ADVANCES IN THE ECOLOGY OF LAKE KARIBA

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Cover Top:	Typical ringnets as utilized in Kapenta fisheries on Lake Kariba
Bottom:	Lake Kariba: The littoral area and draw-down zone
Back cover:	Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

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ECOLOGY OF THE VEGETATION IN THE DRAW-DOWN ZONE OF LAKE KARIBA

Christina Skarpe

INTRODUCTION

The present contribution is a study of the vegetation of the "draw-down zone" e.g. the area between highest and lowest water level in a reservoir, of the artificial Lake Kariba. It aims at providing a renewed description of the shore vegetation along the Zimbabwean side of the lake for comparison with the older records (see, for instance, White 1965, Bowmaker 1968, Child 1968, Magadza 1970). In addition, pilot studies of above-ground biomass production of the dominating vegetation types and on relations between grazing by large herbivores and growth form of *Panicum repens*, a largely dominant species, were intended as a base for further research.

In this contribution, names of plant species follow 'Flora Zambeziaca' (London 1960–1990), and for genera not yet treated there, 'Flora of Southern Africa' (Pretoria 1963–1989).

GENERAL BACKGROUND

The vegetation in the Zambezi River

Lake Kariba is situated in the Zambezian Regional Centre of Endemism, the Kariban Subcenter (White 1965 and 1967). Physiognomically, the region is dominated by deciduous woodlands and forests and mosaics with savanna.

The Zambezi valley is characterized by dry woodlands, often dominated by *Colophospermum mopane* (mopane) (Wild and Barbosa 1967) or the *C. mopane* catena type (Boughey 1958 in Magadza 1970). Above the valley, miombo woodlands or forests dominate with *Brachystegia boehmii* and *Julbernardia globiflora*. Gwembe Valley, where Lake Kariba now is situated, was described (Child 1968) as woodland with mainly mopane, and in the driest parts thicket vegetation. Along the river was a fringe of ever-green riparian forest, and, where the valley was wider, seasonally inundated grassy floodplains. The area had a sparse human population and was virtually without livestock, as a result of tsetse infestation.

The valley was fairly rich in game during the last century (Selous 1881). Animal populations, particularly buffalo, dropped drastically when rinderpest spread into the area in the late 1890's. Populations later recovered, and Child (1968) reported good game populations in areas far from human habitations before the lake was filled. The flooding of the valley resulted in a sharp decline in large herbivore populations, especially in grazing as opposed to browsing species.

With the spread of the "torpedo grass", *Panicum repens*, on the shores, the decline turned into a rapid increase in numbers of particularly elephant, hippopotamus, buffalo and impala (R. Taylor, personal communication)

The creation of Lake Kariba

With the creation of the lake, the most fertile parts of the valley, i.e., the riparian forests and the floodplains, largely on alluvial soils, became flooded. The new shoreline consisted of the comparatively infertile hillsides with dry *C. mopane* catena. In a few places the trees were cut before the reservoir was filled, in order to facilitate fishing operations, but in most places the trees were left standing. In 1984–1986 the dead mopane trees were still standing both in the lake and on the lower parts of the shores. In some of the bays larger tree skeletons with another architecture were found, and were claimed by the local population to be remnants of the riparian forest, among other species *Kigelia africana*.

The annual fluctuations of the water level of the lake which occured during the last 30 years, as well as the nature of the shores, are described in the introduction of this volume.

During the first years, the new shore, i.e., the area between highest and lowest water level of the reservoir, the "draw-down zone", was sparsely vegetated both in its terrestrial and aquatic sections (Bowmaker 1968), probably as a result of a new substrate, a different inundation regime and low availability of diaspores of suitable species, as the original shore vegetation was killed by the rising water. The shore vegetation along the tributary rivers differs from most of that eventually developed along the lake.

Among the plant species that dominated the shore vegetation during the present study, *Panicum repens*, *Cyperus articulatus* and *Polygonum senegalense*, only the two former were mentioned in the vegetation survey of the shores of Lake Kariba from the summer 1965–66 (Magadza 1970). *P. repens* is presumed to have spread to the lake shores by floating pieces of rhizome, and was recorded to increase rapidly during 1966. It probably originated from within the Zambezi system, as it was recorded by H. F. Meyer (Taylor 1985) from the tributary Ume river before the construction of the dam.

Magadza (1970) predicted the dominating role of *P. repens*, and meant that the species spread both by vegetative means and by seed. It has since been claimed that *P. repens* at Lake Kariba generally does not produce viable seed (seemingly normal seed has been collected at a few places during this study, but not tested for germination). *C. articulatus* and *P. senegalense* were not dominant until the receeding water in the 1980's exposed large areas of silty soils, offering these two species a suitable habitat.

METHODS

Field sampling

The vegetation of the geolittoral on the Zimbabwean side of Lake Kariba was sampled in November 1984 and again in February 1985 when some of the plots from the previous year were re-examined, and a number of new plots were added. Vegetation was better developed at the last sampling occasion, and the following description is from that sampling unless otherwise stated. Seventy quadrats of 10 x 10 m, were used, and all species recorded using a 9 degree cover-abundance scale (Braun-Blanquet 1964, modified in van der Maarel 1979) Substrate was recorded as rocks, sand or silt/clay ("fine"). Plots were not levelled, but in four cases placed in short transects perpendicular to the shore line, with one plot close to the shore line, one about halfway to the highest lake level, and one just below that level.

A pilot study for estimation of above-ground biomass for the different vegetation types was carried out in February 1985. February, in the later part of the rainy season, is often the time for peak standing crop (Taylor 1985). In 35 plots of $1 m^2$ all vegetation was cut at ground level, sorted in grasses, sedges and forbs, and oven dried at 90°C until constant weight. Five plots were cut in heavily grazed *P. repens* vegetation, 5 plots in little grazed *P. repens*, 6 plots in *C. articulatus and P. senegalense*, 10 plots in various vegetation on rocky shores, 4 plots on shores of tributary rivers and 5 plots on mixed, low sedge and herb vegetation. In February, the standing crop was supposed to be close to peak standing crop, and was used for a rough indication of minimum above ground net primary production in the major vegetation types. For *P. repens* the highest biomass from the little grazed vegetation was used, to compensate for losses to herbivores.

Differences in growth form of *P. repens* between areas with different grazing pressure, were recorded in a small pilot study in November 1984 in different places along the lake. Grazing pressure was estimated as high, intermediate or low by counting of dung (pats or groups of pellets) usually in 2 plots of 10 x 10 or 5 x 5 m per site. The plots had not been cleared from dung before, and no effort to age the dung or to separate between species (mostly buffalo and elephant) was made. Usually, density of *P. repens* shoots was estimated by counting in 6 quadrats of $0.25 m^2$. Height of undamaged shoots, length and maximum width of undamaged leaves, numbers of all leaves and of green leaves per shoot and often numbers and length of internodes on undamaged shoots were recorded. A sample of rhizomes was dug up; depth of the rhizome system and length and width of the internodes were also measured.

