

Zonation of submerged vegetation in Lake Kariba, Zimbabwe and its  
ecological interpretation.

Lake Kariba Fisheries Research Institute

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By

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## KEY WORDS

Lake Kariba, TWINSPAN, Principal components analysis, Canonical correspondence analysis, Ordination, competition, growth form.

## ABSTRACT

The submerged vegetation of Lake Kariba is described in relation to degree of slope (lake morphometry), depth and light transparency. The direct gradient analysis technique - canonical correspondence analysis and the TWINSPAN classification programs were used to analyse the data set. The western end of the lake with low transparency has a low species diversity (with Vallisneria aethiopica dominating). Species diversity increases with increased transparency in the other parts of the lake. The classification revealed monospecific communities for all species as well as mixed communities with Lagarosiphon as the associate species with the broadest distribution. The ordination revealed a first axis strongly related to the depth and transparency gradients and the second axis related to slope. Vallisneria aethiopica has a growth form adapted to grow in shallow areas subjected to wave action. Potamogeton octandrus also growing in shallow areas is restricted to sheltered areas. Lagarosiphon ilicifolius precluded from the shallow exposed areas grows at medium depth but has a growth form adapted to tap light at the surface. Najas pectinata and Ceratophyllum demersum are adapted to grow in deep water.

## INTRODUCTION

This paper deals with the community pattern of the submerged vascular vegetation and its relation to environmental gradients, as studied in Lake Kariba, Zimbabwe. Multivariate techniques for classification and ordination can be used to explain community structure (Robertson, 1978; Van der Maarel, 1979; Greig-Smith, 1983 ), and to generate hypotheses about community structure and environment interactions (Swaine & Greig-Smith, 1980; Greig-Smith, 1983; Ter Braak, 1986 , 1987).

Few applications of numerical classification and ordination to aquatic vegetation have been published ( Seddon, 1972; Howard- Williams & Walker, 1974; Jensen, 1978, 1979 ). Apart from a few cases in Africa, the patterns and processes governing aquatic littoral vegetation are not well understood ( Gaudet, 1981; Howard-Williams & Walker, 1974).

Studies in temperate water bodies tend suggest that light (Spence et al, 1971; Spence, 1973; Lloyd et al, 1977; Segal, 1971 ) and competitive interactions between the various species ( Grace & Wetzel, 1981; Andrews et al, 1984 ) are major factors determining the distribution of aquatic macrophytes.

### THE STUDY AREA

The study was carried out in Lake Kariba ( 16° 28' - 18° 06' S ; 26° 40' - 29° 03' E ) (Fig. 1 ). The lake is shared between Zambia and Zimbabwe and has an area of 5 250 km<sup>2</sup>. The lake exhibits a complex and varied shoreline with gentle and steep slopes; sheltered and exposed, sandy, rocky and muddy shores as well as bottoms cleared of trees and uncleared once. The lake which filled was made in 1963 by damming the Zambezi River. It has a mean annual draw down of 3m and is subdivided into 5 hydrological basins. The hydrological gradient is largely determined by the Zambezi River which contributes 70% of the lake's inflow. See further Machena & Kautsky (1987 ).

### MATERIAL AND METHODS

#### (i) Field analysis

The study was carried out along 18 vertical transects (Fig. 1) which were spaced to cover the hydrological gradient and all shoreline types along the whole length of the Zimbabwean shore.

The S.C.U.B.A. ( Self Contained Underwater Breathing Apparatus ) diving technique was used in the sampling. Along each transect diving was carried out by two divers in two phases, and sampling was done as recommended in Dybern et al (1976) and elaborated in Kautsky et al (1981). On diving from the shore, the following were recorded:

distance from the shore; depth; species composition; cover of the vegetation by a visual estimation of bottom surface cover and the approximate extent of each homogeneous belt.

Quadrats (0.5 x 0.5m) were placed on the bottom in a stratified manner and 2 to 3 samples were taken in each defined belt. Randomisation within the strata was achieved by swimming towards the surface and dropping the frame. The quadrat size used is the quickest and most efficient sample unit in sampling benthic vegetation by S.C.U.B.A. diving (Pringle, 1984).

The vegetation data used in this paper are % cover values and the environmental variables measured are: secchi-disc transparency (m); degree of slope (%) and depth of vegetation colonisation (m). Secchi disc depths were taken within each basin from Basin 1 to Basin 5 (Fig. 1), along the main axis of the lake. Degree of slope and depth of colonisation were taken at each transect from shore to deep water.

