Montrichardia arborescens*.

As on the Mánamo, in the Macareo river, sites MAC 4 and 5 (Fig. 6.5), free-floating species are established at the external borders of the meadows and those inner areas which are protected from the currents. Floating plants such as *P. repens* and to a lesser degree *E. azurea* occupy those intermediate areas that are in contact with open waters on the top of the levées. Beyond that, are found plant populations of varying densities, composed of *E. polystachya* (at a depth of 0.7-0.9 m) and finally *P. fasciculatum*, associated with other Poaceae such as *Panicum elefanthipes* in the shallower areas between 0.2 and 0.6 m. Similarly, formations of *M. arborescens* occupy the shallow areas between depths of 0.5 and 0.7 m. This vegetation zonation along the edges of the main channels has been similarly reported in the Amazon system with virtually the same species assemblages (Junk, 1970; 1986), undoubtedly, as a response to similar hydraulic flow conditions.

The higher species diversity found in the intermediate section of the Macareo river in contrast with the Mánamo river, is associate with the number of vegetation belts found in the floating meadows of each channel. In each belt, one or two species have a competitive advantage for one resource over other species in the meadow. This assemblage agrees with the spatial heterogeneity model discussed by Tilman and Pacala (1993) to explain high plant richness. In the Macareo the meadows consist of 4 to 7 successive belts with different species composition which are related to different water depth caused by a topographic variation (Appendix 12 and 13 shows this in sites MAC 4, MAC 5 and MAC 6). Instead, in the Mánamo no more than 4 belts are found in each meadow.

6.3.3.2 Textural composition of sediments

The differences in species composition and diversity along the uppermost and lowermost Mánamo and Macareo sections, which undergo the major disturbances, could be explained by the water level oscillation and saline influence. In the middle section of both rivers the spatial heterogeneity seems to be an important factor. The sediments were also considered important thus the characteristic of the two meadows located in this sector of the river were investigated.

The textural composition of sediments in the meadows of the lower section of the Mánamo river (referred to as MAN 3, 4) are shown in Table 6.4. The materials are homogenous and composed of clay silts (organogenic) throughout the profile with a mean grain size (Mz) ranging between 7.8 and 6.4 'phi'. These sediments are characterised by a poor sorting which is indicator of the prevailing lentic conditions of this environment (low kinetic energy of the depositional environment). Among the sediments at the edges of the meadows a change in the texture occurs, from a poor sorting of clay silts to silt and sandy silts.

Table 6.4. Soil properties, 'phi' number and textural classes. MZ= grain size; ECM= Kinetic energy.

Meadows Properties	MAN 3		MAN 4		MAC 4		MAC 5	
m	0-60	70-100	0-60	70-100	0-60	70-100	0-60	70-100
Mean (Mz) phi MKE	6.38	6.15	7.22	5.16	6.19	3.53	6.63	3.85
	Very Low	Very Low	Very Low	Low	Very Low	Moderate	Very Low	Moderate
Est. Dev. (Qd)phi Sorting	1.67	1.96	1.94	1.96	1.77	0.45	1.65	0.63
	Poor	Poor	Poor	Poor	Poor	Good	Poor	Moderate
Textural Class	Silt-	Silt	Silt-	Silt-	Silt-	Sand	Silt-	Sand-
	Clayey		Clayey	Clayey	Clayey		Clayey	Silty

The sediments in the inner part of the meadows in the lower section of the Macareo river, identified as MAC 4 and 5 (Table 6.4), are the same as those of the MAN in terms of their texture and distribution along the transect, as a result of their common origin. They are constituted of poorly selected organogenic clay silts with a mean 'phi' that oscillates between 6.93 and 6.92. This also holds true for the Mánamo river. In the convex part of the meanders of these rivers, the current velocity is notably reduced due to the shallow waters and the vegetation established on the banks. However, there exist notable differences among the sediments found at the open-water edge of the meadows. The MAC presents a belt of sand measuring between 3.85 and 3.52 'phi' with a good grade of sorting, forming the slope of the banks (as can be observed during low waters). The good sorting of these sands reveals a constant energy in the sedimentary environment which permits the deposition of materials of a limited size range within the granulemetric spectrum. Any other finer material which is deposited during the rest of the cycle of the river is carried away by new flood waters.

The homogeneous sequence, found in the sediments composed of clay silts throughout the profile could be explained by a mixing process of coarse and fine material. Due to the dynamic characteristics of this particular channel, silts have either precipitated over pre-

existing sands or, materials are being redistributed along the length of the river course due to current dynamics.

It could be expected that the sedimentation rate of silts is low because of a lack of new incoming sediments, which are restricted by the dam. This is indeed the case, as most of the sediments transported by the Mánamo river precipitate in the lagoon like system which has been formed above the dam, creating sand bars on which communities of aquatic plants have become established (Plate 2.2).

6.4 Final remarks

Water dynamics and its associated parameters, such as velocity, turbulence and erosive forces, is one of the most important and specific abiotic variables influencing species composition and distribution of plant communities in rivers (Fox, 1992). The species composition of the meadows appears to be dependent on the hydrological regime of each part of the water course of both the Mánamo and Macareo. In the Upper Delta flow differences between both channels establish the patterns and timing of colonisation on the banks the coverage and dominance of each plant. This is particularly evident where bank morphology and flow dynamics differ between both channels. In the Mánamo, the water fluctuations are small and constant (see section 5.2.1) and the current velocities are moderate, in contrast with large seasonal flow fluctuations about 7 m and higher current velocities, up to 150 cm s^{-1}, in the Macareo.

In the Mánamo the meadows are extensive and permanent with just a few dominant species, including E. crassipes, P. repens, Sacciolepis striata and Montrichardia arborescens. In the Macareo several plant species and communities including both free-floating and emergent species occur for short periods of time. Relatively permanent constituent species include P. fasciculatum and Gynerium sagittatum which became established at the top of the levées and tolerate vigorous hydrodynamics for long periods, as well as at periods of drought. G. sagittatum has a very wide distribution in the country occupying a range of habitats from wet to very dry habitats. Those species located close to the shoreline, such as P. repens and E. polystachya, should be capable of resisting the potential uprooting during the high water levels.

In the Lower Delta, the physical factors, terrain characteristics and hydrology, that determine the establishment of plants, are similar for both channels. In the same way, the substrate textural classes are very similar with the exception of the external outer fringe, several metres in depth, where only free-floating plants may establish. The main floristic differences in this sector are between the emergent species. A few species appear to be exclusive to each

channel (Table 6.2). In the Mánamo *S. striata, Crinum erubescens, Crenea maritima*, and *Echinochloa colona* were present whilst *Hibiscus striatus, Panicum elefanthipes*, and *Tessaria integrifolia* were exclusive to the Macareo.

In contrast, the results of the study by Baattrupp-Pedersen and Riis (1999) showed that the coverage of coarse-textured substratum and substratum heterogeneity in Danish stream beds, correlated positively with coverage and diversity of mostly emergent macrophytes. Likewise Nilsson *et al.* (1989) reported a correlation between species richness and substrate heterogeneity and was at its maximum at intermediate levels of substrate fineness.

According to Fox (1992), there is uncertainty about how dependent the emergent macrophytes are on the substrate type. However, it seems clear that substratum particle size influences macrophyte colonization with respect to root depth and stability. Consequently this will affect the aquatic species diversity. The results from the study of the Macareo and Mánamo channels suggest that substrate type and the microtopography are not a limiting factor for the colonisation of emergent species such as *Panicum elephantipes* and *Tessaria integrifolia*. Instead it seem to be the regulated hydrological regime as found in the Mánamo river that maintains a permanent non fluctuating condition, which favour the establishment of floating species, excluding new species from being established. The hydrological regime of unregulated rivers, in contrast allows occasional drought as observed in the edges of other large distributaries, that establishes gradients of flooding and habitat heterogeneity.

In the Macareo river *Echynochloa polystachya* is dominant, although it is very scarce in the Upper and Middle Mánamo. Where it is only found in the large flooded area created upstream from the dam. A site which maintain in a certain extent the prior species composition of the regulated river. A common emergent species to both courses is *Montrichardia arborescens.* This species, which can only tolerate a partial flooding of 1-1.5 metres, is distributed all along the Mánamo banks, whilst in the Macareo, where the water oscillations are high, it is only found in the lower stretch of the channel, where seasonal water fluctuation is smaller (meadow MAC 5, Appendix 13).

Salinity should be considered as another important factor in addition to the river bank morphology helping to determine the distribution of meadows of emergent macrophytes in the lower river stretches. Table 6.1 shows the salinity gradient along the Mánamo river. The greatest increase in salinity was observed during the low water stage at Bagre Island (close to MAN 6), making the habitat unsuitable for the survival of freshwater species in the lower Mánamo stretch. Consequently the species composition of the few meadows encountered is

dominated by halophytic species. In the Macareo the last meadow composed of *Paspalum repens* (a non halophytic plant), is located at some 24 km upriver from the open sea while in the Mánamo the last anchored meadow (containing *P. repens*) was found at close to 34 km from the ocean. The variation in infiltration of saline water led to significant differences in the distribution of the aquatic meadows.

In this respect, the dam regulation established clear differences between the two rivers, both in the morphology-vegetation characteristics and in the species composition of the meadows along the courses. The floating mats (rafts) of vegetation behaved in different ways in the Mánamo and in the Macareo rivers. In the Mánamo the time of residence was found to be much longer whilst in the Macareo the rising water stage was associated with the uprooting and separation of rafts of aquatic species which then drifted down-river. Table 6.5 provides a comprehensive summary of the main differences and similarities between the two channels as found in this study.

Table 6.5. Summary of the main differences and similarities between the Mánamo and the Macareo rivers. Ch= channel; fresh= freshwater plants.

	Mánamo	Macareo
Upper Section		
Channel morphology	High sinuosity/narrow	Straight sections/narrow
Water oscillation	ca. 1 m - tidal regime	ca. 7 m - seasonal regime
Bank height /slope	3-4 m / 10-20 %	8-9 m / 45-70 %
Current velocity	High up to 155 cm s^{-1}	Low up to 75 cm s^{-1}
Sediment type	Sandy-loam	Sandy-loam
Salinity	Very low -3 10^{-3} g l^{-1}	0
Species diversity	Variable	Variable
Species type dominance	Floating - emergent fresh	Emergent - floating fresh
Middle section		
Morphology	High sinuosity	High sinuosity
Water oscillation	ca. 1 m	2-3 m
Bank height /slope	2-3 m / steep	3-4 m / steep
Current velocity	Up to 60 cm s^{-1}	Up to 130 cm s^{-1}
Sediment type	Silt-clayey and silt-sandy	Silt-clayey and sand/sand silty
Salinity	7 10^{-3} g l^{-1}	0
Species diversity	High	High
Species type dominance	Floating fresh	Emergent - floating fresh
Lower section		
Morphology	Sinuous wide	Sinuous to straight wide
Water oscillation	ca. 1 m	ca. 1,5 m
Bank height /slope	1-0 m	1-0 m
Current velocity	55 cm s^{-1}	Up to 120 cm s^{-1}
Sediment type	Not determined	Not determined
Salinity	Up to 8.26 g l-1	Not determined
Species diversity	Low	Low
Species type dominance	Emergent halophytes	Floating - emergent fresh

The river regulation established a number of differences among the Mánamo and Macareo rivers as seen above. In site MAN 1 extensive meadows of floating macrophytes were documented in contrast to the reduced communities of these plants found in the Macareo river edges, site MAC 1. The biomass production of the principal species, *Eichhornia crassipes* and *Paspalum repens* was investigated to establish the response of the species productivity to the river regulation.

Chapter 7 Comparative biomass production of *Eichhornia crassipes* and *Paspalum repens*

An inspection of the upper stretches of the regulated Mánamo river and unregulated Macareo river, from aerial photographs, reveals two contrasting environments, a lentic water body system with aquatic meadows extending along the edges of the Mánamo (Plate 7.1) and a dynamic fast flowing water system with no obvious floating vegetation along the edges of the Macareo.

7.1 Aims

• The aims of this chapter are to analyse the biomass production of the principal species of the floating meadows in relation to changes in physical chemical and hydrological factors, comparing the regulated Mánamo river with the unregulated Macareo river.

The original basic research hypothesis in this chapter is that the larger meadows of *Eichhornia* and *Paspalum* found in the upper stretches of the Mánamo, and rafting transported by the currents in the middle course, in contrast with the Macareo, are a consequence of changes in the physico-chemistry of the waters. This is in contrast with the Macareo river. However, the chemical component was further discarded as the water samples taken indicated similar chemical conditions as seen in chapter 5.

7.2 Methods

7.2.1 Study sites

Communities of *E. crassipes* (a free-floating plant) and *P. repens* (a floating plant) were selected on the Mánamo river, 1.5 km downstream of the dam, and on the Macareo river, 1 km downstream from where it divides from Mánamo river (location in same sites of MAN 1 and MAC 1, Fig. 6.1). The sites on the latter river were subsequently relocated several hundred of metres downriver due to removal of the floating mats by the current. The selection of a new sampling site with slightly different environmental condition and /or plants with different stage of development, could produce differences in the results, as the data might show a variant of the main plant assemblage. Junk (1973), reported the same methodological problem of site uniqueness in his study of the aquatic meadows.

7.2.2 Leaf length

The total length of the leaves (for number of leaves see below) of *E. crassipes* was measured, including both the petiole and leaf blade. In *P. repens*, only the blade length was considered. The data were divided into categories, and expressed as percentages.

PAGE

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AS ORIGINAL

7.2.3 Plant biomass production

Samples were always taken in a 2-3 metre belt from the border of the floating mats, and consisted of five samples during the period of rising water level (April to August 1994) two during high water (September and October 1994) and three during the period when the waters were receding (December 1994 and January 1995). An additional sample was taken in April 1995 at the beginning of the next phase of water level increase. Sample collection was closely linked with the collection of physico-chemical data (see chronogram in Table 5.1). Unlike in temperate climates, aquatic sampling in the tropics cannot usually be carried out isochronically (as proposed by Neiff 1990a).

A destructive sampling method was employed. According to Catchpole and Wheeler (1992), this method is very accurate and suitable for homogeneous vegetation, such as the aquatic meadows in Mánamo and Macareo. Inaccuracies are only introduced in making estimates for large areas.

At each site, five sub-samples (0.25 m^2 in area) of plant material were taken. This quadrat size was selected because of it allowed the inclusion of several individuals of *Eichhornia crassipes* (Fig. 7.1) and *Paspalum repens* in each sample, and produced an amount of material that could be processed within the available budget.

In the case of *E. crassipes*, the whole plant was collected. For *P. repens* however, only the green leaves were harvested, due to the difficulty in collecting the long stems of these floating plants (Fig. 7.1). *E. crassipes* plants were washed to remove the sediments. The material was then divided into leaves and into the submerged fraction, then oven-dried to constant weight following standard procedures.

Problems encountered during collection of plant material from aquatic macrophytes included entanglement in very dense mats. Also the collection of entire plants was not possible without loosing some root material or decomposing leaves. Similarly with *P. repens*, the semi-floating stems might be so long (up to 4-5 m) as to make the collection of the full plant very difficult.

As a consequence for *E. crassipes* biomass was measured for leaves and then for the complete plant, while in *P. repens* was measured only for leaf biomass.

All data were analysed in order to identify significant differences using the 't paired' method(Abacus Concepts StatView, 1992).

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Paspalum repens

0.25 sq.m

Eichhornia crassipes
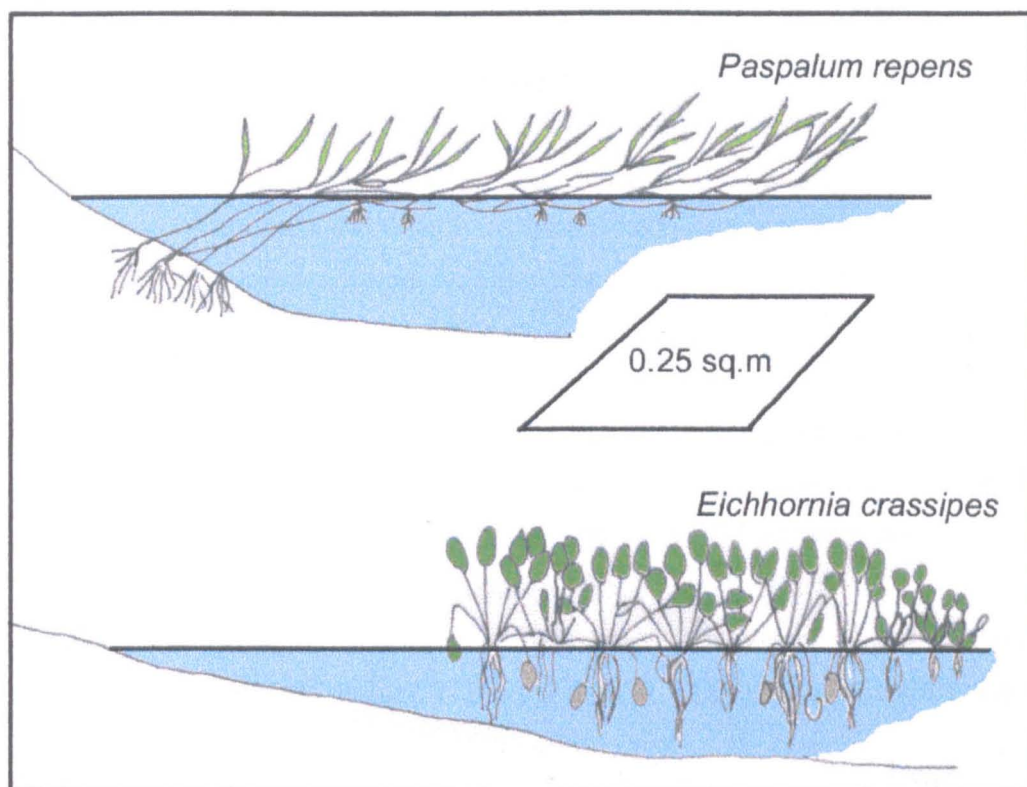
Fig.7.1. Sampling quadrat for biomass analysis.

7.3 Results

7.3.1 Size, total length and density of the leaves of *E. crassipes* and *P. repens*

Fig. 7.2 shows the size dimensions of the leaves of *E. crassipes* and *P. repens* in the Mánamo and Macareo rivers. In the Mánamo river *E. crassipes* produced longer leaves than in the Macareo throughout the entire study period. The longest leaves in the Mánamo, ranging between 90 and 120 cm, were produced during the period of rising water, from June to September. A general decrease of leaf size followed the falling waters.

In the unregulated Macareo, the same pattern can be seen, with the longest leaves (110 cm) being produced in July and August. The migration downriver of the meadows that were first selected for sampling and the selection of new meadows (see Section 3.3.5) to some extent affected the results in the Macareo. This was because from September onward, most of the leaves of the new sites did not measure more than 80 cm being a reflection of their growth cycle. The leaf sizes of between 0 to 20 cm increased from June and then subsequently decreased toward the dry season probably due to the availability of nutrients. The Macareo shows this pattern more clearly than the Mánamo.

In the case of *P. repens*, the classes of leaf length are more homogeneous, especially on the Mánamo, where there is a constant increase in the smaller length size classes. These are apparently not directly associated with the hydrological cycle of the unregulated section of the river, but rather more with the constant, regulated regime (Fig. 5.2 a). In the Macareo, this trend shows a bimodal pattern with a maximum in the month of August, falling in September, followed by an increase towards the end of the dry period. This shows a positive relation with the periods of rising and falling river water (Fig. 5.2 a).

The mean total leaf length for both species and both channels are shown in Fig 7.3 a, revealing that the values for the two species are statistically different in the two rivers (t-test $<0.0001<P<0.0051$). *Eichhornia* leaves in the Mánamo river (mean 67.8 cm, maximum 120 cm) are longer than those in the Macareo (mean 59.4 cm, maximum 110 cm). Similarly *Paspalum* leaves in the Mánamo (mean 42.9 cm) were longer than in Macareo (mean 36.8 cm). Both species show some increase in leaf length during the period of high water and a decrease during the phase of receding waters.
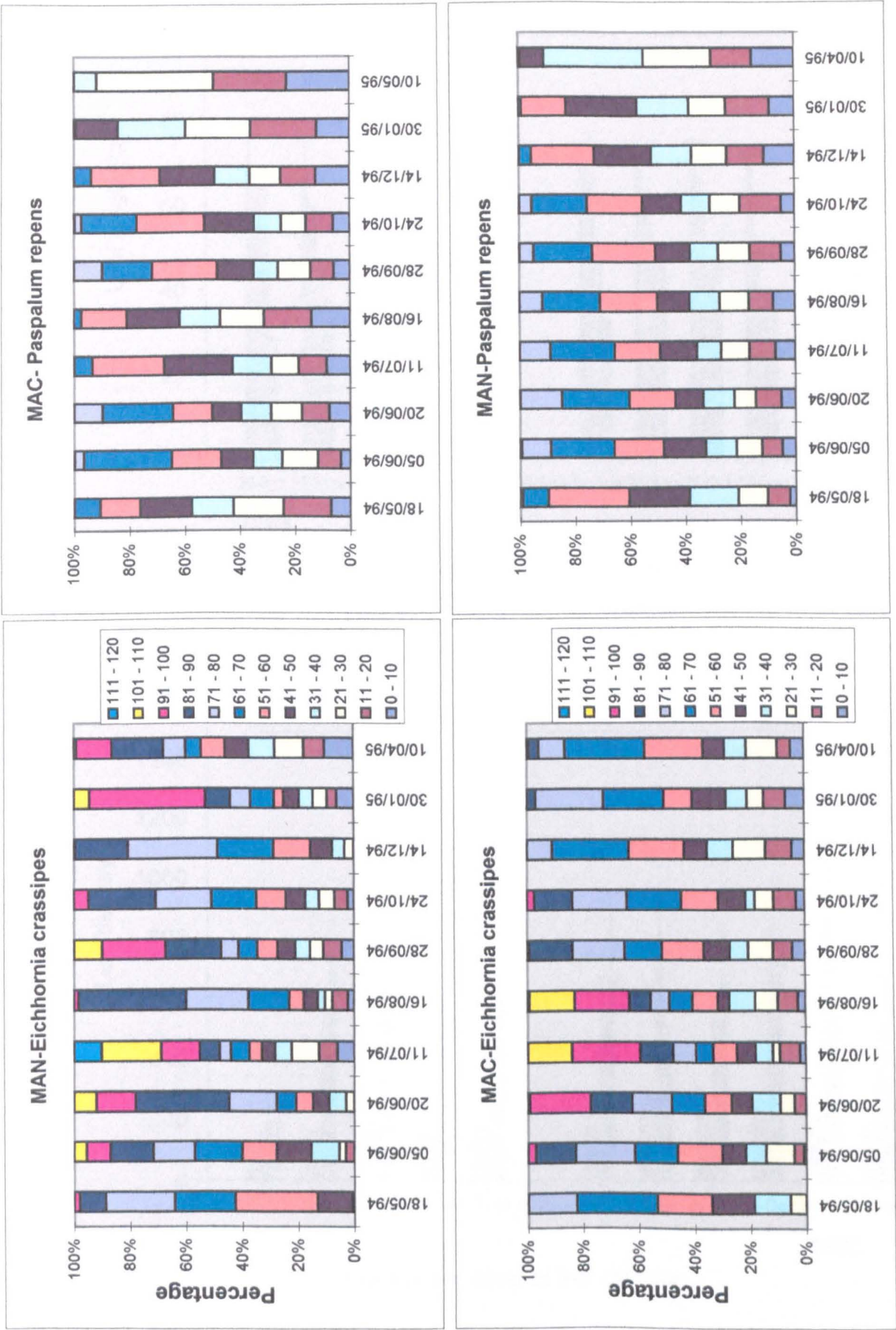
Fig. 7.2. Seasonal variation on leaves length of E. crassipes and P. repens

Density values for the *Eichhornia* and *Paspalum* leaves are shown in Fig 7.3b. There is no apparent seasonal variation in the data and the comparative values between both channels indicate no statistical differences (*t*-test 0.11<P<0.34). *Paspalum* densities in the Mánamo (mean 651.4 leaves m^{-2}) and Macareo (mean 555.5 leaves m^{-2}), showed more marked variations throughout the study period than those of *Eichhornia* (mean 173.0 leaves m^{-2}), in the Mánamo river and, mean 163.2 leaves m^{-2} in the Macareo.

7.3.2 Comparative leaf biomass production data of *E. crassipes* and *P. repens*

for leaf biomass of both species are presented in Fig. 7.4. The dry weight (DW) of *E. crassipes* in the Mánamo river was significantly higher (mean 498.1 g m^{-2}) than that of the Macareo river (mean 378.4 g m^{-2}). In both rivers the leaf biomass of *E. crassipes* increased during the rising water stage, decreased during the receding stage, and increased again at the beginning of the new rainy season. Similar results were obtained by Esteves (1981). The DW values of *P. repens* in the Mánamo are also significantly higher (mean 135.8 g m^{-2}) than those of the Macareo (mean 84.8 g m^{-2}).

7.3.3 Total biomass production for *E. crassipes*

Data on submerged biomass for *E. crassipes* showed that the dry weight (DW) in the Mánamo river (mean 370.84 g m^{-2}) was statistically higher (*t*-test, P=0.0011) than in the Macareo river (mean 259.81 g m^{-2}).

Data for total biomass showed a similar trend. Dry weight (DW) in the Mánamo river (mean 909.14 g m^{-2}) was significantly higher (*t*-test, P = 0.0002) than in the Macareo river (mean 661.03 g m^{-2}). Maximum values were obtained in the month of July (1,15 g m^{-2}), coinciding with the maximum submerged biomass and with the samples with the longest leaves (see Fig. 7.2 and 7.3a). The general tendency is an increase from the beginning of the rising water stage to the peak of the flooding period (September) followed by a steady decrease.

7.4 Discussion

7.4.1 Physical and chemical parameters

The main physical and chemical characteristics of the two rivers considered during the study period were as follows. The transparency values in the Mánamo river ranged from 10 to 140 cm, in contrast with the Macareo river, whose values varied between 10 and 65 cm (Fig. 5.8b).
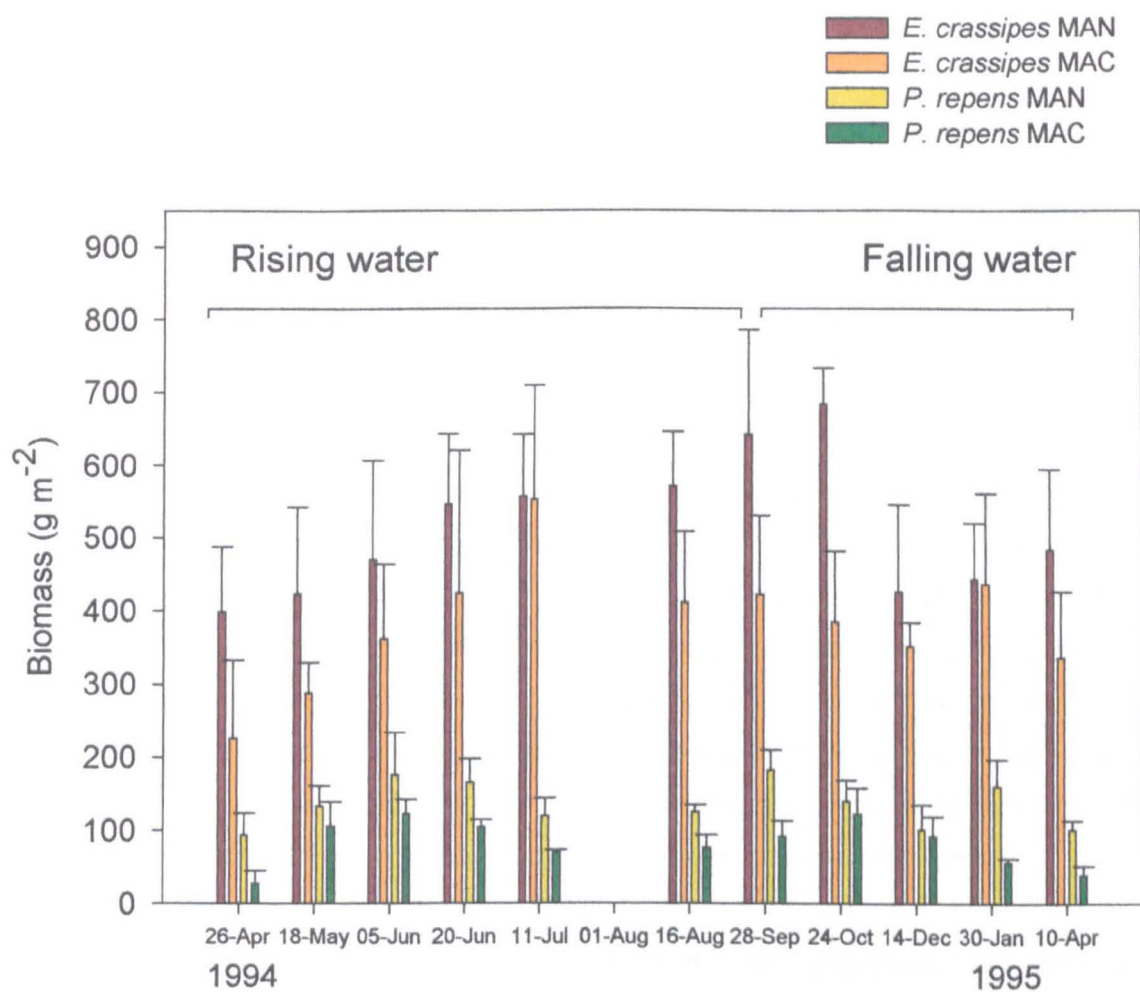
Fig. 7.4. Seasonal variation of leaf biomass production

The annual variations of the water level in Macareo was 7.5 m, compared with approximately 1.5 m in the Mánamo (see Chapter 4), which has tides influencing the entire water course below the dam twice a day (Fig. 5.2 a). Variations in the main chemical variables from low to high water conditions were as follows: DO from 5.5 to 7.4 mg l⁻¹, conductivity from 32 to 65 μS cm⁻¹, and pH from 4.8 to 7.3, phosphorus from 0 to 0.17 mg l⁻¹ and nitrogen from 0.3 to 2.3 mg l⁻¹ (refer to Figs 5.3 to 5.5). In general, these values showed no significant differences between the two water courses. Current velocity in the Macareo ranged from 0 to 75 cm s⁻¹, whilst that of the Mánamo did not exceed 55 cm s⁻¹ (see section 5.3.6).

7.4.2 Size, total length and density of the leaves of *E. crassipes* and *P. repens*

The general tendency observed in the Mánamo and Macareo is the increase of the leaf size with the rising water period and the decreasing with the receding water stage. Inconsistencies such as the second peak of leaf size increase seen in *P. repens* in the Macareo may be due to a change in sample site following the uprooting of the meadow (29 Sept), caused by the sudden drop of 30 cm, in water level. This occurred a few days earlier, as seen in Fig. 5.2.b.

Few data are available concerning the proportion of different leaf sizes and their variation along with the seasonal fluctuation associated with the hydrological cycle. The association of the relative growth rate (RGR) and the leaf elongation has been well documented (Lambers *et al.*, 1998). Our results show that at least in the Mánamo, longer leaves occur (*Eichhornia*) than recorded in the data provided by Lallana (1980). But Lallana's data set was for a natural pond of a Middle Paraná River (Argentina), where the leaves showed mean maximum lengths of 52.7 (± 12.0) cm. Also Boyd and Scarbrooks (1975) reported mean maximum lengths of 78 (± 7.5) cm, after 4 months of intense fertilisation with N-P_2O_5-K_2O, in artificial ponds.

The densities found in our plots are higher than those documented by Boyd and Scarbrooks (1975) (115 stem m²). Their highest fertilisation treatments are similar to those reported by Lallana (1980) (156-420 stem m²). They are much lower than the range of 828 to 1,050 stem per m² observed by Raghuveer *et al.* (1984) in a natural pond of the Yamuna River in India. The stem density is so high in the Mánamo plots that a physical limit has probably been reached.

7.4.3 Comparative leaf biomass production of *E. crassipes* and *P. repens*

Total leaf biomass production of *E. crassipes* from the MAN site was 5,645 kg m⁻², which is significantly higher (*t*-test, P=0.018) than the 4,195 kg m⁻² recorded from the MAC site, in spite of the high standard deviation of each sample. Results for *P. repens* showed an even greater difference: 1.5 kg m⁻² from MAN, compared with 0.91 kg m⁻² for MAC (*t*-test, P=0.004).

The high current velocity that was reached at the beginning of July (75 cm s^{-1}) and the speed with which the waters rose in July and receded during September-October, removed part of the *E. crassipes* and *P. repens* communities from the MAC, necessitating the selection of a different sampling site. This new site produced values for *E. crassipes* biomass similar to those of the MAN in July and October of 1994 (Fig. 7.4).

The water chemistry is similar in both channels for the stretch of the river considered as seen in chapter 5. Rodríguez and Betancourt (1999) found no significant correlation between the biomass production of *E. crassipes* and the water nutrient content in their survey of a floodplain lagoon in the Middle Orinoco River. This was in an aquatic environment resembling the physical conditions in the Mánamo. We may suggest therefore that it is the hydrodynamic factors that bring about the observed differences in the biomass between the two rivers.

Two aspects seem worthy of particular comment:
1. The high water flow in the MAC may reduce the uptake and the cycling of nutrients in the roots of the macrophytes as suggested by Chambers *et al.* (1991) and Sand-Jensen and Pedersen (1999), as well as from the sediments of the floating mats of *E. crassipes*, as shown by Carignag and Neiff (1992) for the Paraná River.
2. The rapid variation in water level and in peak flows modifies the habitat where the communities of *Paspalum repens* are rooted.

As pointed out by Reddy *et al.* (1999), phosphorus retention by plants in stream systems is dominated by physical processes such as flow velocity, discharge and water depth.

In contrast to the results of this study Maine *et al.* (1999) reported no significant differences between the total biomass production of *E. crassipes* in a lotic and lentic environment of the Paraná river system in southern South America. The authors, however, do not show the magnitude of the hydrological differences between the habitats.

Rooted plants growing in such conditions must elongate their shoots continuously, to keep the leaves floating. They may grow at a rate of 20 cm day^{-1} in the Amazon system (Junk, 1986) or even more in the case of the stems of *Nymphoides* that may elongate some 30 cm daily when submerged, in the Paraná system (Neiff 1986). Thus a number of researchers suggest that is the flow dynamics which prevent the plants from reaching their maximum development. Samples of well developed plants taken from lentic waters of the Macareo river showed similar biomass levels to those of the Mánamo river. Raghuveer *et al.* (1984) found analogous results in their comparisons of a pond habitat of standing waters, which showed a greater number of plants, higher densities of leaves per sq. metre, and higher biomass

productions, than in flowing water environments. Likewise Robb (1989), obtained higher biomass, number of species per plot and number of stems per sq. m in impounded dikes, with no flowing water conditions vs. undiked wetlands connected to the Lake Eire. Mitsch and Gosselink (2000), discuss the Robb (1989) results on the basis of:

1. The coastal fluxes may be serving as a stress as well as a subsidy on the macrophytes;
2. The open marshes may be exporting a significant amount of their productivity; and
3. The diked wetlands have a more predictable hydroperiod.

7.4.4 Total biomass production for *E. crassipes*

Data for total biomass showed a dry weight (DW) in the Mánamo river (mean 909 g m^{-2}) which was significantly higher (*t*-test, P = 0.0002) than in the Macareo river (mean 661 g m^{-2}). Maximum values were obtained in the month of July (1,150 g m^{-2}), coinciding with the maximum submerged biomass and with the samples with the longest leaves (see Fig. 7.2 and 7.3a). The general tendency is an increase from the beginning of the rising water stage to the top of the flooding period (September) followed by a steady decrease.

Comparing the results, *E. crassipes* mean biomass production for the Mánamo river for other environmental conditions (Table 7.1) is smaller than that reported by Penfound (1956), Lallana (1980), Esteves (1981), as an average from six reservoirs of Sao Paulo State, Maine *et al.* (1999), Rodríguez and Betancourt (1999) in a floodplain lagoon of the Orinoco River.

Our results for the Macareo river are similar to those presented by Sahay and Sinha (1970), 720 g m^{-2}. Most of the measurements in the previously mentioned studies have been taken from meadows in standing waters, with only a few in flowing water environments. However the values of biomass production reported in the literature show a wide range of variation, with values as high as 2,213 g m^{-2} (Lallana 1980) and as low as 298.2 g m^{-2} (maximum values in a very nutrient poor environment) found by Schiavetti *et al.* (cited in Camargo and Esteves, 1995). Likewise Da Silva (1990) cited in Camargo and Esteves (1995), indicated a wide variation between 380 and 1480 g m^{-2} in several lentic environment in the Pantanal region in Brazil.

Ours results from *Paspalum repens* which yield a biomass values ranging from 0.9 to 1.5 kg m^{-2}, are comparable with data presented by Junk and Piedade (1993) for similar species in the Amazon Basin.

Table 7.1. Biomass production for *E. crassipes*.

Biomass g m^{-2}	Source	locality	Habitat
298	Schiavetti et al. in press in Camargo and Estevez, 1995	Preto river	Lotic
661	This study	Upper Macareo	Lotic
720	Sahay and Sinha, 1970	India Sub-Continent	Lentic
380-1,480	Da Silva (1990) in Camargo and Estevez, 1995	Pantanal-Brazil	Lentic
909	This study	Upper Mánamo	Lotic
1,020-2,213	Lallana, 1980	Middle Paraná	Lentic
1148	Esteves, 1981	Sao Paulo State	Lentic
1200	Rodriguez and Betancourt, 1999	Middle Orinoco	Lentic
1276	Penfound , 1956	Louisiana USA	Lentic
1318	Maine et al., 1999	Middle Paraná	Lentic

7.5 Final remarks

In tropical regions, cyclic variation of the biomass of aquatic communities through the year is not as obvious a phenomenon as in temperate regions (Esteves, 1988). Biomass production values show a large degree of variation as a function of the ecological factors of the environment, acting in conjunction with such factors as variations in water level, availability of nutrients, turbulence of water column and temperature (Camargo and Esteves, 1995). Moreover Menezes (1988, cited in Esteves, 1988) pointed out that ambient factors, as well as water level fluctuations, may produce dramatic differences in the productivity of aquatic such plants as *Nymphoides indica* in the Lobo reservoir in Brazil.

Mitsch and Gosseling (2000) presented abundant evidence regarding the positive correlation of primary productivity with flowing conditions vs. stagnant waters. However, there must be an upper limit to productivity, where the positive effect of nutrient input, is counteracted by the negative effects of changes in river flow. The data collected, showed a higher macrophyte production in the regulated river against the unregulated river, and also suggested that the hydrodynamic factor plays an important role in the plant development as proposed by Mitsch and Gosselink (2000). Likewise the physical river environment has a major impact on the development and growth of submerged macrophytes (Scultorpe, 1967; Grasmuck *et al.*, 1995). The relative coverage of the species (not quantified in this study) is, however, clearly higher in the lentic habitat of the Mánamo river.

The changes in hydrological patterns that result from river regulation has led to the formation of extensive meadows of floating and emergent species in the upper sectors of Mánamo

river. The combination of reduced water level oscillations and currents dynamic, plus the more suitable habitat constituted by the large sand bars has promoted these alterations. This increase in the total biomass of the riverine community after the river regulation, is seen not only in the upper section but also in the lower stretches of the river, where communities of mangroves thrive (chapter 8).

Chapter 8 Mangroves community changes induced by the dam construction

Mangrove communities are characteristic forests formations found in coastal aquatic habitats within the tropics. The evidence for expanding communities of mangroves associated with salt water in the middle and lower stretches of the Delta distributaries, was researched - possibly as a consequence of the Mánamo river regulation.

8.1 Aims

- To document the spread of upriver colonisation of mangrove communities resulting from changes in freshwater flow following the construction of the Mánamo Coffer-dam in 1965.
- To document the dynamics of the salinization process by measuring the ionic relations of interstitial soil water and plants along transects specially where at present, mangrove and non-halophytic aquatic communities are found within the same habitat.
- To ascertain the correlation between floristic composition and soil and plant ion contents.

The research hypotheses are

1. The dam construction has extended the salinity zone upriver along the Mánamo river with a consequent increase of the soil salinity along the river margins.
2. The change in soil condition favoured the colonisation of mangroves further upriver in the Mánamo river

8.2 Methods

8.2.1 Study sites

Vegetation composition and soil chemical properties were studied at selected sites in non disturbed areas in the upper and lower sections of the river (Fig. 8.1). Specific sites were selected based on the availability of aerial photographs before and after the construction of the dam. Site 1 is located in the upper section, a few kilometres downstream from the dam (09° 01' 34" N and 62° 03' 06" W) and is characterised by a mid-stream island. Site 2 is located in the lower section in a concave sector of the Mánamo river (09° 31' 50" N and 62° 35' 06" W), where sediments transported by the river settle to form a beach with shallow waters. The sandbar has been colonised by emergent aquatic plants,
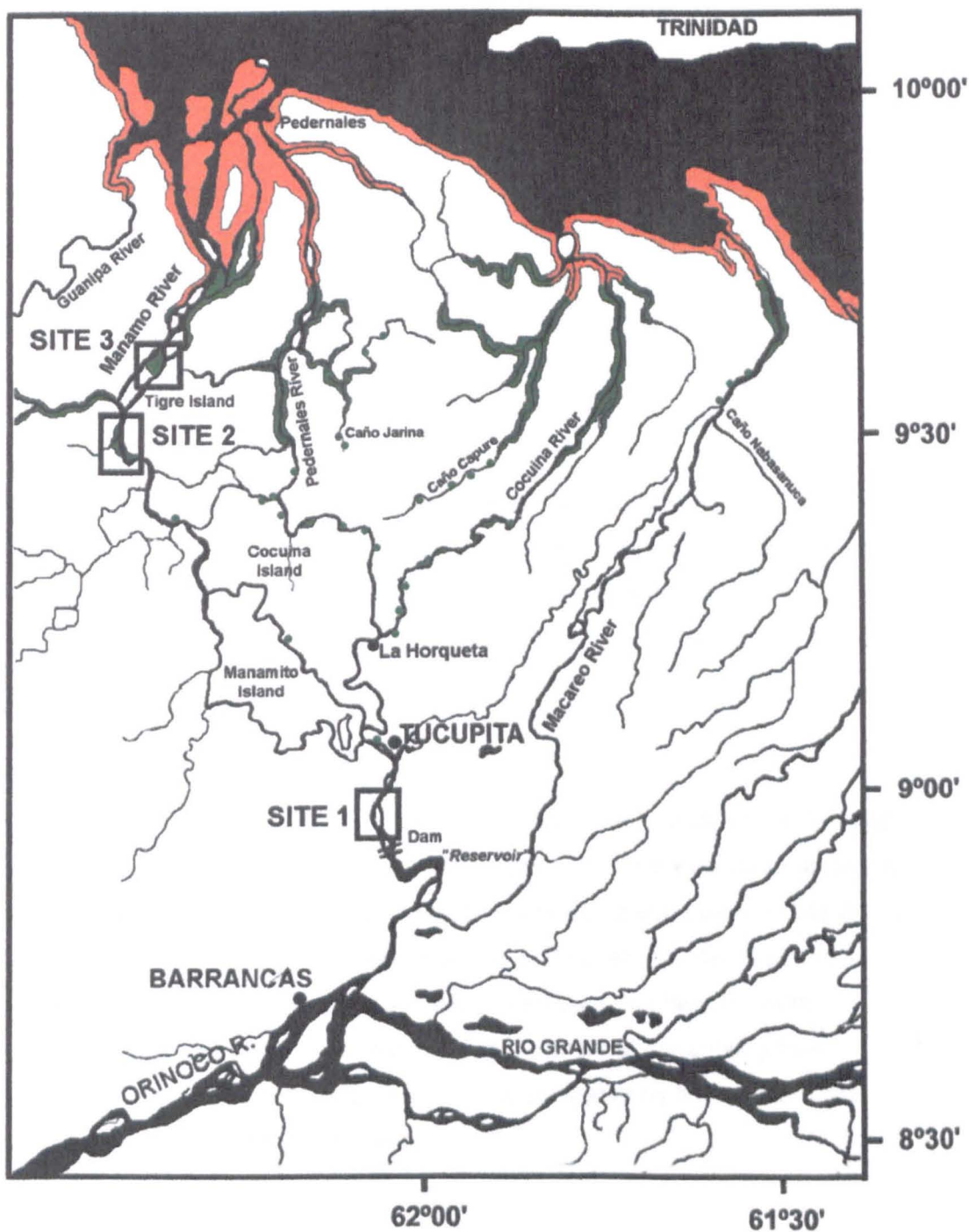
Fig. 8.1. Study sites, previous and present distribution of mangrove communities.

🟧 Previous distributions
🟩 Present distributions

mainly *Paspalum repens* and *Polygonum acuminatum*. Site 3 is located further downstream, on the right bank of Isla Tigre in the main river stream (09° 38' 23" N and 62° 23' 26" W). Sedimentation at this site has allowed narrow marshes of emergent, aquatic plants to develop which are dominated by *Ludwigia octovalvis* in the deeper areas and *Echinochloa polystachya* in the shallower parts (see also description of site MAN 3 and MAN 4 in chapter 6).

8.2.2 Geomorphological evolution

The evolution of riverine and associated landforms and vegetation ensembles over the past 64 years was evaluated at each site using aerial photographs taken in 1932, 1965 and 1982 and by a field survey in 1996. Changes in the distribution of forest and marshes and sedimentation patterns were determined for three periods 1932-1965 (before dam construction), 1966-1982 (except site 1), and 1982 to 1996. Aerial photographs were taken from the following missions: 'Venezuelan Aerial Survey' (1932, scale 1:20,000); Servicio Autónomo de Geografía y Cartografía Nacional de Venezuela, including missions 040510 (1965, scale 1:25,000) and 040543 (1982, scale 1:20,000). Plant community coverage and geomorphological features were identified using stereoscopic analysis of paired aerial photographs and areas measured with a planimeter. The total area analysed was about 640 ha at each site.

8.2.3 Vegetation analysis

A series of 100 m long transects, at right angles to the river fringe, were established through the mixed mangrove communities at sites 2 and 3. Vegetation structure was documented in 100 m^2 plots established every 10 m along the transects, there being eight plots at site 2 and seven at site 3 (Fig. 8.2). In the plots species composition and cover (estimated as the breast-height diameter, dbh) of woody species with more than 2 cm in diameter were recorded. Three main vegetation types were distinguished: marshes, comprising free-floating or emergent aquatic plants; swamp forests on soils saturated by freshwater, and mangrove forests on soils saturated by saline waters.

8.2.4 Sediments analysis

Sediment/soils samples were collected at two approximate depths (0-30 and 80-150 cm) every 10 m on each transect. The sample sediments were transported to the laboratory in an ice box. A sub-sample was collected in a plastic syringe and interstitial water was obtained by pressing the syringe according to standard procedure.
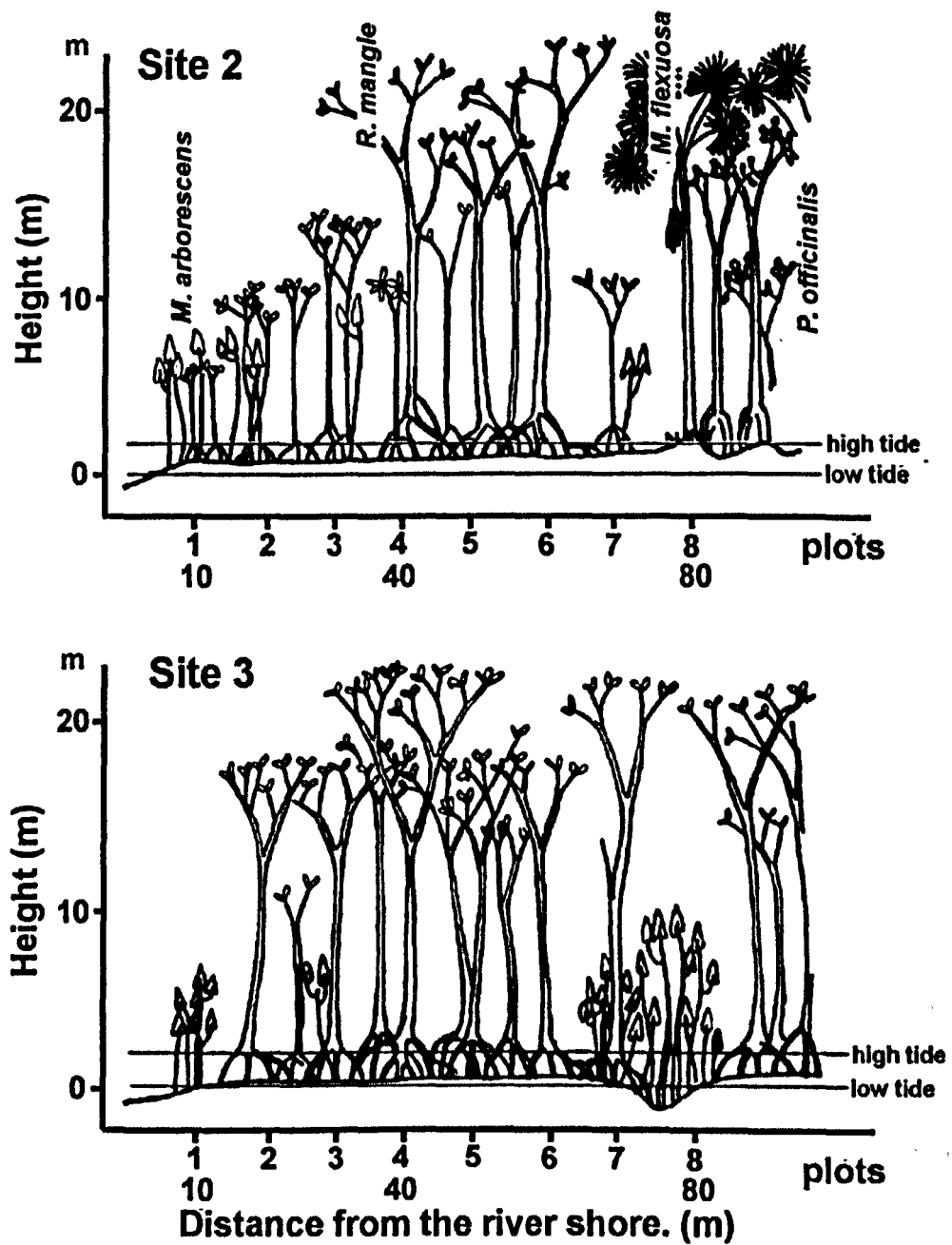
Fig. 8.2. Vegetation profiles in transects of site 2 and site 3.

8.2.5 Chemical analysis in water

Water samples were analysed for sodium, magnesium, chloride and sulphate to determine the influence of sea water. In addition, leaf samples of the dominant species in each transect were collected for measuring their content of soluble sodium, potassium and magnesium using atomic absorption spectrophotometry. Ion concentration data were analysed using parametric one-way analysis of variance and a Kruskal-Wallis test (Abacus Concepts StatView, 1992). Analytical procedures have been described elsewhere (Medina and Francisco,1997).

8.3 Results

8.3.1 Fluvial dynamics and vegetation cover

Site 1 was not photographed between 1965 and 1982. However, available aerial photographs show that during the period between 1932 and 1992 an extensive sandbar developed which increased the surface of the island in the centre of site 1 by 30%. On this sandy soil, secondary succession has lead to the formation of a deciduous forest, 15-25 m in height, with species characteristic of the Upper Delta region such as *Ceiba pentandra*, *Ocotea* sp., *Inga* sp, *Spondias mombin*, *Triplaris* sp and *Licania densiflora* (Huber and Alarcón, 1988).

Site 2 had, about 31.4 ha of rooted emergent marsh vegetation in 1932 (Table 8.1). By the end of 1965 circa 7 ha of sandbars had developed and the marsh cover increased to 39.6 ha. Swamp forest increased by 14 ha with denser tree cover developing behind a belt of shrub communities along the bank. By 1982 marsh vegetation was reduced to about 25 ha and the forested area was reduced by about 12 ha. Simultaneously, mangroves developed in this area of the river and occupied 10 ha in two narrow littoral bands, occupying sparse terrestrial vegetation and marsh areas. Currently (third period), 22 ha of marshes of floating and emergent species are present along a homogenous band of mangroves that follows the natural waterway. Between 1965 and 1996, the mangrove area increased by almost 4 times from 10 to 39 ha (Fig. 8.3).