Mapping of shore types using Landsat MSS

Shore or vegetation types were mapped in 1987 by Christer Surell (Surell 1987) using Landsat MSS satellite recordings. The two major vegetation types, *P. repens* and *C. Articulatus and P. senegalense*, were distinguished in the satellite material and mapped, and their areal extension calculated. The rocky shores were too narrow to be distinguished with the resolution used. Where no shore zone was detected, rocky shore with a width of 20 m was presumed. Minor shore types along tributary rivers were not included.

Statistical methods

The vegetation relevees were classified using two-way indicator species analysis TWINSPAN (Hill 1979), a hierarchical, divisive procedure, and by FLEXCLUS (van Tongeren 1986), a non-hierarchical, cumulative classification method.

As a nonlinear, although not necessarily unimodal, model was presumed, ordination was performed using correspondence analysis (CA) (Hill 1974) and canonical correspondence analysis (CCA) from the programme package CANOCO (ter Braak 1987, 1990). In CA the sample scores were calculated as the weighted average of species scores, and the axes of the ordination were defined by the direction of the largest variation in the data set. The ability of the recorded environmental variables, the substrates "rock", "sand" and "fine", to explain the variation in the species data was tested in an indirect gradient analyses by stepwise partial regression, selecting the environmental variables one by one, starting with the one with the best fit.

Direct gradient analysis was performed with CCA, in which the axes of the ordination are constrained to be linear combinations of the provided environmental data, i.e. only the portion of the variation in the species data that falls along these gradients is taken into account. With the version 3.10 of CANOCO centroids for the three nominal substrate variables are obtained in spite of collinearity.

Morphological differences in *P. repens* between areas with different grazing pressure were tested with one-factor analysis of variance, and significance tests carried out using Fisher PLSD and Scheffé tests, included in the statistical package STATVIEW.

RESULTS

Classification and ordination

The classification by FLEXCLUS on cover and by TWINSPAN on cover and binary data gave similar results, but the binary data gave the poorest separation between clusters. Both procedures with cover data distinguished two big clusters, one with *P. repens* including most plots on sand, and the other with *C. articulatus* and *P. senegalense* including the majority of the plots on finer substrate. Two small, well-separated clusters were characterized by *Rhynchelytrum repens/Sesamum* sp. and *Aristida* spp. *Cynodon dactylon* respectively. Both included relevees from rocky shores. Another small cluster with *Eragrostis* sp. and the only relevee from a reed bed with *Phragmites* sp. contained relevees both from rocky shores and sandy shores. The most species rich group was characterized by *Ludwigia stolonifera* and *Echinochloa stagnina, Eleusine indica, Fimbristylis bisumbellata, Phyla nodiflora* and *Eclipta alba*. This group also included plots from shores of tributary rivers, but also from a few mud shores in shallow bays on the lake itself, two relevees from a clay shore heavily grazed and trampled by game, and two from sheltered rocky shores.

The ordination by CA showed strong correlation of the data with the first two axes; e.g. values 0.688 and 0.645 respectively (Figure 5.1). The extremes on both axes were species poor relevees from rocky substrate (axis 1) and a reedbed on sand (axis 2).

Forward selection of environment variables showed significant fit, $p < 0.01$, for the substrate variables rock, sand and fine material. Best fit was obtained for sand (F ratio: 2.77).

A biplot from CCA showing selected species and the centroids of the substrate variables is shown in Figure 5.2.

The vegetation types

A map of shore types (Figure 5.3), and areas covered by the different types (Table 5.1) are from Surell (1987).

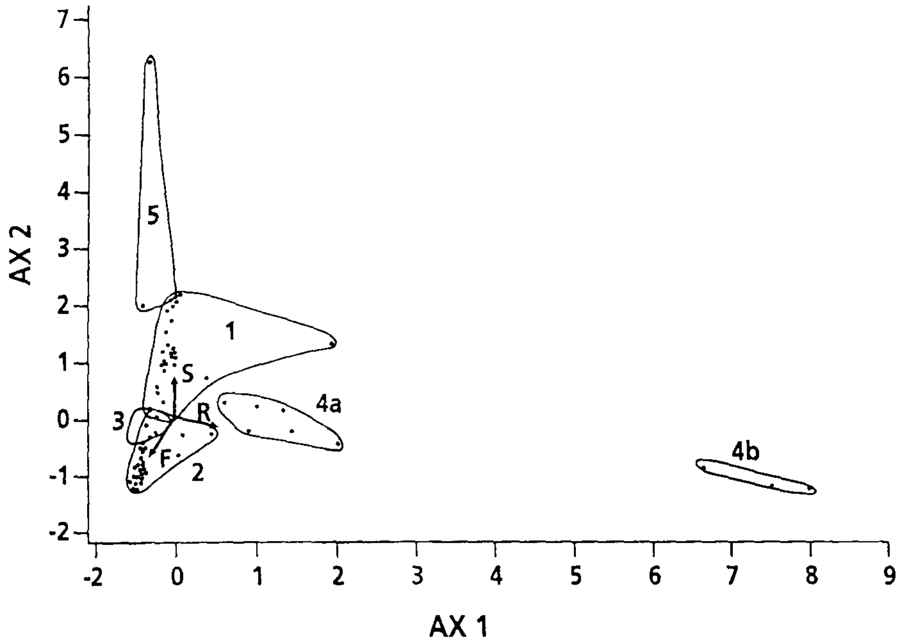


Figure 5.1 Ordination diagram from correspondence analysis with TWINSPAN classes outlined. Ordination and classification on cover data

Abbreviations: Environmental factors: S–sand, R–rock, F–fine material; clusters: 1. *Panicum repens*, 2. *Cyperus articulatus-Polygonum senegalense*, 3. *Ludwigia stolonifera*, 4. a and b rocky shore vegetations, 5. reedbed

Table 5.1 Estimates of absolute area and % of total shore area of major vegetation and shore types of the Zimbabwean side of Lake Kariba (from Surell 1987)

	%	km^2
Panicum repens vegetation	61.8	35
Cyperus-Polygonum vegetation	85.0	48
Rocky and sandy shores	29.2	16

Panicum repens vegetation

This type is almost exclusively found on sand, from the highest inundation level down to near the waters'edge. *P. repens* may grow in the water down to ca. 1 m depth, but with the rapidly receeding water at the time of sampling, the grass had not had the time to colonize the most recently emerged bottoms. *P. repens* seems to spread mainly by vegetative means, which makes it efficient in following the decreasing water level in sites where it is already established, but slow to colonize new areas, as sand banks emerging as off-shore islands.

P. repens is usually strongly dominant in the grasslands with cover of 50–100% and height from 2–5 cm in heavily grazed areas to 100 cm in little disturbed grassland. Particularly in the uppermost zone, the grasslands also included *Waltheria indica*, *Cassia* sp., *Solanum incanum*, *Digitaria milanjiana*, *Heteropogon contortus* and seedlings and saplings of *C. mopane*, usually less than 100 cm tall, presumably as a result of four seasons without flooding. This form of the *P. repens* vegetation was distinguished by TWINSPAN in the last division, but is not delineated in the ordination plot (Figure 5.1)

P. repens is preferred grazing for most large-sized grazers in the area, including elephant, hippopotamus, buffalo, zebra and waterbuck, and probably constitutes a large proportion of the diet also for species like impala, roan and sable. When inundated it is also grazed by herbivorous fish, notably *Tilapia rendalli* (Caulton 1977).

