ECOLOGICAL ASPECTS OF THE MANGROVE FOREST IN FRENCH GUIANA

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RESUMEN

Este trabajo trata del manglar en la Guyana Francesa.
En primer lugar, el autor discute la repartición de las especies vegetales que se encuentran en los estados de desarrollo, de juventud y de madurez del manglar y enfatiza que la vegetación pionera sólo se compone de Laguncularia racemosa *Gaertn., mientras* Rhizophora mangle *L. se desarrolla en las orillas de los ríos y que las salinas se encuentran detrás del manglar, en el cual sólo crece* Avicennia nitida.
En la segunda parte del artículo, el autor, siguiendo el trabajo de Oldeman, describe la morfogénesis y los modelos arquitecturales de algunas especies encontradas en los estados pioneros del manglar. Después se analiza en este manglar, la arquitectura dentro de cuadrados escogidos en estados pioneros y de madurez y por fin se discute su silvigénesis.
En tercer lugar, el autor describe brevement las relaciones entre las poblaciones de aves y la estructura arquitectural que ha descrito.

INTRODUCTION

Nearly the whole coastline of French Guiana is bordered by mangroves which may extend inland from a few meters up to approximately 15 kilometers. On the coastal edge, the mangroves' appearance depends on the sedimentation conditions which vary along the coast according to the play of sea currents. These currents give rise to areas which are heavily attacked by the sea, alternating with vast areas of mud flats (Rossignol, 1978).

These mud flats gradually emerge at low tide and it is found that they extend way out to sea. When these flats are sufficiently raised, they are colonized by pioneer mangrove species. Two types of colonization are observed: *Laguncularia racemosa* Gaertn. (Combretaceae) and *Spartina brasiliensis* Raddi. (Poaceae).

Along the banks of rivers crossing the mangroves, there are pure stands of *L. racemosa*, upstream of the estuaries. These stands, more or less dense, are associated further upstream with a small Lythraceae, *Crenea maritima* Aubl.. *L. racemosa* stands have juvenile individuals as well as mature ones. Further upstream these *L. racemosa* stands are pure, yet lose their young individuals, only mature trees remain. Further inland, sometimes 3 km from the estuary, (Approuague and Sinnamary), *Rhizophora mangle* is associated with *L. racemosa*, eventually becoming the dominant species.

Only *R. mangle* constitutes the riparian vegetation of the upper estuaries, associated with *Montrichardia arborescens* (Araceae).

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Between the coastal pioneer formations and the riparian formations, the mangrove forest is almost uniquely populated by *Avicennia nitida* Jacq. (Verbenaceae). On the inland edge of these stands there is either a belt of *R. mangle*, if it is swamp, which is usually the case, or a senile population of a *A. nitida* covered with epiphytes underneath which spread a thick layer of *Acrostychum aureum*.

Figure 1 is a diagram showing the distribution of plants in the mangroves of French Guiana. This distribution is original due to the extensive populations of *A. nitida* and the pioneering role of *L. racemosa*, whilst *R. mangle* is banished upstream of the estuaries.

Before discussing the architecture of the various stands found, it is necessary to give architectural models, (Halle and Oldeman, 1970) of the plants populating these stands (Figure 2).

Laguncularia racemosa Gaertn. (Combretaceae)(Fig. 2-1)

After a brief unbranched phase during which an orthotropic stem forms with opposite leaves and 7 or 8 internodes, the plant branches in a slightly rhythmic manner into sequences of 3 to 5 pairs of secondary axes which are relatively weak and are followed by one stronger pair. The secondary axes, although sometimes parallel to the ground, have no plagiotropic differentiation at the level of the leaves. The plant may bear axes of the third order possessing a terminal and lateral inflorescence. Flowering is early -it may occur in individuals 1 m high. Taking into consideration the discretely rhythmic branching of the main stem, this initial model of *L. racemosa* would therefore be an Attims one, as described by Halle and Oldeman (1970).

In individuals of this species, it is found that reiteration of the model may occur very early, before the plant has reached 1 m high. These reiterated stems are often very slanting, enabling the plant to cover the ground. The reiterations are not due to any traumatism of the apex; they are of an adaptive nature.

Avicennia nitida Jacq. (Verbenaceae)(Fig. 2-2)

The main stem of a young plant is vertical and orthotropic, bearing opposite, decussate leaves. During the unbranching phase 7 or 8 internodes are formed. Branching is diffuse and the secondary axes are not very slanting. The axes of the 3rd order have a lateral and terminal inflorescence. Sexual maturity is reached when plants are 2 to 3 m high. All lateral axes have a slight plagiotropic differentiation as seen by the arrangement of the leaves on the horizontal plane. The initial model of *A. nitida* could therefore be placed between those of Attims and Roux as described by Halle and Oldeman (1970).

Reiteration may appear on young individuals of 2.5 to 3 m high. These early reiterations, which are traumatic, are always subapical and related to the death of the apex. The reiterated stems straighten up very quickly and then grow vertically.