At site 3 sandbars on the existing islands were reduced by 62 ha from 1932 to 1965. These changes were associated with an expansion of mangroves (34 ha) and by erosive processes, represented by a decrease in the cover of marshes (25.6 ha), and an increase in open water (54.4 ha) (Table 8.1). The total increase in mangrove area represented 31.8% of the total area surveyed. They replaced areas covered by marshes and, to a lesser
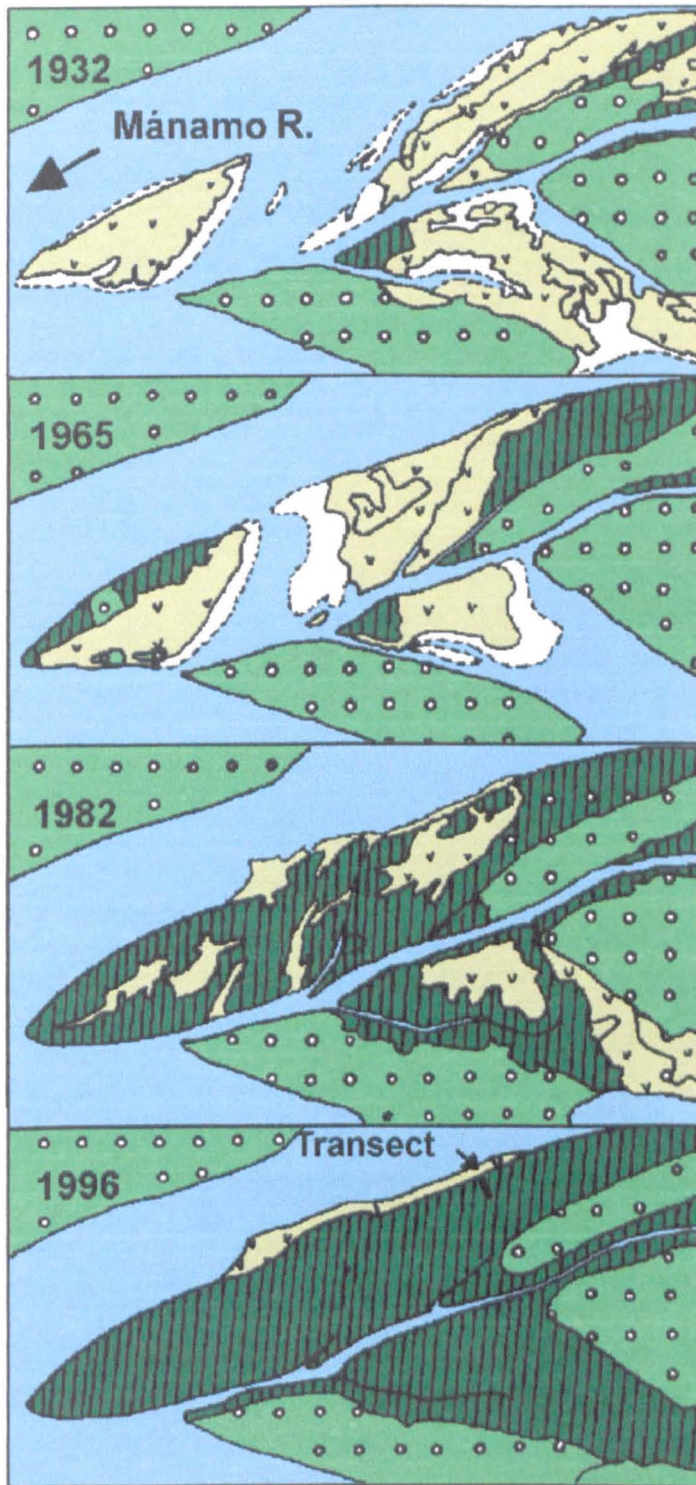
Fig. 8.4. Distribution of plant communities in site 3. Light green: meadows of aquatic plants; middle green: swamp forest; dark green: mangrove communities; dotted lines: areas of sand bars.

degree, swamp forests. Mangrove areas adjacent to swamp forests on the east shore, already present in 1932, did not undergo significant change.

Table 8.1. Area (ha) of the main geomorphic and vegetation features of the study sites.

Period	1932	1965	1982	1996
Site 2				
Swamp forest	408.4	422	414	402.2
Mangroves	0	0	10.5	39.2
Marshes	31.4	39.6	25.2	22.0
Open sand bars	0	7.2	8.8	0
Water surface	202.0	173.2	183.4	175.2
Total	641.8	642.0	641.7	641.6
Site 3				
Swamp forest	179.8	180.8	175.2	170.4
Mangroves	15.6	49.6	176.4	261.6
Marshes	114.8	89.2	61.6	12.6
Open sand bars	94.4	32	14	0
Water surface	235.6	290.0	214.0	196.4
Total	640.2	641.6	641.2	641

During the second period (1965-1982) mangrove communities expanded further, by about 126 ha in site 3. Swamp forest area decreased slightly (by 5 ha), while there were also reductions of marshes and non-vegetated sand bars. The total area covered by mangroves increased to 176.4 ha. During the last 14 yrs (1982-1996), the area of riverine marshes decreased to 12 ha. Since 1932, the marshes decreased from 19% to less than 2% of the total area surveyed. The small scarcely visible, channels that flow through the island are remnants of former larger water ways (Fig. 8.4). The arboreal vegetation is presently dominated by *Rhizophora mangle*.

Summarising, mangrove cover at sites 2 and 3 increased markedly during the last thirty years, after the construction of the Mánamo river dam. The increase was more pronounced at site 3, north of Isla Tigre, but changes in site 2 upriver, south of Isla Tigre, were more dramatic because mangrove communities appeared where they had not grown previously.

Estimates of mangrove expansion at sites 2 and 3 clearly show the effect of changes in river hydrology caused by dam construction (Table 8.2). In site 2 the expansion rate (1983-
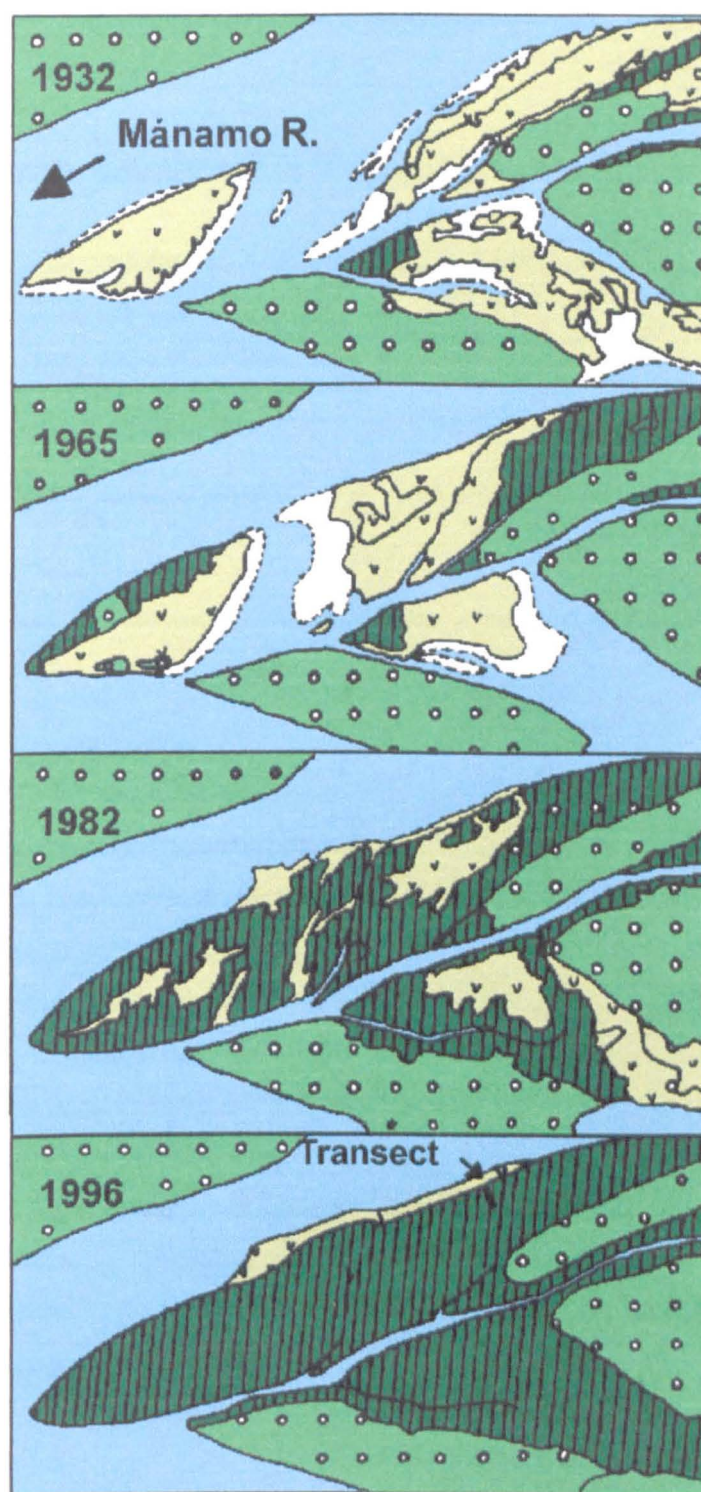
Fig. 8.4. Distribution of plant communities in site 3. Light green: meadows of aquatic plants; middle green: swamp forest; dark green: mangrove communities; dotted lines: areas of sand bars.

1996) reached 2.2 ha yr^{-1}, compared to 1 ha yr^{-1} at site 3 before 1965. At site 3 the rate of increase was 7.9 ha yr^{-1} between 1965 and 1982, and has remained high, at about 6 ha yr^{-1}, during the last 14 years.

Table 8.2. Mangrove community expansion rates in the studied sites.

Period	Years	Increase (ha)	Rate (ha yr^{-1})
Site 2			
1983-1996	13	28.7	2,2
Site 3			
1932-1965	33	34	1,0
1966-1982	16	126,8	7,9
1983-1996	13	85,2	6,6

8.3.2 Floristic and structural composition

The mangrove formation at site 2 in 1995 consisted of a 100 m wide belt parallel to the river shore. The outermost plots were dominated by *Montrichardia arborescens*, a herbaceous Araceae, developing a sturdy trunk up to 8 m tall (Table 8.3). This species formed a narrow fringe, less than 10 m wide with 80% cover, disappearing gradually inland and being substituted by *Rhizophora mangle* (Fig. 8.3). Further inland, other species appeared associated with mangroves; *Crinum erubescens*, a Liliaceae, *Tabebuia* aff. *aquatilis*, an Bignoniaceae endemic to the swamp forests along the Orinoco and Amazonas rivers and *Pterocarpus officinalis,* a Papilionaceae, one of the commonest trees in this region. Towards the interior, where tidal flooding is limited, mangrove communities were substituted by species characteristic of fresh water swamp forests such as *Mauritia flexuosa* (Arecaceae) and *Symphonia globulifera* (Guttiferae) (Huber and Alarcón, 1988). The profile also shows that *Rhizophora* individuals increased in diameter and height (up to 25 cm and 20 m respectively) towards the middle section of the transect.

Table 8.3. Composition, cover and species density in Site 2.

Transect point	1	2	3	4	5	6	7	8
Rhizophora spp.								
Cover (%)	20	50	80	80	70	100	60	-
N°. Ind/ 100 m^2	1	5	8	5	5	5	5	-
Average tree dbh (cm)	5	10	15	25	20	25	15	a
Average tree height (m)	5	15	20	25	20	25	10	-
Montrichardia arborescens and other species								
Cover (%)	80	50	20	b	c	d	-	10 e
N°. Ind/ 100 m^2	25	20	21	-	-	-	-	-
Average tree dbh (cm)	8	8	15	-	-	-	10	-
Average tree height (m)	8	8	10	-	-	-	6	-

[a] Trunk of dbh > 70 cm. In periphery.
[b] _Tabebuia aquatitis_ (30%).
[c] _Pterocarpus officinalis_ (30%)
[d] _Crinum erubescens_
[e] _Mauritia flexuosa_ (60%).
P..officinalis (30%)

At site 3 the arboreal community was chiefly dominated by _Rhizophora_ sp, whose dominance was shared with _M. arborescens_ at either end of the transect (Table 8.4). This pattern was associated with an internal channel carrying part of the freshwater from the main river (see profile in Fig. 8.2). However, beyond this channel _Rhizophora_ sp. became dominant again and covered the rest of the island. Mean and maximum dbh values of mangrove trees in this transect were larger than those of site 2 with a mean dbh of 30 cm, and a maximum height of 25 m.

8.3.3 Interstitial water ions
The salinity of interstitial water was higher at site 3 than at site 2 as evidenced by the concentrations of Na^+, Mg^{2+}, Cl^- and SO_4^{2-} in interstitial water (Fig. 8.5, note differences in y-axis). Sodium concentrations at both soil depths at site 2 increased from the river fringe towards the middle of the transect, and decreased again in the last two sample points. Highest values were always below 2 mM. At site 3, sodium concentrations were higher in the deeper samples and increased steadily from the river fringe towards the interior of the island. A similar but much weaker trend was observed in the upper soil layer. At the river fringe in site 3, sodium was always below 5 mM, while maximum concentrations were found between 60 and 80 m from the shore and reached 10 mM at the surface and 30 mM below 80 cm (Fig. 8.5).
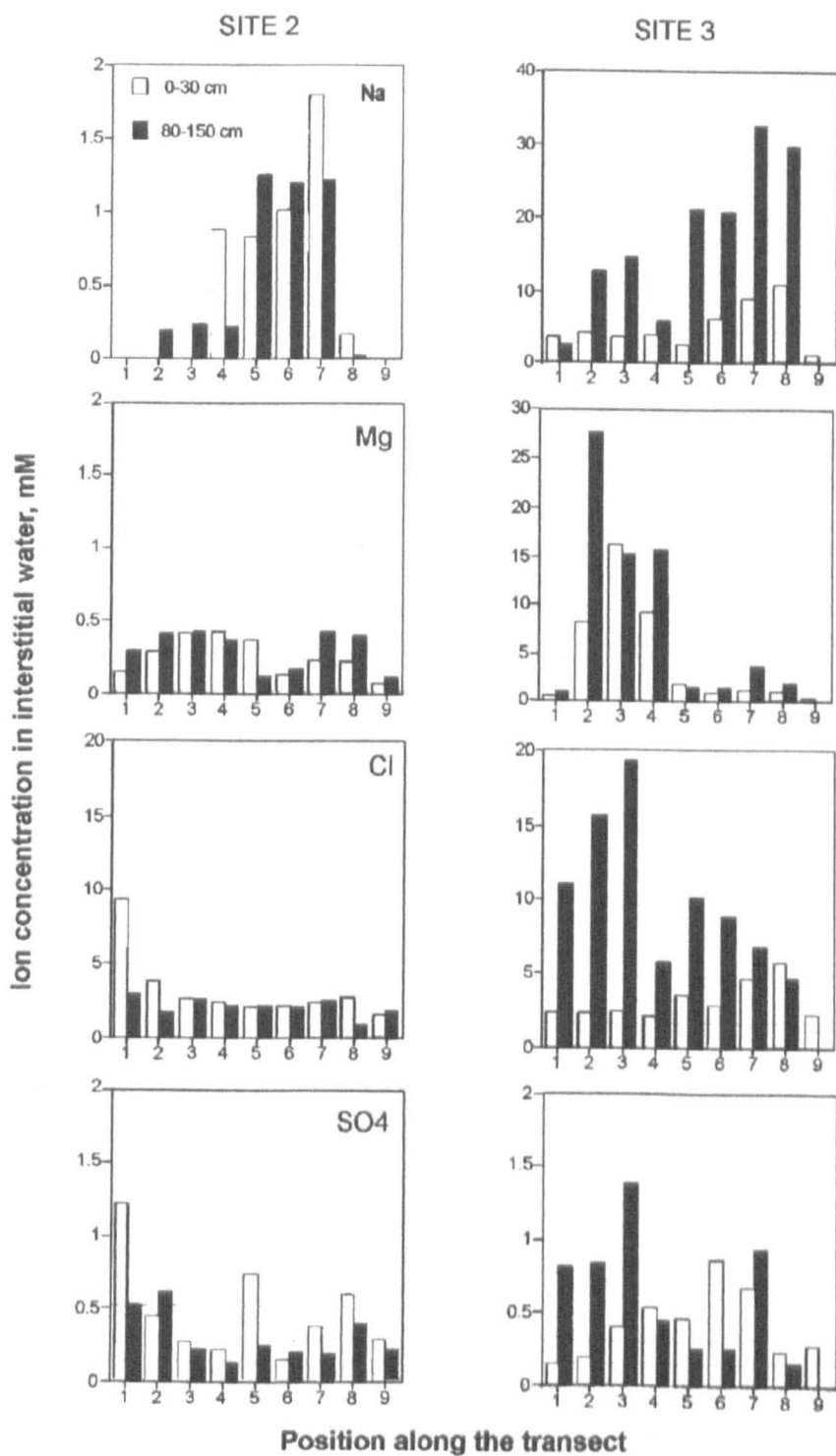
Fig. 8.5. Ion concentration in interstitial water from Sites 2 and 3.

Table 8.4. Composition, cover and density of the species in the Site 3.
+= few individuals.

Transect point	1	2	3	4	5	6	7
Rhizophora spp.							
Cover (%)	5	100	100	100	100	100	20
N°. Ind/ 100 m^2	5	5	8	5	8	3	1
Average tree dbh (cm)	5	20	15	30	20	20	30
Average tree height (m)	2	20	20	25	20	20	25
Montrichardia arborescens							
Cover (%)	95	-	+	-	-	10	100
N°. Ind/ 100 m^2	40	-	3	-	-	8	30
Average tree dbh (cm)	8	-	3	-	-	5	8
Average tree height (m)	5	-	8	-	-	5	10

Magnesium was between one and two orders of magnitude lower in site 2 as compared to site 3. In both transects concentrations tended to be similar at both soil depths. At site 3, samples from plots 2-4 had much larger concentrations than both river fringe and samples from interior areas, plots 4-8 (Fig. 8.5). The concentrations of sodium and magnesium did not follow the same pattern in any of the sites sampled.

Chloride was always higher than sulphate in both sites (2 and 3) (Fig. 8.5). The upper soil layers had similar chloride concentrations in both transects, but at site 3 deeper soil layers had chloride concentrations 2-4 times higher in interstitial water. Also, chloride concentrations in this transect tended to be higher near the river margin.

8.3.4 Plant cation content
In _Rhizophora_ sp sodium was the dominant cation in leaf tissue at both sites (Fig. 8.6). In the lower salinity site 2, leaf sodium concentration along the transect increased landwards, while potassium and magnesium remained at similar levels. In the higher salinity site 3, the concentration of measured cations was similar throughout the transect. Therefore, Na$^+$/K$^+$ molar ratios increased steadily along the transect from around two to more than six in site 2, while in site 3 ratios were above three in plots 1 and 6 and around 6 in the rest.

Rhizophora sp.

Montrichardia arborescens

Site 2

Site 3

Position along the transect
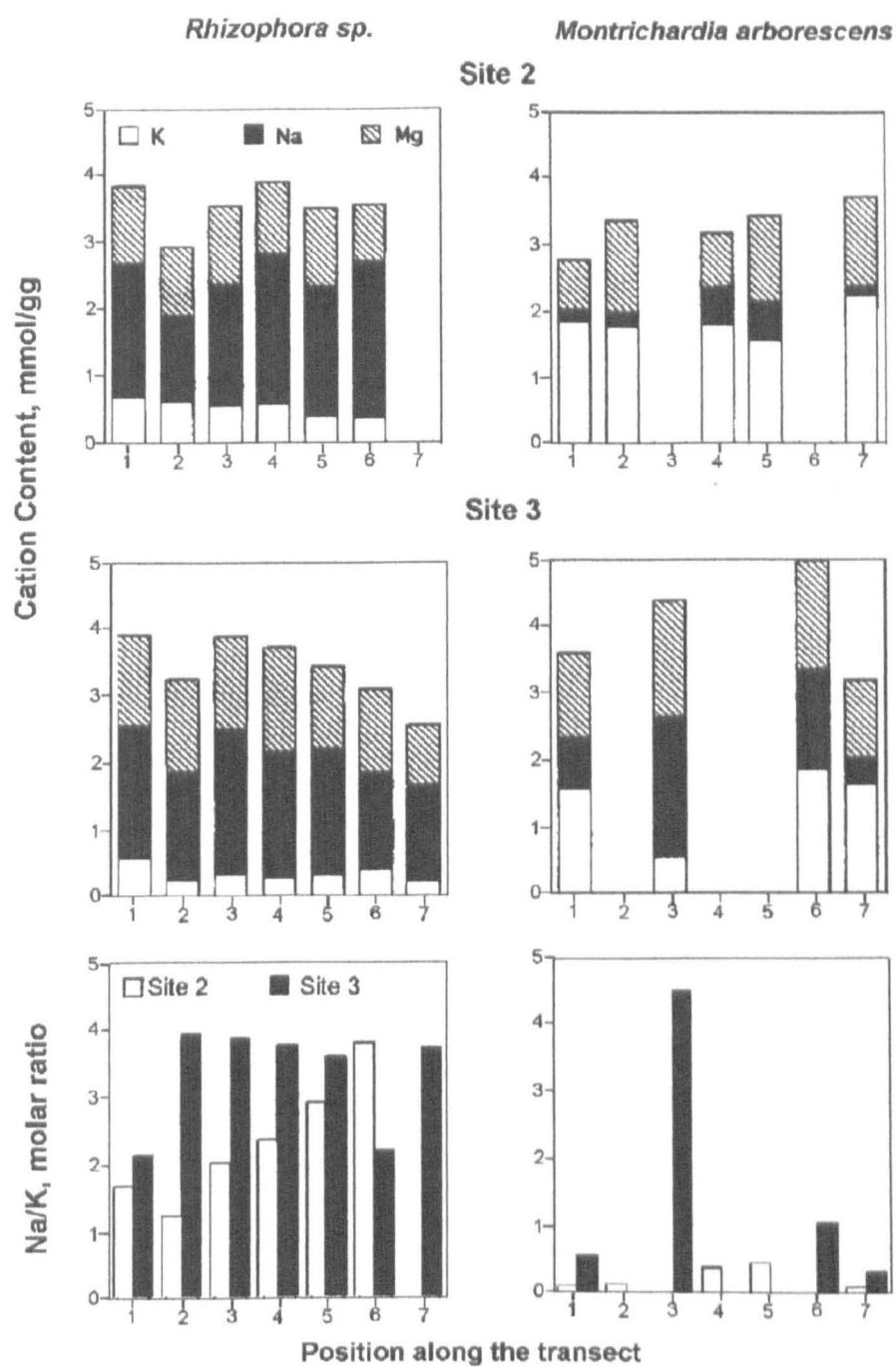
Fig. 8.6. Cation concentration and Na/K ratios of Rhizophora sp and Montrichardia arborescens

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Montrichardia arborescens showed a contrasting pattern in cation concentration and molar Na^+/K^+ ratios (Fig. 8.6). At the lower salinity site potassium was the dominant cation, being 4-8 times more concentrated than sodium. At site 3 however, sodium increased markedly in the middle positions of the transect, reaching similar or higher concentrations than potassium. Magnesium showed a slight increase from site 2 to site 3. The Na^+/K^+ molar ratios were below one along the transect except for sample 3 at site 3. Such soil conditions are less favourable for the growth of this species. Other non-halophyte species were found only in site 2 (*Crinum erubescens, Pterocarpus officinalis* and *Mauritia flexuosa*). Their Na^+/K^+ ratios varied from 0.01 to 0.24 indicating that these species are truly non-halophytes. Although they may be found growing along with *R. mangle*, they are using the upper, less saline soil layers as a source of nutrients and water (see Fig. 8.5).

The average cation concentrations of interstitial water were higher at site 3. Within each site, concentrations increased with depth (Table 8.5). The anion differences between sites were significant only at the deeper sediment layers. In water samples from 0-30 cm depth the site 3/site 2 ratio was nine for sodium and seventeen for magnesium. At a depth of 80-150 cm, these ratios increased to twenty-eight for both cations. Anion ratios were close to one (unity) for upper sampling level, while at the deeper level values reached 4.9 and 2.1 for chloride and sulphate, respectively. Increases of sodium and chloride at site 3 were far more pronounced than those of sulphate.

Changes in the ion concentration of leaf tissues were more conservative. Average values in each transect indicate that in *Rhizophora* sp, concentrations of sodium and magnesium remained at a similar level, while in *M. arborescens* only sodium increased significantly at site 3. Leaf concentration of potassium was significantly higher in *M. arborescens*. Increasing salinity lowered the potassium concentration in both species (Table 8.6).

Table 8. 5. Average concentrations (mM) of ions in interstitial water and plant tissues of low (Site 2) and high (Site 3) salinity Sites and Site 3/Site 2 ratios. Within columns for each sample type numbers followed by the same letter are not statistically different (Fisher's Protected Least Significant Difference, P=0.05). Variance analysis for plants confirmed using a non-parametric test (Kruskal-Wallis test).

Sample		n	Na^+	Site 3/ Site 2	Mg^{2+}	Site 3/ Site 2	Cl^-	Site 3/ Site 2	SO_4^{2-}	Site 3/ Site 2
Intertitial water										
(0-30 cm)	Site 2	9	0.52a	9	0.25^a	17	3.25a	0.9	0.47ab	0.9
	Site 3	9	4.93a		4.30^a		3.00a		0.42a	
(80-150 cm)	Site 2	9	0.48a	28	0.30^a	28	2.09a	4.9	0.30b	2.1
	Site 3	8	13.37b		8.45b		10.20b		0.63c	

		n	K^+	Site 3/ Site 2	Na^+	Site 3/ Site 2	Mg^{2+}	Site 3/ Site 2		
Leaf tissues										
Rhizophora sp	Site 2	6	0.6a	0.6	1.9a	0.9	1.1a	1.2		
	Site 3	7	0.4a		1.8a		1.3a			
M. arborescens	Site 2	5	1.8b	0.8	0.3b	3.7	1.1a	1.3		
	Site 3	4	1.4c		1.2c		1.5a			
Kruskal-Wallis test P values for plants			0.001		0.007		0.097			

8.4 Discussion

Mangrove communities constitute the dominant coastal vegetation, covering the Atlantic coast of the Orinoco Delta, including the mouth of the Mánamo river (Hueck, 1960). There are few historical documents which depict the past coverage of mangroves in the Mánamo river. Aerial photographs dating back to 1932, show that mangroves reached Isla de Tigre 55 km upstream from the Paria Gulf. Beyond Isla Tigre, up to Isla Bagre (see Fig. 8.1), mangroves occupied narrow fringes on sand bars situated on the concave banks of the main stream, lining the narrow channels between islands and also along areas of sedimentation. Twenty years later, Sifontes (1951) observed extensive mangrove communities along the river in this area. However, his observations referred only to river bank vegetation. Unfortunately, no estimates of mangrove expansion can be made based on these reports. More recent cartographic reports (Canales, 1985; MARNR, 1982b) using remote sensing techniques show that mangroves in this river section were restricted to narrow bands, with the colonisation of any larger areas inland being rather exceptional.

The modification of the salinity and hydrological regimes led to rapid changes in the structure and composition of mangrove communities, resulting in community deterioration and extinction (Pannier, 1979; Rodríguez, 1987; Botero, 1990; Twilley *et. al.*, 1995; Botero and

Mancera-Pineda,1996). Reduction in fresh-water availability in coastal, low rainfall areas has resulted in hypersaline levels, affecting mangrove tree growth and eventually causing tree mortality as in the Magdalena river Delta in Colombia (Botero, 1990). However, in high rainfall areas, such as occur in the Orinoco Delta, a reduction in fresh water flow may lead to an increase in the area favourable for mangrove community development. This is the case in the lower course of the Mánamo river and other rivers of the Mánamo sub-basin such as the Pedernales and Cocuina as was predicted by Pannier (1979). Today, pioneer individuals of Rhizophora mangle are already established close to Tucupita city, some 150 km upriver from the sea.

Damming of the Mánamo river a few kilometres downriver from its origin, resulted in rapid and marked changes in sedimentation patterns along the entire river. Sand bars developed in the shallow areas in the upper (site 1) and lower (site 2 and 3) stretches of the river by a combination of erosive and sedimentary processes. Close to the dam (site 1), the decline in water level and flow velocity increased the exposed surface of the islands. At site 2 the first period (1932-1965) was dominated by sediment accumulation, the second period (1965-1982) by sediment erosion, and the third (1982-1996) again by sediment accumulation. At site 3, however, high rates of sediment deposition were predominant through the whole period under study. Despite fresh water flow reduction, currents generated by tidal pulses (at least 49 cm s^{-1}) in the lower river are strong enough to relocate sandy materials according to Hjulstrom's diagram (cited in Trask, 1955).

Vegetation colonisation of new sedimentary surfaces in the Mánamo river is associated with:
1. Availability of propagules;
2. Flooding regime determined by the tides; and
3. Salinization of superficial sediments, resulting from the penetration of saline water. Colonisation of these areas by Rhizophora sp., detected after the construction of the dam, indicates that propagule availability was high. Panapitukkul et al. (1998) reported an average of 3715 ± 920 and 1900 ± 808 fruits day^{-1} released by the mangrove community (Avicennia alba) in each of the channels they examined in Pak Phanang in SE Thailand. The colonisation of Rhizophora also resulted from the lack of competition by other flood resistant species, that are adversely influenced by increased salinization of sediments. Current species composition of sites 2 and 3 corresponds to that of an estuarine mangrove community in an approximately 100 m wide fringe, interspersed with halophobic species of the swamp forest and M. arborescens, a tall herbaceous species that seems to be slightly salt tolerant. New sedimentation areas near the dam have not yet been affected by salinization.

The heterogeneity in soil salinity, both with distance from the river shore and with soil depth, helps explain the coexistence of halophytic and halophobic species. In general, the floristic composition at sites 2 and 3 is more closely associated with salinity values of the superficial soil samples. Ionic concentrations of the deeper soil samples indicate how far the salinization process has advanced. In flooded areas with sulphate rich waters, potential toxic effects develop because of semi-anoxic conditions. At the sites studied here, the increase in overall salinity resulted in increased Cl/SO_4^{2-} ratios. Thus we do not expect any limitation in plant growth due to increased sulphate concentration.

The expansion rates in mangrove areas on site 3 averaged 1 ha yr^{-1} before dam construction (observation period: 33 yrs). This rate increased to 7.8 ha yr^{-1} during the first 16 yrs, and slowed down to 6.6 ha yr^{-1} during the last 14 yrs. The decline in the expansion rate could indicate that mangroves are reaching their new distribution limit, although the process will certainly continue for several years. At site 2, where mangrove establishment is definitively more recent than at site 3 (compare Figs 8.3 and 8.4), the rate of expansion during the last 13 yrs has only been 2.2 ha yr^{-1} (See further discussion in section 10-5 and Fig. 10.4).

In minor distributaries of the Mánamo sub-basin, such as the Capure, Pedernales (see section 4.3.2.2) and Cocuina, the establishment of mangrove communities upriver has been much faster than in the Mánamo and has reached the town of La Horqueta (see Fig. 8.1). In these minor rivers, the tidal influence favours the movement of mangrove propagules upstream due to the slow water hydrodynamics, facilitating the seeds germination. On the other hand the muddy edges (soils salinity has not been measured) in the river bends are optimal habitats for the mangrove establishment. The sinuosity of the rivers is an important factor. For example, the Pedernales river, which has a straighter course, possesses fewer mangrove communities than the more sinuous Cocuina river. Well established communities along the Pedernales are found at some 70 Km from Tucupita, while along the Cocuina they are found at only 45 Km from Tucupita.

8.5 Final remarks

In the same way that mangroves have been invading marsh communities of emergent plants or mud flats in the Mánamo estuary, there has been research in England and Thailand of an apparent autogenic succession where newly emerged flats are been invaded by marsh and mangrove vegetation- similar to that found in the Mánamo.

1. Salt-marsh and woodland. One of the most thorough of these studies collected evidence from a variety of sources including historical maps, satellite imagery and stratigraphic records of plant remains at different depth in the soils (Ranwell, 1974, in Begon *et al.*

1990). The estuary of the River Fal in Cornwall, England, is subject to a quite rapid deposition of silt (increased somewhat by the china clay workings in its catchment). This accumulation can occur at a rate of 1 cm per year on the mud flats which are found 15 km into the estuary. As a result salt-marshes have extended 800 m seaward during the last century, while valley woodland has kept pace by invading the landwards limits of the marshland (Begon et al., 1990); and

2. From the same type of documentary source, Panapitukkul et al. (1998), described an average mangrove progression of 30 m year-1 on recently deposited muds and suggest that the mangroves colonisation will increase by 33 ha yr^{-1} in the eastern bank of Pak Phanang Bay in SE Thailand.

The impact of water management projects on mangroves differs, at least in part because of fluctuations in rainfall in the mangrove area and in the catchment. For example in the Ciénaga de Santa Marta on the Colombian Caribbean coast, reduction in freshwater supply from the Magdalena River has produced massive mangrove mortality (Botero, 1990). La Ciénaga is characterised by an arid climate, where mangrove swamps constitute a fragile coastal ecosystem possessing high salinity levels, as well as being extremely dependent on fresh-water runoff for its survival (Botero and Mancera-Pineda, 1996).

The Mánamo situation is quite the opposite, for this is where a humid climate allows mangroves to occupy new habitats as fresh water supply decreases. Water diversion results in an increase in salinity, and the development of new open sites. These favour the upriver migration and colonisation of mangrove communities leading to an apparently 'robust' estuarine ecosystem.

The expansion of mangrove communities along the middle and lower stretches of the Mánamo river, has provided an undisputed ecological effect of river regulation. It was clearly visible after thirty years, a period where the successional replacements of species lead to important changes in the ecosystem.
The mangrove community is not the only ecosystem that has been undergoing structural and spatial change as a result of river regulation. Forest vegetation communities have also altered.

Chapter 9 Succession dynamics of the swamp communities

Discussion has already taken place on the changes that have occurred within the ecology of the swamp vegetation following the regulation of the Mánamo. There are two further aspects to be explored. The first is to interpret such changes employing the theory and ideas embodied in succession dynamics and second, to investigate the wider aspects of interference. This latter investigation focuses on human activities, especially those that influence ecological aspects. The purpose is to ascertain the extent to which regulation or other human induced changes are responsible for detectable alterations to the ecosystem.

Many subsistence Indian cultures in Latin America, are still dependent on harvesting natural resources for their livelihood. The Mánamo river impoundment affected large territories of the Lower Delta that were the traditional habitat for the native Warao Indians. They were the most · affected by the changes to the environment, due to their closer relationship and dependence on traditional subsistence activities.

9.1 Aims
The aim of the study may therefore be summarised as follows:
* To document the successional vegetation dynamics of a sector along the Pedernales river in the Middle Delta, in the period 1932 to 1996, with respect to the Mánamo river regulation.

The research hypothesis in this case may be formulated as follows: that the primary and secondary vegetation that currently occurs in this area is the result of:
1. The regulation of the Mánamo's flow;
2. The resource exploitation activities of the Creole populations that settled there; and
3. The Warao Indians who migrated into the area.

9.2 Methods
The methods that were employed in order to establish relationships between the dynamic of the vegetation in the Middle Delta region and the impoundment of the Mánamo river involved the choice of sampling sites, the methods of data collection and the analysis of the results.

9.2.1 Study site
The study area is located in the western Middle Delta (see Fig. 4.1) in the region of the Pedernales river, as defined by the following coordinates: 09° 21' and 09° 26' N and 62° 07' and 62° 13' W. The Pedernales distributary branches off from the Cocuina channel near the town of La Horqueta; flowing in a generally northerly direction until its confluence with the Mánamo river, close to its

mouth before entering the Atlantic Ocean. The total study region covers an area of 9,856 ha as shown in Table 9.1.

9.2.2 Vegetation communities

Between 1996 and 1997 the designated site was visited on three occasions. An inventory of the dominant species was documented in the following four environments:

1. the gallery forest (GF) along the Pedernales river;
2. the 'morichal' community or swamp palm forests (SPF);
3. the tall and dense swamp forests (SF td) of the Caño Jarina;
4. in the herbaceous marshes (M) near the settlements of Pepeina and Guacajara (see Fig. 9.1, 1997).

The heights of the individual vegetation communities as well as the level of standing waters were also recorded. In order to check that the selected sites were representative, a reconnaissance flight was undertaken. This enabled the validation of the initial classification and the determination of tree density over large areas. This was based upon the spacing of tree crowns in the canopy as follows: high overlapping (high density); little overlapping (medium density); and sparse, separate crowns (low density).

The inventory included the structural, physiognomic and management data (anthropogenic intervention caused by gathering and hunting activities) registered in the sites analysis described in chapter 4. Testimonies of local inhabitants, about the past and present environmental conditions were also documented.

9.2.3 Successional vegetation dynamics

The changes in vegetation over the past 64 years were established at each site using remotely sensed images. These images consisted of:

1. Aerial photographs taken in 1932, 1960, 1975 and 1997;
2. Satellite images taken in 1975 and 1997; and
3. Aerial photographs of the area taken from a helicopter (scale 1: 1000) during the field survey in 1997-1998.

Changes in forest and meadow vegetation were determined for two periods: 1932-1960 (before the construction of the dam), and 1960 to the present.

Aerial photographs were taken from the following missions: 'Venezuelan Aerial Survey' (1932, scale 1:20.000); Servicio Autónomo de Geografía y Cartografía Nacional de Venezuela, including missions from 1970 (scale 1:50000) and 040526 (1975, scale 1:80000).

Key of symbols in fig 9.1

M: Marshes permanently flooded, 30-70 cm in depth, located in lower depressions consisting of herbaceous and scrubby vegetation, 1 to 4 m tall, dominated by species of emergent Poaceae such as *Leersia hexandra*, *Hymenachne amplexicaulis* and *Panicum grande*; Cyperaceae such as *Eleocharis interstincta* and *Oxycarium cubensis*; and Onagraceae such as *Ludwigia* spp.

M & P ms: Marshes with palms. Permanently flooded, 30 to 70 cm in depth. The meadows are interspersed by sparse palm trees *(Mauritia flexuosa)* of medium size, 10 to 15 m tall.

M & P mm: Marshes with palms. Permanently flooded. Medium density of palm trees (higher than M & P ms), and medium height (15 to 20 m).

SGF md: Medium dense swamp gallery forests. This formation corresponds to the plots Buenaventura north, Guacajara west and Guacajara 2 described in section 4.3.2.2. The mean forest height is 35 m, and the density is high.

SF & P td: Tall and dense swamp forest with palms. This formation corresponds to the Jarina 2 site described in section 4.3.2.3. The mean forest height is tall (30 m), and the density is high.

SF md: Medium-dense, swamp forest, showing low flooding depth (0-10 cm). It corresponds to the Jarina 1 site described in section 4.3.2.3. The mean forest size is medium (30 m) and the density is high.

SF & P td: Tall-dense, swamp forest, located between the levées and depressions, with intermediate levels of flooding (0-20 cm). The species composition is similar to that of 'SF td', but with the inclusion of *M. flexuosa*. The mean forest height is 30 m, and the density is high.

SF & P md: Medium-dense, swamp forest, very similar to 'SF & P td', but with a mean height of 25 m.

SF ls: Low-sparse swamp forest. Secondary vegetation, resulting from significant anthropogenic intervention of 'SF & P md'. It has lower structure and very low density, appearing as a brushwood vegetation.

SPF mm: Medium-medium swamp palm forest. This formation corresponds to the Buenaventura south site described in section 4.3.2.1. The forest height is medium 15-20 m tall, and has medium density.

SPF md: Medium-dense swamp palm forest. This formation corresponds to the Pepeina site described in section 4.3.2.1. The trees are a medium sized, 15 to 20 m tall and with high density.

SPF ls: Low-sparse swamp forest. The palm trees are of a low size, 10 to 15 m tall, and have a low density.

C: Crops and plantations under active cultivation

1932

N

• Creole anthropogenic influence
 –Cultivation (on levees)
 –Clearing

–Reduction of forest land (SF)
(north side of the river)

•Indian anthropogenic influence
(negligible)

SF td   SF md
SF & P td
SF ls   SF & P md
M
Pedernales R.   M & P ms
SGF & P md
SPF ms
SM

09°25'

09°23'

1960

• Creole anthropogenic influence
 –Logging
 –Clearing
 –Hunting

–Reduction of forest land (SF)
(north side of the river)

•Indian anthropogenic influence
(negligible)

–Increase of palm
communities (PSF)

**Dam construction
downriver (1965)**

SF md
SF td
M
SF & P md
SF & P td
Pedernales R.   M & P ms
SPF md
SGF & P md
SPF mm   SM & P mm
SM

09°25'

09°23'

1997

• Creole anthropogenic influence
(negligible)

–Recovery   of the forest land
(north side of the river)

•Indian anthropogenic influence
 – Clearing (fires)
 – Gathering palm products

–Reduction of the swamp palm
communities (SPF & M /P)
(south side of the river)

Jarina channel
SPF ls
SF td   SF md
SF & P ts
Guacajara
SF & P td
SF & P ms   SF & P md
M
Pepeina
SPF ls
SGF & P md
M & P ms
SPF md   Pedernales R.

09°25'

09°23'

62° 10'   62° 08'   62° 06'

Fig. 9.1. Vegetation communities distribution in the three studied years.

221

The Landsat images used were
(1975, scale 1:50000; 1997, scale 1:75000). Community distribution was measured using planimetric methods. Plant distribution, structure and coverage were analysed with a mirror stereoscope.

9.3 Results

9.3.1 Vegetation communities

The inventory and brief description of the forest and herbaceous communities documented in the study area (Fig. 9.1) is presented below. For general relationship of the communities in relation to Delta physical morphology see Figs. 2.4 and 2.5 (chapter 2).

M: Marshes permanently flooded, 30-70 cm in depth, located in lower depressions consisting of herbaceous and scrubby vegetation, 1 to 4 m tall, dominated by species of emergent Poaceae such as *Leersia hexandra, Hymenachne amplexicaulis* and *Panicum grande*; Cyperaceae such as *Eleocharis interstincta* and *Oxycarium cubensis*; and Onagraceae such as *Ludwigia* spp.

M & P ms: Marshes with palms. Permanently flooded, 30 to 70 cm in depth. The meadows are interspersed by sparse palm trees *(Mauritia flexuosa)* of medium size, 10 to 15 m tall.

M & P mm: Marshes with palms. Permanently flooded. Medium density of palm trees (higher than M & P ms), and medium height (15 to 20 m).

SGF md: Medium dense swamp gallery forests. This formation corresponds to the plots Buenaventura north, Guacajara west and Guacajara 2 described in section 4.3.2.2. The mean forest height is 35 m, and the density is high.

SF & P td: Tall and dense swamp forest with palms. This formation corresponds to the Jarina 2 site described in section 4.3.2.3. The mean forest height is tall (30 m), and the density is high.

SF md: Medium-dense, swamp forest, showing low flooding depth (0-10 cm). It corresponds to the Jarina 1 site described in section 4.3.2.3. The mean forest size is medium (30 m) and the density is high.

SF & P td: Tall-dense, swamp forest, located between the levées and depressions, with intermediate levels of flooding (0-20 cm). The species composition is similar to that of 'SF td', but with the inclusion *of M. flexuosa*. The mean forest height is 30 m, and the density is high.

SF & P md: Medium-dense, swamp forest, very similar to 'SF & P td', but with a mean height of 25 m.

SF ls: Low-sparse swamp forest. Secondary vegetation, resulting from significant anthropogenic intervention of 'SF & P md'. It has lower structure and very low density, appearing as a brushwood vegetation.

SPF mm: Medium-medium swamp palm forest. This formation corresponds to the Buenaventura south site described in section 4.3.2.1. The forest height is medium 15-20 m tall, and has medium density.

SPF md: Medium-dense swamp palm forest. This formation corresponds to the Pepeina site described in section 4.3.2.1. The trees are a medium sized, 15 to 20 m tall and with high density.

SPF ls: Low-sparse swamp forest. The palm trees are of a low size, 10 to 15 m tall, and have a low density.

C: Crops and plantations under active cultivation

9.3.2 Community dynamic

The most prominent changes discovered over the two periods were:

1. The transformation of swamp forest to herbaceous vegetation;

2. An increase in palm swamp forests; and

3. A reduction in the area of cultivated land.

Figure 9.1 shows the vegetation communities distribution in the two periods, while Table 9.1 details the formation's surface and the variation between the two periods.

From 1932 to 1960, 775 ha. of 'medium and dense swamp forest' (SF md) and 'tall and dense swamp forests with palms' (SF & P td), located on the right bank of the Pedernales river, was transformed into marshes with a medium to sparse cover of moriche palms. The total net increase in surface area of the marshes was 680 ha (6.92 % of the total study area).

On the other hand, in the southern sector of the channel, the morichal communities (SPF) increased in cover and density, changing from low density to medium density formations, with a net increase of 245 ha. Similarly, 286 ha of marshes (M) with very scant cover of moriche, increased to medium cover. Furthermore, the 823 ha of lowland swamp forest (SF) of this sector increased in density, becoming a medium and high-density community.

The marshes exhibited a slight increase in area (150 ha), partly as a result of the reduction of the gallery forest (347 ha) along the Pedernales river. Lastly, the areas of extensive cultivation along the levées of the north bank were reduced by 61ha.

From 1960 to 1997, the forested areas of the northern sector of the Pedernales that had suffered a decline during the previous period showed signs of partial recovery. The gallery forest community (GF) along the main channel increased by 524 ha, or 5.32 % of the total study area. However, the 'medium and dense swamp forests with palms' (SF & P md) and the 'tall and sparse swamp forest with palm' (SF & P ts) increased only slightly (5 ha and 2.96 ha respectively). The latter two formations vary considerably with respect to density, of which the moriche palm constitutes an important component.

Table 9.1. Area variation of the communities in the periods 1932 to 1960 and 1960 to 1997.

Year	1932		1960		Variation		1997		Variation	
	ha	%	ha	%	ha	%	ha	%	ha	%
M	1368.13	13.88	1517.87	15.4	149.7	1.52	2048.79	20.78	530.9	5.38
M & P mm	-	-	285.8	2.9	-	-	-	-	-	-
M & P ms	1388.55	14.08	2069.2	21,00	680.6	6.98	912.08	9.25	1156.9	-11.75
SF td	558.14	5.66	626.2	6.35	68.06	0.69	605.79	6.14	20.4	-0.21
SF md	2089.63	21.2	1456.61	14.77	633,00	-6.43	1436.19	14.57	79.5	-0.2
SF ls	823.6	8.35	-	-	-	-	-	-	-	-
GF md	1708.46	17.33	1361.32	13.8	347.1	-3.53	1885.43	19.12	524.1	5.32
SPF md	-	-	245.03	2.48	-	-	313.1	3.17	-	-0.69
SPF mm	-	-	251.84	2.55	-	-	-	-	-	-
SPF ms	251.84	2.55	-	-	-	-	-	-	-	-
SPF ls	-	-							626.2	6.36
SF & P td	864.44	8.77	721.5	7.32	142.9	-1.45	639.82	6.49	81.68	-0.83
SF & P ts	-	-			-	-			292.68	2.96
SF & P md	401.59	4.07	980.15	9.94	578.5	5.78	360.75	3.66	619.4	-6.28
SF & P ms	-	-	-	-					490.07	4.97
Za	156.55	1.58	95.29	0.96	61.2	-0.62	-	-	-	-
River	245.03	2.48	245.03	2.48	-	-	245.03	2.48	-	-
Total	9855.96	99.95			9855.96	99.95			9855.96	99.95

The treeless marshes (M), especially those of the southern bank, increased in cover largely as a result of a thinning of 1157 ha (11.75 % of the study area) of the marshes with 'medium and low density of palms' (M & P ml). Dense morichales communities (SPF) and gallery forests (GF) that together, represented approximately 872 ha (8.84 % of the study area), were reduced in extent and became low-growing and low-density communities. Simultaneously, other morichal (SPF mm) communities became denser (SPF md) in the area whilst becoming fragmented towards the extreme south of the site.

The cultivated areas, accounting for157 ha by 1932 virtually disappeared in the 1997 from the levées of this sector of the Pedernales river during this period, leaving partially abandoned

coconut and cacao plantations that have been invaded by forest. Only few spots of crops may be observed.

9.4 Discussion

From the available cartographic sources (Canales, 1985; MARNR, 1982b) the distribution of the vegetation communities of the Middle Delta and in general in all the Delta fan showed the following sequence of development according to a general gradient of flooding from the Upper to the Lower Delta. At a regional scale (see diagram on Fig. 2.8):

1. In the southern region, the tall semi-deciduous forests are located along both older and more recent levées (which do not undergo flooding), whilst the low-lying land, between the channel levées, contains the herbaceous marshes;

2. The 'morichal' swamp palm forests are generally located in the intermediate region;

3. The swamp forests are mostly found toward the lower range; and

4. Mangrove communities are distributed along the outlets of the main channels.

This sequence is also to be seen at a community level from the levées to the depressions, as reported observed in the study area (Fig. 9.1) (see also Fig. 2.5):

1. Semi-deciduous to evergreen forests (GF) in the levées;

2. Medium swamp forests (SF) with palms and swamp palm forest (SPF) in the intermediate position; and

3. Swamp forests, or marshes with swamp palm forests, in the inland basins.

The composition of each vegetation community is fundamentally related to the variation in depth and duration of the flooding that affects most of the land (see chapters 3 and 4). On the Image for 1932 (Fig. 9.1), the northern sector of the study area reveals a pattern of gallery forest (GF) along the levées, swamp forest with a high proportion of palms (SF & P td and SF & P md) occupying the intermediate positions at the flooding fringe on both sides of the channel, and 'medium and dense swamp forest with few palms' (SF md) located in the depressions. These relationships, even if apparent for the semi-deciduous and swamp forests which are unambiguously related to dry and waterlogged soils, do not explain the distribution of marshes and swamp palm forests in the depressions where substrate is permanently waterlogged.

These two formations seems to occupy very similar habitats with regard to the soil substrate and flooding intensity. The soil heterogeneity discussed by van der Voorde (1962) may, however, provide an explanation. The hypotheses is based in the soil heterogeneity produced by the differential deposition of sediments transported by the waters overflowing the levées,

as discussed in section 2.3. This produces a heterogeneity of habitats available for community differentiation. Detailed analysis of the substrates and the changes in water level associated with the swamp vegetation communities of this type of environment has not been carried out (Medina, 1995) and a few relationships have been suggested by van der Voorde (1962) in the Delta and in the Venezuelan Llanos (González, 1987). The scarcity data indicates low nutrient content and high water acidity (González, 1987) , while the few physiochemical data from the inland waters in the Delta (see Table 5.3.), do not allow any conclusion.

However there is uncertain by whether the major pattern of vegetation currently observed, such as the marshes that presently occur in the lower areas of the Upper Delta, and which presumably replace the swamp palm forests, are stable communities adapted to certain environmental conditions or communities resulting from anthropogenic intervention. The Warao inhabitants or their ancestors who have become established in the region during the last 9,000 yrs (Wilbert, 1996), may have played an active role in modifying the forest cover. Heinen et al. (1995) report the artificial plantation of moriche palms in the surroundings of the Warao villages, in areas dominated by mangroves, suggesting the active horticultural practices of the Indians. The management of the environment in pre-Columbian times, leading to the modification of vegetation formations in the Amazon Basin has been proposed (Junk,1995; López-Zent, 1998). According to Dufor (1990), the Amazonia inhabitants population in pre-Columbian times declined from an estimate of 6.8 million to less than 200000 in present times.

Another anthropogenic factor that has had a profound influence in more recent times and has undoubtedly been significant in the Delta region is fire, practised by cattle farmers in order to expand the area of their ranches following the closure of the Mánamo channel, when the previous agricultural practices in the region (Escalante, 1993) were abandoned. However the Indian inhabitants may have also practised this method of control.

9.4.1 First study period: 1932-1960

The most important changes that occurred in this period were the reduction of the forests and the expansion of marshes with palms (see the images for 1932 and 1960 in Fig. 9.1), associated with the occupation and exploitation of the area by Creole people.

Until 1930, the two principle settlements of the region, Tucupita and La Horqueta, represented the main centres of the Creole population and to lesser extent of a few Indians (Salazar-Quijada, 1990). During the decades between 1930 and 1960, the Delta was a prosperous

region with an important and diverse agricultural base that exported products to the main markets of the country, as well as to Trinidad and even to England (Escalante, 1993). Within the study area, the 'Criollos' cultivated the levées along the Pedernales river. Their main crops were plantations of coconuts, *Cocos nucifera*; cocoa, *Teobroma cacao*; plantain, *Musa* spp, corn, *Zea maiz*; and yucca, *Manihot esculenta* (Salazar-Quijada, 1990).

At the beginning of this period, extensive areas of gallery forests were felled to make way for the plantations; events that have been confirmed by aerial photographs taken in 1932. The Buenaventura north site described in section 4.3.2.2 still shows the effects of these activities and as well as sparse remnants of these crops. The timber industry, situated in the nearby Mánamo river (Escalante 1993, Heinen D, *pers. com.*), exploited trees of valuable wood such as the Cachicamo (*Calophillum lucidum*) and the Peramancillo (*Symphonia globulifera*). Additionally, large areas were burned to facilitate hunting, which further reduced the area of the woody communities (see variation of gallery forests in Fig. 9.2). In the image from 1932 (Fig. 9.1) a community classified as 'low-growing and sparse swamp forest' (SF ls) can be seen containing scattered groups of trees as well as many shrubs and lianas, constituting a typical 'matorral formation' that becomes established after major disturbances such as a fire. As a consequence the cover of swamp forests diminished (see variation in Fig. 9.2). During the same period, the 'medium and low density swamp palm forests' (SPF ml) and 'marshes with medium and low palms' (M & P ml) in the southern sector of the Pedernales channel increased in cover and density (Fig. 9.2). In effect, these types of permanently flooded communities are composed of plant species, which hold no economic or social value for 'Criollo' inhabitants.

On the other hand, the indigenous people, the Warao, established their settlements along the littoral fringe (60 to 80 km wide) which had been their traditional territory in the Lower Delta (Urbina and Heinen, 1982; Wilbert, 1996). The domestic units generally formed a population of between 25 and 100 people (Urbina and Heinen, 1982; Wilbert, 1996). Their subsistence activities centred on the seasonal harvesting of sago and fruit, fishing and hunting of rodents and birds. For the Warao; as well as other indigenous people that live in inundated regions of the Orinoco (Gragson, 1992) and Amazon Basins (Kahn *et al.*, 1993), the moriche palm fulfils practically all the requirements of daily life. It serves as:
1. Food (Heinen *et al.*, 1995);
2. Enables the manufacture of utensils, hammocks and clothing (Heinen *et al.*, 1994-1996);
3. Serves as natural medicines for various types of illness (Wilbert, 1996);

1. A secondary product is also derived, the larvae of two species of beetle *Rhynchosporum palmarum* and *Rhina barbirrostris*. These larvae until very recently constituted a crucial source of fat (Suárez, 1968).

At certain times of the year, all the members of a community could be found in the marshlands and morichales, collecting a variety of plant and animal products, especially those derived from the moriche palm (Heinen *et al.*, 1995). This process involved the felling of the palm. But due to the relatively low density of population and the abundance of the palm, the impact of the Warao on the vegetation has been minimal (Wilbert, 1994-1996). As a result the swamp palm forests in the study area have increased (Fig. 9.2).

As a result, during the period 1932-1960, the main impact was seen in the forest communities due to the Creole practices of exploitation.