#### (ii) Data analysis

Usually there is a need to transform cover values before further analysis because of their large range and the implied emphasis on dominants in multivariate methods (Van der Maarel, 1979; Jensen & Van der Maarel, 1980; Gauch, 1982).

Jensen (1978) discussed the effect of various transformations of cover values on the interpretability of both classification and ordination of lake vegetation and stressed on the need for transformation.

Three computer programs were used to analyse the data set. Two of the programs TWINSpan (Hill, 1979a) and CANOCO (Canonical correspondence analysis - Ter Braak, 1986) transform the data by standardization. In the third program ORDINA (Principal components analysis) the data were transformed into a 1-9 scale (Van der Maarel, 1979). The results of this ordination did not provide new insight in the data structure and will therefore not be presented here.

#### (a) TWINSpan

TWINSpan is a polythetic divisive method of classification by a

continued dichotomy of reciprocally averaged data. Three "pseudospecies" cut levels of 1%, 25%, and 75% were used.

Pseudospecies with 75% cover or more in a plot were considered dominant in that plot. This is convenient in largely monospecific vegetation.

In the Lake Kariba study, the vegetation revealed much monospecific zonation, but where two zones merged the species mixed to various degrees. It was in the mixed zones that the pseudospecies cut levels were found practical.

#### (b) CANOCO

Canonical correspondence analysis (CCA) is a modified form of (detrended) correspondence analysis (Hill, 1979b); it is a technique for multivariate direct gradient analysis (Ter Braak, 1986).

CCA provides ordination axes that maximally show the relationship between the vegetation and the environment because the ordination axes are "constrained" to be linear combinations of the environmental variables. Detrending is optionally incorporated in the CCA technique and the program leads to an ordination diagram in which points represent species and sites; and vectors represent environmental variables.

The algorithm gives regression coefficients (canonical coefficients) that define the axes. As many constrained axes can be extracted as there are environmental variables though often most of the variation extracted may be concentrated in the first few axes. If desired a higher-numbered axes may be defined as "residual axes" reflecting the floristic variation not accounted for by the environmental variables. Here, I have extracted the maximum number (three) of constrained axes and a fourth residual axis.

### RESULTS

#### (i) TWINSPAN classification

On the basis of TWINSPAN classification with 3 pseudospecies cut

levels and 6 levels of division, there are 27 groupings (Fig. 2). The first level of division had Vallisneria as indicator species (Fig. 2).

The Vallisneria group is largely monospecific, with no less than 115 "monospecific plots". The subsequent divisions of this group led to different Vallisneria groupings with different cover values, and mixtures with other species. With respect to the other main group, subsequent divisions led to both monospecific and mixed groupings, where each of the remaining species served as an indicator (fig. 2).

On the whole TWINSpan leads to monospecific communities of the 5 recorded species - P.octandrus, C.demersum, L.ilicifolius, N.pectinata and V.aethiopica. Beside these monospecific communities are the various possible combinations of the species to result in the various mixed communities. Lagarosiphon forms more mixed communities than other species and in fact mixes with all the other species. On the other hand Potamogeton does not mix with Ceratophyllum and Najas.

#### (ii) CCA ordination

Fig. 3 presents the graphic representation of the canonical correspondence analysis for axes I and II. Community structure and distribution along the 3 environmental variables are clear.

Table 1 shows that axis I represents both a depth and a transparency gradient and it accounts for 66.5% of the extracted variation. Axis II relates strongly to slope and accounts for 20% of the extracted variation. It follows that of the environmental factors measured, depth and transparency are by far the most important in the structuring of the submerged vegetation of Lake Kariba. Axis I explains most of the distribution of Vallisneria, Lagarosiphon and Najas and part of the variation for Potamogeton and Ceratophyllum. Axis III is unimportant, accounting for only 5% of the variation. Some other environmental factors (which had not been measured) are presumed to be important in the distribution of Potamogeton which dominates axis IV, the residual axis (Table 2).

Since transparency was measured along the main axis of the lake, from Basin 1 to Basin 5 (Fig. 1) and depth was measured on transects from shore to deep water, axis I represents both a geographical

(transparency) and a depth gradient.

(iii) Community pattern in the CCA ordination

Najas and Ceratophyllum occur in habitats with high transparency mainly in the central and eastern parts of the lake (Fig. 4) whereas Vallisneria and Potamogeton occur in habitats of low transparency found in the western parts of the lake. Lagarosiphon takes an intermediate position.