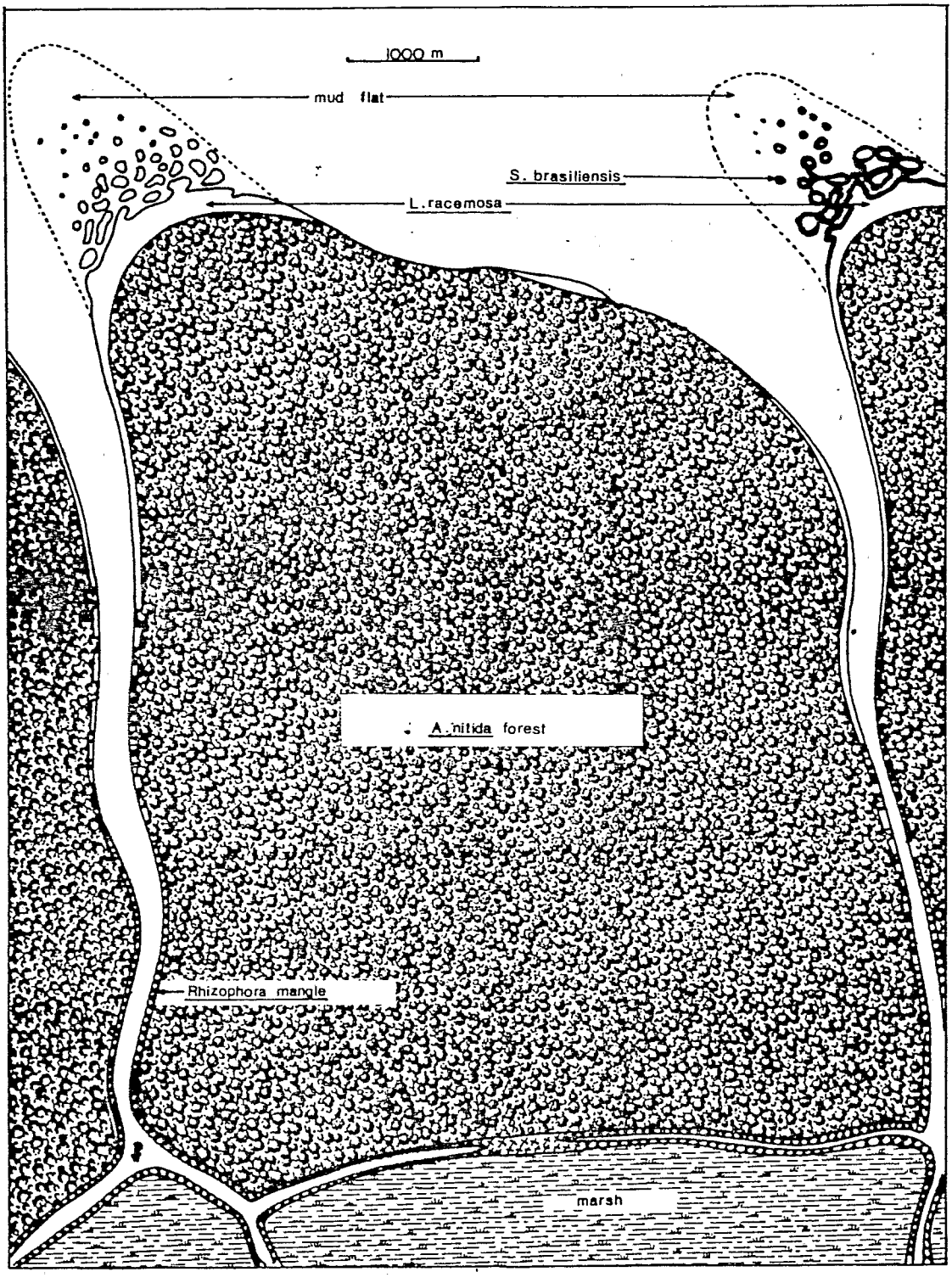

Fig. 1 - Distribution of plants in the mangrove forest of French Guiana.