9.4.2 Second period: 1960-1997

During this period, the most notable changes were the reduction of the palm communities of the southern bank of the Pedernales river and the recovery of forest vegetation on the northern bank (see Figs 9.1 and 9.2). This phenomenon is linked to the withdrawal of the Criollos and the occupation and exploitation of the area by the Warao.
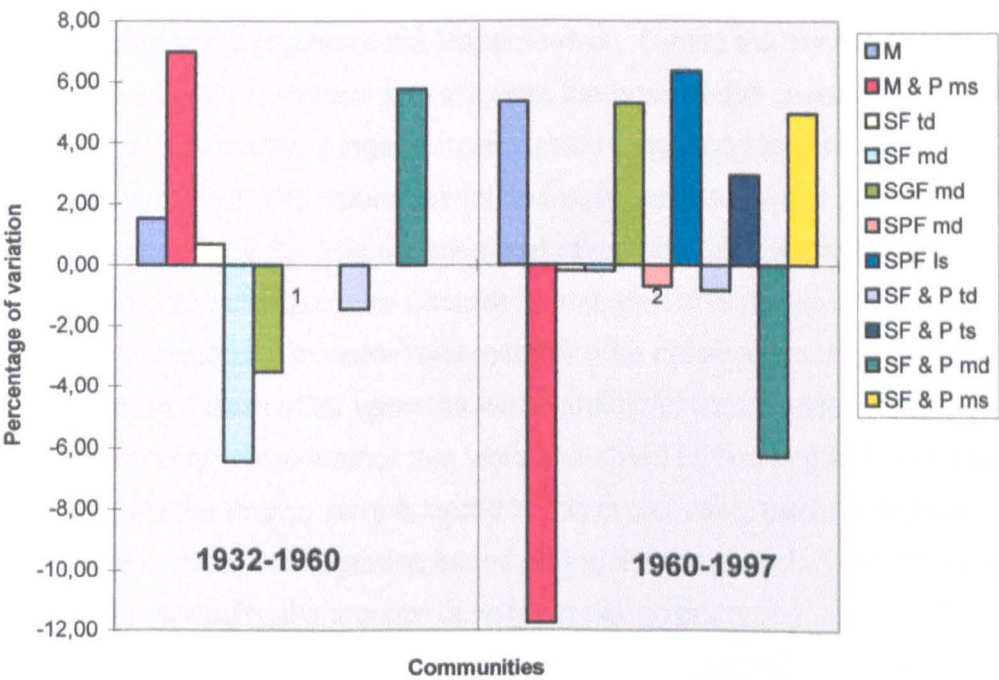
Fig. 9.2. Area variation of the communities in the two periods

The Mánamo river regulation project was carried out in 1965. It had significant effects upon the inhabitants of the Delta. The Criollos of the Upper Delta were affected with respect to

their agricultural activities and traditional subsistence strategies. True, the area's soils were protected from flooding by the project, but the same also prevented the natural fertilisation of the levées where cultivation was carried out. The suspended sediments formally introduced by the Mánamo river were reduced to one third (see section 5.3.5). But in the Pedernales area, which is disconnected from the main course, the input from suspended sediments is very low (0.005 g l^{-1})(Infrawing & Asociados, 1997).

The soils themselves were also altered by drainage projects that prompted their complete desiccation. These events led to the formation of acid-sulphate soils, causing a decline in agricultural production. Many farmers abandoned or sold their properties (Escalante, 1993; García and Heinen, in press) and moved to larger settlements or to neighbouring states. The number of people working in agriculture declined from 62.3 % of the population in 1961 (before the channel regulation), to 44.4 % in 1971, whilst the percentage of people dedicated to other activities simultaneously increased (Buróz and Guevara, 1976). This outmigration of the Criollos from the Pedernales river, from rural to urban areas, would explain the slow regeneration of the cover of woody vegetation communities in the northern sector of the study area (see variation in Fig. 2.9).

For the Warao, the consequences of the regulation works were also related to changes that took place in the hydrological regime of the Mánamo river. During the dry season (November-April), whilst the channels were at their lowest levels, the ocean tides created a subsurface saline wedge along a wide coastal fringe that penetrated deep into the channels of the Delta habitat. On the Mánamo river this influence reached as far as the apex of the Delta, near the river town of Barrancas (Fig. 2.2). The situation was reversed during the rainy season, when the water level of the channels rose (see Chapter 5) and the entire region resumed its typical freshwater regime. Fluctuations in water level maintained a dynamic balance between the influence of saltwater and freshwater upon the fauna and floral communities of the banks, as well as on the communities of the interior that were inundated by flooding of the channels. As a semi-nomadic people the Warao were adapted to this cycle, using freshwater from the channels in the rainy season and migrating inland during the dry period. Today they are sedentary and have resorted to the storage of water in plastic drums.

The permanent salinisation of the channel also brought about important changes in the riparian biota, such as the upstream expansion of mangrove communities (Colonnello and Medina, 1998), and the forcing of the Warao communities to migrate southward to a non-saline environment (Escalante, 1993; García and Heinen, in press). In the Middle Delta they relocated along the Guacajara and Pedernales channels (Delavaud, 1977), and established

two settlements (Pepeina and Guacajara de la Horqueta) which quickly became towns. The date of establishment of these settlements can be deduced from the aerial photograph of 1975. Other villages were established along the upper course of the Mánamo river, the towns of Santo Domingo de Guacajarita, El Pajar and Playa Sucia (Heinen and Urbina, 1986).

The migration to the south has been documented by the National census undertaken in 1963 and 1992. The population estimated by the 1963 census in the Pedernales municipality , corresponding to the outer Delta comprised 2,038 inhabitants distributed in 46 villages, while the southern municipality of Tucupita was inhabited by 2,492 people. In the 1992 census the number of inhabitant in the Lower Delta was reduced to 998 distributed in 12 villages. In contrast their number increased in the Upper Delta to 4,496 living in 33 villages (mean of 132) (OCEI, 1993).

Today, Guacajara has an indigenous population of 402 inhabitants; including residents and those people engaged in itinerant activities (Pfiste C, *pers. com.*). The utilisation of the areas for subsistence activities, especially the morichal community and marshland with palms, has lead to an overexploitation of their resources, causing a reduction in their cover in terms of the density of the area occupied for each community, particularly in the southern sector of the Pedernales river (see Figs 9.1 and 9.2). In the sites Guacajara east and Guacajara west described in section 4.3.2.1 and 4.3.2.2 respectively, the felling of many moriche palms was noted. Kahn and de Granville (1992) in a study of the palms in Amazonia stressed that, in order to maintain a density sufficient for the pollination of female moriche palms and the associated fruit production, the exploitation by local indigenous people should be actively controlled. The authors suggest few male individuals per hectare in the Amazonia, while the proportion of male/female trees in the Mánamo region has not been investigated.

Today, however, there are other forms of subsistence activity such as cultivation of ocumo (*Colocassia* spp), the processing of coconut, as well as occasional salaried work in the nearby towns. During fieldwork carried out on the north side of the Pedernales and Cocuina rivers, clear signs of recent fires were observed in the marshes (with palms). This practice continuously expands the herbaceous vegetation and may also have been the cause of the conversion of forested areas to marshes in recent years, to the south of the Jarina channel (see the 1997 image in Fig. 9.1).

As a result, the major anthropogenic influence in the period 1960-1997, was due to the Warao people, who were principally responsible for modifying the communities containing the moriche palm.

9.5 Final remarks

The traditional culture of the Warao people contains clear concepts of conservation with reference to avoiding the overexploitation of available resources. Both hunting of large animals and felling of trees is prohibited by a set of beliefs that maintain the natural communities; palms however are excluded. According to the indigenous taxonomic system, the trunks of palms are formed of fibre rather than wood. Therefore they do not constitute trees and can be exploited as needed (Wilbert, 1996). Furthermore, some authors have highlighted other possible environmental impacts caused by the Warao (Heinen *et al.*, 1994-1996).

The adoption of the 'ocumo' cultivation in recent years, promoted by the missions established in the area of the eastern Lower Delta, has brought about a change in the traditional forms of subsistence and settlement. This is probably transferring a significant percentage of anthropogenic pressure from the morichales of the interior to the narrow levées along the channels. These areas are more susceptible to deterioration than the morichales which occupy wide belts (ca. 18 % of the total vegetation, see section 2.4.2). Similarly, the rate of recovery of the woody vegetation of the levées as well as the structure and fertility of their substrates, which are greatly affected by cultivation, is much longer than that of the extensive palm communities. In certain areas of Caño Guiniquina in the lower and eastern Delta, cultivation activities have altered the soil structure to the point that they remain very loosely aggregated. This process has long-term effects considering that after 28 years of fallow, soil structure of many sites, has not recovered. The newly acquired dependence on this type of food acquisition is resulting in a progressive and serious modification of the natural vegetation (Wilbert W, *pers. com.*)

Figure 9.3 shows a schematic representation of the changes that have taken place in the vegetation communities during the two periods. The complicated pattern may be compared with a theoretical model (Fig. 9.3) presented by González (1987) for these types of vegetation communities. According to this hypothesis, the marsh community can become a dense swamp palm forest or even a swamp forest through a series of successional stages. The edaphic habitat and microclimate is modified progressively by the growth of palms, facilitating the invasion of new species and development of a new formation where palms share the dominance in the different height strata (diagram A to D and vice versa). The process may be initiated by natural events such as the increase in flooding periodicity and intensity, or by anthropogenic intervention (diagrams E to K, and vice versa) as has occurred in the area. This is where some palm communities increased in density and then reverted to marsh in the next. The climax formation, swamp forest with or without palms (G), representing the final
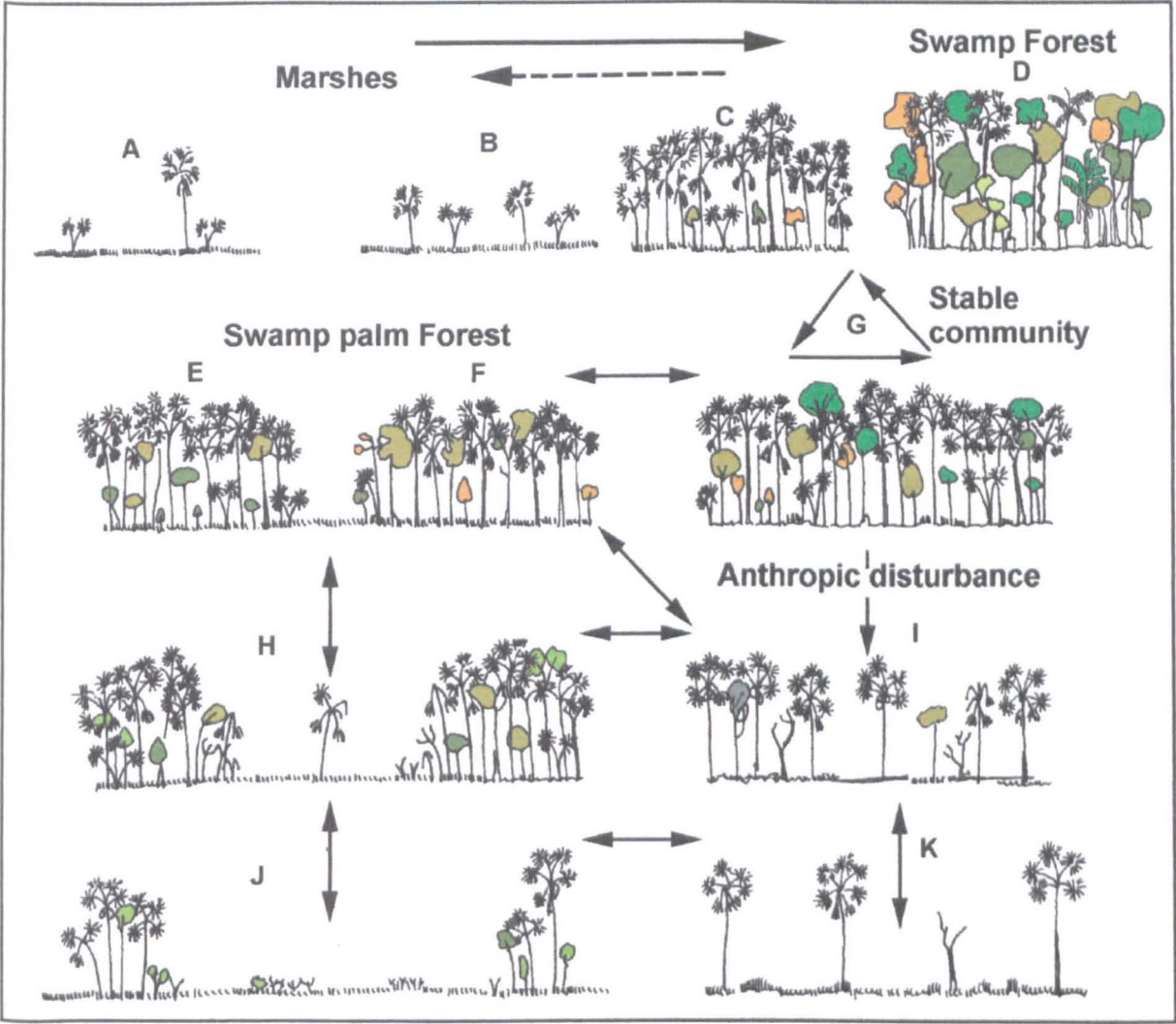
Fig. 9.3. Schematic diagram of the successional stages of the vegetation in the Middle Delta (adapted from González, 1987).

stages of a moriche palm community takes place over a period of about 20-25 years. In addition to its rapid growth, the moriche produces enormous quantities of fruit that are easily dispersed in the flooded environment or transported by the people and animals that consume them (Heinen *et al.*, 1994-1996). A complete discussion of the successional steps is presented in section 10.5.1.

The consequences of a large scale river regulation are far more extensive than that observed in the plant communities along the main rivers. Reduced flooding or modification of peak flows as a consequence of the river regulation might decrease the cultivated area or fisheries, resulting in serious consequences on the rural economy, leading to overexploitation of the remaining agricultural areas and cause a deterioration of local living conditions (Roggieri 1995). In other cases people have left the villages to settle in other areas where the influx of migrants may lead, also, to potential overexploitation of resources (IUCN/CML 1989 in Roggeri 1995). Similar to the changes observed in the vegetation, the fauna (subsistence species) of a wetland can be altered as a result of changes in the hydrological regime, by affecting the flora and habitats of the area, or by direct human interference. This may be seen in Mozambique, for example, where hunting pressure in the Zambesi Delta has increased significantly after the construction of large dams upstream (Roggieri 1995).

The cases documented in chapter 8 and 9, indicate the need to increase impact studies of the inland communities on the ecology. The importance of remote sensing methods coupled to geographical information systems should be stressed and then linked to extensive surveys of territories affected by large engineering projects.

Chapter 10 General discussion

The comparative studies of two distributary rivers presented in this thesis represent the first attempt to describe qualitatively and quantitatively the varied ecological units of the Orinoco Delta and the impacts of the Mánamo dam construction on the regional environment, focusing in particular on its vegetation communities. Since the river regulation, the Delta region has remained relatively untouched and forgotten once the agriculture development, that was planned in the region failed to take place (CVG, 1972). The case received very little publicity, with only few documents including a documentary movie (1978) and anthropological reports (1993) covering the topic. Since (1996), the exploitation of the oil reserves that lie beneath the Delta and the associated development of the oil industry, has renewed public interest in the Delta environment, including the regulation of the Mánamo and its environmental impact. The perception of the scientific community toward the Delta has changed too. The region has been receiving increasing attention and is actually the focus of several meetings and symposia (Colonnello 1998a).

10.1 The wetland communities types

In the Orinoco Delta the wetlands occupy almost all the terrain with the exception of the upper regions currently protected from the flooding. They are identified through the analysis of the geomorphological and ecological environments, these being characterised by:

1. The confluence of low and flat land (minimal land slope);
2. The 'plate' shape of the landscape (islands), slightly depressed in the centre and high along the edges;
3. Poor drainage;
4. Intense precipitation;
5. Seasonal flooding of the Orinoco; and
6. The tidal sea waters that influence regional flooding, and thereby maintain a state of quasi permanent stagnant water inland (MARNR, 1979; Canales, 1985).

According to the classification proposed by Mitsch and Gosselink (2000) and Roggieri (1995), the Mánamo sub-basin region contains almost all the wetland types found in tropical regions (Table 10.1).

In the Upper Delta, along the river courses and in the inter-riverine depressions, ecosystems subject to periodic flooding are found. These include forests and grasslands (wet meadows) with predominantly mineral soils that are mostly used for cattle raising, seasonal shallow lakes and lagoons, which are filled either during river floods or during the rainy season, and fresh-

water marshes mainly found in the lower terrain. These regions were once flooded by the river and rains but have since experienced falling water tables and as a consequence the drying out of the soils.

In the Middle Delta, marshes (low herbaceous, some grass species) that generally occur in a mosaic of herbaceous swamps (tall herbaceous and scrubs species) are particularly well dispersed. Their soils have mineral composition or peat and may be treeless or show a varied cover of palms. The forested communities are dry semi-deciduous (or mangroves) forests along the river banks, and swamp palm forests were dominated by *Mauritia* palms on constantly inundated soils, or swamp forest without *Mauritia* palms on more dry (waterlogged) substrates.

In the lower Delta, the herbaceous types are restricted to the lowest positions. The hardwood communities dominate, particularly those of the swamp forests. The mangrove forests are to be found in the coastal belt and along the lower (and middle) stretches of the river shores. Meadows composed of grasses and other emergent species (halophytic near the sea) are distributed along the shores of the entire river courses.

In some particular sites of the lowland marshes a type of bog and fen landscape may be found (according to Nilsen and Orcutt, 1996). They are characterised by their source of water, with a high acidity of 4.4 pH, the floral dominant composition of Cyperaceae and the occasional presence of insectivorous plants such as *Drocera* sp. Occasionally shallow ponds and water bodies are found in the Upper, Middle and Lower Delta. These water bodies are replenished by rains and are typically acidic (pH 3-5.5), with emergent species such as Cyperaceae and floating macrophytes such as *Nymphaea* spp.

Table 10.1. Main types of wetlands described in the Mánamo sub-basin

Region of main location	Type Formation	Term	Soil type	Topographical position	Main water source
Upper Delta					
	Herbaceous	Wet meadows	Mineral	Uplands	Rain & rivers
		Fresh. T. marshes	Mineral/Peat	Lowland	Rain & rivers
		Emergent plants	Mineral	River banks	Rivers
		Floating meadows	Mineral	River edges	Rivers
		Lagoons/ponds	Mineral	Uplands(PA)	Rains/seepage
	Forested	Deciduous forests	Mineral	Uplands	Rains
Middle Delta					
	Herbaceous	Fresh. T. marshes	Mineral/Peat	Lowland	Rain & rivers
		Emergent plants	Mineral	River banks	Rivers
		Floating meadows	Mineral	River edges	Rivers
		Lagoons /ponds	Peat/mineral	Lowland	Rains/seepage
	Forested	Riverine forests	Mineral	River banks	River
		Riverine mangroves	Mineral	River banks	River(Tidal)
		Swamp palm f. (SPF)	Peat	Lowland	Rains&seepage
		Swamp forests (SF)	Peat	Lowland	Rains&seepage
		Swamp forests (SF)	Peat/mineral	River banks	River (Tidal)
Lower Delta					
	Herbaceous	Salt Tidal. marshes	Peat	Lowland	Rains/seepage
		Ponds/lagoons	Peat/mineral	Lowland	Rains/seepage
		Haline meadows	Mineral	River banks	Rivers
	Forested	Swamp palm f. (SPF)	Peat	Lowland	Rains & seepage
		Swamp forests (SF)	Peat	Lowland	Rains & seepage
		Mangrove forests	Mineral	River edges	River (Tidal)

T: Tidal

At a country scale some of the communities described are restricted to the fluvio-marine lowlands of the Orinoco Delta and, in particular, to the fresh water marshes (Broad-leaved meadows according to Huber, 1995). Similar communities are solely found in the Delta of the Catatumbo river (González V, *pers. com.*) that flows into the Maracaibo Lake in the north-western part of the country (Fig. 2.1). The most widely distributed wetland type is that of the wet meadows (graminous meadows or grassland according to Huber (1995)) that are observed in the Llanos region - flat, largely treeless plains stretching westward from the Delta area (Ramia, 1967; Sarmiento, 1990). Communities of emergent and floating species are found in a variety of flooded habitats throughout the country (Velásquez, 1994) and particularly along the floodplains of the Orinoco and other big rivers such as the Apure (white waters)(Sánchez and Vásquez, 1986). Other large rivers such as the Caura River (clear waters) (Fig. 2.1) that drains the Guayana Shield, have a markedly reduced population of macrophytes (Hamilton and Lewis, 1990b).

Included into the forest communities, in Venezuela, are the swamp forests found in the Amazonas State along the upper reaches of the Orinoco and Ventuari rivers. Their species composition show a high percentage of palm species, *Euterpe*, *Mauritia* and *Manicaria*, along with other tree species that resemble the Delta forest. However its flora has been insufficiently studied (Huber, 1995). The swamp palm forests, 'morichales' are found in several lowland regions particularly in the eastern (high-plains of the Mesa Formation) and south-eastern region along the Caroní river basin (González, 1987). On the other hand, the seasonal flooded forests along the large floodplains, where only a few of the main species (e. g. *Pterocarpus officinalis*) are common to the Delta formations (Colonnello, 1990b).

On the other hand mangrove forests and herbaceous halophytic communities are dispersed across the Venezuelan estuarine environments (Pannier, 1979; Pannier and Fraino de Pannier, 1989). Particularly significant communities are found along the San Juan River (Fig. 2.2) north of the Orinoco Delta and the El Limón river that flows into the Venezuelan Gulf (Fig. 2.1) (Medina and Francisco, 1997).

10.2 The wetland conceptual model
In the 1960s the construction of a dam was proposed. It was to serve the purpose of opening up the resources of the Delta and the north-western region of the country, that had been economically disadvantaged since colonial times (1850). After 1959 the steel factories of the Bolívar State required a large expansion of the labour market linked with a big demographic expansion, creating a market for agricultural products that initially had to be brought from other regions of the country (CVG,1972). The nearby Orinoco Delta with its abundant

flatlands and close proximity to the industrial zone was considered the natural choice for agricultural development.

This massive agricultural development project was planned to occupy an area of 300,000 ha, judged to be suitable for agricultural activities and cattle raising, that should be protected from the problems caused by the seasonal floods. Additionally the project needed to protect the cities and towns from the economic effects of the annual floods that affected even the slightly more elevated parts of the region. To achieve these goals, the original project of the Mánamo regulation included the construction of a dam, with a sluice to control the flow in the Mánamo. Additionally, 174 km of cofferdams were to be constructed to protect the area from the water intrusion from the floods of the neighbouring Macareo river. In a proposed second stage, the protected area would be extended to 2,000,000 ha (CVG,1967). There is no evidence that this phase will be brought into effect.

Such a development should have incorporated a comprehensive analysis (environmental assessment) of all the biotic, physical and socio-economic parameters that might be involved. However by 1965 there was no specific environmental legislation on the Statute books in Venezuela. Elsewhere, the 'National Environmental Policy Act' became a law in the United States only in 1969 (McCall and Flowerdew, 1976). Moreover by the time the Mánamo project was proposed, the wetlands were considered by many to be an unproductive area. This was because there was a lack of scientific knowledge -a view that was stated by Ewel in 1990, when he wrote

> "Sensitivity to the importance of wetlands increased dramatically in the last two
> decades as scientist became aware of the nature and magnitude of losses resulting
> from conversion of large wetlands to agriculture or urban development" (Ewel, 1990).

It is not surprisingly, then to find that there were few predictions available on the likely impact on the physical and biotic environment. General concern was expressed by the Coffee and Cacao plantations owners working along the affected Mánamo river particularly in regard to the possible effect of salinization and deterioration of the potable water for human consumption, and the use of good quality water for domestic animals and crop irrigation (CVG, 1967).

A conceptual framework that would be appropriate to the Delta case, was proposed by Twilley et al. (1998) to investigate the 'forcing function' of ecological and economic processes that determine management decision in coastal environments. This conceptual model, modified for the Mánamo case (Fig. 10.1) treats solar energy, river flow, and tides as forcing functions that control the properties of estuarine ecosystems. The model also includes socio-economic

constraints such as international markets, trade and Indian ethnic policies, and political and cultural ambitions.

The following schematic diagram (Fig. 10.1) shows the 'forcing function' of ecological and economic processes that have helped determine management decision in coastal environments (Twilley *et al.*,1998).
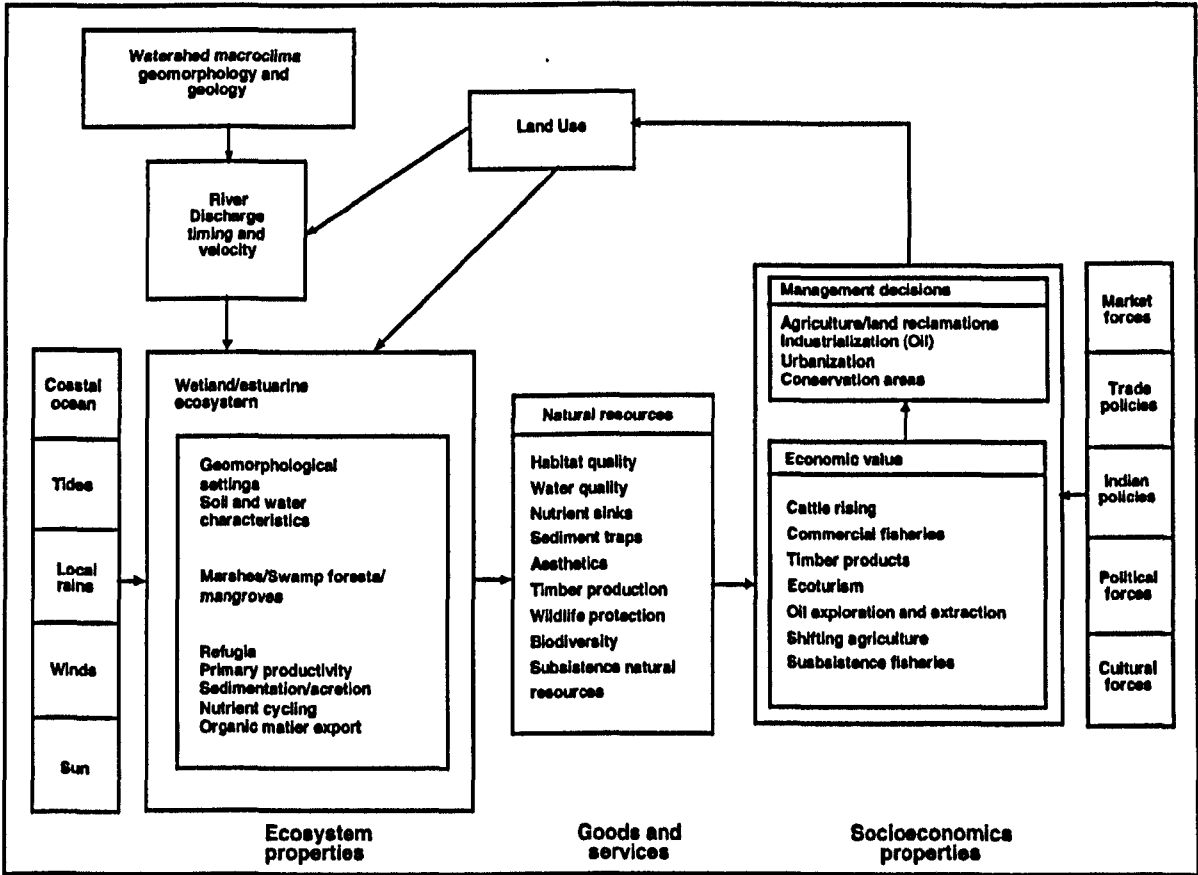
Fig. 10.1. Conceptual model, for 'forcing function' of ecological and economic processes that determine management decision in coastal environments (Adapted from Twilley *et al.* (1998).

In the view of many researchers working in the National Universities, market and political forces dominated the dam construction decisions (García and Heinen, in press). The preparatory work started before the preliminary studies on crop productivity were even published (CVG, 1967). The policies established by the official agencies and the cultural pressures and needs of the indigenous and Criollos people were conveniently ignored in the plans so that the potential economic wealth of the region could be realised. Market forces prevailed because it was thought necessary to expand the crop production for the growing population of the neighbouring states. Political and trade objectives became important, not

least because a few landowners saw an opportunity to manage and control extensive areas of land (García and Heinen, in press). Finally, the 'protection' of the state capital city of the Delta, Tucupita, was deemed a necessary political objective.

The conceptual model (Fig. 10.1) envisages that ecological and socio-economic functions largely determine the values of ecosystem components (the planned large crop production and cattle raising in the Mánamo case), thereby indirectly controlling coastal (wetland) zone management decisions (Twilley et al., 1998). Management decisions were made without considering the pre-existing small holders and the characteristics of their ecological and economic management of the land, nor were the Warao Indians consulted about the maintenance of the cultural (ecologically sound) and economic use of the subsistence activities they practised. Moreover the existing socio-economic value of the Delta was underestimated both in terms of traditional activities such as the commercial fisheries. Nor were other aspects taken into account such as the 'Delta' production method, that was adapted to seasonal flooding, the potential of eco-tourism, the gathering of forest fruits (palm hearts) and of biodiversity resources. The culture of the Warao Indians, who settled in the region thousand of years ago was largely marginalised (García and Heinen, in press).

If the appropriate evaluation of all the ecological constraints involved in the project, had been made, it would probably have led to a less ambitious project, where the social goals such as the inundation protection of the cities against flooding would still have been possible as well as increasing the extent of arable land and maintaining the water quality in most of the lower Delta regions. This would have preserved the Warao Indians habitat. Engineering provisions such as a greater regulation of the water discharge capacity, would also have made possible the longer term adjustments in the riverine environment to the regulated flow of the Mánamo.

10.3 The environmental impact model

Hydrological engineered changes, alteration in plant community structures, storage of surface water, pollutants inputs, in-filling, agriculture and management are disturbances that may be examined as possessing potential cumulative impacts (Hemond and Benoit, 1988; Winter, 1988) on the Delta region.

Impoundment of the Mánamo channel almost 40 years ago, resulted in important associated environmental events. These led to primary and secondary impacts, that modified the whole basin of the Mánamo distributary channel. This massive impact may be linked to other important environmental alterations such as:

1. The dredging of the Río Grande river (main Orinoco distributary), which is causing important changes to both fish habitat and channel morphometry;
2. The disposal of the waste waters of the human settlements; and
3. The shore and bank erosion caused by the ocean-going cargo and oil vessels as well as ocean cruise liners. These anthropogenic influences when viewed together have a wide cumulative impact on the whole of the Delta environment.

According to Bedford and Preston (1988), the appropriate dimension for cumulative assessment is the interacting system of wetlands located within watersheds, landscapes, and regions. The assessment then becomes bounded by the distribution (spatial and temporal) of the resources that may be of concern.

10.3.1 The application of the impact model to the fluvio-estuarine wetland of the Mánamo river sub-basin

The schematic diagram of Fig.10.2, shows the direct and indirect effects of the river regulation on the different components of the Delta environment. The primary impact of the regulation was on the hydrological patterns of the flooding frequency and amplitude, that determine virtually every characteristic of the wetlands (Mitsch and Gossenlink, 2000; Carter, 1986). However, many other indirect effects (indicated with the arrows) occurred.
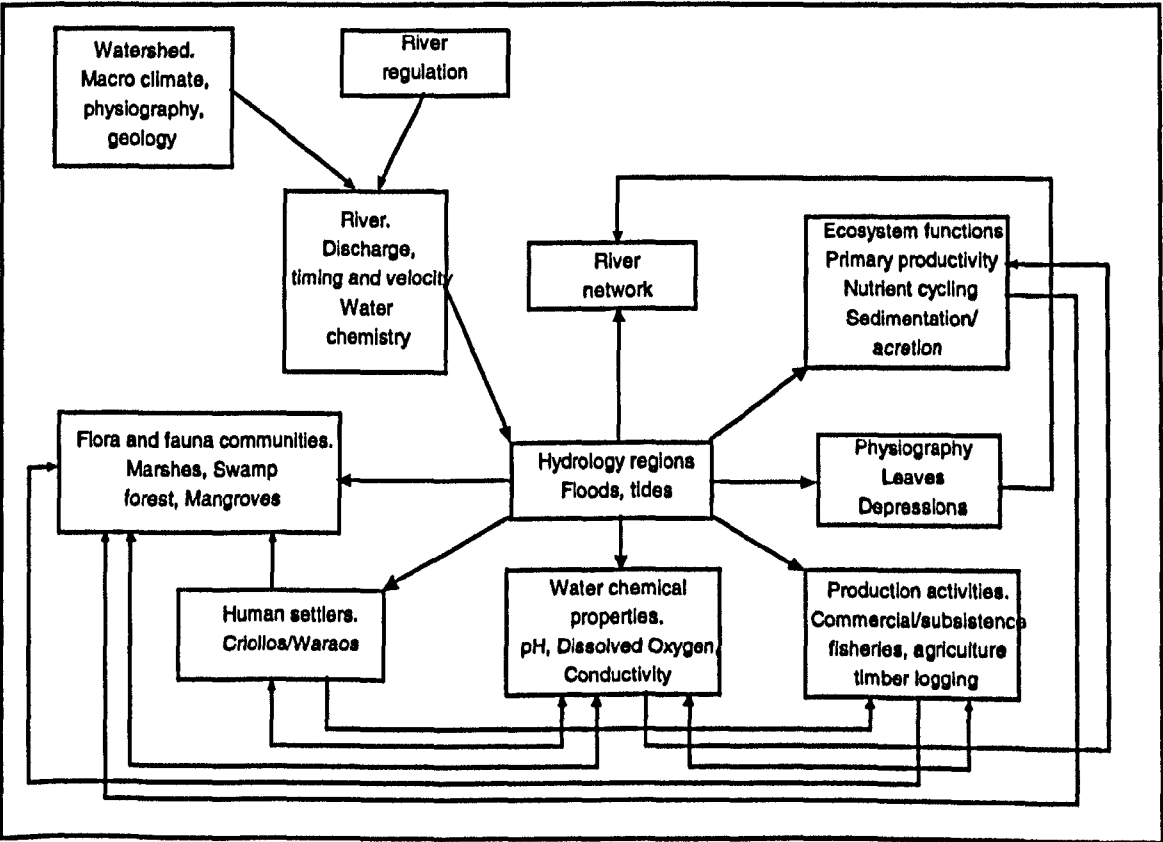
Fig. 10.2 Direct and indirect impacts effects of the river regulation.

A number of aspects are highlighted in this schematic representation.:

1 Hydrology changes affected physiography because of differential transport rates of . sediments and processes of accretion and erosion.

2 Hydrology changes affected river networks because processes of accretion and erosion created shore structures that impeded water flow. In addition, reduction of seasonal flooding accelerated the filling of shallow channels.

3 Hydrology changes affected water chemistry and water physical properties, because of the differential input and release of nutrients from decomposing plants and mud, and reduction of transported suspended sediments (pH, water transparency, electrical conductance).

4 Hydrology changes affected vegetation and faunal distribution and diversity because of the modification to the aquatic habitats along river edges and inter-riverine terrain.

5 River hydrology changes affected ecosysteml functions such as primary production, nutrient input and sedimentation due to modification of physical parameters including both current velocity which affects nutrient input, and wind effects which modify the water temperature and dissolved oxygen etc.

6 Hydrology changes affected subsistence production activities such as fish harvesting and crops production, because modification of the tidal and flooding regimes affected the land and nutrient availability for such activities.

7 Hydrology changes affected human settlers because of alterations in the availability of resources.

In addition to these 'primary' indirect effects, a series of 'secondary' indirect effects can also be identified as having taken place. These include:

1. Water chemistry (sediments/nutrients) affecting ecosystem functions such as productivity and nutrient cycling increased.

2. Modifications to ecosystem functions affecting production activities such as fish harvesting, timber (mangroves) production, and crop yield.

3. Modifications of ecosystem functions affected flora and faunal communities modifying the biomass production, distribution and composition of species.

4. Incoming migrant workers who have modified the biotic communities as well the species distribution due to over exploitation of resources and intensive use of fire for clearance (agricultural development and cattle ranches).

5. Human settlers who have degraded the water quality. This in turn influenced the water chemical characteristics due to local or regional waste and sewage disposal. This is an

increasingly urgent problem along rivers bordered by the major Creole and Warao communities whose population may have exceeded the carrying capacity of the area.

6. Changes in landforms affected the river network, such as the closure of channels and the creation of oxbow lakes.

7. In the same way, water chemistry affected the flora and faunal communities through positive feedback, such as that of the extensive carpets of floating plants that, when decomposing, add large amounts of debris and organic matter to the water.

The reported impacts are common in managed wetlands where channelization, dredging, dam constructions and other human developments have been undertaken (Hopkinson *et al.*, 1995; Bravard and Petts, 1996). The consequences of the Mánamo regulation are almost identical to those reported for the Aswan dam on the Nile (Collier *et al.*, 1973; Din 1977), where there are impacts such as the macrophyte explosion, the sediment reduction, the salt intrusion and soil salinization and even changes in the socio-economic activities of the indigenous people.

The topographic gradient of slope from the Upper to the Lower Delta determines many physical and biotic characteristics of each section. In the Upper Delta, the soils are mostly mineral and the terrain and banks are high and protected from average water rise flooding. The productive activities are directed toward agriculture, cattle raising and marketing and are mainly in hands of the Creole people. In the Middle and Lower Delta, land is flooded, soils are high in organic content and productive activities are mostly subsistence farming fishing and food gathering. The effects of the river regulation were different, both in magnitude and type, in the upper, middle and lower river sections of the Mánamo (Table 10.2).

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Table 10.2. Differential effects of the river regulation, on the upper, middle and lower river sections. The strongest effects are shown in bold and underlined, smaller impacts are in italics or in normal characters.

Upper Delta

> **Hydrology: water velocity, timing and discharge**
> **Soils: chemical and physical properties**
> *Vegetation: cover, distribution and composition (diversity)*
> Agriculture productivity, diversification. Livestock farming increase
> Criollos traditional settlement, local inhabitant migration, changes in
> life style

Middle Delta

> **Hydrology: water velocity, timing and discharge**
> **Vegetation: mangroves, marshes and swamp forests**
> **distribution, species composition**
> *Water quality: chemical (pH, Conductivity, salinity, sediments*
> *transported) and physical (timing, velocity, transparency) properties*
> Geomorphological changes: deposition, accretion. River network
> changes
> *Indians subsistence resources quality (fauna and flora products)*

Lower Delta

> **Hydrology: water velocity, timing and discharge**
> **Vegetation: mangroves, marshes and swamp forests**
> **distribution, species composition (along the river edges)**
> Geomorphological changes: deposition, accretion
> **Water quality: chemical (pH, Conductivity, salinity, sediments**
> **transported) and physical (timing, velocity, transparency)**
> **properties**
> **Subsistence resources quality (fauna and flora products)**
> **Water quality: chemical (pH, conductivity, salinity) and physical**
> **(timing, velocity, transparency) properties**
> **Local inhabitants: migrations**

10.4 Disturbance and type of successional response

All biotic succession processes commence with a disturbance. As pointed out by Peet (1992) it is largely a problem of scale, thus a fallen tree in a forest community is certainly a disturbance that redefines the environment for the tree seedlings, herbs and bryophytes beneath the tree. But disturbance may also be recurrent or large fires that affect the whole arboreal community and lead to a series of successional processes that replace the whole forest.

In this sense, the damming of the Mánamo river may be viewed as an event that redefined the whole Delta environment, particularly along the Mánamo river course but to a certain extent along the other large distributaries. This redefining was also at a community scale, including the habitat of most of the faunal and floral component and the Indian and Creole settlers who, 40 years ago (and to some extent still today), were intimately associated with the natural environmental processes.

According Lake(2000) the damming of a river may be considered as a "press" disturbance because it arise sharply and reach a constant level that is then maintained. A "ramp" disturbance (sensu Lake (2000))may be considered the increasing salinization of the soils of the Mánamo shores, due to the tidal influence. Due to its constant increase for several decades.

Following the definitions of Huston (1994) for perturbation and disturbance, the impoundment of the Mánamo sub-basin is a case of where a large perturbation have been followed by a multi-disturbance pattern. This is because the first term refers to

> "the displacement of some property of a community or ecosystem, such as the total biomass, reproductive rate or nutrient influx, away from its typical value, which is generally considered to represent an equilibrium value" (Huston,1994).

On the other hand disturbance is evidenced in the mortality of organisms, that is in any process or condition which is external to the natural physiology of living organisms that results in the sudden mortality of biomass in a community in a relatively short time scale. In the study of the Mánamo impoundment this could be over several weeks in the case of meadows of emergent plants but over many years in the case of the forest communities of the middle Mánamo sub-basin.

The change of the hydrological patterns may be considered as a perturbation while the following effects particularly on biotic properties of the ecosystem should be considered as disturbances.

In Table 10.3, are listed the series of disturbances, the successional processes that have been initiated and the new equilibrium attained.

Table 10.3. Main disturbances caused by the river regulation in the Mánamo basin, the ecological parameters affected, the prior environmental (biotic) condition, the type of succession initiated; the environmental (biotic) response and predicted species diversity and biomass, L: lower ; H: higher; N-C: no-change; V: variable. U: Upper; M: Middle; L: Lower; D: Delta.

Disturbances	Prior state	Succession	New equilibrium	Diversity	Biomass
Land desiccation (UD)	Natural grassland	Allogenic, indirect	Secondary sedge herbs	L	N-C
Hydrology (U-M-L)	Aquatic. Meadows	Allogenic, direct	New species assemblage	L	V
Hydrology (M-LD)	Aquatic meadows	Allogenic, indirect	Mangrove community	L	H
Hydrology (M-LD)	Sand bars	Allogenic, direct	Mangrove community	L	H
Hydrology (MD)	Swamp forest	Autogenic, indirect	Mangrove community	L	N-C
Hydrology (M-L D)	Sand bars	Allogenic, direct	Emergent meadows	H	H
Hydrology (UD)	Aquatic meadows	Allo/autogenic, indirect	Low semi-deciduous forest	H	H
Hydrology (UD)	Sand bars	Allo/autogenic, indirect	Low semi deciduous forest	H	H
Hydrology (LD)	emergent/floating sp.	Allogenic, indirect	New halophytic assemblage	L	N-C
Land clearance (UD)	Swamp forest	Allogenic, indirect	Marshes/Herbaceous swamp	L	L
Over exploitation (MD)	Swamp palm com.	Allogenic, indirect	Marshes/Herbaceous swamp	L	L

The disturbances affected primarily the species and community diversity and biomass, as discussed below.

10.4.1 Primary and secondary succession

Immediately after the river regulation and the draining of the land, most of the terrain in the Upper Delta which was supposed to become a highly productive region, became acidic causing the failure of the agricultural projects. The acidification of the land, particularly in the depressed areas, impeded the planned crop production. A successional allogenic process allowed sedges to replace the original species *Paspalum fasciculatum, Hymenachne amplexicaulis* and *H. donacifolia* (CVG, 1970) and other species (Cyperaceae) that were unable to grow under the new soil conditions. This led to a fall in agriculture productivity over a number years (Escalante, 1993). However, the subsequent introduction of some Poaceae such as *Urochloa mutica*, the tanner grass, which is a successful invader of the waterlogged soils competing against the native grasses, favoured cattle and more recently buffalo. The latter is an active consumer of some Cyperaceae, such as *Eleocharis mutata* and has led to increases in animal production.

The communities of aquatic plants along the river-shore of the Mánamo river were subject to an initial drastic change due to the perturbation caused by the changes in the level of the

water fluctuations. These are not detailed in this research because of the lack of detailed historical documents and archived studies. The distribution and biomass of aquatic plants is primarily affected by hydrological regime changes (van der Valk, 1981b; Greening and Gerritsen, 1987; Hill *et al.*, 1998; Coops *et al.*, 1999). The biomass production of the dominant macrophytes showed an increase in the Mánamo river (Upper Delta) in contrast to the Macareo river by 29 % for *Eichhornia crassipes* and 40 % for *Paspalum repens*. The new conditions of the lentic habitat allowed more aggressive development and expansion of the macrophytic meadows (chapter 6). Evidence of the reduction of biomass may be seen in the floating meadows that have drifted down-river in the lower Mánamo (see Plate 6.1 in chapter 6), where the plants succumb to the increased salinity, and eventually decompose.

Changes in seral communities such as the disappearance of some notable species that have been indicated during interviews with elderly fishermen and farmers, have undoubtedly taken place since1965. The communities are now considered to have reached a new equilibrium or climax. It is of interest to note that, the species diversity in the unregulated river remains higher than that of the regulated river, particularly in their middle courses (see chapter 6). Results from Greening and Gerritsen (1987) of a study of species composition and biomass dynamics in a marsh plant community, suggest that changing water levels results in natural (seasonal, but uneven) seasonal drought (the Macareo banks case), may produce higher macrophytic diversity and greater variability in biomass. The contrasting case would be if there were more frequent changes in river levels, or if there was a period of continuous waterlogging.

However, statements about equilibrium and climax stages must be viewed with caution. According to the successional stages depicted by Glenn-Lewin and van der Maarel (1992), the development of a seral community will develop, so long as there are always processes at work promoting community diversity. For instance, this is the case of the secular succession, where very long term phenomena are continuously influencing the communities. The possibility of temperature change and sea level rise due to global warming is an example of increasing disturbance that might be initiating successional processes at a global scale (Larcher, 1995; Boucher,1999). The seral processes may not follow a clear direction. At least over short periods of time, Dethier (1985), established that none of the assemblages of species in the tide pools he studied, was stable over many generations. Rather, they seem to exist in a changing dynamic state where disturbances are viewed as the stochastic factor overlying other, more predictable community structuring factors such as tidal height or pool size.

A case of primary succession occurred in this study when a new water level was established along the Mánamo river, creating permanently exposed sand bars (nudation process as defined by Clements (1916) cited in Begon *et al*, 1990). Previously the seasonal flooding used to cover the substrates exposed during the 4-5 months of the low water period, where every year an ephemeral community of species became established that were then removed by the ensuing floods (Glenn-Lewin and van der Maarel, 1992). The cyclic changes were mostly in the dominance of the invading plants because the primary pool of species that develops annually tends to be similar. Analogous processes have been viewed in the sand shores of the Macareo river. In the Upper Mánamo the primary succession continued and lead to the meadow community noted today, largely dominated by *Eichhornia crassipes* and *Paspalum repens*. These species show competitive traits such as large density branches, rhizomes, high potential relative growth rate and tendency to deposit a dense layer of litter (Grime, 1973). Similarly the dry forest at the top of the levées, is another case of primary succession (see Plate 6.1), that in most cases is been currently managed through agriculture practices. In the Middle and Lower Delta the newly exposed sand-bars have led to a mangrove formation and halophyte species assemblages.

Primary succession in Delta environments, however, may be akin to secondary succession (Glenn-Lewin and van der Maarel, 1992). Delta river development and salt marshes may be recipients of biological materials from many upstream sites before succession starts or during the seral stages. Their substrates may incorporate organic material from upstream. On the other hand, propagules and organic matter would always be moved downstream. They may also move upstream if tides are favourable. The *Rhizophora* seeds, across the Mánamo sub-basin for example, have colonised the upriver reaches of the rivers (chapter 8) by mean of this transport mechanism. However, this may also be the case for a bare substrate surrounded by forest vegetation where the organic matter, and seeds, continuously shed from the trees (Glenn-Lewin and van der Maarel, 1992).

Succession processes have to be evaluated over various periods of time, particularly the natural systems that are dynamic such as the Deltas, where the hydrologic and geomorphological processes may not be predictable.

The knowledge of the species composition before the disturbance allows the determination of the seral stages of the succession and the species composition of the future equilibrium (Henry *et al.*, 1996). In general, the sequence of the vegetation colonisation in the Delta follows the stages proposed by Amoros and Wade(1996). This starts with aquatic emergent and isolated plants of species such as *Eleocharis elegans* and *Cyperus articulatus*. These form small

islands of vegetation and cause a reduction in water velocity increasing the deposition of silt sediments. In the Mánamo (Table 10.4), floating plants, particularly *E. crassipes,* and to a lesser degree *Pistia stratiotes*, *Salvinia auriculata* and *S. sprucei* anchor themselves and their organic matter serves to enrich the substrate. Later, other emergent species such as *Ludwigia* spp and *Paspalum repens*, form dense communities. Finally there appear tall herbaceous species (*M. arborescens*) and woody bushes composed of *S. exasperata, Ludwigia* spp or *Mimosa pigra*, which are in turn followed by trees.

The successional sequence in the Macareo river is similar but rooted species dominate the successional sequence(Table 10.4). It starts with the colonization of the sand banks by *Paspalum repens* and *Echinochloa polystachya* at the margin of the river and *Paspalum fasciculatum* on the levées, these are species that allow sediment deposition, facilitating the establishment (Connell and Slatier, 1977) of a shrubby pioneer stage. A second shrubby stage is also composed of tall Poaceae such as *Gynerium sagittatum* followed by the arboreal stages. This kind of sequence is likely to occur along the banks of the Macareo during the lateral migration of the channel (G. Colonnello, unpublished data) and has also been reported in the Peruvian Amazon by Lamotte, (1990).

Table 10.4. General stages of successional development in the Delta river edges.

Mánamo		Macareo
	Herbaceous stage	
Eleocharis elegans	**(primary invaders)**	*Paspalum fasciculatum*
Eleocharis mutata		(Top of banks)
Cyperus articulatus		*Paspalum repens,* (water level)
		Echinochloa polystachya
		Eichhornia azurea
↓ ↓		
	Herbaceous stage	
Eichhornia crassipes,	**(secondary invaders)**	*Ludwigia* spp.
Pistia stratiotes		*Polygonum acuminatum*
Paspalum repens,		
Ludwigia spp.		
↓		↓
Montrichardia arborescens	**Scrubb stage**	*Ginerium sagittatum*
Mimosa pigra		*T. integrifolia*
Sesbania exasperata		*Sesbania exasperata*
↓		↓
	Characteristic first	
Erithryna sp., *Cecropia* sp.	**arborescent stage**	*Cecropia* sp.

Several simultaneous processes may occur, because allogenic succession is promoted by a large perturbation or disturbance such as the barrage construction . Autogenic succession is promoted by the modification of the habitat which prepares it for the pioneer species such as occurs when sediments and organic debris are trapped between the stems of species that colonise bare sand bars. According to Connell and Slatier, (1977), the new invading species found more conducive conditions in which to become established. Competition is also observed, such as juvenile mangrove trees shading the pioneer heliophillous community which inhibits their establishment and growth as observed in the Middle-Lower Delta (see chapter 8) (Connell and Slatier, 1977). Competition may be intense when mangrove species invade the meadows of floating and emergent plants in the Lower Delta. The increasing soil salinity observed in the Middle Delta gives them a competitive advantage over freshwater species because their tolerance to salinity levels of up to 6 g l^{-1} (Pannier and Rabinovich,1976). However in the Upper Delta, where substrates are not yet influenced by increasing salinity, the aquatic macrophytes are stronger competitors than other species, preventing the mangrove seeds from becoming established.

10.4.2 The case of the Middle Delta communities

The swamp forests and swamp palm forests of the Middle Delta were affected by the continuous fires and logging activities in the period prior to the dam construction (1965) and subsequently by over-exploitation and fire in the period after the river regulation resulting in a high frequency of disturbance of the natural cover. This anthropogenic influence facilitated the reduction of the community diversity, diminishing the dominance of low rates of growth (k-strategy) (MacArthur and Wilson, 1967); or C-S selection (Grime, 1979) species and favouring the dominance of species with high rates of growth (r-strategy) (MacArthur and Wilson, op.cit.) or R selection (Grime, 1979), as was seen in the case of the forest communities in chapter 4. The species which could not reach the maturity and consequently did not produce seeds before the next disturbance event, were substituted by species, mostly herbaceous plants, that were able to do so.

The impact of regulation on palm communities has been indirect, because prior to the regulation, infrequent disturbances allowed the forest species to recover; such as natural or anthropogenic fires. However the added impact of the Warao inhabitants in the region, increased the frequency of fires and palm felling, making the forest biota less able to recover. This process resembles the 'dynamic equilibrium model' proposed by Huston (1994) for the coexistence of functional analogous species within the same community type.

The disturbance produced by the Warao across the marshes and swamp communities in the vicinity of their new settlements, is likely to diminish in the near future. This is because the Indian groups are undergoing cultural adjustments as they adopt Creole traditions of subsistence. Many people are increasingly dependent on their part-time cash jobs in the cities. They are also migrating to urban areas in search of improved life styles. At the same time, the cultural values of Indian artisan crafts and the indigenous knowledge of how to use such natural resources are rapidly being forgotten. It would not be surprising if the successional processes within the forest communities had suffered further change since 1996 (see chapter 9).

The reverse process, is characterised by tree-less marshes evolving to swamp palm communities and swamp forests, that occurred after the river regulation, along the right bank of the Pedernales river (see chapter 8). This was aided by the reduction in the 'disturbance frequency' as the Creole people abandoned the region. The different stages of the vegetation patches in the Middle Delta, allow us to depict the main seral stages. The principle single species that starts the successional processes is the moriche palm (*Mauritia flexuosa*) showing an *r*-strategy by outcompeting other forest species.

The characteristics that promote the dominance of the moriche palm (*Mauritia flexuosa*) are:
1. Widespread seed dispersion by rivers, birds, small mammals and humans;
2. Medium longevity, up to 60 years;
3. Short period of seed production, 8-10 years;
4. High annual production of fruits, 1,500 to 5,000;
5. High levels of light saturation;
6. Germination of seeds not requiring high solar radiation inputs in the photosynthetically active band (PAR); and
7. Seedlings responding to high levels of light, characteristic of late morning radiation levels in the tropics.