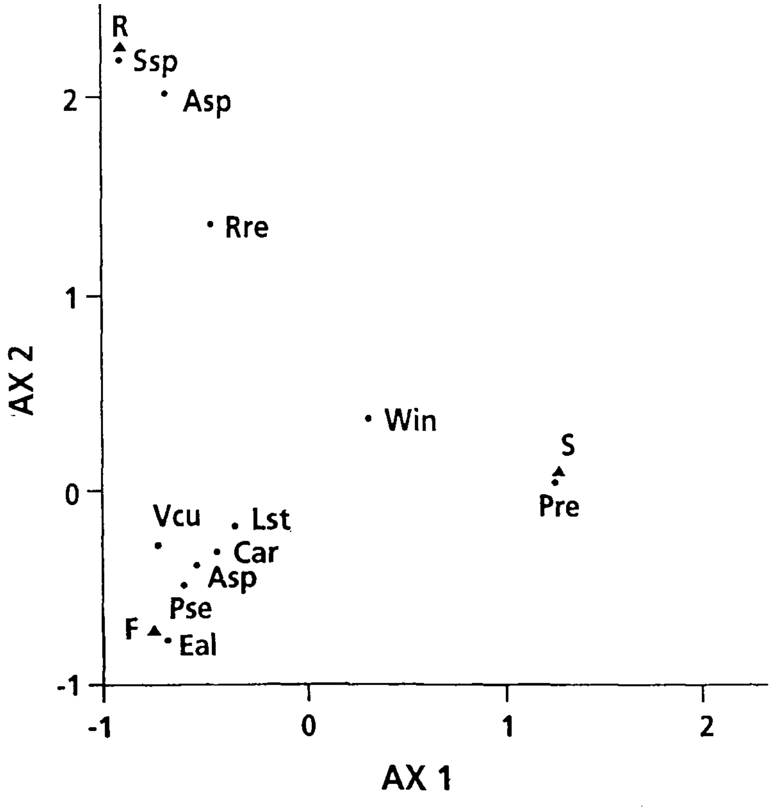


Figure. 5.2 Ordination biplot from canonical correspondence analysis showing centroids of the nominal environmental variables: R–rocky, S–sandy and F–fine material shore

Species are: Ssp. = *Sesamum* sp., Asp. = *Aristida* sp., Rre = *Rhynchelytrum repens*, Win = *Waltherica indica*, Pre = *Panicum repens*, Lst = *Ludwigia stolonifera*, Vcu = *Vossia cuspidata*, Car = *Cyperus articulatus*, Alsp. = *Alternanthera* sp., Pse = *Polygonum senegalense*, Eal = *Eclipta alba*.

