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Patterns and processes in a seasonally flooded tropical plain: the Apure Llanos, Venezuela

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Abstract

Aim The factors and processes determining the ecology and distribution of ecosystems in the Apure lowlands, Venezuela, are critically discussed.

Location The Middle Apure region, an alluvial Quaternary plain built by the Arauca and Apure rivers, occupies a subsidence area caused by faulting of the geological basement during the last and most active phases of the Andean uplift.

Methods To assess the determinants of the hydrological and ecological variability in this region, we used remote imagery and field surveys.

Results The hydrological and ecological variability responds to a set of interconnected processes of different nature: geological, climatic and paleoclimatic and hydrographic, which together have conditioned the geomorphological history of the regional landscape. This evolution, in turn, has guided the soil forming processes and the functional behaviour of the different types of savanna, forest and wetland ecosystems. The continuously subsiding trend of the Llanos that accompanied the Andean Orogeny, together with the Quaternary climatic oscillations, settled the framework in which successive depositional and erosional events took place. Five Quaternary depositional events, gave rise to the actual landscape pattern. The youngest, Q_{0a} is the actual flood plain, Q_{0b} is the Holocene flood plain, Q_1 is from Upper Pleistocene, Q_2 from Middle Pleistocene, while Q_3 the oldest sedimentary material in this area, is of Lower Pleistocene age. Within each sedimentary unit, we analysed the pattern of land forms, soils and natural ecosystems. The Q_0 and Q_1 land units show a characteristic unstable drainage system, with frequent changes in the course of rivers and their affluents and diffluents. Soil genesis mainly correlates with the contrasting characteristics of the wet and dry tropical climate, and with the water regime of each land form on each sedimentary unit. So, a sequence from entisols, through inceptisols and alfisols, to ultisols, correlates with the sequence of land units from Q_0 to Q_3. Different vegetation types predominate on each land form/soil unit. Gallery forest (evergreen and semi-evergreen) exclusively occurs on Q_{0a} entisols, semi-deciduous forest characterizes Q_{0b} and Q_1 inceptisols, semi-seasonal savanna is almost entirely restricted to Q_0 and Q_1 units, hyperseasonal savanna widely dominates on Q_2 and Q_3 alfisols and ultisols, while seasonal savanna just occurs on the well-drained Q_1 and Q_2 alfisols, and on dunes.

Main conclusions The genesis and dynamics of the various land forms and soils throughout the Quaternary, provide the key to their particular hydrology, and determines the kind of plant formation able to occupy each habitat, thus explaining the complex pattern of quite different ecosystems found in the region.

Keywords
Wetlands, water regime, soil genesis, landscape evolution, tropical savannas, tropical forests, Venezuelan Llanos.

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INTRODUCTION

The Colombo-Venezuelan Orinoco Llanos, a half million square kilometres region predominantly covered by tropical savanna, constitutes an active economic frontier where annual crops and cattle raising have been rapidly expanding for the last 30 or 40 years (Silva & Moreno, 1993; Sarmiento, 2000). Within this large Quaternary plain, the upland, well-drained soils, formerly occupied by seasonal savannas, have been increasingly converted into field crops and improved pastures; whereas the lowlands, suffering various degrees of seasonal flooding, have remained almost exclusively devoted to an extensive livestock system that almost entirely depends on the herbage resources of the natural savannas.

The most widespread seasonally flooded area of the Venezuelan Llanos occurs in Apure state, and it continues across the Colombian frontier in the Arauca and Casanare plains. In the central part of the Apure lowlands (Fig. 1), between the formerly forested lands to the west, and the young inner delta in the northeast, bordering the Orinoco, the Venezuelan government promoted, and in most cases built, a system of low, earth dykes, aimed to control the inundations and to improve the livestock-based economy. The terrains encircled by dykes and river levees were called 'módulos' (modules), as they operate both as hydrological and as grazing units. In spite of their ecological impact and important economic role, neither the functioning of these modules nor their effects on the distribution and the functioning of the natural ecosystems under modulated conditions, are fully understood.

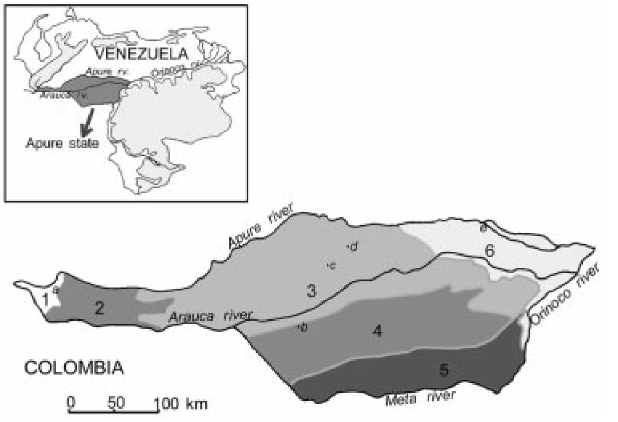

Figure 1 Situation of Apure State within Venezuela, and delimitation of its major landscapes. (1) Forested piedmont; (2) Q_0 flood plain, mainly under evergreen and semi-deciduous forests; (3) Middle Apure plains, a mosaic of Q_0, Q_1, Q_2, and Q_3 land units, mostly covered by flooded savannas; (4) aeolian plains, on Q_2 and Q_3 land units, with seasonal savannas; (5) high plains, on Q_4 land units, dominated by seasonal savannas; (6) inner delta flood plains, on Q_0, a mosaic of gallery forests, semi-seasonal savannas and swamps. The study area belongs to unit 3. Sites mentioned in text: a. El Nula, b. Elorza, c. Bruzual, d. Mantecal, e. Hato El frío, f. El Samán, g. San Fernando. Adapted from ECOSA (1980).

An international cooperation research project was established in 1997, as a part of the European Union International Cooperation with Developing Countries (INCO DC) program (European Commission, 1997), on the 'Ecological bases for the sustainable management of tropical flooded ecosystems: case studies in the Llanos, Venezuela, and in the Pantanal, Brazil'. The project was centred in the region of the Apure Llanos and took the Nhecolândia area of the Brazilian Pantanal (Adámoli, 1999), as a second study case to be compared with the Apure. In the context of this research project, the objective of this preliminary study is to provide an overall picture of the environmental conditions of the Middle Apure area. We want to integrate the dynamic processes of various kinds: geological, climatic and palaeoclimatic, geomorphological and pedological, into a single conceptual framework, in order to demonstrate their part in the patterning and functioning of its ecosystems. Our ultimate goal is to achieve a more coherent view of the dynamics of the various natural ecosystems and their potential use.