Najas and Ceratophyllum occur in deeper water whereas Potamogeton and Vallisneria occur in shallow water habitats. Again Lagarosiphon takes an intermediate position. The picture of the vertical distribution of the vegetation is similar to that drawn from direct observations (Fig. 5).

Ceratophyllum is the only species that relates strongly to slope on axis II. Ceratophyllum occurs in deep water and occupies habitats of high transparency, while also being confined to steep slopes.

Fig. 3 indicates the "centres" of species distribution (marked by letters). These mark the sites where the species dominate. The differential positions of the "centres" of different species along the depth gradient reflects zonation. Between these "centres" there is a varying degree of mixing between the species. Fig. 3 shows that the Lagarosiphon community occurs near the centroid in the analysis or the centre of gravity in the community composition. This indicates that Lagarosiphon is the most abundant species and has the ability to mix with the other species, whereas Vallisneria, Potamogeton, Ceratophyllum, and Najas are found towards the extremes of the 3 environmental gradients measured, Lagarosiphon mixes along all of them.

DISCUSSION

As CCA relates the ecological amplitudes (response curves) of the different species to the weighted environmental variables, the ordination diagram visualises the response of the species to the variation in specific environmental factors (Ter Braak, 1987). For example, the main gradient in Fig. 3 fits the profile in Fig. 5. The



position of the species centres along the ordination axes represents their respective optima along the environmental gradient.

Peripheral species along the axes indicate narrow distributions and stronger indicator potential (Hill, 1973; Gauch et al, 1977). In the CCA diagram Vallisneria, Potamogeton, Ceratophyllum and Najas are therefore species with restricted niches with respect to the environmental variables measured. On the other hand Lagarosiphon, as indicated by its central position in the gradient, should have a broad environmental tolerance (Gauch, 1982) and this is reflected in its capacity to mix with all other species.

The community structure as obtained in the TWINSpan classification, is found back in the CCA ordination: zones with monospecific communities separated by zones with mixed communities. Of particular interest is the zonation of the vegetation, along the depth gradient. Where vegetation stratification is evident, competitive exclusion is likely to take place. Goldberg & Werner (1983) argue for an equivalence of competition among species within a community, but where gradients are marked competitive exclusion takes place (Grace & Wetzel, 1981, 1982). Rydin (1985) gives an elaborate picture of competitive exclusion among Sphagnum species along a topographic gradient from hummocks to hollows. Mueller-Dombois & Ellenberg (1974) and Grime (1983) point out that plants of a low growth rate are commonly displaced from their physiological optimal habitats, because other plants with faster growth rates may find their optimal conditions on the same habitat. Plants that are pushed to the extremes of an environmental gradient do not necessarily prefer those extreme conditions; alternatively they may be able to survive because they have greater ecological tolerances for these environmental conditions (Mueller-Dombois & Ellenberg, 1974).

In Lake Kariba, with a depth gradient (Fig. 5) Ceratophyllum and Najas, must tolerate habitats with low light availability because they grow in deep water.

Vallisneria and Potamogeton growing in shallow water are adapted to have higher light availability but are susceptible to wave action. Wave action would also affect any other species that occurs near the shore. The differences in the growth forms between these plants

entails a different response to wave action. Vallisneria has a short growth form, with the shoot only a few centimeters above the substratum, therefore having its major biomass near the sediment surface. The effect of waves on Vallisneria is to truncate the leaves, while the shoots are often not harmed, and because of firm attachment the plants are not uprooted. Vegetative reproduction through rhizomes is also an adaptation to growing in shallow areas. The vegetative shoots, are firm and resist uprooting through waves because they are attached to their mother plants. Ward & Talbot(1984) report Isoetes alpinus in Lake Alexandria ( New Zealand) to respond in a similar way to wave action, with truncation in exposed areas. Vallisneria, having its major biomass at the sediment surface, is unable to compete in deep water where irradiance is low. It is therefore restricted to shallow waters where it is a better competitor because of its adaptation to withstand wave action. Monospecific Vallisneria communities can be very extensive and very dense (V3 on Fig.2) or they could be much less dense (V2 or V1 on Fig. 2). The height of the Vallisneria plants (length of leaf from point of intersection with shoot to the apex), is determined by the physical characteristics of the bottom substrate and wave action. The height varied as much as from 50cm on soft bottoms in protected shores to 3cm on rocky and exposed shores.

Potamogeton growing in shallow water as well, is heterophyllous (with floating leaves), has tall slender stems with little branching and few rhizomes. The floating leaves are structurally and physiologically similar to the leaves of terrestrial plants adapted to a high light conditions (Barko et al,1982). Potamogeton can therefore grow in turbid waters but the tall stems make it susceptible to wave action and the species is therefore restricted to sheltered areas.