In this way marsh vegetation, dominated as it is by herbs such as *Cyperus giganteum*, *Eleocharis mutata* and *Leersia hexandra*, is colonised by the seeds and fruits of the palm in relatively dry years, when the water level of the wetland is shallower. This allows a community of seedlings to be established. The continuous growth of this community of juveniles (diagrams A and B in Fig. 9.3), marks the beginning of a series of environmental autogenic changes:
1. The reduction of the light levels reaching the soil surface, which produces an overgrowth and competition which eliminates eliminates the heliophyllous grasses and sedges;

2. The creation of mounds of organic matter basically comprising the fallen megafilous leaves, which elevate the edaphic substrate and thereby create an ideal habitat for the germination of shade tolerant species; and

3. The gradual reduction of the water level by the increasing of transpiration. At the point when the Moriche palm dominates, the formation may be called a swamp palm forest or 'morichal'.

The creation of a particular environment, shady, dry and with abundant organic matter, permits the establishment of a 'more K-strategy species' or late-successional species such as *Erythrina fusca, Symphonia globulifera* and *Virola surinamensis* (diagrams C and H in Fig. 9.3). These are essentially heliophyllous species whose seedlings and saplings tolerate low levels of light. These successional processes fit into the 'facilitation' model of Connell and Slatyer (1977), the later species becoming established and growth only after primary plant invasions have suitably modified the conditions. The newly established species may, in turn, reduce the competition due to overgrowth. This sequence is evidenced by the high growth rate of this type of forest tree which yields, 2.39 to 3.76 m^3 ha^{-1} yr^{-1} (Veillon, 1977). The change in the availability of light for the moriche palm, validates the resource-ratio hypothesis of succession (Tilman, 1985). The formation may then be termed a swamp forest (diagram D in Fig. 9.3).

The coexistence of several different communities, and in turn of different species types, during the successional processes, in a relatively small area as seen in the Middle Delta is supported by the existence of multiple niches (the niche diversification hypothesis; Connell, 1978; Denslow, 1987; Welden, *et al.*, 1991). The high spatial and temporal heterogeneity of habitats and niches, is based in the soils micro-heterogeneity encountered in the interior of the Delta basins This is where layers of different proportions of silt, sand and clay are mixed with layers of peat in different stages of maturity (van der Voorde, 1962) and the particular consistency of the peats which absorb water, creating mounds of variable dimensions (Dost, 1971). As Huston (1994) pointed out,

> "physical heterogeneity such as geology, soils and topography also increases the number of functional types that can occur, as well facilitating the landscape scale coexistence of functional analogues whose relative competitive ability is altered by environmental conditions".

The same author, also indicated that

> "in physical homogeneous landscape is still possible to have dramatic heterogeneity that is produced by the asynchronous patch dynamics of disturbances and succession".

On the other hand the diversity of ecological niches provided by the physical heterogeneity allows for total or partial survival of the communities during a disturbance facilitating a quicker recovery after a disturbance, enhancing, for instance, the following successional processes.

10.4.3. Diversity reduction and biomass increase

Several cases have been investigated where the species diversity is reduced as a consequence of the river regulation. However the effect may be seen not only at a regional level in the Mánamo sub-basin, but also in its upper region by the reduction of the surface area of the wetlands. The lentic environments support the higher macrophyte species diversity as established in this study (see chapter 3). The construction of the main dam and the 174 kilometres of cofferdams built to protect the inhabited Upper Delta, restricted the seasonal formation of lagoons and marshes (as is partially seen in Plate 2.2). Two sites that sustained high species diversity in the Upper Delta such as Lag. Ataguía and Lag. Terraplén for instance, are found in the 'unregulated' side of the cofferdam close by the Macareo overflow.

Huston (1994) observed that one group of organisms in a community may be increasing along a productivity gradient (from a fluvial to an estuarine system), while the diversity of another group is decreasing along the same gradient. On the other hand the biomass reveals a reverse pattern where the increase in the diversity correlates positively with the decrease of biomass, which is particularly clear in the upper and lower reaches of the Mánamo. Fig. 10.3, shows a hypothetical diagram relating the species diversity to biomass in the regulated and unregulated terrain. The riparian communities show the higher species diversity in the middle stretches of the river courses (intermediate disturbance hypothesis, Connell, 1979; Huston, 1994), where the flooding has an intermediate effect allowing the existence of a wider variety of habitats. This is particularly evident in the Macareo river that continues to show seasonal fluctuations as well as a gradient in seasonal water level rise, from the upper to the lower river section (see Table 6.5). In the Mánamo the diversity shows a similar curve but it tends to be low in the upper section where floating meadows composed of few species e.g. *Eichhornia crassipes* dominate, and in the lower section where one species of mangrove dominates. Downriver toward the sea, as the freshwater species become less frequent, the salt tolerant species help to maintain the diversity. On the other hand the curve of the biomass is the inverse to that of the species diversity.
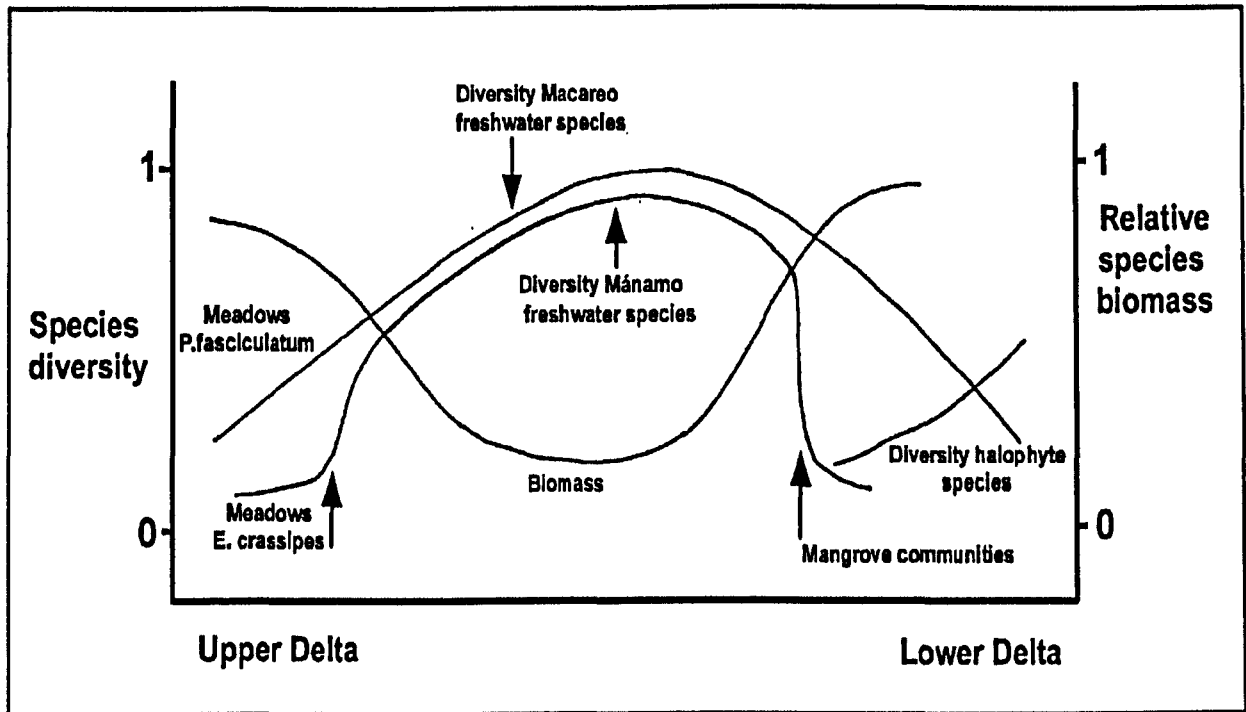
Fig. 10.3. Relation of species diversity and biomass

10.5 The equilibrium model

This process may be schematically represented by the hypothetical curve of a model shown in Fig. 10.4. which include three distinct phases:

1. The 'initial equilibrium', the state preceding the disturbance;

2. The 'disturbance phase', where the environmental parameters are changed; and

3. The 'new equilibrium' phase where the biotic and physical factors compensate for the changed environment.

In fact after a 'disturbance' the multiple environmental factors (biotic and physical) of a wetland ecosystem are forced into a response but with decreasing magnitude over time as the 'forcing' environmental factors diminish in strength
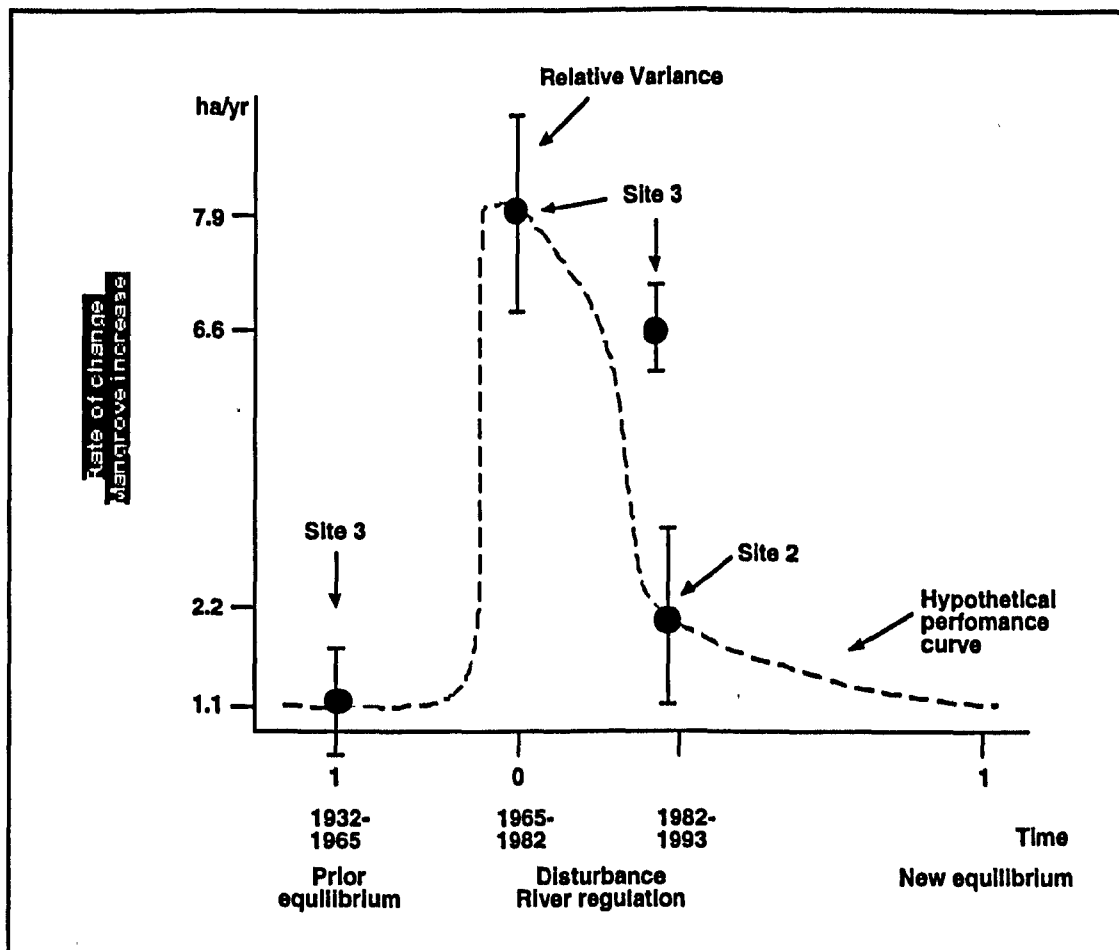
Fig. 10.4. The 'Equilibrium model' for the environmental response of the anthropogenic impact of the Mánamo dam. Example of the mangroves community increase in the studied sites (chapter 8)

This equilibrium model is similar to the 'model of ecosystem restoration' proposed by Molles Jr. *et al.* (1998) for the restoration of riparian of habitats which also involves three phases:

1. the disconnected phase, prior to the re-establishment of the flood-pulse (in the case of the floodplain management),
2. the reorganisation phase and
3. the steady-state phase.

Both models are based on the capacity of natural systems to respond to a particular disturbance, stressing the period of renewal. This period is equivalent to the 'relaxing' period between the perturbation and a new equilibrium which is finally reached, as Bender *et al.* (1984) asserted. According to Rapport and Witford (1999), the ecosystems do not 'bounce back', indicating that the new equilibrium will be always different from the previous one.

Several examples in the case of the Mánamo regulation may be proposed. Figure 10.4 shows data for the mangrove invasion of the sand-bars that remained dry after the change in the hydrological regimes of the Mánamo river. The increase in the mangrove communities along the Middle and Lower course of the Mánamo river was 1 ha yr^{-1} (see chapter 8, Table 8.2) before the river regulation in the period 1932-1965, reaching a maximum rates of 7.8 ha yr^{-1} in site 3, after the river closure in the period 1965-1982 due to the increase in the salinity levels, but it later declined to a rate of 6.6 ha yr^{-1} in the period 1982-1996. For example Site 2, located upriver from Site 3, showed a rate of 2.2 ha yr^{-1} in the period 1982-1996. This may be considered as a potential rate for site 3 in the future - at such a time when the mangrove community reaches an equilibrium with the new salinity values in the waters observed after the dam construction.

The model may also be applied, even if somewhat hypothetically - to the case of the riparian meadows developing along the Mánamo river. Prior to the dam construction, the biomass production and distribution of the floating meadows (*E. crassipes*) in Mánamo should have been similar to that of the Macareo river, at a level of 378 g m^2. After the closure, the dam gates remained closed for a year causing an explosion of macrophytes due to nutrient enrichment, supplied by the untreated sewage from Tucupita (Escalante 1993). The production may have reached values around 2,200 g m^2, which are evidently among the highest levels that can be found (Boyd and Scarbrook, 1975; Lallana, 1980). The only currents were due to the tides. The prevailing chemical and physical conditions should have been optimal for the development of these plants. *E.crassipes* shows a maximum growth rate at high temperatures (26 °C) (Bock, 1969) and a daily incremental factor of 1.148 (Penfound and Earle, 1948). The eventual opening of the sluice gates created a surge of water toward the mouth that surged through part of the meadows and created the new condition as we see today that mean a production of 900 g m^{-2}.

The equilibrium model may be also applied to the effects of the human population. The life of Warao Indians was noticeably affected by the change in the water chemistry. The salinity increased in the river network of the coastal belt, as the seasonal flooding was suppressed and the tidal influence from the sea lasted all through the year. The sources of potable water became salty and the soils started to become saline. The initial effect was profound, causing even the death of many people due to the unhealthy waters and the decline of the *Colocassia* sp crops. The population of entire towns migrated or were moved to the south of the Delta, where the availability of freshwater was not at risk. Today, the human communities are expanding again supported by a new life style (Heinen and Rodriguez, In press).

The length of time required to restore the equilibrium condition is likely to be different in every situation because of the variety of ecological constraints involved in each. Begon *et al.* (1990) pointed out that there is likely to be an important parallel between the properties of a community and the properties of its component populations. In stable environments, populations will be subject to a relatively high degree of *K* selection; in variable environments they will be subject to a high degree of *r* selection. The *K*-selected populations high competitive ability, high inherent survivorship, but low reproductive output (MacArthur and Wilson, 1967), will be resistant to perturbations, but once perturbed will have little capacity to recover (low resilience). The *r*-selected populations, by contrast, will have little resistance but higher resilience.

In the case of the environment of the Mánamo some of the changes caused by the regulation may reach their new equilibrium faster than others such as the forest or mangrove ecosystems. Their main components are *K*-selected species stretching over several decades, by which time the changes in the riparian meadows should have reached a new equilibrium, within a period of few years, as they are composed mainly of *r*-selected species. The re-establishment time of macrophytes in rivers after a disturbance caused by floods is much shorter as established by Henry *et al.* (1996). Ponds and other aquatic systems with rapidly changing phytoplankton populations or annual grasses show greater recovery ability than do terrestrial systems such as evergreen and deciduous forests, as found by O'Neill (1976) in a simulation of standard perturbations on different models of communities.

The seral steps that occur between the disturbance and the new equilibrium may be marked by a reduction of biomass or the temporal extinction on one species indicating a 'subsidy-stress' gradient in the model of Odum *et al.*, (1979). In this model, increasing the intensity of a specific perturbation is plotted on the x-axis and the response plotted on the y-axis including the enhancement, reduction or extinction of the community (Fig. 10.5). The two hypothetical curves show the response to:
1. The 'usable input' that produces a convex performance curve as a response and;
2. The 'toxic input', the performance curve of which tends to diminish.
The biomass production of floating and emergent macrophytes in the upper stretches of the Mánamo river may fit into the first response type, which is the subsidy effect. The reduction of the water discharge in the upper reaches of the Mánamo river created a lentic environment where aquatic species such as *Eichhornia crassipes* and *Paspalum repens* increased their biomass production compared with the lotic habitats in the unregulated rivers as the Macareo river (see chapter 7). However a significant reduction of the water discharge is likely to increase the salinization of the waters, instigating a further successional process. This may

lead to the replacement of the total community, as occurred in the lower Mánamo lower course when the fresh water herbaceous communities were replaced by halophytic meadows.
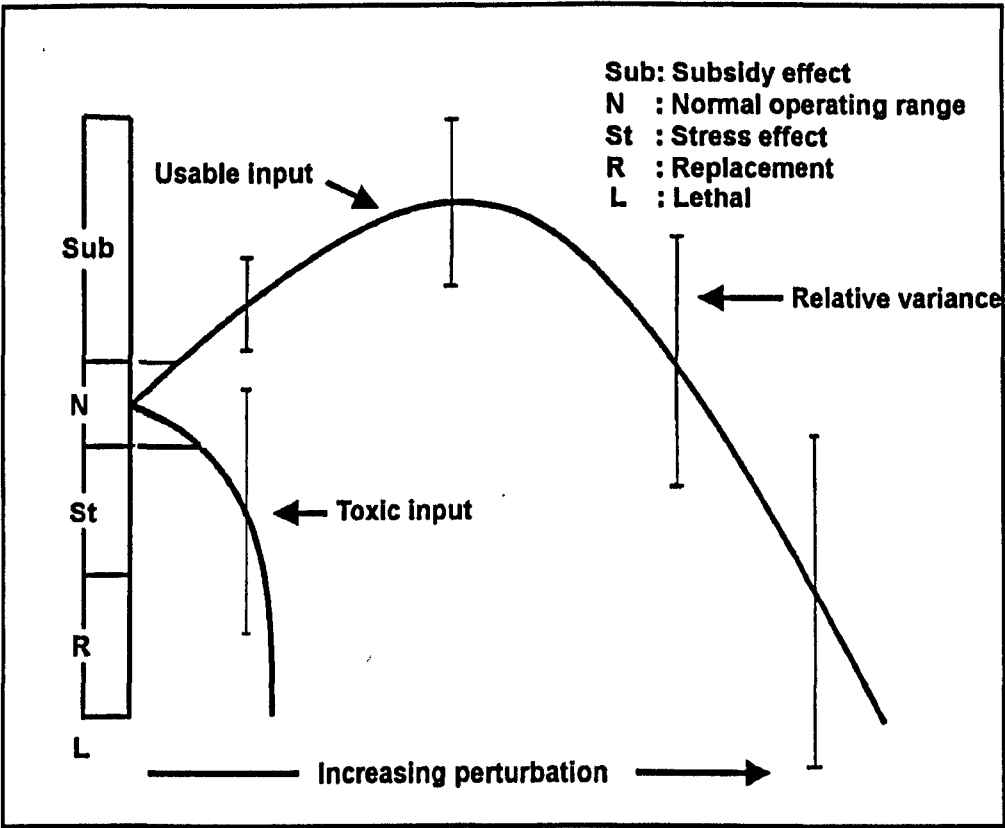
Fig. 10.5. The subsidy-stress gradient model (Odum, *et al.*, 1979)

On the other hand, the virtual disappearance of species such as *Echinochloa polystachya* and *Eichhornia azurea* from the Upper Delta river edges and their substitution by emergent species (*Montrichardia arborescens*) are examples of the second response type, the toxic input. This is where the perturbation caused an immediate stress situation, as the species were unable to adapt, and were replaced by other species, more tolerant to the new environmental conditions.

10.6 Importance of the Orinoco Delta and its restoration

Deltaic wetlands around the world that have been intensively managed by people have been studied in order to estimate the value as a natural resource. This is because the wetland environments possess a potential for economic growth (Coleman *et al.*1998, Elster *et al.*,1999).

Junk (1995) summarised the following ecological importance of the tropical wetlands:

1. Wetlands have multiple functions in the landscape. Large-scale modification will have far-reaching consequences on biodiversity, local and regional climate, hydrology and sediment load of rivers down to their mouth and adjacent marine habitats;

2. Wetlands harbour many highly adapted plant and animal species. They are of great ecological value, and should be managed in a way assuring the maintenance of this value;

3. Most wetlands belong to a category of floodplain, which means that they have a distinct dry and wet phase. Changes in the hydrological regimes will have far-reaching consequences for the structure and function of the wetlands and their actual and potential use;

4. Wetlands of low nutrient status, such as the extensive swamp forests and marshes over acidic organic matter, have a low natural production capacity. They are extremely vulnerable to human impact and should be used to a limited extend only. Logging for timber production and agriculture are not recommended, because of the slow growth of trees and the low nutrient status of the soils; and

5. Wetlands of high nutrient status such as the floodplain of nutrient-and sediment-rich-white water rivers, require management concepts, which consider the interests of different users (fishermen, farmers, and foresters) to fully exploit its production potential.

Worldwide wetland ecosystems represent an economic resource whose value to society is only now becoming realised. Their average global value is without doubt, among the more valuable natural systems in existence, and is estimated as follows :

14,785 $ ha^{-1}yr^{-1} for wetlands;

9,900 $ ha^{-1}yr^{-1}for tidal marshes or mangroves

19,580 $ ha^{-1} yr^{-1} for swamps/floodplains

22,832 $ ha^{-1}yr^{-1} for estuaries (Costanza *et al.* 1997, 1998).

The value given to a particular ecosystem, was not available or even understood almost 40 years ago when the Mánamo regulation was projected. The annual value of the wetlands may be affected by large anthropogenic interventions and these could be evaluated, according to Costanza et al., (1997, 1998) by such methods. Such a monetarist approach might be valuable in explaining to politicians and development managers why natural ecosystems and particularly wetlands should be protected.

10.6.1 The case for partial amelioration of the effects of regulation

In the recent years as a consequence of the general concern about the ecological impacts caused by the Mánamo dam, it has been suggested by some non-governmental organisations (NGOs) that there should be a partial restoration of the hydromorphic situation as existed prior to the building of the barrage (Monente, 1998). As pointed out by Wissmar and Beschta (1998), the development and re-establishment of riparian ecosystems depends on very

complex dynamic processes, including non-linear interactions. An effective strategy for restoration requires a careful review of the analysis of the baseline data at both local and regional scales. Moreover, fluvial ecosystems are remarkably resilient in their ability to adapt to and recover from physical and chemical disturbances. However if the disturbance is prolonged and causes a complete loss of critical habitat elements, ecological integrity cannot be maintained (Gore and Shields Jr.,1995).

To be feasible, restoration must take into account the new environmental and social characteristics of the region. In particular the Orinoco Delta is still predominantly a wilderness area supporting a wide range of natural systems as well as indigenous Indian activities which are adapting to the new environment. If this is so, a return to a former subsistence system might not be feasible (García A, *per. com.*). The restoration of the river flow would affect most of the river margins downriver of the dam and in particular would cause the waters to re-inundate areas in the Upper Delta. On the other hand, the economic activities such as cattle raising, would be adversely affected.

Rasmussen (1994) proposed the idea of a 'string of beads' restoration. Applying his concept to the Mánamo "not all of a river's floodplain needs to be reopened to the riverine floodplain to revitalise ecosystem integrity". In the same vein, Sparks *et al.* (1998) proposed that 'relaxation' of the constraints on the water management of wetlands should be considered as a viable alternative. Likewise, Middleton (1999) stressed that an alternative approach to dam removal for flood pulse in rivers is to provide controlled releases of water to simulate flood flow conditions. Adapting these concepts to the case of the Mánamo river, it may be proposed that the opening of the sluice gates up to a certain level should be permitted in order to allow increased discharge to occur.

According to the opinion of several hydrologists with expertise in the Mánamo system (Córdoba,J, *pers. com.*), the water discharge should be increased to a level similar to the previous water discharge during the low water period, that is about 800 m^3 s^{-1}. This water inflow, simulating a seasonal discharge such as that of the Orinoco, would permit an increase in between 1 and 2 m in the water level (see Fig. 10.6). An automatic telemetric system would send a message daily to enable optimal dischage to be effected. Any suggested discharge should be validate by the installation of an ongoing research programme.

The study has indicated a number of benefits, ecologically, socially and economically in the environs of the Macareo and unregulated regions of the Delta that are absent in the Mánamo. The advantages in partial restoration can be placed into three categories, these are:

1. Ecological, as the natural system may reassume some of the properties such as a higher biodiversity.
2. Social, in terms of the melioration of the living standard of the Creole and Warao populations.
3. Economic, as a greater number of people might improve their income through the agriculture and the sustainable exploitation of the natural resources.

From the studies undertaken in this thesis it is now possible to identify the advantages of partial restoration of the Mánamo sub-basin to a more 'natural' flow regime.
1. Increase of the flow of freshwater (see Fig 10.6) during the rainy season reducing the saline intrusion and mangrove colonisation upriver (see chapters 6 and 8). This is probably the most obvious natural benefit derived from the amelioration of regulation. The extensive mangrove communities have been managed since the1950s (Canales, 1985) and there is no sign that this will decline, since the annual authorisation for exploitation has been constantly increased.
2. An improvement in the water quality for the river communities, by allowing effluents and sewage to be partially treated and then discharged safely into the ocean. This is an important task since a few years ago a cholera epidemic killed several people in the Lower Delta due to the consumption of contaminated crabs (Escalante, 1993). It may also lead to a reduction in the very high child mortality rate of 47 %, mainly caused by diarrhoeal diseases (Layrisse et. al.,1980).
3. To re-open the connections between the channels that are currently blocked would allow the regeneration of the soil or at least impede further salinization along the banks and terrain in Lower Delta. This would encourage the cultivation of *Colocassia* sp and might also re-establish the habitat for freshwater fish species along the coastal belt and allow
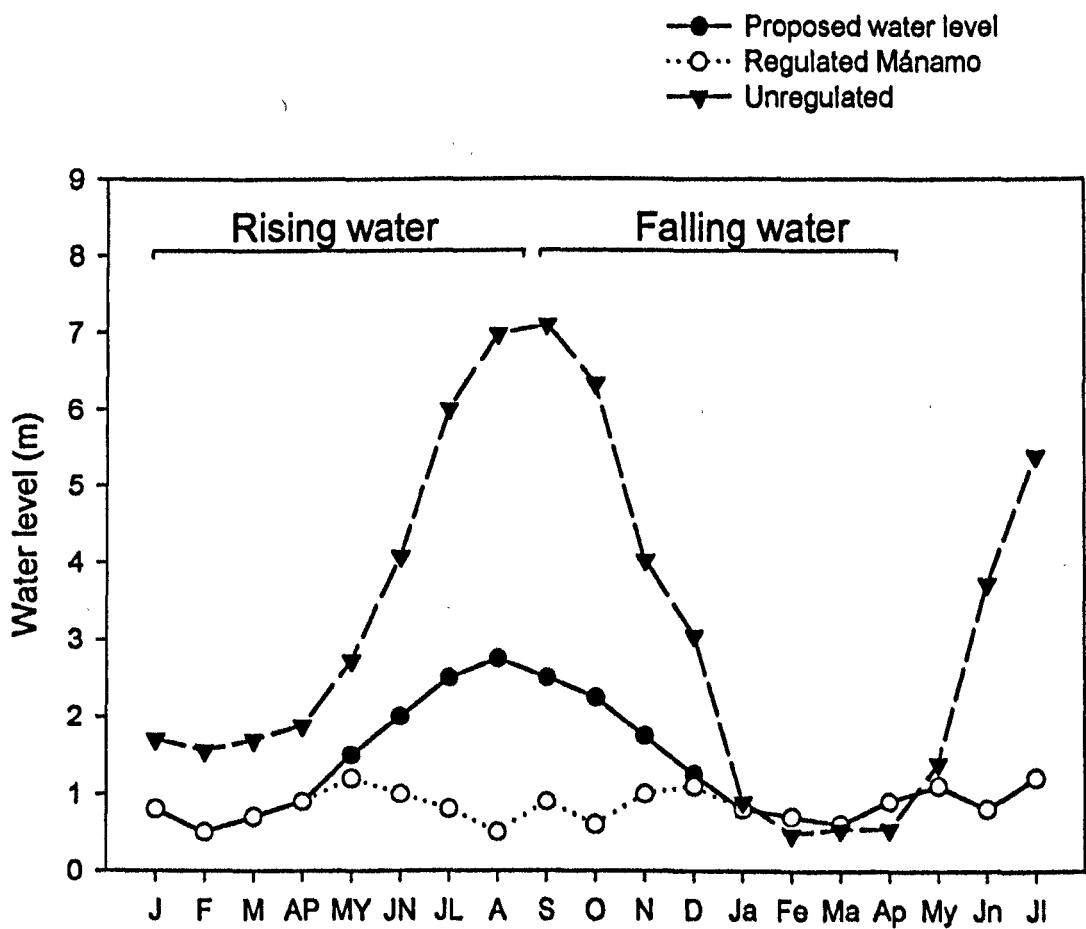
Fig. 10.6. Hydrograph of the regulated and unregulated Mánamo river showing the proposed water level fluctuation.

the re-colonisation by Warao Indians (see chapter 9). This would reverse the conditions that led to the migration of the Warao in the first instance (García and Heinen, in press).

4. To reduce the further salinization of the inter-riverine terrain and alter the community composition, particularly the swamp palm forests, where local inhabitants gather important subsistence products (see chapter 9).

5. To re-establish the seasonal agriculture production and raise the annual income favouring the commercial development of small farmers, many of whom are living in the towns, having abandoned the subsistence (see chapter 9).

6. To improve the local navigation removing the macrophytic floating communities more efficiently to the open sea and improving the quality of life. Several channels such as the Cocuina and Pedernales, should be cleared of debris to improve local river transport (see chapters 6 and 7).

7. To re-establish part of the riparian macrophytic community, currently poor in biodiversity (see chapter 3, 4 and 6) .

A rehabilitation project would need to include the proper management of peak river discharges in order to maintain the functions of the towns as well as the new industrial and agricultural developments. At the same time it should allow the re-establishment of the natural ecosystem of the riverine and wetland system, dependant, as it has been in the past, on the seasonal flow of the Mánamo. Diversity of riverine species may be restored if lost species from the upper Mánamo river could be re-established. It is likely that plant propagules from the unregulated section of the Mánamo (upstream the barrage) would bring about the succession of a diverse flora at the proposed new level of the shoreline (Hill et al., 1998), in a kind of 'self design' of natural recovery as suggested by Mitsch and Wilson (1996), which could be enhanced by 'seeding' through human or natural means Mitsch et al.,(1998).

Proper management of wetlands in the Mánamo sub-basin is of fundamental importance for the human population (Mitsch and Gosselink, 2000). Wetlands have abundant and varied resources, such as plants, aquatic and terrestrial fauna, many of which feature in the diet of communities at the local and regional scale. This is particularly true in a region where little industrial development has taken place. Wetlands therefore play an essential part in the supply of food for many rural communities (Roggeri, 1995). This role of the Orinoco Delta wetlands has been particularly important in the survival of the indigenous and Creole inhabitants (see chapter 9) because the region was almost completely isolated from the rest of the country.

Ignorance of the physical capabilities and properties of wetlands that are to be targeted for reclamation has proved to be a major hindrance. There is also ignorance of the local or traditional systems of exploitation, which may be unfamiliar to western-trained minds. Indigenous systems have been proven to be rich in their use of a considerable range of renewable resources, highly sustainable and low energy-using, and may offer better returns than a conversion to agricultural land use (Williams, 1993b). Examples of this are two industries that flourished besides the traditional agriculture and livestock farming practices. The palmito heart, collected from the palm *Euterpe oleracea* and processed in two factories in La Horqueta town and the mangrove (*Rhizophora mangle*) logging, a valuable construction material favoured by affluent people in their houses.

General conclusions

1. The dam construction in the Mánamo river established a new division in the Delta:
    1. The regulated Delta, including the Mánamo sub-basin, from the Mánamo river course to approximately the Tucupita channel, flowing close to the Macareo river.
    2. The unregulated Delta, including the territories from the Macareo river to the Rio Grande river, the southernmost distributary.

2. The more striking features differentiating the two Delta areas are the hydrologic regimes of their water courses. The Mánamo sub-basin shows a regimen of relatively minor water level fluctuations of less than 1 m and a moderate current velocity (mean: 45 cm s^{-1}) generated by tidal influence. In contrast the rivers in the unregulated region, show seasonal water level fluctuations of up to 7.5 m and current velocities of up to 150 cm s^{-1}.

3. Despite the river regulation, physico-chemical variables, such as ion content, pH, electrical conductivity and DO, do not show significant differences in the upper stretches of the channels of the Mánamo and Macareo. However the increased tidal and saline influence from the ocean have led to increasing changes in the lower reaches of the regulated rivers, where the former seasonal fluvial regime has been replaced by a permanent estuarine regime. This change is seen in an upriver expansion of the halophyte communities, aquatic meadows and mangrove communities.

4. The aquatic and semi-aquatic vegetation of the Orinoco River Delta represents important evidence of biodiversity only brought to light by this study. To date, 174 species have been recorded, some for the first time, giving valuable insight into the floristic composition of the region. Further sampling will permit a more complete vision of the Delta's species and the environmental variables which affect them. The results of this study show that the Orinoco Delta is unique, possessing a higher species richness than other large South American wetlands.

5. Aquatic environments of the Orinoco Delta may divided in to two main groups:(a). Lentic habitats, comprising lagoons, small creeks and marshes of predominately clear waters; and (b) Lotic habitats, represented by the big distributary channels, of white water.

6. The water bodies of the Delta are subject to a wide dynamic hydraulic regime. The lagoons and marshes are either rain fed and/or supplied from the overflowing water of the channels. The reverse process takes place during the dry season.

7. As a result of the physical processes mentioned above, the physico-chemical conditions of the water bodies, such as transparency, pH and electrical conductivity vary during the annual cycle. These variables influenced the establishment of different vegetation communities and the abundance of their characteristic individual species. Controlling variables of the auto-ecology of each community could only be ascertained by frequent sampling during a whole annual cycle.

8. The differences found in the floral composition of the meadows of aquatic plants in the Mánamo and Macareo seems to be the result of the hydrodynamic differences between the channels morphology, bank slope, current velocity, and hydrology regime. These differences have led to the establishment of a unique set of species adapted to conditions in each water course.

9. The hydrological conditions established by the water regulation led to a higher biomass production of *Eichhornia crassipes* and *Paspalum repens* in the upper stretches of the Mánamo than in the Macareo river. This difference was due, essentially, to the great elongation of the stems achieved by the plants, particularly *E. crassipes*, in the Mánamo channel. The chief environmental differences were:

   1. The high water flow in the Macareo river, that reduced the uptake and the recycling of nutrients in the roots of the macrophytes from both water and also from sediments below the floating mats and

   2. The high and rapid variation of the water level in the Macareo that modifies the habitat where the communities are established.

9. The fluvial system of the Mánamo river changed to an estuarine environment. The saline environment is becoming more evident upstream causing the replacement of freshwater species with halophyte species. A significant increase in the surface area of the mangrove communities has taken place with initial expansion rates of 7.8 ha/year. This colonisation has also affected several large neighbouring distributaries such as the Pedernales and Cocuina channels.

10. From the point of view of human population, transformation of the fluvial regime to an estuarine regime brought a series of anthropological changes, of which the most important were:

   1 The abandonment of the former agricultural practices by the Creole inhabitants settled in the Middle Delta. These resulted in secondary vegetation succession in the region - from marshes to palm communities.

   2 The immigration of the Indian populations in some regions of the Middle Delta, also resulting in profound modifications in plant community distribution, from palm communities to marshes. This high level of ecological change, initiated by disturbances, has led to new communities becoming established over the past 30 years. Such rapid secondary succession is promoted by several factors, including the fast growth of the main component of the communities, the Moriche palm and the changing environmental conditions so produced.

In conclusion, whatever the social and economic benefits of river regulation to a catchment may be, the effects on biodiversity, on the evidence presented in this study, must remain a major concern.

As Chapin et al., (2000), have stated

"diversity at all organizational levels, ranging from genetic diversity within populations to the diversity of ecosystems in landscapes, contributes to the global biodiversity" and on the other hand "species diversity has functional consequences because the number and kind of species present determine the organismal traits that influence ecosystem processes".

It is by this overriding reason that a partial return of the Mánamo to its former flow regime is seen as the best option in any attempt to restore biodiversity.

REFERENCES

Abacus Concepts, StatView (1992) *Abacus Concepts, Inc.* Berkeley California

Ali, M.M. and Soltan, M.E. (1996) The impact of three industrial effluents on submerged aquatic plants in the River Nile, Egypt. *Hydrobiologia,* **340,** 67-76

Alvarez, R. (1987) Dinámica sedimentaria en los canales de Margarita-Coche-Araya. *Memoria de la Sociedad de Ciencias Naturales La Salle,* **127-128,** 77-103

Amoros, C., Gilbert, J. and Greenwood, H.T. (1996) Interactions between units of the fluvial hydrosistem. In: Petts, G.E. and Amoros, C. (eds.) *Fluvial hydrosystems.* Chapman and Hall, London. 184-210

Amoros, C. and Wade, P.M. (1996) Ecological successions. In: Petts, G.E. and Amoros, C. (eds.) *Fluvial hydrosystems.* Chapman and Hall, London. 151-172

APHA (American Public Health Association) (1985) *Standard methods for the examination of water and waste water.* 16 th Ed. New York

Armentano, T.V. (1993) Soils and ecology: Tropical wetlands. In: Williams, M. (ed.) *Wetlands: A threatened landscape.* Blackwell Publishers, Oxford. 115-145

Arteca, R.N. (1997) *Flooding.* In: Prasad, M.N.V. (ed.) *Plant ecophysiology.* John Wiley and Sons, New York. 151-172

Aymard, G. (1997) *Forest diversity in the interfluvial zone of the Rio Negro and Río Orinoco in Southwestern Venezuela.* Master Thesis. University of Missouri, St. Louis

Baattrup-Pedersen, A. and Riis, T. (1999) Macrophyte diversity and composition in relation to substratum characteristics in regulated and unregulated Danish streams. *Freshwater Biology,* **42,** 375-385

Barrat-Segretain, M.H. (1996) Strategies of reproduction, dispersion, and competition in river plants: A review. *Vegetatio,* **123,** 13-37

Barrow, C.J. (1987) The environmental impacts of the Tucuri Dam on the Middle and Lower Tocantins River, Brazil. *Regulated Rivers,* **1,** 49-60

Beard, J.S. (1955) The description of Tropical American vegetation-Types. *Ecology,* **36,** 89-100

Bedford, B.L. and Preston, E.M. (1988) Developing the scientific basis for assessing cumulative effects of wetlands loss and degradation on landscape functions: Status, perspectives, and prospects. *Environmental Management,* **12(5),** 751-771

Begon, M., Harper, J.L. & Townsend, C.R. (1990) *Ecology: Individuals, populations and communities.* Blackwell, Oxford

Bender, E.A., Case, T.J. and Gilpin, M.E. (1984) Perturbation experiments in community ecology: Theory and practice. *Ecology,* 65(1), 1-13

Bock, J.H. (1969) Productivity of the water hyacinth Eichhornia crassipes (Mart.) Solms. *Ecology,* 50(3), 400-464

Bockstael, N., Constanza, R., Strand, I., Bointon, W. and Wainger, L. (1995) Ecological economic modelling and evaluation of ecosystems. *Ecological Economics,* 14, 143-159

Bonetto, A.A., Wais, I.R. and Arquez, G.S. (1988) Ecological considerations of river regulations of the Delta basin according to flatland characteristics. *Water International, IWRA, USA,* 13(2-9), 2-8

Bonetto, A.A., Wais, I.R. and H.P. Castello (1989) The increasing damming of the Paraná Basin and its effects on the Lower reaches. *Regulated Rivers,* 4, 333-346

Botero, L. (1990) Massive mangrove mortality on the Caribbean coast of Colombia. *Vida Silvestre Neotropical,* 2(2), 77-78

Botero, L. and Mancera-Pineda, J.E. (1996) Síntesis de los cambios de origen antrópico ocurridos en los últimos 40 años en la Ciénaga de Santa Marta (Colombia). *Revista Academia Colombiana de Ciencias,* 20(78), 465-474

Boucher, K. (1999) Global warming. In: Pacione M. (ed.) *Applied Geography-Principles and Practice.* Routledge, London. 21-35

Boyd, C.E. and Scarsbrook, E. (1975) Influence of nutrient additions and initial density of plants on production of Water hyacinth *Eichhornia crassipes. Aquatic Botany,* 1, 253-261

Braun-Blanquet, L. (1932) Plant sociology: the study of plant communities (transl. By G.D.Fuller and H.S. Conard) *Transl. of 1st. De. Of Pflanzensoziologie* (1928). Mc Graw-Hill, New York

Bravard, J.P. and Petts, G.E. (1996) Human Impacts on fluvial ecosystems. In: Petts, G.E. and Amoros, C. (eds.) *Fluvial hydrosystems.* Chapman and Hall, London. 243-261

Burkart, A. (1957) La vegetación del delta del Río Paraná. *Darwiniana,* 11(3), 457-560

Buróz, C.E. and Guevara, B.J. (1976) Prevención de crecidas en el Delta del Río Orinoco y sus efectos ambientales: El Proyecto Caño Mánamo, Venezuela. In: *Agua, desarrollo y medio ambiente en America Latina.* ONU-CEPAL, 277-302

Calheiros, D.F., Seidl, A.F. and Ferreira, C.J.A. (2000) Participatory research methods in environmental science: local and scientific knowledge of limnological phenomenon in the Pantanal of Brazil. *Journal of Applied Ecology*, **37**, 684-696

Camargo, A.F.M and Esteves, F. (1995) Biomass and productivity of aquatic Macrophytes in Brazilian lacustrine ecosystems In: Tundisi, J.G., Bicudo, C.E.M. and Matsumura Tundisi, T. (eds.) *Limnology in Brazil.* Brazilian Academy of Science, 137-149

Campbell, D.G., Daly, D.C. and Maciel, U.N. (1986). Quantitative ecological inventory of terra firme and várzea tropical forest of the Rio Xingú, Brazilian Amazon. *Brittonia*, **38**, 369-375

Canales, H. (1985) *La cobertura vegetal y el potencial forestal del T.F.D.A. (Sector Norte del Río Orinoco).* M.A.R.N.R. División del Ambiente. Sección de Vegetación

Carignan, R. and Neiff, J.J. (1992) Nutrient dynamics in the floodplain ponds of the Paraná River (Argentina) dominated by water-hyacinth *Eichhornia crassipes. Biochemistry*, **17**, 85-121

Carter, V. (1986) An overview of the hydrologic concerns related to wetlands in the United States. *Canadian Journal of Botany*, **64 (2)**, 364-374

Cathpole, W.R. and Wheeler, C. J. (1992) Estimating plant biomass: A review of techniques. *Australian Journal of Ecology*, **17**, 121-131

Chambers, P.A., Prepas, E.E., Hamilton, J.R. and Bothwell, M.L. (1991) Current velocity and its effect on aquatic macrophytes in flowing water. *Ecological Application*, **1**, 249-257

Chapin III, F.S., Zavaleta, E.S., Eviners, V.T., Naylor, R. L., Vitousek, P.M., Reynolds, H.L., Hooper, D. U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. and Díaz, S. (2000) Consequences of changing biodiversity. *Nature*, **405**, 232-242

Civco, L.D., Kennard, W.C. and Lefor, M.W. (1986) Changes in Connecticut salt-marshes vegetation as revealed by historical aerial photographs and computer-assisted cartographics. *Environmental Management*, **10 (2)**, 229-239

Clinebell, R.R.II, Phillips, O.L., Gentry, A.H., Stark,N. and Zuurihg,H. (1995) Predictions of neotropical tree and liana species richness from soil and climatic data. *Biodiversity and Conservation*, **4**, 56-90

Cochrane, M.A. and Schulze,M.D. (1999) Fire as a recurrent event in tropical forests of the Eastern Amazon: effects on forest structure, biomass, and species composition. *Biotropica*, **31(1)**, 2-16

Coleman, J.M., Roberts, H.H. and Stone, G.W. (1998) Mississippi River Delta: an overview. *Journal of Coastal Research*, **14(3)**, 698-716

Collier, B.D., Cox, G.W., Johnson, A.W. and Miller, P.C. (1973) *Dynamic ecology.* Prentice-Hall, Inc., London

Colonnello, G. (1990a) Physiographic and ecological elements of the Orinoco River basin and its floodplain. *Interciencia,* **15 (6),** 479-485

Colonnello, G. (1990b) A Venezuelan floodplain study on the Orinoco river. *Forest Ecology and Management,* **33/34,** 103-124

Colonnello, G. (1993) Physiographic and ecological aspects of the Venezuelan Orinoco Basin. Animal-plant interactions in tropical environments. In: Barthlott, W., Naumann, C.M., Schmidt-Loske, K. & K.-L. Schuchmmann (eds.). *Results of the annual meeting of the German Society for tropical ecology, held at Bonn,* February 13-16, 1992.- Bonn (Zoologisches Forschungsinstitut und Museum Alexander Koening)

Colonnello, G. (1996) Aquatic vegetation of the Orinoco River Delta (Venezuela). An Overview. *Hydrobiologia,* **340,** 109-113

Colonnello, G. (1997) Estudio de la vegetatión acuática del Delta del Río Orinoco. El Parque Nacional Mariusa y su área protectora. Parte I, comunidades vegetales. Ciencia y conservación en el sistema de Parques Nacionales de Venezuela. In: Novo Torres, I (ed.) *Componente de estudios básicos del programa fortalecimiento del sistema de parques nacionales de Venezuela.* Wildlife Conservation Society, 313-320

Colonnello, G. (1998a) El impacto ambiental causado por el represamiento del Caño Mánamo: cambios en la vegetación riparina un caso de estudio. In: López, J.L., Saavedra, Y and Dubois, M. (eds.) *El Río Orinoco, Aprovechamiento sustentable.* Instituto de Mecánica de Fluidos. Universidad Central de Venezuela, Caracas. 36-54

Colonnello, G. (1998b) Biomass production of *Eichhornia crassipes* and *Paspalum repens* in two contrasting environments of the Orinoco River Delta (Venezuela). *Verhandlungen International Verein von Limnologie,* **4,** 1827-1829

Colonnello, G. (1998c) Effects of the regulation of the Mánamo channel, in the Orinoco River Delta, Venezuela. *Proceedings of VII International Congress of Ecology (INTECOL),* p 94. Florence, July 1998

Colonnello, G. (In press). *Spartina Alterniflora* Loisel. una especie de Poaceae nueva para Venezuela. *Memoria de la Sociedad Ciencias Naturales La Salle*

Colonnello, G., Graves R., and Wade, P.M. (1992) A survey and evaluation of ditch flora of Malltreath Marsh SSSI, Anglesey, with recommendations of the management of the drainage system. Report to Countryside Council for Wales. Bangor

Colonnello, G. and Medina, E. (1998) Vegetation changes induced by dam construction in a tropical estuary: the case of the Mánamo river, Orinoco Delta (Venezuela). *Plant Ecology*, **139(2)**, 145-154

Colonnello, G., Solé, M.A. and Velásquez, J. (1993) Inventario preliminar de las plantas acuáticas vasculares del Delta del Río Orinoco, Venezuela. *Memoria de la Sociedad de Ciencias Naturales La Salle*, **139**, 147-159

Colonnello, G. and Yánez, L. (1999) Dinámica sucesional de la vegetación en un herbazal de pantano en el Delta del Río Orinoco: La regulación del Caño Mánamo y las migraciones humanas como hipótesis de su origen. I Reunión Internacional sobre Biodiversidad Iberoamericana. Pamplona, January 1999

Comiskey, J., Aymard, G. and Dallmeier, F. (1994) Structure and composition of lowland mixed forests in the Kwakwani region of Guyana. *Biollania*, **10**,13-28

Connell, J.H. and Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organisation. *American Naturalist*, **11**, 1119-1144

Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**,1302-1310

Conservation International (1994) *The Tambopata-Candamo Reserved zone of Southeastern Perú: A biological Assessment.* Washington D.C.

Conservation International (1997) *The Cordillera del Condor Region of Ecuador and Perú : A biological assessment.* Washington D.C.

Cook, C.D.K. (1990) *Aquatic Plant Book.* SPB Academic Publishing, The Hague

Coops, H., Geilen, N. and Van der Velde, G. (1999) Helophyte zonation in two regulated estuaries areas in the Netherlands: vegetation analysis and relationships with hydrological factors. *Estuaries*, **22(3a)**, 657-668

COPLANARH (Comisión del plan nacional de aprovechamiento de los recursos hidráulicos) (1979) *Inventario Nacional de Tierras. Delta del Orinoco y Golfo de Paria. Serie de informes científicos*, Zona 2/1C/21. Maracay

Costanza, R., d'Arge, R., Groot, R. de, Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Rasking, R.G., Sutton, P. and M. Van den Belt (1997) The value of the world's ecosystem services and natural capital. *Nature*, **387**, 253-260

Costanza, R., d'Arge, R., Groot, R. de, Faber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Rasking, R.G., Sutton, P. and Van den Belt, M. (1998) The value of the world's ecosystem services. *Ecological Economics*, **25**, 3-15

CVG (Corporación Venezolana de Guayana) (1967) Sin inundaciones 300.000 hectáreas del Territorio Federal Delta Amacuro. *Natura*, **35**, 24-32

CVG (Corporación Venezolana de Guayana) (1970) *Dignóstico ganadero en la zona de influencia del Delta del Orinoco.* Ed. Etapa, Caracas

CVG (Corporación Venezolana de Guayana) (1972) La transformación del Delta del Orinoco. *Natura*, **46-47**, 30-35

CVG (Corporación Venezolana de Guayana) (1980) *Tierras ganadas al agua para el desarrollo agropecuario.* Tucupita

CVG-Tecmín (Corporación Venezolana de Guayana-Técnica minera) (1991) Vegetación, Informe de avance NC-20-11 y 12. Clima, Geología, Geomorfología y Vegetación. CVG Técnica Minera C.A. Gerencia de Proyectos Especiales. Proyecto de inventario de los Recursos Naturales de la Región Guayana, Ciudad Bolívar

Dalmeier, F. (1992) Long-term monitoring of biological diversity in tropical forest areas (Methods for establishment and inventory of permanent plots). *MAB-Digest*, **11**, 9-72.

Danielo, A. (1976) Vegetation et sols dans delta de l'Orénoque. *Annals de Géographie*, **471**, 555-578

Davis, T.A.W and Richards, P.W. (1933-34) The vegetation of Moraballi Creek, British Güiana: an ecological study of a limited area of Tropical rain Forest. Parts I. *Journal of Ecology*, **21**, 106-55

Davis, T.A.W and Richards, P.W. (1933-34) The vegetation of Moraballi Creek, British Güiana: an ecological study of a limited area of Tropical rain Forest. Parts II. *Journal of Ecology*, **22**, 350-384

Day, J.A. and Davies, B.R. (1986) The Amazon river system. In: Davies, B.R. and Walker, K.F. (eds.) *The ecology of river systems.* Dr. W. Junk Publishers, Dordrecht. 289-337

de Cabo, L., Puig, A., Arreghini, S., Olguin, H.F., Seoane, R. and Obertello, I. (1999) Physiochemical parameters and plankton in the Lower Delta of the Paraná river in relation to flow. Manaus' 99 - Hydrological and Geochemical Processes in Large Scale River Basins. 1-7.