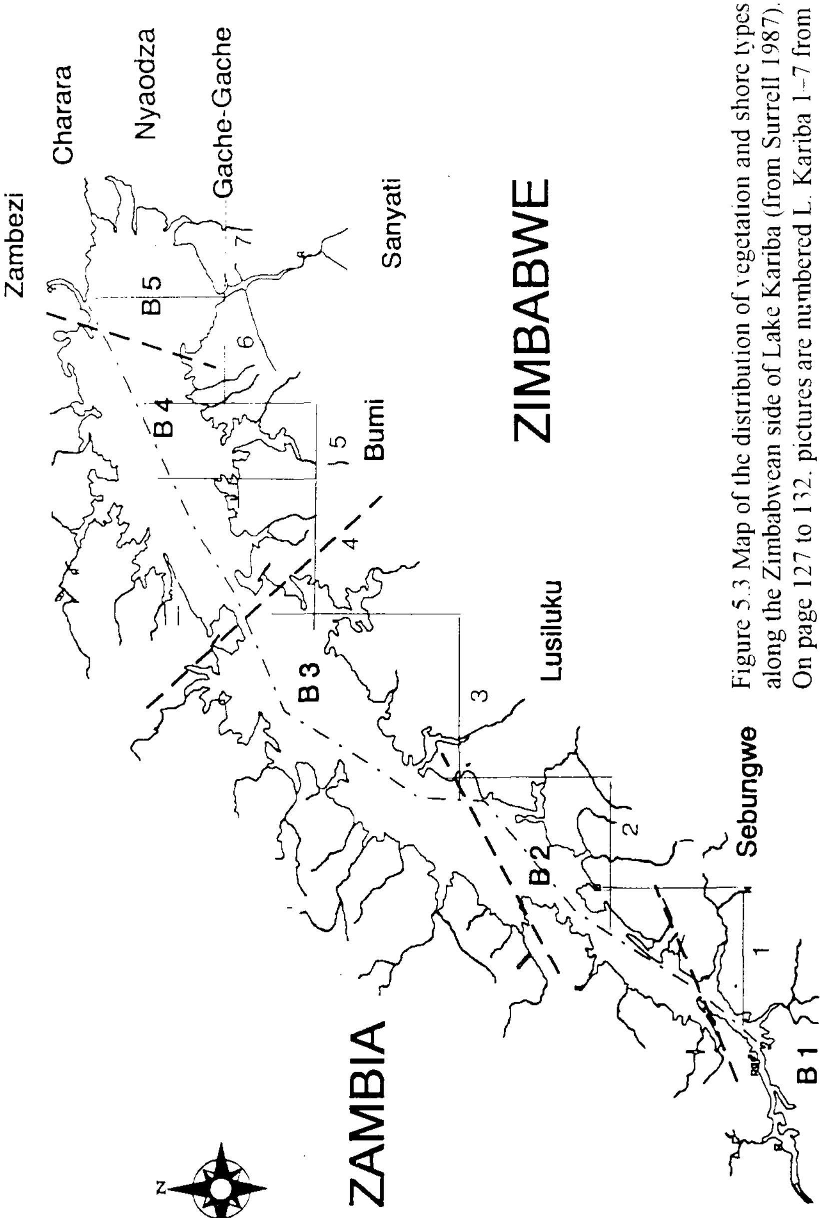
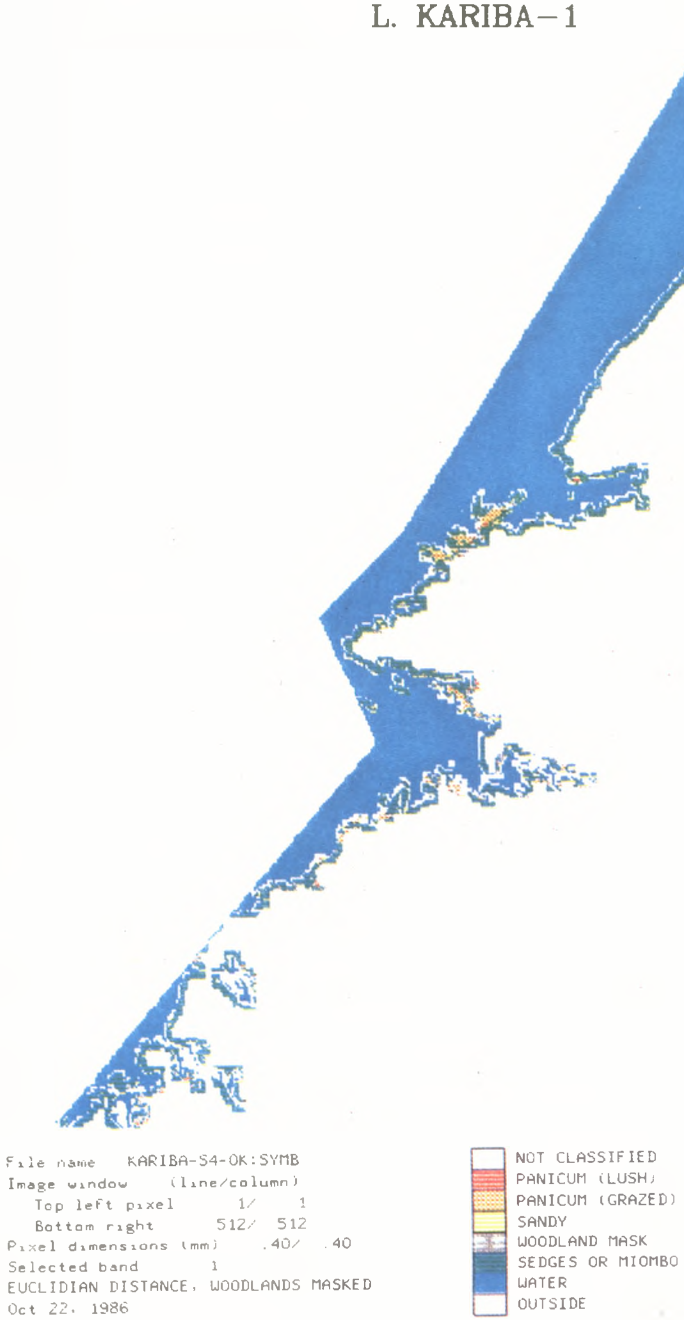
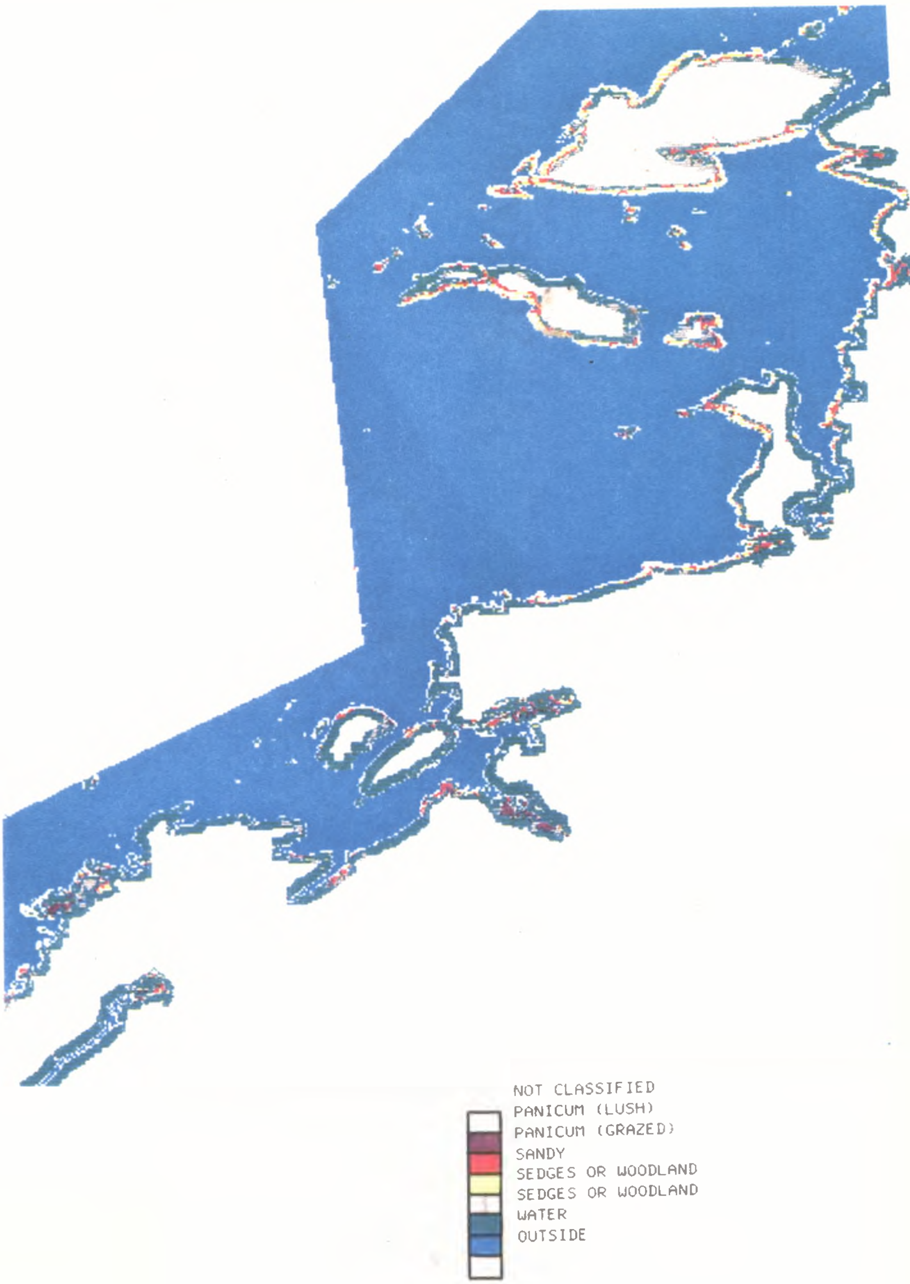


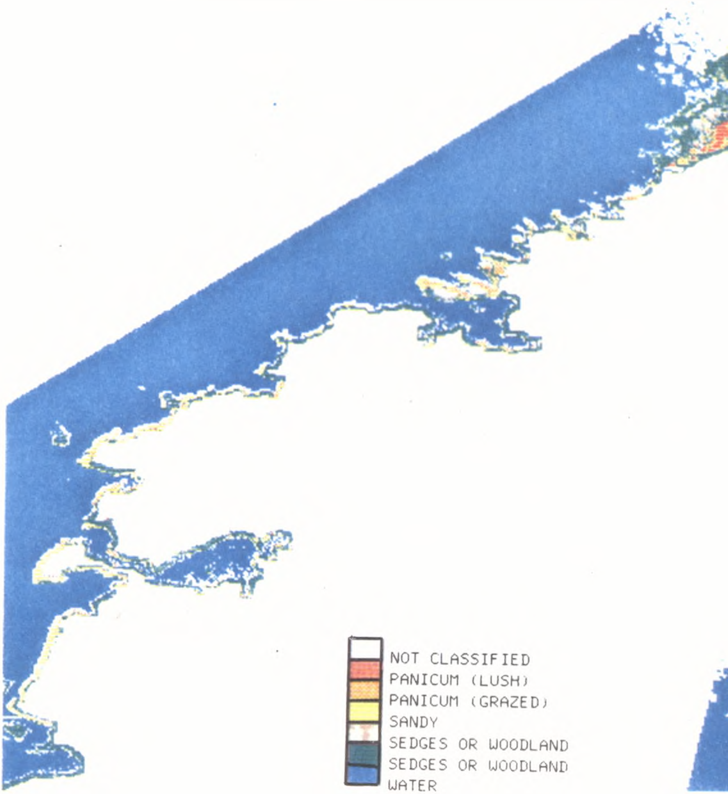
Figure 5.3 Map of the distribution of vegetation and shore types along the Zimbabwean side of Lake Kariba (from Surrell 1987). On page 127 to 132. pictures are numbered L. Kariba 1–7 from SW to NE