A well developed Lagarosiphon community has a forest like structure of tall slender stems (up to 4m high) rising to a dense canopy at the water surface. Branching which normally begins within 0,5m from the surface can be very intense and a thick mat is formed so that the bulk of the photoreceptive biomass is near the surface (where there is more light ). The leaves are many and small ( 1cm long ).These are spirally arranged around the stem. Although roots are developed, they only provide a weak attachment to the substratum. The tall growth form, with the bulk of the biomass is near the surface and the

numerous small leaves (increasing surface area ) are adaptations to growing in deep water with reduced light availability ( Duarte et al, 1986). Lagarosiphon is truncated by wave action and is therefore restricted to protected shores and deep water. Canopy formation at the surface effectively occludes light from deeper water (Grime, 1983), and non - canopy forming species like Najas and Ceratophyllum are outcompeted in this respect. Light is attenuated exponentially with depth within the macrophyte canopy (Westlake, cited in Carpenter & Lodge, 1986). In monospecific Lagarosiphon communities, the density is variable (L3, L2 and L1 on Fig. 2) depending on the physical characteristics of the substratum.

Najas and Ceratophyllum communities look much like the Lagarosiphon community with the important difference that branching occurs at all levels, creating an impenetrable vegetation. These respond in much the same way to wave action as Lagarosiphon but grow in deeper water as they are outcompeted for light by Lagarosiphon. They are therefore shade tolerant. Growth of Ceratophyllum is dependent on nutrient uptake from the water medium only, because it is not rooted. In nutrient poor waters Ceratophyllum would be a poor competitor with other species that supplement their nutrient requirements from sediment uptake (Spence, 1982). It is quite clear from Fig. 3 that Ceratophyllum is pushed to deep water and steep slopes.

In the terminology of Grime (1983), with respect to plant strategies in the vegetative phase, Lagarosiphon is a competitor, whereas Najas, Ceratophyllum and Vallisneria are stress tolerators.

A number of reasons have been advanced to explain the co-existence of different species e.g. different life strategies at both the regenerative and vegetative phases (Grime, 1983) and habitat differentiation (Newman, 1982). In both cases, the species differ in their response to environmental factors. The existence of monospecific stands of Potamogeton within the Vallisneria zone points to the availability of different physical environments in the zone. In Europe Zostera marina and Z. noltii co-exist as mosaics of monospecific stands. Verhoeven et al (1982) explain this by the availability of different physical environments. It is much less clear which factors are causing differentiation in the areas where the communities are really mixed. Outside microhabitat differentiation, perhaps different

life strategies are crucial.

Along the transparency gradient (i.e. along the main axis of the lake) Vallisneria and Potamogeton occur largely in the eastern part of the lake (Fig. 1). This is the end of the lake where the Zambezi River flows in. Seventy percent of the lake's inflow is from the Zambezi River ( Begg, 1970 ). For six months of the year when this river is in flood, transparency precludes the growth of vegetation except Vallisneria which is restricted to a very narrow belt along the shore. This belt is shallow enough to permit sufficient light for this plant. Other species do not grow in this belt probably due to wave action.

This study has shown that the distribution of vegetation in lake Kariba is largely dictated by the environmental gradients of light, depth and degree of slope. Slope in this study is taken as an index of lake morphometry.

Lake morphometry is important since sediment characteristics ( e.g. soil particle size ) and wave action depend on it. The area covered by vegetation (and therefore the biomass ) is inversely related to slope ( Duarte et al, 1986 ). Light availability, sediment characteristics, lake trophy and lake morphometry are believed to be the major determinants of macrophyte cover and biomass ( Duarte et al, 1986 ). Light and depth are (inversely) correlated. Along the gradients measured, the vegetation is stratified in monospecific and mixed belts. I suggest that the stratification of the vegetation along the environmental gradients is maintained by competitive exclusion or displacement. There are some areas where a whole transect is colonised by one species, e.g. Lagarosiphon at station 8 ( Figs. 1 & 4 ); in the presence of other species Lagarosiphon does not colonise the whole transect ( e.g. station 5 ) but occupies a limited zone, probably due to competitive displacement. It can be argued in the presence of other species Lagarosiphon occupies a limited depth interval, its realised niche but has a potential to occupy a whole depth interval, its fundamental niche. However, the species that do not mix e.g. Potamogeton and Ceratophyllum and Potamogeton and Najas, probably do not do so because they occupy opposite ends of environmental gradients.

