ADVANCES IN
THE ECOLOGY OF
LAKE KARIBA

Edited by Jacques MOREAU

Cover and inside photographs supplied by Nils Kautsky and Gertrud Cronberg

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.

ACKNOWLEDGEMENTS

6

THE ORGANIZATION AND PRODUCTION OF THE SUBMERGED MACROPHYTE COMMUNITIES IN LAKE KARIBA

Cecil Machena

INTRODUCTION

Aquatic macrophytes play important roles in the ecology of lakes. At times in large standing crops, they dominate the littoral zone of lakes (Cattaneo and Kalff 1980, Howard-Williams and Allanson 1981, Morgan and Kitting 1984, Denny 1985, Carpenter and Lodge 1986, Machena and Kautsky 1988) forming an important land-water interface. In the process, they benefit animals and lower plants through facilitating sediment stabilization and providing habitat diversity and shelter, as well as being substrata for periphyton and sites of abundant food production for invertebrates and fish (Wetzel and Hugh 1973, Pelican *et al.* 1978, Ramberg *et al.* 1978, Howard-Williams 1981, Machena 1989).

Submerged macrophytes also derive a large proportion of their nutrients from the sediments and simultaneously act as nutrient pumps (Denny 1972 and 1980, DeMarte and Hartman 1974, Best and Mantai 1978, Carignan and Kalff 1980, Carignan 1982, Barko and Smart 1986, Machena *et al.* 1989). In many ways, macrophytes therefore influence the diversity, abundance and population patterns of aquatic invertebrates and vertebrates, fish, crocodiles and birds.

In Lake Kariba, the succession of macrophyte communities has been documented since its formation 40 years ago. The development of vegetation during the early phase of the lake has been described by Mitchell (1969) and Marshall and Junor (1981). In 1959, when the lake was filling, there was a population explosion of the blue-green *Microsystis* and floating rafts of *Salvinia molesta* Mitch., *Pistia stratiotes* L., *Utricularia* spp., and *Lemna* spp. were noticed. In 1960, *Ceratophyllum demersum* L. was noticed as well as the development of an emergent hydrophyte shoreline vegetation, with *Typha* spp., *Cyperus* spp., *Ludwigia stolonifera* Guill. and Perr., *Scirpus cubensis* Poepp. and Kunth, *Phragmites mauritianus* Kunth and *Pycerus* spp. Between 1960 and 1962 there was an extensive growth of *Salvinia* which covered 22% of the lake by 1962 (Mitchell 1969, Marshall and Junor 1981) and by 1964, *Salvinia* had substantially declined. The decline probably followed changes in physico-chemical characteristics of the lake (Coche 1968) and the stabilisation in water level fluctuations that occured.

Benthic macrophytes did not establish until after 1964 due to the rapid rise in the water level during the filling phase of the lake and the extensive cover of *Salvinia* which occluded light to the bottom. In areas where *Salvinia* could not

form permanent mats, such as river mouths, *Ceratophyllum demersum* grew. In 1964, *Potamogeton pusillus* L. established in suitable areas and rapidly colonized depths of up to 4 m.

The stabilisation of water levels made possible for benthic macrophyte and mussel communities to establish. This locked up large amounts of nutrients that had earlier been available for *Salvinia*, which led to a shift from the dominance of floating vegetation to benthic organisms. (Marshall and Junor 1981, Machena 1989).

By 1966, *Potamogeton pusillus*, and *P. schweinfurthii* occupied the depths between 1 and 1.5 m. At depths between 1.5 and 3 m *P. pusillus* was the dominant plant giving way at 3 m to dense stands of *C. demersum* which colonized depths of up to 7.5 m. In 1966, *Lagarosiphon ilicifolius* first appeared in the lake and Donnelly (1969) noted that it was replacing *P. pusillus* in the upper reaches of the lake. In 1969, *Vallisneria aethiopica* (Frenzl) was noticed for the first time. *Najas pectinata* (Parl) was first recorded in 1971 (Bowmaker 1973). Dispersal and colonization of new species may still take place and this may change the current composition of the vegetation.

