An Outline of the Vegetation of the Okavango Drainage System

P. A. SMITH, Ministry of Agriculture, Maun

Introduction

The Okavango drainage system, a part of the Kalahari hydrographic basin, consists of:

(a) Upper Okavango: the catchment of the Cubango and Cuito Rivers in Angola
(b) Namibian section: the Okavango River between Mucusso and Mohembo
(c) Panhandle: the Okavango River and Swamp between Mohembo and the Delta
(d) Delta: all areas liable to flooding within the Gomare and Thamalakane fault-troughs
(e) Boteti River
(f) Makgadikgadi Depression.

At Fig. 1, the system and part of its surrounds are divided into zones, each containing one or more main vegetation types. These zones represent simplified versions of vegetation maps that have already been published. No such information is readily available for the Namibian section which is left blank. Seven zones are selected for description. Some important data on their physical background are listed below:

			Principal river			
Zone	*Mean annual rainfall mm*	*Altitude m.a.s.l.*	*Length km*	*Descent m*	*Gradient*	*Conductivity micromhos/ cm^{-1}*
1	1 260/1 350	1 710/1 830	35	120	1: 300	4,2/8
2	860/1 340	1 200/1 810	400	500	1: 800	21/35
3	520/ 860	1 018/1 200	540	182	1:3 000	38
Namibian section	?	994/1 018	50	24	1:2 100	36
4	520					
5	410/ 490	932/ 994	442	62	1:7 130	24/102
6	?					
7	472/ 490	900/ 932	260	30	1:8 666	?
			1 727	918	1:1 880	

The whole system is embedded on Kalahari sand, except that soils in Zone 1 and the Cubango part of Zone 2 are derived from crystalline rock.

ZONE 1: UPLAND GRASSLAND

This zone has one main vegetation type, and is found in the area of highest rainfall and elevation in the Kalahari Basin — on the slopes of the Angolan "Planalto Central." The Cubango River rises here from a network of sponges, but varies from little more than a series of trickles to a stream, at most, a few metres broad by one

metre deep. A very steep gradient ensures swift flow of its waters, which are sparkling-clear and of exceptional purity.

At the sponges where water oozes out of black, peaty turf, grow typical bogland plants, eg, *Xyris, Eriocaulon, Genlisea* and *Drosera spp.* Surrounding the sponges and close to the stream herbaceous cover, mostly under one metre in height, forms a thick mat, rich in variety: *Compositae, Araceae, Gentianaceae, Labiatae, Rubiaceae, Umbelliferae* spp., many grasses, sedges, ferns, brackens and some spectacular *Dissotis* and *Polygala.* The small stream dimensions are reflected in a paucity of aquatics with only one in any abundance: the submerged *Limnophila ceratophylloides.* Occasional clusters of yellow water-lilies *(Nymphaea sulphurea)* add colour to the scene. A low, shrubby form of beechwood *(Faurea saligna)* dominates the banks. Two heather-like bushes and a dwarf *Syzygium* complete the list of riverine woody plants.

In the drier conditions, away from the Cubango, stretch vast fields of grass. Among the many different kinds to be seen, *Loudetia simplex* is the commonest. Trees are scarce and stunted. The only woody species best suited to this environment are rhizomatous suffrutices or shrublets with a large underground stock and several such plants occur here, eg, *Parinari capensis* and *Protea tricophylla.*

ZONE 2: THE "MIOMBO" ZONE

"Miombo" is a vernacular term widely applied in Central Africa to areas where *Brachystegia, Julbernardia* and similar trees predominate. This zone contains four main vegetation types, ranging from dry, deciduous forest through woodlands to wooded grasslands. Principal trees are:

Brachystegia spiciformis, B. bakerana, B. boehmii, Julbernardia paniculata, Pteleopsis anisoptera, Cryptosepalum pseudotaxus.

In the "Miombo," the Cubango soon becomes a river and descends a massive half-km in elevation — more than in all the other zones combined. A chain of rapids punctuate the whole of this part of its course and the bed is frequently strewn with boulders.

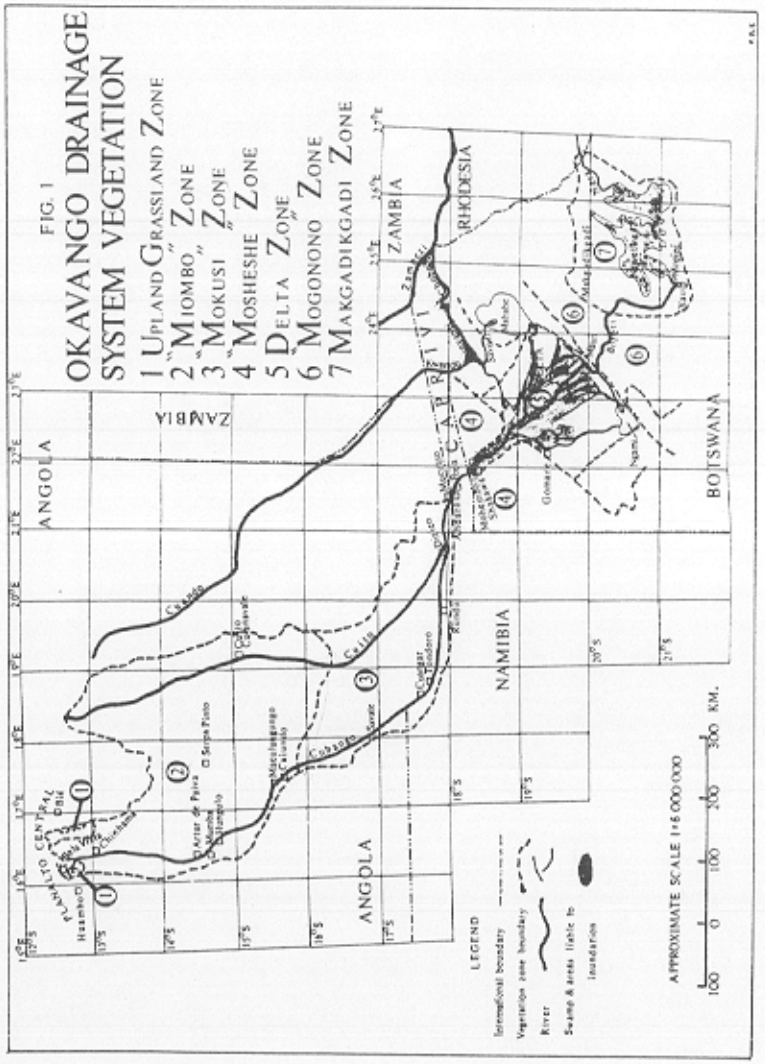
Almost from the start, *Phragmites mauritianus,* a reed, appears in a thin fringe at the riversides, together with another tall grass, *Pennisetum glaucocladum.* A river bank community develops around the *Phragmites* increasing downstreamwards and dominates wherever conditions are sandy enough. A typical profile is illustrated in Fig. 2. Associated plants in the reed bed (Section 1) are *Mikania cordata* (creeper) and other emergents: *Polygonum pulchrum, P. senegalense, Commelina macrospatha, Ethulia conyzoides* and *Kosteletzkya buettneri.* At Section 2, the pool, which is created only where allowed by the slope, contains water-lilies *(Nymphaea caerulea, N. lotus), Ludwigia stolonifera, Lagarosiphon ilicifolius, Sacciolepis africana* and *Oryza longistaminata.* The commonest plant in the pool is the legume with long-floating stems, *Aeschynomene fluitans.* In the upper reaches of the zone, where water levels are slightly more stable, ferns *(Cycloserus interruptus),* sedges *(Cyperus distans, Scirpus muricinux)* and *Floscopa glomerata* enter the pool. The three tall grasses at Sections 4, 5 and 7 usually grow in pure stands. *Vetiveria nigritana* is always at the highest watermark. The majority of plants in this community are adapted to withstand a wide fluctuation between minimum and maximum water levels, which, at the end of the zone, seems to be as much as 3 m. Floods are probably passed in waves and not sustained for long periods.

