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The vegetation of seasonally flooded areas of the Pongolo River Floodplain

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ABSTRACT

The Braun-Blanquet method of phytosociological analysis has been used to identify the plant communities of the seasonally flooded areas of the Pongolo River Floodplain. Six communities and two sub-communities, whose distribution is closely related to relative periods of exposure and inundation, were recognized. The structure and interrelationships of the communities are considered and the rôle of human activities in determining their extent is commented upon. Comparison is made with similar situations elsewhere in Africa.

RÉSUMÉ

VÉGÉTATION DES ZONES PÉRIODIQUEMENT INONDÉES DANS LE LIT MAJEUR DE LA RIVIÈRE PONGOLO

On a utilisé la méthode d'analyse phytosociologique de Braun-Blanquet pour identifier les communautés végétales des zones périodiquement inondées dans le lit majeur de la rivière Pongolo. On y a reconnu six communautés, dont la distribution est en corrélation étroite avec les périodes relatives d'exposition et d'inondation. On considère la structure et les interrelations des communautés et l'on commente le rôle joué par les activités humaines dans la détermination de leur amplitude. La situation est comparée à d'autres du même genre qui se présentent ailleurs en Afrique.

INTRODUCTION

The impoundment of rivers inevitably results in changed conditions downstream and where this involves a floodplain, the effects are likely to be of considerable importance (Attwell, 1970; Begg, 1973; Phélines, Coke & Nichol, 1973; Townsend, 1975). This may be particularly pertinent in the African context since some of the most important fisheries are located on floodplains (Welcomme, 1974).

The object of this study was to define and to determine the factors influencing the distribution of the plant communities of the seasonally flooded areas of the Pongolo River Floodplain. It forms part of a multi-disciplinary research programme whose objective is an assessment of the long-term effects of impounding the waters of the Pongolo River on the floodplain ecosystem.

This paper presents the results of a Braun-Blanquet analysis carried out between June and September 1974.

THE STUDY AREA

The Pongolo River Floodplain (27°S, 37°E) is situated on the low-lying coastal plain (75 m above mean sea level) in the north-eastern corner of Natal, South Africa (Fig. 1). It is approximately 60 km long and 0,8 km wide. Although the floodplain covers 10 416 ha (Welcomme, 1974), this study only considered 8 800 ha, because the floodplain in the vicinity of Nhlanjane Pan, which had not been flooded since construction of the Pongolopoort Dam (1972) (Fig. 1), was excluded.

Flooding is predominantly a summer phenomenon, and prior to construction of the Dam, the major floods were of relatively short duration: 28 cumec flows lasted for periods of up to 100 days and caused minimal flooding; 56 cumec flows for up to 60 days; and flows in excess of 85 cumecs for only between two and ten days (Table 1). The major floods, arising from either the very high flows or lower flows for longer periods, annually recharge a number of shallow

FIG. 1.—Map of the Pongolo River Floodplain showing the Pongolopoort Dam, the pans (named) and the Ndumu Game Reserve at the confluence of the Pongolo and Usutu Rivers.

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TABLE 1.—The duration of different flow rates on the Pongolo River Floodplain. High flows have the shortest duration. Data compiled from information provided by the Department of Water Affairs, Pretoria

River flow (cumecs)	Average number of days per year that flow exceeds stated value
28	102,0
56	41,0
85	20,0
113	11,0
141	8,0
170	5,0
198	4,0
226	3,0
255	2,5
283	2,0

waterbodies, locally referred to as pans (Hutchinson, Pickford & Schuurman, 1932). These have a total area of *c.* 2 600 ha (Musil, Grunow & Bornman, 1973), but this is reduced considerably by evaporation to less than 1 000 ha during the dry season.

Fluctuating water levels have been shown to influence both the species composition and the distribution of individual species in wetland areas (Howard-Williams, 1972; Howard-Williams & Walker, 1974; Howard-Williams, 1975). On the Pongolo River Floodplain some 8 000 ha lies between high flood level (HFL) and maximum retention level (MRL) of the pans, i.e. the level at which pan and river lose contact (Breen *et al.*, 1978), and is therefore normally only flooded for relatively short periods. A further approximately 1 000 ha becomes exposed gradually during the dry season as levels drop below MRL, and is therefore inundated for longer periods than that between HFL and MRL. The natural flooding regime has been altered by the impounding of the river at Jozini (Fig. 1), and the effects of these changed conditions on the floodplain vegetation will be discussed in a subsequent paper.

Inhabitants of the higher area immediately around the floodplain make extensive use of the alluvial soils for subsistence agriculture and most of the floodplain vegetation is disturbed (Fig. 2). However, since a portion of the floodplain was incorporated in the Ndumu Game Reserve (Fig. 1) when it was established in 1924, a relatively undisturbed area was available for comparison.

METHODS

The Braun-Blanquet method of sampling and synthesis as described by Werger (1974) was adopted. Using aerial photographs, physiognomically distinct vegetation areas were demarcated and field checks were carried out to ensure that they were correctly assigned. Optimal plot size was determined by increasing the area until the number of species recorded remained more or less constant. Plot size was determined as 100 m² (5 m × 20 m) for the forest community and, although it may be adapted to vegetation type (Werger, 1974), all communities were sampled by 100 m² plots. A total of 106 plots was investigated during August and September 1974. All species present were listed and, since most annuals only appear after the floods have receded (usually in April), it is probable that most were still recognizable at the time of the survey.

After communities had been checked and demarcated on the aerial photographs (1:25 000), they were subjectively transcribed onto a map of the same scale.

The following site factors, soil pH in 1 N KCl (Jackson, 1958), and proportions of clay, silt and sand (Black, 1965), were determined. With the aid of 1: 6 000 contour maps the height of each plot above MRL and below HFL was estimated.

Plant nomenclature follows Ross (1972).

THE PLANT COMMUNITIES

Six communities have been recognized and they may be grouped according to their relative periods of exposure and inundation: (1) the communities (two) of high-lying areas, which are only inundated for short periods; (2) those (three) of low-lying gently sloping areas, which only become exposed as water approaches and drops below MRL, i.e. those having the longest submergence and shortest period of exposure; and (3) the community which occupies the intermediate areas, where the slope is slightly steeper

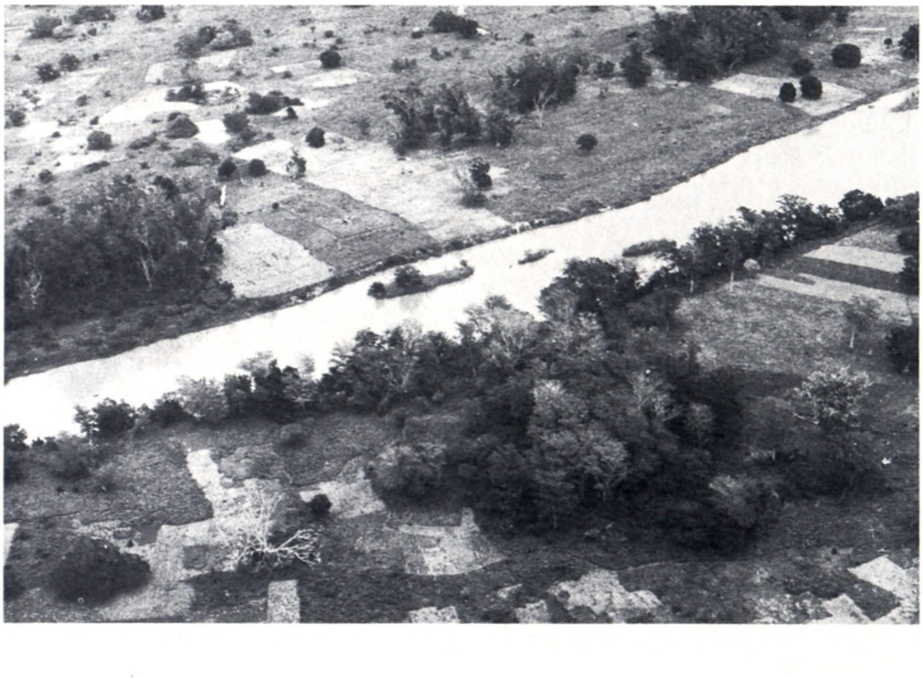

FIG. 2.—An aerial view of part of the Pongolo River Floodplain showing the extensive cultivation along the levees and riverbank. Only small pockets of the *Ficus sycomorus* — *Rauvolfia caffra* Community remain outside the Ndumu Game Reserve.