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TABLE 1 : Kariba species data: canonical coefficients (regression coefficients of the ordination axes) and the correlations of the environmental data with the first 2 axes.  
 Option : 2 ordination axes related to 3 environmental variables.

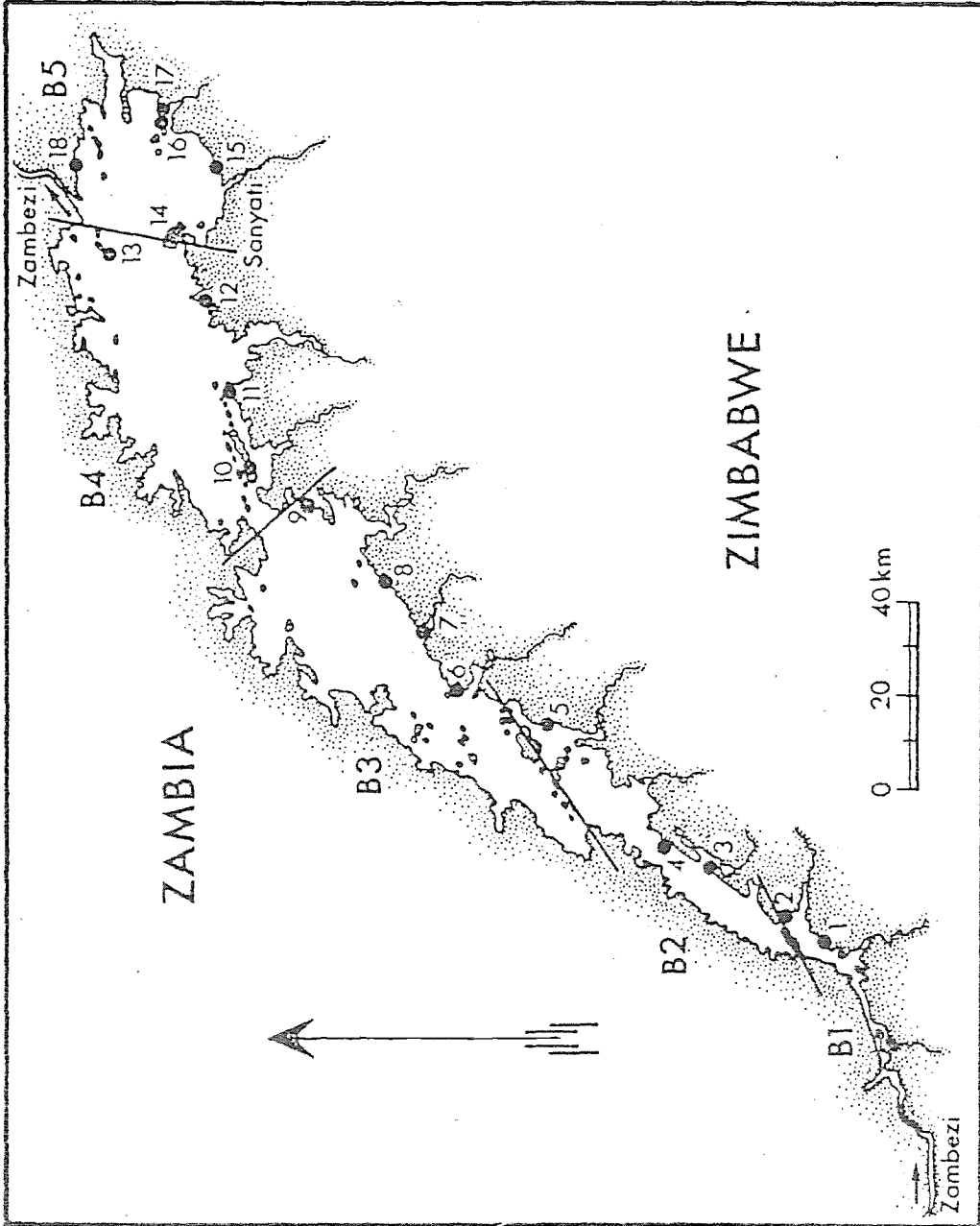
<u>AXIS</u>	<u>COEFFICIENTS</u>		<u>CORRELATIONS</u>	
	1	2	1	2
Eigen value	0,66	0,38		
<u>VARIABLE</u>				
Depth	8,05	2,25	0,85	0,67
Slope	-2,86	4,92	0,007	0,88
Transparency	6,82	0,87	0,83	0,38

TABLE 2 : Species scores and eigen values in the CCA ordination of Lake Kariba vegetational and environmental data. Option : 3 ordination axes related to 3 environmental variable, one residual axis.