Swampy conditions are rare on the Cubango itself, but are frequently obtained at dams in the "mulolas" or minor-side drainages. Bullrushes *(Typha sp.), Limnophyton* and submerged *Najas, Ceratophyllum* and *Rotala spp.* are plentiful in the "mulolas," but rare on the main river.

FIG. 1

OKAVANGO DRAINAGE SYSTEM VEGETATION

1 UPLAND GRASSLAND ZONE
2 "MIOMBO" ZONE
3 "MOKUSI" ZONE
4 "MOSHESHE" ZONE
5 DELTA ZONE
6 "MOGONONO" ZONE
7 MAKGADIKGADI ZONE



Swift currents at the rapids establish a niche for some highly-specialised aquatic rock flora *(Podostemaceae* and *Hydrostachyaceae).* Elsewhere in the riverbed, no other aquatics are able to survive, except at the banks, as already described.

Riverine woodlands in the Cubango are sparse in this zone, but trees are numerous locally at the rapids. Bands of *Syzygium guineense spp. barotsense* line some of the lower reaches. Other woody species encountered are:

> *Syzygium benguellense, S. cordatum, Phoenix reclinata, Antidesma venosum, Rhus quartiniana, Neorosea andongensis, Tarenna gossweileri, Croton pyrifolius, Salix subserrata* and *Bequaertiodendron magalismontanum* — all trees; *Ficus pygmaea, Myrica serrata* — shrubs and *Canthium henriquesianum,* a liane.

The Cuito River rises in the north-east part of the "Miombo" zone, but, unfortunately, little information is obtainable on this and most of the other large tributaries.

ZONE 3: (MOKUSI) AND THE NAMIBIAN SECTION

At 16°S latitude, the Cubango flows into the Kalahari sand area, and an alab dunefield, which extends south as far as the shoulders and western flank of the Delta. "Omuramba," or fossil drainages, lie in some interdunal depressions. The main vegetation types for the mokusi and mosheshe zones (and the Namibian section) are so similar, that they can all be treated together. Trees on the dunes are *Baikiaea plurijuga* (mokusi), *Burkea africana* (mosheshe), *Guibortia coleosperma, Pterocarpus angolensis, Pseudolachnostylis maprouneifolia, Erythrophloeum africanum, Dialium engleranum* and *Combretum psidioides.* In the northern parts, mokusi is dominant, and in the southern parts, mosheshe dominates — probably the result of differences in rainfall.

The *Phragmites* community outlined earlier carries on here too, and, in fact, well into the Delta. Along the line, a few extra plants join in: *Mimosa pigra, Echinochloa stagnina, Sesbania cinerascens, Aeschynomene nilotica* and *Ipomoea rubens.* After Dirico, competition is faced with papyrus, which is reported to be very prevalent in the lower Cuito Valley. The link between the Cuito and panhandle papyrus populations is tenuous, however, and is only maintained as a sporadic fringe fronting the reedbeds.

Swamp development on the Cubango begins near Tondoro, where the river changes course eastwards, and meandering increases. Initially, it is confined to small sites at backwaters, omuramba and tributary junctions. Between Mucusso and Popa Falls, a large outcrop of quartzite crosses the river's path, forcing it into wildly-braided channels between wooded islands. In places, e.g. at Andara, parts of this rocky barrier act as weirs, sufficiently stabilising water levels to permit growth of ferns, sedges and other swamp aquatics at the sides.

Between Tondoro and Andara, many of the riverine trees so familiar in the Delta make their debut near the Cubango, such as *Diospyros mespiliformis, Garcinia livingstonei, Hyphaene palm, Kigelia pinnata, Sclerocarya caffra, Acacia nigrescens, Ficus sycomorus* and *F. burkei.* Closer to the water's edge, *Syzygium guineense spp., barotsense* and *Phoenix* palm are the species mostly seen at the few sites favourable for tree growth.

Grasslands and wooded terraces separate the river from the mainland proper, in a valley which is consistently narrow until broadening appreciably at Tondoro. Groves of mongongo *(Ricinodendron rautanenii)* are notable at the mainland ecotones with the highest terraces. In the rest of the valley, trees and bushes of *Combretaceae* and *Mimosoideae (Leguminosae)* families are commonest.

ZONE 5: PANHANDLE AND DELTA

Soon after crossing the international boundary, the Okavango enters a complex of perennial and seasonal swamp and floodplain. The perennial swamps are always