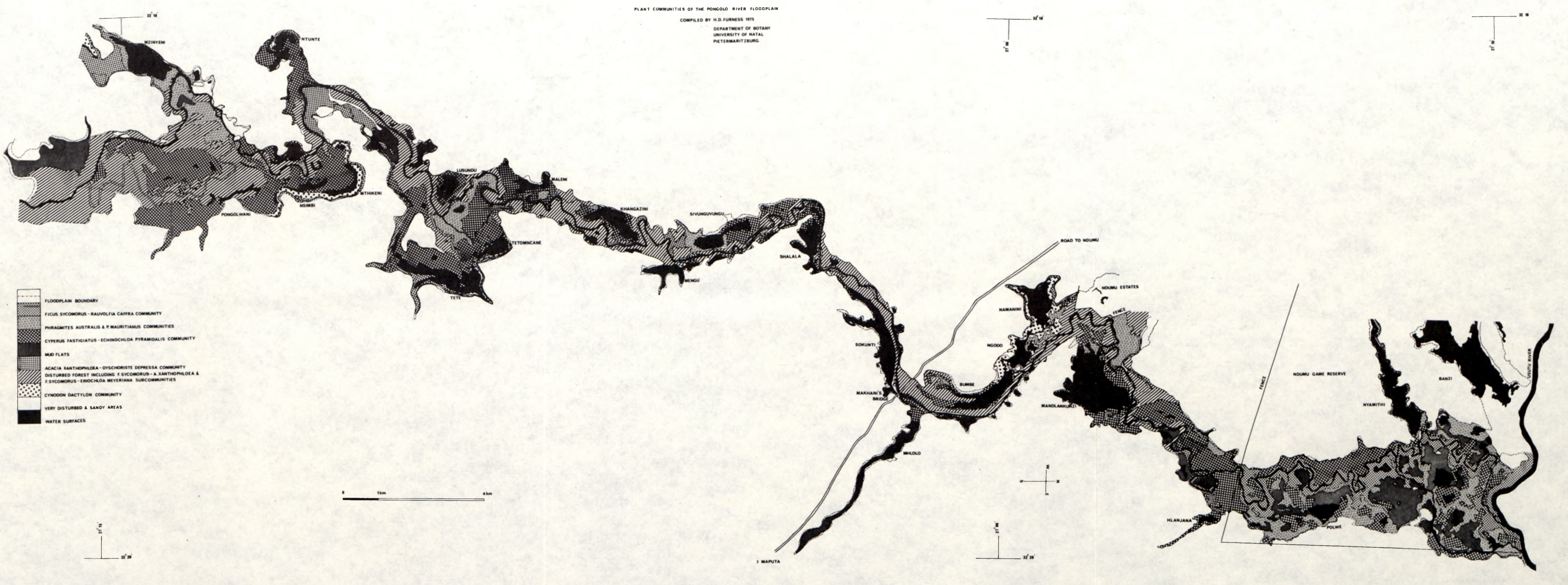

Fig. 3.—Map showing the distribution of the plant communities of the seasonally flooded areas of the Pongolo River Floodplain between Mzinyeni Pan and the confluence of the Pongolo and Usutu Rivers.

[illegible]—Map showing the distribution of the plant communities of the seasonally flooded areas of the Logone River Floodplain between [illegible] and the confluence of the Logone and Chari Rivers.

so that water drains off fairly rapidly thereby preventing the development of communities typical of the low-lying areas.

1. *Communities of the high-lying areas* (Fig. 2)

Two communities may be recognized: the *Ficus sycomorus—Rauvolfia caffra* Community with two subcommunities, occupying 406 ha, which is restricted to levees on either side of the main river channel, and the *Acacia xanthophloea—Dyschoriste depressa* Community, 128 ha in extent, which is confined to narrow bands along the margin of the floodplain (Figs 3 & 4).

1.1 *The* Ficus sycomorus—Rauvolfia caffra *Community*

This community forms a distinct vegetational unit. Since most of the species present do not occur in any other community, they may be regarded as character or differential species (Table 2). They include *Ficus sycomorus, Rauvolfia caffra, Trichilia emetica, Entada spicata, Syzygium guineense, Adina microcephala, Allophylus decipiens, Kraussia floribunda* and *Monanthotaxis caffra.*

Outside the Ndumu Game Reserve (Table 3: relevés 90, 65, 96, 81, 80, 87, 83 & 104), the community usually has only two strata: a tall tree stratum (12–15 m), formed principally by *Rauvolfia caffra, Ficus sycomorus* and *Trichilia emetica* with cover of 60–80%, and a 2-3 m shrub stratum of *Allophylus decipiens, Grewia caffra, Monanthotaxis caffra, Ficus capreifolia, Syzygium guineense* and *Adina microcephala* with cover of 10–20%. Within the reserve a further two strata of shade tolerant species are evident (relevés 73, 72, 68, 69, 70, 71 & 74), the taller (0,75–1,25 m, cover 15–20%) of *Dicliptera heterostegia* and *Setaria chevalieri,* while in some relevés (81 & 87) the grass *Oplismenus hirtellus* forms a low stratum (0,1–0,25 m) with cover not exceeding 10%. The tendency for these two strata to be developed within the Reserve reflects the agricultural disturbance on the levees outside the Reserve.

Two sub-communities are recognizable:

(a) *The* Ficus sycomorus—Eriochloa meyeriana *Subcommunity*

This develops where the impact of agriculture is severe. Because of clearing, the upper stratum (8–10 m, cover 40 %) is only occasionally present (Table 3: relevés 93, 91, 49 & 48), and the middle shrub and lower herb strata are poorly developed. The second stratum of *Dicliptera heterostegia, Monanthotaxis caffra, Kraussia floribunda* and *Setaria chevalieri* is