L. KARIBA-1
File name KARIBA-S4-OK:SYMB
Image window (line/column)
Top left pixel 1/ 1
Bottom right 512/ 512
Pixel dimensions (mm) .40/ .40
Selected band 1
EUCLIDIAN DISTANCE, WOODLANDS MASKED
Oct 22, 1986
NOT CLASSIFIED
PANICUM (LUSH)
PANICUM (GRAZED)
SANDY
WOODLAND MASK
SEDGES OR MIOMBO
WATER
OUTSIDE

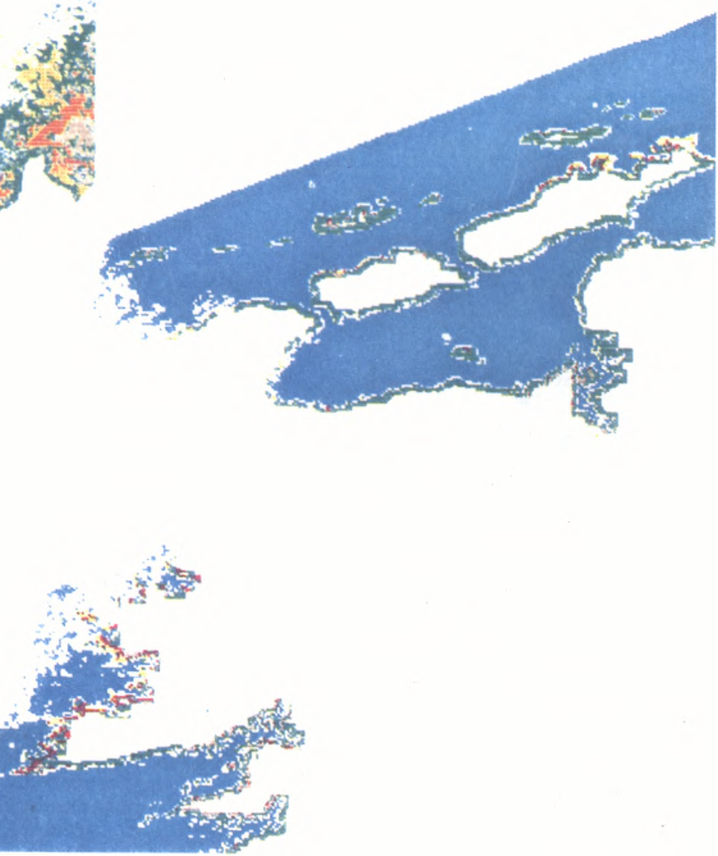
L. KARIBA−2


NOT CLASSIFIED
PANICUM (LUSH)
PANICUM (GRAZED)
SANDY
SEDGES OR WOODLAND
SEDGES OR WOODLAND
WATER
OUTSIDE

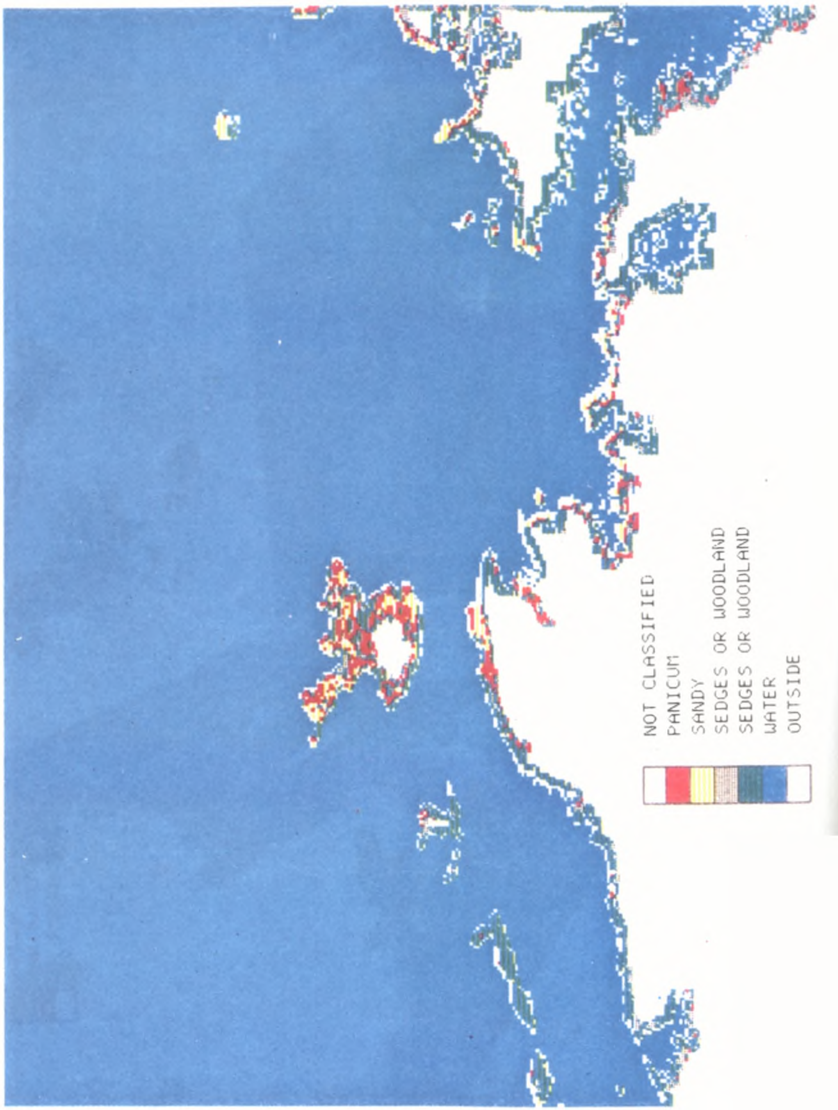
L. KARIBA-3

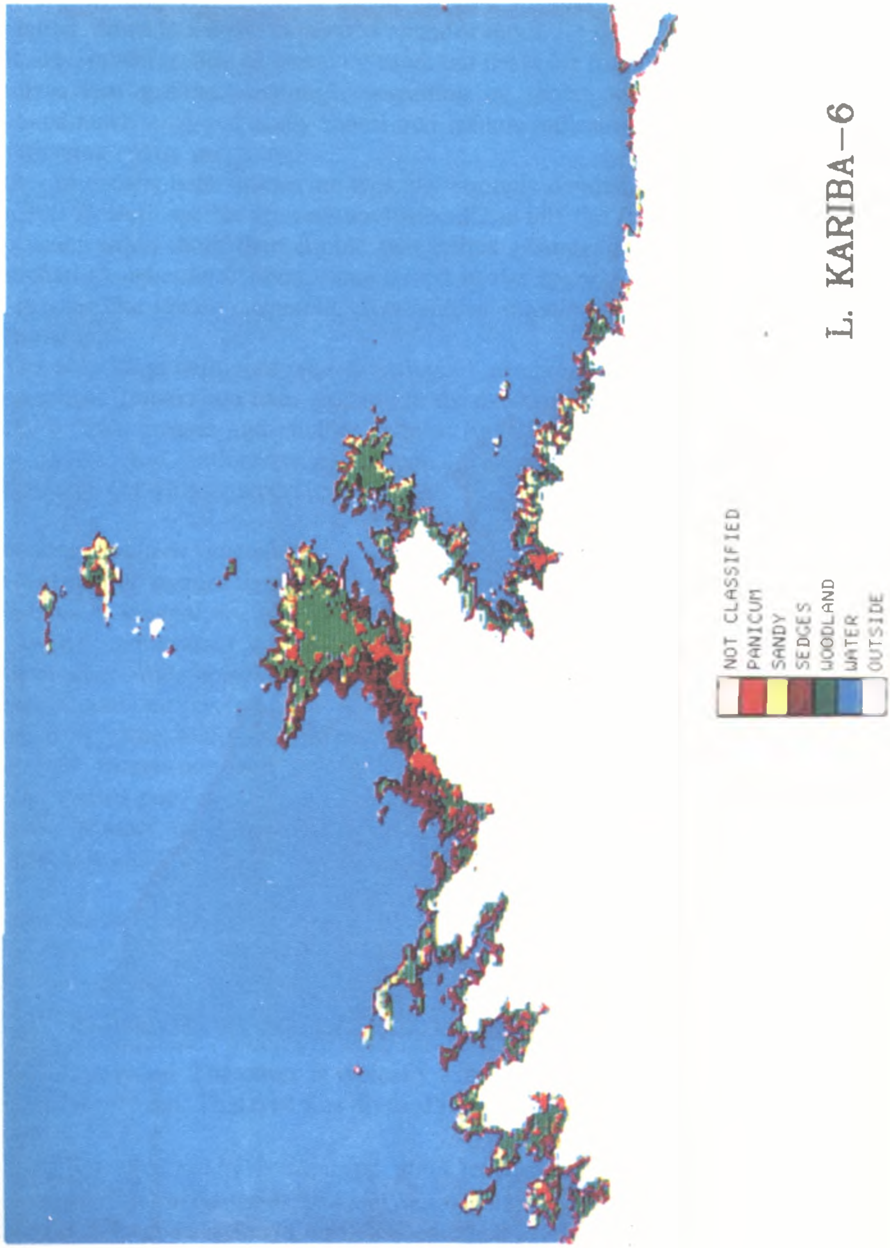

NOT CLASSIFIED
PANICUM (LUSH)
PANICUM (GRAZED)
SANDY
SEDGES OR WOODLAND
SEDGES OR WOODLAND
WATER

L. KARIBA—4

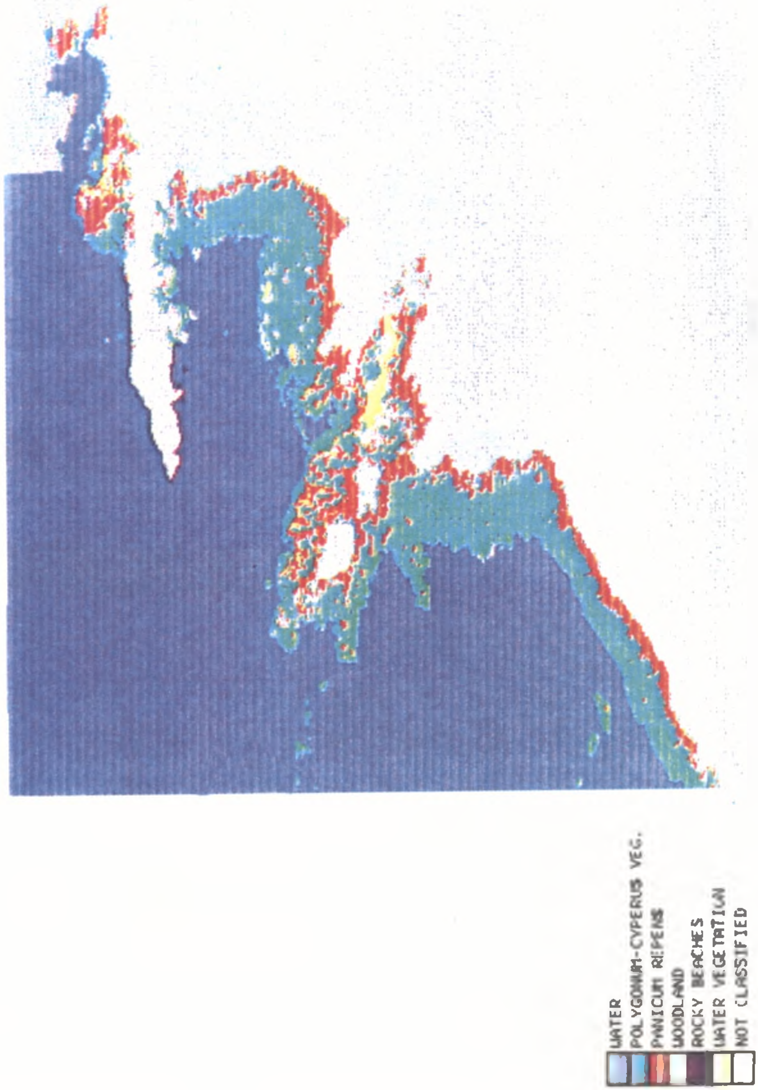


L. KARIBA – 5


NOT CLASSIFIED
PANICUM
SANDY
SEDGES OR WOODLAND
SEDGES OR WOODLAND
WATER
OUTSIDE


L. KARIBA—6
NOT CLASSIFIED
PANICUM
SANDY
SEDGES
WOODLAND
WATER
OUTSIDE

L. KARIBA 7


WATER
POLYGONUM-CYPERUS VEG.
PANICUM REPENS
WOODLAND
ROCKY BEACHES
WATER VEGETATION
NOT CLASSIFIED

Cyperus articulatus - Polygonum senegalense vegetation
Most typical this vegetation is found on fine material, below the *P. repens* vegetation, down to a water depth of a meter or more.

It may, however, also be found on sand, but never far from the water. It rapidly colonizes new ground, seemingly spreading by seeds. A number of sparsely vegetated newly emerged sandy shores and islands indicate that it may be slower in colonizing coarse substrates.

One or usually both species are typically strongly dominant, with a joint cover of ca.100 %. Both species are commonly about 2 m tall, but *P. senegalense* may in deep water attain more than double that height (Ramberg *et al.* 1987). Sedges other than *C. articulatus* often occur mixed in the upper zone, and occasionally also grasses like *Vossia cuspidata, Echinochloa stagnina, Cynodon dactylon* and *Digitaria* sp..