This chapter deals with the present organization of macrophyte communities, the operative physical factors underlying this organization, their production and the role of these communities in Lake Kariba.

SPECIES DIVERSITY IN LAKE KARIBA

Seven species of submerged macrophytes have been recorded in Lake Kariba (Machena and Kautsky 1988). These species are *L. ilicifolius* Oberm., *Najas pectinata* (parl) Magnus, *Vallisneria aethiopica* Frenzyl, *Ceratophyllum demersum* L., *Potamogeton octandrus* L, *P. pusillus* L. and *P. schweinfurthii* A. Benn. This number of species is low in comparison to other lakes. Eleven submerged vascular species have been recorded in Lake Tanganyika (Coulter 1991). There are twelve species in Loch Leven, Scotland (Jupp and Spence 1977) and 16 species in Lake Memphremagog, Canada (Chambers 1987).

There are probably a number of reasons to explain the low species diversity in Lake Kariba. The hydrolittoral zone is subjected to annual lake level fluctuations of about 3 m, creating a physically unstable habitat (Introduction, this volume). This may be a limiting factor to colonization by many plant species as noted by Grime (1979) and Sousa (1979); a high frequency of disturbance will reduce species diversity or even inhibit species establishment in an area. Generally, plant species that tolerate physically unstable habitats are short-lived and experience non-equilibrium coexistence with their environment (Huston 1979. Sousa 1979. Werner 1979). Successful plant colonizers in unstable habitats need broad tolerance limits to cope with the rapidly changing environment and rapid dispersal mechanisms to colonize new bottoms as environment changes (Gould 1981, Pianka 1981, 1983). In Lake Cahora Bassa (Mozambique), for example, no submerged vascular macrophytes have established in the hydrolittoral zone because of annual drawdowns of up to 10 m (Bernacsek and Lopez 1984). Environments experiencing an intermediate frequency and magnitude of disturbance may have a higher diversity of species because of the suppression of dominance (Grime 1979, Sousa 1979, Keedy and Rednicek 1986).

Competitive interference by *Lagarosiphon* in Lake Kariba could be strong and could also contribute to the low species diversity. *Lagarosiphon* which is canopy forming is dominant in the nutrient rich and less disturbed areas (Machena 1987, Machena and Kautsky 1988). Competitive canopy-forming species often dominate completely (in their suitable habitats) because of their capability to elongate and concentrate their photoreceptive biomass at the water surface (Barko and Smart 1981, Duarte and Kalff 1987, Chambers and Kalff 1987, 1990).

PRESENT DISTRIBUTION, ABUNDANCE, STRUCTURE AND ZONATION OF THE VEGETATION

Biomass distribution of the vegetation

The biomass distribution of submerged vascular vegetation has been investigated by SCUBA diving in the lake (Machena and Kautsky 1988). Diving was conducted along 18 vertical transects (extending from the shore to the depth of maximum colonization by the vegetation) that were spaced to cover the hydrological gradient and all shoreline types along the whole length of the Zimbabwe shore (Figure 6.1). The Zambian shore was not sampled but only slight differences are expected between the two shorelines (Coche 1974). Hence the results from the Zimbabwean shore were extrapolated to cover the two shorelines. The total standing stock of the vegetation in the lake was obtained by multiplying the average biomass in each metre depth interval by 105.22 sq. km recalculated from Balon and Coche (1974).

Both the lengthwise and depth distributions of the vegetation are shown in Figures 6.2 and 6.3. The mean vertical distribution is shown in Figure 6.4.