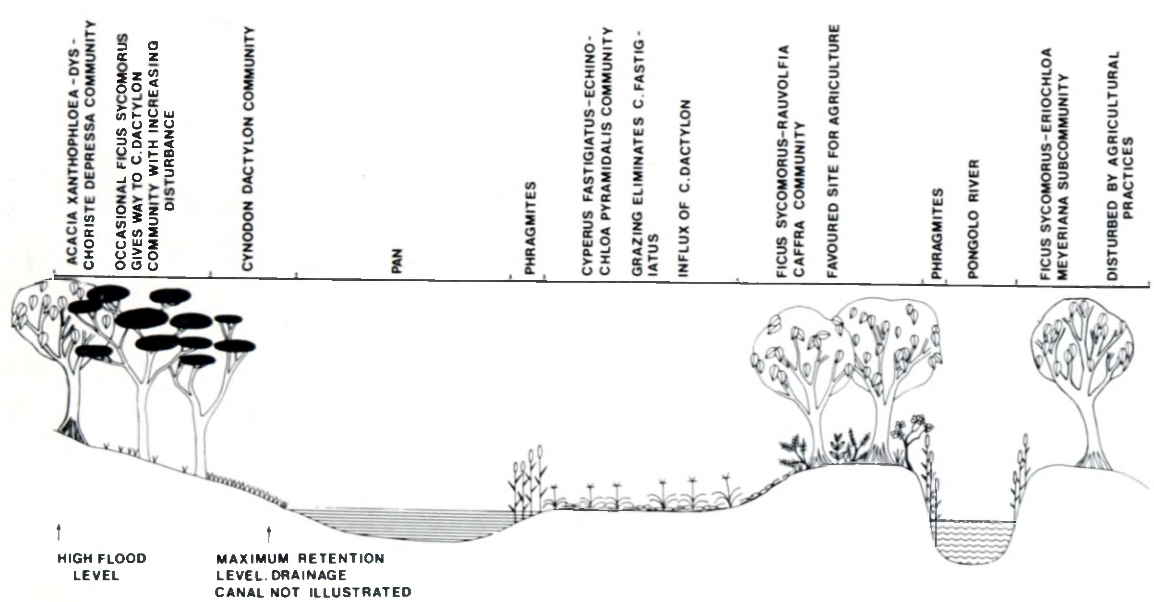

FIG. 4.—Diagrammatic representation of a cross-section of the Pongolo River Floodplain showing the relative positions of the different plant communities.

TABLE 2.—Character* and differential† species of the Floodplain communities

Community	Species	Community	Species
Ficus sycomorus—Rauvolfia caffra	Ficus sycomorus*† Rauvolfia caffra*† Trichilia emetica*† Dicliptera heterostegia*† Entada spicata*† Adina microcephala*† Syzygium guineense*† Setaria chevalieri*† Ipomoea digitata*† Allophylus decipiens*† Kraussia floribunda*† Oplismenus hirtellus*† Monanthotaxis caffra*†	Acacia xanthophloea—Dyschoriste depressa Cynodon dactylon Cyperus fastigiatus—Echinochloa pyramidalis Phragmites australis Phragmites mauritianus	Acacia xanthophloea*† Dyschoriste depressa*† Cynodon dactylon* Cyperus fastigiatus* Phragmites australis*† Phragmites mauritianus*†

0,75–1,25 m tall with slightly higher cover (15%) compared with the *Ficus sycomorus—Rauvolfia caffra* Community. The lower stratum (0,1–0,25 m, cover 15–60%) contains a number of species which is found in other communities e.g. *Sida alba, Eriochloa meyeriana* and *Commelina africana*. In moister areas, *Echinochloa pyramidalis* forms quite dense mats (relevés 49 & 48). The presence of opportunist species such as *Sida alba* and *Commelina africana*, and the extent (2 142 ha) and the distribution of this sub-community (Fig. 3) suggest that it results from disturbance. It is thus present along the levees and between the old and present river course north and east of Mzinyeni and south of Pongolwani Pans, sites that are favoured for agriculture and where, under undisturbed conditions, the *Ficus sycomorus—Rauvolfia caffra* Community would normally be present.

(b) *The* Ficus sycomorus—Acacia xanthophloea *Sub-community*

This sub-community has a very restricted distribution (10 ha, Fig. 2) and is represented only by two small stands (Table 3: relevés 86, 85 & 58).

Four strata are present, the upper (8–10 m, cover 40–50%) being comprised of *Ficus sycomorus, Acacia xanthophloea* and two climbers, *Ipomoea digitata* and *Jasminum fluminense*. The 2–4 m shrub stratum, dominated by *Ficus capreifolia* and *Grewia caffra*, but also containing *Acacia xanthophloea*, has relatively low cover (10–20%). A third stratum of approximately 0,75 m, comprising mainly *Kraussia floribunda, Mimosa pigra* and young *Acacia xanthophloea*, is present with cover not exceeding 30%. The lowest stratum (0,4 m) is characterized by both the greatest species diversity and, at times, the highest cover. Dominant species are *Dyschoriste depressa, Cissampelos mucronata, Eriochloa parvispiculata, Cardiospermum halicacabum, Hemarthria altissima, Eriochloa meyeriana* and *Echinochloa pyramidalis*.

The two sites where this sub-community has developed, to the south-west of Khangazini and west of Mengu Pans (Fig. 2), are areas where the river levees and the margin of the floodplain are close together. Such a situation would facilitate an intergrading of the *Ficus sycomorus—Rauvolfia caffra* and the *Acacia xanthophloea—Dyschoriste depressa* Communities. This sub-community is therefore regarded as transitional.

1.2 *The* Acacia xanthophloea—Dyschoriste depressa *Community* (Fig. 5)

Acacia xanthophloea and *Dyschoriste depressa* are confined to this community and the *Ficus sycomorus—Acacia xanthophloea* Sub-community and they may, therefore, be regarded as either character or differential species (Table 2: relevés 99, 18, 53, 23, 16, 11, 13, 15, 17, 45, 102, 30, 26, 32, 36, 100, 98 & 75). A striking feature of this community is that it is formed of two strata only, the tree stratum being composed entirely of *Acacia xanthophloea* (8–12 m, cover 20–50%). The second stratum is made up of low-growing (0,15–0,45 m) herbs with sparse cover (usually 7–10%). *Dyschoriste depressa* is the most prominent, others being *Sida alba, Heliotropium ovalifolium, Heliotropium indicum, Cynodon dactylon, Ambrosia artemisiifolia* and *Cardiospermum halicacabum*. These latter species tend to be widely distributed and have low cover-abundance values (r or +). Many may be regarded as opportunists, reflecting the unstable conditions brought about by flooding and grazing. In some areas outside the relevés investigated a few well-established *Ficus sycomorus* are present. These stands are, however, not considered typical. They do, however, serve to indicate the close relationships between this community and the *Ficus sycomorus—Rauvolfia caffra* Community.

1.3 *Interrelationships*

Both communities of the high-lying areas develop on widely varying soils, usually slightly acidic (pH 4–6,6) and with extremely variable clay (9–68%), silt (3–49%) and sand (16–62%) fractions. This suggests that some other factor(s) predominate in determining their distribution. Because of topographical variation along the floodplain, different pans at MRL have different elevations with regard to both the river level and HFL. This has a striking influence on the vegetation, those communities intolerant of flooding being closely related to HFL, where those communities, which are more hygrophilous and more tolerant of flooding, have a distribution that is closely related to MRL irrespective of its height relative to HFL.

FIG. 5.—A view of the *Acacia xanthophloea — Dyschoriste depressa* Community taken during the extended summer floods of 1976. At this time the herb layer becomes incorporated into the aquatic system.

