

A phytogeographic survey of Southern Benin

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ABSTRACT

Southern Benin has a dry subequatorial climate with a rainfall gradient from 850 mm in the west to 1 500 mm in the east, the geomorphology is varied and the vegetation has been subjected to strong human influence. There are numerous plant formations, namely:

1, forest islands which are probably relics of the primitive vegetation and include (a) dense semi-deciduous forests of several types, (b) swamp forests of two types, (c) periodically flooded forest of two types, (d) *Lophira lanceolata* (Hutchinson & Dalziel, 1954–72) woodlands and (e) mangrove swamps;

2, formations which are probably derived and include (a) thickets of several types, (b) tree savannas and shrub savannas, (c) grassy savannas and prairies varying according to soil characteristics and (d) halophytic grasslands; and

3, floating vegetation on fresh-water lakes.

RÉSUMÉ

APERCU PHYTOGEOGRAPHIQUE SUR LE SUD BÉNIN

Le Sud-Bénin, en climat subéquatorial sec avec un gradient de pluies d'ouest en est (de 850 à 1 500 mm), ayant une géomorphologie variée et ayant subi un fort impact anthropique présente de nombreuses formations végétales. On peut distinguer:

1, Des îlots forestiers (restes vraisemblables de la végétation primitive) comprenant des: (a) forêts denses semi-décidues, de plusieurs types et occupant les plateaux, les bords de vallée et la dépression argileuse de la Lama, (b) forêts marécageuses de deux types (un type à nombreuses espèces dans les vallées continuellement inondées et à écoulement permanent de l'eau; un type dominé par *Ficus congensis* dans les dépressions littorales à eau stagnante en saison sèche), (c) forêt périodiquement inondée de deux types (un sur sable littoral à *Symphonia globulifera*; un sur les terrasses de bord des fleuves), (d) forêt claire à *Lophira lanceolata* sur le sable roux littoral, (e) mangrove en bordure de la lagune de l'ouest;

2, Des formations vraisemblablement dérivées, comprenant: (a) des fourrés (à *Manilkara obovata* près de l'océan; à *Dalbergia ecastaphyllum* près des mangroves; à nombreuses espèces près des îlots de forêt dense semi-décidue, (b) des savanes arborées et arbustives (à *Lophira*; à *Mitragyna inermis* et *Phoenix reclinata* dans les vallées; à *Terminalia glaucescens* et autres espèces dans la dépression de la Lama), (c) des savanes herbeuses et des prairies variées suivant les caractères du sol (à *Ctenium newtoni*; à *Andropogon gayanus*; à *Vetiveria nigriflora*; à *Cynodon dactylon*; à *Loudetia phragmitoides*; à *Echinochloa pyramidalis*; à *Typha australis*; à *Paspalum vaginatum* . . .), (d) des pelouses halophiles à *Sesuvium portulacastrum* et *Philoxerus vermicularis*;

3, Une végétation flottante sur les lacs d'eau douce (à *Cyclosorus striatus*, *Pistia stratiotes* . . .).

L'action humaine actuelle tend à détruire les derniers îlots forestiers et à favoriser les fourrés et la végétation herbeuse.

Since Adjanohoun's report on conservation of vegetation in Le Dahomey (1968), several investigations have been carried out on the vegetation of Southern Benin (see References). This article endeavours to take stock of the phytogeographic knowledge of that region.

1 ENVIRONMENT

1.1 Geomorphology

Southern Benin consists solely of sedimentary rocks from the Upper Cretaceous to the Quaternary. Its geomorphology is dominated by two series of plateaux separated by an east-west depression and by north-south valleys.

The east-west depression, called Lama, is chiefly argillaceous and flooded for part of the year (August–September). The northern plateaux, called Aplahoué, Abomey, Kétou, reach 100–150 m in

altitude, with red sandy argillaceous soil and lateritic crusts. The southern plateaux, called Bopa, Allada, Sakété, rise to 20 m in the south and 90 m in the north; they consist of argillaceous, red to ochre sand, pleistocene, called 'terre de barre.' Circular depressions and small flat-bottomed valleys cut through them. The north-south valleys correspond to small rivers the Ouémé (and the So), the Kouffo (and Lake Ahémé and the Aho), the Mono (and the Sazué). These valleys have a rather varied topography viz. sandy buttes which are never covered by flood waters, low argillaceous and silty clay banks which are flooded every year, constantly hydromorphic peaty parts and open expanses of water (Lakes Aziri, Sélé, Hounhoun, Ahémé).