To achieve these goals we started reviewing the pertinent literature on the physical environment in the area, in particular geology, geomorphology and soils. Afterwards, three types of remote sensing imagery were visually analysed: the two existing air photographic missions, one Landsat TM image, and three ASL radar images. Finally, in several field missions, land forms, soils and vegetation were sampled all along the area, in different seasons, during three consecutive years. Although these materials were mainly used in another aspects of the INCO DC project, the field experience and the interpretation of remote imagery greatly helped to understand the land form patterns and the ecological processes determining the distribution of regional ecosystems.

The Middle Apure covers about 30,000 km^2 (Fig. 1). It is mainly occupied by flooded savanna ecosystems of the two types recognized in the literature: hyperseasonal and semi-seasonal savannas (Sarmiento, 1984). Forests also cover important extensions, as do various types of semi-permanent wetlands, permanent swamps and lagoons. The whole area is very flat, with a general SW–NE slope in the order of 0.2%. Human influence has been limited to livestock introduction two centuries ago, and to road and dyke construction from the 1960s onwards.

THE OVERALL ENVIRONMENTAL SETTING

Geological framework

In order to understand the crucial processes that cause the outstanding features of the Llanos landscapes, specifically those related to the study area, we adopted a wide spatio-temporal overview, embracing the last part of the geological history of the northern Andes and of their adjacent sub-Andean subsidence zone. The Colombo-Venezuelan Llanos are a part of the huge subsidence system that, in concordance with the Andean uplift, runs all along the eastern, inward border of the mountain chains, and extends to the craton (Guiana Shield), that together with the Brazilian Shield, make up the core of the South American continent. The Llanos del Beni, in northeastern Bolivia, between the Andes and the Brazilian Shield, seem to be the mirror image in the southern hemisphere of the geological, hydrological and ecological conditions of the Orinoco Llanos in northern South America (Hanagarth, 1993).

The sub-Andean subsidence zone, the Llanos geosyncline in Venezuela (Feo Codecido, 1972), has been filled up with alluvial materials that accumulated in thick continental deposits from the Miocene to the Quaternary (Fig. 2). These materials overlie folded and faulted Cretaceous and Eocene rocks of marine origin, that in turn cover the undifferentiated Palaeozoic-Precambrian basement. Towards the end of the Eocene, one of the strong pulses of the Andean Orogeny uplifted the Sierra Nevada, leading to an active erosion period in the plains. Later, the Upper Tertiary and Quaternary sediments piled up in the basin, forming a mighty sequence that, near to the piedmont, attains more than 3000 m in thickness (Gonzalez de Juana *et al.*, 1980).

A system of faults, parallel or perpendicular to the Andes, reflects the last strong uplift events, one in the Eocene, the other in Mio-Pliocene times, when the final, vertical uplift took place. The fractures in the basement below the unconsolidated sedimentary materials left evident surface traces. The drainage system in particular acquired a pattern directly imposed by these faults (Fig. 3).

The faulting of the basement gave rise to slightly uplifted horsts and depressed grabens. In spite of Quaternary processes of filling and erosion, which tended to erase these tectonic imprints, the faults roughly delimit the Llanos major subregional units (Sarmiento, 1983). The upraised blocks remained as the actual high plains, the Venezuelan *mesas* and the Colombian *altillanuras*, well above the younger alluvial plains. Besides the actual flood plains (Q_{0a}), five successive Quaternary depositional units have been recognized in the northern Andes and their surrounding plains, Q_4 being the oldest (Lower Pleistocene), and Q_0 the youngest (Holocene) (Tricart & Millies-Lacroix, 1962; ECOSA, 1980). The southern Apure high plain is a Q_4 surface (Fig. 1, landscape 5), while both Q_2 and Q_3 materials outcrop in the aeolian plains (landscape 4). The sunk blocks correspond to the depressed lowlands, or alluvial overflow plains (FAO, 1964), where flooded savannas and swamps predominate (Fig. 1, landscapes 2, 3 and 6). Landscapes 2 and 6, the youngest in the Apure, are Holocene flood plains (Q_0), while our study area, the Middle Apure (landscape 3), the most heterogeneous, shows surface materials from Q_0 to Q_3.

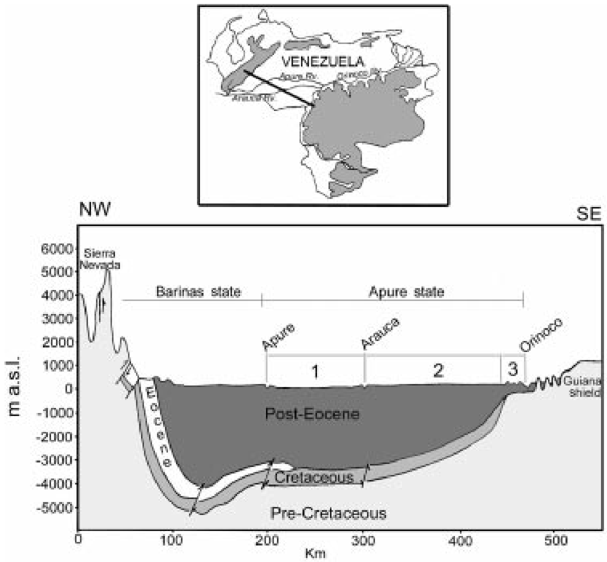

Figure 2 A NW–SE geological profile from the Andes, across the Venezuelan Llanos, to the Guiana Shield. The Venezuelan map shows the position of the transect. The depth of post-Eocene sediments and the main faults are shown. Apure State extends between the Apure and the Orinoco rivers. Its major landscapes are indicated: (1) Middle Apure plains, (2) aeolian plains, (3) high plains. Adapted from Feo Codecido (1972).

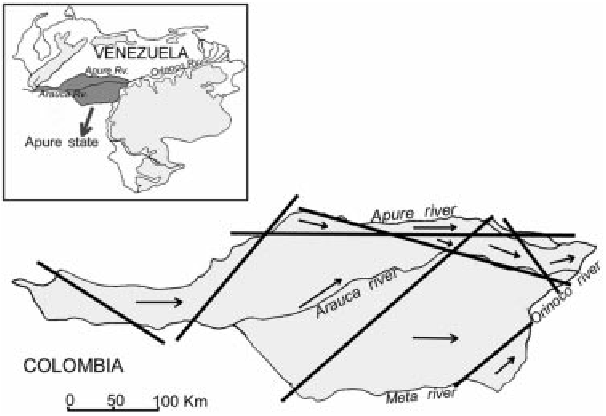

Figure 3 The major fault system in Apure State and its influence on the drainage. The arrows indicate the orientation of the drainage system in each block. Adapted from ECOSA (1980).