TABLE 3.—Communities of the seasonally flooded areas of the Pongolo River Floodplain

Phragmites australis Community

RELEVÉ NUMBER	76	77	92	94	95
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	0	0	0,3	0,6	0,3
HEIGHT BELOW HIGH FLOOD LEVEL (M)	2,7	2,7	2,1	1,8	1,8
TOTAL NUMBER OF SPECIES	2	2	7	8	5
TOTAL COVER (%)	90	90	50	85	85
CLAY (%)	38	28	16	43	33
SAND (%)	48	65	73	27	51
SILT(%)	14	19	11	30	16
pH (N KCl)	6,4	6,3	5,6	5,6	4,9

Phragmites mauritianus Community

RELEVÉ NUMBER	51	52	57	101	88	64
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	0,6	0	0,6	0	0	0
HEIGHT BELOW HIGH FLOOD LEVEL (M)	1,2	1,8	0,6	1,8	3,0	3,0
TOTAL NUMBER OF SPECIES	4	5	6	7	7	3
TOTAL COVER (%)	100	100	100	90	90	100
CLAY (%)	71	46	56	39	69	66
SAND (%)	20	31	22	21	25	18
SILT(%)	9	23	22	40	6	16
pH (N KCl)	5,3	4,4	4,1	4,9	3,6	5,0

Cyperus fastigiatus — Echinochloa pyramidalis Community

RELEVÉ NUMBER	37	4	59	105	106	89	84	82	55	42	44	97	34	3	33	2	14	61	46	54	40	1	38	103	39	66	78	24	79	63
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	0,6	0,3	0,3	0,3	0,3	0,3	0,3	0,3	0,6	0,3	0,3	0,3	0,6	0,3	0	0,6	0,3	0,3	0,3	0,3	0,3	0,3	0,6	0,3	0,6	0,3	0,3	0,9	1,8	0,3
HEIGHT BELOW HIGH FLOOD LEVEL (M)	1,2	2,4	1,2	1,5	0,9	2,7	2,7	2,7	0,6	1,8	1,8	0,9	0,9	0,9	2,4	1,5	2,4	3,3	2,7	1,8	2,1	2,7	2,4	1,2	2,4	2,4	2,7	1,8	1,5	2,7
TOTAL NUMBER OF SPECIES	7	8	8	8	8	12	9	7	12	14	8	14	10	6	11	7	13	13	13	13	14	12	11	12	13	9	6	7	8	11
TOTAL COVER (%)	40	65	90	80	40	80	90	90	60	80	60	85	75	70	45	40	60	95	75	90	80	90	90	80	60	60	90	75	80	10
CLAY (%)	58	60	43	56	65	59	68	28	46	71	72	54	68	72	48	64	32	63	67	51	62	70	56	51	66	70	68	72	63	65
SAND (%)	30	14	43	27	21	29	18	57	33	20	14	21	21	12	34	15	57	18	21	30	18	16	34	36	22	10	16	17	22	17
SILT(%)	12	33	14	17	14	12	14	15	21	31	14	25	11	35	18	21	11	19	12	19	20	14	10	13	12	20	16	24	15	18
pH (N KCl)	4,4	4,1	3,4	3,3	3,8	4,2	3,8	3,9	4,8	3,4	3,7	4,5	4,0	4,3	5,3	4,0	5,2	4,9	3,4	5,3	3,8	4,4	4,0	3,4	3,9	4,1	4,9	4,0	4,1	3,9

Nodum of indeterminate rank

RELEVÉ NUMBER	56	21	19	35	20
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	0,3	0	0	0,9	0
HEIGHT BELOW HIGH FLOOD LEVEL (M)	1,5	2,1	2,4	1,2	2,4
TOTAL NUMBER OF SPECIES	17	23	24	20	17
TOTAL COVER (%)	60	55	70	70	75
CLAY (%)	46	45	69	22	62
SAND (%)	33	35	19	71	20
SILT(%)	21	20	12	7	18
pH (N KCl)	6,1	4,3	4,8	4,7	4,3

Cynodon dactylon Community

RELEVÉ NUMBER	5	8	22	9	28	7	31	29	10	25	6	27
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	0,9	1,2	1,5	1,8	0,6	0,9	0,3	0,3	0	0,3	0,6	1,2
HEIGHT BELOW HIGH FLOOD LEVEL (M)	1,8	2,4	1,2	0,3	3,3	2,7	0,9	3,0	1,5	3,3	2,7	1,8
TOTAL NUMBER OF SPECIES	4	4	7	4	17	14	13	9	5	9	5	11
TOTAL COVER (%)	90	75	55	80	50	60	55	70	85	65	75	50
CLAY (%)	37	29	63	49	56	57	50	58	50	73	47	56
SAND (%)	55	63	20	25	38	22	47	21	20	11	42	38
SILT(%)	14	13	17	26	6	21	8	21	30	16	11	6
pH (N KCl)	4,8	6,8	4,6	4,9	5,7	6,2	6,3	4,8	4,5	5,4	5,5	5,9

Acacia xanthophloea — Dyschoriste depressa Community

RELEVÉ NUMBER	99	43	18	53	23	16	11	13	15	17	45	102	30	26	32	36	100	98	75
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	1,5	3,0	1,5	1,2	2,7	2,1	3,0	2,1	2,7	0,3	1,5	1,5	3,0	2,7	0,9	1,5	1,5	1,5	2,7
HEIGHT BELOW HIGH FLOOD LEVEL (M)	0,3	0	0,3	0,6	0	0,9	0,6	0,6	0,6	1,8	0,6	0	0,3	0,3	0,3	0,3	0,3	0,3	0
TOTAL NUMBER OF SPECIES	12	11	12	6	8	15	12	13	17	12	7	14	9	6	8	12	7	11	3
TOTAL COVER (%)	50	60	70	40	45	65	50	45	60	45	40	50	75	55	75	55	60	35	50
CLAY (%)	63	28	51	26	60	53	32	38	44	51	46	46	63	47	38	54	63	59	33
SAND (%)	30	62	17	45	20	30	58	50	39	27	45	22	16	44	42	21	30	32	51
SILT(%)	7	10	32	29	20	17	10	12	17	22	14	32	21	9	22	25	7	9	16
pH (N KCl)	4,1	5,3	4,5	5,1	4,6	4,9	4,8	4,9	4,6	4,8	4,9	4,5	4,5	6,8	4,7	5,7	4,3	6,4	6,6

F. sycomorus — A. xanthophloea Sub-Community

RELEVÉ NUMBER	86	85	58
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	1,8	1,8	1,5
HEIGHT BELOW HIGH FLOOD LEVEL (M)	0,3	0,3	0
TOTAL NUMBER OF SPECIES	19	16	19
TOTAL COVER (%)	90	90	90
CLAY (%)	66	54	28
SAND (%)	21	31	33
SILT(%)	13	15	39
pH (N KCl)	4,6	4,7	5,0

Ficus sycomorus — Eriochloa Meyeriana Sub-Community

RELEVÉ NUMBER	90	93	91	49	48
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	3,3	2,1	2,4	3,0	2,4
HEIGHT BELOW HIGH FLOOD LEVEL (M)	0	0,3	0	0	0
TOTAL NUMBER OF SPECIES	9	13	9	16	14
TOTAL COVER (%)	85	80	60	75	80
CLAY (%)	14	30	23	43	50
SAND (%)	79	56	59	27	43
SILT(%)	7	14	18	30	7
pH (N KCl)	4,0	6,2	6,8	5,5	5,5

Ficus sycomorus — Rauvolfia coffra Community

RELEVÉ NUMBER	65	67	73	72	68	69	70	71	74	96	81	80	87	83	104
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	3,3	1,2	2,7	2,7	2,7	2,7	2,7	2,7	2,7	2,1	3,0	3,0	2,7	3,0	2,1
HEIGHT BELOW HIGH FLOOD LEVEL (M)	0	1,5	0	0	0	0	0	0	0	0	0,3	0,3	0,3	0	0
TOTAL NUMBER OF SPECIES	5	5	9	9	13	11	8	8	9	12	12	10	10	10	7
TOTAL COVER (%)	65	70	90	90	90	70	90	90	80	90	70	75	80	70	75
CLAY (%)	33	68	38	27	21	46	21	9	30	14	31	49	17	11	59
SAND (%)	18	17	42	56	67	17	62	26	46	83	56	33	75	57	29
SILT(%)	49	23	20	20	12	37	17	65	24	3	13	18	8	32	12
pH (N KCl)	4,8	4,8	5,5	5,2	5,7	5,5	5,0	4,8	6,4	5,8	5,4	6,1	5,1	5,6	5,4