A coastal complex of variable width (3–5 km) lies a short distance from the ocean, consisting of old offshore bars, recent bars, depressions corresponding to former lagoons, and present-day lakes and lagoons (lagoon of Porto-Novo, Lake Nokoué, coastal lagoon).

Fig. 1A shows the geology of the southern part of Benin.

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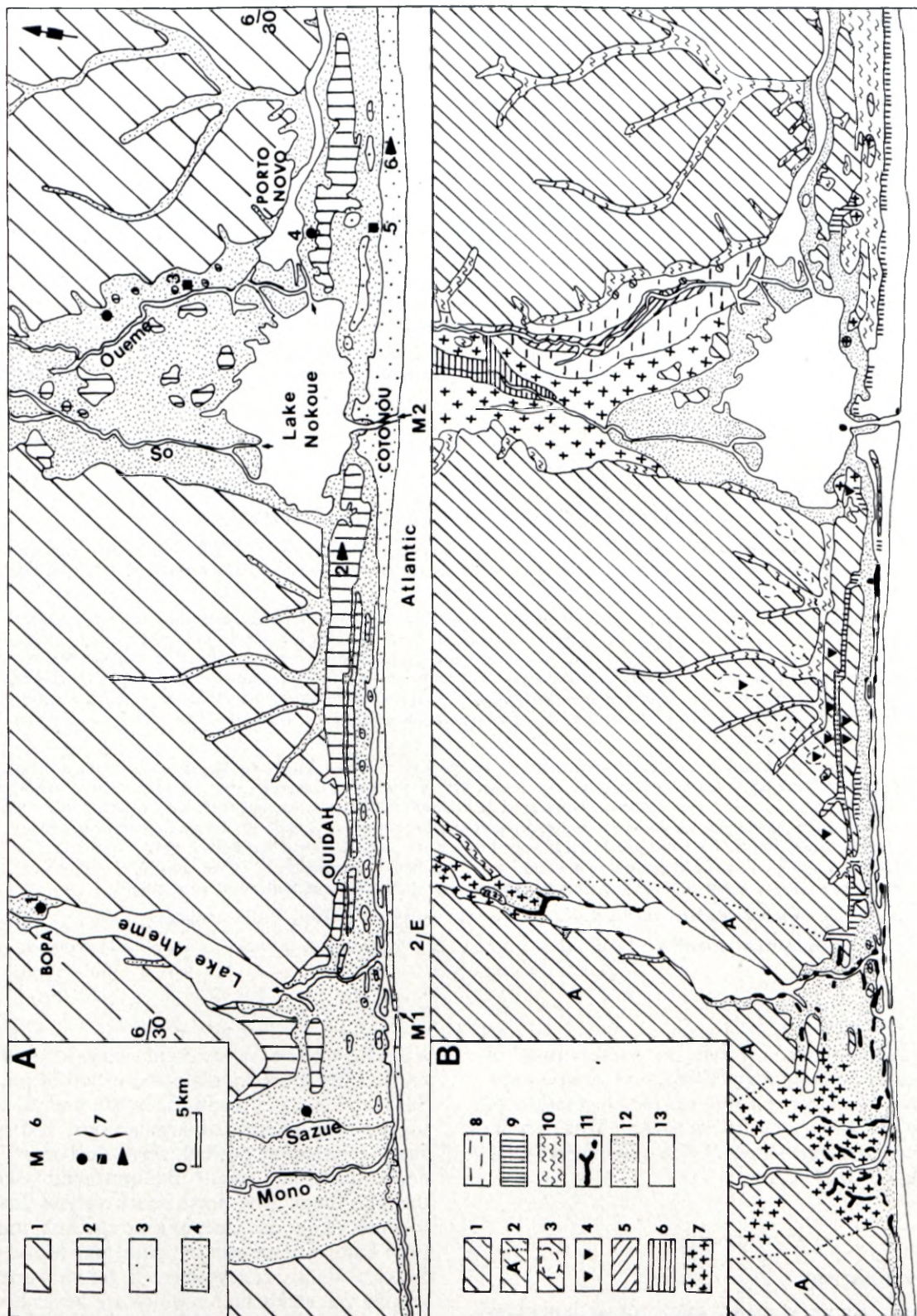