Delascio, F. (1975) *Aspectos biológicos del Delta del Orinoco.* Instituto Nacional de Parques, Dirección de Investigaciones Biológicas, División de Vegetación, Caracas

Delavaud, C.C. (1977) Le milieu et l'occupation humaine dans le Delta de L'Orenoque. *Bulletin Associacion Francaise Géographie*, **447**, 295- 302

Del Valle, J.I. (1996) Los bosques de Guandal del delta del río Patia (Colombia). Revista de la Academia Colombiana de Ciencias, **78**, 796-489

Delta Centro Operating Company (1998) *Estudio de impacto ambiental. Proyecto de perforación exploratoria Bloque Delta Centro, Fase 1.* Technical Report, Caracas

Delta Centro Operating Company (1999) *Plan de supervisión ambiental. Proyecto de perforación exploratoria Bloque Delta Centro. Pozo Jarina.* Technical Report, Caracas

Denslow, J.S. (1987) Tropical rainforests gaps and tree species diversity. *Annual Review of Ecology and Systematics,* **18**, 431-451

Dethier, M.N. (1985) Disturbance and recovery in intertidal pools: maintenance of mosaic pattern. *Ecological Monograph,* **54(1)**, 99-118

Devall, M.S. (1990) Cat island swamp: Window to a fading Louisiana ecology. *Forest Ecology and Management,* **33-34**, 303-315

Din, S.H.S. (1977) Effects of the Aswan high dam on the Nile flood on the estuaries and coastal circulation pattern along the Mediterranean Egyptian coast. *Limnology and Oceanography,* **22**, 194-207

Di Persia, D.H. and Neiff, J.J. (1986) The Uruguay river system. In: Davies and K.F.Walker B.R.(eds.) *The ecology of river systems.* Dr. W. Junk Publishers, Dordrecht, 599-622

Dorr, J.L. (1995) Plant collecting along the Lower Orinoco, Venezuela: H.H. Rusby and R.W.Squires (1896). *Brittonia,* **47(1)**, 1-20

Dost, H. (1971) Orinoco Delta. Cat-clay investigations, Main results of 1970-1971. C.V.G.-I.R.I. Tucupita

Downing, J.A. and Anderson, M.R. (1985) Estimating the standing biomass of macrophytes. *Canadian Journal Fisheries and Aquatic Science,* **42**, 1860-1869

Drury, W.H. and Nisbet, I.C.T. (1973) Succession. *J. Arnold Arboretum,* **54**, 331-368

Dufour, D.L. (1990) Use of tropical rainforests by native Amazonians. *BioScience,* **40(9)**, 652-659

Dumont, J.F., Lamotte, S. and Kahn, F. (1990) Wetland and upland forest ecosystems in Peruvian Amazonia: Plant species diversity in the light of some geological and botanical evidence. *Forest Ecology and Management,* **33-34**, 125-140

Dye, P.J. and Walker, B.H. (1980) Vegetation-environmental relations on sodic soils of Zimbabwe Rhodesia. *Journal of Ecology,* **68**, 589-606

Elster, C., Polania, J. and Casas-Monroy, O. (1999) Restoration of the Magdalena River delta, Colombia. *Vida Silvestre Neotropical,* **7(1),** 23-30

Emery, K.O. (1938) Rapid method of mechanical analysis of sand. *Journal of Sedimentary Petrology,* **8(1),** 105-111

Erickson, P.A. (1994) *A practical guide to environmental impact assessment.* Academic Press, London

Escalante, B. (1993) La intervención del Caño Mánamo en el Delta del Orinoco y su repercusión en el medio ambiente vista por los deltanos. In: Monente, J. and Vásquez, E. (eds.). *Estudio limnológico y aportes a la etnología del Delta del Río Orinoco.* Fundación La Salle de Ciencias Naturales, Caracas

Esteves, F. de A. (1981) Biomass and analysis of the major inorganic components of floating aquatic macrophyte (*Eichhornia crassipes* (Mart.) Solms) in six reservoirs of Sao Paulo State (Brazil). *Ciencia e Cultura,* **34(9),** 1196-1200

Esteves, F. de A. (1988) *Fundamentos de Limnologia.* Editora Interciencia/FINEP, Rio de Janeiro

Ewel, K.C. (1990) Multiple demands on wetlands. *BioScience,* **40 (9),** 660-666

Faber, S. and Costanza, R. (1987) The economic value of wetlands systems. *Journal of Environmental Managements,* **24,** 41-51

Fassett, N.C. (1975) *A manual of aquatic plants.* The University of Wisconsin Press, Winsconsin

Fearnside, P.M. (1989) Brazil's Balbina dam: Environment versus the legacy of the Pharaons in Amazonia. *Environmental Management,* **13 (4),** 401-423

Fearnside, P.M. and Barbosa, R.I. (1996) Political benefits as barriers to assessment of environmental costs in Brazil's Amazonian development planning: The example of the Jatapu dam in Roraima. *Environmental Management,* **20(5),** 615-630

Finol, H. (1981) *Planificación silvicultural de los bosques ricos en palma Manaca (Euterpe oleraceae), en el Delta del Río Orinoco.* Universidad de Los Andes, Mérida.

Finol, H. (1993) La palma manaca (*Euterpe oleraceae* Mart.) en el Delta del río Orinoco. In: De las Salas, G. and Padehla, F. (eds). *Actas de la V Reunión Internacional de Silvicultura y Desarrollo Sostenible en América Latina.* 58-65. Universidad Distrital Francisco José de Caldas, Palmira.

Folk, R.L. and Ward, W.C. (1957) Brasos river bar: A study in the significance of grain-size parameters. *Journal of Sedimentary Petrology ,* **27(1),** 13-26

Fox, A.M. (1992) Macrophytes. In: Calow, P. and Petts, G. (eds.) *The rivers handbook, hydrological and ecological principles.* Blackwell Scientific Publications, London. 216-233

Franceschi, E.A. and Prado, D.E. (1989) Distribution of herbaceous communities of the river Parana valley along an elevation gradient after a catastrophic flood. *Coenoses,* **4(1)**, 47-53

Frangi, J.L. and Lugo, A. (1985) Ecosystem dynamics of a subtropical floodplain forest. *Ecological Monographs,* **55(3)**, 351-369

Funindes-USB (1999) Caracterización del funcionamiento hidrológico fluvial del Delta del Orinoco. Desarrollo armónico de Oriente DAO. PDVSA, Caracas.

Furch, K. and Junk, W.J. (1980) Water chemistry and macrophytes of creeks and rivers in Southern Amazonia and Central Brazilian Shield. In: Furtado, J.I. (ed.) *Tropical ecology and development,* 771-796

Furch, K. (1984) Water chemistry of the Amazon basin: The distribution of chemical elements among freshwaters. In: Sioli, H. (ed.) *The Amazon, limnology and landscape ecology of a mighty tropical river and its basin.* Dr. W. Junk Publishers, Dordrecht. 167-199

Galvis, G., Mojica J.I. and Rodríguez, F. (1989*) Estudio ecológico de una laguna de desborde del Río Metica.* FONDO FEN Colombia. Universidad Nacional de Colombia, Bogotá

García-Castro, A.A. and Heinen, H.D. (in press) Planificando el desastre ecológico: Los indígenas Warao y el impacto del cierre del Caño Mánamo (Delta del Orinoco, Venezuela). *Antropológica*

García Lozano, L.C. and Dister, E. (1990) La planicie de inundación del medio-bajo Magdalena: restauración y conservación de habitats. *Interciencia,* **15(6)**, 396-410

Gentry, A.H. (1982) Patterns of neotropical plant species diversity. *Evolutionary Biology,* **15,** 1-84

Geohidra Consultores (1998) *Estudio de Impacto ambiental, proyecto perforación exploratoria. Area Prioridad Este, Bloque Punta Pescador.* AMOCO, Caracas

Gill, C. (1970) The flooding tolerance of woody species-a review, *Forestry Abstracts,* **31(4),** 671-688

Givnish, T.J. (1999) On the causes of gradients in tropical tree diversity. *Journal of Ecology,* **87,** 193-210

Glenn-Lewin, D.C. and Van der Maarel, E. (1992) Patterns and processes of vegetation dynamics. In: Glenn-Lewin, D.C, Peet, R.K. and Veblen, T.T. (eds.) *Plant succession-theory and prediction.* Chapman and Hall, London. 11-59

Gómez, O. and Medina, E. (1998) The vegetation distribution patterns from a Landsat-4 TM image along the San Juan river (Monagas State), Venezuela. *International Journal of Remote Sensing,* **19(6),** 1017-1020

González, C.V. (1987) *Los morichales de los llanos orientales. Un enfoque ecológico.* Ediciones Corpoven, Caracas

González, V., Cauz, C., Quiroz, Y. and Marín, F. (1983) *Bases para el diseño de unidades de mitigación y control de las cuencas hidrográficas de los ríos Caris y Pao, Edo. Anzoátegul. Tomo IV: Ecosistemas Morichal.* UCV-MENEVEN-IZT, Caracas

Gopal, G. and Goel, U. (1993) Competition and allelopathy in aquatic plant communities. *The Botanical Review,* **59(3),** 155-210

Gore, J.A. and Shields Jr., F.D. (1995) Can large rivers be restored? *BioScience* **45(3),** 142-158.

Gortz-Van Rijn, A.R.A. (1990) *Flora of the Güianas.* Poaceae. Koeltz Scientific Books, Berlin

Gosselink, J.G., Shaffer, G.P., Lee, L.C., Burdick, D.M., Childers, D.L., Leibowitz, N.C., Hamilton, S.C., Boumans, R., Cushman, D., Fields, S., Koch, M., and Visser, J.M. (1990) Landscape conservation in a forested wetland watershed. *BioScience,* **40(8),** 588-600

Grasmuck, N., Haury, J., Léglize, L. and Muller, S. (1995) Assessment of the bio-indicator capacity of aquatic macrophytes using multivariate analysis. *Hydrobiologia,* **300-301,** 115-122

Gracson, T.L. (1992) The use of palms by the Pume Indians of southern Venezuela. *Principles,* **36(3),** 133-142

Greening, H.S. and Gerritsen, J. (1987) Changes in macrophyte community structure following drought in the Okefenokee swamp, Georgia, U.S.A. *Aquatic Botany,* **28,** 113-128

Greenwood, M.T., Bickerton, M. and Petts, G. E. (1995) Spatial distribution of spiders on floodplain of the River Trent, UK. The role of hydrological setting. *Regulated Rivers,* **10,** 303-313

Greig-Smith, P. (1983) *Quantitative plant ecology.* Blakwell, Oxford

Grime J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature,* **242:** 344-347

Grime J.P. (1979) Plant strategies and vegetation processes. John Wiley and Sons, Chichester

Haller, W.T., Sutton, D.L. and Barlowe, W.C. (1974) Effects of salinity on growth of several aquatic macrophytes. *Ecology,* **55,** 891-894

Hamilton, S.K. and Lewis Jr., W.M. (1987) Causes of seasonality in the chemistry of a lake on the Orinoco River floodplain, Venezuela. *Limnology and Oceanography,* **32(6),** 1277-1290

Hamilton, S.K. and Lewis Jr., W.M. (1990a) Physical characteristics of the fringing floodplain of the Orinoco River, Venezuela. *Interciencia,* **15(6),** 491-500

Hamilton, S.K. and Lewis Jr., W.M. (1990b) Basin morphology in relation to chemical and ecological characteristics of lakes on the Orinoco River floodplain, Venezuela. *Archiv für Hydrobiologie,* **119(4),** 393-425

Harper, J.L. (1977) *Population biology of plants.* Academic Press, London

Haynes, R.R. (1988) Reproductive biology of selected aquatic plants. *Annals of the Missouri Botanical Garden,* **75,** 805-810

Heinen, H.D. (1987) Los Warao. In: *Los aborígenes de Venezuela*-Vol III-Etnología contemporánea. Fundación La Salle de Ciencias Naturales, Caracas. 585-692

Heinen, D., Lizarralde, R. and Gómez, T. (1994-1996) El abandono de un ecosistema: El caso de los morichales del Delta del Orinoco. *Antropológica,* **81,** 3-36

Heinen, H.D., San José, J.J., Arias, H.C. and Montes, R. (1995) Subsistence activities of the Warao Indians and anthropogenic changes in the Orinoco Delta vegetation. *Scientia Gûaianae,* **5,** 312-334

Heinen, H.D. and Urbina, L. (1986) Proyectos de desarrollo en Guayana y el problema de la tierra indígena. *Boletín Antropológico. La Universidad de Los Andes,* **10,** 110-124

Hemond, H.F. and Benoit, J. (1988) Cumulative impacts on water quality functions. *Environmental Management,* **12(5),** 639-653

Henry, C.P., Amoros, C. and Bornette, G. (1996) Species traits and recolonization processes after flood disturbances in riverine macrophyte. *Vegetatio,* **122,** 13-27

Herrera, L.E., Febres, G.A. and Avila, R.A. (1981) Las mareas en aguas venezolanas y su amplificación en la región del Delta del Orinoco. *Acta Científica Venezolana,* **32,** 299-306

Hill, M.O. (1979) *DECORANA-A FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Section of ecology and systematics, Cornell University, Ithaca, New York

Hill, N.M., Keddy, P.A. and Wisheu, I.C. (1998) A hydrological model for predicting the effects of dams on the shoreline vegetation of lakes and reservoirs. *Environmental Management,* **22(5),** 723-736

Hopkinson Jr., C.S. and Vallino, J.J. (1995) The relationships among man's activities in watersheds and estuaries: a model of runoff effects on patterns of estuarine community metabolism. *Estuaries*, **18(4)**, 598-621

Huber, O. (1995) Venezuelan Guayana, vegetation map. 1:2,000,000. CVG-Edelca- Missouri Botanical Garden

Huber, O. and Alarcón, C. (1988) Mapa de la vegetación de Venezuela. 1:2,000,000. Caracas: MARNR, The Nature Conservancy

Hueck, K. (1960) Mapa de Vegetación de la República de Venezuela. 1:2,000,000 Instituto Forestal Latinoamericano de Investigación y Capacitación, Mérida

Hullbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54(2)**, 187-211

Huston, M. (1994) *Biological diversity. The coexistence of species on changing landscapes.* Cambridge University Press, Cambridge

Huston, M. and Smith,T. (1987) Plant succession: Life history and competition. *American Naturalist,* **130**, 168-198

Hutchinson, G.E. (1975) *A treatise of limnology. III. Limnological botany.* Wiley & Sons, New York

Infrawing y Asociados (1997) *Estudio de factibilidad de cinco locaciones.* Delta Centro Operating Company, Caracas

Infrawing y Asociados (1998) *Estudio de Impacto Ambiental, proyecto de perforación exploratoria. Bloque Delta Centro, fase 1.* .Delta Centro Operating Company, Caracas

IRNR (USB)-Ecology and Environment. (1999) *Estudio de factibilidad ambiental del proyecto cierre del Caño Tórtola.* Informe Técnico, Caracas

Jean, M. and Bouchard, A. (1991) Temporal changes in wetland landscapes of a section of the St. Lawrence river, Canada. *Environmental Management,* **15(2)**, 241-250

Jedicke, A., Furch, B., Ulrich, S. and Schluter, U.B. (1989) Increase in the oxygen concentrations in Amazon waters resulting from the root exudation of two notorious water plants, *Eichhornia crassipes* (Pontederiaceae) and *Pistia stratiotes* (Araceae). *Amazoniana,* **6(1)**, 53-69

Jorgensen, S.E. (1994) Models as instruments for combination of ecological theory and environmental practice. *Ecological Modelling,* **76/76**, 5-20

Junk, W. (1970) Investigations on the ecology and production-biology of the "floating meadows" (Paspalo-Echinochloetum) on the Middle Amazon. Amazoniana, II(4), 449-495

Junk, W. (1973) Investigations on the ecology and production-biology of the "floating meadows" (Paspalo-Echinochloetum) on the Middle Amazon, Part II. The aquatic fauna in the root zone of floating vegetation. Amazoniana, IV(1), 9-102

Junk, W. (1983) Ecology of swamps on the Middle Amazon. In: Gore, A.J.P (ed.) Ecosystems of the World. Mires, Swamp, bog, fen and moor. B. Regional studies. Elsevier Scientific Publishing Company, Amsterdam. 269-294

Junk, W. (1986) Aquatic plants of the Amazon system. In: Davies and K.F.Walker B.R.(eds.) The ecology of river systems. Dr. W. Junk Publishers, Dordrecht, 319-338

Junk, W. (1990) Die Krautervegetation der Uberschwemmungsgebiete des Amazonas (Varzea) bei Manaus und ihre Bedeutung fur das Okosystem. Max-Plank-Institut fur Limnologie, Arbeitsgruppe Tropenškologie. Plön/Holstein

Junk, W. (1995) Human impacts on neotropical wetlands: Historical evidence, actual status, and perspectives. Scientia Güaianae, 5, 299-311

Junk, W., Bayley, P.B. and Sparks, E.P. (1989) The flood pulse concept in river-floodplain systems. In: Dodge,D.P. (ed.) Proceedings of the International large river symposium. Canadian Special Publication Fisheries Aquatic Science, 106, 110-127

Junk, W. and Furch, K. (1991) Nutrient dynamic in Amazonian floodplains: Decomposition of herbaceous plants in aquatic and terrestrial environments. Verh. International Verein. Limnol., 24, 2080-2084

Junk, W. and Howard-Williams, C. (1984) Ecology of aquatic macrophytes in Amazonia. In: Sioli, H. (ed.) The Amazon, limnology and landscape ecology of a mighty tropical river and its basin. Dr. W. Junk Publishers, Dordrecht. 269-293

Junk, W. and Nunes de Mello, J.A.S. (1987) Impactos ecologicos das represas hidroelétricas na bacia Amazónica Brasileira. Tubinger Geographisshe Studien, 95, 367-385

Junk, W, and Piedade, M.T.F. (1993) Biomass and primary production of herbaceous plant communities in the Amazon floodplain. Hydrobiologia, 263, 155-162

Kahn, F. and de Granville, J. (1992) Palms in forest ecosystems of Amazonia. Springer, Berlin

Kahn, F. and Mejía, K. (1990) Palm communities in wetland forest ecosystems of Peruvian Amazonia. Forest Ecology and Management, 33/34, 169-179

Kahn, F., Mejía, K., Moussa, F. and Gomez, D. (1993) VIII. *Mauritia flexuosa* (Palmae), La más acuática de las palmeras amazónicas. En: Kahn, F., León, B. and Young, K.R. (compilers) *Las plantas vasculares en las aguas continentales del Perú.* IFEA, Lima. 287-308

Kent, M. and Coker, P. (1992) *Vegetation description and analysis, a practical approach.* Belhaven Press, London

Kershaw, K.A. (1974) *Quantitative and dynamic plant ecology.* Eduard Arnold Limited, London

Khedr, A.H. and El-Demershad, M.A. (1996) Distribution of aquatic plants in relation to environmental factors in the Nile Delta. *Aquatic Botany,* **56,** 75-86

Krumbein, W.C. (1936) Aplication of logarithmic moments to size frequency distributions of sediments. *Journal of Sedimentary Petrology,* **6(1),** 35-47

Klinge, H. Junk, W.J. and Revilla, C.J. (1990) Status and distribution of forested wetlands in tropical South America. *Forest Ecology and Management,* **33/34,** 81-101

Lahitte, H.B., Hurrell, J.A., Mehltreter, K., Belgrano, M.J., Jankowski, L.S., Haloua, M.P. and Canda, G. (1997) *Plantas de la costa. Delta del Paraná- Isla Martín Garcia y Ribera Platense.* L.O.L.A., Buenos Aires

Lake, P.S. (2000) Disturbance, patchiness, and diversity in streams. *Journal of North American Benthological Society,* **19 (4),** 573-592

Lallana, V.H. (1980) Productividad de *Eichhornia crassipes* (Mart.) Solms. en una laguna isleña de la cuenca del Río Parana Medio. II. Biomasa y dinámica de población. *Ecología Argentina,* **5,** 1-16

Lambers, H., Chapin III, F.S. and Pons, T.L. (1998) *Plant physiological ecology.* Springer, New York

Lamotte, S. (1980) Fluvial dynamics and succession in the Lower Ucayaly, Peruvian Amazony. *Forest Ecology and Managment,* **33-34,** 141-256

Lande, R. (1996) Statistics and partioning of species diversity, and similarity among multiple communities. *Oikos,* **76,** 5-13

Larcher, W. (1995) *Physiological plant ecology.* Springer, Berlin

Laurance, W.F., Bierregard Jr., R.O., Gascon, C., Didham, R.K., Smith, A.P., Lynam, A.J., Viana, V.H., Lovejoy, T.E., Sieving, K.E., Sites Jr., J.W., Andersen, M., Tocher, M.D.,

Kramer, E.A., Restrepo, C. and Moritz, C. (1997) Tropical forest fragmentation: Syntesis of a diverse and dynamic discipline. In: Schelhas, J. and Greenberg, R. (eds.). *Forest patches in tropical landscapes*. Island Press, Washington D.C. 502-514

Layrisse, M., Salas, G. and Heinen D. (1980) Vital statistics of five Warao Subtribes. In: Wilbert, J. and Layrisse, M. (eds.). Demographic and Biological Studies of the Warao Indians. UCLA University of California, Los Angeles.

Lentino, M. and Bruni, A.R. (1994) *Humedales costeros de Venezuela: Situación ambiental.* Sociedad Conservacionista Audubon de Venezuela, Caracas

León, B. and Encarnación, F. (1993) Las plantas acuáticas comunes de la amazonia Peruana. In: Kahn, F., León, B. and Young, K.R. (compilers) *Las plantas vasculares en las aguas continentales del Perú.* IFEA, Lima. 231-247

Lewis Jr., M.W. and Saunders III, J.F. (1990) Chemistry and element transport by the Orinoco Main stem and lower tributaries. In: Weibezahn, F.H., Alvarez, H. and Lewis Jr., W.M. (eds.) *El Río Orinoco como ecosistema/The Orinoco River as an ecosystem.* Fondo Editorial Acta Científica Venezolana, Caracas. 211-239

Lincoln, R.J., Boxshall, P.F. and Clark, P.F. (1982) A dictionary of ecology, evolution and systematics. Cambridge University Press, Cambridge

López-Zent, E. (1998) A creative perspective of environmental impacts by native amazonian human populations. *Interciencia,* **23,** 232-240

Lubchenco, J. (1978) Plant species diversity in a marine intertidal community: Importance of herbivore food preference and algal competitive abilities. *American Naturalist,* **112,** 23-39

Lundberg, J. (1998) *A history of Southamerican rivers: 90 Ma to recent.* (Mimeograph)

MacArthur, R.H. and Wilson, E.O. (1967) *The theory of island biogeography.* Princeton University Press, Princeton

Magurran, A.E. (1989) *Diversidad ecológica y su medición.* Ediciones VEDRA, Barcelona

Maine, M.A., Suñe, N.L., Panigatti, M.C., Pizano, M.J. and Emiliani, F. (1999) Relationships between water chemestry and macrophyte chemeistry in lotic and lentic environments. *Archives für Hydrobiologie,* **145 (2),** 129-145

Maltby, E. (1991) Wetlands: Their status and role in the biosphere. In: Jackson, M.B., Davis, D.D. and Lambers, H. (eds.) *Plant life under oxygen deprivation.* SPB Publishing, The Hague. 3-21

MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1979) *Inventario nacional de tierras region oriental Delta del Orinoco-Golfo de Paria.* Dirección

General Sectorial de Información e Investigación del Ambiente. Serie Informes Científicos-Zona2/1C/21, Maracay

MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1982a) *Estudio preliminar de ordenación del Territorio Federal Delta Amacuro. Parte I, Inventario Analítico.* Serie Informes Técnicos, Zona 12/IT/174

MANRN (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1982b) *Mapa de la vegetación actual de Venezuela.* Dirección General Sectorial de Información e Investigación del Ambiente. Proyecto VEN 79/001/B. Sistemas Ambientales Venezolanos

MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1983) Taller de trabajo: El proyecto Orinoco-Apure y sus impactos ambientales. Caracas

MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1988) *Estudio agroclimatológico del territorio Federal Delta Amacuro.* Caracas.

MARNR (Ministerio del Ambiente y de los Recursos Naturales Renovables) (1992) *Areas naturales protegidas de Venezuela.* Serie aspectos conceptuales y metodológicos. DGSPOA/ACM/01

McCall, S.M. and Flowerdew, R.T.N. (1976) Measurement techniques in environmental impact assessment. *Environmental Conservation,* **3(3),** 209-217

Meade, R.H., Nordin, C.F., Pérez-Hernández, D., Mejia, A. and Pérez Godoy, J.M. (1983) Sediment and water discharge in Río Orinoco, Venezuela and Colombia. *Proceedings of the second international symposium on river sedimentation.* Water Resources and Electric Power Press, Beijing. 1134-1144

Medina, E. (1995) *Evaluación ecológica y manejo ambiental de la región sur-este de Maturín, Edo. Monagas.* Informe elaborado para FUNDIATE como parte del proyecto de evaluación de impacto ambiental de operaciones de exploración y explotación petrolera en el área de desarrollo de Maturín Este

Medina, E., Cuevas, E., Popp, M. and Lugo, A. (1990) Soil salinity, sun exposure, and growth of *Acrostichium aureum,* the mangrove fern. *Botanical Gazzette,* **151(1),** 41-49

Medina, E. and Francisco, M. (1997) Osmolality and $\delta^{13}C$ of leaf tissues of mangrove species from environments of contrasting rainfall and salinity. *Estuarine, Coastal and Shelf Science* , **45,** 337-344

Middleton, B. (1999) *Wetland restoration - Flood pulsing and disturbance dynamic.* John Willey and Sons. Inc, New York

Mirza Qader, M.M. (1998) Diversion of the Ganges water at Farakka and its effects on salinity in Bangladesh. *Environmental Management*, **22(5)**, 711-722

Mitsch, W.J. and Gosselink, J.G. (2000) *Wetlands*. John Wiley & Sons, Inc. New York

Mitsch, W.J. and Wilson R.F. (1996) Improving the success of wetland creation and restoration with know-how, time and self-design. *Ecological Applications*, **6(1)**, 77-83

Mitsch, W.J., Wu, X., Nairn, R.W., Weihe, P.E., Wang, N. Deal, R. and Boucher, C.E. (1998) Creating and restoring wetlands. *Bioscience*, **48(12)**, 1019-1030

Moffat, D. and Lindén, O. (1995) Perception and reality: Assessing priorities for sustainable development in the Niger River Delta. *Ambio*, **24(7-8)**, 527-538

Monente, J.A. (1993) Materiales en suspensión transportados por el Río Orinoco. *Memoria de la Sociedad de Ciencias Naturales La Salle*, **131-134**, 5-13

Monente, J.A. (1998) Consecuencias de la intervención de los humedales en el Delta del Orinoco y areas adyacentes, con especial énfasis en los caños. Congreso Iberoamericano del medio ambiente. USB, Caracas

Monente, J.A. and Colonnello, G. (1997) Hidroquímica del Delta del Orinoco. *Memoria de la Sociedad de Ciencias Naturales La Salle*, **148**, 109-131

Monente, J.A. and Wiscovitch, R. (1993) Introducción General. In: Monente, J. and Vásquez, E. (eds.) *Estudio limnológico y aportes a la etnoecología del Delta del Río Orinoco*. Fundación La Salle de Ciencias Naturales, Caracas. 9-47

Molles Jr., M.C., Crawford, C.S., Ellis, L.M., Valett, H.M.and Dahm, C.N. (1998) Managed flooding for riparian ecosystem restoration. *Bioscience*, **48(9)**, 749-756

Moss, B. (1988) *Ecology of fresh waters-man and medium*. Blackwell Scientific Publications, London

Mueller-Dombois, D. and Ellenberg, H. (1974) *Aims and methods of vegetation ecology*. Wiley & Sons, New York

Mwalyosi, R.B.B .(1998) Environmental impacts of the proposed Stiegler's Gore Hydro-power project. *Tanzania.Environmental Conservation*, **15(3)**, 250-254

Natura SA (1998) *Expansión del campo petrolero Pedernales. Evaluación ambiental específica*. British Petroleum, Caracas

Neiff, J.J. (1986) Aquatic plants of the Paraná system. In: Davies, B.R. and Walker, K.F. (eds.) *The ecology of river systems*. Dr. W. Junk Publishers, Dordrecht. 557-571

Neiff, J.J. (1990a) Aspects of primary productivity in the lower Paraná and Paraguay riverine system. *Acta Limnologica Brasiliensis*, **3**, 77-113

Neiff, J.J. (1990b) Ideas para la interpretación ecológica del Paraná. *Interciencia*, **15(6)**, 424-441

Neiff, J.J. (1996) Posibles impactos de la Hidrovía Paraguay-Paraná sobre la vegetación. In: *Evaluación del impacto ambiental de la Hidrovía Paraguay-Paraná. CIH-PNUD/BID, Buenos Aires, Argentina, T11: Impactos sobre el Ambiente Biológico.* 11-1, 1-54

Nilsen, E.T. and Orcutt, D.M. (1996) *The physiology of plants under stress.* John Wiley and Sons, New York. 362-400

Nilsson, C., Grelsson, G., Johanson, M. and Sperens, U. (1989) Pattern of plant species richness along riverbanks. *Ecology*, **70(1)**, 77-84

Nilsson, C.N., Ekblad, A., Gardfell, M. and Carlberg, B. (1991) Long-term effects of river regulation on river margin vegetation. *Journal of Applied Ecology*, **28**, 963-987

OCEI (Oficina Central de Estadística e Informática) (1993) *Censo indígena de Venezuela, Tomo 1,*. Caracas

Odum, E.P. (1983) *Systems ecology: an introduction.* Wiley-Interscience, New York

Odum, E.P., Finn, J.T. and Franz, E.H. (1979) Perturbation theory and the subsidy-stress gradient. *BioScience*, **29(6)**, 349-252

Olivares, E. and Colonnello, G. (2000) Salinity gradient in the Mánamo river, a damned distributary of the Orinoco delta, and its influence on the presence of *Eichhornia crassipes* and *Paspalum repens. Interciencia*, **25(5)**, 242-248

O'Neill, R.V. (1976) Ecosystems persistence and heterotrophic regulation. *Ecology*, **57**, 1244-1253

Panapitukkul, N., Duarte, C.M., Thampanya, U., Kheowvongsri, P., Srishal, N., Geertz-Hansen, O., Terrados, J. and Boromthanarath, S. (1998) Mangrove colonization: mangrove progression over the growing Pak Phanang (SE Thailand) Mud Flat. *Estuarine, Coastal and Shelf Science*, **47**, 51-61

Pannier, F. (1979) Mangroves impacted by human-induced disturbances: A case study of the Orinoco Delta Mangrove Ecosystem. *Environmental Management*, **3**, 205-216

Pannier, F. (1986) Las costas venezolanas: un reto y una oportunidad para la investigación, conservación y gestión ambientales. *Boletín Academia Ciencias Físicas, Matemáticas y Naturales*, **46**, 53-155

Pannier, F. and Rabinovich, J. (1976) Aspectos ecológicos del Delta del Río Orinoco. In: *Agua, desarrollo y medio ambiente en America Latina.* Anexo ONU-CEPAL, 1-.35

Pannier, F. and Fraino de Pannier, R. (1989) *Manglares de Venezuela.* Cuadernos Lagoven, Caracas

Paolini, J., Herrera, R. and Nemeth, A. (1983) Hydrochemistry of the Orinoco and Caroní Rivers. *Mitt. Geol.-Palaont. Inst. Univ. Hamburg,* **55,** 223-236

Parkison, R., DeLune, R.D. and White, J.R. (1994) Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean Region. *Journal of Coastal Research,* **10(4),** 1077-1086

Pautou, G., Girel, J. and Borel, J. (1992) Initial repercussions and hydroelectric developments in the French upper Rhone valley: A lesson for predictive scenarios propositions. *Environmental Managements,* **16(2),** 231-242

Pedrozo, F. and Bonetto, C. (1989) Influence of regulation on Nitrogen and Phosphorus mass transport in a large South American river. *Regulated Rivers,* **4,** 59-70

PDVSA (Petróleos de Venezuela, S.A.) (1992). *Imagen de Venezuela. Una visión espacial.* Instituto de Ingeniería, Caracas

Peet, R.K. (1992) Community structure and ecosystem functions. In: Glenn-Lewin, D.C., Peet, R.K. and Veblen, T.T. (eds.) *Plant succession- Theory and prediction.* Chapman and Hall, London. 103-150

Penfound, W.T. (1956) Primary production of vascular aquatic plants. *Limnology and Ocenography,* **1,** 92-101

Penfound, W.T. and Earle, T.T. (1948) The biology of water hyacinth. *Ecological Monograph,* **18,** 447-472

Pérez Hernández, D. and López, J.L. (1998) Algunos aspectos relevantes de la hidrología del Río Orinoco. In: López, J.L., Saavedra, Y. and Dubois, M. (eds.) *El Río Orinoco. Aprovechamiento sustentable,* Instituto de Mecánica de Fluidos, Facultad de Ingeniería, Universidad Central de Venezuela, Caracas. 88-98

Petrell, R.J. and Bagnall, O. (1991) Hydromechanical properties of water hyacinth mats. *Aquacultural Engineering,* **10,** 133-147

Petts, G.E. (1990) Regulation of large rivers: Problems and possibilities for environ-mentally-sound river development in South America. *Interciencia,* **15(6),** 388-395

Petts, G.E. and Amoros, C. (1996) Fluvial hydrosystems: a management perspective. In: Petts, G.E. and Amoros, C. (eds.) *Fluvial Hydrosystems*. Chapman and Hall, London. 263-278

Pfefferkorn, H.W., Kaldried, F., Hetch, C., Hofmann, C., Rabold, J.M. and Wagner, T. (1988) Recent geology and taphonomy of the Orinoco river Delta. Overview and field observations. *Heidelberger Geowissenschaftliche Abhandlungen*, **20**, 21-56

Pickett, S.T.A., Collins, S.C. and Armesto, J.J. (1987) A hierarchical consideration of causes and mechanisms of succession. *Vegetatio*, **69**, 109-14

Pieczynska, E. and Zalewskis, M. (1997) Habitat complexity in land-inland water ecotones. In: Lacharvanne, J. and Juge, R. (eds.) *Biodiversity in land-inland water ecotones*. Man and the Biosphere Series, UNESCO, Paris. 61-80

Poi de Neiff, A., Neiff, J.J., Orfeo, O. and Carignan, R. (1994) Quantitative importance of particulate matter retention by the roots of *Eichhornia crassipes* in the Paraná floodplain. *Aquatic Botany*, **47**, 213-223

Primack, R. and Hall, P. (1992) Biodiversity and forest change in Malaysian Borneo. *BioScience*, **42**, 829-837

Ramia, M. (1967) Tipos de sabana en los Llanos de Venezuela. *Boletin de la Sociedad de Ciencias Naturales*, **27(112)**, 264-288

Ramsar Convention (1971) *International conference on conservation of wetlands and water fowl, Ramsar, Iran, 30 January - 3 February 1971. Proceedings.* International Wildfowl Research Bureau, Slimbridge

Rapport, D.J. and Witford, W.G. (1999) How ecosystems respond to stress. *BioScience*, **49(3)**, 193-203

Rasmussen, J.L. (1994) Environmental restoration, floodplains vs. potholes. *Water Resources Uptade*, **97**, 29-33

Raughuveer, P., Chandra, R. and Sirohi, G.S. (1984) Estimations of bioproductivity of water hyacinth (*Eichhornia crassipes*): A case of study. In: Thyagarajan, G. (ed.) *Water hyacinth UNEP reports and Proceedings Series*, **7**, 264-274

Raunkier, C. (1937) *The life forms of plants and Statistical Plant Geography*. Clarendon Press, Oxford

Reddy, K.R. (1984) Water hyacinth (*Eichhornia crassipes*) biomass production in Florida. *Biomass*, **6**, 167-181

Reddy, K.R., Kadlec, R.H., Flaig, E. and Gale, P.M. (1999) Phosphorus retention in streams and wetlands: A review. *Critical Reviews in Environmental Sciences and Technology*, **29(1)**, 83-146

Richards, P.W. (1983) The three dimensional structure of a tropical rain forest. In: Sutton, S.L., Withmore, T.C. and Chadwick, A.C. (eds.) *Tropical Rain Forests: Ecology and Management,* Special Publication No. 2 of the BES, Blackwell Scientific, Oxford

Rigler, F.H. (1982) Recognition of the possible: an advantage of empirism in ecology. *Canadian Journal Fisheries Aquatic Science*, **39**, 1323-1331

Robb, D.M. (1989) *Diked and undiked freshwater coastal marshes of Western Lake Erie.* Master Thesis. The Ohio State University, Columbus

Rodríguez Altamiranda, R. (Comp.) (1999) *Conservación de humedales en Venezuela: Inventario, diagnóstico ambiental y estrategia.* Comité Venezolano de la IUCN. Caracas

Rodríguez, G. (1987). Structure and production in Neotropical Mangroves. *Tree,* **2(9)**, 264-267

Rodríguez, C.J. and Betancourth, J.A. (1999) Caracterización físico-química de una laguna de inundación del tramo Orinoco Medio y su relación con la biomasa de la cobertura de bora (*Eichhornia crassipes* (Mart.) Solms). *Interciencia,* **24(4)**, 243-250

Roggieri, H. (1995) *Tropical freshwater wetlands.* Kluwer Academic Publishers, Dordrecht

Roldán Pérez, G. (1996) *Fundamentos de Limnología Neotropical.* Editorial Universidad de Antioquia, Antioquia

Ronghua, C. and Twilley, R.R. (1998) A gap dynamic model of mangrove forest development along gradients of soil salinity and nutrient resourses. *Journal of Ecology,* **86**, 37-51

Rosales Godoy, J., Petts, G. and Jukka, S. (1999) Riparian flooded forests of the Orinoco and Amazon basins: a comparative review. *Biodiversity and Conservation,* **8**, 551-586

Rosenberg, N.J. (1974) *Microclimate. The biological environment.* Wiley-Interscience, New York

Sahay, R. and Sinha, A.B. (1969) Contribution to the ecology of Indian aquatics.I Seasonal changes in Biomass in water hyacinth (*Eichhornia crassipes*). Mart. (Solms). *Hydrobiologia,* **35**, 376-382

Salazar-Quijada, A. (1990) *Toponimia del Delta del Río Orinoco.* Universidad Central de Venezuela, Caracas

Sánchez, J.C. (1990) La calidad de las aguas del Río Orinoco. In: Weibezahn, F.H., Alvarez, H. and Lewis, W.M. Jr. (eds) *El Río Orinoco como ecosistema/The Orinoco River as an ecosystem*, Fondo Editorial Acta Científica Venezolana, Caracas. 241-268

Sánchez, L. and Vásquez, E. (1986) Notas sobre las macrofitas acuáticas de la sección baja del Río Orinoco. *Memoria de la Socidad de Ciencias Naturales La Salle*, **46 (125-126)**, 107-126

Sanderson, E.W., Ustin, S.L. and Foin, T.C. (2000) The influence of tidal channels on the distribution of salt marsh plant species in Petaluma Marsh, CA. USA. *Plant Ecology*, **146**, 29-41

Sand-Jensen, K. and Pedersen, O. (1999) Velocity gradients and turbulence around macrophyte stands in streams. *Freshwater Biology* , **42**, 315-328

Sarmiento, G. (1990) Ecología comparada de ecosistemas de sabanas en América del Sur. In: Sarmiento, G. (Comp.) *Las Sabanas Americanas*. Fondo Editorial Acta Científica Venezolana, Caracas. 15-56

Seinfeld, J.H. and Pandis S.N. (1998) Atmospheric chemistry and physics-From air pollution to climate change. John Wiley & Sons,INC. New York

Schalles, J.F. and Shure, D.J. (1989) Hydrology, community structure, and productivity patterns of a dystrophic Carolina Bay wetland. *Ecological Monographs*, **59(4)**, 365-385

Scheffer, M. (1990) Multiplicity of stable states in freshwater systems. *Hydrobiologia 200-201/Dev. Hydrobiol.*, **61**, 475-487

Scheffer, M. and Beets, J. (1994) Ecological models and the pitfalls of causality. *Hydrobiologia*, **275*276**, 115-124

Scott, D.A. and Jones, T.A. (1995) Classification and inventory of wetlands: a global overview. *Vegetatio*, **118**, 3-16

Sculthorpe, C.D. (1967) *The biology of aquatic vascular plants*. Edward Arnold Ltd, London

Sedell, J.R., Richey, J. and Swanson, F.J. (1989) The river continuum concept: a basis for the expected ecosystem behaviour of large rivers? *Canadian Special Publication.*

Fisheries Aquatic Science, **106**, 49-55

Segal, S. (1971) Principles on structure, zonation and succession of aquatic macrophytes. *Hydrobiologia*, **12**, 89-95

Sheppard, F.P. (1954) Nomenclature based on Sand-silt-clay ratios. *Journal of Sedimentary Petrology*, **24(3)**, 151-158

Sifontes, E. (1951) El Orinoco, su navegación entre Ciudad Bolívar y Pedernales. *Notas hidrometereológicas. Hidrología venezolana.* Imprenta Nacional, Caracas

Silvertown, J.W. (1980) The dynamic of a grassland ecosystem: botanical equilibrium in the park grass experiment. *Journal of Applied Ecology,* **17**, 491-504

Sioli, H. (1965) Bemerkung zur typologie amazonischer Flussen. *Amazoniana,* **1(1),** 74-83

Sklar, F.H. and Browder, J.A. (1998) Coastal environmental impacts brought about by alterations to freshwater flow in the Gulf of Mexico. *Environmental Management,* **22 (4),** 547-562

Sobrevila, C and P. Bath (1992) *Evaluación ecológica rápida. Un manual para usuarios de America Latina y El Caribe.* The Nature Conservancy, Arlintong

Sparks, R.E., Nelson, J.C. and Yao, Y. (1998) Naturalization of the flood regime in regulated rivers. The case of the upper Mississippi River. *BioScience,* **48 (9),** 706-720

Stallard, R.F, Koehnken, L., Johnsson, M.J. (1991) Weathering process and the composition of inorganic material transported by through the Orinoco River system, Venezuela and Colombia: *Geoderma,* **51,** 133-165

Stodola, J. (1967) *Encyclopedia of water plants.* TFH Publications Inc., New Jersey

Suárez, M.M. (1968) *Los Warao. Indígenas del Delta del Orinoco.* Departamento de Antropología, Instituto Venezolano de Investigaciones Científicas, Caracas

Swetnam, W.T., Allen, G.D. and Betancourth, J.L. (1999) Applied historical ecology: Using the past to manage for the future. *Ecological Applications,* **9(4),** 1189-1206

Tabacchi, E., Planty-Tabacchi A.M. and Décamps, O. (1990) Continuity and discontinuity of the riparian vegetation along a fluvial corridor. *Landscape Ecology,* **5,** 9-20

Tabacchi, E., Correl, D.L., Hauer, R., Pinay, G., Planty-Tabacchi, A.M. and Wismar, R. (1998) Development, maintenance and role or riparian vegetation in the river landscape. *Freshwater Biology,* **40,** 497-516

Tams (Tippets-Abbott-McCarthy-Stratton Engineers & Architects) (1956*) Informe sobre el canal navegable propuesto de Pto Ordaz al mar en el Río Orinoco.* Informe al gobierno de Venezuela

Ter Braak, C.J.F. (1987-1992) *CANOCO-a FORTRAN Program for canonical community ordination.* Microcomputer power, Ithaca, New York

Thomaz, S.M., Roberto, M. do C. and Bini, L.M. (1997) Caracterização limnológica dos ambientes aquáticos e influencia dos níveis fluviométricos. In: Vazzoler, A.E.A.M.; Agostinho,

A.A. and N.S.Hahn (eds.) *A planície de inundação do alto rio Paraná: Aspectos físicos, biológicos e socioeconômicos.* Editora de Universidade Estadual de Maringá, Maringá. 73-102

Tilman, D. (1985) The resource-ratio-hypothesis of plant succession. *American Naturalist,* **125,** 827-852

Tilman, D. and Pacala, S. (1993) The maintenance of species richness in plant communities. In: Ricklefs, R.E. and Schluter, D. (eds.) *Species diversity in ecological communities. Historical and geographical perspectives.* The University of Chicago Press, Chicago. 13-25

Toner, M. and Keddy, P. (1997) River hydrology and riparian wetlands: a predictive model for ecological assembly. *Ecological Applications,* **7(1),** 236-246

Toth, L.A., Stefani, L.M., Arrington, D.A. and Chamberlain, J. (1998) Hydrologic manipulations of the channelised Kissimee river. *BioScience,* **48(9),** 757-764

Trask, P.D. (1955) *Recent marine sediments: A symposium.* The American Association of Petroleum Geologists. Dover Publications, Tulsa, Oklahoma

Twilley, R.R., Gottfried, R.R., Rivera-Monroy, V.H. Zhang, W., Armijos M.M. and Bodero, A. (1998) An approach and preliminary model of integrating ecological and economic constrains of environmental quality in the Guayas River estuary, Ecuador. *Environmental Science & Policy,* **1,** 271-288

Twilley, R.R., Snedaker, S.C., Yáñez Arancibia and Medina, E. (1995) Mangrove systems. In: Heywood, V.H. (ed.) *Global biodiversity assessment. Biodiversity and ecosystems functions: Ecosystems analyses United Nations Environment Programme.* Cambridge University Press, Cambridge. 387-393

Urbina, L. and Heinen, D. (1982) Ecología, organización social y distribución espacial: estudio de caso de dos poblaciones indígenas: Pemon y Warao. *Antropológica,* **57,** 25-54

Valle Ferreira, L. and Stohlgreen, T.J. (1999) Effects of river level fluctuation on plant species richness, diversity, and distribution in a floodplain forest in Central Amazonia. *Oecologia,* **120,** 582-587

Van Andel, T.H. (1967) The Orinoco Delta. *Journal of Sedimentary Petrology,* **37,** 297-310

Van der Brink, F.W.B. and Van der Velde, G. (1993) Growth and morphology of four freshwater macrophytes under the impact of the raised salinity level of the Lower Rhine. *Aquatic Botany,* **45,** 285-297

Van der Kevie, W. (1972) Physiography, classification, and mapping of acid sulphate soils. In: Dost, H. (ed). *Acid suphate soils.* Vol I, ILRI. 204-222

Van der Valk, A.G. (1981a) Succession in wetlands: a Gleasonian approach. *Ecology,* **62(3)**, 688-696

Van der Valk, A.G. (1981b) Effects of prolonged flooding on the distribution and biomass of emergent species along a freshwater wetland coenocline. *Vegetatio,* **110**, 185-196

Van der Voorde, J. (1962) Soil conditions of the Isla Macareo, Orinoco Delta, *Medelingen Stichting Bodemkartering,* **12**, 6-24

Vásquez, E. and Wilbert, W. (1992) The Orinoco: Physical, Biological and Cultural Diversity of a Major Tropical Alluvial River. In: Calow, P. and Petts, G. *The Rivers Handbook, hydrological and ecological principles.* Blackwell Scientific Publications, London. 448-471

Veillón, J.P. (1977) *Los bosques del Territorio Federal Delta Amacuro. Venezuela. Su masa forestal, su crecimiento y su aprovechamiento.* ULA-FCF, Mérida

Velásquez, J. (1994) *Plantas Acuáticas Vasculares de Venezuela.* Universidad Central de Venezuela. Consejo de desarrollo científico y humanístico, Caracas

Vila, M.A. (1964) *Aspectos geográficos del territorio Delta Amacuro.* Ediciones del Departamento de Relaciones Públicas, Corporación Venezolana de Fomento, Caracas

Walker, K.F. (1992) The river Murray, Australia: A semiarid lowland river. In: Calow, P. and Petts, G. (eds.) *The rivers handbook, hydrological and ecological principles.* Blackwell Scientific Publications, London. 472-492

Wallinford (1969) Orinoco Delta, Venezuela. Second report of hydraulic model investigation on some effects of closing the Caño Mánamo and Caño Macareo distributaries. Hydraulic Research Station, Wallingford.

Weibezahn, F. (1990) Hidroquímica y sólidos suspendidos en el alto y medio Orinoco. In: Weibezahn, F.H., Alvarez, H. and Lewis Jr., W.M. (eds.) *El Río Orinoco como ecosistema / The Orinoco River as an ecosystem.* Fondo Editorial Acta Científica Venezolana, Caracas. 151-210.

Welden, C.W., Hewett, S.W., Hubbell, S.P. and Foster, R.B. (1991) Sapling survival, growth and recruitment: relationship to canopy height in a neotropical forest. *Ecology,* **72**, 35-50

Wentworth, C.K. (1936) Discussion: The method of moments. *Journal of Sedimentary Petrology,* **6(3)**, 158-159

Werkhoven, M.C.M and Peeters, G.M.T. (1993) Aquatic macrophytes. In: Ouboter, P.E. ed.) *The freshwater ecosystems of Suriname. Monographiae Biologicae,* **70**, 99-112

Wetzel, R.G. (1981) *Limnología*. Ediciones Omega S A, Barcelona

Whittaker, R.H. (1973) Direct gradient analysis: Results. In: Whittaker, R.H. (ed.) *Handbook of Vegetation Science. Part V. Ordination and classification of communities*. Dr. W. Junk Publishers, The Hague. 35-52

Wilbert, J. (1996) *Mindfull of famine. Religious Climatology of the Warao Indians*. Harward University, Center for the Study of World Religions, Cambridge. 3-22

Wilbert, W. (1994-1996) *Manicaria saccifera* and the Warao In the Orinoco Delta. *Antropológica*, **81**, 51-66

Williams, M. (1993a) Protection and retrospection. In: Williams, M. (ed.) *Wetlands, a threatened landscape*. Blackwell Publishers, Oxford. 323-353

Williams,M. (1993b) Understanding wetlands. In: Williams, M. (ed.) *Wetlands, a threatened landscape*. Blakwell Publishers, Oxford. 1-42

Wilson, M.A. and Carpenter, S.R. (1999) Economic valuation of freshwater ecosystem services in the United States: 1971-1997. *Ecological Applications*, **9(3)**, 772-783

Winter, C.T. (1988) A conceptual framework for assessing cumulative Impacts on the hydrology of non tidal wetlands. *Environmental Managements*, **12(5)**, 605-620

Wissmar, R.C. and Beschta, R.L. (1998) Restoration and management of riparian ecosystems: a catchment perspective. *Freshwater Biology*, **40**, 571-585

Wolda, H. (1981) Similarity indices, sample size and diversity. *Oecologia*, **50**, 296-302

Yánez, C.E. (1997) *Estudio geoquímico regional de los ríos del escudo de Guayana*. Doctoral Thesis. Universidad Central de Venezuela, Caracas

Zutchi, D.P. and Gopal, B. (1990) Structure and dynamics of plant communities. In: Brij Gopal (ed.) *Ecology and management of aquatic vegetation In the Indian Subcontinent*. Kluwer Academic Publishers, Dordrecht. 127-146

Appendix 1. Study sites, geographical co-ordinates

Curiapo	(8° 32' N and 61° 01' W)
Caño Ibaruma	(8° 18' N and 61° 02' W)
Caño Guiniquina	(9° 10' N and 61° 09' W)
Pozo Jarahuaja	(9° 14' N and 61° 04' W)
Caño Mariusa	(9° 00' N and 61° 34' W)
Caño Coboina	(9° 03' N and 61° 18' W)
Laguna Travesía	(8° 34' N and 61° 38' W)
Isla Mariusa	(9° 18' N and 61° 18' W)
Caño Cuberina	(9° 19' N and 61° 23'W)
Caño Macareo	(9° 14' N and 61° 45' W)
Caño Guapoa	(9° 09' N and 61° 41' W)
Caño La Florida	(9° 08' N and 62° 05' W)
Laguna Las Clavellinas	(9° 11' N and 62° 05' W)
Caño Pedernales	(9° 19' N and 62° 05' W)
Laguna Ataguía	(8° 32' N and 62° 03' W)
Laguna Terraplén	(9° 00' N and 61° 55' W)
Caño Tucupita	(9° 17' N and 61° 48' W)
Ciénaga Los Guires	(9° 13' N and 61° 56' W)
Caño Acoimito	(8° 30' N and 61° 34' W)
Laguna Alamilla	(8° 25' N and 61° 31' W)
Barra Meregina	(8° 50' N and 60° 48' W)
Caño Mánamo	(9° 10' N and 62° 10' W)
Alto Araguao	(8° 50' N and 61° 35' W)

Appendix 2. List of species collected.