RELEVÉ NUMBER	50	62	12	47	41	60
HEIGHT ABOVE MAXIMUM RETENTION LEVEL (M)	1,2	2,4	1,8	2,4	0,3	0,3
HEIGHT BELOW HIGH FLOOD LEVEL (M)	0,6	0,3	0,9	0	1,2	2,7
TOTAL NUMBER OF SPECIES	6	7	11	16	19	9
TOTAL COVER (%)	75	90	50	45	95	100
CLAY (%)	51	66	51	33	61	66
SAND (%)	26	25	20	32	24	13
SILT(%)	23	9	29	35	15	21
pH (N KCl)	4,5	4,5	5,3	5,4	3,4	4,4

PHRAGMITES AUSTRALIS (CAV.) TRIN. EX STEUD.
PHRAGMITES MAURITIANUS KUNTH
ECHINOCHLOA PYRAMIDALIS (LAM.) HITCHC. & CHASE.
POLYGONUM PULCHRUM BLUME
LUDWIGIA STOLONIFERA (GUILL. & PERR.) RAVEN
POLYGONUM SALICIFOLIUM WILLD.
POLYGONUM SENEGALENSE MEISN.
CYPERUS FASTIGIATUS ROTTB.
ALTERNANTHERA SESSILIS (L.) DC.
ERIOCHLOA MEYERIANA (NEES) PILG.
RANUNCULUS MULTIFIDUS FORSK.
CENTELLA ASIATICA (L.) URBAN
CYNODON DACTYLON (L.) PERS.
GNAPHALIUM PENSYLVANICUM WILLD.
GRANGEA MADERASPATANA (L.) POIR.
GLINUS LOTOIDES L.
SENECIO MADAGASCARIENSIS POIR.
POLYGONUM AVICULARE L.
HEMARTHRIA ALTISSIMA (POIR.) STAPF & C.E. HUBB.
RORIPPA MADAGASCARIENSIS (DC.) HARA
COMMELINA AFRICANA L.
CONYZA BONARIENSIS (L.) CRONQUIST
COTULA AUSTRALIS (SPRENG.) HOOK. f.
CARDIOSPERMUM HALICACABUM L.
AMBROSIA ARTEMISIIFOLIA L.
HELIOTROPIUM INDICUM L.
EUPHORBIA INAEQUILATERA SOND.
COTULA ANTHEMOIDES L.
CAPERONIA STUHLMANNII PAX
CYPERUS SEEDLING
HELIOTROPIUM OVALIFOLIUM FORSK.
LEGUME SEEDLING
PASPALUM COMMERSONII LAM.
SIDA ALBA L.
ERIOCHLOA PARVISPICULATA C.E. HUBB.
CISSAMPELOS MUCRONATA A. RICH.
ACACIA XANTHOPHLOEA BENTH.
DYSCHORISTE DEPRESSA NEES
FICUS SYCOMORUS L.
RAUVOLFIA CAFFRA SOND.
TRICHILIA EMETICA VAHL
DICLIPTERA HETEROSTEGIA PRESL EX NEES, NON CHEV.
ENTADA SPICATA (E.MEY.) DRUCE
ADINA MICROCEPHALA (DEL) HIERN.
SYZYGIUM GUINEENSE (WILLD.) D.C.
SETARIA CHEVALIERI STAPF EX STAPF & C.E. HUBB.
IPOMOEA DIGITATA L.
AGERATUM CONYZOIDES L.
ALLOPHYLUS DECIPIENS (SOND.) RADLK.
GREWIA CAFFRA MEISN.
FICUS CAPREIFOLIA DEL.
KRAUSSIA FLORIBUNDA HARV.
OPLISMENUS HIRTELLUS (L.) BEAUV.
MONANTHOTAXIS CAFFRA (SOND.) VERDC.
JASMINUM FLUMINENSE VELL.

OTHER ACCOMPANYING SPECIES

ABUTILON GUINEENSE (SCHUMACH.) BAK. f & EXELL
SESBANIA SESBAN (L.) MERRILL
MIMOSA PIGRA L.
PSILANTHES MAURITIANA (PERS.) DC.
GOMPHRENA CELOSIOIDES MART.
PHYLA NODIFLORA (L.) GREENE
CHENOPODIUM ALBUM L.
XANTHIUM STRUMARIUM L.
SOLANUM NIGRUM L.
ECLIPTA PROSTRATA (L.) L.
GNAPHALIUM LUTEO-ALBUM L.

INFREQUENT SPECIES IN RELEVÉS OF TABLE 3.

AMBROSIA ARTEMISIIFOLIA L. (95: +)
AZIMA TETRACANTHA LAM. (13:+, 15:+, 17:r)
BARLERIA SP. (11: r)
CENTEMA SUBFUSCA (MOQ.) LOPR. (32: 1)
COTULA AUSTRALIS (SPRENG.) HOOK. f. (890:+, 74 :+, 96 :+)
EUCLEA UNDULATA THUNB. (15: r)
GNAPHALIUM SP. (96 :+, 92:+, 94 :+)
GREWIA SUBSPATHULATA N.E. Br. (16 :1, 13 : r)
HYGROPHILA AURICULATA (SCHUMACH.) HEINE (75 :+, 96 : 1, 99 :+)
LEPIDIUM SULUENSE MARAIS (15 : +)
LUDWIGIA STOLONIFERA (GUILL. & PERR.) RAVEN (20 : r, 28 : r)
MAYTENUS SENEGALENSIS (LAM.) EXELL (6 :+)
SPOROBOLUS SMUTSII STENT (35 :+)

Fig. 6a reveals that although the distribution of both communities is relative to height below HFL, and therefore to the period of inundation while the river is in flood, the *Ficus sycomorus—Rauvolfia caffra* Community is the more sensitive to flooding in that it develops on the highest areas. Clearly, however, distribution of the community is not only determined by period of inundation, because it is absent from areas around the margin of the floodplain, even where they may have an almost identical flooding regime to that of the levees. It seems likely that seasonal availability of soil moisture acts in conjunction with inundation, because proximity to the river would prevent the development of the very dry conditions which arise along the edge of the floodplain during the dry winter months (unpublished data). The seasonally drier conditions along the margin of the floodplain eliminate *Monanthotaxis caffra* and other hygrophilous woody species, while the presence of occasional *Ficus sycomorus* suggests that it may be somewhat more tolerant. Although more favourable soil moisture conditions might be found at lower elevations along the floodplain margin, development of the woody component is prevented by the longer period of inundation. The combination of these factors is probably responsible for the distinct separation of the *Ficus sycomorus—Rauvolfia caffra* and *Acacia xanthophloea—Dyschoriste depressa* Communities.

The *Acacia xanthophloea—Dyschoriste depressa* Community tends to develop in slightly lower-lying areas than the *Ficus sycomorus–Rauvolfia caffra* Community, but above MRL (Fig. 4). It is, therefore, inundated only while the river is in flood, and the period of inundation is greater than that experienced by the *F. sycomorus—R. caffra* Community.

2. *The communities of low-lying areas*

Three communities were recognized (Table 3). The *Phragmites australis* and the *P. mauritianus* Communities together occupy an area of *c.* 234 ha, most of which (65%) is in the Ndumu Game Reserve. The *Cyperus fastigiatus—Echinochloa pyramidalis* Community is one of the largest, covering *c.* 2 471 ha, with particularly extensive stands occurring west of Tete and Nsimbi Pans and in the Ndumu Game Reserve (Figs 3 & 7).