FIG. 1.—A, simplified geological map of Lower Benin. 1, 'Terre de barre' (pleistocene, argillaceous red sand); 2, yellow sand on old bars (recent pleistocene or holocene?); 3, sand of recent marine bars; 4, clay, mud and peat of valleys and depressions; 6, estuaries (entrance of salt water) with M 1 (estuary of the Mono and of the coastal lagoon) and M 2 (mouth of the channel of Cotonou); 7, organic evidence located at some depth (black circles: peat of mangrove swamps; squares: shells of brackish environment; triangles: charcoal). Number 1 was dated from 5 700 BP (GIF-2847), number 2 from 2 670 (DaK-199), number 3 from 2 670 BP (GIF-3347), number 4 from 5 430 BP (GIF-2848), number 5 from 1 050 BP (GIF-3350), number 6 from 830 BP (GIF-3973). B, schematic phytogeographic map of Lower Benin. 1, non hydromorphic formations (islands of dense semi-deciduous forest, thickets, *Elaeis* groves, fallow land in various stages); 2, *idem*, but with abundant *Adansonia digitata*; 3, savannas apparently included in past extension of dense semi-deciduous forest; 4, formations with *Lophira lanceolata* (woodlands and savannas); 5, low prairie with *Cynodon dactylon*, near the Ouémé; 6, periodically-flooded forest on the low banks of the Ouémé and So; 7, varied savannas with *Mitragyna inermis* and *Andropogon gayanus* var. *squamulatus*; 8, medium prairie with *Echinochloa pyramidalis*; 9, periodically-flooded forest (with *Symphonia globulifera*) and prairie (with *Fuirena umbellata*); 10, swampy fresh-water forests and thickets; 11, mangrove swamps; 12, prairie with *Paspalum vaginatum* (with occasional *Typha australis*); and 13, coastal vegetation (littoral thicket, littoral grassland, coconuts).

1.2 Climate

Southern Benin has a dry subequatorial climate with two rainy seasons and two dry seasons of unequal length: the long rainy season from April to July, the short rainy season in October, the long dry season from December to February and the short dry season in August. Two gradients characterize the region:

— a light south-north gradient with a tropical tendency with decrease in the length of the short dry season and increase in the length of the long dry season;

— a strong east-west gradient of decreasing annual rainfall (1 350 mm at Porto-Novo, 1 100 mm at Ouidah, 850 mm at Grand-Popo). Another characteristic is the great irregularity of annual rainfall from one year to the next.

The mean monthly temperatures vary little, for example Cotonou is 28°C in March, 25°C in August, with a mean temperature of 26.5°C. The maximum temperatures are close to 34°C on the coast and a little higher in the interior. The largest temperature variations occur during the days of the Harmattan (from December to February).

The dominant winds come from the south-west except during the Harmattan.

1.3 Hydrology

Rivers, lakes and lagoons are at their lowest depth from November to May. Most years, they are highest in September and October. Thus, in the valleys, there is an annual alternation of submersion and emersion which, with the topography, is one of the determining factors of phytocoenoses.

In the dry season, salt water from the ocean can enter the Mono River and Lake Nokoué through inlets: this explains the presence of halophytic phytocoenoses very far inland (Fig. 1B).

1.4 Human influence

Lower Benin appears to have been inhabited for a long time. The density of villages is high. The crops (maize, cassava, taro), the plantations (palm-oil from the last century onwards, coconut), the techniques of salt extraction (by boiling) and fishing (by placing a great number of branches in the water) and the gathering of fire wood, have brought about the destruction of forests (only a few forest islands remain) and their replacement by thickets and grassy phytocoenoses.

Man probably brought the baobab to the south-west part and very likely modified the distribution of palm trees (*Borassus* sp., *Phoenix reclinata*, *Raphia* spp.).