The only large herbivore seen to utilize *C. articulatus* and/or *P. senegalense* was elephant. Impala and roan, grazing in the outskirts of this vegetation, seemed mainly to take grasses and smaller sedges. Egyptian geese were seen to graze fresh shoots and inflorescenses of small sedges, *Cynodon dactylon* and *Digitaria* sp. (M. Eriksson pers. comm.).

Ludwigia stolonifera vegetation
This vegetation merges both in the field and in the ordination with the *C. articulatus-P. senegalense* type. The *L. stolonifera* vegetation is characterized by low sedges and grasses and dicotyledonous herbs like *Ludwigia stolonifera, Euclipta alba, Phyla nodiflora* and *Alternanthera* sp.. This vegetation is found in a species poor variety, on well protected fine material heavily trampled and disturbed by game, and also in a more luxuriant form along tributary rivers. The cover of the species poor vegetation is 10–50%, of the species rich one 50–100%.

The species poor and species rich types were not separated by TWINSPAN with the number of divisions requested. The *L. stolonifera* vegetation type occupies only small areas, and was not distinguished in the satellite data.

Annual vegetation on rocky shores
The rocky shores were characterized more by the sparseness of vegetation than by a particular species composition. Annual species dominate, rooted in sand or gravel often deep down between the rocks. Particularly in the highest zone, there are some perennials as *Panicum repens, Heteropogon contortus* and seedlings and saplings of mopane. The cover is typically less than 30%, often only 10 %, and the height 20–70 cm. This type was divided in two by both TWINSPAN and CCA (see Figure 5.1):

- 4a characterized by *Aristida* spp. and *Cynodon dactylon* and
- 4b by *Rhynchelytrum repens* and *Sesamum* sp.

Similar vegetation is found on newly emerged sandy or gravelly beaches and islands where *P. repens* has not yet developed. Resampling of a number of the plots two or more times also showed high variation in time, as is common in annual assemblages.

Phragmites reeds
A small cluster of three relevees was composed of the only sample from a reed bed with *Phragmites* sp. plus two species poor grassy plots.

Evaluation of the above-ground biomass

The plots cut for biomass determination included grazed and ungrazed swards of *P. repens*. The average oven-dried above-ground biomass was 462 g m^{-2}. Standing crop was 792 g m^{-2} for little grazed swards and 132 g m^{-2} for heavily grazed ones. For *C. articulatus and P. senegalense* vegetation the average standing crop was 1240 g m^{-2}. For the other types, i.e. *Ludwigia stolonifera* vegetation (3), the annual vegetation on rocky shores (4a and 4b in Figure 5.1) and *Phragmites* reeds (5), lumped together 192 g m^{-2}.

Interaction between *P. repens* and large herbivores

In intensely grazed areas, shoots of *P. repens* were low in stature with short internodes, sometimes to the extent that the leaves seemed to grow directly in rosettes from the rhizomes and no culms could be distinguished (Table 5.2). One-factor analysis of variance showed significant correlation with grazing pressure of all measured variables.

Table 5.2 Mean values and standard error (between brackets), for measured variables in *Panicum repens* with different relative grazing intensities. 95% significance (Fisher PLSD and Sheffé F-test) indicaded by letter

relative grazing intensity	*shoot density (no m^{-2})*		*shoot length (cm)*		*leaves per shoot (no shoot)*	
low	583	(153)	58	(3.9)	9	(0.5)
medium	612	(188)	9	(1.2)	5	(0.5)
high	8205	(1780)	4	(0.2)	5	(0.3)
relative grazing intensity	*live leaves per shoot (no shoot)*		*leaf length (mm)*		*leaf width (mm)*	
low	8	(0.3)	127	(12.2)	5	(0.2)
medium	5	(0.5)	41	(9.6)	5	(0.2)
high	4	(0.3)	25	(1.3)	4	(0.1)
relative grazing intensity	*LAI (m^2 m^{-2})*					
low	1.2	(0.4)				
medium	0.5	(0.2)				
high	1.8	(0.6)				

Density of shoots was higher and width of leaves less with heavy grazing than with medium and low grazing pressure. Shoot length, internode length, leaf length, number of leaves and green leaves per shoot were higher in areas with low grazing pressure than in such with medium or high (Table 5.2). There was no difference in leaf area index with grazing pressure.

The rhizomes of *P. repens* varied in internode length between sites from ca. 32 mm to 15 mm, without any clear relation to intensity of herbivory. Rhizome width varied little and was between 2.5 and 3.5 mm for most sites. The bulblike outgrowths up to ca. 15 mm in diameter, presumably containing stored carbohydrates, were only seen on rhizomes in not or lightly grazed vegetation. The depth of the rhizomes varied between 2 and 40 cm, seemingly increasing with height of the locality above the lake surface.

INTERPRETATION AND DISCUSSION

Vegetation types

The previously barren sandy and silty shores of Lake Kariba are now largely occupied by dense and highly productive vegetation. The exposed rocky shores have no preconditions for any denser plant cover; on the contrary, continuing erosion of fine material from between rocks may lead to further reduced vegetation cover.

The *P. repens* vegetation has been confined to the draw down zone. When the study was performed, the upper part of that zone had not been inundated for four years, and the vegetation showed signs of a beginning succession towards mopane woodland.

The *C. articulatus and P. senegalense* vegetation became common around the lake only since the rapid drop in the lake level, similarly to *P. senegalense* in the Ikowa reservoir in Tanzania (Backéus 1993) . If the lake level remains low, *P. repens* may expand downwards, and soon meet the *Cyperus-Polygonum* vegetation, leading to competition for space and other resources. Both communities grow in the transition zone between land and water, but the *Cyperus-Polygonum* vegetation was never found as far inland as *P. repens*. *P. repens* grows mainly on sandy soils, whereas *C. articulatus* and *P. senegalense* are primarily found on finer substrate. The distribution pattern may, however, be a result of most newly exposed areas open for colonization by vegetation being on fine material, rather than a preference for certain substrates. Where wave action is noticeable, the fine material may continue to erode, making the new shore increasingly sandy. If, on the contrary, the lake level rises again, the *Cyperus-Polygonum* vegetation will be drowned and if it has not the ability to move into the existing *Panicum* vegetation, it may decrease drastically, as happened for *P. senegalense* in the Ikowa reservoir (Backéus 1993).

Although the vertical pattern of vegetation along the shore was not studied in detail, it is obvious that the vertical zonation characterizing the vegetation in the mid–1960's (Magadza 1970) is much weakened.

This may be caused by most plots not having been flooded for 2–4 years. Vegetation patterns are large scale, and the only obvious zonation is where the *Cyperus-Polygonum* vegetation occupies the recently emerged bottoms below the *Panicum* grasslands, and on sandy and rocky shores where the uppermost parts show a species change towards a woodland not influenced by the fluctuating water.

The draw-down zone is a typical ecotone, i.e. a boarder zone characterized by a fluctuating environment rather than by a successive gradient as in an ecocline (van der Maarel 1990, Backéus 1993). The large-scale spatial pattern of fairly homogeneous vegetation types along the shores is a characteristic of ecotones (van Leeuwen 1966 in Backéus 1993). Ecotones are generally poor in species, as is the case with most vegetation in the present study. The increase in species number close to the highest water level, that has been above the flooding for four subsequent years, suggests a succession towards a vegetation unaffected by water level fluctuations. The relatively species rich vegetation along some tributary rivers is not influenced by the lake level fluctuations, but by a less variable moisture gradient, perhaps with more traits of an ecocline.