2.1 *The* Phragmites australis *Community*

This community is dominated by *Phragmites australis,* which may be regarded as the character/differential species (Table 2). Under protection in the Ndumu Game Reserve (Table 3: relevés 76 & 77), it forms dense stands growing to a height of 2,0–3,0 m with high cover-abundance values and few other species (relevés 76 & 77). Where its vitality is reduced by cutting and burning (relevés 92, 94 and 95), invasion by other species occurs, principally *Echinochloa pyramidalis* and *Eriochloa meyeriana* that form a stratum between 0,3 and 0,45 m.

2.2 *The* Phragmites mauritianus *Community*

Phragmites mauritianus is the dominant and differential species (Table 2), growing to a height of 1,5–3,5 m and forming dense stands with high cover-abundance values (Table 3). It is usually associated

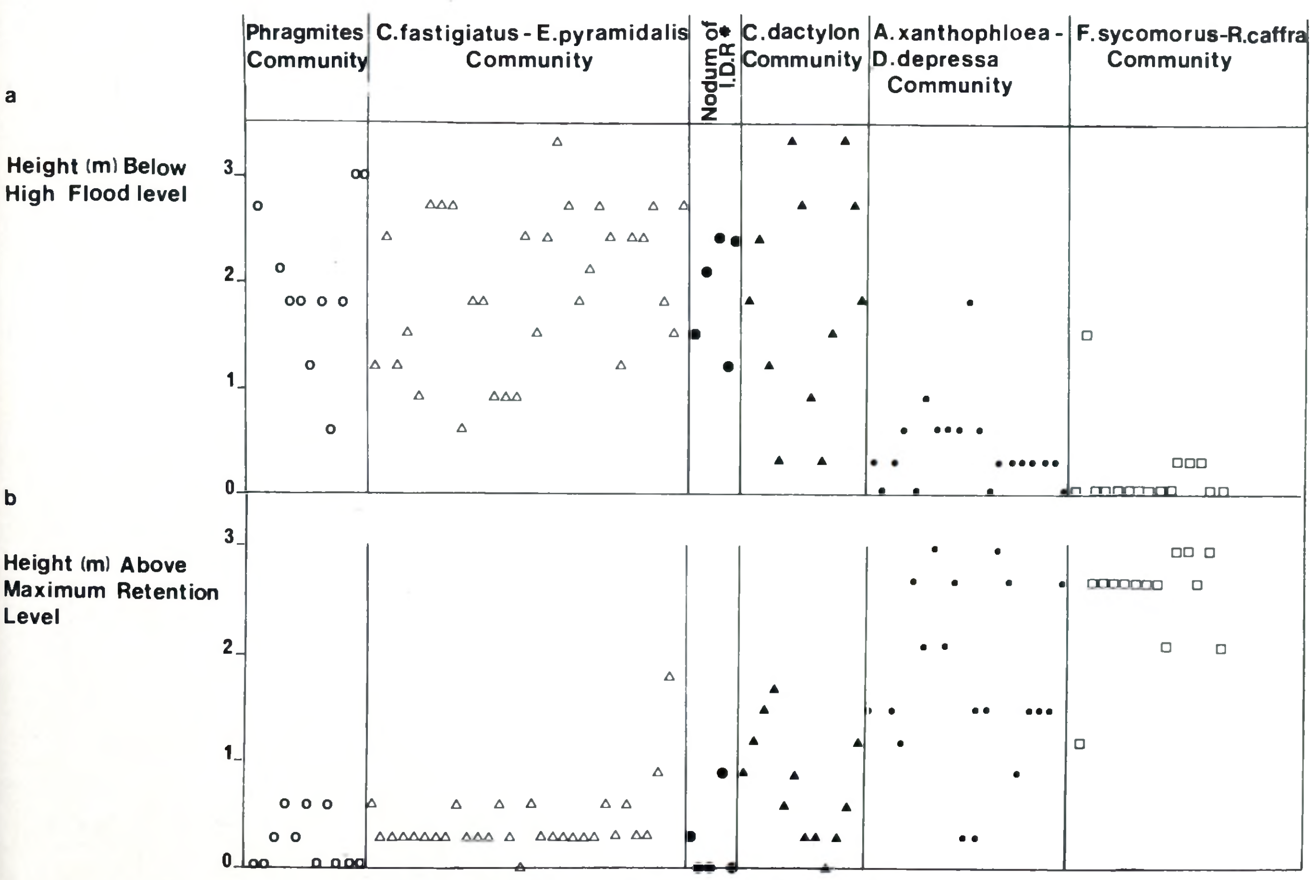

FIG. 6.—Position of the relevés relative to: (a) height below high flood level; (b) height above maximum retention level. Relevés are ordered in the sequence defined by the phytosociological Table 3. *Nodum of indeterminate rank.

with *Echinochloa pyramidalis* and *Alternanthera sessilis*, although other species are also found in this community (e.g. *Eriochloa meyeriana, Sida alba* and *Cynodon dactylon*), particularly outside the Ndumu Game Reserve. Only one relevé (64) was, however, examined within the Reserve. Where present, these species form a low-growing stratum (0,15–0,4 m) with low cover-abundance values.

2.3 *The* Cyperus fastigiatus—Echinochloa pyramidalis *Community* (Fig. 7)

Cyperus fastigiatus and *Echinochloa pyramidalis* are differential species (Table 2), for this community (Table 3) and, when they have high cover-abundance values (relevés 59 & 105), few other species are present. Where cover-abundance of the differential species is lower, opportunist species such as *Glinus lotoides, Heliotropium indicum* and *Cardiospermum halicacabum* are more common. Three strata may be recognized, an upper comprising mainly *Cyperus fastigiatus* (1–2 m; cover 20–80%), intermediate (0,3–0,4 m; cover 15–80%) dominated by *Echinochloa pyramidalis*; and a layer formed by prostrate species such as *Cynodon dactylon* and *Polygonum aviculare* (0,1–0,15 m; cover 5–20%).

2.4 *Interrelationships*

The three communities of the low-lying areas all develop on acidic soils with a pH of 3,3–6,4 and of rather variable texture (Table 3). It seems that the *Phragmites australis* Community develops on soils that are more sandy (27–73%) than those of the *Phragmites mauritianus* and *Cyperus fastigiatus—Echinochloa pyramidalis* Communities (10–57%).

The development of all three communities is closely associated with MRL (Fig. 6b). This suggests that it is not so much inundation as the presence of a more stable water supply that controls the position of these communities. The *Phragmites* Communities tend to occupy the lower positions, *P. australis* favouring swampy areas as opposed to *P. mauritianus*, which prefers sites where there is water movement, such as river banks. The *Cyperus fastigiatus—Echinochloa pyramidalis* Community develops only on flat and gently sloping draining areas adjacent to pans, and in depressions that remain wet for most of the dry season (Fig. 4).

The *Cyperus fastigiatus—Echinochloa pyramidalis* Community shows marked affinities with the *Phragmites* Communities through the extension of the distribution of *Echinochloa pyramidalis* into these semi-aquatic habitats, and with the *Cynodon dactylon* and *Acacia xanthophloea—Dyschoriste depressa* Communities because of the presence of *Cyperus fastigiatus* in these higher-lying areas. The degree to which these rather broad distributional patterns reflect the distribution under natural and undisturbed conditions is debateable, because reduction in the cover of the *Phragmites* Communities might favour intrusion of *Echinochloa pyramidalis*, whereas grazing of *Cyperus fastigiatus* seems to favour an increase in the *Cynodon dactylon* component. Where both differential species are grazed, particularly in the areas west of Sivungu-vungu and to the south and south-west of Khangazini Pans, their cover-abundance values are lower and a wider variety of species is present (Table 3: relevé 46, 38 & 39).