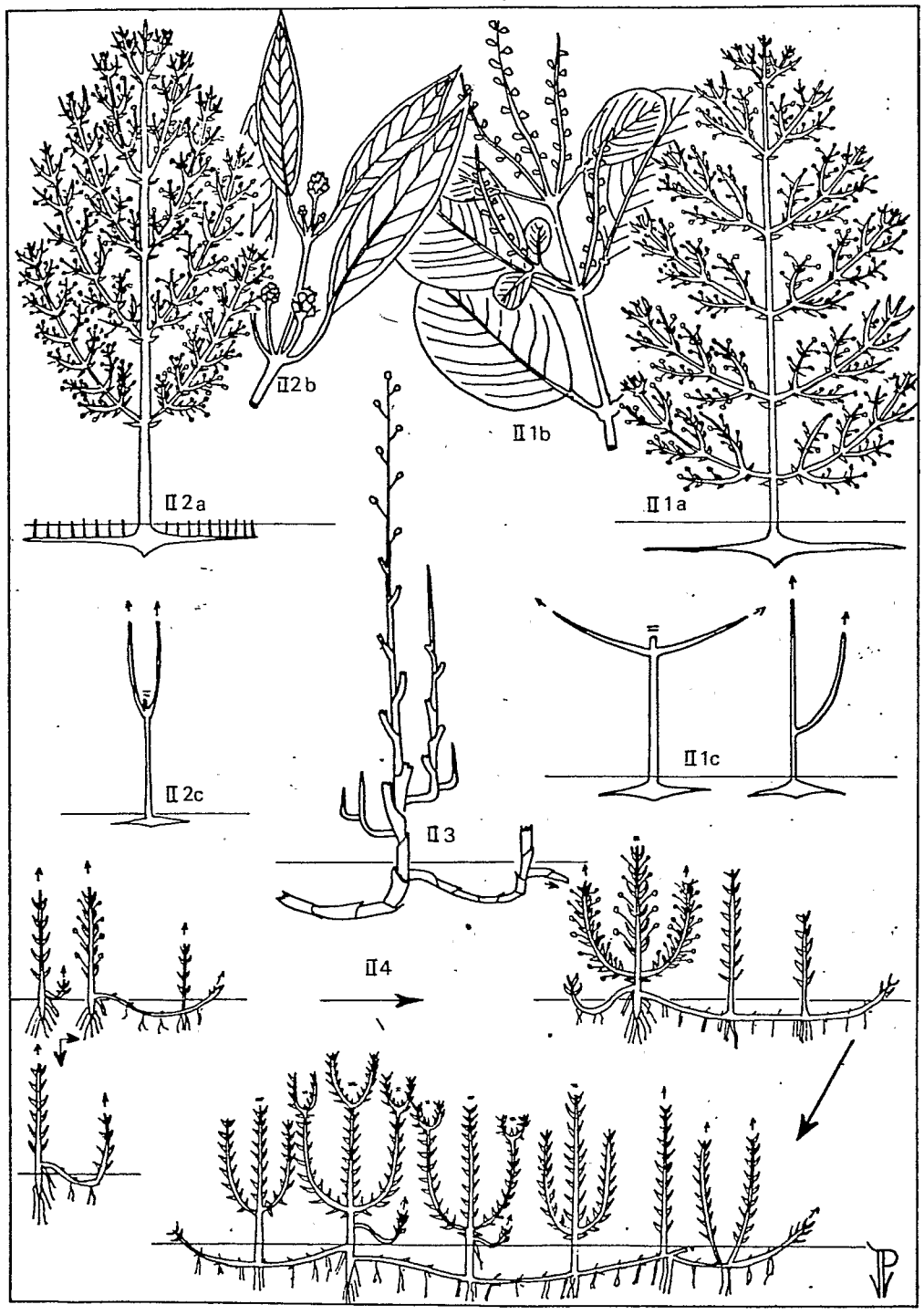

Fig. 2 - Morphogenesis of the main plants in the mangrove forest of French Guiana.

It must also be noted that the main stem of A. *nitida* cannot bear to be sloping: any stem sloping by accident immediately produces a series of reiterated stems which are perfectly vertical.

Spartina brasiliensis Raddi (Poaceae)(Fig. 2-3)

This plant is a grouping of branched units. Each of these units is made up of a main stem bearing alternate leaves and possessing a horizontal underground portion with small leaves void of chlorophyll. This portion has roots at each node. The aerial portion, made up of 7 to 8 internodes, has long leaves. The stem has an apical sexuality.

This main stem gives rise to two types of lateral axes:

- on the one hand, small sterile lateral axes which grow from the first two or three aerial nodes of the main stem. Each of these small axes may produce an axis of superior order, also sterile, at the first node. The main stem and these axes comprise one branched unit.

- on the other hand, a lateral axis which appears at the point where the main stem straightens up. This lateral axis then creates another branched unit.

Each of these units seems to represent a branching sequence and corresponds to the article as described by Halle and Oldeman (1970). This plant corresponds to Tomlinson's model rendered more complicated by extra elements which are purely vegetative.

Crenea maritima Aubl (Lythraceae)(Fig. 2-4)

This plant is also made up of branching units. Each unit has a vertical stem with opposite, decussate leaves and axillary inflorescences. Maturity of the flower begins at the base of the plant. The apex of this stem degenerates quite quickly whilst two lateral, opposite axes appear. These axes come from buds on one of the lowest nodes of the main stem. They straighten up quickly and possess lateral sexuality. Their apexes then degenerate and axes of a 3rd order, with axillary inflorescence, appear at the last node of the 2nd order axes.

At the same time there exists an underground, caulinary morphogenesis which is neither limited by time or space. A lateral axis forms in the area of the root neck of the young orthotropic main stem and grows in a creeping manner, bearing small, opposite, decussate leaves. Small roots appear at each node. This axis may either straighten up and send out a new main aerial stem which will form a new unit, or, more often the case, grow along underground. In this case, it sends out aerial, vertical axes sideways which then branch out.