AXIS	1	2	3	4
EIGEN VALUE	0,41	0,10	0,02	0,90
SPECIES SCORE:				
<u>M. pectinata</u>	19	-12	11	-5
<u>C. demersum</u>	17	43	15	9
<u>L. illicifolius</u>	4	0	-10	5
<u>V. aethiopica</u>	-14	0	3	-14
<u>P. octandrus</u>	-17	-14	31	236

## Legends to Figures

- Figure 1. Map of Lake Kariba showing divisions between major basins and the sampling stations where diving transects were laid out.
- Figure 2. TWINSpan dendrogram of 279 samples from 18 diving transects along the Zimbabwe shore of lake Kariba. Similar samples are joined at a low level in the dendrogram. Dissimilar samples are not joined until higher levels. Each species served as an indicator species and the respective levels are shown.
- Figure 3. CCA ordination diagram of the submerged vascular vegetation of Lake Kariba with plant species (letters), environmental variables (arrows) and plot numbers. (Identical plots are not shown).
- Figure 4. Distribution of the submerged vascular vegetation of Lake Kariba. Valley 4 designates the western third part of the lake.
- Figure 5. Depth profile of the submerged vascular vegetation of Lake Kariba.



Vall - Vallisneria  
 Pot - Potamogeton  
 Lag - Lagarosiphon  
 Cer - Ceratophyllum  
 Naj - Najas  
 3 > 75 % cover  
 2 25 - 75 % cover  
 1 < 25% cover