GENERA SPECIES	FAMILY	Type
Justicia laevilinguis (Nees)Lindau	Acanthaceae	Emergent
Echinodorus bolivianus		
E.b. (Rusby)Holm-Nielsen ssp. *intermedius*	Alismataceae	Helophyte
Echinodorus grandiflorus (Cham. & Schl.) Mich.	Alismataceae	Helophyte
Echinodorus tenellus (Mart.) Buchenau		Helophyte
Sagittaria guayanensis H.B.K.		Emergent
Sagittaria latifolia Willd.		Emergent
Sagittaria planitiana Agostini		Emergent
Alternanthera philoxeroides (Mart.) Griseb	Amaranthaceae	Helophyte
Alternanthera sessilis (L) R. Br.		Emergent
Crinum erubescens Ait.	Amaryllidaceae	Subm-Emer
Hydrocotyle umbellata L.	Apiaceae	Floa-Emer
Hymenocallis tubiflora Salisb.		Emergent
Montrichardia arborescens (L.) Schott	Araceae	Emergent
Pistia stratiotes L.		Free-floating
Urosphata sagittifolia (Rudge) Schott		Helo-Emer
Ambrosia cumanensis HBK	Asteraceae	Emergent
Eclipta prostrata (L.)L.		Emergent
Mikania congesta D.C.		Helophyte
Tessaria integrifolia R .& P.		Helophyte
Trichospira verticillata (l.) Blake		Helophyte
Azolla filiculoides Lam.	Azollaceae	Free-floating
Begonia patula Haw.	Begoniaceae	Emergent
Blechnum serrulatum L.C. Rich.	Blechnaceae	Emergent
Rorippa nasturtium-aquaticum (L.)Hayek	Brassicaceae	Emergent
Canna glauca L.	Cannaceae	Helophyte
Cabomba aquatica Aubl.	Cabombaceae	Floating
Mimosa pigra L.	Caesalpiniaceae	Emergent
Machaerium lunatum (L.f.)Duke		Emergent
Aeschynomene sensitiva Sw.		Helophyte
Aeschynomene evenia C.Wright		Helophyte

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Sesbania exasperata H.B.K.		Emergent
Neptunia oleracea Lour.		Floating
Ceratophyllum demersum L.	Ceratophyllaceae	Sub-Free-swim
Hippobroma longifolia (L.) R.Br.	Campanulaceae	Emergent
Commelina sp.	Commelinaceae	Helophyte
Aniseia martinicensis (Jacq.) Choisy	Convolvulaceae	Helophyte
Ipomoea sobrevoluta Choisy		Helophyte
Ipomoea sp.		Helophyte
Cayaponia metensis Cuatr.	Cucurbitaceae	Helophyte
Cyperus articulatus L.	Cyperaceae	Emergent
Cyperus distans L.f.		Emergent
Cyperus imbricatus Retz.		Emergent
Cyperus luzulae (L.)Retz.		Emergent
Cyperus odoratus L.		Emergent
Cyperus sphacellatus Rottb.		Emergent
Cyperus surinamensis Rottb.		Emergent
Cyperus sp. L.		Helophyte
Eleocharis elegans (H&B.)Roem.&Schult.		Emergent
Eleocharis filiculmis Kunth		Emergent
Eleocharis geniculata (L.) Roem. & Schult.		Emergent
Eleocharis interstincta (Vahl)R.&S.		Emergent
Fimbristilis complanata (Retz.)Link.		Emergent
Fimbristilis miliacea (L.)Vahl		Emergent
Eleocharis mutata (L.)Roem.&Schult.		Emergent
Fuirena incompleta Nees		Emergent
Fuirena umbellata Rott.		Emergent
Lagenocarpus guianensis Nees		Emergent
Oxicarium cubense (Poepp & Kunth)K.Lye		Emergent
Rynchospora holoschoenoides (L.C.Richard)Herter		Emergent
Scleria macrophylla Presl. & Presl.		Emergent
Scleria microcarpa Nees ex Kunth		Emergent
Scleria pterota Presl.		Emergent
Tonina fluviatilis Aubl.	Eriocaulaceae	Sub-Floa-emer
Alchornea castaaeifolia(Willd.) Juss.	Euphorbiaceae	Helophyte

Caperonia palustris (L.) St. Hill.		Emergent
Phyllanthus fluitans (Mull.)Arg.		Free-floating
Chelonanthus alatus (Aubl.)Pulle	Gentianaceae	Emergent
Limnobium laevigatum (H&B ex Willd) Heine	Hydrocharitaceae	Note 1
Hydrolea elatior Shott.	Hydrophyllaceae	Emergent
Hydrolea spinosa L.		Helophyte
Hyptis pulegioides Pohl. ex Benth.	Lamiaceae	Helophyte
Lemna perpusilla Torrex	Lemnaceae	Floa-free-swim
Lemna minor L.		Free-swimming
Wolffiella lingulata (Hegelm)Hegelm.		Free-swimming
Spirodela intermedia W. Koch		Free-floating
Utricularia foliosa L.	Lentibulariaceae	Submerged
Utricularia gibba L.		Submerged
Utricularia hydrocarpa Vahl		Submerged
Utricularia inflata Walter		Submerged
Utricularia sp1		Submerged
Hydrocleis nymphoides (Willd.)Buch.	Limnocharitaceae	Floating
Hydrocleis parviflora Seub.		Floating
Cuphea melvilla Lindl.	Lythraceae	Helophyte
Rotala ramosior (L.)Koehne		Helophyte
Crenea maritima Aubl.		Emergent
Hibiscus striatus Cav. ssp *lambertianus* (H.B.K.) O. Blancha	Malvaceae	Emergent
Hibiscus bifurcatus Cav.		Emergent
Hibiscus sororius L.		Emergent
Urena lobata L.		Emergent
Thalia geniculata L.	Marantaceae	Emergent
Marsilea polycarpa Hook.&Grev.	Marsileaceae	Floating
Nepsera aquatica (Aubl.) Naud.	Melastomataceae	Helophyte
Miconia sp.		Helophyte
Nymphoides indica L. Kuntze	Menyanthaceae	Floating
Heliconia hirsuta L.f.	Musaceae	Helophyte
Heliconia psittacorum L.f.		Helophyte
Nymphaea connardii Wiersema	Nympheaceae	Sub-floating
Nymphaea rudgeana G.F.W. Mey.		Sub-floating

Ludwigia decurrens Walt.	Onagraceae	Emergent
Ludwigia helminthorrhiza (Mart.) Hara		Floating
Ludwigia hyssopifolia (G. Don) Exell		Emergent
Ludwigia leptocarpa (Nutt.) Hara		Emergent
Ludwigia octovalvis (Jacq.)Raven		Emergent
Ludwigia sedoides (H.&B) Hara		Emergent
Ludwigia torulosa (Arnott)Hara		Emergent
Habenaria longicauda Hook. ssp. *longicauda*	Orchidaceae	Helophyte
Teramnus labialis Spreng.	Papilonaceae	Helophyte
Vigna jurvana (Harms) Verdecourt		Helophyte
Vigna longifolia (Benth) Verdecourt		Helophyte
Ceratopteris pteridoides (Hook.)Hieron.	Parkeriaceae	Sub-emer
Peperomia pellucida (L.) Kunth	Piperaceae	Helophyte
Acroceras zizanioides (Kunth)Dandy	Poaceae	Emergent
Coix lacrima-jobi L .		Emergent
Cynodon dactylon (L.) Pers.		Emergent
Echinochloa colonum (L.)Link		Emergent
Echinochloa polystachya (H.B.K.) Hitchc.		Emergent
Eragrostis japonica (Thunb.)Trin.		Emergent
Eragrostis hypnoides (Lam.)Britton Sterns and Pogg		Emergent
Gynerium sagittatum (Aubl.) Beauv.		Emergent
Hymenachne amplexicaulis (Rudge)Nees.		Note 2
Isachne polygonoides (Lam.)Doell and Mart.		Emergent
Leersia hexandra Swartz.		Note 2
Leptochloa scabra Nees.		Emergent
Luziola subintegra Swallen		Free-floating
Oryza latifolia Desv.		Emergent
Oryza rufipogon Griff.		Emergent
Panicum elephantipes Nees. in Trin.		Note 2
Panicum dichotomiflorus Michx.		Emergent
Panicum grande Hitch & Chase		Emergent
Panicum laxum Sw.		Emergent
Panicum maximum Jacq.		Emergent
Panicum mertensii Roth		Emergent

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Panicum parvifolium Lam.		Emergent
Panicum pilosum Swartz		Emergent
Panicum scabridum Doell. in Mart.		Emergent
Paspalum conjugatum Bergius		Emergent
Paspalum fasciculatum Willd.		Emergent
Paspalum repens Berg.		Floating
Paspalum wrightii Hitch. & Chase.		Emergent
Urochloa arrecta (L.) Stapf.		Emergent
Urochloa mutica (Forsskal) Nguyen.		Emergent
Sacciolepis striata (L.) Nash.		Floating
Spartina alterniflora Loisel		Emergent
Sopobolus virginicus (L.) Kunth.		Emergent
Polygonum acuminatum H.B.K.	Polygonaceae	Emergent
Acrostichum aureum L.	Polipodiaceae	Helophyte
Acrostichum danaeifolium langsd. &Fischer		Helophytet
Pityrogramma calomelanos (L.)Link		Helophyte
Thelypteris interrupta (Willd.) Iwatsuki		Helophyte
Eichhornia azurea (Sw.)Kunth.	Pontederiaceae	Floating
Eichhornia crassipes (Mart.)Solms		Free-floating
Eichhornia heterosperma Alexander		Floating
Heteranthera reniformis Ruiz & Pav.		Sub-emer
Pontederia rotundifolia L.f.		Emergent
Diodia multiflora D.C.	Rubiaceae	Helophyte
Diodia hyssopifolia (Roem.& Schult.) Cham. & Schlecht.		Helophyte
Mitracarpus hirtus (L.) DC.		Helophyte
Oldenlandia lancifolia (Schum.)DC.		Helophyte
Salvinia auriculata Aubl.	Salvinaceae	Free-floating
Salvinia sprucei Kuhn.		Free-floating
Agalinis hispidula (Mart.) D«Arcy	Scrophulariaceae	Helophyte
Bacopa aquatica Aubl.		Emergent
Bacopa saltzmannii (Benth.) Ewall.		Emergent
Capraria biflora. L.		Helophyte
Lindernia dubia (L.) Pennell		Helophyte
Thelypteris gongyloides (Schkuhr) Small.	Thelypteriaceae	Helophyte

Thelypteris serrata (Cav.)Alston		Helophyte
Sphenoclea zeylanica Gaertn.	Sphenocleaceae	Emergent
Typha dominguensis Pers.	Typhaceae	Emergent
Lippia betulifolia H.B.K.	Verbenaceae	Helophyte
Phyla nodiflora (L.) Green		Helophyte
Xyris caroliniana Walter	Xyridaceae	Helophyte
Costus arabicus L.	Zingiberaceae	Helophyte

Note 1: Species that may adopt different habit (Eco-phases) according to the level of flooding. Floating - emergent. Note 2: Species that may show floating leaves and slender culms (floating) when flooding is deep and be emergent in shallow waters.

Appendix 3. Key to the species of the Poaceae in the Orinoco Delta

The key includes several species not collected in this study but, recorded for the Delta region.

1A.-Aquatic plants with floating culms, at least during its maximum development------------------2

1B.-Aquatic plants emergent, culms not floating from the bottom to the summit------------------11

2A.- Culms aerenchymatous ---3

2B.-Culms hollow--4

3A.-Culms Leaves with blades tipically broad, cordate. Ligules membranous 1-2 mm long
--*Hymenacne amplexicaulis*

(not to be confused with *Acroceras zizanioides*)

3B.-Leaves attenuate at the base. Ligules 3-4.5 mm ciliate---
--*Echinochloa polystachya*

4A.-Auricles present at both sides of the sheath summit---5

4B.-Auricles absent. --6

5A.-Culms robust. Sheats greatly inflated. Inflorescence 100-200 racemes--*Paspalum repens*

5B.- Culms weak. Sheats not inflated. Inflorescence an open panicle. Spikelets flushed with
pink or purple--*Leersia hexandra*

6A.-Ligules 1-3 cm long Spikelets unisexual, one-flowered
in separate panicles---*Luziola subintegra*

6B.-Ligules lower than 1 cm long. Spikelets bisexual--7

7A.-Culms weak----------- ---8

7B.-Culms robust--9

8A.-Tufted plants, frecuently much branched at the base. Leaves up to 45 x 1.4 cm, totally
glabrous. Inflorescence an open panicle (2-) 5-20 cm, wide.---------------*Panicum dichotomiflorus*

8B.-Sprawling plants. Leaves up to 18 x 0.11 cm, glabrous except for few cilia in the margins
near the summit of the sheath. Inflorescence a loosely spicate panicle 1-2 cm wide---------------
--*Sacciolepis striata*

9A.-Inflorescens an open panicle---10

9B.-Inflorescence a racemes. Spikelets paired in two rows. Nodes purple----------------------------
--*Paspalum writii*

10A.- Culm aerenchimatous. Ligule membranous 0.4-0.5 mm long, surmounted by a row of cilia
1-1.3 (-1.7) mm long---*Panicum elephantipes*

10B.- Culm hollow. Ligule membranous 1-2.6 mm long surmounted by a row of cilia
0.4-0.8 mm long---*Panicum grande*

11A.-Plants growing in a halophitic environment, specially along the coast--------------------12

11B.-Plants growing in a fresh-water environment inland--14

12A.-Cespitose plants. Culms 2-3 m long. Nodes purple. Inflorescence an open
panicle--*Panicum altum*

12B.-Rhizomatous plants. Culms less than 1.5 m long--13

13 A.-Culms 30-40 (-60) cm long, 3-4 mm wide. Leaves strongly overlapping and distichous,

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blades 5-17 cm long. Inflorescence 3-10 cm long------------------------------------*Sporobolus virginicus*

13B.-Culms 80-100 cm long, 7-10 mm wide. Leaves not overlapped nor distichous, blades15-25 cm long. Inflorescence 10-25 cm long------------------------------------*Spartina alterniflora*

14 A.-Plants rarely more than 50 cm tall--15

14B.- Plants more than 50 cm tall--20

15 A.-Blades, 10-25 mm long. Inflorescence ovate congested, 10-20 mm long------------------------

--*Eragrostis hypnoides*

15B.- Blades longer than 25 mm. Inflorescence not as above----------------------------------16

16 A.-Inflorescence a panicle--17

16B.-Inflorescence a raceme---19

17 A.-Sprawling plant and rooting at the lower nodes. Inflorescence 13-30 cm long----------------

----------------------------   *Acrocera zizanioides* (not to be confused with *Sacciolepis striata*)

17B.- Erect plants. Inflorescence less than 13 cm long--18

18 A.-Ligule 1-2 mm long, ciliate. Spikelets globose to slightly obovate, ciliate. Florets (2) round plano-convex, 8-1.2 mm long--*Isachne polygonoides*

18B.-Ligule 0.5 mm long, membranous. Spikelets elliptical, glabrous----------------------------

--*Paspalum parviflorum*

19 A.-Racemes 3-5, 2.5-6 cm long--*Cynodon dactylon*

19 B.-Racemes 2 rarely 3, 7-12 cm long, divergents, arching, conjugate-----------------------

--*Paspalum conjugatum*

20 A.-Plants taller than 0.5 (-4) m---21

20 B.-Plants taller than 4(-20) m---37

21 A.- Inflorescence subtended by a hollow, bony bead. Blade subcordate at the base-----------

--*Coix lacryma-jobi.*

21 B.-Inflorescence not subtended by a bony bed---22

22 A.-Awned spikelets ---23

22 B.- Awnless spikelets---25

23 A.- Culms solid, aerenquimatous----------------------------------*Echinochloa polystachya*

23 B.- Culm hollow--24

24 A.-Ligule 3-7 mm long. Basal branches of inflorescence in small fascicles--------------------

--*Oryza latifolia*

24 B.-Ligule 8-35 mm largo. Basal branches of inflorescence alternate-----------------------

--*Oryza rufipogon*

25 A.-Inflorescence a raceme of racemes (only few short secondary branches in *Urochloa mutica*)--   ------------------------------ 26

25 B.-Inflorescence a panicle--32

26 A.-Culms solid, internodes reddish, 1-2 m long-----------------------*Paspalum fasciculatum*

26 B.-Culms hollow---27

27 A.- Ligule absent--28

27 B.-Ligule present--29

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28 A.-Racemes, 20-75. Spikelets 2.3-2.8 mm long ----------------------------------*Echinochloa colona*

28 B.-Racemes, 5-12. Spikelets 1.3-1.8 mm long----------------------------------*Panicum pilosum*

29 A.- Spikelets (2-6) laterally compressed--*Leptochloa scabra*

29 B.- Spikelets dorsally and ventrally compressed----------------------------------30

30 A.- Culms branched forming a complex of inflorescences---------------------------------

--*Andropogon bicornis*

30 B.- Culms not branched, terminal inflorescence----------------------------------31

31 A.-Basal branches of the inflorescence not divided----------------------------*Urochloa arrecta*

31 B.-Basal branches of the inflorescence with few short divisions-----------------------------

--*Urochloa mutica*

32 A.-Inflorescence with the branches alternate--33

32 B.-Inflorescence with at least the lowermost branches, whorled-----------------------------35

33 A.- Inflorescence spicate---34

33 B.- Inflorescence broadly cylindrical--*Panicum laxum*

34 A.- Blades cordate at the base. Dewlap prominent, purple ---------------------------------

--*Hymenacne amplexicaulis*

34 B.- Blades attenuate at the base. Dewlap yellowish ----------------------------*Eragrostis japonica*

35 A.- Inflorescence with all the branches whorled---------------------------------*Panicum mertensii*

35 B.-Inflorescence with the lowermost branches whorled-----------------------------------36

36 A. Nodes and collars glabrous, reddish ----------------------------------*Panicum elefanthipes*

36 B.-Nodes and collars densely and finely pubescent, not reddish---------------------------------

--*Panicum maximum*

37 A.-Culms hollow 5-15 cm wide. Blades 6-12 cm long----------------------------*Bambusa vulgaris*

37 B.-Culms solid, 1.5-2 cm wide. Blades 100-150 cm long -------------------*Gynnerium sagittatum*

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Appendix 4. Descriptions and Illustrations of the Poaceae from the Orinoco Delta.
UD: Upper Delta; MD: Middle Delta; LD: Lower Delta.

Acroceras zizanioides (Kunth) Dandy

Plants sprawling and rooting at the lower nodes, the erect part of culms ca 50 cm tall. Leaves, glabrous; ligules 0.3-0.4 mm long membranous, ciliolate; blades 8-17 x 1-2.5 cm, lanceolate to lanceolate- ovate, cordate at the base. Inflorescence, an open panicle with few branches, 12-30 cm long, ovate. Spikelets, 5-6.2 mm long, narrowly obovate, glabrous.

Ecology: growing in marshes of standing waters, with some levels of eutrophication, muddy soils. Along river edges of white waters, forming dense patches in rooted meadows in sandy islands. In open sun to shady areas in the ecotone with the flooded forest.

Sites of collection: Laguna Ataguia, U D; Ciénaga Los Guires (marshes), U D; Caño Tucupita, UD; Caño Mánamo, UD.

Andropogon bicornis L.

Robust, erect, cespitose plants. Culms hollow 100-200 cm tall. Leaves coarse, shiny, often with a reddish cast when old. Sheaths slightly inflated; ligules 1-2 mm long, membranous. Blades 20-35 x 3-8 mm, flat to inrolled. Inflorescence a broomlike mass of numerous bracteate racemes, 15-50 x 10-15 cm. Spikelets paired, one sessile 2.5-3.3 mm long, linear lanceolate. One pedicelled and falling first.

Ecology: Growing in marshes of standing and slightly saline waters. Forming dense stands.

Sites of collection: Guacajara oeste, MD.

Bambusa vulgaris Schrad. ex J. C. Wendl.

Giant, cespitose bamboos. Culms 10-20 m x 5-12 cm, glabrous. Foliage leaves in complements (7-9); inner ligules 0.5 mm long, membranous; outer ligules, 0.3-1 mm long, indurate; blades (12-) 20-30 x 1.5-4 cm, in complements, lanceolate, glabrous, deciduous, truncate to round at base. Inflorescence produced as a series of loosely fasciculate, 2-3 cm long clusters. Pseudospikelets 14-20 mm long, narrowly ovate to lanceolate.

Ecology: In the delta region has been found in a dry secondary forest, nearby the mouth of the Mánamo River.

Sites of collection: Capure, LD.

Coix lacrimae-jobi L.

Robust maiz-like plant. Culms up to 2 m x 1 cm, glabrous. Leaves glabrous; sheaths much shorter than the internodes; dewlaps prominent; ligules 1 mm long, membranous; blades 20-40 x 2-4 cm, lanceolate, subcordate at the base. Inflorescence numerous from axillary to terminal nodes; beads 9-12 x 6-9 mm elliptical to ovate, becoming bony when mature. Spikelets 6-9 x 1.5-2 (-3) mm, lanceolate to oblanceolate.
Ecology: Found in the flooded strip along the rivers of the lower delta, in muddy soils. Probably introduced by Waraos Indians. The bony beads are used, when dry, to make adorns.
Sites of collection: Caño Guiniquina, LD.

Cynodon dactylon (L.) Pers.

Creeping plant. Culms erect (flowering portion up to 40 cm long), glabrous, freely branching at the lower nodes. Leaves with sheaths keeled, glabrous, the summit with a row of cilia, 2-3 mm long. Ligules 0.3 mm long, ciliate. Blades 2.5-8 x 1-3 cm, attenuate at the base. Inflorescence of 3-5 subequal racemes (1.5-) 2.5-6 cm long. Spikelets 2-2.5 mm long, strongly laterally compressed.
Ecology: Sandy edges along river channels. Annually flooded. Open sun.
Sites of collection: Caño Macareo, AD,MD.

Echinochloa colona (L.) Link

Plant tufted or branching and decumbent, rooting at the lower nodes. Culms 55-100 cm tall, slender, glabrous or the nodes hispid. Leaves with sheaths glabrous or few auricular , pilose hairs; ligule absent; blades 8-18 x 0.4-1.1 mm. Inflorescence 5-15 cm long, of 5-12 ascending racemes. Spikelets 2.3-2.6 mm, ovate, pubescent, plano-convex.
Ecology: Shallow lagoons or marshes, with some saline influence. Sandy to muddy soils. Open sun.
Sites of collection: Capure, LD.

Echinochloa polystachya (Kunth) Hitchc.

Plant robust. Culms to over 5-7 m long, 1-2 cm in diameter, aerenchymatous; glabrous or the swollen nodes brown-hispid. Leaves with sheaths slightly inflated, glabrous to papillate-hispid; ligules 3-4.5 mm long, ciliate; blades 35-75 x 1-2.5 cm. Inflorescence 15-32 cm long, ovate to pyramidal. Spikelets with body 4.3-6 mm long, ovate; lemna usually awned, up to 15 mm long.

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Ecology: Growing in standing waters and lentic environments on river banks, influenced by tidal or seasonal high water level oscillations. Specimens collected in rivers of black waters as the Caño Acoimito coming from the Guayana shield have a shorter and thinner culms than those growing in the white water courses as Caño Macareo in the middle Delta.

Sites of collection.: Caño Mánamo, LD; Caño Coboina, LD; Caño Acoimito, LD; Caño Macareo, LD; Boca del Caño Merejina, LD; Caño Araguaito, MD; Capure, LD.

Eragrostis hypnoides (Lam.) Britton, Stern, & Poggenb.

Plants extensively stoloniferous. Culms freely branching below, erect part of culms erect, 5-10 (-20) cm tall. Leaves with sheaths shorter than internodes, glabrous or marginally short-ciliate; ligules 0.3-0.7 mm long, ciliate; blades 5-23 x 1-1.8 mm. Inflorescence 10-20 cm long, ovate, congested. Spikelets 5-13 mm long, linear- oblong, often curving.

Ecology: Forming mats in muddy shores of rivers and lagoons beds after the water evaporation. Open sun.

Sites of collection: Caño Macareo, MD; Boca de Macareo; UD.

Eragrostis japonica (Thunb.) Trin.

Tufted plants. Culms up to 100 cm tall, glabrous. Leaves glabrous, rigid; ligules 0.5-0.6 mm long, membranous; dewlaps yellowish; Blades 18-23 x 3-7 cm long. Inflorescence a bushy contracted panicle, 20 cm long; branches appressed. Spikelets (1.7-) 2.3-3.5, linear- oblong.

Ecology: Muddy areas on lagoons and river shores. Open sun.

Sites of collection: Caño Macareo,UD; Caño Macareo, MD; Boca Caño Merejina, LD.

Gynerium sagittatum (Aubl.) P. Beauv.

Giant, reedlike plant. Culms erect, 5-8m x 1.5-2.5 cm, solid. Leaves strongly overlapping, sheaths glabrous except densely woolly along margins and midvein near the summit; dewlaps prominent; ligules 1 mm long; blades 100-200 x 3-6 cm, the margins extremely scabrous to serrulate; the midvein slightly sunken and sparingly pilose on the upper surface, raised into a broad (to 6 mm wide) low dom on the lower surface. Inflorescence a panicle 100-150 cm long, plumose or bushy; the filiform branches borne in pendent fascicles. Female spikelets 9-11 mm long, plumose, V- shaped. Male spikelets, 21.7-3.5 mm long, only sparingly pubescent.

Ecology: Along riverbanks in wet areas, often forming the ecotone between the rooted meadows and the forest. Also in rooted meadows. Muddy to sandy soils. Open sun.

Sites of collection: Not collected. Very wide distributed along all the delta habitats.

Hymenachne amplexicaulis (Rudge) Nees
Plants with erect or decumbent, floating culms to over 2 m long. Leaves glabrous; ligule 1.4-2 mm long, membranous; blades 15-25 x 1.4-2 cm, cordate at the base. Inflorescence 16-40 x 0.7-1.2 cm, densely spicate. Spikelets 3.8-5.3 mm long, slenderly lanceolate.
Ecology: Edges of lagoons and rivers of white, clear and black waters. Forming colonies in shallow waters.
Sites of collection: Cienaga El Garcero, UD; Laguna Las Clavellinas, UD; Laguna La Travesia, MD; Guara island, UD; Caño Guapoa, MD; Caño Ibaruma, LD; Caño Guiniquina, LD;

Isachne polygonoides (Lam.) Doell in Mart.
Sprawling plant. Culms decumbent, the erect flowering portion 12-35 cm tall. Internodes glabrous, nodes bearded. Sheaths shorter than internodes, densely pilose; ligules 1-2 mm long, ciliate; blades 20-35 x 6-12 mm, subcordate at the base, the margins papillate-pilose. Inflorescence 4-9 cm long, ovate. Spikelets 1.2-1.7 mm long broadly elliptical.
Ecology: Forming extensive colonies in rooted meadows along river courses. In shallow waters and muddy grounds in lagoons. White waters. Open sun.
Sites of collection: Curiapo (Río Grande), LD; Laguna Terraplen, UD.

Leersia hexandra Sw.
Rhizomatous plant. Culms weak, becoming decumbent and rooting at the nodes, the erect portion 30-50 cm tall. Leaves with sheaths glabrous to scabrid, keeled; summit of sheath prolonged in an elongate-triangular auricle in one side. Dewlaps brown; ligules 2-4 mm long, truncate or lacerate, whitish; blades 10-26 x 0.3-1 cm, linear, rounded at the base. Inflorescence, 10-20 cm long, ovate. Spikelets 3.4-3.8 mm long, elliptical, whitish or flushed with pink or purple.
Ecology: Forming large floating mats, on shallow waters, on lagoons or muddy grounds and marshes. Occasionally in river edges. Open sun.
Sites of collection: Herbazal Pepeina, MD; Laguna Las Clavellinas, UD; Laguna Terraplen, UD; Laguna Travesia , MD; Caño Acoimito, LD; Herbazal de Pepeina, MD.

Leptochloa scabra Nees

Tufted, somewhat succulent plants. Culms 50-80 cm tall; foliage glabrous and generally scabrous; leaves usually scabrid, dewlap often blackish; ligules 1.5-2.3 mm long, membranous with a fringe of cilia; blades 12-23 x 0.5-12 cm. Inflorescence, slender racemes 13-25 cm long, narrowly pyramidal. Spikelets 3.3-4.5 mm long, sometimes flushed with purple.

Ecology: Growing on river edges, forming rooted mats; on muddy and sandy substrates. Scarce. Open sun.

Sites of collection: Caño Macareo, MD, LD.

Luziola subintegra Swallen

Stoloniferous plant, with abundant branches. Culms decumbent, shining, glabrous. Sheaths overlapping, somewhat inflated, glabrous to puberulent; ligules 1-2 cm long, membranous, narrowly triangular , adnate to sheaths auricles; blades25-42 x 0.5-1 cm. Female inflorescence, an umbelliform panicle, 1-several, borne near base to culms, at the water surface. Female spikelets 4-4.8 mm long, ovate, caudate, terete, yellowish. Male inflorescence, an aerial panicle, 2-8 cm long, borne 20-50 cm above the surface of the water. Male spikelets 3-5 mm long, narrowly lanceolate to elliptical, yellowish.

Ecology: Forming dense, floating mats, in shallow to deep waters in lagoons or river fringes. White, clear and black waters. Shade to open sun.

Sites of collection: Caño Mánamo, UD; Laguna Alamilla, LD; Laguna Terraplen, MD; Laguna travesia, MD; Caño Capure (observed).

Oriza latifolia Desv.

Robust, cespitose plant. Culms erect, 1-2 (-2.5 m) tall, hollow, weak. Leaves with sheaths finely scaberulous or glabrous; sheaths summit often with a small purplish dewlap and a few 1-2 mm long cilia; ligules 3-7 mm long, membranous surmounted by a dense row of cilia; blades 40-60 x 2-4 cm, scabrous on the margins. Inflorescence a terminal panicle, 20-35 cm long. Spikelets 5.5-7.5 mm long, elliptical, deciduous. Lemna with an awn straight or slightly flexuous, 15-25 mm long.

Ecology: Along lagoons shores, in shallow water and muddy soils. Forming rooted meadows on river banks. Clear to black waters.

Sites of collection: Laguna Alamilla,LD; Laguna Merecure,MD; El Rosario, UD; Caño Ibaruma, LD.

Oriza rufipogon Griff.

Cespitose, weak, perennial plant. Culms erect, 1-2 m tall, unbranched above the base, hollow. Leaves with sheaths glabrous, the summit often with inconspicuous dewlaps;

ligules 8-18 mm long, membranous; blades 25-35 cm, scabrous on the margins. Inflorescence a terminal panicle, 18-25 cm long. Spikelets 7.5-10 mm long, elliptical, deciduous. Lemna awn 25-60 mm long.

Ecology: Along lagoon shores, in shallow waters and muddy soils.

Sites of collection: Laguna Alamilla, LD.

Panicum altum Hichc. & Chase

Cespitose plants. Culms 2-3 m tall, often becoming decumbent and rooting at the lower nodes, hollow. The leaves shorter than the internodes; sheaths somewhat inflated at the base; ligules 0.3-0.4 mm long, surmounted by a dense beard of cilia 1-2.5 mm long; blades 25-45 x 0.8-1.3 cm, linear. Inflorescence terminal, 20-25 cm long, an open panicle. Spikelets 2.8-3.2 mm long, ovate.

Ecology: Sandy and muddy coastal areas, saline environments of the river mouths.

Sites of collection: Not collected. Herbarium samples from Pta. Brava, Mouth of Caño Guiniquina.

Panicum dichotomiflorum Michx.

Weak, tufted plant, frequently much branched at the base. Culms 50-130 cm long, hollow, glabrous, frequently becoming decumbent and rooting at the nodes; erect portion 30-50 cm. Leaves with sheaths about as long as the internodes, glabrous, straminous to purplish; ligules 1-3 mm long, membranous or ciliate; blades 8-45 x 0.3-1.4 cm, subcordate at the base. Inflorescence terminal and axillary panicles, 2-25 cm long, ovate. Spikelets 2-3 mm long, elliptical to slightly obovate.

Ecology: Floating on river fringes in quite waters. White waters.

Sites of collection: Caño Macareo, MD.

Panicum elefanthipes Nees in Trin.

Robust plant, the basal part submerged and rooted at the nodes. Culms 1-1.5 m tall, aerenchimatous, glabrous; the nodes purple. Leaves with sheaths somewhat inflated at the base, the margins hyaline; dewlaps prominent, purple; collars brownish to purplish; ligules 0.4-0.5 mm long, membranous surmounted by a dense row of cilia 1-1.3 mm long. Inflorescence a panicle, usually enclosed in summit of uppermost leaf sheath, 15-50 cm long, pyramidal, broomlike. Spikelets, 3-4.5 mm long, slenderly lanceolate.

Ecology: Belonging to a rooted meadows in the shallow waters along river, lagoons and marshes. White to clear waters. Muddy soils, open sun.

Sites of collection: Caño Mánamo, UD; Caño Macareo, MD; Caño Acoimito.

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Panicum grande Hichc. & Chase

Robust, perennial plant. Culms decumbent and rooting at the lower nodes, 1-3 m tall, hollow, the nodes dark, densely covered with fine pubescence. Leaves with sheaths glabrous; dewlaps prominent, purplish-brown; the margins scabrous; ligules membranous, 1-2.6 mm long, surmounted by short cilia 0.4-0.8 mm long; blades 50-80 cm long, glabrous to hirsute. Inflorescence terminal, 30-70 cm long, a tangled, ovate panicle, the lowermost nodes bearing verticils of 4-8 branches. Spikelets 2.3-2.8 mm long, lanceolate.

Ecology: Often forming floating mats in river edges. White waters. Open sun.

Sites of collection: Caño Coboina, LD.

Panicum laxum Sw.

Sprawling, creeping plants, rooting at the nodes. Erect portions of the culms 50-80 cm tall, glabrous to sparingly pilose. Leaves with sheaths glabrous to somewhat papillate-pilose, collars often conspicuous, hairy; ligules 0.3-0.5 mm long, membranous, ciliolate or lacerate; blades 4-30 x 0.3-1 cm, linear to linear-lanceolate, inrolling when dry. Inflorescence terminal a broadly cylindrical panicle, 5-30 cm long. Spikelets 1.1-1.7 mm long, lanceolate-elliptical.

Ecology: Along strembanks, forming rooted meadows on clear to black waters. Open sun.

Sites of collection: Caño Ibaruma, LD.

Panicum maximum Jacq.

Robust, cespitose, plant. Culms 1-2.5 m tall, the nodes typically densely and finely pubescent, hollow. Leaves with sheath glabrous to variably pubescent, typically papillate-pilose in the margins and near the summit; collars and dewlaps evident, densely bearded with papillate-pilose hairs; ligules 1 mm long, membranous, surmounted by a dense row of cilia, 1 mm long; blades 25-60 x 0.8-2.3 cm, linear, rounded at the base. Inflorescence terminal, 25-60 cm long, an ovate open panicle, the lowermost branches whorled, the uppermost alternate or opposite. Spikelets 3-3.8 mm long, elliptical.

Ecology: Riverbanks belonging to rooted meadows in white waters. Open sun.

Panicum mertensii Roth in Roem. & Schult.

Rhizomatous, perennial plant. Some culms becoming decumbent and rooting at the nodes; 1-3 m tall, solid at the lower intrernodes; the nodes dark. Leaves with sheaths shorter than the internodes, the margins membranous; dewlaps well developed in

robust plants; ligules 2-4 mm long, membranous surmounted by a row of short cilia; blades 22-40 x 12.5-3.5 cm, linear to narrowly lanceolate, subcordate or rounded at the base. Inflorescence terminal, 20-50 cm long, an ovate panicle, branches disposed in 4-8 nearly equidistant verticils. Spikelets 3.2- 4 mm long, obovate.
Ecology: Belonging to marshes of shallow waters. Open sun.
Sites of collection: Isla Guara, UD.

Panicum parvifolium Lam.
Straggling and extensively sprawling plant, freely branching, creeping and rooting at the nodes. Erect portions of culms 20-50 cm tall, often purplish, the nodes compressed dark. Leaves remotely spaced along culm. Sheaths much longer than the internodes; ligules 0.1-0.2 mm long, membranous, transparent, backed by a row of cilia, 1 mm long; blades 17-33x 0.25-0.7 mm, lanceolate-elliptical. Inflorescence terminal, 3-6 cm long, an ovate, open panicle. Spikelets1-1.8 mm long, sub-globose, elliptical to ovate.
Ecology: Marshes of shallow, clear to black waters. Ponds edges, sandy soils. Open sun to shady areas.
Sites of collection: Pozo Jarahuaja (pond), LD; Caño La Pava (marsh), LD.

Panicum pilosum Sw.
Sprawling, creeping and rooting at the nodes plants. Erect portion of culms 50-100 cm tall; nodes brownish to purplish. Leaves with sheaths inrolled, diverging from the internodes, commonly glabrous with the margins strongly ciliate; ligules absent or occasionally present, small and membranous; collars pubescent; blades 5-25 x 1-1.7 cm, linear-lanceolate. Inflorescence terminal, 8-25 cm long, narrowly-pyramidal, with numerous raceme-like branches, more or less pilose. Spikelets1.3-1.8 mm long, lanceolate.
Ecology: On thick floating meadows in black water river.
Sites of collection: Caño Ibaruma, LD.

Paspalum conjugatum Berg.
Colonial, stoloniferous plant, the erect culms borne in small tufts, the foliage, often crowded at the base. Erect portion of the culms 25-45 cm tall, the nodes purple. Leaves with sheaths glabrous, somewhat succulent, collars usually well developed, ciliolate, resembling an external ligule; ligules 1 mm long, arcuate, membranous; blades 8-15 x 0.6-1.2 cm, narrowed at the base. Inflorescence a pair (rarely 3) of divergent,

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arching, conjugate recemes. Spikelets 1.2-1.8 mm long, orbicular to ovate, strongly dorsally compressed.

Ecology: Disturbed areas and river edges, in muddy soils. Open sun.

Sites of collection: Caño Guiniquina, LD; Caño Jotanana, MD.

Paspalum fasciculatum Willd.

Cespitose, perennial plants. Culms, solid, 1-2 m tall, glabrous, reddish, the nodes with corky swellings. Leaves with sheaths somewhat inflated at base; dewlaps prominent, brown; ligules 1-1.5 mm long, membranous; blades 25-40 x 1-2.2 cm, lanceolate. Inflorescence 13-22 cm long, 14-20 ascending racemes 7-15 cm long. Spikelets 3.7-4.6 mm long, broadly lanceolate.

Ecology: Forming extensive mats in dry river banks, sandy to muddy soils. White to clear waters. Also in drying lagoons. Open sun. Tolerates the seasonal (4-6 months) flooding, that may covers all the plant.

Sites of collection: Caño Araguao, MD; Caño Mariusa, MD; Caño Araguaito, MD; Caño Macareo, UD; Laguna Terraplén, UD.

Paspalum repens Berg.

Robust, floating plants. Culms 2-indefinite m long, erect portion, 30-60 cm tall. The basal leaf sheaths greatly inflated up to 1.5 cm in diameter. Leaves with sheaths glabrous below, finely papillate- pilose near the summit; ligules 2-3 mm long, puberulent, brown, erose, Sheaths auricles present, 3-10 mm long attenuate; dewlaps purple, collars pubescent; blades 20-30 x 0.5-1.8 cm, lanceolate. Inflorescence 8-15 cm long, ovate bearing 20-100, deciduous, spreading, solitary or verticilled racemes, 4-7 cm long. Progressively shorter upward.

Spikelets 1.7-2.2 mm long, lanceolate-elliptical.

Ecology: Forming wide floating meadows in shallow waters, of small to large rivers, also in lagoons. Associated with *Eichhornia crassipes* and other aquatic plants. Attached to muddy soils. Open sun. The strong currents detach big portions of the floating mats, carrying them as rafts. Plants growing on white water (rich in nutrients) are more robust and large than those found in black waters (poor in nutrients).

Sites of collection: Caño Mánamo, UD; Caño Manamito, UD; Caño Coboina, LD; Caño Ibaruma, LD; Caño Macareo, MD; Laguna Travesia, MD; Laguna Alamilla, MD.

Paspalum wrightii Hichc. & Chase

Erect plant. Culms up to 1 m tall, spongy, shining, the nodes purple. Leaves glabrous to sparingly papillate-hispid or sericeous on the margins and summit of sheaths and

blades. The blades abruptly differentiated from the sheaths, much narrower; ligules 1 mm long, membranous; blades 15-18 x 3-5 cm, coarse, flat or inrolled. Inflorescence 15-20 cm long, narrowly pyramidal , of 5-25 ascending, progressively smaller racemes. Spikelets 2.1-2.3 mm long, narrowly elliptical, orangish-brown.

Ecology: Stream banks in shallow and drying lagoons, muddy soils. Clear to black waters.

Sites of collection: Laguna Alamilla, LD; Caño Acoimito, LD.

Sacciolepis striata (L.) Nash

Sprawling, decumbent plant. Culms weak, the erect portion 30-50 cm tall. Leaves with sheaths slightly shorter or equal than the internodes, glabrous, except for a few cilia on the margins near the summit; ligules 0.2-0.4 mm long, ciliate-membranous; blades 13-18 x 6-11 cm, flat, somewhat speudopetiolate. Inflorescence 10-17 cm long and 1.2 cm in diameter, a loosely spicate panicle. Spikelets 3-3.7 mm long, lanceolate-elliptical.

Ecology: Very common in the delta region. Riverbanks and lagoon beaches of white, clear and black waters. Muddy soils.

Sites of collection: Ciénaga El Garcero, UD; Caño Mánamo, UD; Caño Cuberima, LD; Caño Ibaruma, LD; Caño Coboina, LD; Laguna La Florida, UD; Pozo Jarahuaja, LD.

Spartina alterniflora Loisel.

Rhizomatous, robust plant. Culms to 1 m tall and 0.7 cm in diameter, hollow. Leaves, glabrous, smooth, coarse, the uppermost leaves reduced; sheaths with hyaline margins; dewlaps sometimes present, small yellow; ligules 0.6-0.9 mm long, ciliate; blades 15-25 x 0.5-0.9 cm, widest at base, inrolled when dry, pungent, striate in the upper surface. Inflorescence a narrow panicle 10-25 cm long. Spikelets 11-14 mm long, lanceolate.

Ecology: Saline environments, muddy beaches on river mouths. Associated with *Sporobolus virginicus*. Open sun.

Sites of collection: Capure, Caño Mánamo mouth, LD. First record for Venezuela.

Sporobolus virginicus (L.) Kunth

Strongly rhyzomatous, perennial plant. Culms in row in very long rhizomes, 30-60 cm tall, hollow, glabrous, shining, shrunken. Leaves strongly overlapping and distichious, appearing subopposite; sheaths often with delicate cilia along the margins, otherwise glabrous; dewlap often present, yellowish; ligules 0.1 mm long, densely ciliolate; blades 5-17 x 0.3-0.6 cm, linear, widest at the base, typically ascending at about 45 degree angle, flat to slightly inrolled. Inflorescence 3-10 cm long, narrowly-elliptical, compact, densely flowered.

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Spikelets 2-2.6 mm long, lanceolate.

Ecology: Saline habitats, muddy soils on river mouths. Associated with *Spartina alterniflora*. Open sun.

Sites of collection: Capure, Caño Mánamo mouth, LD.

Urochloa arrecta (L.) Stapf.

Sprawling plant, with culms rooting ate the lower nodes. Erect portion of culms, 50-90 cm tall, hollow, glabrous. Leaves glabrous, with sheaths shorter than the internodes; dewlaps present, yellowish; ligules 1 mm long; blades 12-15 x 0.6-1.5 cm, attenuate to subcordate at the base. Inflorescence 12-15 cm long, of 6-8 racemes, the lowest spreading and rather distant; racemes 5 cm long. Spikelets 3.5-4 mm long, narrowly ovate.

Ecology: Shallow waters of ditches and rooted meadows in large rivers. Polluted and white waters. Muddy to sandy soils, Open sun.

Sites of collection: Caño Tucupita, UD; Caño Mánamo, LD.

Urochloa mutica (Forsskal) Nguyen.

Robust plant. Culms readily becoming decumbent and rooting at the nodes. Erect portions of the culms 1-3 m tall, the nodes woolly; sheaths glabrous to softly and sparingly papillose-pilose; dewlaps well-developed, often pubescent; ligules 1.5 mm long, ciliate-membranous; blades 15-21 x 1-1.6 cm long. Inflorescence ovate, of 10-18 ascending, loosely flowered recemes, the lowest, sparingly rebranched. Spikelets 3-3.4 mm long, ovate.

Ecology: Growing in shallow, somewhat polluted waters, of ditches.

Sites of collection: Caño Tucupita, UD.

Acroceras zizanioides (HBK) Dandy

1 cm
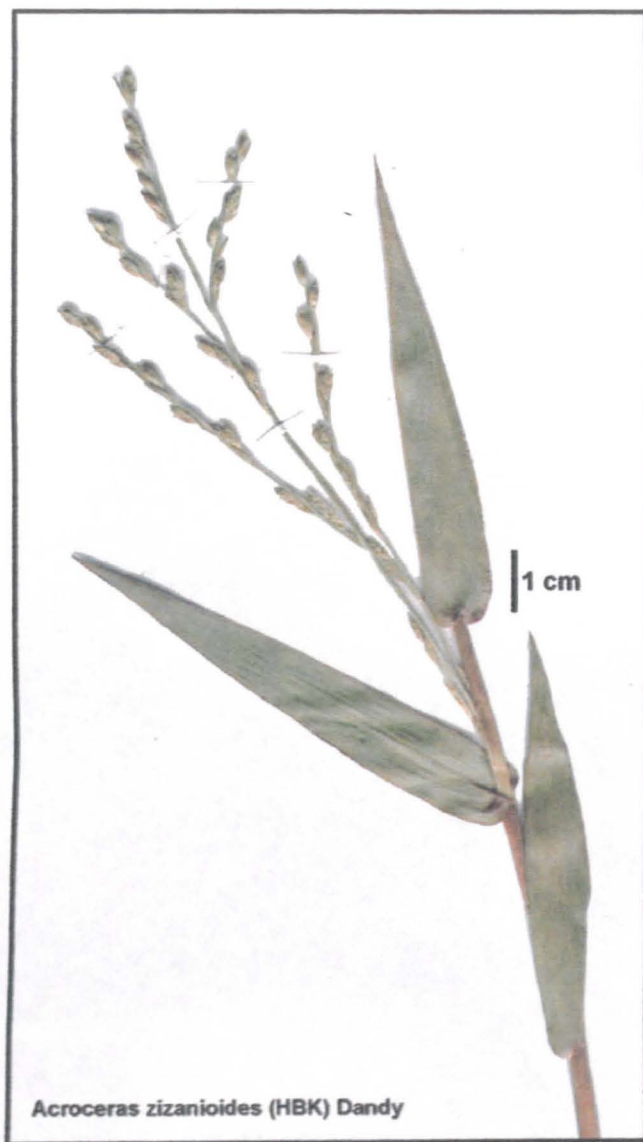
Fig. 1. *Acroceras zizanoides* (HBK) Dandy

Andropogon bicornis L.

1 cm

Fig. 2. *Andropogon bicornis* L.

Coix lacrima-jobi L.

1 cm

Fig. 4. *Coix lacrima-jobi* L.

Bambusa vulgaris Schard.

1 cm
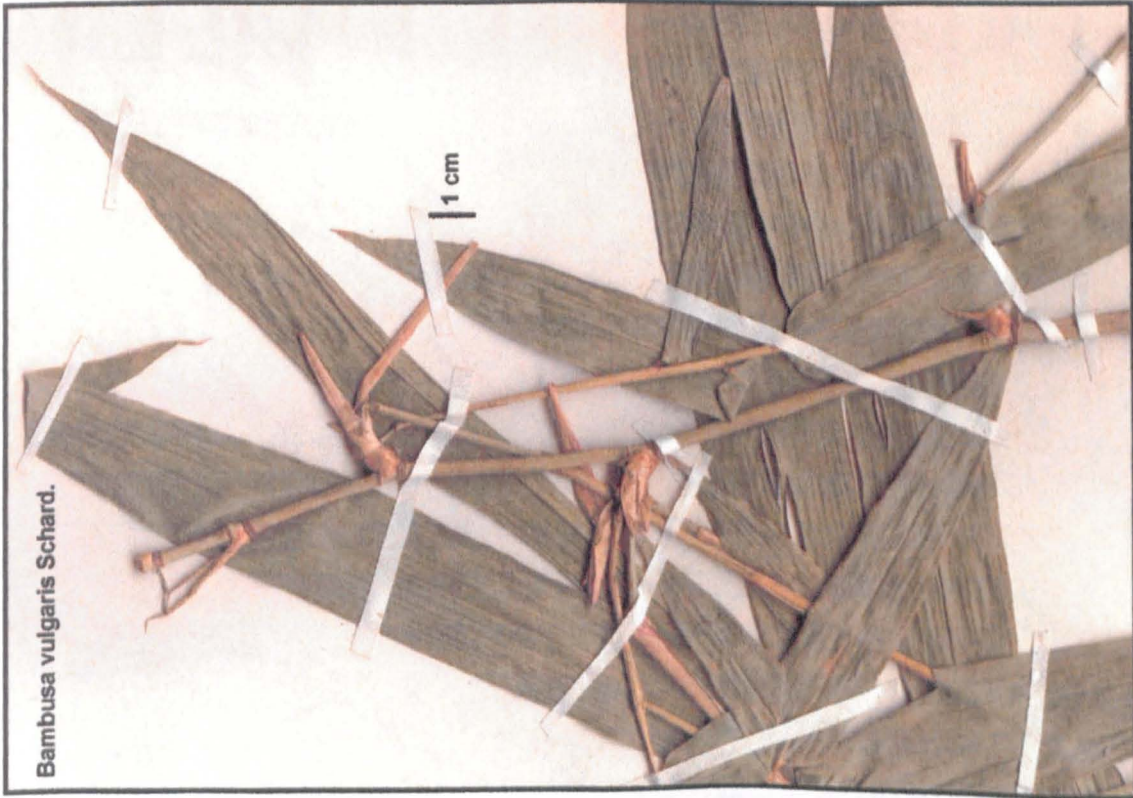
Fig. 3. *Bambusa vulgaris* Schard.

Fig. 5. *Cynodon dactylon* (L.) Pers.

Fig. 6. *Echinochloa colona* (L.) Link.
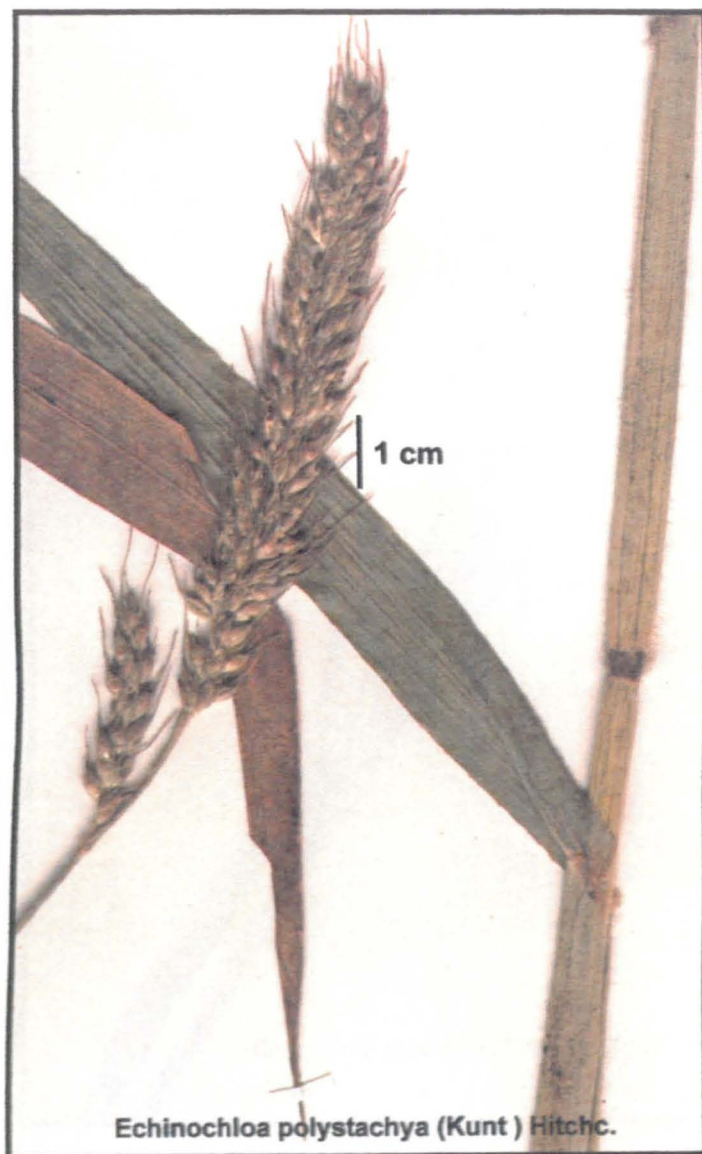
Fig. 7. *Echinochloa polystachya* (Kunt) Hitchc.

Fig. 8. *Eragrostis hypnoides* (Lam.) B.S.P.

1 cm

Eragrostis japonica (Thunb.) Trin.
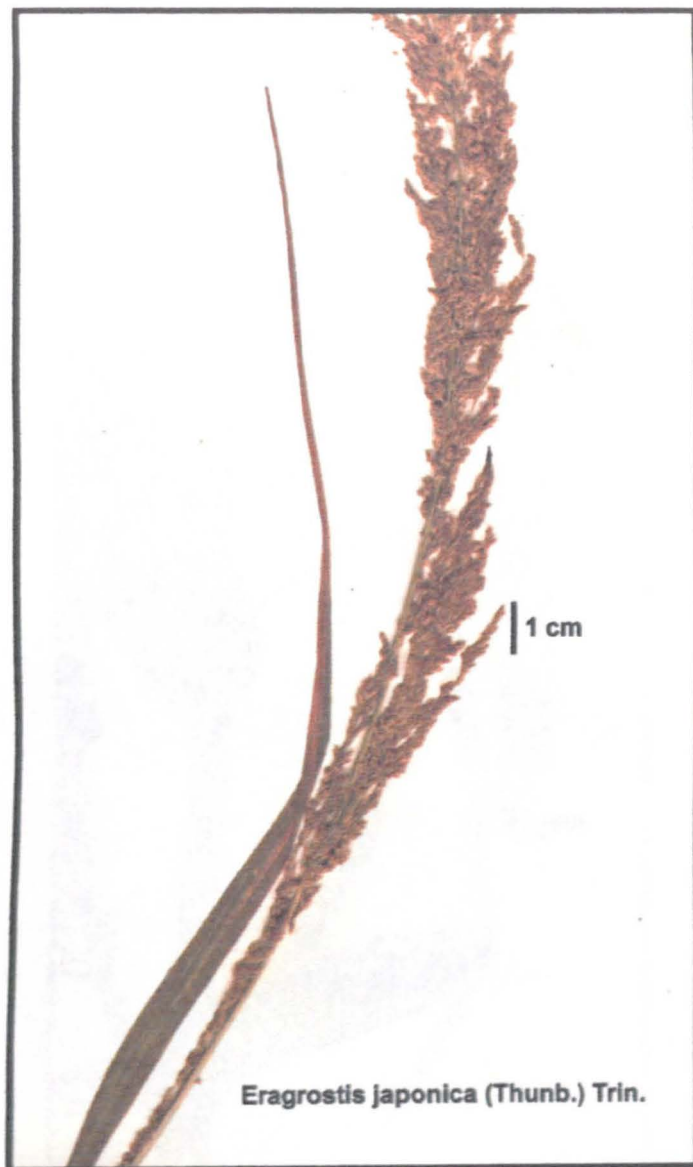
Fig. 9. *Eragrostis japonica* (Thunb.) Trin.

Gynerium sagittatum (Aubl.) Beauv.

1 cm

Fig. 10. *Gynerium sagittatum* (Aubl.) Beauv.
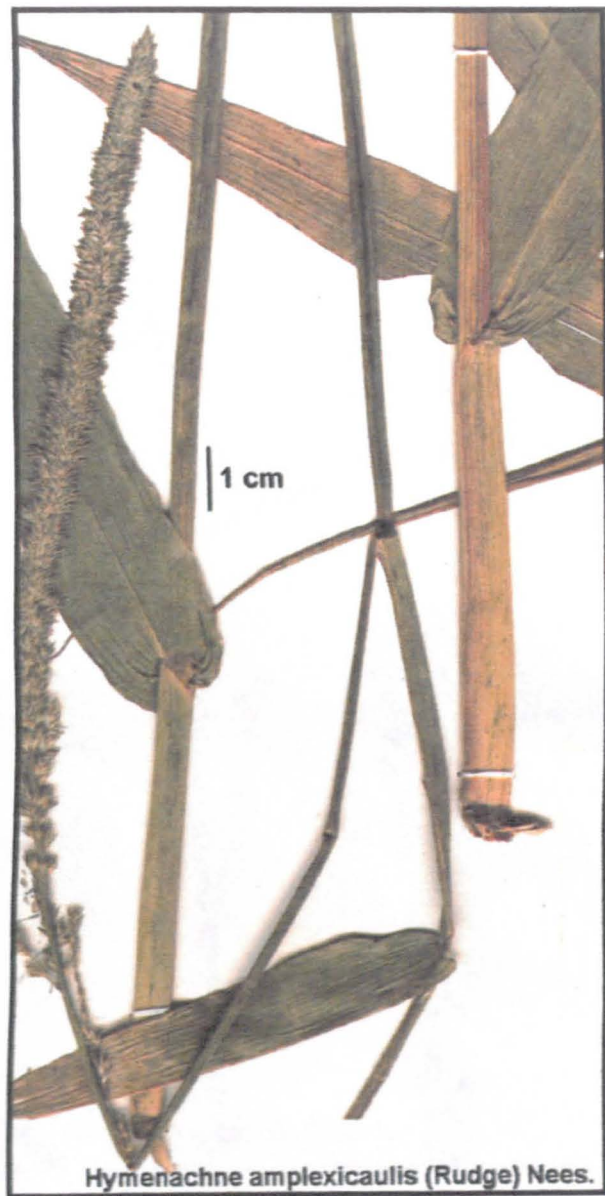
Fig. 11. *Hymenachne amplexicaulis* (Rudge) Nees.