The study area represents one of the most noticeable subsidence areas in the whole Colombo-Venezuelan Llanos. It is located in the central and northern parts of the Venezuelan Apure state, and consists of alluvial plains built by the Arauca and the Apure rivers from the Middle Pleistocene to the Holocene (Q_3–Q_0). Several geological formations provided the materials that were later deposited therein by these two rivers. Cretaceous sandstones are almost the only rock type outcropping on the eastern flanks of the Colombian *Cordillera Oriental* in the Sierra Nevada del Cocuy, where the sources of the Arauca river are found (González *et al.*, 1988). In Venezuela, the slopes of the Sierra Nevada de Mérida overlooking the Llanos, are the sources of the Uribante and Caparo rivers, that later converge forming the Apure. They are somewhat more heterogeneous from a litho-stratigraphic viewpont, as Cretaceous and Jurassic sandstones, Palaeozoic micaschists and Precambrian migmatites and gneisses outcrop across the mountain slopes. But as in the *Cordillera Oriental*, there is a wide predominance of sandstones and other related coarse-textured sedimentary rocks (Bellizzia, 1976).

The exclusive presence of sandstones in the upper basin explains the nature of the Arauca sediments. In fact, they mostly are quartzitic silts, originated from the erosion of the sandstones, and the subsequent abrasion of the sand during their long transport from the Andes to the Middle Apure region. In contrast, the Apure river alluvial materials are granulometrically and mineralogically more heterogeneous. However, it should be noticed that most of the study area has been filled with the Arauca alluvial materials, and only in the northernmost part of the region does the Apure river flow over its own sediments.

Summarizing, three important ecological consequences derive from the geological history of these plains. First, the drainage pattern, that approximately reflects the Late Tertiary and Pleistocene tectonic events. Secondly, the differentiation of large landscape units according to the upward and downward movement of the blocks resulting from those tectonic events. Thirdly, the nature of the surface alluvial materials, composed of poor quartzitic sands and silts, almost entirely derived from Mesozoic sandstones.

Climatic factors and palaeoclimatic events

Quaternary climatic oscillations seem to be one of the most relevant factors influencing nature, speed and extent of the various processes involved in the genesis of the landscape. The available palynological evidence clearly points out how frequently climate and vegetation changed in the tropical South América lowlands throughout the Quaternary (Wijmstra & van der Hammen, 1966; van der Hammen, 1974, 1984) During the moist periods, tropical rainforests predominated, while under somewhat drier and more seasonal conditions, the savannas rapidly became the dominant regional ecosystems. In the Llanos in particular, a pollen diagram from 'Laguna de Agua Sucia' (Fig. 4), in the southernmost part of the Colombian Llanos, in an area nowadays dominated by savannas and gallery forests, shows that *c.* 5000 years ago forests and savanna elements about equally shared the local landscape. Later, forest elements became dominant and, at *c.* 2000–2200 years ago, a savanna woodland replaced the forest, to be thereafter slowly replaced by a more open savanna vegetation (van der Hammen, 1974).

In concordance with the climatic cycles that characterize the last 2 Myr, successive morphogenetic phases did occur. In some of them, active erosive processes worked on the mountain slopes and the river beds, and the eroded materials were subsequently transported to and, whenever the flow of the streams decreased, accumulated in the flood plains. In other phases, corresponding to more stable climatic conditions, the processes of river dissection and sedimentation in the plains slowed down. The more energetic phases have been called 'rhexistatic', and the more calm ones 'biostatic' (Zinck, 1981; Hanagarth, 1993). All through the Quaternary, the genesis of the relief, both in the Andes and in the Llanos, was deeply influenced by the occurrence of these kinds of climatic and morphogenetic fluctuations, with rhexistatic phases roughly coincident with the dry glacial periods, and biostatic phases coincident with the humid interglacials.

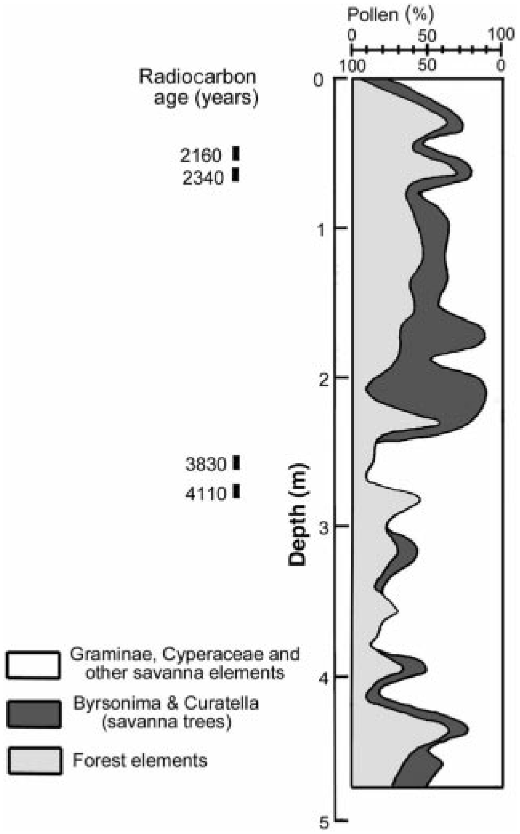

Figure 4 Pollen diagram from 'Laguna de Agua Sucia' (Colombian Llanos). The core covers about 6000 years, the last part of the Holocene, and shows the alternation of open savanna, savanna woodland and forest. From van Der Hammen (1974).

Superimposed on the complex array of land units and land forms produced by the successive climatic phases and their corresponding geomorphogenetic processes, the modern climate, marking the start of the Holocene period, that began to prevail about 14,000 years ago, determined the broad characteristics of each type of habitat and the conditions of existence of the various ecosystems. So, nowadays, the tropical savannas predominate under a tropical wet and dry climate, where a considerable rainfall seasonality is coupled with high mean temperatures and a high atmospheric evaporative demand (Nix, 1983).

In the Apure plains, the mean annual precipitation, estimated from a 26-year record at several meteorological stations, shows a slight but clear east–west gradient. Thus, rainfall is 1300 mm in San Fernando de Apure, and 2760 mm in El Nula, 500 km westwards, showing a sharp increase directly related to the proximity of the Andean chains. The interannual rainfall variability also is quite remarkable. Mean monthly precipitation, their standard variations and absolute ranges, in two localities in the Apure plains, are shown in Fig. 5. The rainfall regime corresponds