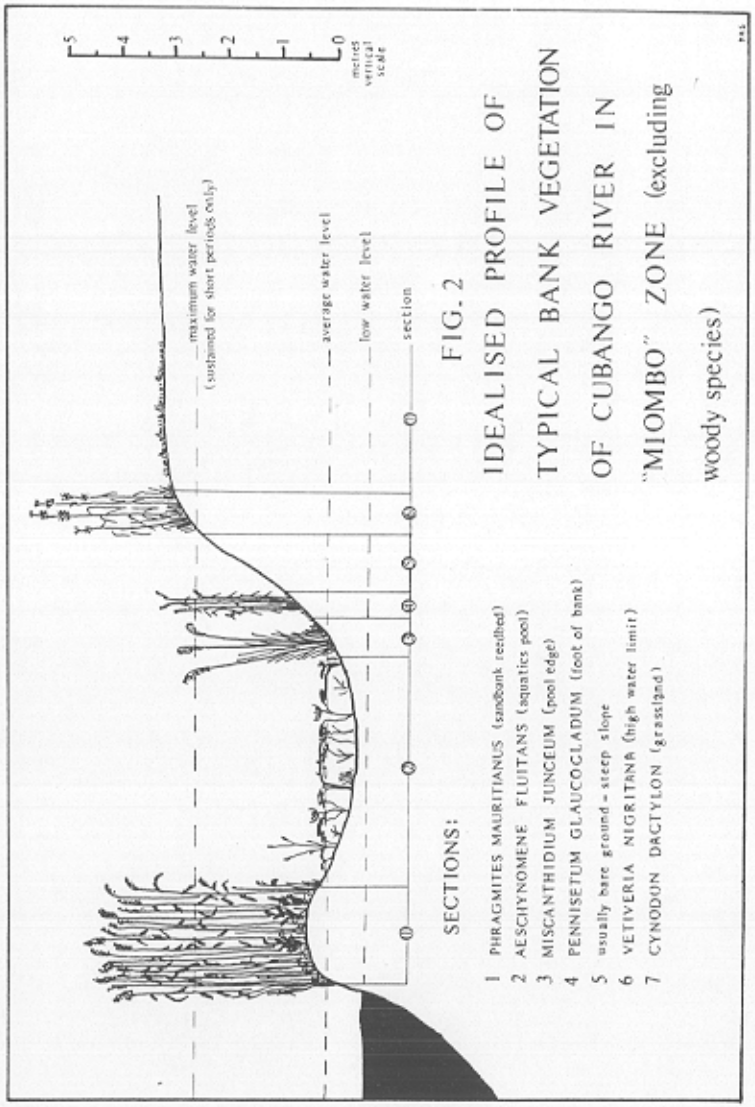


FIG. 2

IDEALISED PROFILE OF TYPICAL BANK VEGETATION OF CUBANGO RIVER IN "MIOMBO" ZONE (excluding woody species)

under water and never dry out. At the other extreme, the floodplains are areas liable to inundation, which, when flooded, remain so only for part of a year at a time. Seasonal swamps are the intermediate category. Lists of plants found in, or close to, these wetlands in the panhandle and Delta are given in Tables 1-5.

The *Phragmites mauritianus* community, after having dominated more than 1 000 km of riverbank, is ousted by papyrus in the upper parts of the panhandle. The outer sections become widely dispersed; *Vetiveria* now marks the limits of the seasonal swamp, but is rare and confined to the upper Delta and panhandle. *Miscanthidium* soon becomes a major dominant in its own right. *Aeschynomene fluitans* switches to a channel-liner in the lower perennial swamp. Although thus shorn, reedbeds persist along the Okavango/Nqogha banks, but cease to be very noticeable beyond the Boro junction. Relict patches survive on the Thaoge as far as Seokgwe.

Perennial swamp

There are five important communities in the perennial swamp: papyrus in the deeper waters, *Miscanthidium* in the shallow-flooded sites, and between these two, another species of reed, *Phragmites australis,* bullrush *(Typha latifolia spp. capensis)* and *Pycreus* communities occur.

Papyrus is a giant sedge, producing leafless culms (or stems), 4 m tall from perennial rhizomes. It grows so quickly — culms are replaced every three months — and so densely, that rhizomes get entangled and form a mat. New plants pile on top of old and mats thicken with their own debris and sediments trapped from the water. They can build up to such an extent on banks, that channel-flow is raised to a higher level than in the swamp alongside. Insofar as rhizome-ends in the upper layers and at the edges can move freely beyond the grip of this mat, the latter can be said to be floating. On the whole, however, mats are usually so compact and heavy, that they remain firmly lodged on top of the substrate.

Papyrus beds occupy bands of varying width beside major channels to the limits shown in Fig. 3. The greatest expanses are in the lower panhandle and above the Nqogha blockage. Towards the downstream limits on open rivers, mats attenuate into fringes and culms reduce to 1-2 m before the plant disappears completely. On moribund rivers (eg, Thaoge above Gomare, Gomoti), papyrus chokes the riverbed solidly, but does not spread onto the banks or beyond. Elsewhere in the swamp, it is found in circular patches at the edges of its distribution.

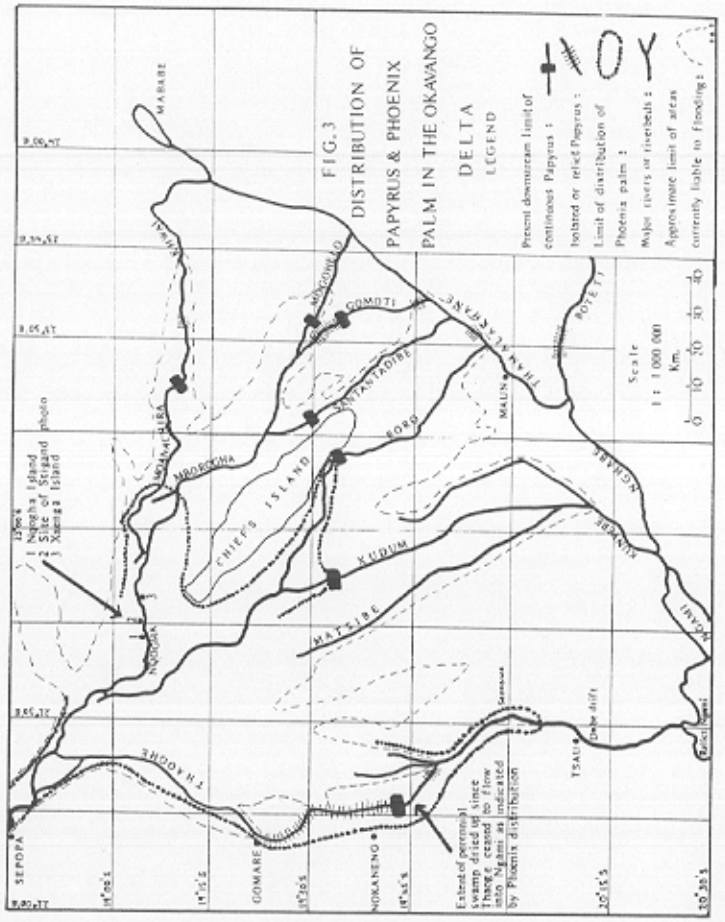
Although sometimes growing in pure stands, papyrus beds often contain varying admixtures of competitor plants (e.g., reeds, *Miscanthidium,* bullrush). Among a large number of smaller associates, the more plentiful species are a fern (e.g., *Cyclosorus interruptus), Polygonum pulchrum* and various *Commelinaceae.*

Papyrus is restricted to low-conductivity waters — not exceeding 45-60 micromhos/cm^{-1}, except in moribund and abandoned channels. Waters emerging from its swamps are much less turbid than those entering them. These facts suggest that papyrus plays an important role in the treatment of suspended solids.