3. *Communities of intermediate areas*

Only one community, the *Cynodon dactylon* Community, has been recognized, covering 171 ha of the floodplain. It is generally found on gently sloping areas that become exposed gradually as the flood-waters recede (Table 3, Fig. 6). The soils vary from acidic (pH 4,5) to almost neutral (pH 6,8), with very variable texture: clay 29–73%, silt 6–36% and sand 11–63%. *Cynodon dactylon* is extremely tolerant of extended periods of dry conditions foı owing exposure, and of submergence. Not surprisingly, therefore, the distribution of the *C. dactylon* Community does not show marked relationships with either height above MRL or below HFL (Fig. 6a & b). It therefore extends from below maximum retention level to above high flood level (Fig. 4). *C. dactylon* may be found in all the communities, particularly where disturbance has occurred.

3.1 *The* Cynodon dactylon *Community* (Fig. 8)

Cynodon dactylon, the differential species (Table 2) for this community, forms dense, almost pure, stands

FIG. 7.—A good example of the *Cyperus fastigiatus—Echinochloa pyramidalis* Community. This stand on the north-western edge of Tete Pan has been reduced in size and in height. Most of the area is now a mixture of *Cyperus fastigiatus, Echinochloa pyramidalis* and *Cynodon dactylon* forming a stratum of about 50 cm in height.

FIG. 8.—The *Cynodon dactylon* Community is grazed extensively during the late winter period when pasturage elsewhere is low.

of considerable extent around some pans (e.g. Namanini-Bumbe 42 ha, east of Mthikeni and Nsimbi 27 ha). It forms a single stratum (0,2 m) with up to 90% cover where conditions are most favourable (Table 3: relevés 5, 8 & 10). Elsewhere, where cover is reduced (relevés 27 & 28), and grazing more intense, the height may be less (0,05 m) and the weeds (*Ambrosia artemisiifolia, Conyza bonariensis* and *Polygonum aviculare*) become more prominent. These species form an ill-defined stratum of 0,2–0,3 m in height.

3.2 *Interrelationships*

The close relationships of the *Cynodon dactylon* Community with other communities on the floodplain are emphasized not only by the distribution of *C. dactylon,* but also by five relevés (56, 21, 19, 35 & 20) that form a nodum of indeterminate rank between the *C. dactylon* and *Cyperus fastigiatus–Echinochloa pyramidalis* Communities.

It seems probable that this community would normally develop in areas where the inundation period was too long for the woody communities and where it became too dry for communities characteristic of the low-lying areas (Fig. 6). Since it presently extends into areas that clearly show relics of other communities, it must be concluded that disturbance has increased the extent of this community. At the lower levels it is principally by replacement of *Cyperus fastigiatus,* which is adversely affected by grazing and trampling and, at higher levels, by clearing, which reduces competition and allows more direct illumination, both of which favour *Cynodon dactylon.*

4. Relevés of undetermined affinity

Six relevés (50, 12, 47, 41, 60 & 62) do not appear to fit satisfactorily into the communities outlined above. Although they could have been allocated to specific communities, thereby improving the information on total floristics, the degree of affinity did not, in our opinion, justify this action. They are included in the table because an advantage of the Braun-Blanquet method is that new relevé data may continuously be added, thereby facilitating recognition of communities that may not be presently recognizable (Werger 1973).

DISCUSSION

The studies by Tinley in 1958 (published in 1976) are the earliest reports on the Pongolo River Floodplain vegetation. He recognized two formations, the Riparian Forest, which included the disturbed and undisturbed vegetation of the levees and high-lying margins of the floodplain, and the Aquatic and Marginal Pan Vegetation. This broad classification, which does not take into account the observed marked influence of the flooding regime, does not agree well with the community distinctions drawn up in this study.

More recently, De Moor *et al.* (1977) and Pooley (1978) have reported on the vegetation within the Ndumu Game Reserve (Fig. 1). Only a portion of this Reserve includes the floodplain of the Pongolo River. De Moor *et al.* (1977) using the system of Fosberg (1967), recognized six formations (Table 4) of which five corresponded well with those recognized in this study. The microphyllous deciduous shrub savanna is, however, difficult to relate to our communities, because it includes species such as *Sesbania sesban, Echinochloa pyramidalis* and *Phragmites australis,* which appear to exhibit markedly different responses to inundation, and it therefore probably forms a transition between "forest and grasses" as has been suggested by Pooley (1978). Neither De Moor *et al.* (1977) nor Pooley (1978) have, however, attempted to relate the plant communites to flooding regimes.

TABLE 4.—Comparison of the formations determined by De Moor *et al.* (1977) with communities of this study

	De Moor *et al.* (1977)	Present study
	Formation	*Community*
1	Dry season deciduous forest	*Ficus sycomorus—Rauvolfia caffra*
4	Tall evergreen graminoid marsh	*Phragmites mauritianus*
4a	Tall evergreen graminoid marsh	*Phragmites australis*
4b	Seasonal orthophyll tall grass	*Cyperus fastigiatus—Echinochloa pyramidalis*
4c	Microphyllous deciduous shrub savanna	Probably transitional between *Cyperus fastigiatus—Echinochloa pyramidalis* and *Ficus sycomorus—Rauvolfia caffra*
5	Seasonal orthophyll meadow	*Cynodon dactylon*

Werger (1974a) has suggested that in areas exposed to extreme conditions, emphasis should be placed on permanently recognizable species in phytosociological analysis. This concept was applied to the floodplain vegetation because, particularly above MRL where both inundation and exposure have to be tolerated, conditions may be considered to be extreme. It reduces the number of species from 64 to 25, but does not alter the definitions of the communities (Table 5).

None of the communities recognized on the Pongolo River Floodplain is unique. They have been recorded from widely separated areas on the African continent, on floodplains and areas of fluctuating water levels.

Phragmites australis and *P. mauritianus* have a world-wide distribution (Clayton, 1967; Fernandes *et al.*, 1971), although *P. mauritianus* tends to be more tropical and is frequently encountered in swampy and seasonally flooded areas (Gordon-Gray & Ward, 1971; Howard-Williams & Walker, 1974; Rzóska, 1974). The distinction in ecological preference between *P. australis,* which favours standing water, and *P. mauritianus* which prefers moving water, supports the observations of Gordon-Gray & Ward (1971). Howard-Williams & Walker (1974) reported similar environmental conditions in stands of *P. mauritianus* in Lake Chilwa, although it was also present in alkaline swamps. In other parts of Central Africa, Vesey-Fitzgerald (1963) recorded *Phragmites* in Riverine Grasslands and "lakes" where it formed dense stands on silt banks, sand bars and in lagoons. He did not record it from "pans" or "alkaline swamps and flats", but this may, in the former instance, reflect the fact that the pans being investigated were shallow depressions that normally dried up during the dry season. They are clearly different from those of the Pongolo system. Vesey-Fitzgerald did not record the specific names of *Phragmites* and from the distribution (Clayton, 1967; Fernandes *et al.,* 1971) it seems likely that, although both *P. australis* and *P. mauritianus* could have been present, *P. mauritianus* would be the more common.