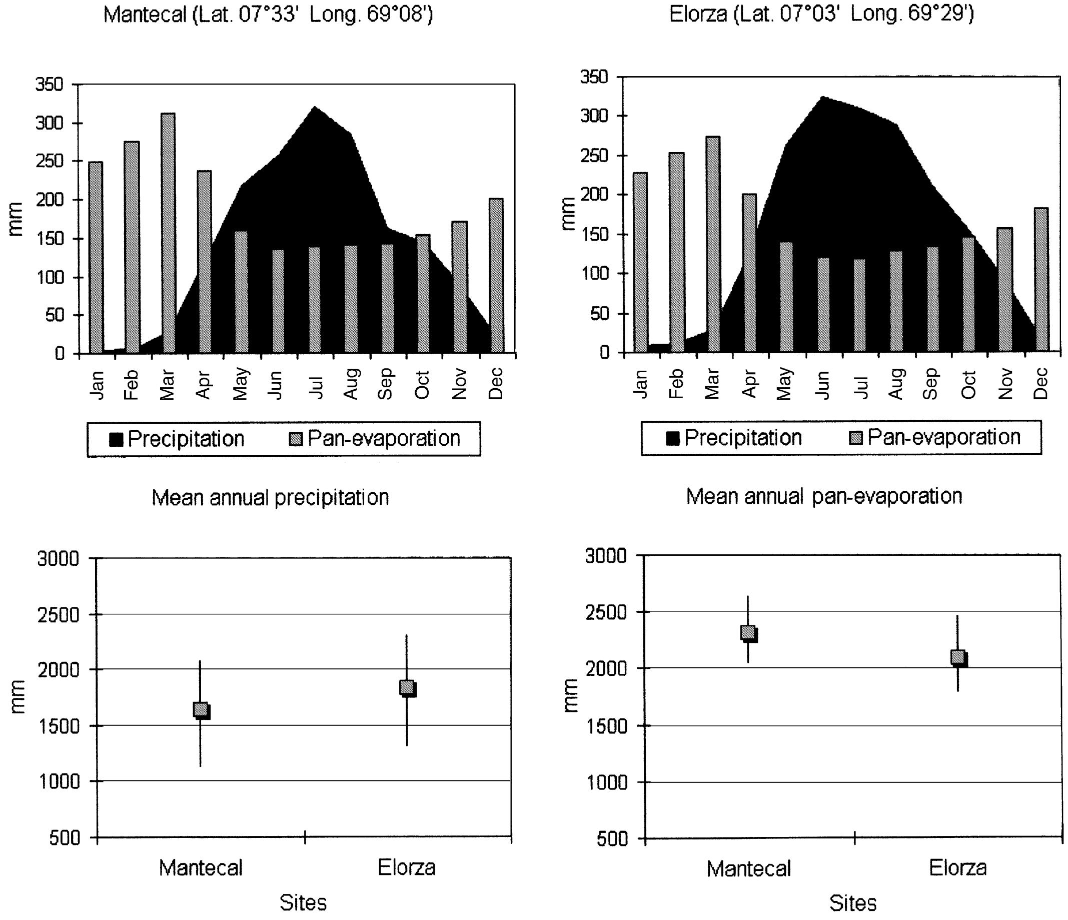

Figure 5 Monthly and annual precipitation and pan-evaporation in two localities of the Middle Apure. Both localities show a clear one-peaked rainfall pattern, with almost negligible precipitation during the 4 month long dry season. Notice how the highest evaporation occur at the end of the dry season. Standard errors and ranges indicate the great interannual variability in rainfall, and to a lesser degree, in evaporation.

to the typical one-peaked 'llanos pattern', highly seasonal and with its maximum at the middle of the year. This pattern mainly obeys two different climatic phenomena: first, the presence of local convective systems fed by an increase in solar radiation during the passage of the Intertropical Convergence Zone (ITCZ) over this latitude. Secondly, a mesoscale climatic system determined by the heat difference between the north and south hemisphere during the austral winter, that activates the southeast trade winds. When these winds, blowing from the high pressure zone on the Tropic of Capricorn towards the ITCZ, hit the Andean chains, the air mass rises in the troposphere, adiabatically cool, and discharge their humidity as rainfall. Consequently, these events are responsible for the peak in precipitation in June or July, during the maximum of the austral winter (Snow, 1976).

As in all tropical regions, the temperature regime is very stable throughout the year, with mean values oscillating around 26 °C, with the rainy areas tending to show the lowest mean temperatures (ECOSA, 1980). The difference in monthly mean temperatures between the warmest and coldest months are never higher than 3 °C. In contrast, daily temperature cycles are remarkable, ranging from 7 to 8 °C during the rainy season, to 12 °C and even more, during the dry season. Evaporation also shows important seasonal differences, positively correlated with the annual progression of air temperatures (Fig. 5). It reaches the highest values, in the order of 8 mm day^{-1}, during the dry months.

In summary, there have been two kinds of climatic influences on the pattern and processes of natural ecosystems. One is indirect, as a consequence of climatic fluctuations over the distribution of ecosystems. The other, more direct, affects the seasonal behaviour of ecosystems, deeply dependent on rainfall pattern and its variability, on the high evaporative demands, and on the constantly high air temperatures (Sarmiento *et al.*, 1985).

Hydrological processes and drainage patterns

The study area is located south of the Apure river, and is part of the 161,000 km^2 that conform to the watershed of this big

Venezuelan river, one of the major tributaries of the Orinoco. Most of the streams in this sector are diffluents and/or abandoned arms of the Arauca river. For instance, the Guaritico river originates as a diffluent of the Arauca in the western sector of the study area, while the Macanillal creek arises as a diffluent of the Caicara river, which in turn is a diffluent arm of the Arauca. From this point of view, the landscape genesis relates to the hydrographical dynamics of the Arauca river from the Middle Pleistocene (Q_2) to the Holocene. Moreover, we consider that the Apure and the Arauca watersheds constitute a single hydrographic unit, at least in this sector, as their alluvial plains originated from multiple depositional events through the system of channels that interconnect both rivers.

In general, all streamflows exhibit very wide seasonal variations because of the seasonal rainfall regime in the plains and in the catchment areas. In fact, both the slopes of the Colombian Cordillera Oriental, as well as those of the Venezuelan Sierra Nevada de Mérida overlooking the Llanos, show very contrasting rainy and dry seasons. From the point of view of water resources management, such a wide annual variation in the discharge of rivers produces a high probability of flooding during the rainy season.

The two rivers originating in the Andes (Arauca and Apure), sharply differ in terms of discharge, overflow frequency, bed shape and sediment charge, from the numerous creeks that arise in the plains. Finally, one of the most characteristic features in the behaviour of all streams, is their low competence, both because of the slight regional slope and the dam effect exerted by each major river over their affluents (inner delta situation) (ECOSA, 1980; Zinck, 1981). Therefore, sediments tend to accumulate on the stream bed, leading to their uprise above the surrounding level. As a consequence, the water courses become quite unstable and often change, by breaking their natural levees. The resulting drainage system is more like a network of affluents and diffluents than like an ordered pattern of tributaries of various orders (Fig. 6).