Although able to tolerate a wide range of hydrological regimes, papyrus is best developed in perennial waters that vary little between minimum and maximum levels. It is a good indicator of perennial swamp, but does not occupy all the deeper waters therein. A possible explanation for this is that Okavango papyrus appears to reproduce only vegetatively, because seedlings have not yet been found in the Delta. This may limit its ability to expand, except along channels.

Perennial and seasonal swamp

The other perennial swamp-dominants also extend far into the regularly-inundated parts of the seasonal swamp. *Phragmites australis* reedbeds grow best in



sluggish waters of medium depth, and are prominent around madiba edges and at channel-sides away from the papyrus area. They are particularly noticeable on the Thamalakane between the Santantadibe and Boro junctions, and alongside the moribund Thaoge. Less obvious, but more extensively distributed, are areas in which individual plants are widely separated from each other in fairly open waters. At 5 m, this reed is the tallest of the swamp herbaceous plants, and it has the deepest and toughest root system.

Miscanthidium is scarce in the panhandle near the Okavango, but large fields start to vie with papyrus on the Nqogha. They become a serious challenge on the Moanachira, where they ultimately take over almost completely. At its prime expression, this grass, 3¾ m high, grows in densely-packed tussocks and is almost impossible to walk through. It has long, spike-like, cylindrical leaves. Beyond the open waters behind papyrus, a reticulated pattern of *Miscanthidium* "ribbons" suggest that it colonises deposits of sediments trickling through from the Nqogha. It enjoys a very wide distribution throughout the Delta, and is usually found in pure stands, except at channel-sides.

Bulrushes are the least abundant of the taller dominants, but are common locally around madiba and pools, channel corners and backwaters. They flourish mostly in the "middle" swamps where beds line reaches of the lower Moanachira and Boro Rivers and the Santantadibe.

Open-water communities are very varied, but feature in both perennial and seasonal swamp. In the former, mats of short sedges float among open waters vegetated by submerged or floating-leaved aquatics. The sedge *Pycreus nitidus* best typifies this community. Other sedges, eg, *Cyperus nudicaulis, Scirpus cubensis* and a grass, *Leersia friesii,* also float in mats, which are often colonised by a small insectivorous plant, *Drosera madagascariensis.* Among the aquatics, *Brasenia schreberi* and *Nymphaea caerulea* are the commonest floating-leaved plants, and underneath, submerged *Najas pectinata, Ceratophyllum demersum* and *Lagarosiphon ilicifolius* grow in patches. A thick layer of plant detritus is found on the bed in this community, and when disturbed, releases gas-bubbles. Thinly present are rooted emergents: reed, bulrush, other sedges, particularly *Eleocharis spp.* and grasses *(Sacciolepis spp.* and *Eriochrysis pallida).* Clods of peat-like matter can be seen at the surface in places, and they are utilised by *Xyris* and *Utricularia spp.*

When intergrading into its seasonal swamp-form, this open-water community loses many of the species noted above. *Nymphaea caerulea* becomes the more abundant plant. Floating sedge and grass mats are replaced in the shallower waters by emergent plants, notably *Panicum repens, Oryza longistaminata, Leersia hexandra* (grasses), *Rhynchospora, Fimbristylis* and *Fuirena spp.* (sedges). The submerged plants are restricted to only the deepest parts of the seasonal swamp. Floating-leaved aquatics, besides the *Nymphaea,* now include more *Potamogeton thunbergii, Nymphoides indica* and *Caldesia reniformis.* The emergent sedges, *Eleocharis,* continue to be an important element.

Ficus verruculosa, a shrubby tree, is widespread on sites slightly elevated above water level in the lower perennial and regularly-inundated seasonal swamps. It is also abundant in a variety of smaller sizes.

In the remaining drier parts of the seasonal swamp, two sedges, *Scirpus inclinatus* and *Cyperus articulatis,* are overwhelmingly dominant at most sites. Besides being conspicuous in the open-water communities, together or singly, they form vast sedgefields throughout the Delta. They are very similar in appearance and height (range 1-2 m), both having leafless, cylindrical, dark-green culms with small inflorescences at the tip. This community, dubbed "Sica," has many associates — especially *Cyperus longus, C. denudatus* and *Panicum repens,* but the extent to which they accompany the dominants varies considerably. Many "Sica" fields on the periphery

of the seasonal swamp are very dense and stands are correspondingly pure. As the space between individual plants widens, so the community becomes more diverse.

Floodplains

Floodplains are mostly grasslands and border all island and mainland edges with the swamps. While they occur mostly beyond the seasonal swamp, some floodplains commence directly from rivers or perennial swamp — especially in the panhandle. The wettest types are covered by *Vossia, Echinochloa, Leersia, Oryza, Acroceras* and *Paspalum spp.* The driest have either a lawn-cover *(Cynodon dactylon)* or terraces of such tall *spp.* as *Hyparrhenia rufa* and *Cymbopogon excavatus.* Bordering the perennial swamp, a "red band" is common and includes *Andropogon, Sorghastrum* and *Eulalia spp.* Following at higher ground, dense swards of *Imperata cylindrica* are found. The sandier, well-watered floodplains are dominated by *Eragrostis inamoena, E. lappula, Setaria angustifolia* and *Trachypogon spicatus.* Saline soils are indicated by *Sporobolus spicatus, S. tenellus* and a sedge, *Cyperus laevigatus.* Broad-ranging floodplain grasses are *Setaria anceps* and *Chloris gayana.*

Rivers, melapo and watercourses

As in the Angolan and Namibian sections, the major rivers in the upper Delta and panhandle are largely devoid of bed vegetation. Aquatics there are restricted to sides, sheltered bays and corner sandbanks. Deep sites are sought by *Eichhornia natans, Potamogeton octandrus, Nymphaea lotus* and *Ceratophyllum, Najas* and *Lagarosiphon spp.* Cut-off river sections are filled with *Trapa natans.* Throughout both the perennial and seasonal swamps, *Vossia cuspidata,* a floating grass, and *Nymphaea caerulea* are ubiquitous at channel-sides.

As soon as waters become clearer and velocities reduced in the lower papyrus areas, the following submerged aquatics begin to invade riverbeds:

> *Rotala myriophylloides, Nesaea crassicaulis, Ottelia ulvifolia, O. muricata, Limnophilia ceratophylloides* and *Wiesneria schweinfurthii.*

Rotala beds, especially, dominate seasonal melapo, giving way only to *Limnophila* at shallower reaches and occasionally to *Wiesneria.* Some melapo are so broad, the vegetation becomes more a modified version of the swampy, open-water communities, with water-lilies, *Nymphoides* and *Potamogeton thunbergii* particularly to the fore.