Finally, the opening of the channel of Cotonou (1885), and the construction of the Port of Cotonou (1960) have had a great impact on the environment.

As evidence of past human involvement, we were able to date with C14 some charcoal associated with neolithic quartz at Godomey* and with pottery at Kraké.**

2 PRINCIPAL PHYTOCOENOSES

2.1 Forest islands

2.1.1 Dense semi-deciduous forests

Only a few rare stands of secondary forest remain on the southern plateaux—on their slopes and in the Lama depression.

(a) On the southern plateaux.

The greatest number of species is found on the Sakété Plateau, with a very sharp decrease in number of species from east to west. An example of a typical forest island is that of Ké (northwest of Porto-Novo; area: 4 hectares) with the following strata and main species:

— rare megaphanerophytes (*Cola gigantea* var. *glabrescens*, *Ceiba pentandra*, *Antiaris africana*, *Pycnanthus angolensis* and *Triplochiton scleroxylon*);

— macrophanerophytes (*Bosqueia angolensis*, *Blighia unijugata*, *Celtis brownii*, *C. mildbraedii*, *C. zenkeri*, *Chlorophora excelsa*, *Chrysophyllum albidum*, *Parkia bicolor*, *Sterculia tragacantha*, *Tabernaemontana pachysiphon* and *Trichilia prieureana*);

— microphanerophytes (*Agelaea obliqua*, *Capparis erythrocarpos*, *Carpolobia lutea*, *Dracaena arborea*, *Newbouldia laevis*, *Oncoba spinosa*, *Cola millenii*, *Connarus africanus* and *Salacia pallescens*);

— nanophanerophytes (*Angylocalyx oligophyllus*, *Chassalia kolly*, *Cnestis ferruginea*, *Deinbollia pinnata*, *Dracaena surculosa*, *Mallotus oppositifolius* and *Ritchiea pentaphylla* . . .).

— lianas (*Alafla barteri*, *Dioscorea minutiflora*, *Leptoderris brachyptera*, *Ritchiea reflexa* and *Smilax kraussiana* . . .).

In the villages various trees which are typical of these forests can be seen. It has sometimes been assumed that all the southern plateaux were covered by a dense semi-deciduous forest (Mondjannigni, 1969), but that does not seem to be the case for the southern part of the Bopa and Allada Plateaux (Paradis *et al.*, 1978): there, the forest-savanna mosaic appears to be of long standing. Around Porto-Novo, throughout the centuries, an *Elaeis* plantation replaced the dense forest through human activity (Brasseur-Marion & Brasseur, 1953).

(b) Lama depression (Paradis & Houngnon, 1977). A forest expanse of 8500 hectares still exists, composed of:

— some megaphanerophytes deciduous during the dry season, over 30 m in height, and widely spaced (*Ceiba pentandra*, *Antiaris africana*, *Chlorophora excelsa* and *Triplochiton scleroxylon*);

— a continuous stratum of evergreen trees, 15–25 m in height (*Dialium guineense*, *Diospyros mespiliformis* and *Mimusops andongensis*), with *Afzelia africana*;

— a stratum 7–10 m in height with the same species as above but, in addition, *Celtis brownii* and *Drypetes floribunda*, and

— a very dense undergrowth (from 1–5 m tall) with *Sorindeia warneckei*, *Cremaspora triflora*, *Chassalia*

* 2670 ± 120 BP (DaK-199)

** 830 ± 90 BP (GIF-3973) (Paradis, 1977).

kolly, *Pancovia bijuga* and *Gardenia triacantha* predominating.

Here and there in the forest, can be found isolated stands of *Anogeissus leiocarpus* — evidence of former land-clearing, and which must not be interpreted as relics of a southward extension of dry plant formations.

It seems likely that the clay of the entire transversal depression between the northern and southern plateaux was formerly occupied by a forest of this type. The planting of crops (maize) destroyed it almost everywhere, and today, the subsisting island, despite being theoretically a reserve, is in the process of being destroyed.

2.1.2 Swampy fresh-water forests

These are of two types.