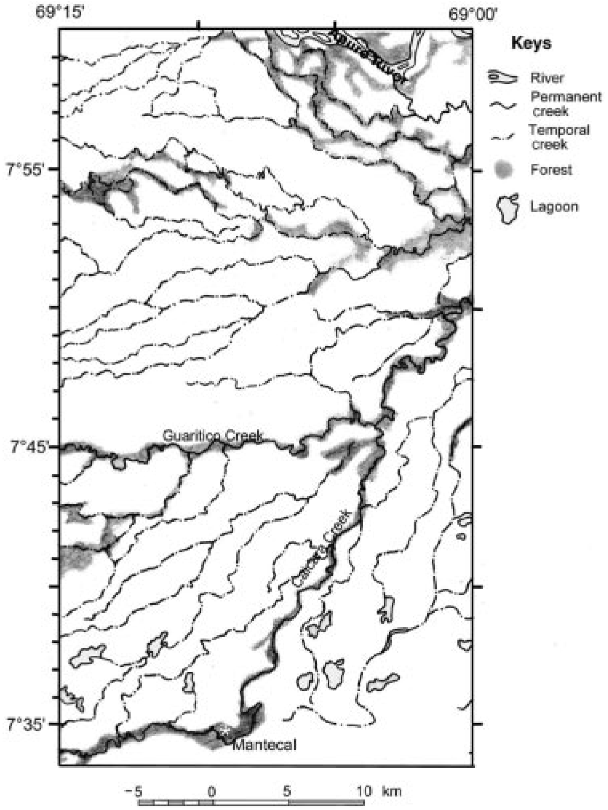

Figure 6 Sector of the 1 : 250,000 topographic map of the Middle Apure plains. It can be seen the intrincate drainage network characteristic of this landscape, and the occurrence of many large lagoons. Gallery forest accompanies rivers, permanent creeks and some seasonal creeks. The Apure river appears at the top. Sheet NB 19-2 ELORZA, Dirección de Cartografía Nacional, Venezuela.

The origin of the land forms

As we have already discussed, the genesis of the landscape was linked with deposition and erosion processes clearly correlated with the Quaternary climatic oscillations. Thus for instance, the dunes, typical wind-induced land forms, originated during the driest periods of the Quaternary, and their orientation reflects the direction of the dry season trade winds (NE–SW). These aeolian land forms were later strongly eroded and frequently fossilized by deposition of younger alluvia, every time the regional climate switched from a dry desert climate to a dry-and-wet savanna climate. Four or five such arid cycles may have occurred during the last glacial periods (Tricart, 1974; Khobzi, 1981).

In the Middle Apure, a first distinction of landscape units is based on the different deposition periods, from Q_3 to Q_0. The corresponding alluvia either still remain on the surface or underlie younger depositions. Generally, these sedimentary landscapes have been later dissected by the drainage system or were buried under new fluvial deposits. The first case occurs when the surface is higher than the stream base level, as in the Q_3 and Q_2 surfaces. The second process occurs in the more depressed areas, where the sedimentary surface lies below the level of the stream channels. We have to take into account the long-term morphoclimatic regime (rhexistatic or biostatic), under which the genesis of the landscape has occurred, as it determines the frequency and the extension of the river overflooding, and of course, of the new depositions (Coplanarh, 1975; Hanagarth, 1993).

When a river changes its course abandoning its former flood plain, the original fluvial land forms start to erode and their materials redeposited, in a process that may be considered as a slow landscape homogenization and levelling. In this way, the various processes of formation and dismantlement of the alluvial forms occur simultaneously, but in different land units, determining the active dynamics and the geomorphological complexity of the landscape (Fig. 7).

Finally, we would like to remark that, as a consequence of the biostatic character of the climate prevailing during the Holocene, the energy of the rivers has decreased, in such a

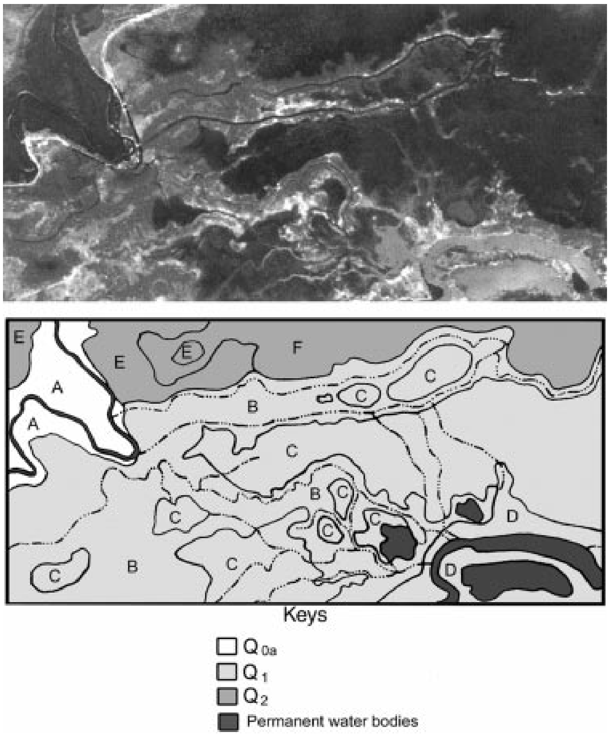

Figure 7 *Above*: Air photograph from the Middle Apure plains (Hato El Frío). Approximate scale 1 : 50,000. The photograph corresponds to the dry season, during the rainy season almost the entire area is flooded. *Below*: Delimitation of land units and land forms. The creek in the northwest corner is the 'Guaritico' and the wide creek in the southeast is the 'Macanillal'. In this area Q_{0b} is absent. (A) Actual river shore complex under semi-evergreen gallery forest; (B) mosaic of small deltaic arm levees and overflow mantles, slightly to moderately flooded, mostly under hyperseasonal savannas; (C) overflow and decantation cuvettes, moderately to deeply flooded, under semi-seasonal savannas and swamps; (D) non-flooded high levees, under seasonal savannas, with small patches of semi-deciduous forest; (E) low levees and overflow mantles, slightly to deeply flooded, under hyperseasonal and semi-seasonal savannas; (F) overflow cuvettes, deeply to permanently flooded, under semi-seasonal savannas and swamps.

way that the most recent sediments (Q_{0a}, or actual and Q_{0b}, or early Holocene), just form narrow strips bordering the actual river channels. These *river shore complexes* (ECOSA, 1980), mainly occur on the convex shores of the streams, and show a very irregular and broken relief of juxtaposed, predominantly sandy, alluvial forms. However, there also exist other areas of predominantly Holocenic deposition, possibly subsidence zones, where the Q_0 land forms are more widely segregated from each other (Coplanarh, 1975).