In ephemeral watercourses, such as the lower Thaoge and Mogohelo Rivers, emergents, such as *Polygonum,* flourish more than any other type.

The major factors governing riverbed aquatics are clearly: current velocity, water depth, turbidity (light penetration) and water level fluctuation.

Madiba

In the open waters of large madiba, where waves prevent growth of floating-leaved plants, masses of *Najas* and *Lagarosiphon* colonise the bed to depths of 3 m and more. At the sides, water-lilies, *Trapa, Eleocharis* and "Sica" bands shield open-water and bank communities similar to those already described. The smaller madiba are usually smothered by water-lilies.

Islands and mainland edges

Island and mainland boundaries with floodplains are usually marked by a tree-line (or by other woody plants). Trees which are widely distributed throughout the Delta and panhandle comprise most of those listed in Table 1 (i) (c), and they can be ranked fairly predictably according to their preferences for water supply, eg,

Lonchocarpus capassa, which has a relatively small demand, appears infrequently and then only on the highest elevations of islands in the perennial swamp, but is very common in the drier seasonal swamp islands. Many islands in the perennial and wetter seasonal swamps have a thick riparian woodland, which, in a few places, is developed into forest, but their composition is usually very mixed, except that *Hyphaene* palm and *Acacia nigrescens* often occur in pure stands. *Phoenix* palm and the hybrid *Syzygium* are found exclusively within the perennial swamp, except in relict areas. *Ficus verruculosa* and *Vernonia amygdalina* (a shrub) characterise the lower perennial and wetter seasonal swamp island edges. *Rhus, Combretum, Maytenus* and *Diospyros* shrubs and herbs of *Amaranthaceae* and *Acanthaceae* are common in the understorey.

Termitaria feature throughout the Delta and are particularly common in the seasonal swamp and floodplains. They often carry much woody vegetation, including, especially, the small tree *Euclea divinorum* and climbing shrub *Capparis tomentosa.*

Mainland

Relicts of a former, more extensive swamp system are obvious in the whole of the Delta mainland (including the centres of large island masses). The main vegetation type is a mosaic of grassland, woodland and wooded (tree/shrub) grassland. Principal genera are:

Trees: *Acacia, Boscia, Colophospermum, Combretum, Lonchocarpus, Terminalia* and *Ziziphus.*

Shrubs: *Acacia, Dichrostachys, Grewia, Rhus, Ximenia, Maytenus* and shrub-forms of trees listed above.

Grasses: *Aristida, Cenchrus, Digitaria, Schmidtia, Stipagrostis* and *Urochloa.*

ZONE 6: (MOGONONO) AND THE BOTETI RIVER

This is a zone of wooded (tree/shrub) grassland, and two types of dunes constitute the landform: transverse, hummocky dunes and longitudinal dunes about 200 m apart. Mogonono *(Terminalia sericea),* both as a tree or shrub, dominates the sandier dune crests and *Acacias,* the bases. Other plants are mosheshe, *Peltophorum, Combretum, Lonchocarpus, Croton, Boscia* — trees, *Rhus, Grewia, Acacia, Ximenia, Croton, Bauhinia* and *Commiphora* — shrubs, and *Aristida, Eragrostis, Anthephora* and *Triraphis* — grasses.

The Boteti section contains only riverine-type vegetation and swamps are absent. The dominant riverbank community is *Phragmites australis,* and large reedbeds are common in the upper reaches, especially just below the Thamalakane junction and near Chanogha. In the lower reaches they become sparser, but revive again in full force to surround "Lake" Xau. "Sica" and bulrush communities are also present, but *Miscanthidium* is absent. A small, relict papyrus fringe lines the river below Samadupe Bridge. The riverbed vegetation is similar to the Delta seasonal swamp channels.

Acacia tortilis lower terraces are prominent alongside the river in the upper reaches. Higher terraces here have a dense *Sansevieria deserti* storey under an erratically-developed riparian woodland. Isolated, individual *Diospyros mespiliformis, Garcinia livingstonei* and *Kigelia pinnata* are seen, but riverine trees are mostly *Acacia spp., Combretum imberbe, Cassine transvaalensis, Terminalia sericea, Lonchocarpus capassa* and *Ziziphus mucronata.* Below Bushman Pits and near Khumaga, the tree-line is very thin, and only a few tall specimens are interspersed between dense thorn thickets of *Acacia* and *Dichrostachys* — vegetation induced by livestock overgrazing.

ZONE 7: MAKGADIKGADI DEPRESSION

The natural outlet of the Boteti is into Ntwetwe Pan, which is linked to Sua Pan. The latter is more strictly part of the eastern Makgadikgadi drainage system, formed by the Nata, Semowane, Mosetse, Lepashe and Mosupa Rivers. The eastern Makgadikgadi drainage is the only other actively-operating system in the Kalahari Basin, but cannot be considered as part of the Okavango, although they share the same terminal sink.

Ntwetwe Pan is too saline to support any vegetation at all. It is encircled by a semi-desert plant community of *Sporobolus* and *Odyssea paucinervis* grasses and a succulent *Suaeda plumosa.* These, in turn, give way to higher ground of fringing dunes covered by *Cynodon* lawn grasses. Small, damp depressions among the dunes contain reed *(Phragmites australis),* a sedge *(Scirpus maritimus)* and an aquatic *Alternanthera* with *Dichanthium* and *Panicum* grasses. The main and more extensive Pan border behind the dunes is grassland in which, again, *Sporobolus* and *Odyssea* grasses are common, together with *Aristida, Cymbopogon, Chrysopogon, Eragrostis, Cenchrus* and *Schmidtia spp.* Scattered tree-clumps occur on raised hummocks where baobab, *Acacia, Terminalia, Albizia* trees and *Hyphaene* palms grow.

Outline of vegetation: summary

The Okavango dryland area contains a wide spectrum of vegetation types, ranging from semi-desert, halophytic and upland grasslands of edaphic formation, to grasslands, bush, scrub, thicket, woodlands and forests of climatic formation. In the wetland part of the system, there are relatively stable riverine communities on the one hand, and unstable, perennial and seasonal swamp floodplain and ephemeral watercourse types on the other. The significant feature in the wetland group is the predominance of the reed genus *Phragmites,* over almost three-quarters of the total 1 727 km length of the principal river. It is only in the Delta that this pattern of uniformity is broken. Gradient alone cannot be blamed, because the Boteti has a flatter slope than the Delta. Obviously, the topography or landform is primarily responsible, because the Delta is the only zone lacking a sufficiently incised valley to keep the system's flow within narrow limits. The absence of high banks in the Delta prevents an orderly transition between the two different reed species. In the swamps which result in the interval, papyrus is the dominant plant initially. Rivers associated with papyrus are known to have very erratic flow regimes, which have caused disruptions throughout the Delta ecosystem. The question of whether these changes have been brought about by papyrus itself, by sediment transport problems, by seismicity or by any other cause, awaits further investigation. The effect of these changes on plant communities is evidenced by many anomalies in their patterns of distribution. To sort them out requires knowledge of the history of their environment and such information is sometimes difficult to obtain for the Delta, especially its interior regions.