(a) *In the low ground with permanently flowing water (vales of the southern plateaux, the edge of the valley of the Ouémé).* For example, the forest of the vale of Igolo, near the Nigerian border can be described (Paradis, 1975a) with:

— a discontinuous stratum 8–15 m in height (*Anthostema aubryanum*, *Alstonia congensis*, *Symphonia globulifera*, *Cleistopholis patens*, *Mitragyna ciliata*, *Syzygium owariense*, *Carapa procera*, *Anthocleista vogelii*, *Dracaena perrottetii*, *Homalium molle*, *Ficus vogeliana* and *Xylopia rubescens*).

— a stratum 2–8 m tall (*Raphia hookeri*, *Alchornea cordifolia*, *Mussaenda isertiana*, *Sabicea africana* and *Ixora brachypoda*);

— lianas (*Lygodium microphyllum*, *Canthium setosum*, *Eremospatha macrocarpa*, *Oligocodon cunliffeae*, *Sherbournia bignoniiflora* and *Zacateza pedicellata*);

— grasses and forbs (*Cyclosorus striatus*, *Impatiens irvingii*, *Acroceras zizanioides*, *Eulophia horsfalli*, *Brachiaria mutica* and *Palisota hirsuta*).

(b) *In the constantly flooded depressions without permanent water flow.* Such zones exist in the coastal complex and correspond to the courses of former rivers, quite evident from Cotonou to Nigeria. For example, near Krake, the forest is dominated by *Ficus congensis* with *Anthocleista vogelii*, *Syzygium owariense*, *Chrysobalanus ellipticus*. Only during the flood season (August to November) does the water flow freely. The rest of the year it is stagnant.

In such an environment, a *Ficus congensis* forest can be found in the old course of the Kouffo to the north of Lake Ahémé.

Man has had an influence on the swampy forests, by cutting down tall trees with straight trunks (*Alstonia*, *Cleistopholis*, *Mitragyna* and *Symphonia*), by planting *Raphia* palms to be used in various ways, by penetrating into the clearings to harvest species of forbs (*Thalia welwitschii*, *Cyrtosperma senegalense*), the leaves of which are used to wrap food sold in the markets. In the Ouémé Valley, taro is grown at the site of a swampy forest which was almost entirely cleared away for that purpose. Now, in that valley, rice-growing, through the extension of draining, is modifying the environment. The final result of

human influence is an abundance of thickets and marshy prairies with a few scattered, tall trees.

2.1.3 Periodically-flooded forests

They are of three types, according to the substrate (Paradis, 1975a, 1975b; Berding, 1976).

(a) on the low banks of the Ouémé and the So. To the north of Adjohoun, along the edge of these two rivers, made up of silty argillaceous soil, a riverbank forest lies on the low banks, forming a veritable gallery forest. It is inundated during the flood season for one to two months a year. Its composition is as follows:

— a stratum of trees (8–12 m) with *Azelia africana*, *Cynometra vogelii*, *Dialium guineense*, *Lonchocarpus sericeus*, *Manilkara obovata* and *Pterocarpus santalinoides*;

— a stratum of shrubs with *Cola laurifolia*, *Memecylon blakeoides* predominating and *Mimusops kummel*, *Mitragyna inermis*, *Morelia senegalensis*, *Pachystela brevipes* and *Pavetta owariensis*;

— lianas: *Flagellaria guineensis*, *Leptoderris brachytera* and *Paullinia pinnata*.

— a herbaceous stratum with *Crinum jagus*, *Haemanthus rupestris*, *Amorphophallus atrovirens*, *Herderia truncata* and *Hypolytrum poecilolepis*.

(b) *On the sand along the edge of the depressions of the coastal complex.* Here, the level of phreatic water fluctuates throughout the year, rising to one metre above ground from June to November, and falling to one metre below during the dry season. Such an environment is occupied by forest in which *Symphonia globulifera* is abundant, along with such species as *Cleistopholis patens*, *Alstonia congensis*, *Memecylon blakeoides*, *Anthocleista vogelii*, *Berlinia grandiflora*, *Syzygium guineense*, *Chrysobalanus ellipticus* and *Ancistrophyllum secundiflorum*.

Man has, in many places, transformed this forest into *Elaeis* groves and grass savanna with *Loudetia phragmitoides* and *Panicum congoense* (Paradis, 1975a).