Soils and soil forming processes

In the study area, the soil features are clearly linked with the position along the topographical gradient and with the characteristics of the corresponding land forms. From this point of view, the levees, the highest position in the gradient, have sandy soils, while in the overflow mantles of intermediate topographical positions, loamy to moderately light-textured soils occur, and in the overflow and decantation cuvettes, fine to very fine textures predominate (Schargel & González, 1972). Soil evolution times superimpose this granulometric gradient, differentiating the soils according to the degree of profile development. So, entisols and inceptisols predominate on the Q_0 and Q_1 units, while alfisols and vertisols dominate on the Q_2 land forms (Table 1). Even so, the early development of alfisols on well-drained sites of Q_1 units is possible, because of the strong climatic seasonality, the constantly high temperatures, and the free percolation, which accelerate clay illuviation and the chemical degradation of primary minerals. Moreover, buried ultisols often appear near to the surface (when thin Q_2 layers cover Q_3 materials), with characteristic plinthitic aggregations, deep red colours and very slow hydraulic conductivities, which notoriously influence the water budget of the overlying soil (Malagón & Ochoa, 1980).

The soils in the study area are highly desaturated (Schargel & González, 1972; Malagón & Ochoa, 1980; Mogollón & Comerma, 1994), probably because of both the intensity of leaching and the poverty in cations of the parental alluvial materials. Their low cation exchange capacity (Table 1), as a result of the high proportion of 1 : 1 kaolinitic clays, also favours leaching. Even if desaturation generally occurs, soils may differ in their relative fertility. Thus for instance, the soils developed over sediments deposited by the Andean rivers are richer than those deposited by the local streams. The clear trend towards the transformation of clay minerals from the 2 : 1 to the 1 : 1 type favours nutrient losses, acidifies the soil, increases the amount of changeable aluminium, and promotes the immobilization of phosphorus. In this way, in terms of chemical fertility, the oldest soils always are the poorest.

The organic matter content of soils in the study area is rather low, generally less than 1.5% (Schargel & González, 1972; ECOSA, 1980). It seems that the soil carbon content of savanna ecosystems is positively correlated with their primary productivity (Montgomery & Askew, 1983). Forest and swamp soils tend to have the highest organic carbon content (Table 1), while seasonal savannas generally show the lowest values. In any case, the low soil organic matter content of savanna ecosystems could also be attributed to frequent fires and to the high below-ground decomposition rates, which in turn are a consequence of the constantly high soil temperatures, higher than in forest or in swamp, that promote carbon mineralization.

Finally, the formation of argillic horizons, because of the accelerated clay illuviation caused by the strongly seasonal climate, characterizes alfisols and ultisols (ECOSA, 1980; Malagón & Ochoa, 1980). The argillic horizons are often associated with ferric concretions, mainly between layers of sharply contrasted hydraulic properties, which eventually lead to the differentiation of plinthitic horizons (hardpan) with almost null saturated hydraulic conductivity. The soil

Table 1 Some physico-chemical features of the topsoil in four soil profiles of different age (land unit), land form, and vegetation. Adapted from Schargel & González (1972)

Soil group	Depth (cm)	Land unit	Depositional environment	Vegetation	Sand (%)	Silt (%)	Clay (%)	Cation exchange capacity (Cmol kg^{-1})	Saturation (%)	Organic carbon (%)
Ustipsamment	0–33	Q_1	Deltaic arm High levee	Wooded cerrado-like seasonal savanna	71	22	7	9.20	17	0.72
Ustropept	0–12	Q_1	Overflow mantle Low bank	Semi-deciduous forest	10	61	29	23.32	64	1.20
Haplustalf	0–11	Q_2	Breakage axis Low bank	Seasonal savanna	82	15	3	3.10	41	0.50
Plinthaqult	0–26	Q_3	Overflow mantle	Hyperseasonal savanna	37	57	6	4.4	16	0.50

hydromorphism, initially promoted by slow surface drainage and by the sharp rainfall seasonality, then becomes more evident, and determines the appearance of perched water-tables near to the surface, during the rainy season (Malagón, 1995).

In summary, the morphogenetical dynamics of the Apure plains (deposition–erosion–burying of sedimentary layers), results in land forms where different materials have been superimposed along geomorphological time. This phenomenon has led in many sites to a succession of buried soils, some of them near to the surface, distinguished by their different mineralogical and hydraulic properties, degree of development and texture. As a consequence, some of the horizons in the soil profile have not been formed during the current pedogenesis, but inherited from a former one. These polycyclic and polygenic features make the spatial analysis of the different soil units in the study area and the prediction of their properties from the morphology of the landscape, much more complex.

ECOLOGY OF THE REGIONAL ECOSYSTEMS

In the plains of the Apure region, as a result of the spatio-temporal complexity of their syngenetic processes, a wide variety of ecosystems occur. These range from permanent swamps, where the primary productivity is mainly of aquatic macrophytes, to tropical savannas, where the grass layer is dominant, to tropical forests, with a closed canopy of evergreen and semi-deciduous trees. In this section, we discuss some distinctive features of these ecosystems and their relationships with the overall environmental setting.

Rainforests

As a consequence of the sharp seasonality in rainfall, physionomically and phenologically the rainforests of the study area mostly correspond to the tropical semi-deciduous forest, although the evergreen type also occurs. According to our field observations, three forest types are recognized, each located over a particular land unit.

The Q_{0a} gallery forest

This ecosystem characteristically appears on the flood plain of rivers and creeks, over the entisols developed on the newly deposited alluvia of the river shore complex. As a consequence of the already mentioned surface roughness of the flood plains, the gallery forest either becomes deeply (bottomlands) or shallowly (higher topographic positions) flooded by rivers and streams, during the rainy season. This flood gradient is more evident in the wider flood plains, where the alluvial land forms are better defined than in the narrower strips. The Q_{0a} gallery forest appears as almost continuous and interconnected bands along the drainage system. It can be considered as a *várzea* or seasonal swamp forest, well adapted to an extended inundation period (Pires & Prance, 1985; Sarmiento, 1992). The degree of evergreeness of these forests is related to the annual cycle of water availability. Thus, the large permanent rivers maintain an evergreen forest gallery, while the smaller, more seasonal streams, show a semi-evergreen gallery forest, where leaf fall mostly occurs during the dry season.

The semi-deciduous forest on Q_{0b} and Q_1 land units

A tropical semi-deciduous forest borders abandoned river arms and ancient river courses, where the fluvial morphogenesis is not active anymore. It appears as discontinuous bands, or even as isolated forest patches, covering the highest topographic positions (levees). It can be considered as a *terra firme* rainforest (Pires & Prance, 1985), sensitive to flooding but needing, under this contrasting climate, a permanent water-table within reach of the roots. It seems that this ecosystem is suffering a gradual and slow disintegration process, as the land form, where it occurs, ages and the soil water supply becomes entirely dependent on rainfall. In addition, the former forest inceptisols show signs of evolution towards alfisols by developing an argillic horizon. We might predict that on sandier and deeper levees, where the volume of water available to deep-rooted trees throughout the dry season is larger and the argillic horizon formation is slower, the forest will persist the longest, forming islands in a rather continuous matrix of savanna ecosystems.