Finally, it must be noted that several stolons may shoot out from an aerial stem, the oldest ones being the lowest. This architecture is not found in any model defined by Halle and Oldeman (1978).

ARCHITECTURE OF THE MANGROVE FOREST

I. *Pioneer phases*

L. racemosa facies. (Fig. 3-1)

The most elevated areas of the mud flats, which are only covered by a few decimeters of water at high tide, are colonized by small groups of *L. racemosa* which form small vegetative islets. On nearing the mainland, these small islets increase in size, eventually joining up to form a continuous, dense population of plants no higher than 1.50 m. Beneath this canopy there are a few young A. *nitida* stems. This continuous stand, approximately 100 m wide, gradually reaches about 5 m high. It is then abruptly replaced by a pure stand of A. *nitida* approximately 7 m high.

S. brasiliensis Raddi facies (Fig. 3-2)

This formation differs from the previous one in that the first islets are made up purely of *S. brasiliensis*, only later being associated with *L. racemosa*. *S. brasiliensis* disappears when the *L. racemosa* canopy becomes continuous.

II. *Riparian vegetation*

C. maritima facies (Fig. 3-3)

This facies is found at the mouth of the river for about 100 m. Following a line perpendicular to the river, one finds a pure, dense stand of *C. maritima*, 3 m wide and 50 cm high. This stand overshadows numerous young plants of *L. racemosa* and A. *nitida*. Beyond this belt of *C. maritima* lies a stand of *L. racemosa* about 12 m wide, whose height reaches approximately 4 m at the furthest point from the river. Under its canopy there are some young stems of A *nitida*. This stand is suddenly replaced by a forest of A. *nitida*, as for the coastal formation.

L. racemosa facies (Fig. 3-4)

This formation is situated upstream of the previous facies for approximately 3 kilometers. The riparian population is a pure stand of *L. racemosa*. Following a combination of numerous reiterations, the stand fans out over the river in a similar way to Oldeman's description (1972).

Rhizophora mangle facies

This facies is found upstream of the *L. racemosa* one. Both species gradually mix, with *L. racemosa* eventually disappearing. The pure riparian stand of *R. mangle* is characterized, of course, by the barrier of aerial roots which it constitutes. The trees are higher, reaching up to 25 m. Whilst small ones reiterate stems to give a fan-shaped structure, bigger ones escape this development, growing upwards and then reiterating at the crown.