Fig. 12. *Isachne polygonoides* (Lam.) Doell in Mart.
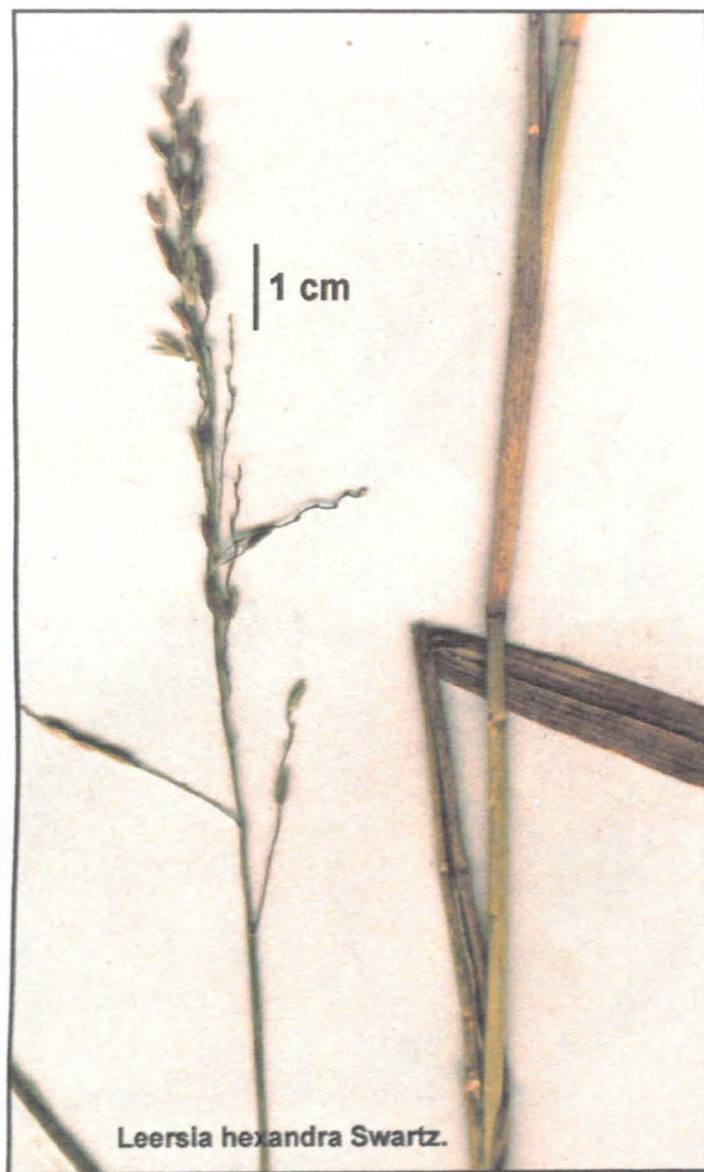
Fig. 13. *Leersia hexandra* Swartz.

Fig. 14. *Leptochloa scabra* Nees.

Fig. 15. *Luziola subintegra* Swallen
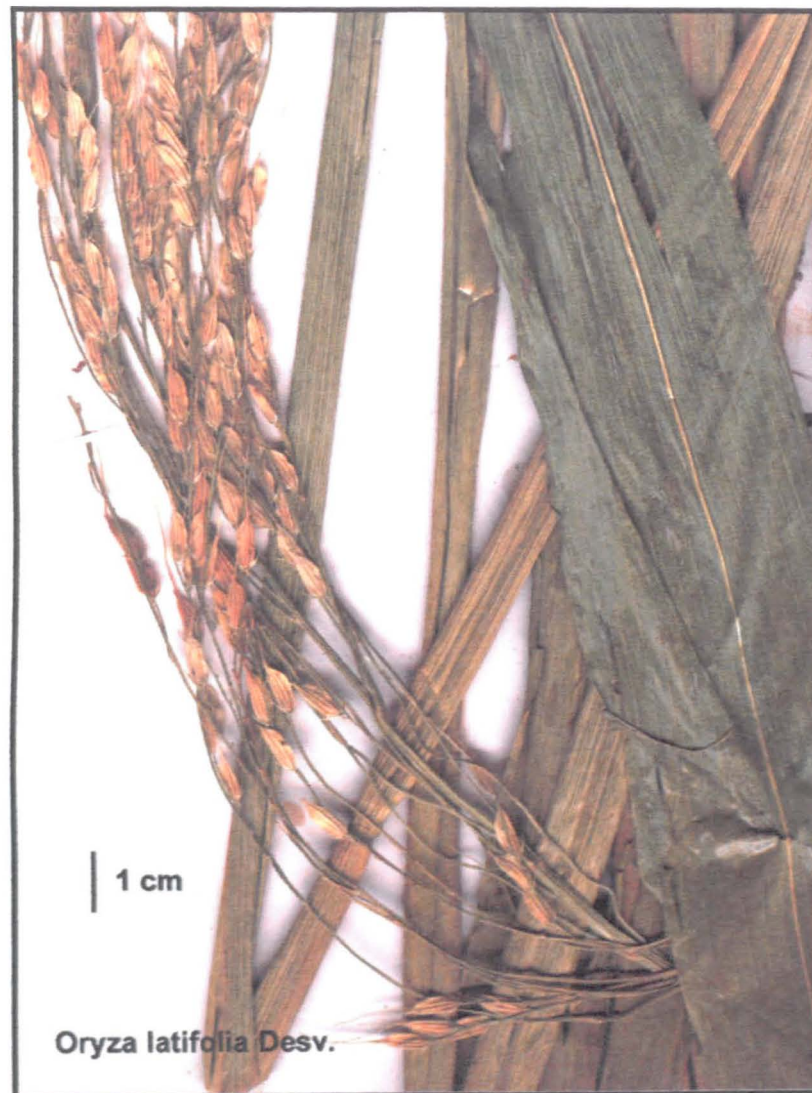
Fig. 16. *Oryza latifolia* Desv.
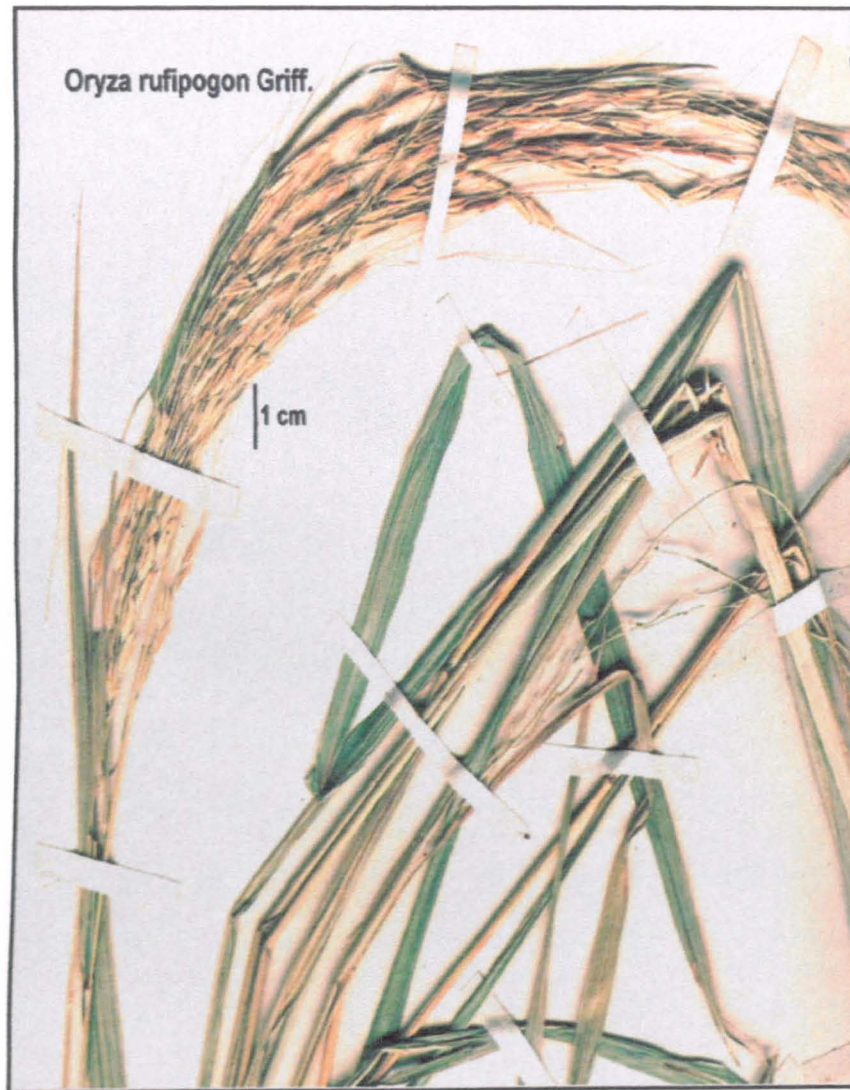
Fig. 17. *Oryza rufipogon* Griff.

Fig. 18. *Panicum altum* Hitchc. & Chase

Fig. 19. *Panicum dichotomiflorum* Michx.

Fig. 20. *Panicum elephantipes* Nees.

Fig. 21. *Panicum grande* Hitchc. & Chase

Fig. 22. *Panicum laxum* Sw.

Panicum mertensii Roth

Fig. 24. *Panicum mertensii* Roth.

Panicum maximum Jacq.
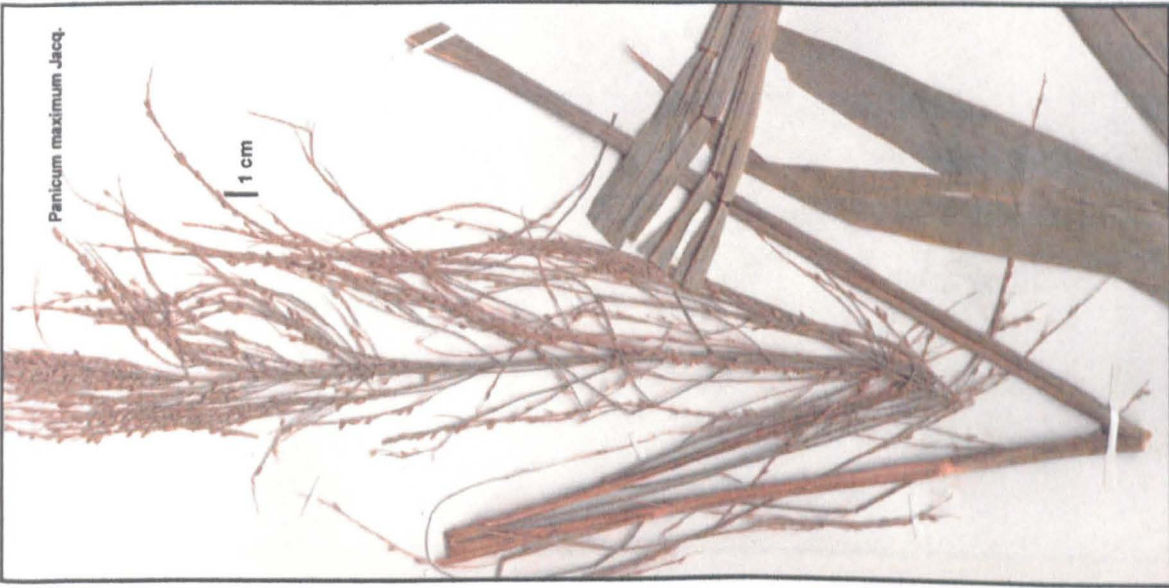
Fig. 23. *Panicum maximum* Jacq.

1 cm

Panicum parvifolium Lam.
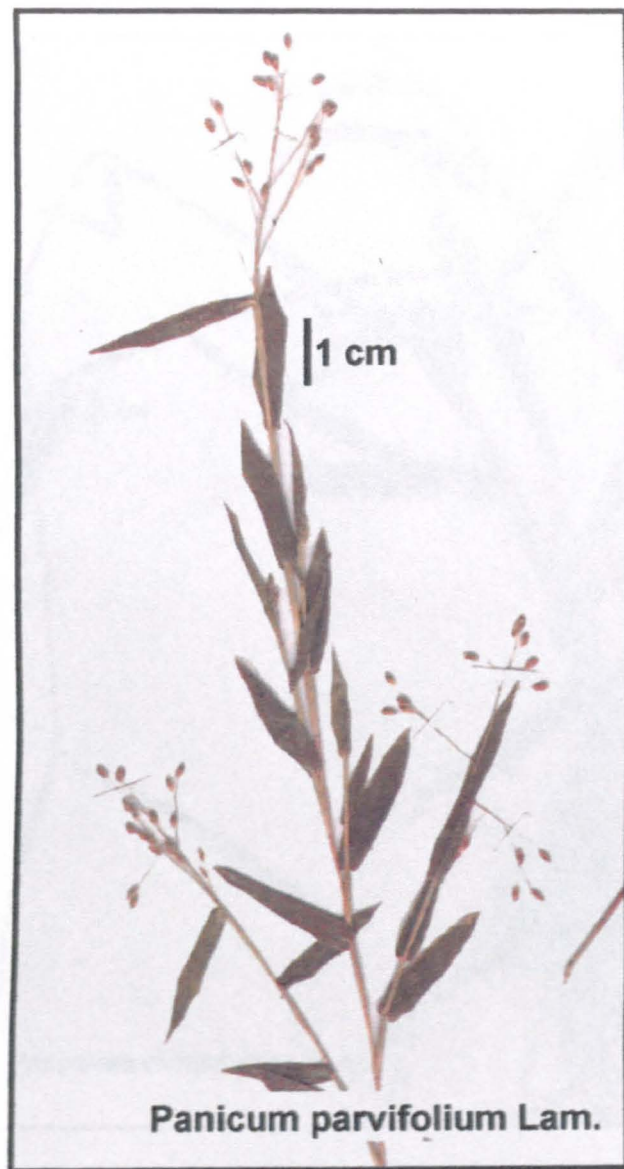
Fig. 25. *Panicum parvifolium* Lam.

1 cm

Panicum pilosum Swartz.

Fig. 26. *Panicum pilosum* Swartz.

Paspalum fasciculatum Willd.

1 cm

Fig. 28. *Paspalum fasciculatum Willd.*

Paspalum conjugatum Berg.

1 cm

Fig. 27. *Paspalum conjugatum Berg.*
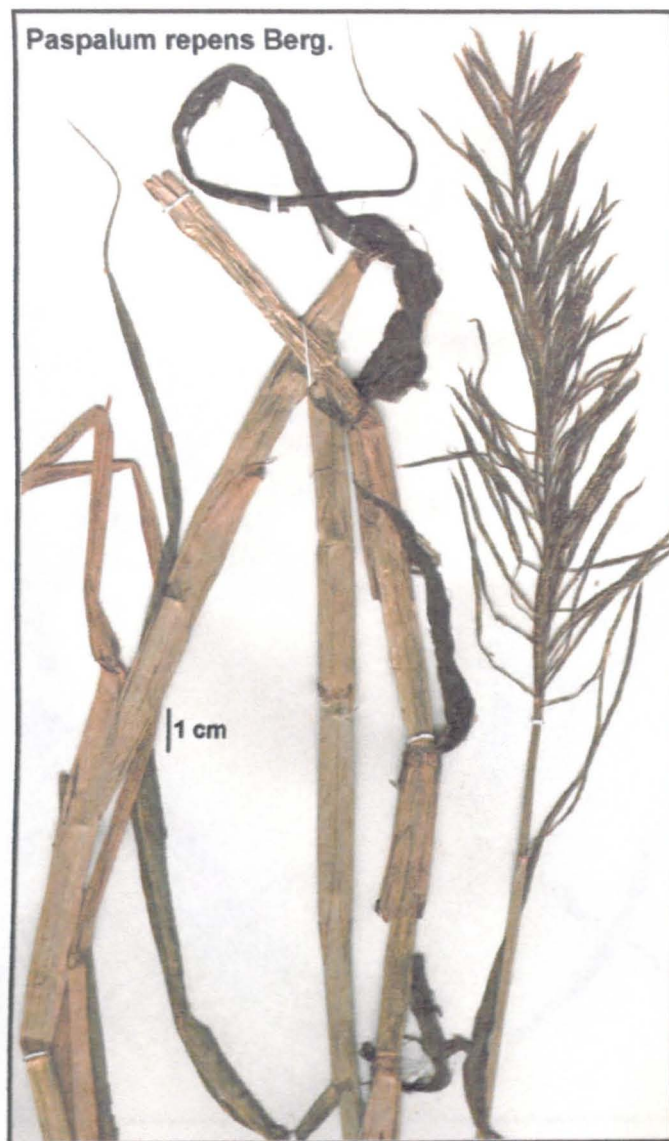
Fig. 29. *Paspalum repens* Berg.

Fig. 30. *Paspalum wrightii* Hitchc. & Chase

Fig. 31. *Sacciolepis striata* (L.) Nees.

Fig. 32. *Spartina alterniflora* Loisel

Fig. 33. *Sporobolus virginicus* (L.) Kunth.
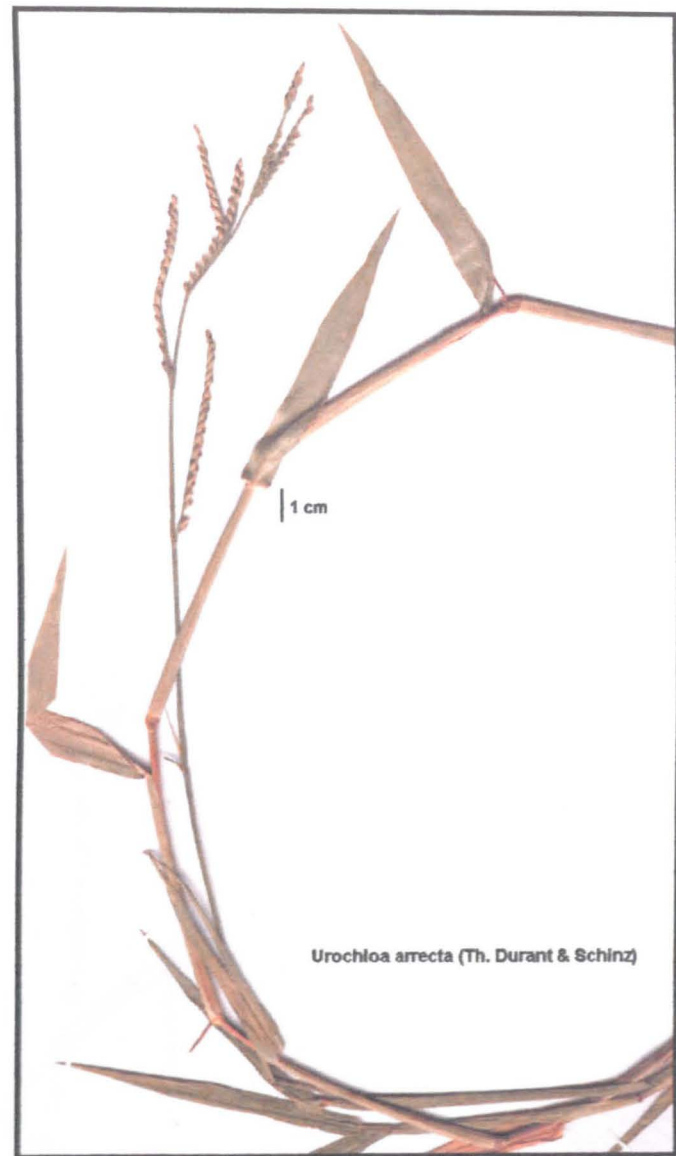
Fig. 34. *Urochloa arrecta* (Th. Durant & Schinz)

1 cm

Urochloa mutica (Forssk.) T.Q. Nguyen

Fig. 35. *Urochloa mutica* (Forssk.) T.Q. Nguyen

Appendix 5. Description of study sites.

Curiapo
The Curiapo site is located on the banks of the Río Grande in the extreme southeast of the Lower Delta. Here the width of the white water distributary channel is approximately 400 m. The site is subjected to major diurnal tidal oscillations, whose mean values reach 1.47 m (Herrera *et al.*, 1981). The bank-slope is gentle and composed of sandy clays. A gradient was observed, from floating (*Eichhornia crassipes*) and rooted plants with floating stems (*Paspalum repens*), to small erect rooted species. In the highest positions, nearly pure communities of *Montrichardia arborescens* followed by *Mauritia flexuosa* were found. On the external portions of the sandy levees, extensive communities of reeds (*Eleocharis elegans*) were found alternating with patches of *E. crassipes, E. azurea, P. repens,* and *Salvinia auriculata.*

Caño Ibaruma
The Caño Ibaruma site is situated along the mainstream of the Ibaruma River, whose black waters originate from the foothills of the Imataca Mountain Range and discharge into the Río Grande in the extreme south-east of the Lower Delta. At the site, the river is approximately 20-40 m wide. This area is subject to tidal oscillations. The banks are steep and the river bottom is composed of sand and gravel with a high content of iron oxides. Rooted plants with floating leaves were encountered along with species, which rooted on the floating mattresses. Also present were pure communities of *Cabomba aquatica* and *Nymphaea* spp. The forest along the banks was an ombrofillous evergreen type.

Caño Guiniquina
At the sample site, the main channel is approximately 30-50 m in width. Near its mouth this distributary channel converges with the Araguabisi River before flowing into the Atlantic Ocean. It is a black water channel due to its catchment in the bordering lowlands, which are covered with dense evergreen forests. The mean daily tidal oscillations measure approximately 1.10 m. The banks are steep and the river bottom is predominantly clay. Plant communities rooted to the riverbanks were observed. These are composed mainly of *P. repens, E. polystachya, Eichhornia azurea* as well as free-floating species, among which is *E. crassipes.* In open areas, colonies of rooted species such as *Pontederia rotundifolia* and *Coix lacrimae-jobi* were found. Because of the tidal effect, the current through the lower course of the distributary carries large groups of water hyacinth (*E. crassipes*).

Pozo Jarahuaja

A small lagoon, of approximately 20-25 m in diameter, containing clear waters that have drained over herbaceous formations and the morichales of the Lower Delta. The banks are abrupt and the soils sandy. In this water body was found a diverse community composed of species belonging to the Cyperaceae (*Rhynchospora holoschoenoides*, *Oxicarium cubense*), Pteridophytae *(Blechnum serrulatum, Acrostichium aureum)* which were rooted on the banks, as well as floating species which include *Nimphaea rudgeana*. From this site was collected the only specimen *of Phillanthus fluitans* from the Lower Delta.

Caño Coboina

The Caño Coboina site is located on the banks of the distributary channel of the same name. Here, the white water channel measures were between 40 and 80 m in width. It runs parallel to the Araguao channel located in the centre east area of the Lower Delta. An evergreen forest subject to the daily oscillations of the tides represents the riverine vegetation. Eddies are a common occurrence. The soil of the site is a muddy clay with abundant organic material. A gradient beginning with free-floating plants, dominated by the water hyacinth, and rooted species with floating stems such as *E. azurea* and *E. polystachya* occurred with decreasing depth, continuing on to rooted erect species. On the higher part of the levee we found *M. arborescens* followed by the red mangrove *Rhizophora mangle*.

Caño Mariusa

This distributary is between 80 and 200 m wide. It discharges predominantly black waters, originating principally from waters that have percolated through forest and herbaceous formations of the Middle Delta. Along its lower course the distributary is heavily influenced by diurnal tidal fluctuations. Towards the headwaters eddy formations are common. The bottom is composed of clay sediments, on which was observed a gradient of free-floating plant communities grading in to rooted species with floating stems and then to rooted erect species. On the higher part of the profile (towards the banks) one finds a herbaceous formation, composed mainly of *Paspalum fasciculatum* near the shoreline and *Gynerium sagittatum* occupying drier areas. On the lower course of the Mariusa relatively small communities of *E. azurea* and *M. arborescens* were observed, followed by a community of mangroves, principally *Rhizophora racemosa*, inhabiting the ecotone with the forest.

Laguna Travesía

The Laguna Travesía is situated in the headwaters of Caño La Playa (and Caño Mariusa) in the upper Middle Delta. It is an area of herbaceous flooded savannahs (4-5 m deep). The lagoons of this region are formed by seasonal rains and flood waters of the Araguao and Macareo distributaries. Although the waters are initially white, local contributions of water and settling of the sediments result in clear waters. Extensive carpets of macrophytes were found, dominated by a few Poaceae e.g. *Leersia hexandra, Oriza latifolia,* and *Luziola subintegra* and free-floating species such as *E. crassipes* and *Salvinia* spp.

Isla Mariusa

The Isla Mariusa is an island formed by a sandy bar, 30 m wide and 80 m long, located in the Middle Delta in the mainstream of the Mariusa channel. The site with a bottom of muddy clays, is surrounded by black waters, is regularly flooded with the oscillation of the tides. An heterogeneous community of floating plants dominated by *Eichhornia crassipes* was observed along the shores, while the higher elevations supported erect rooted species among which were distinguished various different reeds (*Eleocharis interstincta, E. mutata*), climbers, bushes, and forest seedlings.

Caño Cuberina

A Waraoan term indicating the abundance of the Cuberú tree *(Pachira inundata)*.

The Caño Cuberima site is situated on the gently sloping banks of a channel (50-100m wide) which discharges black waters. The bottom sediments are of clay with a high content of organic matter. Along its lower course this particular channel connects the Caño Mariusa with the Caño Caiguires, where is subjected to a strong tidal influence with a salinity up to 5 0/00. Along the length of the channel are small colonies of *E. azurea* and *E. polystachya*, a few communities of *M. arborescens* and red mangrove. In the shallower waters were observed several species of rooted plants with floating leaves and erect rooted plants (including *Hymenocallys tubiflora*).

Caño Macareo

This site contained various sampling localities chosen from along the banks of the white water channel. The distributary measures between 200 and 300 m in width. Its banks have abrupt slopes and the current is relatively fast flowing (particularly during the annual flood seasons). During the dry period (low waters) this area is influenced by the diurnal tides whose amplitude vary from the sea to inland. The most extensive aquatic communities are established in those areas sheltered from the currents. Here the

3

dominant species are rooted plants with floating stems (*P. repens* and *E. polystachya*). Near the banks, floating plants (*E. crassipes*) anchor to semi-submerged tree trunks and develop dense communities. Along the banks are communities of emergent species (*Ludwigia* spp. *Costus arabicus*, *Hymenachne amplexicaulis* and *O. cubense*). In the ecotone with the forest one observes dense Gramineae formations dominated by *P. fasciculatum*. During the annual floods, it is not uncommon to observe the greater part of the floating carpets of vegetation transported away by the strong currents.

Caño Guapoa

The Caño Guapoa is a black-water channel between 10 and 30 m wide. It receives waters draining from forest formations of the Middle Delta and empties into the Caño Macareo. Its banks have abrupt slopes and organic soils on which are established rooted plant communities. Formations of rooted plants that grow over floating mattresses of aquatic plants and organic matter are common, and dominated by *Justicia laevilinguis*, *Ludwigia* spp. *Hidrocotile umbellata*, *Begonia patula* and *O. cubense*. During the August, especially near the headwaters, navigation along this course is blocked by accumulation of Water hyacinth.

Caño La Florida

The Caño La Florida site is located on the Caño Cocuina; a 10-20 m wide channel which originates in the Upper Delta and empties out into the Boca de la Serpiente just below the island of Trinidad. It also collects wastewater from various riverside settlements and agricultural lands. The course is subject to diurnal oscillations produced by the tides. Apparently due to pollution, extensive communities of several species e.g. *E. crassipes*, *P. repens*, *H. umbellata*, *L. laevigatum*, *Lemna perspusilla*, *P. stratiotes* and *S. striata* have developed which prevents navigation along a major portion of its upper course.

Laguna Las Clavellinas

This site consists of a small lagoon measuring approximately 20 m wide by 80 m long and up to 2.5 m deep. It is constituted by rainwater. The banks show a gentle slope with organic-clayey soils on which are found a community of rooted plants with *Typha dominguensis* as dominant, surrounded by *M. arborescens*, *G. sagittatum* and *P. fasciculatum*. On the open water are found communities composed of *Hydroclels nymphoides*, *S. auriculata*, *Spirodella intermedia* and *N. rudgeana*.

Caño Pedernales

The site include the banks of the canal of the same name (20-30 m wide) on its upper stretches. It is composed of clear to black waters and clay soils. This watercourse originates from the Caño Cocuina near the settlement of La Horqueta and empties into the Gulf of Paria. It is subject to daily tidal oscillations. A few rooted macrophytes (*O. cubense, B. serrulatum, E. azurea*) grow along the shores in the shallow areas while on the higher elevations are dominated by *Machaerium lunatum* and interspersed by individuals of *Rhizophora mangle*. Rooted in the bottom *Nymphaea* spp was observed. Floating plants, including the water hyacinth, are transported by the fluvial currents.

Laguna Ataguía

A lagoon system several kilometres long and up to 4 m deep. The system was formed as a consequence of the damming of the Mánamo channel. These low-lying areas are initially flooded with rainwater and later with the overflow of the Macareo channel during the flood season. The banks have a gentle slope and are composed of clay sediments. Observed in this environment were several rooted species of Gramineae with floating stems (*L. hexandra, L. subintegra*). Additional species (*H. amplexicaulis* and *Cyperus distans*) form dense borders. *Ludwigia sedioides* and *Nymphaea* spp. were observed among the species rooted in the shallow areas. Large areas of the open water were covered by *Eichhornia* spp. Several submerged plants (*C. aquatica, Utricularia* spp.) were observed to develop once the transparency of the waters increased as a result of the settling out of suspended matter.

Laguna Terraplén

A large lagoon that formed as a result of the construction of a retaining wall which protects Tucupita and other river towns from flooding by the Caño Macareo. The banks have a gentle slope and a depth of 2-3 m. The physico-chemical characteristics of the waters and their floristic composition were very similar to the lagoons of Ataguía. However, they have a greater extension of rooted meadows among which were distinguished several uncommon species such as *Habenaria repens* and *Chelonanthes alatus*.

Caño Tucupita

Caño Tucupita is a channel (approximately 15-25 m wide) connecting the Caño Mánamo with the Caño Macareo. The banks have abrupt slopes and clay soils. A large part of its course passes through towns such as Tucupita where it has been polluted and obstructed by dense carpets (over 100 m long) of *E. crassipes, P. repens, E.*

polystachya and *P. stratiotes.* At the same time some species such as *Azolla filiculoides, L. perspusilla, L. laevigatum* and *H. umbellata,* form patches of tens-of-square meters. Especially during the wet season, flood control on the Caño Mánamo, and the presence of floodgates in its union with the Macareo downstream, impedes the natural control, which the currents had over the accumulation of aquatic plants.

Ciénaga Los Guires

A swamp which is fed by seasonal rains. It also receives waters originating from the agricultural lands of the Middle Delta. It is a shallow community (20-50 cm deep) with clay soils and dominated by erect rooted plants (e.g. *M. arborescens, C. distans, H. amplexicaulis, F. umbellata, Ludwigia* spp.), anchored floating plants e.g. *L. hexandra,* free floating plants (e.g. *Lemna* spp.) and semi-submerged species such as *Utricularia* spp..

Caño Acoimito

In Warao the term "*acoi*" means "putrid", probably referring to the colour of the waters. A river originating from the run-off of the Imataca foothills and which empties into the Brazo Imataca channel in the Middle Delta. The banks are abrupt, with a clay-mud bottom, and black waters. It is also subject to the daily influence of the tides. During the floods season, this channel inundates large areas of savannahs in its middle section and forms an extensive lagoon system. In this environment there dominated communities of free or rooted floating species (e.g. *E. azurea, Eichhornia heterosperma, Nimphoides indica, L. hexandra*). Of note among the submerged species is *Utricularia inflata.*

Laguna Alamilla

A lagoon fed by rainwater runoff (up to 3 m deep) from the piedmont of the Imataca mountains. Although it connects with the Caño Acoimito, and partially shares the same type of water during the maximum flood stage, it presents some distinct species such as *Ludwigia torulosa, Paspalum wrightii, Xiris caroliniana* and *Utricularia hydrocarpa,* which have been collected only in this area.

Barra Meregina

This site is composed of extensive sandbars found at the mouth of the Meregina channel. Because of its geographical location the area is subjected to tidal fluctuations of approximately 1.10 m. The salinity was measured at 4-5 0%. The slopes of the banks are gentle and the bottoms are mud soils, colonised by extensive mangrove

formations. The communities are composed of a few species; principally *E. crassipes* and rooted plants with floating stems e.g. *P. repens* and *E. azurea*. Further along the fringe were encountered *M. arborescens*. *Avicennia germinans* and *Rhizophora racemosa* represent the mangroves found here, which form small colonies on shallow waters.

Caño Mánamo

Diverse riverbank sites were found along this channel In the Upper Delta (150-250 m wide). They showed abrupt banks and clay-mud bottoms. The zone is subject to the continual action of the tides. Aquatic plant communities were comprised of a few floating species dominated by *P. repens* and *E. crassipes*. The communities of rooted plants are found especially on the islands (see chapter 5); of these *Eleocharis elegans* and extensive colonies of *M. arborescens* are notable.

Alto Araguao

The Upper Araguao is a white water (partially of clear waters during the dry season) distributary channel, approximately 200-300 m wide with abrupt banks. Due to the lotic environment only few species are found rooted along these banks. Several Isolated patches of *Cyperus* sp., *O. cubensis* and *Tessaria integrifolia* were encountered along sandy belts in the convex shores. Present in the ecotone with the forest are dense fringes of *Paspalum fasciculatum* behind which dominate *Gynerium sagittatum*.

Appendix 6a. Distribution of floating species in the studied sites. 5 = 70-100 %; 4 = 30-70 %; 3 = 10-30 %; 2 = 3-10 %; 1 = 0-3 %.

Species/Sites	Lag. Terraplen	Lag. Travesia	Lag. Alamilla	Lag. Ataguia	Lag. Clavellinas	C. Guiniquina	P. Jarahuaja	C. Mariusa	Isla Mariusa	C. Ibaruma	C. Acoimito	C. Guapoa	C. Cuberima	C. Pedemales	C. Florida	C. Tucupita	Cien. Guires	C. Macareo	Curiapo	Barra Meregina	C. Manamo	C. Coboina	Alto Araguao	Constancy	Frecuency (%)
E. crassipes	5	4		4		4		3	2	1	1		2	1	5	1		4		2	4	4	3	17(1-5)	74
S. auriculata	1	3	2	1	1		1	2	3	2	2	1	2					2	1		3	2	2	17(1-3)	74
P. repens	1	1		2		3		2	1	1					1			3	1	4	4	2	3	14(1-4)	61
E. azurea		2	2	3		3			3	3	4		1	1				3		2		3		12(1-4)	52
E. polystachya		2	2	1	2								1			3	4	4				2	3	10(1-4)	44
P. stratiotes				1	1					1			1	2	1	3	5		2					9(1-5)	39
L. hexandra	4	3	3	3	3			3			4						3						3	9(3-4)	39
L. laevigatum	1	1		1					3	2	1				3	3	1							9(1-3)	39
N. rudgeana	2	8	2	4				3	2	3			1											8(1-3)	35
Nymphaea sp.	3		1	2		1		1						2		2	1							8(1-3)	35
S. sprucei	1	2	1		1				2		1					1		1						8(1-2)	35
H. umbellata	1		3					2	2				2	2		3								7(1-3)	30
Utricularia sp.1	2	1	2	1			2						2				2							7(1-2)	30
L. helminthorrhi	2	1		2									2						2					5(1-2)	22
S. polyrhiza				1									2		1	2								4(1-4)	17
N. indica			1	3							4		1											4(1-4)	17
U. foliosa			1	3							2								2					4(1-3)	17
C. pteridoides	1	2								1			1											4(1-2)	17
M. polycarpa	1		1						1	2														4(1-2)	17
L. minor				1												3	2							3(1-3)	13
C. aquatica	3	4								2														3(2-4)	13
T. fluviatilis		1									3	2												3(1-3)	13
P. rotundifolia						2					1											1		3(1-2)	13
L. sedioides			3	4																				2(3-4)	9
U. inflata		2									3													2(2-3)	9
E. heterosperma		1									3													2(1-3)	9
N. oleraceae	1			2																				2(1-2)	9
A. filiculoides	2			1																				2(1-2)	9
U. sagittifolia								1					2											2(1-2)	9
Utricularia sp.2			2								2													2(2)	9
O. latifolia	3	3																						2(3)	9
H. nimphoides				5																				1(5)	9
P. fluitans					1																			1(1)	4
U. hydrocarpa			2																					1(2)	4
S. latifolia									1															1(1)	4
H. reniformis																1								1(1)	4

Appendix 6b. Distribution of emergent species in the study sites   5 = 70-100 %; 3 = 10-30 %; 2 = 3-10 %; 1 = 0-3 %.

Species/Sites	Lag. Terraplen	Lag. Travesia	Lag. Alamilla	Lag. Ataguia	Lag. Clavellinas	C. Guiniquina	P. Jarahuaja	C. Mariusa	Isla Mariusa	C. Ibaruma	Caño Acoimito	C. Guapoa	C. Cuberima	C. Pedemales	C. Florida	C. Tucupita	Cien. Guires	C. Macareo	Curiapo	Barra Meregina	C. Manamo	C. Coboina	Alto Araguao	Constancy	Frecuency(%)
L. octovalvis	2	1	3	1				2	2	2	2					1	3	1	3	1	2	2	3	16(1-3)	69
O. cubense		2	2		3		2	2	3	4			2	1		3	2	3			2	2	3	15(1-4)	65
M. arborescens	3		3		3	2		3	2	3			2	2		1	3		3		4	3		14(1-4)	61
H. amplexicaul	4	1	3	3	2					1	4	2				4	3	3		2				12(4-4)	52
P. acuminatum	1	1					1	1	1	2			2				2	2		2				10(1-2)	43
M. pigra	2	1	2	3				2	1	1	1												2	9(1-3)	39
F. umbellata		2		1				2	2	2	1						2							7(1-2)	30
L. subintegra	3	2	3	2						2							3							6(2-5)	26
C. distans				2				1	2							3	4	2						6(1-4)	26
S. striata				2				2	1			2		1						1				6(1-2)	26
Ipomoea sp.	2		2					2				2						2		1				6(1-2)	26
J. laevilinguis				1					2	1						1	2							5(1-2)	22
B. serrulatum			2	1		1			1											1				5(1-2)	22
A. philoxeroide	2			2				2	1	1														5(1-2)	22
P. fasciculatum			3						4								3						4	4(3-4)	17
E. elegans								3	3									4		2				4(2-4)	17
M. congesta								1	1			2								1				4(1-2)	17
A. zizanoides																2	3	2						3(2-3)	13
B. aquatica			3									2	2											3(2-3)	13
E. mutata				1					3							2								3(1-3)	13
Scleria sp.										1	1	2												3(1-2)	13
C. melvilla									2										2	1				3(1-2)	13
X. caroliniana	2			2								1												3(1-2)	13
A. aureum			1	1										1										3(1)	13
B. patula	2											3												2(2-3)	7
G. sagittatum			3						2														3	2(3)	7
C. sphacellatus								1									2							2(1-2)	7
F. millacea															1	2								2(1-2)	7
Cyperus sp.	1	2															2						2	2(1-2)	7
E. interstincta									2	2														2(2)	7
R. holoschoenoides			2	2																				2(2)	7
C. surinamensis									1	1														2(1)	7
C. biflora									1	1														2(1)	7
H. venezuelensis												1						1						2(1)	7
S. zeylanica												1				1								2(1)	7
P. wrightii	4																							1(4)	4
C. arabicus																		4						1(4)	4
T. geniculata																2								1(2)	4
T. dominguensis			2																					1(2)	4
P. elepanthipes												2												1(2)	4
E. prostrata												2												1(2)	4
L. decurrens								1																1(1)	4
L. leptocarpa										1														1(1)	4
L. torulosa		1																						1(1)	4
Solanum. sp.								2																1(1)	4
Hyptis sp.								1																1(1)	4
A. hispidula								1																1(1)	4
Bacopa sp.										1														1(1)	4
C. articulatus																	1							1(1)	4
E. filiculmis			1																					1(1)	4
L. scabra				1																				1(1)	4
P.grande																						1		1(1)	4
P.parvifolium					1																			1(1)	4
P. pilosum										1														1(1)	4
P. scabridum										1														1(1)	4

Appendix 7. Similarity matrix for floating specis in study sites

	Lag. Alamilla	C. Acoimito	Lag. Ataguia	Lag. Travesia	Lag. Terraplen	C. Ibaruma	Lag. Clavellina	C. Guiniquina	C. Guapoa	C. Florida	C. Tucupita	C. Mariusa	Isla Mariusa	C. Cuberima	C. Pedernales	Alto Araguao	C. Manamo	Cien Guires	C. Macareo	P. Jarahuaja	Curiapo	C. Coboina	B.Meregina
Lag. Alamilla		0.415	0.286	0.364	0.216	0.182	0.25	0.154	0.207	0.087	0.087	0.222	0.154	0.258	0.276	0.231	0.167	0.167	0.222	0.24	0.174	0.231	0.25
C. Acoimito			0.367	0.356	0.286	0.3	0.222	0.148	0.25	0.286	0.258	0.214	0.258	0.222	0.267	0.323	0.323	0.16	0.267	0.2	0.286	0.364	0.24
Lag. Ataguia				0.383	0.4	0.2	0.313	2.58	0.276	0.267	0.276	0.313	0.303	0.323	0.286	0.286	0.286	0.323	0.174	0.16	0.276	0.25	
Lag.Travesia					0.242	0.368	0.285	0.276	0.345	0.285	0.24	0.286	0.276	0.345	0.35	0.182	0.25	0.24	0.345	0.261	0.296	0.2	
Lag. Terraplen						0.278	0.489	0.323	0.353	0.231	0.222	0.231	0.364	0.214	0.231	0.231	0.174	0.24	0.286	0.25	0.308	0.231	0.19
C. Ibaruma							0.462	0.345	0.333	0.333	0.296	0.308	0.417	0.333	0.357	0.261	0.32	0.19	0.357	0.25	0.273	0.308	0.286
Lag. Clavellina								0.111	0.32	0.211	0.2	0.4	0.2	0.19	0.211	0.222	0	0.3	0.286	0.235	0.235	0.21	0.143
C. Guiniquina									0.211	0.381	0.3	0.133	0.3	0.348	0.381	0.333	0.4	0	0.435	0	0.267	0.435	0
C. Guapoa										0.364	0.211	0.3	0.211	0.2	0.222	0.133	0.235	0.133	0.222	0.25	0.25	0.222	0.267
C. Florida											0.381	0.143	0.154	0.3	0.333	0.267	0.353	0.154	0.333	0	0.167	0.286	0.182
C. Tucupita												0.133	0.125	0.286	0.316	0.267	0.267	0.333	0.235	0	0.154	0.133	0.182
C. Mariusa													0.316	0.222	0.25	0.267	0.154	0.154	0.25	0.286	0.167	0.25	0
Isla Mariusa														0.348	0.316	0.333	0.333	0	0.471	0.154	0.267	0.381	0.375
C. Cuberima															0.125	0.316	0.381	0	0.364	0	0.25	0.333	0.267
C. Pedernales																0.267	0.353	0.154	0.333	0	0.286	0.333	0.4
Alto Araguao																	0.444	0.167	0.421	0.182	0.308	0.421	0.333
C. Manamo																		0	0.625	0.167	0.308	0.421	0.333
Cie. Guires																			0	0.182	0	0	0
C. Macareo																				0.2	0.285	0.455	0.4
P. Jarahuaja																					0.333	0.167	0.222
Curiapo																						0.286	0.222
C. Coboina																							0.4

Appendix 8. Similarity matrix for emergent species in study sites

	Isla Manusa	C. Ibarama	C. Acoimito	Lag. Alamilla	G. Clavellinas	Cien. Guires	C.Guapoa	C. Coboina	C. Manusa	P. Jarahuaja	Curiapo	Lag.Terraplen	C. Tucupita	Lag. Travesia	Lag Ataguia	C. Manamo	C. Florida	Alto Araguao	C. Cuberina	Borra Meregina	C. Macareo	C. Pedernales	C. Guiniquira
Isla Manusa		0.340	0.273	0.318	0.311	0.286	0.222	0.391	0.333	0.235	0.316	0.242	0.194	0.242	0.138	0.267	0.258	0.250	0.207	0.207	0.138	0.160	0.910
C. Ibarama			0.372	0.359	0.235	0.400	0.207	0.303	0.182	0.222	0.276	0.286	0.231	0.333	0.231	0.261	0.308	0.240	0.214	0.250	0.167	0.200	0.118
C. Acoimito				0.381	0.229	0.316	0.250	0.250	0.125	0.154	0.313	0.276	0.276	0.364	0.323	0.250	0.240	0.231	0.240	0.240	0.160	0.190	0.222
Lag. Alamilla					0.242	0.294	0.200	0.313	0.100	0.167	0.250	0.387	0.296	0.387	0.296	0.273	0.261	0.250	0.190	0.261	0.174	0.211	0
G. Clavellinas						0.162	0.148	0.207	0.129	0.323	0.160	0.167	0.231	0.167	0.091	0.190	0.100	0.240	0.182	0.100	0.286	0.273	0
Cien. Guires							0.200	0.214	0.133	0.167	0.333	0.240	0.296	0.296	0.240	0.273	0.190	0.250	0.190	0.190	0.296	0.211	0.125
C.Guapoa								0.333	0.077	0.250	0.308	0.320	0.190	0.261	0.190	0.222	0.211	0.200	0	0.211	0.190	0.133	0.143
C. Caboina									0.143	0.308	0.357	0.320	0.261	0.261	0.190	0.300	0.348	0.200	0.211	0.286	0.105	0.235	0.000
C. Manusa										0	0.154	0.087	0.087	0.160	0.087	0.100	0.095	0.167	0	0.095	0.160	0	0
P. Jarahuaja											0.200	0.118	0.118	0.118	0	0.250	0.235	0.125	0.235	0	0.118	0.353	0
Curiapo												0.286	0.211	0.286	0.118	0.200	0.316	0.222	0.133	0.235	0.211	0.267	0
Lag.Terraplen													0.364	0.364	0.300	0.267	0.143	0.235	0.143	0.250	0.125	0.167	0
C. Tucupita														0.364	0.300	0.267	0.250	0.133	0.143	0.250	0.222	0.167	0
Lag. Travesia															0.417	0.267	0.333	0.381	0	0.333	0.333	0.167	0
Lag Ataguia																0.154	0.143	0.316	0.143	0.250	0.125	0	0
C. Manamo																	0.308	0.286	0.182	0.182	0.154	0.364	0
C. Florida																		0.267	0.167	0.286	0.143	0.200	0
Alto Araguao																			0	0.154	0.235	0.182	0
C. Cuberina																				0.167	0	0.200	0
Borra Meregina																					0.143	0	0
C. Macareo																						0.167	0
C. Pedernales																							0
C. Guiniquira																							

Appendix 9. Species in common with other South American wetlands (Sources in text)

	Amazonas basin	Paraná	Surinam	Delta Paraná	Altogether
Acroceras zizaniodes	X				
Alternanthera hasseleriam	X				
Alternanthera phylloxeroides		X		X	
Azolla filiculoides				X	
Cabomba aquatica			X		
Canna glauca		X			
Ceratopteris pteridoides	X		X		
Coix lachryma-jobi	X				
Cuphea melvilla	X				
Cynodon dactylon	X				
Cyperus distans	X				
Cyperus imbricatus	X				
Cyperus luzualae	X	X			
Cyperus sphacelatus	X				
Cyperus surinamensis	X				
Echinochloa crus-pavonis	X				
Echinochloa ꜰ polystachya	X	X		X	
Echinodorus grandifolius		X		X	
Eichornia azurea	X	X	X	X	X
Eichornia crassipes	X	X	X	X	X
Eichornia heterosperma			X		
Eleocharis elegns		X			
Eragrostis hypnoides	X	X			
Fimbristylis miliacea	X				
Gynerium sagittatum	X				
Hibiscus sororius	X	X			
Hidrocleis nymphoides		X	X	X	
Hymenachne amplexicaules		X			
Ipomoea alba	X				
Isachne polygonoides	X				
Justicia laevilinguis	X				
Leersia hexandra	X				
Leptochloa scabra	X				
Limnobium laevigatum	X	X			
Ludwigia decurrens	X				
Ludwigia helminthorrhiza	X				
Ludwigia leptocarpa	X				
Ludwigia octovalvis	X				
Marsilea polycarpa	X		X		
Mikania congesta	X				
Mitracarpum hirtum	X				
Montricharia arborescens	X				
Neptunia oleracea	X				
Nymphaea rudgeana			X		
Nymphoides indica		X	X	X	
Oldenlandia lancifolia	X				
Panicum dichotomiflorum	X				
Panicum elephantipes		X		X	
Panicum laxum	X				
Panicum maximun	X				
Panicum mertensis	X				
Paspalum conjugatum	X				

Species	1	2	3	4	5
Paspalum fasciculatum	X				
Paspalum repens	X	X			
Peperonia pellucida	X				
Phylantus fluitans	X	X			
Pistia stratiotes	X	X	X	X	X
Pityrogramma calomelanos	X				
Polygonum acuminatum	X	X		X	
Pontederia rotundifolia	X	X	X	X	X
Rhynchospora corymbosa		X		X	
Salvinia auriculata	X		X		
Salvinia sprucei	X				
Scleria microcarpa	X				
Scleria pterota	X				
Sesbania exasperata	X				
Spirodela intermedia	X		X	X	
Thalia geniculata	X			X	
Thelypterys gongyloides		X			
Tonina fluviatilis			X		
Typha domingensis		X			
Urena lobata	X				
Utriculari foliosa	X	X	X	X	
Utricularia gibba	X		X		
Utricularia hydrocarpa			X		
Utricularia inflata			X		
Wolffiela lingulata			X		

Appendix 10. Descriptions of the forest in the studied sites.

Guacajara east site

The Guacajara east site is located on the right bank of the Pedernales River and north of the Guacajara village, in an highly disturbed ecotone between a swamp palm forest and a marsh community. The area has been utilised for several decades by Creole people for hunting purposes and the Warao who harvest sago.

Species composition and structural analysis.

The total of the IVI's value (Importance Value Index) corresponds to the only 7 woody species taller than 2 m reported: *Erythrina fusca, Mauritia flexuosa, Euterpe oleracea, Virola surinamensis, Annona* sp. *Symphonia globulifera* and *Carapa guianensis*. (Appendix 10).

The profile of the plot displays three levels of trees. The upper level is represented by *Erythrina fusca* and *Mauritia flexuosa* (species that reach 20-22 m in height). The intermediate level ascends from 10 to 15 m, and is composed of *Virola surinamensis* as well as smaller trees of *Erythrina* and *Symphonia globulifera*. The lower level is dominated by juveniles of the former and particularly *Euterpe oleracea* and *Annona* sp. Herbaceous plants, floating and rooted species form the lowermost stratum.

The proportion of stems is similar between the smaller size classes, up to 15 m in height, containing the 85% of the individuals (120 stems). The size class from 15 to 20 m included 17 plants, a few trees that attained heights of 35 m, and one individual of *Virola surinamensis* that has reached more than 30 m, stand as witness of the former structure of the vegetation in this intensively disturbed plot.

The palm trees Moriche (*Mauritia*) and Manaca (*Euterpe*) still constitute a most important group of plants in the parcel showing the 152% of the IVI's value which corresponds to a density of 390 and 250 individuals/Ha respectively.

The most constant species, lower than 2 m in height (Appendix 10) are rooted emergent species: *Costus arabicus, Montrichardia arborescens, Urospatha sagittifolia* and the floating species *Wolfiella lingulata, Salvinia auriculata* and *Azolla filiculoides*. However the dominance is very low, because only in few subplots reaches the 10% of cover.

1

The Calentura site
The Calentura site is located along the Cocuina river. The vegetal formation is defined by the geomorphology of the area; a depression behind the levees of the river permanently flooded. It represents an extreme case of a swamp palm forest severely disturbed by frequently fires.

Species composition and structural analysis.
Only 14 species of woody plants higher than 2 m tall were registered (Appendix 10): *Mauritia flexuosa, Erythrina fusca, Ficus* sp. *Pterocarpus officinalis, Tabebuia insignis, Cecropia peltata* and *Euterpe oleracea* constitute the 88% of the IVI's total value.

Four strata levels were recognised in this forest community, the upper level from 18 to 25 m constituting an emergent layer composed of *Erythrina fusca* and *Mauritia flexuosa*; an intermediate level between 10 and 18 m dominated by *Mauritia flexuosa, Ficus* sp, *Euterpe oleracea, Cecropia peltata, Pterocarpus officinalis* and smaller individuals of *Erythrina*; a lower level dominated by young palms of *Mauritia* dominates as well as juveniles of *Tabebuia insignis* and *Ficus* sp. The palms of the upper layer appear healthy in contrast to the second strata, where the number and development of the big leaves is reduced; probably do to the effects of the almost continuous fire evidenced among the stems. In this plot, the herbaceous species, *Montrichardia arborescens*, reaches an unusual development of up to 8 m, accounting for 1106 individuals higher than 2 m and contributing to the general physiognomy of the community. This proliferation is a response to the open distribution of the canopy affected by the periodic fires because the size distribution shows a disproportional abundance of the 2-5 m class and very few in the higher size classes.