The forest strips along the dams

Even if these forest strips are hardly visible at the scale of our analysis, as they appear over the raised sides of the dykes and roads built in the area during the last two or three decades, they may be important in the overall regional vegetation dynamics. According to our field observations, these forest strips seem to represent early successional stages of the above mentioned *terra firme* forest type, being mainly dominated by pioneer shrub and tree species. They contribute to the stabilization of the roadsides, but apparently do not proceed further away from this particular habitat.

In general, we assume that there are two relevant constraints for the establishment of forests in the plains of the Middle Apure region: nutrient availability and water supply throughout the year. In addition, seasonal flooding may represent a third severe ecological constraint that restricts the *terra firme* type of forest to the highest and best drained land forms of the Q_0 and Q_1 land units. The remaining units, with heavy soils, will be quickly colonized by flooded savannas and permanent swamps. In the bottomlands of the Q_0 landscapes, the transition from the *várzea* type forest to seasonal herbaceous swamps and other wetland ecosystems, may result from seasonal changes in the soil water content, given that when their clay soils dry out, the water potential sharply decrease, favouring the competitive ability of herbaceous plants.

Parallelly, the nutrient constraint may explain the restricted localization of the semi-deciduous forest to young, relatively richer soils (entisols and inceptisols), given the fast processes of leaching, acidification and base desaturation that impoverish the soil in a relatively short pedogenetic time. However, for the Q_0 and Q_1 forests, this transition from inceptisols to alfisols may be slower, because of the occurrence of rather impermeable clay layers near to the surface. In these cases, even if leaching does occur, the effective soil volume for water storage becomes greatly restricted, leading to an oversaturation during the rainy season and to strong water deficits during the dry season. Both situations represent severe constraints to this non-flooded type of forest ecosystem.

On the other hand, taking into account that the sandier a soil is, the less active the clay illuviation process, we suggest that the change from entisols towards alfisols will also be slower in the sandier units, even if the leaching losses are faster under these conditions. We think that, even in extreme dystrophic conditions, as long as the soil's effective volume for water storage and root penetration is large enough, the forest will change from semi-deciduous towards evergreen sclerophyllous forms, as is the case with the *cerrado* and the *cerradâo* in the Brazilian Pantanal area (Dubs, 1992). Our hypothesis about spatial and temporal forest dynamics in the area is summarized in Fig. 8.

Tropical savannas

Seasonal savannas occur on the relatively high topographical positions. According to its original definition (Sarmiento, 1984), the seasonal savanna ecosystem has a 6–9-month period of soil water availability (in the top soil, for grasses, and/or in deeper subsoil layers for trees), followed by a 3–6-month dry period where soil water, at least in the uppermost horizons exploited by the grasses, decreases below the permanent wilting point (PWP).

Under the wet-and-dry tropical climate of the Venezuelan Llanos, this soil water regime is only possible on well-drained sites, without an impermeable layer (clay or iron hardpan), and where the water-table is deep or absent. In our area such conditions do not occur in any land form developed on Q_0–Q_3 units, except on the relict dunes. All the other high positions have either an oscillating water-table approaching the surface during the rainy season, or a perched water-table over a soil hardpan. For this reason, the Middle Apure Llanos essentially appear as an area of wetlands consisting of flooded forests, wet savannas and swamps.

The driest type of seasonal savanna, a tree savanna, only occurs in the study area on the old, fixed dunes. Another type of dry, wooded, seasonal savanna, appears on high topographical positions on Q_3, particularly where the erosion, after having swept away the topsoil of the former ultisol, leaves the hardened illuvial horizon exposed, often plinthitic and with an incipient ferric induration. When fragmented, this material is not an impermeable layer any more and acts as a new parent material for soil evolution. However, true plinthitic cuirasses only appear on the Q_4 surfaces, southwards from the Middle Apure area.

The Q_1 and Q_2 river levees maintain a somewhat moist type of seasonal savanna grassland. In fact, this savanna shows some features transitional to an hyperseasonal system. This transitional condition is mainly because of its occurrence on

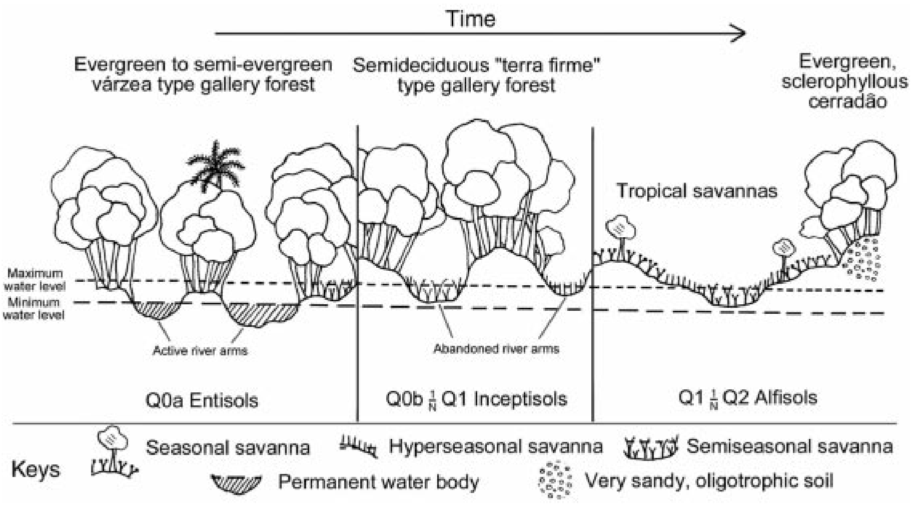

Figure 8 Idealized transect across the geochronological land units, showing the distribution of the major vegetation types as influenced by the level of flooding and the degree of soil evolution.

alfisols, where a perched water-table appears over the argillic horizon, at intermittent periods during the rainy season.

The hyperseasonal savanna, with a highly contrasted annual soil water regime where soil water switches in a few days from a dry situation to water saturation, characterizes silty materials (overflow mantles). There the soil fills up quickly at the start of the rainy season, remains near to saturation during this whole season, being even intermittently waterlogged for some weeks, and dries off again shortly after the rains end. In the Middle Apure, these savannas extend almost uninterrupted over the widespread Q_2 and Q_3 overflow mantles. They are pure grasslands, green during the rainy season and quite dry after the end of rains. Normally, they remain waterlogged with 5–10 cm of water for short periods. A peculiar trait of all these savannas is the broken microrelief, caused by closely packed earthworm mounds whose upper part emerges from the shallow, discontinuous water sheet.