"Indicator plants"

Certain plants have very specific requirements which make them useful indicators of a narrow range of environmental factors. *Phoenix* palm and papyrus thrive and multiply only where a permanently-high water table exists. This condition can only be met in the semi-arid climate of the Delta by perennial swamp. Established plants will survive subsequent dessication for a limited period, but for so long as they are able to live in a changed environment, they provide proof of the former existence of perennial swamp conditions. Papyrus, being an herbaceous plant, responds more quickly to changes than *Phoenix,* a woody plant.

Distribution of *Phoenix* and papyrus

The areas presently occupied by these plants are illustrated in Fig. 3. The Thaoge River used to flow into Lake Ngami until c.1884. Perennial swamps used to extend to at least as far south as Dobe Drift, but have now retreated to above Gomare. These facts are well known, but using the *Phoenix* line as a guide, Fig. 3 shows that perennial swamps on the Thaoge achieved a greater degree of consolidation than is apparent elsewhere in the Delta today.

On the Boro and Xudum Rivers, *Phoenix* and papyrus have reached the same limits of distribution, suggesting that perennial swamp expansion beyond these points has been halted for some time — enabling the slower palm to catch up with the sedge. This idea is corroborated by the fact that Ellenberger, in his 1931 survey, found that papyrus on the Boro was limited to the same area in which it is found today.

The situation in the Nqogha network is very interesting, because papyrus has far outstripped the *Phoenix* line along all its outlets. A photograph taken by Stigand (1923) of an island on the Nqogha, shows one small clump of short *Phoenix* and a *Miscanthidium* bank. Today, that island-front is a mass of tall *Phoenix* with such a thick papyrus fringe, it is almost impossible to get onto the beach. It is obvious that perennial swamp consolidation in this region has only begun during this century. Stigand was informed by local residents that the Nqogha was merely a shallow molapo, while the Thaoge was a major river.

The changes in regimes on papyrus-lined rivers previously referred to, are associated on the Thaoge and Nqogha, with papyrus debris blockages, but, as already intimated, the causes of change are, as yet, not well understood. It would seem that the Nqogha blockage upstream of the Mborogha junction is responsible for the over-extension of papyrus on the Gomoti, and its conversion from a major outlet to a moribund river. The Nqogha blockage is now threatening the supply of the Moanachira River. It is considered that the key to an understanding of most of the changes occurring in the Delta today, lies within the investigation of the causes of blockages.

TABLE 1

Trees of the Delta and panhandle: riverine and swamp areas, floodplain and island/mainland edges

1. **Found *mostly* at island edges within the perennial and seasonal swamps**

(a) **Semi-aquatic: perennial swamps only:**

Ekebergia capensis
Phoenix reclinata
Rhus quartiniana var. quartiniana
Syzygium guineense × cordatum (hybrid)

(b) **Semi-aquatic: perennial and seasonal swamps**

Ficus verruculosa

(c) **Other**

Acacia galpinii
Acacia nigrescens
Albizia versicolour
Berchemia discolor
Cassine transvaalensis
Diospyros mespiliformis
Ficus sycomorus
Hyphaene beguellensis var. ventricosa
Lonchocarpus capassa
Acacia karroo
Albizia harveyi
Antidesma venosum
Carissa edulis
Croton megalobotrys
Ficus burkei
Garcinia livingstonei
Kigelia pinnata
Sclerocarya caffra

2. **Found *mostly* at floodplain-edges with the mainland**

Acacia erioloba (giraffae)
Acacia hebeclada
Acacia sieberana var. woodii
Colophospermum mopane
Gardenia spatulifolia
Zizyphus mucronata
Acacia fleckii
Acacia tortilis spp. heterecantha and *spp. spirocarpa*
Combretum imberbe
Terminalia sericea

3. **Found at miscellaneous sites**

Acacia leuderitzii
Boscia albitrunca
Commiphora sp.
Lonchocarpus nelsii
Adansonia digitata
Combretum hereroense
Euclea divinorum
Peltophorum africanum

4. **Found very rarely**

Burkea africana
Combretum apiculatum
Euphorbia ingens
Lannea stuhlmannii var tomentosa
Olax dissitiflora
Pterocarpus angolensis
Cassine matabelica
Combretum zeyheri
Kirkia acuminata
Ochna Pulchra
Piliostigma thonningii
Ricinodendron rautanenii

5. **Found *only* in the upper panhandle**

Acacia albida (islands)
Cassine aethiopica (islands and mainland-edge)
Syzygium guineense ssp. barotsense (semi-aquatic)
Acacia hebeclada ssp. chobiensis (islands)
Rhus quartiniana var. zambesica (islands)

Note:

(a) At Sections (1(c) and 2) it is emphasised that some trees listed as occurring mostly at island edges were often at floodplain edges and *vice versa.*

(b) Some of the ssp. listed at 2, 3 and 4 are mainland "strays."

TABLE 2

Shrubs and other woody *ssp.* of the Delta and panhandle: riverine and swamp area, floodplain and island/mainland-edges

1. **Semi-aquatic or aquatic**

Ficus capreifolia
Hibiscus diversifolius ssp. rivularis
Rubus exsuccus
Ficus fygmaea
Myrica serrata
Tacazzea apiculata

2. **Island and mainland-edges**

Bauhinia macrantha
Combretum albopunctatum
Commiphora africana var. rubriflora
Capparis tomentosa
Diospyros lycioides
Ehretia coerulea
Grewia bicolor
Grewia flavenscens
Lantana angolensis
Maytenus heterophylla
Pavetta lasiopeplus
Plumbago zeylanica
Rhus tenuinervis
Tricalysia allenii
Vernonia amygdalina
Ximenia americana
Boscia mossambicensis
Combretum sp.
Cordia ovalis
Dichrostachys cinerea
Ehretia amoena
Flacourtia indica
Grewia flava
Grewia schinzii
Markhamia acuminata
Maytenus senegalensis
Phyllanthus reticulatus
Rhus pyroides var. gracilis
Securinega virosa
Vangueria infausta
Ximenia caffra