Cyperus fastigiatus is widespread in the province of Natal in South Africa (Ross, 1972), but has not been recorded in tropical areas (Vesey-Fitzgerald, 1955; 1963; Dean, 1967; Cook, 1968; Howard-Williams & Walker, 1974; Imevbore & Bakare, 1974; Rzóska, 1974). Ross (1972) claims that *C. fastigiatus* is closely allied to the more tropical *C. auricomus* Sieber ex Spreng., which is also placed with *C. digitatus* Roxb. subsp. *auricomus* by Kükenthal (in Ross, 1972). Howard-Williams & Walker (1974) reported *C. digitatus* from relatively acidic soils (pH below 6,0) in their neutral to acidic marsh vegetation type. These conditions are similar to those in which *C. fastigiatus* is found on the Pongolo system.

Unlike *Cyperus fastigiatus, Echinochloa pyramidalis* is widespread in wet areas where it is often associated with a variety of other species (Vesey-Fitzgerald, 1955; 1963; Dean, 1967; Cook, 1968; Imevbore & Bakare, 1974; Howard-Williams & Walker, 1974). The description of its growth in floodplain grassland by Vesey-Fitzgerald (1963) aptly describes its behaviour in the Pongolo system: "Growth starts at the onset of the rains but the stature depends on the extent of flooding. Under optimum conditions the previous season's accumulation of rough rots away in the water and the new growth is very vigorous". Although *E. pyramidalis* is grazed by hippopotamus (Scotcher *et al.*, 1978), the numbers of hippopotamus outside the Ndumu Game Reserve on the Pongolo Floodplain are small and they do not exert a marked effect. However, as soon as the floods recede and the marshy areas become dry enough for cattle, both *E. pyramidalis* and *C. fastigiatus* are grazed. As in tropical areas, even when drying out and being grazed, node shoots remain green until quite late in the season. In areas where grazing is particularly heavy and where drainage is slightly more rapid following the floods, *E. pyramidalis* may form a mosaic with *Cynodon dactylon* as has been observed by Vesey-Fitzgerald (1955) and Dean (1967).

The development of *Cynodon dactylon* Communities under conditions of fluctuating water levels is well documented, both as pure stands (Lea & Van V. Webb, 1939; Vesey-Fitzgerald, 1955; Dean, 1967; Greenway & Vesey-Fitzgerald, 1969) and in association with other species (Lea & Van V. Webb, 1939; Burnett, 1951; Anderson & Herlocker, 1973; Howard-Williams & Walker, 1974). These short-grass lawns develop on a wide range of soils from acid to alkaline in areas where prolonged flooding is not experienced. Dean (1967) noted that *C. dactylon* was easily killed by flooding. On the Pongolo, it regularly tolerates periods of submergence of up to 150 days, apparently without much detrimental effect.

During summer the *C. dactylon* around the pans may be inundated, thereby becoming an integral part of the aquatic system. Even if it is not completely inundated, the substrate is generally too wet for access by cattle and goats. Thus it is only during the drier parts of the year that these lawns become accessible to terrestrially based grazers, for which it provides a valuable source or pasturage.

The distribution of *Acacia xanthophloea* along tropical and sub-tropical river courses and in damp depressions is well documented (Anderson & Herlocker, 1973; Greenway & Vesey-Fitzgerald, 1969). Vesey-Fitzgerald (1974) concluded that the cyclic and seral status of groves of *A. xanthophloea* were substantially influenced by drainage conditions. A consequence of this is that trees along the lake-shore may succumb during periods of high lake levels (Greenway & Vesey-Fitzgerald, 1969), a situation observed on the Pongolo Floodplain particularly in the vicinity of Mzinyeni Pan (Figs 1 & 5) during the unnaturally extended floods caused by discharge of water from the Pongolopoort Dam after its construction.

Ficus sycomorus occurs throughout Africa along river courses, swampy areas and even arid areas where the water table is high (Palmer & Pitman, 1972). Site preference seems to be for those areas where drainage is quite good and yet water is freely available, because the best stands on both the Pongolo Floodplain (in the Ndumu Game Reserve) and in Lake Manyara National Park (Greenway & Vesey-Fitzgerald, 1969) are along the tops of the river banks and levees.

This study has illustrated the importance of the flooding regime in the development of the vegetational communities. As a result, changes in the pattern of flooding, both of frequency and perhaps more importantly of duration of inundation and exposure, can be expected to exert a profound effect on the communities, as has been observed elsewhere (Dean, 1967; Townsend, 1975, Attwell, 1970). With the very sandy nature of the soils of the floodplain, particularly of the levees and around the pans, destruction of vegetation, resulting either directly from changes in the flooding pattern, or indirectly as a result of allowing cultivation and grazing in areas that were formerly too wet, could increase erosion, thereby having a profound impact on the floodplain system as a whole.

TABLE 5.—Communities of the Pongolo River Floodplain delineated on the permanently recognizable species only

	Phragmites australis community	Phragmites mauritianus community	Cyperus fastigiatus–Echinochloa pyramidalis community	Nodum of indeterminate rank	Cynodon dactylon community	Acacia xanthophloea–Dyschoriste depressa community	F. sycomorus–A. xanthophloea sub-community	F. sycomorus–E. meyeriana sub-community	Ficus sycomorus–Rauvolfia caffra community
Phragmites australis (Cav.) Trin. ex Steud.	55221			1					
Phragmites mauritianus Kunth		444554		+					
Echinochloa pyramidalis (Lam.)Hitchc.& Chase	2122	443323	4243241+3234222214+2+1+311	1		1 + +			
Cyperus fastigiatus Rottb.	+		234433332313223333233224322321	++++1		+ r rr			
Cynodon dactylon (L.) Pers.	2 1		+ 1 1 2r2 + 1 + 1	111	543443445343	+2+r 11+1 1+11			
Acacia xanthophloea Benth.						3+32333333233332333	22+		
Dyschoriste depressa Nees						r1r+11+ +2+1 + 2	112		
Ficus sycomorus L.							333	33223	333333343344432
Rauvolfia caffra Sond.							+		33433222312313
Trichilia emetica Vahl.							1	1 2	221222212222
Dicliptera heterostegia Presl ex Nees non Chev.								+2+	22212222r 2 +
Entada spicata (E.Mey.) Druce									11111111r1+ 1
Adina microcephala (Del.) Hiern.									+11r1+ +
Syzygium guineense (Willd.) D.C.									1+111 +
Setaria chevaliere Stapf ex Stapf & C.E.Hubb.			+					+	2+r 1 +r r
Ipomoea digitata L.							++	1+	2+++ + 1
Allophylus decipiens (Sond.) Radlk.									11 1++ r
Grewia caffra						1r	2+	2	1 + + 4 +1+3
Ficus capreifolia Del.		+ +		1			1+	2r	r + +21 1 2
Kraussia floribunda Harv.							r	+ 1	++1+
Oplismenus hirtellus (L.) Beauv.								+	+1 1 2+
Monanthotaxis caffra (Sond.) Verdc.								+	+ 22 1
Jasmimum fluminese Vell.							1+r	++	
Sesbania sesban (Ll) Merrill			1 + +			r r	1		
Mimosa pigra L.			r r r	++ +			1		

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UITTREKSEL

Die Braun-Blanquet-metode van fitososiologiese analise is gebruik om die plantgemeenskappe van die seisoen-oorstroomde gebiede van die Pongolorivier-vloedvlakte te identifiseer. Ses gemeenskappe en twee subgemeenskappe, waarvan die verspreiding nou in verband staan met die periodes van relatiewe blootstelling en onderwatersetting, is onderskei. Die struktuur en onderlinge verwantskappe van die gemeenskappe is in ag geneem en kommentaar is gelewer oor die invloed van menslike aktiwiteite op die omvang daarvan. Vergelykings met soortgelyke situasies elders in Afrika is getref.

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