In the third ecological type of savanna, the semi-seasonal savannas, the soil never dries below the PWP, but does remain saturated and flooded for several consecutive months. This system appears on shallow soils, easily waterfilled, and in cuvettes where infiltration is so slow that a free water sheet rapidly accumulates. These ecosystems, popularly known as *esteros*, are the most productive herbaceous formations in the region, with the additional advantage that their green biomass persists throughout the dry season, when they constitute quite palatable herbages. It is important to notice that this type of savanna only occurs on Q_0 and Q_1 units because in the older ones the more mature drainage system has drained the bottomlands.

As depicted in Fig. 9, these three ecological types of savanna ecosystems, set apart by the interplay of three different soil water conditions during the year, the three axes of our diagram, represent the extreme situations. Most of the inner space inside the triangle corresponds to intermediate situations, that probably exist in the field, but have yet been neither identified, nor defined on the basis of their floristic composition and function.

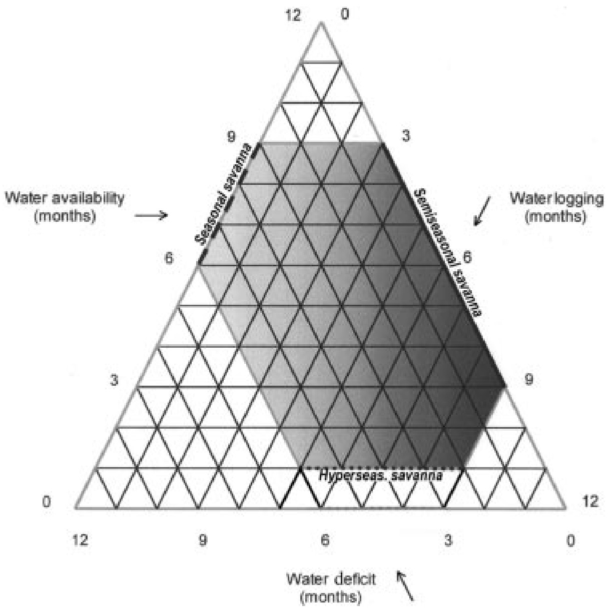

Figure 9 A model of the distribution of savanna ecosystems in the ecological space determined by soil water deficit, water availability and waterlogging. Seasonal savannas occur towards the upper left border, on the right border is the field of existence of semi-seasonal savannas, and towards the centre and the bottom the hyperseasonal savannas occur. The white parts of the triangle correspond to other kind of ecosystems. The pattern of grey follows the primary productivity trend in tropical savanna ecosystems, from the lightest grey corresponding to the lowest productivity values, to the darkest grey, corresponding to the highest values.

CONCLUSIONS

Within the broad geological framework, defined by the Andean uplift and its consequences on the newly formed sub-Andean geosyncline, the gradual construction of the actual landscapes during the last half of the Quaternary forms the basis for understanding the ecology of the Apure Llanos.

The study area stands as a depressed part of the subsiding Llanos, that originated as the surface expression of a structural graben in the deep Pre-Cretaceous basement, produced during the Andean orogeny. During the uplift of the neighbouring Andean chains, a system of faults fractured the plains, leaving unambiguous traces on the drainage system. Thus, the course of the Apure river follows this system of faults, while the Arauca river gradually shifted from a fault-induced SW–NE direction, when it flowed into a now abandoned Apure river bed, to its actual, eastward direction, directly flowing into the Orinoco.

This wide wandering of the principal rivers left its imprints on the landscape, guiding the successive alluvial depositions towards a pattern concordant with the southward divagation of the river. An old Q_3 surface was first dissected, then filled with Q_2 alluvia, and later dissected again and partially filled with Q_1 materials. Meanwhile, several desert climatic events took place, remodelling the fluvial landscapes and redistributing the river sands to form extensive fields of dunes, and silts forming a thin, widespread loessic cover.

The sharp rainfall seasonality together with the high air and soil temperatures, led to a rapid soil evolution. In such a way, entisols are just restricted to the most recent land units (Q_0), an incipient profile differentiation characterizes inceptisols on Q_1 materials, more advanced stages in the pedogenesis (alfisols) prevail on Q_2 units, whereas ultisols appear on the Q_3 surfaces. In any chronological unit, the accumulation of clays in cuvettes promoted the evolution towards vertisols, while on the dunes, the soil became fixed at a quartzipsamment stage, i.e. a young, sandy soil almost entirely composed of quartz grains.

The distribution of the major ecosystems closely follows the soils and geomorphological setting. In each isochronous land unit (Q_0–Q_3), land forms, soil and vegetation evolved together as an integrated functional and dynamic unit: the ecosystem. Seasonal savanna ecosystems characterize the coarse soils on the highest topographical positions of the Q_1 units, providing the occurrence of a hardpan or of an impervious clay layer does not impede free water percolation through the profile. Thus, seasonal savannas do not occur when Q_1 cuvettes have been fossilized by younger, coarser deposits, or on Q_2 and Q_3 units, as all these soils show an impervious claypan. The exception are the dunes, developed on Q_2 and Q_3 units, with free draining, sandy soils (quartzipsamments).

The hyperseasonal savanna appears on the Q_1, covering narrow overflow mantles. It becomes the most widespread ecosystem on the ill-drained Q_2 and Q_3 units, where it occupies almost any landform, except the lowest topographical positions. The semi-seasonal savannas, already appearing in overflow and decantation cuvettes of Q_{0b}, extend over the depressed, ill-drained units of Q_1. But they are mostly absent in Q_2 and Q_3, where they are replaced by a type of highly contrasted, heavily waterlogged, hyperseasonal savanna. This is because, in the relatively higher and older surfaces, the drainage system has attained a greater development, draining all bottomlands.

Finally, permanent swamps and lagoons occupy the mostly undrained, everwet, bottomlands, whose frequency seems to be inversely correlated with the age of the land units. Along the Q_0 flood plains, evergreen to semi-evergreen gallery forests appear in any position, except those permanently flooded, while semi-deciduous forests appear as a relict, post-climax formation, on the disaggregating Q_{0b} to Q_1 levees of already scarcely functional rivers.

In this way, the genesis and dynamics of the various land forms and soils, throughout the Quaternary, collectively outlined the actual landscape, providing the key to understand the distribution and the major ecological trends of the regional ecosystems. This is possible, firstly, because in young sedimentary basins the dynamics of deposition acts as the overwhelming genetic factor in determining land forms, soils and vegetation. In this sense, if the ecosystem concept has to keep its integrated holistic meaning, it must include not just the soils and the biota, but also the land forms and their genesis. Otherwise it would be almost impossible to understand the genesis and to predict the future trends of change in these ecosystems.

A second factor that has allowed the elucidation of the part played by various processes in determining present ecosystem patterns, is the observation of the effects of recent (only two centuries), slight human influence. This has just started to leave their feetprints on the ecosystems. However, the medium and long-term consequences of recent land use intensification based on the building of the dam system still remains to be fully clarified.

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