The more important species of less than 2 m in height are the rooted emergent species (Appendix 10): *Montrichardia arborescens*, with a high cover in all the sub-plots, *Panicum grande*, a species of fern and *Costus arabicus*. Among the free-floating plants were found *Wolfiella lingulata, Lemna perspusilla, Salvinia auriculata* and *Azolla filiculoides*.

The Pepeina site
The Pepeina site is located in a flat inland area, south of the Pedernales river, among the geomorphologic settings in an alluvial depression formed between the levees of the

Pedernales and the Pepeina rivers. The area is covered by herbaceous marshes with a variable cover of moriche palms and swamp palm forests.

Species composition and structural analysis.
In the site were recorded 21 species taller than 2 m (Appendix 10). Six of them, *Mauritia flexuosa* (Moriche palm), *Euterpe oleracea* (Manaca palm), *Ficus* sp.(Higuero), *Virola surinamensis* (Cuajo) , *Cecropia peltata* (Yagrumo) and *Annona* sp., are the dominant plants, accounting 80% of the IVI's total.

The taller trees are *Mauritia flexuosa*, occupying the upper level from 15 to 18 m tall. Euterpe oleracea, Virola surinamensis and Ficus sp. between 10 to 15 m compose the intermediate level, while the Manaca palm, Yagrumo and juveniles of Moriche form the third layer. The number of taller trees (from 10 to 20 m) is 28, 3.4%, the intermediate level 22%, and the smaller class size have the greater number 595 or 73%. This distribution indicates a high rate of natural regeneration. The area showed no signs of major intervention.

The most important species lower that 2 m tall (Appendix 10) are rooted plants, in particular, *Montrichardia arborescens* that has a cover up to 40% in all the sub-plots. If compared to the IVI analysis, it would show a second importance after the Moriche palm. Other relevant species are *Costus arabicus*, *Echinodorus* sp and some Pteridofitae. Free-floating plants such as *Lemna perspusilla* and *Wolfiella lingulata* are also present.

The Buenaventura south site
The site was located in the left bank of the Pedernales River, at approximately 150 m from the river shore in a depressed area behind the levees Due to the permanent flooding, it was not cleared and almost undisturbed.

Species composition and structural analysis.
The dominant species, higher than 2 m tall, according their importance value (Appendix 3) are the moriche (*Mauritia flexuosa*), the Manaca (*Euterpe oleracea*), the Apamato (*Tabebuia insignis*), and a leguminosae (*Macrolobium bifolium*).

The tallest trees are *Mauritia flexuosa* and *Ficus* sp 1. They form the canopy and attain heights of 15 to 20 m. The under story is composed of the upper stratum, extending from 10 to 15 m, and includes species such as *Euterpe oleracea, Erythrina fusca, Virola surinamensis, Cecropia peltata, Ficus velutina, Clusia* sp. and *Tabebuia insignis*. The

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lower stratum (up to 10 m in height) is dominated by *Annona* sp. *Ficus* sp 2, *Ficus* sp 4, *Coccoloba* sp, *Casearia silvestris*, *Piper* sp. and juveniles of other species and the herbaceous stratum composed of *Montrichardia arborescens, Calathea lutea, Costus arabicus, Heliconia* sp. *Urosphata sagittifolia, Echinodorus grandiflorus* and seedlings of *Ficus* spp. Of 312 stems and 40 individuals, 12.8% correspond to the category between 10 to 20 m; 156 stems or 50% belong to the class of 5 to 10 m; and 115 stems or 36.8% belong to the smaller class that ranges from 2 to 5 m.

The palms *M. flexuosa* (Moriche), *E. oleracea* (Manaca) and *Euterpe precatoria* (Guinamora) define the vegetal formation (accumulated IVI : 182.74). The moriche is the most important species with 259 individuals, of which 18 are more than 10 m tall. Its density reaches 2590 palms per ha (180 plants/ha including only the higher specimens), indicating the high rate at which this species regenerates. The Manaca palm is ranked second with 94 specimens and 940 individuals /ha. The dominant class is the 2-5 m class, only two plants reached a height greater than 10 m.

Montrichardia arborescens, a 6-7 m tall herbaceous plant, dominates the herbaceous stratum (Appendix 10). Other important species in the plot are Caña de la India (*Costus arabicus*), Platanillo (*Heliconia* sp.) and Casupo (*Calathea lutea*). Among the seedlings there were several commonly found species of Ficus (Moraceae) and Moriche (*Mauritia flexuosa*).

The Guacajara west site.
The Guacajara west site was located along the west bank of the Pedernales, in a partially disturbed area slightly flooded by the daily tides. The geomorphologic landscape is a levee of very gentle slope along the river shore, where dominates a mangrove (*Rhizophora mangle*), probably favoured by the salinity in the soils, toward the inland a community of gallery forest and swamp palm forests are established.

Species composition and structural analysis.
In this plot, 23 species taller than 2 m were recorded. *Euterpe oleracea, Mauritia flexuosa, Symphonia globulifera, Virola surinamensis,* and *Cecropia peltata* account for 72% of the IVI (Appendix 10). The presence of species such as *Pachira aquatica, Macrolobium bifolium, Manikaria saccifera, Swartzia leptopetala* and *Homandia guianensis* distinguish this plot from the swamp palm forests that are found in depressed and more flooded areas.

The parcel that displays three levels of trees. The upper level, from 18 to 25 m in height, is composed almost exclusively of *Mauritia flexuosa* as testimony of a former continuous canopy that developed in the area (most of the bigger palms have been felled). The intermediate level, from 10 to 15 m, is dominated by *Rhizophora mangle*, growing along the river bank, and *Euterpe oleracea*, *Virola surinamensis* and smaller individuals of the moriche palm. The lower level of trees is represented by the palm trees *Manikaria saccifera* and juveniles of *Euterpe oleracea*, *Cecropia peltata* and *Montrichardia arborescens*. The latter two species are typical of secondary succession following a disturbance. In fact, notorious are the light gaps in the forest canopy that stimulate the growing of a dense mats of vines and scrubs. The size class distribution shown in figure 3.10, indicates that 61,7% of the total stems (314) correspond to the 2-5 m class, 28,6% correspond to the 5-10 m class and only 9.7% to the higher tress, which coincide with the felled trunks. The palm density is high, 1,390 individuals/Ha of *Euterpe oleracea*, 210 of *Mauritia flexuosa* and 30 of *Manikaria saccifera*, favoured by the light incidence on the forest floor.

The most important species lower than 2 m in height (Appendix 10) are the herbaceous plants such as *Costus arabicus*, *Heliconia sp.*, *Acrostichium aureum* an halophytic fern, as well as sapling and juveniles of hardwood species.

The Guacajara 2 site

The Guacajara 2 site is located along the banks of the Pedernales River, north of its confluence with the Guacajara River. As with the Guacajara west site, the forest belt along the rivers is mainly composed of red mangroves.

Species composition and structural analysis.

In this plot 34 species were determined; the most important (higher IVI) were (Appendix 10): the palms Manaca (*Euterpe oleracea*), and Moriche (*Mauritia flexuosa*), Peramancillo (*Symphonia globulifera*), red mangrove (*Rhizophora mangle*), Arepito, Cuajo (*Virola surinamensis*), Cachicamo (*Calophyllum brasiliense*), "Cacho de venado" (an unidentified species) and Clavellino (*Pentaclethra macroloba*). All told, these account for 73% of the total IVI value.

As discussed in the prior section, the vegetation in this plot has two clearly distinct physiognomies. The first is from 0 to 50 m. It shows no significant anthropogenic intervention, which is probably due to in part to the presence of mangrove communities,

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and perhaps to the high salinity in the soils that make them undesirable for cultivation. The second is from 50 to 100 m. The physiognomy resembles a tall scrub formation favoured by the light penetration once the forest canopy disappeared. The presence of an emergent individual of more than 30 m tall and a number of felled moriche palms serve as testimony to the former profile.

In general there was an emergent stratum of up to 35 m tall composed of *Rhizophora* and *Symphonia* individuals. The upper stratum, ranging from 15-25 m, was composed of *Virola surinamensis, Mauritia flexuosa, Hernandia guianensis, Symphonia globulifera,* and *Calophyllum guianensis.* The second stratum, extending from 10 to15 m, was dominated by *Rhizophora mangle, Pterocarpus officinalis Virola surinamensis, Erythrina* cf. *fusca, Ficus* cf, *nymphaefolia* and *Euterpe oleracea.* The third stratum ranging from 2 to 10 m, was establish by such smaller species as *Myrcia* sp. *Annona* sp. *Ficus* sp. and *Cecropia* sp. and juveniles of *Euterpe,* and *Symphonia* among others.

The distribution of the tree size classes showed that of 444 trees, 51,8%, corresponds to a size class from 2 to 5 m, in contrast to the 61,7% from the Guacajara west site. Here, 33,56% corresponded to the size class of 5-10 m, versus 28,6% of Guacajara west plot. The lower strata are very similar, but they do differ in the upper strata where the trees higher than 15 m tall are 31 and 9 respectively. The *Euterpe* palm showed 1390 individuals/ha, the moriche 210 Ind./Ha and *Manicaria saccifera* 30 Ind./Ha. The number of juveniles and seedlings in the plot represented 65% of all the individuals, indicating a high rate of germination. The high light intensity that reaches the soils favours the proliferation of these species.

The dominant species lower than 2 m in high (Appendix 10) are *Calathea lutea* (Casupo), *Costus arabicus* (Caña de la india), *Heliconia* sp (Platanillo), *Montrichardia arborescens* (rábano), *Urospatha sagittifolia,* and seedlings of *Mauritia, Euterpe* and *Symphonia.* form a dense scrub formation. An halophytic herbaceous species, *Acrostichium aureum,* occupies a band of 30 m adjacent to the mangroves.

The Buenaventura north site
Species composition and structural analysis.
This plot shows a relatively high richness (31 wooden species) in spite of the intense intervention, mainly because the river does not flood the banks. The species with higher IVI are (Appendix 10): *Euterpe oleracea Casearia silvestris, Bactris* sp. and *Virola*

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surinamensis. Gynnerium sagittatum and *Cecropia* sp. They are clearly succesional plants. Several species as *Couroupita guayanensis, Nectandra* sp, *Genipa americana, Piper* sp and *Inga* sp. that shows a little importance, are species which are remnants of the original forest or are reintroduced in the bank vegetation.

The plot has two different physiognomies, the first 50 m are characterised by a woody plants and in the last fifty m dominates scrubs and herbaceous species. The upper stratum or canopy with the highest trees reaching 30-35 m was composed of the species *Couroupita guianensis, Spondias mombin* and *Genipa americana.* The second stratum extending from 10 to 25 m was dominated by *Virola surinamensis, Ficus* sp, *Euterpe precatoria* and *Manikaria saccifera.* The third stratum is composed of juveniles and small trees up to 10 m in height, *Cecropia* cf. *peltata, Casearia* silvestris, *Hura crepitans, Euterpe oleracea, Piper* sp, *Inga* sp. Herbs species and seedlings composed the lower stratum. The distribution of the trees size class (Fig 3.10) shows as from the 416 stems higher than 2 m tall, only 6, the 1.44% belongs to the higher class from 20 to 35 m. The main part of the trees belong to the smaller classes, 106 stems the 25,5% between 5 and 10 m and 286 stems, the 68.9% between 2 and 5 m.

The dominant species are rooted emergent plants lower that 2 m in high (Appendix 10): *Montrichardia arborescens, Costus arabicus, Piper* sp, *Calathea lutea* and ferns (Pteridophytae). These species have a high coverage because they form large colonies.

The Jarina 2 site

The site is located between the Jarina and Pedernales rivers in a relatively flat region. The plot occupies the river shores that remain dry because they are not flooded by the tides.

Species composition and structural analysis.

There are 53 tree species, 60% of the IVI's total (Appendix 10). One hundred and eighty are accounted for by the following: Manaca palm (*Euterpe oleracea),* Carapo (*Carapa guianensis),* Temiche palm (*Manikaria saccifera),* Peramancillo (*Symphonia globulifera),* Sangrito (*Pterocarpus* sp.), Cuajo (*Virola surinamensis),* Cocojoro (*Hernandia guianensis),* and Currucay (*Protium* sp.).

The upper stratum, from 20 to 30 m, is generally even and composed mainly of *Protium* cf *Insigne, Pterocarpus* sp, *Hernandia guianensis, Protium* spp, *Euterpe precatoria* and *Pachira aquatica;* with few emergent trees of *Protium* cf *insignis* reaching the 40 m in

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height. This layer accounts for the higher number of trunks, 186. In the second strata, from 10 to 20 m, there dominate such species as *Euterpe oleracea, Campslandra laurifolia, Virola surinamensis, Carapa guianensis* and *Symphonia globulifera*. The mangrove trees (*Rhizophora mangle*) colonise along the river shore. The lower tree layer from 5 to 10 is predominantly formed by *Euterpe oleracea, Manikaria saccifera, Inga* spp., *Sterculia pruriens, Pentaclethra macroloba* and *Manilkara* cf. *nitida* between others species. The under-story is made up of a medium to dense growth of juveniles (particularly those belonging to *Euterpe oleracea*, which has a caespitose growth forming dense clumps), saplings of the mentioned species as well as a number of small unidentified trees.

The more important species belonging to the herbaceous stratum and woody plants less that 2 m tall are: *Ischnosiphon obliquus* (Marantaceae), *Costus arabicus* (Zingiberaceae), *Protium* sp, *Heliconia* sp.(Musaceae) and saplings *of Euterpe oleracea, Virola surinamensis* and *Symphonia globulifera*. The under-story is relatively dense due to the open canopy and is frequent muddy areas and a thick layer of litter and wood debris.

The Jarina 1 site.
This site was selected along the headwaters of the Jarina River, a stream of black waters (according to Sioli, 1965). The area is a flat and undisturbed region covered by a continuous forest formation. The plot occupies a belt adjacent to the river banks and is partially flooded by the tidal effect that maintains the inland soils permanently waterlogged.

Species composition and structural analysis
Of the 41 woody species taller than 2 m found (Appendix 10), 8 accumulated the 56% of the IVI's total value: *Euterpe oleracea, Symphonia globulifera, Manikaria saccifera, Vitex orinocensis*, a not identified species, *Virola surinamensis, Protium* sp. and *Macrolobium bifolium*.

As a result of the physiognomic profile interpretation, three strata were recognised. The upper level between 15 and 25 m composed of *Symphonia globulifera, Macrolobium bifolium, Sterculia pruriens, Virola surinamensis* and the unidentified species n 5. Occasionally, individuals of *Clusia* sp. *Euterpe precatoria* and *Ceiba pentandra* emerge up to 30 m from the general surface of the canopy. The intermediate level, from 10 to

15 m, is dominated by *Vitex orinocensis*, the palm *Manikaria saccifera, Inga* sp., *Manilkara nitida* and smaller individuals of *Virola surinamensis*. Nectandra sp. Erythrina fusca, Tabebuia insignis, Annona sp, Protium sp and Euterpe oleracea represent the lower level. The size class distribution (Fig 3.14), denotes a similar number of individuals in the size classes from 2 to 10 m tall, and a decreasing proportions among the higher size classes. Palm composition is dominated by the Manaca palm, *Euterpe oleracea*, with a density of 1390 individuals/ha, and the Temiche palm, *Manikaria saccifera* with 270 individuals/Ha. This community showed no *Mauritia* palms.

The most important species lower than 2 m in height (Appendix 10) are *Ischnosiphon obliquus, Costus arabicus, Protium* sp. *Heliconia* sp, *Euterpe oleracea, Symphonia globulifera, Virola surinamensis* and vines.

Appendix 11. Forests sites, species composition and IVI

Table 1: Guacajara east. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Species	Common name	Dr	Cr	Fr	IVI
Erythrina fusca	Bucare	17.24	38.82	21.21	77.28
Mauritia flexuosa	Palma moriche	20	37.04	18.18	75.22
Euterpe oleracea	Palma manaca	24.83	13.22	27.27	65.32
Virola surinamensis	Cuajo	19.31	3.25	6.06	28.62
Annona sp.	Catuche	4.14	1.83	12.12	18.09
Symphonia globulifera	Peramancillo	7.59	5.39	12.12	25.09
Carapa guianensis.	Carapa	6.9	0.46	3.03	10.38
Totals		100	100	100	300

If included in the calculations *Montrichardia arborescens* would display a IVI of 17.49

Table 2: Guacajara east. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and tconstancy number (CN) in the sub-plots (16 m²).

Sub-plot	1	2	3	4	5	6	7	8	9	10	NC
Species											
Costus arabicus	10	+	+	+	+	+	+	+	10	10	V
Montrichardia arborescens	10	+	-	10	+	+	+	+	+	+	V
Wolfiella lingulata	+	+	+	+	+	+	+	+	+	+	V
Urospatha sagittifolia	+	+	+	+	+	+	+	+	+	+	V
Salvinia auriculata	+	+	+	+	+	+	+	+	+	+	V
Azolla filiculoides	-	+	+	+	+	+	+	+	+	+	V
Pteridofita	+	-	+	-	+	+	10	10	+	10	IV
Calathea luthea	10	+	+	+	+	-	-	+	+	+	IV
Heliconia sp	-	-	10	-	+	+	-	-	+	+	III
Mauritia flexuosa	-	-	-	-	+	-	+	+	10	-	II
Inga sp.	-	+	-	-	-	-	-	+	+	-	II

Table 3: Calentura site. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Species	Common name	Dr	Cr	Fr	IVI
Mauritia flexuosa	Palma moriche	57.06	21.74	21.74	100.53
Erythrina cf. fusca	Bucare	19.02	19.57	19.57	58.15
Ficus sp.	Lechero	7.98	15.22	15.22	38.41
Pterocarpus officinalis	Sangrito	4.29	10.87	10.87	26.03
Tabebuia insignis	Apamato	4.29	6.52	6.52	17.34
Cecropia cf.peltata	Yagrumo	1.84	6.52	6.52	14.88
Euterpe oleracea	Palma manaca	1.23	4.35	4.35	9.92
Symphonia globulifera		1.23	4.35	4.35	9.92
Virola surinamensis	Cuajo	0.61	2.17	2.17	4.96
Psidium	Guayabo	0.61	2.17	2.17	4.96
Pachira aquatica	Cacao de agua	0.61	2.17	2.17	4.96
Annona sp.	Catuche	0.61	2.17	2.17	4.96
Leguminosae	Arepito	0.61	2.17	2.17	4.96
Totals		100	100	100	300

If included in the calculations *Montrichardia arborescens* would show a IVI of 169.5

Table 4: Calentura. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and constancy number (CN) in sub-plots (16 m²).

Sub-plot Species	1	2	3	4	5	6	7	8	9	10	NC
Montrichardia arborescens	60	60	50	70	70	80	50	50	60	30	V
Cyperaceae	-	+	10	+	10	10	+	10	+	+	V
Pteridofita	+	10	+	+	10	+	+	+	+	+	V
Urospatha. sagittifolia	10	+	-	-	+	+	+	+	+	+	IV
Costus arabicus	10	+	+	-	+	+	10	-	+	10	IV
Symphonia globulifera	-	+	-	-	+	10	+	+	10	-	III
Lemna perspusilla	+	-	-	+	-	+	-	+	-	+	III
Mauritia flexuosa	-	+	+	10	-	+	-	10	-	+	III
Wolfiella lingulata	+	+	+	-	-	+	-	-	+	+	III
Salvinia auriculata	-	+	+	-	+	+	+	-	-	+	III

Erythrina cf. fusca	+	-	-	+	-	-	-	-	+	-	II
Ludwigia sp.	-	-	-	-	+	-	-	-	+	+	II
Azolla filiculoides	+	-	-	-	-	-	+	+	-	-	II
Utricularia sp.	-	-	-	-	-	-	-	+	-	-	I
Hydrocleis nymphoides	+	-	-	-	-	-	-	-	-	+	I
Limnobium laevigatum	+	-	+	-	-	-	-	-	-	-	I

Table 5: Pepeina site. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Woody species: 21.

Species	Common name	Dr	Cr	Fr	IVI
Mauritia flexuosa	Palma moriche	51.09	73.86	12.82	137.77
Euterpe oleracea	Palma manaca	18.61	12.89	10.26	41.76
Ficus sp.	Higuero	12.08	5.64	12.82	30.54
Virola surinamensis	Cuajo	4.16	2.45	10.26	16.86
Cecropia peltata	Yagrumo	1.58	1.24	7.69	10.51
Annona sp.	Catuche	1.58	0.34	7.69	9.62
		1.19	0.45	6.41	8.25
Tabebula insignis	Apamate	2.18	0.38	3.85	6.41
Vitex orinocensis	Caramacate	1.19	0.58	3.85	5.62
Inga sp.	Guamo	0.79	0.1	3.85	4.73
Ficus sp.	Frutero	0.79	0.11	3.85	4.75
Euterpe precatoria	Palma guinamora	1.19	0.81	1.28	3.28
Psidium sp.	Guayabo	0.59	0.13	2.56	3.29
	Casabe	0.4	0.16	2.56	3.12
Symphonia globulifera	Peramancillo	0.4	0.05	2.56	3.01
	Cacho de venado	0.59	0.27	1.28	2.15
Genipa americana	Caruto	0.40	0.23	1.28	1.90
	Lechero	0.4	0.22	1.28	1.9
Faramea sp.	Cafecillo	0.13	0.04	1.14	1.3
Piper sp.		0.2	0.02	1.28	1.5
Psychotria sp.		0.2	0.01	1.28	1.49
Totals		100	100	100	300

If included in the calculations *Montrichardia arborescens* would show a IVI of 72.95

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Table 6: Pepeina site. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and constancy number (CN) in the sub-plots (16 m²).

Sub-plot / Species	1	2	3	4	5	6	7	8	9	10	NC
Montrichardia arborescens	20	20	30	40	10	20	40	30	20	20	V
Echinodorus sp.	+	+	10	40	+	10	+	20	+	10	V
Pteridofita	10	+	+	30	+	+	10	10	+	-	V
Wolfiella lingulata	+	+	+	+	+	+	+	+	+	+	V
Lemna perspusilla	+	+	+	+	+	+	+	+	+	+	V
Costus arabicus	+	10	10	10	10	+	+	+	10	20	V
Urospatha sagittifolia	+	-	-	+	+	30	10	+	+	+	IV
Nimphaea cf. *connardii*	+	+	+	+	+	+	-	-	-	-	III
Inga sp. (Bejuco)	-	+	-	+	+	-	-	+	+	-	II
Melastoma.	-	-	-	-	+	+	+	-	-	-	II
Psychotria sp.	-	-	+	+	-	+	10	-	-	-	II
Solanum sp.	+	-	+	-	-	-	-	-	-	+	II
Cuphea melvilla	-	-	-	-	-	-	-	-	-	10	I
Symphonia globulifera	+	-	-	-	-	+	-	-	-	-	I

Table 7: Buenaventura south. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Species	Common name	DR	CR	FR	IVI
Mauritia flexuosa	Palma moriche	18.27	36.87	9.80	64.94
Euterpe oleracea	Palma manaca	30.45	21.74	8.82	61.02
Tabebuia insignis	Apamato	5.45	5.49	2.94	13.88
Psidium sp.	Guayabo	6.09	2.73	4.90	13.72
Macrolobium bifolium		5.45	4.12	3.92	13.49
Ficus cf. *velutina*	Higuero peludo	3.85	2.47	5.88	12.20
Ficus sp 1.	Higuerón	3.53	2.40	5.88	11.81
Ficus cf. *nymphaefolia*	Ficus hoja ancha	3.85	3.72	3.92	11.48
Erythrina cf. *fusca*	Bucare	2.24	3.82	4.90	10.97
Virola surinamensis	Cuajo	2.56	2.07	5.88	10.51
Cecropia cf.*peltata*	Yagrumo	1.92	1.88	4.90	8.70
Ficus sp 2.	Ficus hoja fina	1.60	3.16	2.94	7.71

	Pata zamuro	1.92	0.49	3.92	6.33
Coccoloba sp.	Uvero	1.28	0.66	3.92	5.86
Casearia cf. silvestris	Tapaculo	1.92	0.90	2.94	5.77
Ceiba pentandra	Ceiba	0.96	0.66	2.94	4.56
Nectandra sp.	Laurel	1.28	0.33	2.94	4.55
	Casabe	1.28	0.28	2.94	4.50
	Leche amarilla	0.96	0.50	2.94	4.41
Ficus sp 3.	Ficus	0.96	2.29	0.98	4.23
Ficus sp 4.	Frutero	0.64	0.87	1.96	3.47
Annona sp.	Catuche	0.64	0.31	1.96	2.91
Inga sp.	Guamo	0.64	0.24	1.96	2.85
Clusia sp.	Semitrepador	0.64	0.70	0.98	2.32
No identi. sp 2		0.32	0.70	0.98	2.00
Pterocarpus officinalis	Sangrito	0.32	0.42	0.98	1.72
Ficus sp 5.	Higuero hoja fina	0.32	0.10	0.98	1.41
Piper sp.	Guaiuyo	0.32	0.07	0.98	1.37
Desmoncus sp.	Camuare	0.32	0.04	0.98	1.34
Totals		100	100	100	300

Table 8: Buenaventura south. Species belonging to the herbaceous stratum. Relative coverage and constancy number in sub-plots (4 m^2)(CN).

Sub-plot Species	1	2	3	4	5	6	7	8	9	10	NC
Montrichardia arborescens	10	+	+	+	50	60	70	50	30	30	V
Costus arabicus	-	+	+	+	+	+	-	10	+	+	V
Urospatha sagittifolia	+	-	+	-	+	+	10	10	-	+	IV
Calathea luthea	-	+	-	+	+	-	10	+	+	10	IV
Heliconia sp.	-	10	-	-	+	+	10	+	10	20	IV
Echinodorus grandiflorus	-	+	50	-	50	-	-	30	-	40	III
Mauritia flexuosa	-	-	-	-	+	10	+	+	10	-	III
Ficus cf. velutina	-	-	-	+	+	-	-	-	+	+	III
Euterpe oleracea	-	-	+	10	-	+	-	-	-	-	II
Ficus cf. nymphaefolia	-	-	+	-	+	-	-	-	+	-	II
Clusia sp.	-	-	-	-	-	-	-	-	-	10	I
Inga sp.	-	-	-	+	-	-	-	-	-	-	I

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Table 9: Buenaventura north. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Species	Common name	DR	CR	FR	IVI
Euterpe oleracea	Palma manaca	15.43	15.79	3.30	34.51
Casearia silvestris	Tapaculo	8.19	7.79	9.89	25.87
Bactris sp.	Corozo	12.05	8.78	1.10	21.93
Tapirira sp.	Patisleño	8.91	6.35	4.37	19.65
Virola surinamensis	Cuajo	7.22	6.40	4.39	18.03
Inga sp.	Guamo	4.82	4.55	7.69	17.06
Gynnerium sagitatum	Caña negra	9.63	6.25	1.10	16.98
Cecropia sp.	Yagrumo	3.16	8.28	4.4	16.3
Spondias mombin	Jobo	1.92	7.00	4.39	13.31
Teobroma cacao	Cacao	2.17	4.14	2.19	8.50
Ficus sp.	Lechero	2.17	3.3	4.39	9.86
Genipa americana	Caruto	0.96	4.06	3.3	8.32
Psidium sp.	Guayabo	2.65	1.10	4.39	8.14
Coccoloba sp.	Uvero	4.81	0.84	2.20	7.85
Hura crepitans	Jabillo	1.2	1.33	4.40	6.93
Protium sp.	Cabimbo	1.44	1.27	3.30	6.01
Couroupita guianensis	Taparon	0.48	2.77	2.2	5.45
	Fruta paloma	1.2	0.66	3.30	5.16
Bixa urucurana	Onotillo	0.72	0.93	3.3	4.96
Nectandra sp.	Laurel	1.2	0.39	3.30	4.89
Inga sp.	Guamo tabla	0.72	0.60	3.3	4.62
Ficus sp.	Higueron	0.48	1.60	2.2	4.28
Desmoncus sp.	Camuare	1.68	1.37	1.10	4.15
Lecythis sp.	Coco mono	1.20	0.60	2.2	4.00
Piper sp.	Guaiuyo	1.44	0.33	2.20	3.97
	Nigua-Nigua	0.96	0.64	2.2	3.80
	Zapatero	0.48	0.33	2.20	3.01
Euterpe precatoria	Guinamorena	0.48	1.41	1.10	2.98
Vismia sp.	Lacre	0.48	0.43	1.10	2.01
Manikaria saccifera	Temiche	0.24	0.19	1.09	1.53
	Hueso pescado	0.24	0.15	1.10	1.49
	Martinica	0.24	0.13	1.10	1.47
	Bejuco	0.24	0.11	1.10	1.45
No ident. sp 1		0.24	0.078	1.09	1.42
Totals		100	100	100	300

Table 10: Buenaventura north. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and constancy number (CN) in the sub-plots (16 m^2).

Sub-plot Species	1	2	3	4	5	6	7	8	9	CN
Costus arabicus	10	+	+	+	+	+	+	+	10	V
Montrichardia arborescens	10	+	-	10	+	+	+	+	+	V
Piper sp.	+	+	+	+	+	+	+	+	+	V
Carapa guianensis	+	-	+	+	+	-	-	-	-	IV
Pteridofita	+	-	+	-	+	+	+	+	+	IV
Calathea luthea	10	+	+	+	+	-	-	+	+	IV
Heliconia sp.	-	+	-	+	-	-	+	-	+	III
Zingiberaceae sp.	-	-	-	-	+	+	-	+		II
Cecropia sp.	-	-	+	-	-	-	+	+	10	II
Gynnerium sagittatum	-	-	-	-	-	-	+	+	10	II
Virola surinamensis	-	-	-	-	+	-	+	+	-	II
Hura crepitans	+	-	-	+	+	-	-	-	-	II
Inga sp.	-	-	+	-	+	+	-	-	-	-	II

Table 11: Guacajara west. Relative density (RD), coverage (RC) and frecuency (RF) of the tree species higher than 2 m tall

Species	Common name	Dr	Cr	Fr	IVI
Euterpe oleracea	Palma manaca	44.69	31.30	11.25	87.25
Mauritia flexuosa	Palma moriche	6.75	15.79	10	32.54
Symphonia globulifera	Peramancillo	10.29	12	8.75	31.04
Virola surinamensis	Cuajo	9	11.99	10	30.99
Rizophora mangle	Mangle rojo	4.18	7.2	3.75	15.13
Pterocarpus officinalis	Sangrito	2.57	4.98	2.5	10.06
Cecropia cf.*peltata*	Yagrumo	3.22	1.64	5	9.85
	Cacho de venado	1.29	0.64	7.5	9.42
Inga sp.	Guamo	2.57	1.38	5	8.95
Psidium sp.	Guayabo	2.57	1.13	3.57	7.45
Pachira aquatica	Cacao de agua	1.28	1	3.75	6.04
Macrolobium bifolium	Arepito 1.29	1.15	3.75	6.18	
Manikaria saccifera	Temiche	0.96	2.36	1.25	4.58
Annona sp.	Catuche	1.29	0.69	2.5	4.48
	Lechero	0.96	0.47	2.5	3.94

Swartzia leptopetala	Congrio	0.64	1.56	1.25	3.46
Desmoncus sp.	Camuare	0.64	0.22	2.5	3.36
Hernandia guianensis	Cocojoro	0.32	1.35	1.25	2.92
Ludwigia sp.	Clavo de pozo	0.96	0.4	1.25	2.61
Spondias mombin	Jobo	0.32	0.76	1.25	2.34
	Fruta de paloma	0.64	0.22	1.25	2.11
Melastomataceae		0.32	0.11	1.25	1.68
Casearia sp.	Tapaculo	0.32	0.04	1.25	1.61
Totals		100	100	100	300

If included in the calculations *Montrichardia arborescens* would display a IVI of 4.56

Table 12: Guacajara west. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and constancy number (CN) in the sub-plots (16 m²).

Sub-plot Species	1	2	3	4	5	6	7	8	9	10	NC
Urospatha sagittifolia	+	+	+	+	+	+	10	10	+	+	V
Calathea luthea	10	+	+	+	+	-	20	10	10	10	V
Costus arabicus	10	+	+	+	+	+	10	10	10	10	V
Heliconia sp.	-	-	10	-	+	+	10	20	20	30	IV
Acrostichium aureum	-	+	50	-	50	-	-	30	-	40	III
Mauritia flexuosa	-	-	-	-	+	10	+	+	10	-	III
Virola surinamensis	-	-	-	+	+	-	-	-	+	+	III
Euterpe oleracea	-	-	+	10	-	+	-	-	-	-	II
Manikaria saccifera	-	-	-	-	-	-	-	-	-	10	I
Montrichardia arborescens	-	+	-	+	-	-	-	-	-	-	I
Inga sp.	-	-	-	+	-	-	-	-	-	-	I

Table 13: Guacajara 2 site. Species higher than 2 m tall, relative density (RD), coverage (RC) and frequency (RF).

Species	Common name	RD	RC	RF	IVI
Euterpe oleracea	Manaca	22.75	19.21	7.14	49.10
Mauritia flexuosa	Moriche	11.94	25.53	7.94	45.41
Symphonia globulifera	Peramancillo	15.77	8.07	7.14	30.9
Rhizophora mangle	Red mangrove	5.85	17.58	4.76	28.20
	Arepito	8.33	4.67	7.14	20.13
Virola surinamensis	Cuajo	3.38	3.61	6.35	13.34
Calophyllum brasiliense	Cachicamo	2.93	2.98	6.35	12.25
	Cacho venado	3.60	2.57	4.76	10.9
Pentraclethra macroloba	Clavellino	4.05	2.57	2.38	9.00
Annona sp.	Catuche	0.45	0.11	7.14	7.70
	Palo negro	2.48	1.27	3.17	6.92
Ficus cf. nimphaefolia	Ficus hoja ancha	0.45	0.08	6.35	6.88
Psidium sp.	Guayabo	1.80	1.03	3.18	6.00
Inga sp.	Guamo	1.35	0.80	3.18	5.32
Pterocarpus officinalis	Sangrito	1.35	1.56	2.38	5.29
Inga sp.	Guamo chigo	1.58	1.03	2.38	4.99
Cecropia peltata	Yagrumo	1.6	0.83	2.38	4.78
Myrcia sp.	Guayabito	3.15	0.57	0.79	4.51
Hernandia guianensis	Cocojoro	0.68	1.62	1.59	3.89
Cecropia sp.	Yagrumo cañero	1.13	0.62	0.79	2.54
Macrolobium bifolium		0.45	0.26	1.59	2.30
Protium sp.	Currucay	0.45	0.22	1.59	2.25
Inga sp.	Guamo	0.90	0.53	0.74	2.22
Pachira aquatica	Cacao de agua	0.68	0.64	0.79	2.12
Erythrina glauca	Bucare	0.45	0.33	0.79	1.57
Ficus sp.	Lechero cuadrado	0.45	0.33	0.79	1.57
	Palo floreado	0.23	0.48	0.79	1.51
Nectandra sp.	Laurel	0.45	0.26	0.79	1.50
Annona sp.	Catuche rebalsero	0.23	0.27	0.79	1.29
Carapa guianensis	Carapo	0.23	0.11	0.79	1.13
Sterculia pruriens	Majagua	0.23	0.18	0.79	1.12
No identif. sp 3		0.23	0.05	0.79	1.07
Rubiaceae sp 2.	Cafecillo I	0.23	0.04	0.80	1.06
	Pata zamuro	0.23	0.03	0.79	1,05
Total		100	100	100	300

Table 14: Guacajara 2. Species lower than 2 m in high, coverage (%) and constancy number (CN) in sub-plots (4 m²).

Sub-plot	1	2	3	4	5	6	7	8	9	10	NC
Species											
Calathea luthea	-	-	-	-	+	-	20	10	20	50	V
Costus arabicus	-	-	-	-	+	+	10	10	10	10	V
Heliconia sp.	-	-	-	-	-	+	10	20	20	30	IV
Acrostichium aureum	-	+	50	-	50	-	-	30	-	40	III
Montrichardia arborescens	-	-	-	-	+	10	+	20	20	+	III
Urospatha sagittifolia	-	-	-	+	+	+	-	-	+	+	III
Mauritia flexuosa	-	-	-	+	10	10	+	+	-	-	III
Virola surinamensis	-	-	+	-	-	+	-	+	+	-	III
Euterpe oleracea	-	-	+	10	-	+	10	-	-	+	III
Symphonia globulifera	-	-	-	-	-	+	-	10	+	+	II
Inga sp.	-	-	-	+	-	-	-	-	-	-	I

Table 15: Jarina 2. Relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall.

Species	Common name	Dr	Cr	Fr	IVI
Euterpe oleracea	Palma manaca	38.72	32.98	6.14	77.84
Carapa guianensis	Carapo	9.40	9.23	5.52	24.15
Manikaria saccifera	Temiche	7.33	8.47	6.14	21.93
Symphonia globulifera	Peramancillo	3.95	4.78	3.68	12.41
Pterocarpus sp.	Sangrito	2.26	6.10	3.68	12.04
Protium cf. insigne	Guacharaco	1.50	4.91	5.20	11.61
Virola surinamensis	Cuajo	3.58	2.68	4.91	11.16
Hernandia guianensis	Cocojoro	2.26	4.97	2.45	9.68
Protium sp.	Currucay rojo	3.20	1.65	4.29	9.14
Mimosaceae	Arepito	2.07	1.54	3.68	7.29
Inga sp1.	Guamo	1.32	1.38	3.68	6.38
Coccoloba sp.	Uvero	1.69	0.76	3.68	6.13
	Palo floreado	1.13	2.79	1.84	5.76
cf. Machaerium	Ñaure	1.88	2.45	0.93	5.26
	Huevo de zamuro	1.32	1.00	2.45	4.78

Rubiaceae sp1	Cafecillo I	1.69	0.42	2.45	4.57
Manilkara cf. *nitida*	Purguo	0.94	2.45	1.11	4.50
Vines	Bejucos	2.06	1.23	1.10	4.39
Pachira aquatica	Cacao de agua	1.50	2.17	0.61	4.29
Macrolobium sp.	Arepito	0.94	0.80	2.45	4.20
*Campsiandra laurifolia**	Guamo chigo	1.13	0.56	2.45	4.14
Protium sp 1.	Currucay blanco	0.94	2.45	0.37	3.76
cf. *Piranhea* sp.	Pata zamuro	0.94	0.24	2.45	3.63
Pentaclethra macroloba	Clavellino	0.75	0.53	1.84	3.12
Sterculia pruriens	Majagua	0.75	0.32	2.45	3.52
Tabebuia insignis	Apamate	0.56	1.22	0.77	2.56
Calophyllum lucidum	Cachicamo	0.56	0.18	1.23	1.97
Protium sp.2	Cabimbo	0.56	1.23	0.09	1.88
	Cacao	0.19	0.61	1.06	1.86
	Lacre	0.38	0.12	1.23	1.73
Nectandra sp.	Laurel	0.38	0.09	1.23	1.69
No ident. sp8		0.19	0.79	0.61	1.60
Swartzia leptopetala	Congrio	0.19	0.61	0.79	1.59
Rizophora mangle	Mangle rojo	0.19	0.62	0.61	1.42
Clusia sp.	Copey	0.19	0.61	0.62	1.42
No identi. sp 9		0.19	0.49	0.61	1.30
No ident. sp 5		0.19	0.61	0.44	1.24
Cecropia sp.1	Yagrumo lag.	0.38	0.19	0.61	1.18
Inga sp.	Guamo cañero	0.19	0.61	0.32	1.12
No ident. sp6		0.19	0.61	0.32	1.12
No ident. sp		0.19	0.61	0.26	1.06
	Palo negro	0.19	0.14	0.61	0.94
Cecropia sp 2.	Yagrumo	0.19	0.12	0.61	0.93
	Macanilla	0.19	0.12	0.61	0.93
Rubiaceae sp 3	Cafecillo sp3	0.19	0.61	0.089	0.89
No ident. sp7		0.19	0.07	0.61	0.87
Ficus sp.	Higueron	0.19	0.05	0.61	0.85
	Nigua -nigua	0.19	0.04	0.61	0.84
Rubiaceae sp 2	Cafecillo sp 2	0.19	0.61	0.026	0.83
	Ñame	0.19	0.03	0.61	0.83
	Fruta paloma	0.19	0.03	0.61	0.83
Casearia silvestris	Tapaculo	0.19	0.03	0.61	0.83
Totals		100	100	100	300

Table 16: Jarina 2. Species belonging to the herbaceous stratum. Relative coverage and constancy number (CN) in sub-plots (4 m^2).

Sub-plot	1	2	3	4	5	6	7	8	9	10	NC
Species											
Ischnosiphon - obliquus	-	+	30	+	+	+	+	+	30	50	V
Costus	10	+	+	+	+	+	+	+	+	+	V

arabicus											
Euterpe oleracea	10	+	+	10	10	+	-	10	+	10	IV
Protium spp.	+	+	-	+	+	+	+	+	-	+	IV
Heliconia sp.	+	+	+	-	10	+	-	+	+	-	IV
Symphonia globulifera	+	-	-	10	+	-	+	10	+	+	IV
Bejucos	-	-	+	+	-	10	-	-	-	+	III
Virola surinamensis	+	-	-	+	+	-	-	-	+	+	III
Manikaria saccifera	-	+	+	-	10	-	-	+	-	10	III
Pteridofita	-	-	+	+	-	-	+	-	-	+	II
Calathea luthea	-	-	+	-	-	-	+	+	-	-	II
Montrichardia arborescens	10	+	-	+	-	-	-	-	-	-	II
Inga sp.	-	+	-	-	-	+	-	-	-	-	I
Pentaclethra macroloba	-	-	-	-	-	+	-	-	-	-	I

Table 17: Jarina 1. The relative density (RD), coverage (RC) and frequency (RF) of the tree species higher than 2 m tall

Species	Common name	Dr	Cr	Fr	IVI
Euterpe oleracea	Palma manaca	24.69	25.44	6.08	56.21
Symphonia globulifera	Peramancillo	10.48	10.8	6.76	28.03
Manikaria saccifera	Temiche	4.80	10.9	6.76	22.46
Vitex orinocensis	Caramacate	5.86	4.79	4.05	14.71
No ident. sp3		4.44	3.67	6.08	14.2
Virola surinamensis	Cuajo	3.37	2.74	5.41	11.52
Protium sp.	Currucay	3.55	1.36	4.05	8.96
Macrolobium bifolium*	Arepito	2.66	4.85	3.38	10.89
Bactris sp.	Palma cubarro	5.33	3.22	1.35	9.9
Tabebuia insignis	Apamato	2.66	2.27	4.05	8.99
Swartzia leptopetala*	Congrio	2.31	2.52	4.05	8.89
Annona sp.	Catuche	3.37	2.86	2.03	8.26
	Perita	2.84	1.31	4.05	8.20
Inga sp1.	Guamo	1.95	1.97	4.05	7.98
	Cacho de venado	2.84	1.49	3.38	7.71
No ident. sp1		1.78	1.45	3.38	6.61
Pterocarpus sp.	Sangrito	0.71	1.75	2.7	5.17
Pachira aquatica	Cacao de agua	2.13	0.66	20.3	4.82
Coccoloba sp.	Uvero	1.24	0.77	2.7	4.71
Psidium sp.	Guayabo	1.42	1.15	2.03	4.6

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	Naure	1.42	1.56	1.35	4.33
Carapa guianense	Carapo	1.42	1.39	1.35	4.17
	Pata de vaca	1.24	1.51	1.35	4.11
Clusia sp.	Copey	0.36	0.94	1.35	2.64
Euterpe precatoria	P. guinamora	0.53	1.25	2.03	3.81
Nectandra sp*.	Laurel	1.07	0.42	2.03	3.51
Sapotaceae	Purguo	0.53	0.62	2.03	3.18
*Campsiandra laurifolia**	Guamo chigo	1.42	0.73	0.68	2.83
Ceiba pentandra	Ceiba	0.18	1.22	0.68	2.08
No ident. sp4		0.36	0.88	0.68	1.91
	Lechero	0.4	0.22	1.28	1.9
*Tapirira guianensis**	Tapaculo	0.36	0.17	1.35	1.87
No ident. sp5		0.18	0.86	0.68	1.72
No ident. sp2		0.53	0.47	0.68	1.68
Pentachletra macroloba	Hueso pescado	0.36	0.53	0.68	1.56
	Majomo	0.18	0.55	0.68	1.41
Ficus sp.	Higuero	0.36	0.10	0.68	1.13
Erythrina cf. fusca	Bucare	0.18	0.18	0.68	1.03
Protium cf. *insigne*	Guacharaco	0.18	0.14	0.68	1.0
*Sterculia pruriens**	Majagua	0.18	0.12	0.68	0.97
No ident. sp6		0.18	0.07	0.68	0.93
Totals		100	100	100	300

Table 18: Jarina 1. Species belonging to the herbaceous stratum lower that 2 m in high, coverage and constancy number (CN) in the sub-plots (16 m^2).

Sub-plot	1	2	3	4	5	6	7	8	9	10	NC
Species											
Ischnosiphon sp.+		20	10	20	+	20	+	+	10	+	V
Costus arabicus	10	+	+	+	+	+	10	+	+	10	V
Protium sp.	+	10	+	+	+	+	+	-	+	+	V
Heliconia sp.	-	-	10	-	+	+	10	+	+	+	IV
Euterpe oleracea	-	+	+	10	-	+	-	10	-	+	III
Symphonia globulifera	-	+	-	-	+	10	+	+	10	-	III
Vines	-	-	+	+	-	10	-	-	-	+	III
Virola surinamensis	+	-	-	+	+	-	-	-	+	+	III
Pteridofita	-	-	+	+	-	-	+	-	-	+	II
Calathea luthea	-	-	+	-	-	-	+	+	-	-	II
Montrichardia arborescens	-	+	-	+	-	-	-	-	-	-	I
Inga sp.	-	-	-	+	-	-	-	-	-	-	I
Manikaria saccifera	-	-	-	-	-	-	-	+	-	-	I

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Appendix 12. Description of the meadows of the Mánamo river. Cover = mean value in the site

Site	Depth (m)	Wide of belt (m)	Species	Cover (%)	Species type	Comments
MAN 1	1.2-0.9	1-3	E. crassipes	35	F-floating	External edge
	0.9-0.6	7	E. crassipes		F-floating	Generally the individuals of these species
		5-7	Sacciolepis striata	15	Floating	are not mixed but forming well delimited
		5-7	Paspalum repens	12	Floating	stands, distributed according to the tolerance to deep and velocity currents on each sector of the meadow.
	0.6-0.3	5-10	Mimosa pigra	8	Emergent	This community is also composed by Araceae
			Sesbania exasperata	2	Emergent	and Bromeliaceae species, growing on the stems of
			M. arborescens	4	Emergent	Montrichardia arborescens
	0.3-0	5-10	H. amplexicaulis	5	Floating-emer.	Ecotone between the meadows and the forest
			Tonina fluviatilis	1	Emergent	vegetation, the dominant species are Genipa
			B.scabiosoides	1	Emergent	americana and Erythrina sp.
			Heliconia sp.	5	Emergent	
			Ludwigia octovalvis	5	Emergent	
MAN 2	2-1.5	3-5	E. crassipes	28	F-floating	Occupying the external border.
	1.5-0.5	10	P.repens	22	Floating	Occasionally occupying the external ridge side
	0.5-0.2	3	S.striata	25	Floating	
	0.2-0	2-3	M. arborescens	25	Emergent	Ecotone between meadow and forest.
MAN 3	2-0.7	35	P. repens	26	Floating	Forming together the external border
			Polygonum acuminatum	1	Emergent	
			Ludwigia helminthorrhiza	5	Floating	
	0.7-0.7	10	P.acuminatum	29	Emergent	
			P.repens		Floating	
			S. striata	1	Emergent	
	0.7-0.8	10	M. arborescens	26	Emergent	Ecotone between the meadow and the
			N. connardii	4	Floating	community of mangroves
			Echinodorus sp.	4	Emergent	
			Crinum erubescens	1	Emergent	
	0.8-0.2	45	Rhizophora mangle	100	Tree-emergen	Mangrove community interspersed with Montrichardia individuals.
MAN 4	1-0.85	10	E. crassipes	41	Floating	P. repens occupy this position some 50 m
			Salvinia auriculata	1	Floating	to the left
			S. sprucey	1	F-floating	
			E. azurea	1	Floating	
			Echinochloa colona	1	Emergent	
	0.9-0.8	40	L.octovalvis	12	Emergent	In a sector adjacent to this area, there grows

			E. crassipes		F-floating	a stand of 60-80 m² of *M. arborescens*.
			Echinochloa polysta			
			Mikania congesta	1	Floating	
					Creeping	
	1.4-1.2	10	*E. polystachya*	20	Floating	Deepest area of the meadow
	1.2-0.9	10-15	*M. arborescens*	20	Emergent	Ecotone between meadow and mangrove
			C.erubescens	1	Emergent	community
	0.9-0	to inland	*R. mangle*	100	Tree-emer.	This area correspond to Site 3 of chapter 8
MAN 5	0.8-0	5-30	*Crenea maritima*	40	Emergent	*C. maritima* is an halophytic plant. The salinity
			Echinochloa colona	58	Emergent	at this sector reach a salinity concentration of
			E. crassipes	1	F-floating	8.26 g l⁻¹, with high water conditions.
			P. repens	1	Floating	Few plants, severely affected by salinity
	0	5	*R. mangle*	50	Tree-emergen	Seedlings
MAN 6	10	0-80	*Sporobolus virginicus*	36	Emergent	Silty edges
			Spartina alterniflora	34	Emergent	
			Rabdadenia biflora	30	Emergent	

Site	Depth (m)	Wide of belt (m)	Species	Cover (%)	Species type	Comments
MAC 1	0-0	2-3	*Paspalum fasciculatum*	60	Emergent	Species occupying the top of the leeves
			E. polystachya	20	Floating	Species occupying the slope (45°) of
			P.acuminatum	10	Emergent	the banks
			Eclipta postrata	1	Emergent	
			Eleocharis elegans	8	Emergent	
			Mimosa pigra	1		
MAC 2	2.5-2	10	*E. polystachya*	31	Floating	The belt of *E. polystachya* has a variable wide depending of the intensity of the currents
	1.5-1.4	10	*E. polystachya*		Floating	
			H. amplexicaulis	5	Emergent	
			P. stratiotes	1	F. floating	
			Ludwigia octovalvis	1	Emergent	
			Ludvigia sp.	1	Emergent	
	1.4-1.25	10	*P. fasciculatum*	39	Emergent	Monospeciphic community
			Ludwigia helminthorrhiza	1	Floating	
	1.25-0.8	20	*P. fasciculatum*		Emergent	
			Salvinia auriculata	1	F. floating	
	1-0.3	50	*P.fasciculatum*		Emergent	
			M.arborescens	11	Emergent	
			Sphenoclea zeylanica	2	Emergent	
	0.3-0.1	15	*Gynerium sagittatum*	4	Emergent	Ecotone between the meadow and
			Costus arabicus	2	Emergent	the forest
			M. pigra		Emergent	
MAC 3	2-0.5	8	*E. crassipes*	28	F-floating	Few plants of *H.amplexicaulis* reach the edge.
	0.5-0.3	3	*H. amplexicaulis*	3	Emergent	
	0.5-0.3	2	*Mimosa pigra*	6	Emergent	Few isolate stands of 20-30 m²
	0.5-0	2-3	*Eichhornia azurea*	3	Floating	Few plants on the edge of the meadow
	0-0	5-10	*G. sagittatum*	50	Emergent	On the top of the levee. Ecotone
MAC 4	2-0.9	5-10	*E.crassipes*	8	F-floating	*E. azurea* Forming stands of 10-15 m²,
			E. azurea	5	Floating	along the edge of the meadow
	0.9-1.6	15	*E. polystachya*	10	Floating	Sand-bar parallel to the river shore
			H. amplexicaulis	5		
	1.6-1	15	*P. repens*	12	Floating	
	1-0.26	20	*Panicum elephantipe*	14	Emergent	

			P. fasciculatum	17	Emergent	
	0.26-0.6	40-50	*P. fasciculatum*		Emergent	
			E. polystachya		Floating	
			P. elephantipes		Emergent	
			Tessaria integrifolia	5	Emergent	
			Hibiscus striatus	6	Emergent	
	0.48-1.2	20	*P. fasciculatum*		Emergent	Depression
			E. polystachya		Floating	
	5-10	5-10	*M. arborescens*	18	Emergent	Ecotone with the forest
MAC 5	1-0.80	5 a 10	*P. repens*	23	Floating	
			Eichhornia azurea	11	Floating	
	0.8-1.2	35	*E. polystachya*	20	Emergent	
			Cyperus giganteus	2	Emergent	
			Oxicarium cubensis	2	Emergent	
			Ludwigia sp 1 .	2	Emergent	
			Ludwigia sp 2.	2	Emergent	
			Eclipta postrata	2	Emergent	
			Mikania congesta	2	Creeping	
	1.2-0.7	25 a 35	*E. polystachya*		Emergent	
			M. arborescens	22	Emergent	
			P. acuminatum	5	Emergent	
	0,7-0	20	*M. arborescens*		Emergent	Ecotone with the forest
			Mikania congesta		Creeping	
			Hibiscus striatus	8		
MAC 6	1.6-1.3	10	*P.repens*	26	Floating	This meadow is formed in a sandy-clayey soils, in a large sedimentation are of the river course.
			Cyperus giganteus	8		
	1.3-1.1	10	*P. repens*		Floating	
			P. acuminatum	4	Emergent	
			H. amplexicaulis	3	Emergent	
	1.1-1.5	10	*E. polystachya*	24	Floating	
			P. repens		Floating	
	1.5	30	*E. crassipes*	14	F-floating	
	0.5	20	*E. polystachya*		Floating	
			T. odoratus	4		
	0.5	10	*P. fasciculatum*	8	Emergent	
			M. arborescens	9	Emergent	
MAC 7	1-0.5		*P.repens*	50	Floating	Directly in contact with the forest Last meadows before the river mouth.
			Salvinia auriculata	1	F-floating	
	0-0.5	30	*M. arborescens*	49	Emergent	