(c) *On the sandy islets of the Ouémé Valley.* Here there are occasionally-flooded forests, comprised of a mixture of riverbank forest species such as *Cynometra vogelii*, *Cola laurifolia*, *Lonchocarpus* spp., *Manilkara obovata*, *Ostryocarpus riparius* and *Pterocarpus santalinoides* and semi-deciduous forest species such as *Ceiba pentandra*, *Cola gigantea* and *Cola millenii*.

2.1.4 Woodlands with *Lophira lanceolata*

In the Ahozon Reserve, on yellow sand, *L. lanceolata* forms a monospecific, 6–10 m-high, closed community with a single stratum. The herbaceous plants, well-developed in October, include a stratum, 1–1.3 m high, with *Ctenium canescens*, *C. newtonii*, *Setaria pallide-fuscae* and *Schizachyrium sanguineum* and a lower stratum with Cyperaceae like *Bulbostylis aphyllantoides*, *Kyllinga erecta* and *Cyperus margaritaceus*. Almost everywhere, these woodlands have been transformed into tree and shrub savannas invaded by small thickets (see below).

2.1.5 Mangrove swamps (Paradis & Adjanohoun, 1974; Paradis, 1979, 1980, 1981)

At some points (north-west of Lake Ahémé, east of the coastal lagoon, between the Aho and Grand-Popo) there remain some relics of a mangrove swamp with *Avicennia africana* and *Rhizophora racemosa*, formerly more extensive. Between Ouidah and the estuary, on the areas degraded for the extraction of salty soil, there are some small populations of *Laguncularia racemosa*.

2.2 Thickets, savannas, prairies, grasslands and floating vegetation

2.2.1 Thickets

(a) *Littoral thicket* (Paradis, 1976; Souza, 1979). In rare places on the coast there remain patches of this thicket with shrubs (*Manilkara obovata*, *Fagara zanthoxyloides*, *Diospyros tricolor*, *Syzygium guineense* and *Chrysobalanus orbicularis*), liana (*Sarcostemma viminalis*) and a geophyte (*Sansevieria liberica*). In addition, there is the occasional *Adenia lobata*, *Agelaea obliqua*, *Carissa edulis*, *Chassalia kolly*, *Flacourtia flavescens*, *Ritchiea reflexa*, *Trema guineensis*, and *Phoenix reclinata*. It seems likely that this coastal thicket constituted the edge of a littoral forest with *Manilkara obovata*, destroyed for the extraction of salt by boiling sea water.

(b) *Thicket with Dalbergia ecastaphyllum* (Paradis, 1979). This species is abundant in readily-flooded parts on the banks of the coastal lagoon, where it is often associated with *Drepanocarpus lunatus*, in the clearings of *Rhizophora* mangrove swamp, and along depressions with *Typha australis* and *Kyllinga peruviana* of the coastal sand. This thicket, 2–4 m in height, is not easily penetrated, and constitutes a phytocoenose of long duration. At the edge of the mangrove swamp, it impedes the reconquest of the environment by *Rhizophora* and *Avicennia*.

(c) *Thicket on yellow sand and 'terre de barre.'* On yellow sand, scattered among the *Lophira lanceolata* formations, thickets 6–12 m in height and 10–100 m in diameter are plentiful. Their flora, which is quite abundant, includes *Barteria nigrifolia*, *Bridelia ferruginea*, *Dialium guineense*, *Fagara zanthoxyloides*, *Annona senegalensis*, *Byrsocarpus coccineus*, *Carissa edulis*, *Cnestis ferruginea* and *Vitex doniana*. The majority of these species are zoochorological (ornithochore and cheiropterochore). These thickets are a stage in the progression of *Lophira* savanna to forest: one can often observe rotting trunks of *Lophira* in the thickets.

On 'terre de barre,' likewise, there is a thicket formed by numerous discontinuous copses more or less extensive, 4–8 m in height. The tallest trees are *Bridelia ferruginea*, *Fagara zanthoxyloides*, *Malacantha alnifolia*, *Phyllanthus discoideus* and *Vitex doniana*. They tower over a number of small shrubs. Here, these thickets are undoubtedly a stage in the progression of old savannas to forest (Paradis *et al.*, 1978).