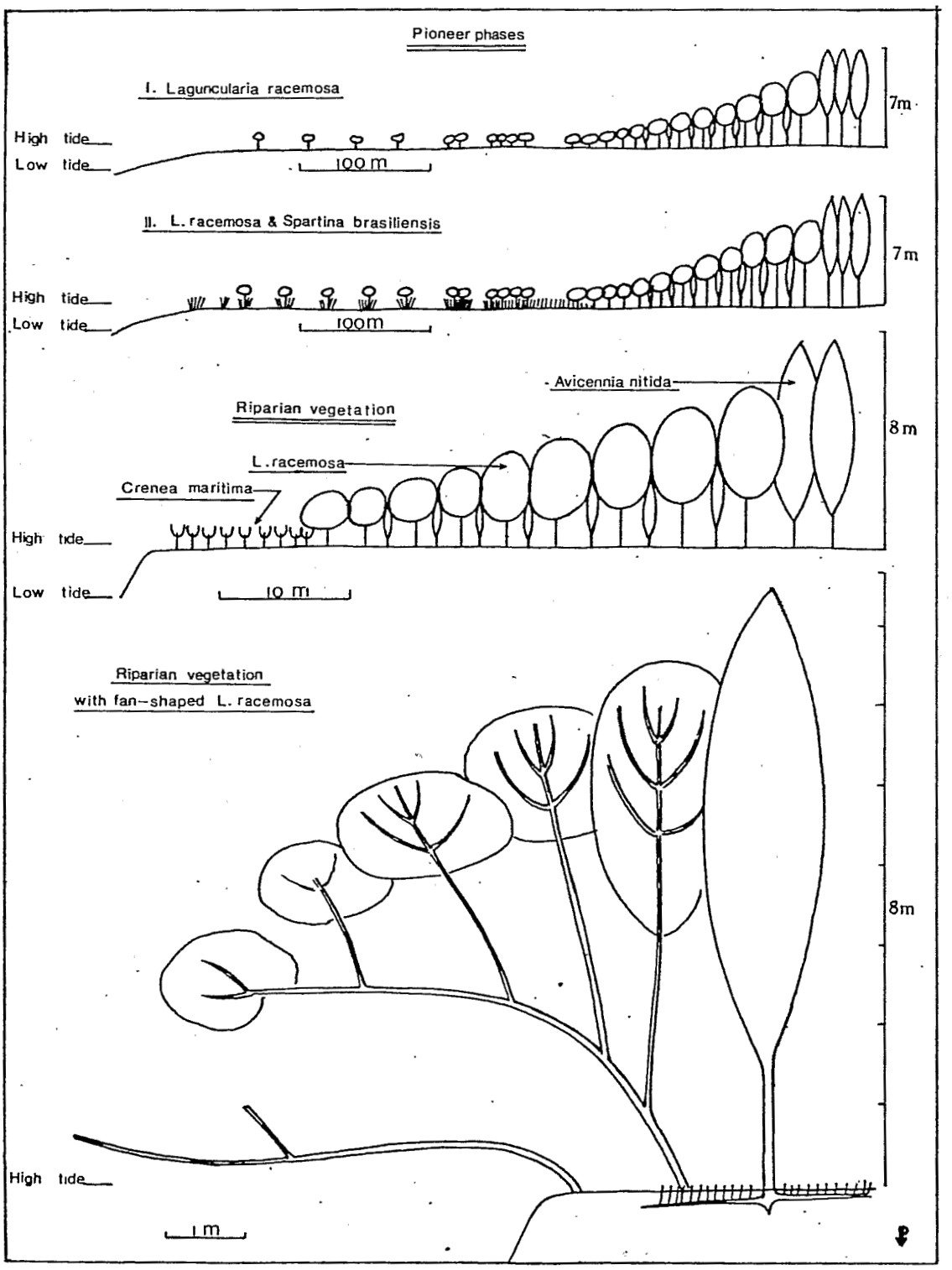

Fig. 3 - Pioneer and riparian populations in the mangrove forest of French Guiana.
1. Pioneer facies with *Laguncularia racemosa*
2. Pioneer facies with *Spartina brasiliensis*
3. Riparian vegetation with *Crenea maritima*
4. Fan-shaped riparian vegetation with *Laguncularia racemosa*.

A. *nitida* forest: different phases of its architecture.

The A. *nitida* forest was studied by taking four plots which seemed to represent different stages. Work was done according to the concepts and methods developed by Oldeman (1974).

Plot 1 (12 m x 6 m) (Fig. 4)

This plot was situated 300 m from the coast.

The trees were quite small, never exceeding 7 m. 42 A. *nitida* and 1 R. *mangle* were counted on 72 m^2. Of these 42 individuals, 7, of the past, were small, often with dead branches. Most individuals belonged to the set of the present as seen by their numerous reiterations, even present in small trees. 5 individuals comprised the set of the future. Devoid of reiterations, these trees, far from being over-topped, were among the highest of the plot. Quite a number of seedlings were noted.

Plot 2 (17 m x 5 m) (Fig. 5)

This plot was situated 400 m from the coast.

The population was still monospecific. Stems were 17 m high. Of 30 individuals, 3 were of the past set, 7, having numerous reiterations, were of the present and the remaining 20 constituted the future set. Trees of the future set were not as high as those of the present set. It was again observed that all trees of the present set were found all along the vertical plane. Numerous seedlings were found.

Plot 3 (17 m x 5 m) (Fig. 6)

This plot was situated 1 km from the mouth of the river.

The population was still monospecific except for a few young shoots of the climber, *Rhabdadenia biflora* Jacq. Hill (Apocynaceae), and for one plant of R. *mangle*. There were 24 individuals of A. *nitida*, some reaching 20 m high. 6 were of the past, 5, well reiterated, were of the present and were found all along the vertical plane. 13 individuals, having no definite reiterations, were considered as trees of the future; some were very tall, four of them exceeding 15 m and four others 10 m.

Plot 4 (20 m x 18 m) (Fig. 7)

This plot was situated 3 km from the mouth of the river.

The A. *nitida* population was considerably sparser than in the previous plots: 35 individuals only, reaching 25 m high. Some small plants of R. *mangle* and R. *biflora* were found in the understorey; seedlings were quite numerous, A. *nitida* predominating