3. **Creepers and lianes**

Clematis brachiata
Cocculus hirsutus
Cynanchum schistoglossum
Gymnema sylvestre
Jasminum fluminense
Rhoicissus tridentata
Clematopsis scabiosifolia
Combretum mossambicensis
Gongrothamnus divaricatus
Hippocratea africana var. richardiana
Pergularia daemii
Sarcostemma viminale

4. **Upper panhandle only**

Canthium huillense (climber)
Mimosa pigra (aquatic)
Pavetta assimilis (shrub)
Citropsis daweana (shrub)
Oncoba spinosa (shrub)

TABLE 3

Aquatic herbs and ferns of the Delta and panhandle: riverine and swamp area and floodplains (excluding "pan" species, grasses and sedges)

1. **Free-floating: leaves on or above surface**

Azolla pinnata var. africana
Lemna sp. (?trisulca)
(Ricciocarpus natans (Liverwort))
Lemna perpusilla
Spirodela polyrhiza

2. **Free-floating: Submerged**

Aldrovanda vesiculosa
Utricularia foliosa
Utricularia reflexa var. reflexa
Utricularia benjaminiana
Utricularia inflexa
Utricularia stellaris

Partly emergent:

Utricularia arenaria
Utricularia gibba ssp. gibba and *ssp. exoleta*
Utricularia subulata
Utricularia scandens
(Chara and *Nitella spp. (algae))*

3. **Rooted: submerged**

Ceratopteris thalictroides (also emergent)
Ceratophyllum demersum (also free-floating below surface)
Eichhornia natans
Limnophila ceratophylloides
Najas pectinata
Ottelia kunenensis
Ottelia ulvifolia
Rotala myriopylloides
Wiesneria schweinfurthii
Lagarosiphon ilicifolius
Limnophila indica
Nesaea crassicaulis
Ottelia muricata
Potamogeton trichoides
Vallisneria aethiopica

4. **Rooted: Floating-leaved**

Brasenia schreberi
Nymphaea lotus
Nyphoides brevipedicellata
Nymphoides thunbergiana
Potamogeton thunbergii
Caldesia reniformis
Nymphaea caerulea
Nymphoides indica
Potamogeton schweinfurthii
Trapa natans var. bispinosa

5. **Rooted: Floating-stemmed**

Aeschynomene fluitans
Ipomoea aquatica

6. **Rooted: Emergent**

Adenostemma caffrum
Alternanthera sessilis
Ammannia prieuriana
Caperonia serrata
Commelina diffusa
Commelina macrospatha
Crassocephalum picridifolium
Drosera madagascariensis
Eulophia latilabris
Floscopa glomerata
Habernaria schimperana
Hygrophila prunelloides
Limnophyton angolense
Ludwigia abyssinica
Ludwigia leptocarpa
Ludwigia palustris
Melanthera scandens ssp. madagascariensis
Oldenlandia lancifolia
Alternanthera nodiflora
Ammannia baccifera
Burnatia enneandra
Centella asiatica
Commelina fluviatilis
Commelina zambesica
Cyclosorus interruptus
Ethulia conyzoides
Eulophia sp.
Haberaria filicornis
Hydrocotyle verticillata
Kosteletzkya buettnen
Lauembergia repens ssp brachypoda
Ludwigia erecta
Ludwigia octovalvis ssp. brevisepala
Ludwigia stolonifera
Microlepia speluncа
Pentodon pentander

Polygonum limbatum
Polygonum salicifolium
Polygonum strigosum
Rhamphicarpa fistulosa
Senecio strictifolius
Torenia thouarsii
Xyris capensis
Xyris straminea

Polygonum pulchrum
Polygonum senegalensis
Pycnostachys coerulea
Senecio leptocephalus
Typha latifolia ssp. capensis
Thelypteris confluens
Xyris rehmannii

7. **Semi-woody**

Aeschynomene cristata var. cristata
Sesbania cinerascens
Sesbania microphylla

Aeschynomene indica
Sesbania bispinosa var. bispinosa
Sesbania rostrata

8. **Creepers**

Cassytha filiformis
Cuscuta capestris
Ipomoea rubens
Vigna luteola

Cissampelos mucronata
Cuscuta australis
Mikania cordata

TABLE 4

Grasses and sedges of the Delta and panhandle: Riverine and swamp areas, floodplain and island/mainland-edges

1. **Found in perennial swamps**

Grasses

Panicum hymeniochilum

Sedges

Cyperus papyrus
Websteria confervoides

2. **Found in perennial and seasonal swamps**

Grasses

Diplachne gigantea

Echinochloa stagnina
Leersia friesii
Panicum parvifolium
Panicum subalbidum
Paspalum scrobiculatum
Phragmites australis
Sacciolepsis africana
Vossia cuspidata

Echinochloa holubii (? pyramidalis)
Eriochrysis pallida
Leersia hexandra
Panicum repens
Paspalidium platyrrhachis
Pennisetum glaucocladum
Phragmites mauritianus
Sacciolepsis typhura

Sedges

Carex cognata
Cyperus articulatus
Cyperus digitatus ssp. auricomus
Cyperus nudicaulis
Eleocharis acutangula
Fimbristylis companata
Fuirena stricta
Pycreus mundtii
Pycreus polystachyos
Scirpus cubensis

Cladium mariscus ssp. jamaicense

Cyperus denudatus var. denudatus
Cyperus papyrus
Eleocharis dulcis
Fuirena pubescens
Fuirena umbellata
Pycreus nitidus
Rhynchospora africana
Scirpus inclinatus

3. **Found in seasonal swamps and floodplains**

Grasses

Acroceras macrum
Andropogon huillensis

Brachiaria dura
Brachiaria rugulosa
Cymbopogon excavatus
Digitaria eylesii
Eragrostis lappula
Eragrostis sarmentosa
Eulalia geniculata
Hyparrhenia rufa
Panicum coloratum
Setaria anceps
Setaria sphacelata
Sorghastrum friesii
Sporobolus ioclados
Sporobolus tenellus
Trichoneura grandiglumis

Andropogon eucomus
Aristida junciformis ssp. welwitschii
Brachiaria humidicola
Chloris gayana
Digitaria debilis
Eragrostis inamoena
Eragrostis namequensis
Eragrostis stapfii
Hemarthria altissima
Imperata cylindrica
Panicum dregeanum
Setaria angustifolia
Sorghum verticilliflorum
Sporobolus africanus
Sporobolus spicatus
Trachypogon spicatus
Vetiveria nigritana

Sedges

Cyperus alopecuroides
Cyperus dives

Cyperus imbricatus
Cyperus longus
Cyperus maculatus

Eleocharis atropurpureus
Eleocharis marginulata
Eleocharis variegata
Fimbristylis dichotoma
Fimbristylis bisumbellata
Kyllinga erecta var. erecta
Kyllinga erecta var. intricata
Pycreus aethiops
Pycreus unioloides
Rynchospora perrieri