(d) *Wooded thicket at the edge of the Lama Forest.* This thicket clearly results from the invasion of savanna by forest. Indeed, it is comprised of:

— large savanna trees, from 5–12 m in height, widely spaced (*Anogeissus leiocarpus*, *Combretum molle*, *Fagara zanthoxyloides*, *Lannea kerstingii*, *Piliostigma thonningii*, *Pterocarpus erinaceus* and *Terminalia glaucescens*);

— a closed stratum, from 0–5 m in height, with the same floristic composition as that of the Lama Forest with much *Dialium guineense*, *Diospyros mespiliformis*, *Mimusops adongensis* and *Celtis brownii*. The diameter of these forest species is small. This wooded thicket on the forest periphery appeared after the area was made a reserve, which put a stop to annual fires. As long as fires occurred each year, the savanna species grew without competition but, as soon as they stopped, the forest species, better adapted to the present environment, were able to occupy the former burnt sites.

2.2.2 Tree savannas and shrub savannas

(a) *With Terminalia glaucescens of the Lama depression and north of Lake Ahémé.* These are Guinean savannas with numerous species, but without *Lophira lanceolata* or the Shea butter tree. It is possible that these savannas have arisen through the destruction of woodlands by man.

(b) *With Lophira lanceolata.* These result from deterioration of the *Lophira* woodlands. Their floristic composition is the same as that of the woodlands.

(c) *With Mitragnya inermis and Phoenix reclinata (in the valleys).* In the Ouémé valley, this savanna is characterized by a tree stratum (with *Mitragnya inermis* and some *Pterocarpus santalinoides*), a shrub stratum (with *Antidesma venosum*, *Drepanocarpus lunatus*, small *M. inermis*, *Mimosa pigra* and *Vitex doniana*) and an herbaceous stratum (with *Andropogon gayanus* var. *squamulatus*, *Axonopus flexuosus*, *Cyperus articulatus*, *Eriosema glomeratum*, *Hibiscus asper* and *Hygrophila auriculata*). In some scattered spots there are copses with *Phoenix reclinata*. In the valleys of the Kouffo and the Mono, these palm-trees are abundant, and in the south-west there is also *Borassus aethiopum*. Near Cotonou and in the south-east there are some dispersed stands of *M. inermis*.

These *M. inermis* savannas occur on soil which is seasonally flooded and composed of clay or silty-argillaceous sand. They appear to have been derived under the influence of fire, from riverside forests.

2.2.3 Grass savannas and varied prairies

These low phytocoenoses, with superficial roots, can be classified according to the characteristics of the substratum.

(a) *On sand never or rarely flooded:*

— on 'terre de barre' grassy savanna with *Andropogon tectorum* and *Imperata cylindrica*, characteristic of exhausted soils, which become very sandy;

— on yellow sand grassy savanna with *Ctenium newtonii* and *Schizachyrium sanguineum*, resulting from the great deterioration of *Lophira* shrub savannas.

(b) *On sand periodically flooded:*

— littoral zone: the highest areas are occupied by a prairie with *Vetiveria nigritana*, the lowest points are covered by a prairie with *Panicum congoense* (Guinko, 1974), the places, topographically very low, by a prairie with *Loudetia phragmitoides*;

— low Ouémé valley: the bulge of the steep river bank, silty and sandy, is occupied by a low *Cynodon dactylon* prairie, used very much for grazing, with numerous ruderal species. In flood season, this bulge is inundated almost every year and invaded by floating vegetation;

(c) *On argillaceous and silty clay soil, periodically flooded:*

— littoral zone (in the depressions parallel to former bars): medium prairie with *Fuirena umbellata*;

— low Ouémé valley: medium prairie with *Echinochloa pyramidalis* and *Brachiaria mutica* (and during the dry season *Aeschynomene indica*, *Digitaria horizontalis*, *Hyptis lanceolata*, *Paspalum orbiculare* and *Pentodon pentandrus*). During the flood season, most of these species become floating. In addition, there are some Cyperaceae (*Cyperus haspan*, *Fuirena umbellata* and *Rhynchospora corymbosa*), and various strictly floating species.