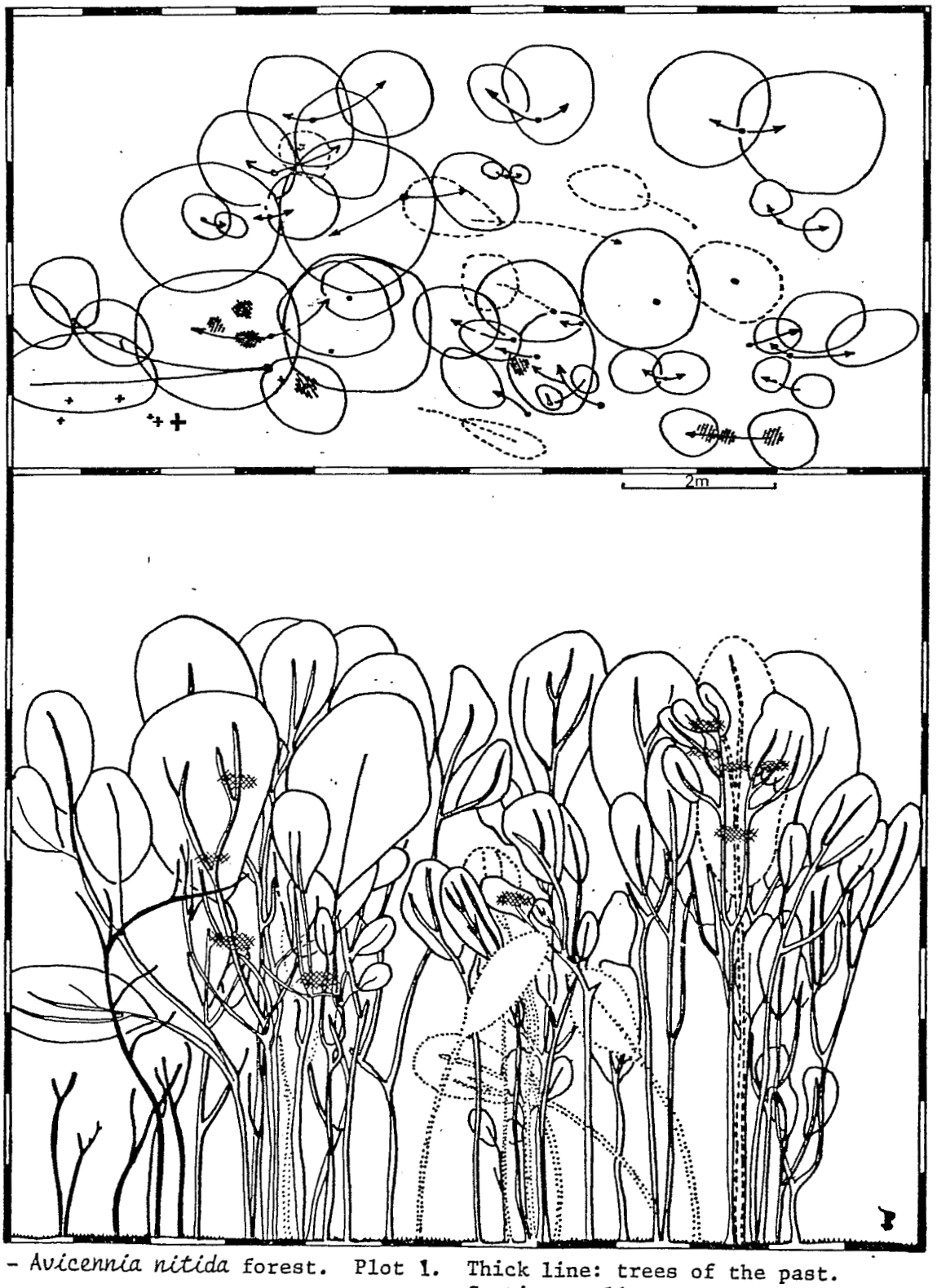

Fig. 4 - *Avicennia nitida* forest. Plot 1. Thick line: trees of the past.
Continuous line: trees of the present.
Dotted line: trees of the future.

Fig. 5 - *Avicennia nitida* forest. Plot 2.
Thick line: trees of the past
Continuous line: trees of the present
Dotted line: trees of the future.

Fig. 6 - *Avicennia nitida* forest. Plot 3.
Thick line: trees of the past
Continuous line: trees of the present
Dotted line: trees of the future.

Fig. 7 - *Avicennia nitida* forest. Plot 4. Thick line: trees of the past.
Continuous line: trees of the present.
Dotted line: trees of the future.

by far. The arborescent population of A. *nitida* was clearly marked by the set of the past comprised of 15 degenerate individuals, that is, 40% of the population. 9 individuals, well reiterated, found all along the vertical plane, represented the set of the present and 11 individuals, six being among the highest trees of the plot, were considered to be in the future set.

Discussion on the genesis of the mangrove forest

It therefore appears that in French Guiana, sedimentation conditions permitting, *L. racemosa* and *S. brasiliensis* are the colonizers. Once the *L. racemosa* population has developed a dense, continuous canopy which happens very rapidly due to its way of reiterating, numerous seedlings of A. *nitida* grow up but always remain over-topped by *L. racemosa*. Suddenly, for reasons which escape us, the *L. racemosa* population is replaced by a pure stand of A. *nitida*.

From then on, the forest is a pure stand of A. *nitida*. Over its whole expanse seedlings were found but no young plants. Between the canopy and the seedling layer there was a leafless space. This leads one to believe that the trees comprising this forest are all contemporaries. As time goes on, they grow but decrease in number as seen in Figure 8. Beyond this phase, one can but think like Richards (1952): "The trees are not rapidly replaced by natural regeneration and as they die the forest becomes more and more open". In fact, while the old A. *nitida* trees, covered in Araceae epiphytes, die, vast open spaces appear colonized by the fern *Acrostichum aureum*. It therefore seems that there is no regeneration in this forest after its establishment. However, it must be noted that due to the sequence of choking up and clearing of silt caused by the sedimentation conditions, the coastal edge of the mangrove forest is constantly renewed: an area heavily attacked by waves later builds up into a mud flat which is soon colonized as already described.