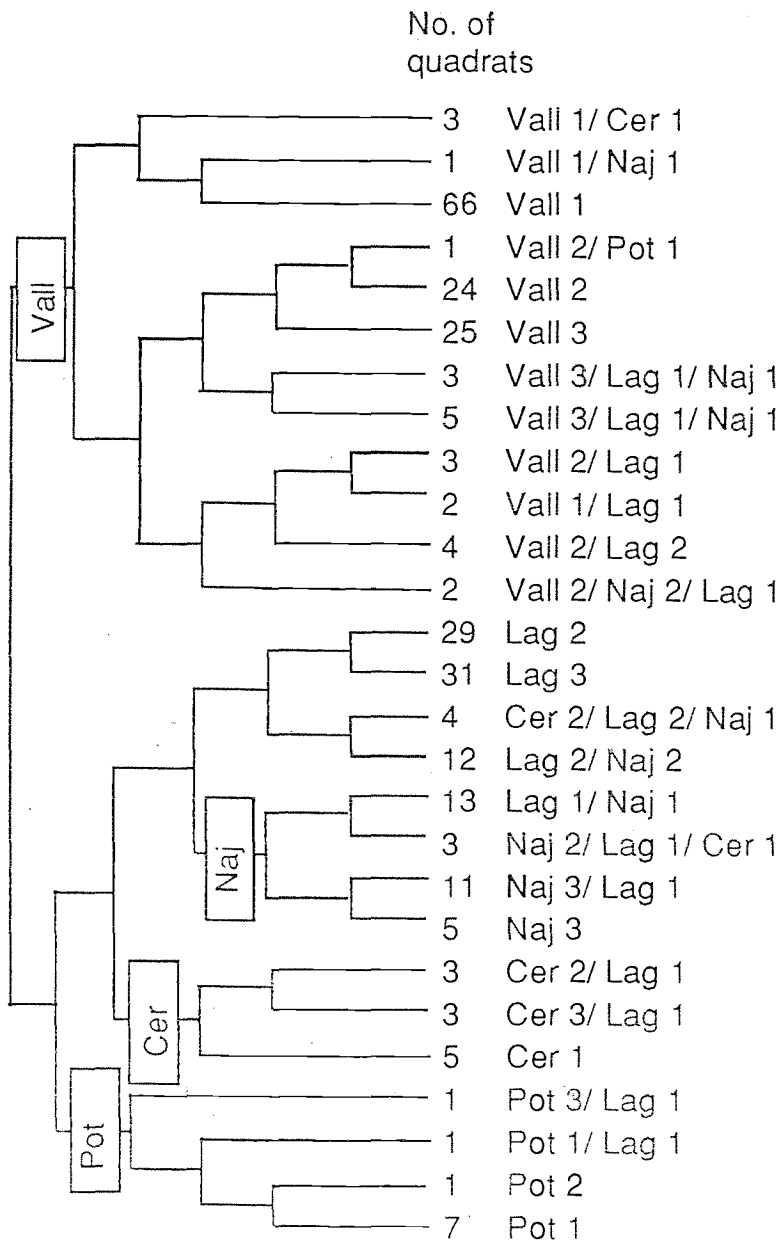


Fig. 2

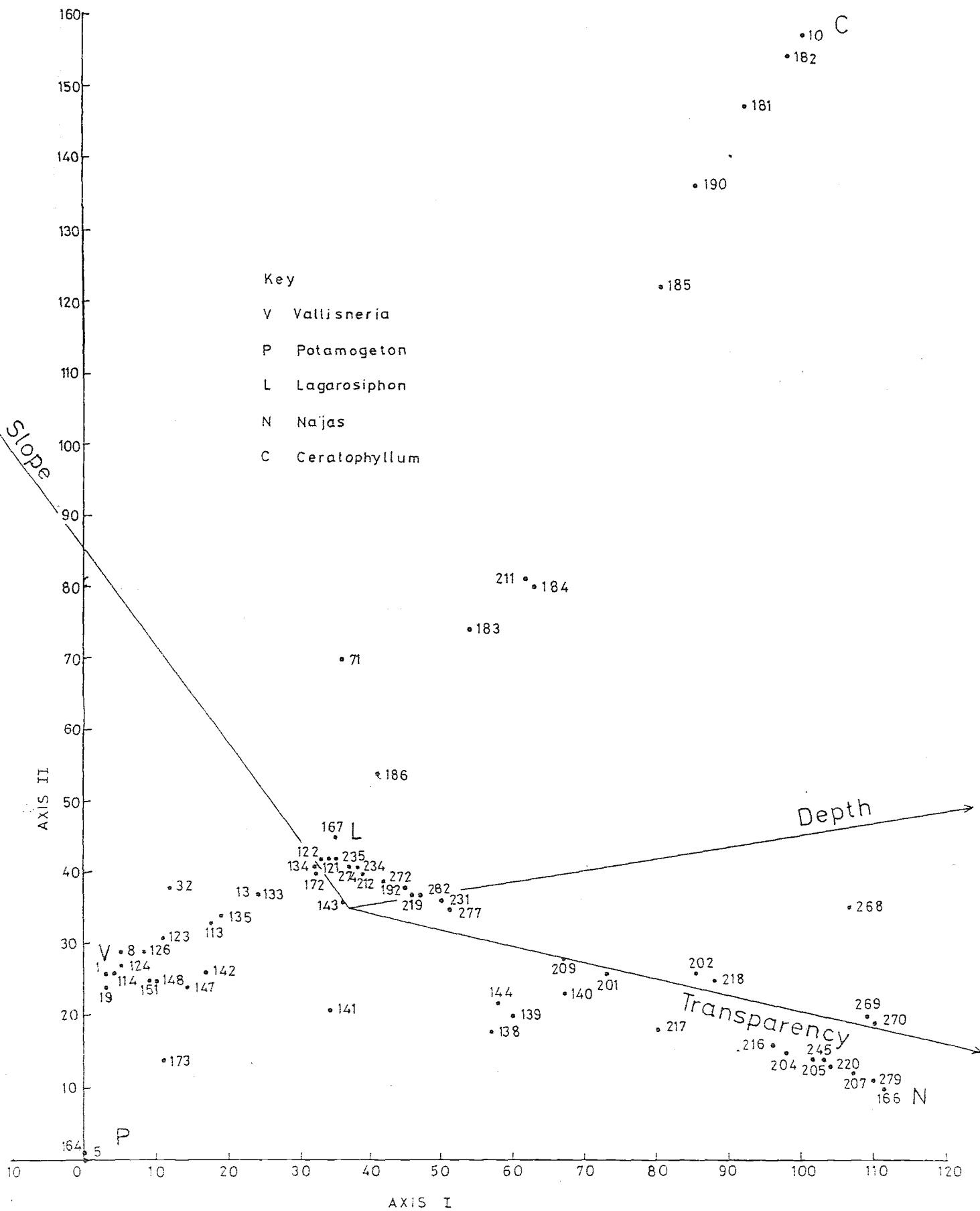


Fig. 3

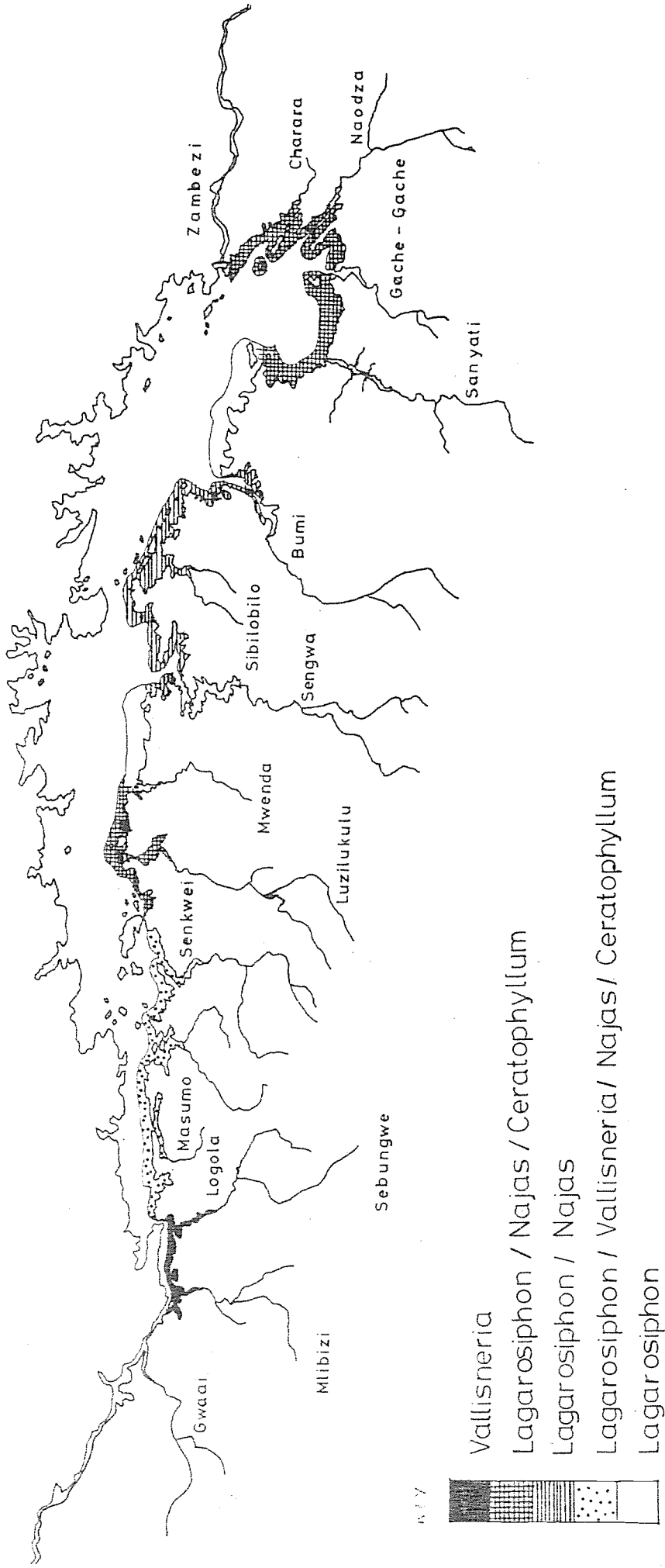