(d) *On substrata saturated with fresh water all year long:*

— high prairie with *Typha australis* (with very few species: *Paspalum vaginatum*, where the salinity increases during the dry season, *Polygonum pulchrum*, *Cyperus papyrus*, *Cyclosorus striatus* and *Cyrtosperma senegalense* where the water remains fresh all the time). Such a prairie is located around the lagoon of Porto-Novo (Paradis & Rabier, 1979), between Cotonou and the eastern limit of the mangrove swamp, in the abandoned meanders of the Kouffo (north of Lake Ahémé), and in the depression between the Allada plateau and the yellow sand (from Pahou to Godomey);

— a community of *Cyperus papyrus*, which is not very extensive (behind the preceding community where the water is acid) with *Phragmites australis* and *Echinochloa pyramidalis*;

— a community with *Nymphaea lotus* in the numerous expanses of open water;

— a community with *Cyclosorus striatus*, very extensive on the periphery of Lakes Aziri and Hounhoun, and in the gaps of swamp forests. This fern floats during floods. The death of the fern, without decomposition of its rhizome, produces floating peat on which seeds from trees of swamp forests can germinate;

— a community with *Pycnus mundii*, localized in one spot (Guinko, 1974).

(e) *On hydromorphic substrata, slightly brackish at certain times of the year.* On these substrata there occur an *Eleocharis* spp. prairie behind the mangrove swamps (from Ouidah to Togbin), and a community behind the offshore bar (between it and the mangrove swamps) with *Kyllinga peruviana*, *Phyla nodiflora*, *Fimbristylis obtusifolia*, *Mariscus*

ligularis, *Pycnus polystachyos*, *Hydrocotyle bonariensis* and *Philoxerus vermicularis*.

(f) *On a salty substratum (Paradis, 1980):*

— grassland with *Sesuvium portulacastrum* and *Philoxerus vermicularis* on the periphery of areas where salty earth is extracted (south-western region).

— low prairie with *Paspalum vaginatum*, very extensive (Fig. 1B), and with other species (*Cyperus articulatus*, *Bacopa crenata*, *Pentodon pentandrus* and *Pycnus polystachyos*). Occasional clusters of *Acrostichum aureum* can be found scattered over the prairie.

— littoral grassland with two features (in the low areas, on prograding, sand, pioneer vegetation with *Ipomoea pes-caprae*, *Remirea maritima* and *Cyperus maritimus*; in the high areas of the offshore bar, grassland with *Sporobolus virginicus*, *Schizachyrium pulchellum*, *Ipomoea stolonifera* and *Diodia vaginalis*, with small dunes having scattered *Scaevola plumieri*).

2.3 Floating vegetation (Paradis & Rabier, 1979; Texier *et al.*, 1980)

Floating vegetation begins to multiply rapidly when floods occur in the low valleys. On the lagoon of Porto-Novo, they constitute floating islands with:

— species floating freely on the surface: *Azolla africana*, *Salvinia nymhellula* and very abundant *Pistia stratiotes*;

— immersed species: *Ceratophyllum demersum*;

— species with creeping stems which can live rooted on the edge of banks: *Aeschynomene indica*, *Commelina congesta*, *Enydra fluctuans*, *Ipomoea aquatica*, *Jussiaea repens* var. *diffusa*, *Leersia hexandra*, *Marsilea diffusa*;

— helophytic species: *Echinochloa pyramidalis*, *Cyperus papyrus*, *Typha australis*, *Paspalum vaginatum*, *Polygonum pulchrum*. Due to its great biomass, this category gives its physiognomy to the floating islands.

In the lagoon of Porto-Novo the floating vegetations spreads from January onwards following an increase in salinity. It begins to take over the lagoon in June-July.

CONCLUSIONS

This phytogeographic overview of Southern Benin shows the great variety of phytocoenoses caused, on the one hand, by climatic, topographic and edaphic factors and, on the other, by human influence on the environment. The result is a mosaic of plant formations in which thickets and savannas of several types predominate.

The natural historical factors, especially paleoclimate, have not yet been elucidated.

Future research should focus on detailed cartography, to a scale of 1: 50 000 (already begun), on the determination of kinds of charcoal (in collaboration with archaeologists) and on the palynological study of soil samples.

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