According to the different types of vegetation, one discovers various wildlife communities dwelling in the mangrove forest.

I. NO VEGETATION

1. *Permanently submerged area*

This area is the habitat of a glow-worm, *Chaetopterus cf variopedatus* (polychete spiomorphe) and the crab, *Callinectes bocourti*. Associated with these two species are a large number of estuary fish capable of tolerating extreme variations of salinity. Among the Siluridae are found *Arius luniscutis*, A. *albicans*, A. *proops*, A. *rugispinis*, *Selenapsis passany* and *Bagre marinus;* among the Centropomidae are found *Centropomus ansiforous* (snooks) and C. *undecimalis*.

Occasionally one comes across other species of fish, for example *Cynoscion acoupa* (Scianidae), *Mugil cephalus* and M. *incilis* (Mugilidae).

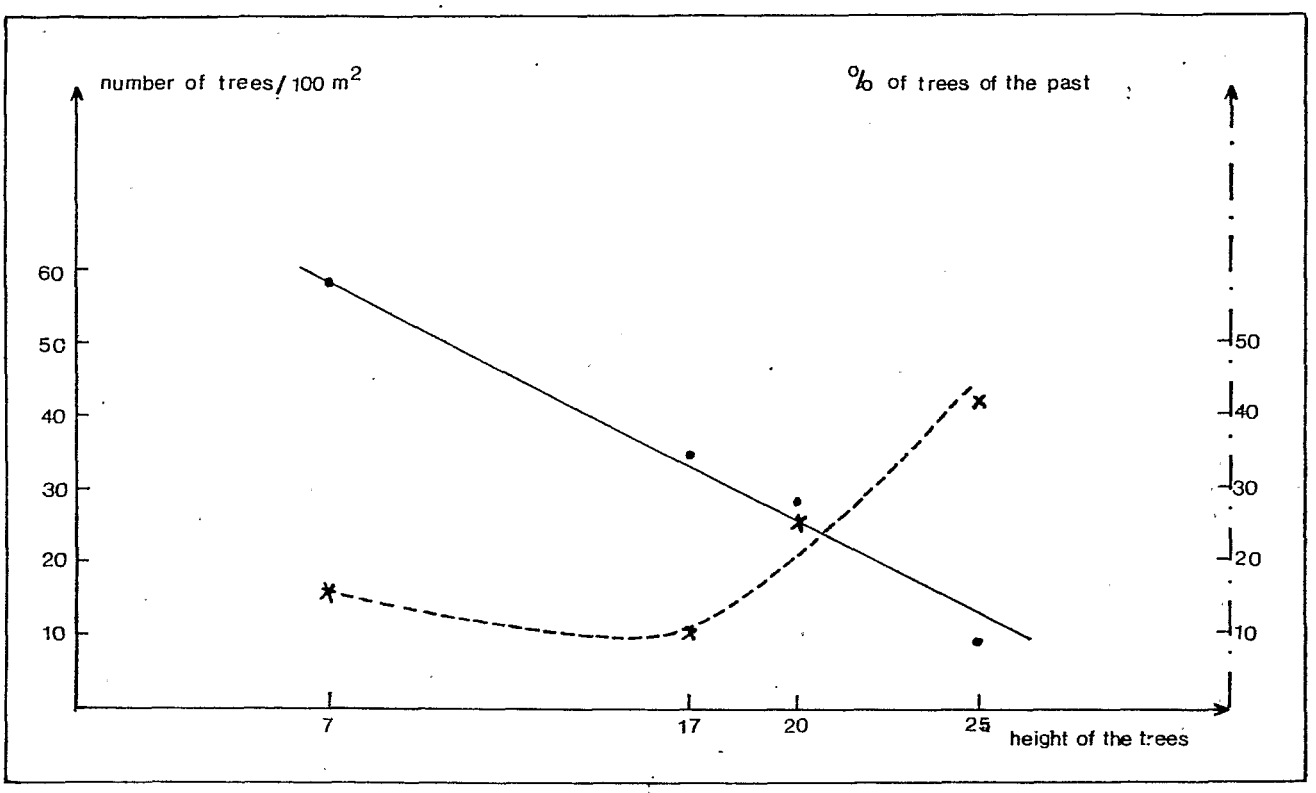

Fig. 8 - *Avicennia nitida* forest. Evolution of the number of stems and percentage of trees of the past in terms of population height.

Shrimp and prawn also dwell in this area, among others may be mentioned the "sea bob", *Xyphopenaeus kroyeri*, which is found both in the sea and the estuaries, as well as other estuary species such as *Palaemon schmitti* and *Macrobrachyum amazonicum* (Palaemonidae), *Hippolysmata oplophozoides* (Hippolytidae) and *Accetes cf Americanus* (Sergestideae).

Of course, this area is also the hunting ground of a large number of sea birds; for example, numerous Laridae such as the Laughing gull, *Larus atricilla* and various species of terns (Sterna).