The above-ground biomass

Taylor (1985) studied the above-ground peak standing crop of *P. repens*, in Matusadona National Park at Lake Kariba and found considerable variations between years and sites. Ungrazed *P. repens* in the floodplains typically had a peak standing crop of more than 1000 g m^{-2} of dry matter. This is more than indicated by this pilot study. The difference may depend on decreasing productivity of the floodplains with the reduced inundation frequency resulting from the low lake level during this study.

Peak standing crop is always less than net seasonal production, due to losses to small and large herbivores and litter. If standing crop, however, is used as a rough indication of minimal production, it would, multiplied by the area estimations by Surell (1987) (Table 5.1), imply that about 50,000 metric tonnes of *P. repens* shoots are produced each year on the Zimbabwean shore of Lake Kariba. The corresponding figure for the *Cyperus-Polygonum* vegetation would be 100 000 tonnes, and for the other shores 5,000 tonnes. Above-ground net production (as different from standing biomass) of grasses is most often similar or higher in moderately grazed areas compared to ungrazed ones (Vickery 1972, McNaughton 1983, Oesterheld and McNaughton 1991); therefore, the standing crop from the ungrazed grasslands was used for the calculation of total biomass of *P repens*. However, it should be stated that these figures are only indications of the order of magnitude.

Vegetation and large herbivores

Herbivory has a number of direct and indirect effects on resource allocation and growth form in plants (Crawley 1983, Detling and Painter 1983, Oesterheld and McNaughton 1988 and 1991). The causal relationship between the growth form of *P. repens* and grazing by large herbivores at Lake Kariba can not be certified without an experimental study, e.g., with exclusures, which was not feasable in the present project. The observed differences in growth form between grazed and ungrazed swards agree, however, well with grazing induced differences recorded in other studies. Peterson (1962) lists shortened internode length, prostrate green leaves, reduced leaf size and depleted carbohydrate reserves among the typical effects of grazing on grasses. McNaughton (1984) found higher shoot density and smaller canopy height, internode length and leaf length in grazed areas as compared to exclusures. One or more of these effects of grazing are also shown by Vesey-Fitzgerald (1969), Grant *et al.* (1981), Oesterheld and McNaughton (1988), O'Connor (1994).

Exchange between terrestrial and aquatic systems

There is strong interaction between the lake and the vegetation and soil in the draw-down zone. The good moisture supply as well as the high rate of herbivory also speed up decomposition rate and nutrient turn-over, which is the base of the high biological productivity in the geolittoral zone, and also supplies nutrients to the lake itself.

Biomass may be washed into the lake as more or less intact plant-or animal parts and decompose in the water; biomass may decompose on land and leak organic or inorganic substances to the water during inundation periods, or nutrients may be transported to the lake by particle erosion or in solution in surface run-off of rain water.

Animal activities contribute to the exchange of energy and nutrients between the lake and the terrestrial surroundings. Herbivory speeds up the carbon and nutrient turn over, and may increase the leakage of nutrients during inundation. Most of the biomass eaten is excreeted as urine and dung, which mineralizes much faster than plant litter. Dung can also easily be carried away intact by the water. Taylor (1985) estimates that at least 60% of the seasonal above-ground production of *P. repens* is grazed by large herbivores.

Hippopotamus has a particular impact on flows between land and water. Hippos are almost entirely grazers, and feed on land during the night, but leave most of their dung well scattered in the shallow water, where they rest during daytime.

Arman and Fields (1973) evaluated the daily food consumption of hippopotamus. From the demographical structure of a protected population and the individual growth of this animal, it can be infered that the life span is about 15 years and the weight at this age is 1.5 tonne (Arman and Fields 1973). As an average, such an animal eats 14 kg (dry weight) of grass per day, e.g. 5.11 tonnes per year. The digestion rate is 35% dry weight. Consequently about 3.32 tonnes (dry weigth) of plant material are released yearly into the water as dung by each individual in Lake Kariba.

Assuming that about 3,000 hippos (Taylor unpublished data) are living on the Zimbabwean shore of Lake kariba, their plant consumption would be 15,330 tonnes which represent 30% of the crop production of *P. repens* which is their main food source near Lake Kariba.

Hippopotamus also stirr up the bottom material while moving around in the water, promoting a high aquatic primary production. Hippos move along preferred paths between grazing lawns on land and the water, the paths often eventually becoming narrow water-filled channels increasing the length of the shore line and thus the contact surface between water and land.

CONCLUSION

The SAREC/UZ Project on Ecology of Lake Kariba has contributed to some basic knowledge on the composition of vegetation communities in the draw-down zone at the end of the 1980's, and has given some indication on the amount of above-ground phytomass production. Through the study by Surell (1987) the most important vegetation- or shore types were mapped and their extension estimated. The interactions between the geolittoral zone and the lake is hypothesized to consist primarily of nutrients and energy transfers, directly through the lake inundations and indirectly through animal activities. The next step is to quantify the flow between land and water, and to rate the significance of different processes, including the activities of hippopotamus and other large herbivores.

SUMMARY

This contribution is a study of the vegetation of the "draw-down zone" e.g., the area between highest and lowest water level in a reservoir, of the artificial Lake Kariba. It provides a description of the evolution of the vegetation before and after the closure of the dam.

Among the plant species that dominated the shore vegetation during the present study, *P. repens*, *C. articulatus* and *P. senegalense* are particularly considered. Their

distribution is analysed using classification and ordination methods and related to various ecological factors. The *P. repens* vegetation has been confined to the draw down zone. The *C. articulatus-P. senegalense* vegetation became common around the lake only since the rapid drop in the lake level. The distribution pattern may be a result of most newly exposed areas open for colonization by vegetation being on fine material, rather than a preference for certain substrates.

The average estimated above-ground biomass of *P. repens* was 462 g m^{-2} (dry weight). Standing crop was 792 g m^{-2} for little grazed swards and 132 g m^{-2} for heavily grazed ones. For *C. articulatus-P. senegalense* vegetation the average standing crop was 1240 g m^{-2}.

An estimate of about 50,000 metric tonnes of *P. repens* shoots are produced each year on the Zimbabwean shores of Lake Kariba. The corresponding figure for the *Cyperus-Polygonum* vegetation would be 100,000 tonnes, and for the other shores 5,000 tonnes.

The interactions between vegetation and grazing large herbivores are briefly outlined even if the causal relationship between the growth form of *P. repens* and grazing by large herbivores at Lake Kariba can not be certified in this project.

Exchanges between terrestrial and aquatic systems through the draw-down zone are also described. A high rate of herbivory and the animal activities in general contribute to the exchange of energy and nutrients between the lake and the terrestrial surroundings. Herbivory speeds up the carbon and nutrient turn over, and may increase the leakage of nutrients during inundation, mainly through excretion. In this aspect, the impact of hippopotamus is particularly considered.