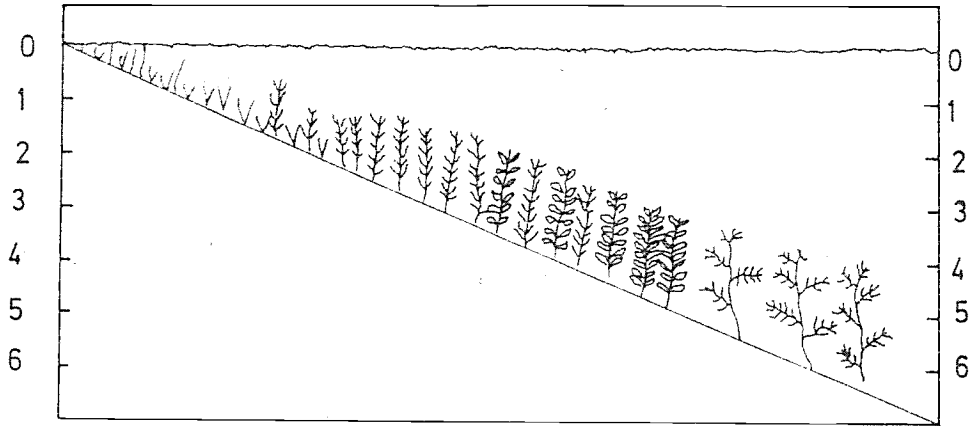


Fig. 4





Key





- VV Vallisneria
-  Lagarosiphon
-  Najas
-  Potamogeton
-  Ceratophyllum

Fig. 5