2. *Area which emerges at low tide: mud flats without vegetation*

At high tide the same animals are found as in the previous area. However, the mud flats are also inhabited by numerous small crustaceans of the Tanaidaceae family, fish and crustacean larvae and burrowing worms, *Annelides polychetes*. At low tide, these mud flats are the domain of numerous waders, the most striking one being the Scarlet Ibis, *Endocimus ruber* (Threskiornithidae). Several Ardeidae are also seen, for example, the small, snowy egret, *Egretta thula thula*, the little blue heron,

Florida caerulea, the tri-coloured heron, *Hydranassa tricolor* and the white-necked heron, *Ardea cocoi*. One also finds Charadriidae, among others the grey plover, *Pluvialis squatarola*, the semi-palmated plover, *Charadrius semipalmatus*, as well as Scolopacidae which are particularly numerous: the whimbrel, *Numenius phaeopus*, the greater yellowlegs, *Tringa melanoleuca*, the spotted sandpiper, *Actitis macularia*, the ruddy turnstone, *Arenaria interpres*, the common dowitcher, *Limnodromus griseus* and several other species of sandpiper of the Calidris genera.

As well as being a feeding ground for the waders, these open mud flats are used as a resting ground by the black skimmer, *Rynchops nigra* (Rynchopidae) and the sea birds mentioned above, especially in the more elevated, drier areas.

II. AREA COVERED WITH VEGETATION

1. *Mud flats with sparse pioneer vegetation*

The marine organisms mentioned above are found at high tide. There are also two crabs, *Uca macacaoni* and *Clibanarius vittatus* and a shrimp, *Alpheus heterochaclis*. The vegetation is also used as a resting ground for some waders of the Scolopacidae family: the whimbrel, *Numenius phaeopus hudsonicus*, the lesser yellowlegs, *Tringa flavipes*, *T. melanoleuca*, *Actitis macularia* and *Catoptrophorus semipalmatus*. All these birds perch on the lower branches of very young *Laguncularia* stems. Other birds seem to treat it as a feeding and resting ground: the pied water tyrant, *Fluvicola pica* (Tyrannidae) and the yellow-hooded blackbird, *Agelaius icterocephalus* (Icteridae).

2. *Mud flats with continuous pioneer vegetation: dense canopy of L. racemosa, overshadowing A. nitida stems.*

Being difficult to penetrate, only the outer edge is used by Ardeidae as a resting ground.

3. *Riparian vegetation with L. racemosa and C. maritima*

At low tide, Ardeidae come to roost on the lower branches of *Laguncularia*, which are also the resting ground for numerous sandpipers, *Calidris pusilla* and *C. mauri*, near the mouth of the river. Further upstream, these branches are covered with the white-winged swallow, *Tachycineta albiventer* (Hirundinidae). Very occasionally one comes across an osprey, *Pandion haliaetus* (Pandionidae), muscovy ducks, *Cairina mochata* (Anatidae) and the ringed kingfisher, *Ceryle torquata* (Alcedinidae) on the branches of *Laguncularia*.

One often sees the curious fish, *Anableps tetraphtalmus* at the very edge of the water.

4. *Avicennia forest: young stems between 7 and 10 m high*

This area is the nesting ground for the Scarlet Ibis. Covering approximately 7 hectares (CONDAMIN), this area holds about 6,000 nests. Associated with the Ibis nests,by far the most numerous there are nests of the snowy egret, *Egretta thula*, the little blue heron, *Florida cerulea* and the tri-coloured heron, *Hydranassa tricolor*, as well as, very occasionally, the common egret, *Egretta alba*, the boat-billed heron, *Cochlearius cochlearius* (Cochlearidae), the white-necked heron, *Ardea cocoi*, the yellow-crowned night heron, *Nycticorax violacea* and the black-crowned night heron, *N. nycticorax* (Ardeidae).

5. *Avicennia forest: Older stems*

One often sees the greater ani, *Crotophaga major* (Cuculidae) and the Rufous crab hawk, *Buteogallus acquinoctialis* (Accipitridae). Among the nocturnal birds are found one *Butorides*, the *Nycticorax nycticorax* and the spectacled owl, *Pulsatrix perspicillata* (Strigidae).

Two fish are seen at high tide in these two areas: *Anableps tetraphtalmus* and *Selenaspis passany*. They are also the biotope of four crabs: *Uca rapax* (Ocipodidae) and *Ucides cordatus* (Gacarcuridae) with which *Goniopsis cruentata* and *Pachygapsus gracilis* (Grapsidae) are associated.

Mammals are rare in these two areas; one may see the crab-eating rat, *Procyon cancrivorous*, little monkies, *Saimiri semreas* and the mangrove deer, *Odocorleus gymnotis*.

Finally, these two areas are literally infested with mosquitos, Dipteres culucidae, the commonest being *Coquillettidia venezuelensis* and *Anopheles aquasalis*, with which numerous Ceratopogonidae are associated.

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