Cyperus compressus
Cyperus denudatus var. sphaerospermum
Cyperus laevigatus
Cyperus longus var. tenuiflorus
Cyperus muvinilungensis var. muvinilungensis
Eleocharis intricata
Eleocharis nigrescens
Fimbristylis sp.
Fimbristylis squarrosa
Fuirena ciliaris

Lipocarpha atra
Pycreus flavescens
Rhynchospora holoschoenoides
Scirpus isolepsis

Scirpus maritimus
Scirpus uninodis
Scleria flexuosa
Scleria sp.
Scirpus sp.
Scleria dregeana
Scleria melanomphala

4. Found in floodplains and islands

Grasses

Aristida meridionalis
Bothriochloa insculpta
Dactyloctenium aegyptium
Digitaria eriantha
Eragrostis rigidior
Eragrostis viscosa
Hyperthelia dissoluta
Stipagrostis uniplumis
Aristida pilgeri
Cynodon dactylon
Dactyloctenium giganteum
Eragrostis pallens
Eragrostis tricophora
Heteropogon contortus
Schizachyrium jefferysii

Sedges

Bulbostylis barbata
Cyperus amabilis
Cyperus fulgens
Cyperus rotundus
Fimbristylis hispidula
Mariscus hamulosus
Mariscus laxiflorus
Scirpus muricinux
Bulbostylis burchellii
Cyperus esculentus
Cyperus margaritaceus
Cyperus zollingeri
Kyllinga alba
Mariscus squarrosus
Pycreus macrostachyus

5. Found on islands (including "pans")

Grasses

Andropogon gayanus
Aristida stipitata ssp. stipitata
Brachiaria deflexa
Chloris virgata
Cymbosetaria sagittifolia
Digitaria perrottetii
Diplachne fusca
Elymandra grallata
Enteropogon macrostachyos
Eragrostis cilianensis
Eragrostis superba
Oplismenus burmannii
Panicum maximum
Pogonarthria squarrosa
Schmidtia kalahariensis
Setaria pallidefusca
Sporobolus fimbriatus
Sporobolus natalensis
Stipagrostis hirtigluma ssp. patula
Tragus racemosus
Urochloa trichopus
Aristida adscensionis
Aristida congesta
Brachiaria nigropedata
Cenchrus ciliaris
Digitaria milanjiana
Digitaria velutina
Echinochloa colonum (? frumentacea)
Enneapogon cenchroides
Eragrostis aspera
Eragrostis echinochloidea
Leptocarydion vulpiastrum
Panicum kalaharense
Perotis patens
Rhynchelytrum repens
Schmidtia pappophoroides
Setaria verticillata
Sporobolus macranthelus
Sporobolus pyramidalis

Tragus berteronianus
Urochloa mossambicensis

Sedges

Cyperus difformis
Mariscus dubius
Pycreus pelophilus
Scirpus articulatis
Mariscus assimilis
Pycreus chrysanthus
Pycreus pumilus
Scirpus jacobii

TABLE 5

Herbs of the Delta and panhandle: floodplains and island/mainland-edges (other than grasses, sedges and aquatics) (genera only)

Islands/mainland-edges

Abutilon
Acalypha
Aerva
Asparagus
Blepharis
Bidens
Cassia
Crotalaria
Cyphostemma
Desmodium
Glycine
Hemizygia
Hoslundia
Hypoestes
Justicia
Leonotis
Lablab
Momordica
Ocimum
Pluchea
Ruellia
Sansevieria
Triumfetta
Wissadula
Achyranthes
Acrotome
Aloe
Barleria
Blumea
Borreria
Commicarpus
Cardiospermum
Diclipteris
Gloriosa
Haemanthus
Hibiscus
Hydnora
Indigofera
Kedrostis
Lupiniphyllum
Monechma
Nelsonia
Peristrophe
Pupalia
Ruspolia
Tragia
Urginea
Zehneria

Floodplains

Acanthosicyos
Bergia
Buchnera
Chenopodium
Conyza
Craterostigma
Crotalaria
Diclis
Dissotis
Enicostemma
Euphorbia
Gisekia
Alectra
Blumea
Cassia
Cleome
Corchorus
Crinum
Dicerocaryum
Dipcadi
Eclipta
Eriocaulon
Evolvulus
Glinus

Gnaphalium
Heliotropium
Hibiscus
Ilysanthes
Indigofera
Kohautia
Limeum
Lobelia
Marsilea
Melochia
Mollugo
Nesaea
Nicolasia
Oldenlandia
Oxygonum
Periglossum
Pollichia
Polygala
Pycnosphaera
Rhamphicarpa
Sesuvium
Sida
Sopubia
Sutera
Tephrosia
Trianthema
Vernonia
Xanthium

Gomphocarpus
Hermannia
Hyptis
Ipomoea
Juncus
Lightfootia
Limosella
Lophiocarpus
Melhania
Mimulus
Monsonia
Neohyptis
Nidorella
Orthanthera
Pavonia
Phila
Polycarpaea
Portulaca
Pterrococcus
Sesamum
Sebaea
Sonchus
Sphaeranthus
Talinum
Trachyandra
Vahlia
Vigna
Zaleya

REFERENCES

Angolan section:

Barbosa, L. A. G. 1970. "Carta Fitogeografica de Angola." *IICA,* Luanda.

Diniz, A. C. 1973. "Caracteristicas Mesologicas de Angola." *MIAA, Nova Lisboa.*

Diniz, A. C. and de Barros Aguiar, F. Q. 1973. "Recursos em Terras com Aptidao para o Regadio na Bacia do Cubango." *IIAA, Nova Lisboa* (Serie Tecnica, No. 33).

Botswana section

Bawden, M. G. (Ed.) 1965. "Some Soils of Northern Bechuanaland." *D.O.S.,* England.

Ellenberger, V. 1931. Unpublished Report. Botswana National Archives, *Ref. S236/7.*

Grove, A. T. 1969. "Landforms and Climatic Change in the Kalahari and Ngamiland." *Geogr. J.,* **135:2,** June.

Peterhouse Natural History Society. 1971-1974. *"The Wagtail,"* Nos. 9, 12, 13 and *Special Number,* Marandellas.

Rains, A. B. and McKay, A. D. 1968. "The Northern Statelands, Botswana." *D.O.S.,* England (Land Resource Study, No. 5).

Stigand, A. G. 1923. "Ngamiland." *Geogr. J., Vol.* **LXII,6,** December.

Weare, P. R. and Yalala, A. 1971. "Provisional Vegetation Map of Botswana." *BNR,* Vol. **3.**