The estimated total biomass for the whole lake was 101 000 tonnes (dry weight) of rooted vegetation composed of *Lagarosiphon ilicifolius* (52%), *Najas pectinata* (33%), *Vallisneria aethiopica* (11%), *Ceratophyllum demersum* (3%) and *Potamogeton octadrus* (0.5%). A biomass of 1,400 g (dry weight) m^{-2} was the maximum recorded while the average for the potentially colonisable 0–12 m zone and for the whole lake was 79.9 +/–32.2 g m^{-2} and 18.8 g m^{-2} respectively.

According to Machena and Kautsky (1988) the maximum depth of colonization by rooted vegetation that they observed was only 6 m beyond the water level when sampling. However, Kenmuir (1975) and Langerman (1984) recorded colonization down to 12 m. The sampling reported by Machena and Kautsky (1988) was carried out in 1984 in the midst of a severe drought and the lake level had dropped by 7 m. Most likely, this drop in the lake level was faster than the rate of recolonization by plants.

The maximum colonizable depth recorded by Kenmuir (1974) and Langerman (1984) is comparable to the maximum observed one in lakes Bangazi-north, Sibaya and Pollela (South Africa) where rooted vegetation is found to depths of 7 to 12 m (Howard-Williams 1984). Generally, angiosperms are not known to grow below 11 m and they seldom extend deeper than 9 m (Hutchinson 1975, Chambers and Kalff 1985). When the regression model of mean summer Secchi disc transparency and maximum colonizable depth of angiosperms (Chambers and Kalff 1985) is applied to Lake Kariba, a Secchi-disc transparency of 35 m is needed to allow growth at 12 m. This is high when compared with the maximum Secchi disk transparency of 10.6 m recorded for Lake Kariba (Coche 1974).
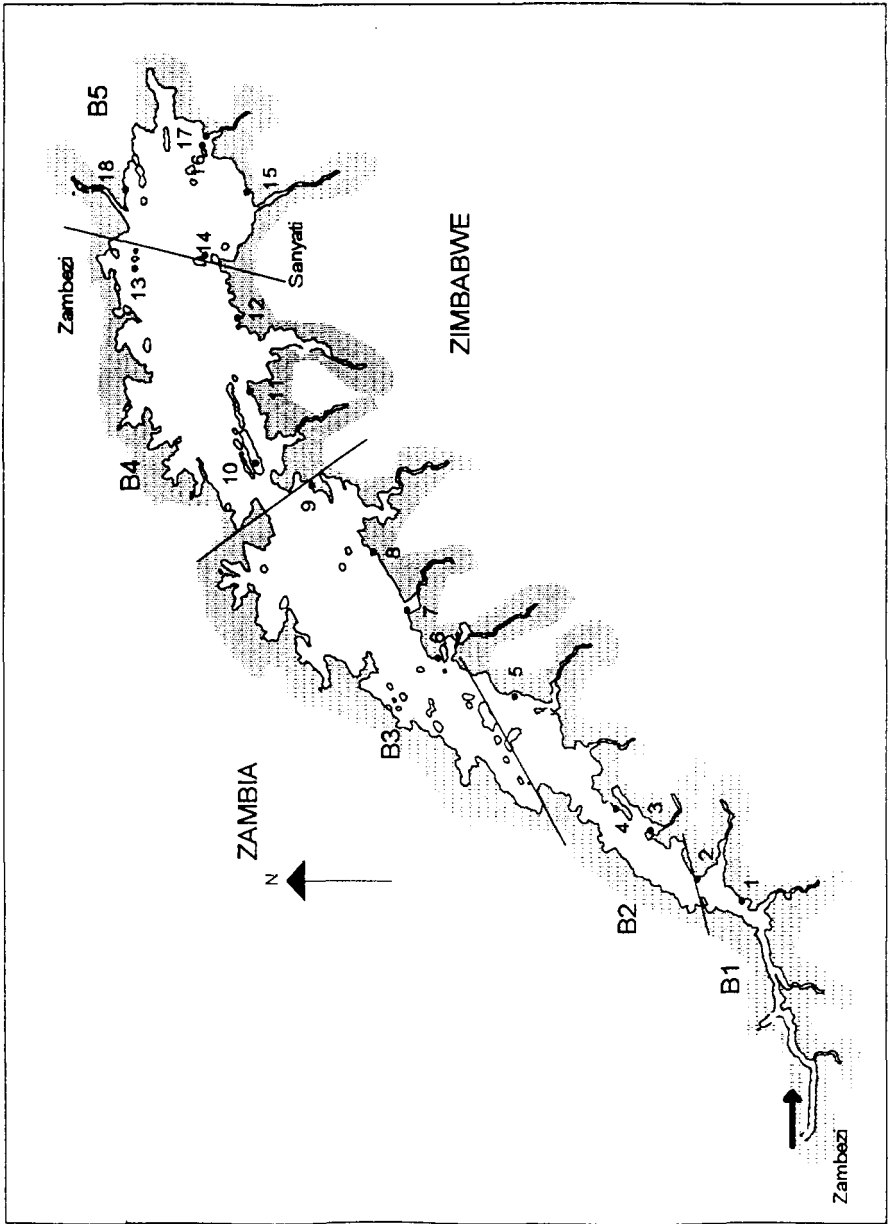
Figure 6.1 Map of Lake Kariba with sampling locations during the 1984 diving survey.
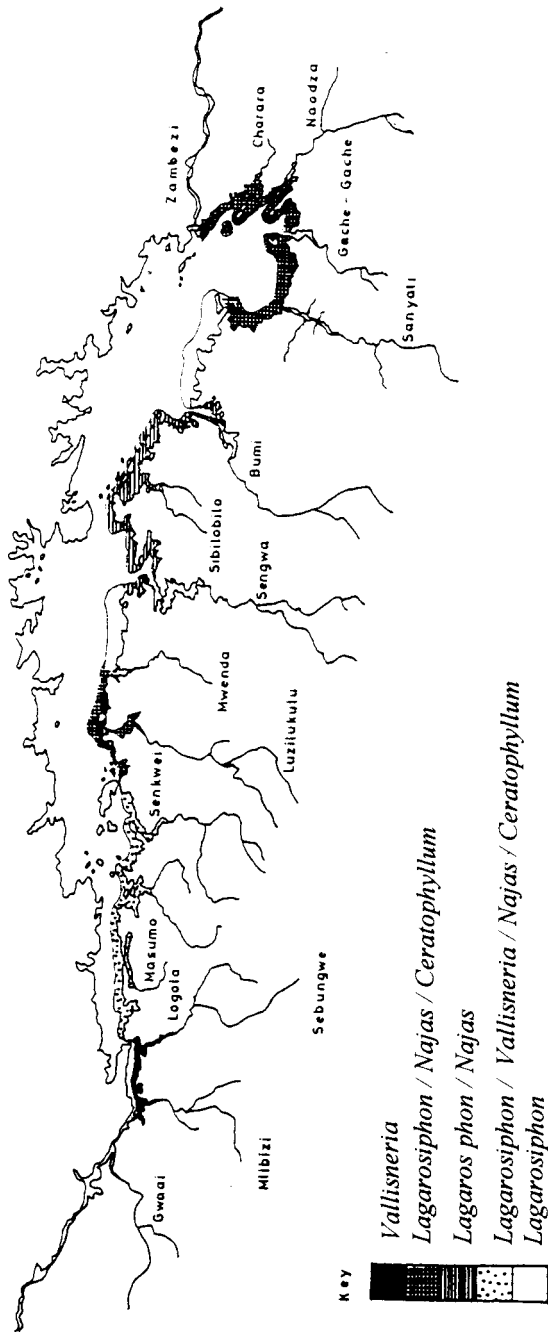
Figure 6.2 Distribution of the submerged vegetation of Lake Kariba (from Machena & Kautsky 1988)
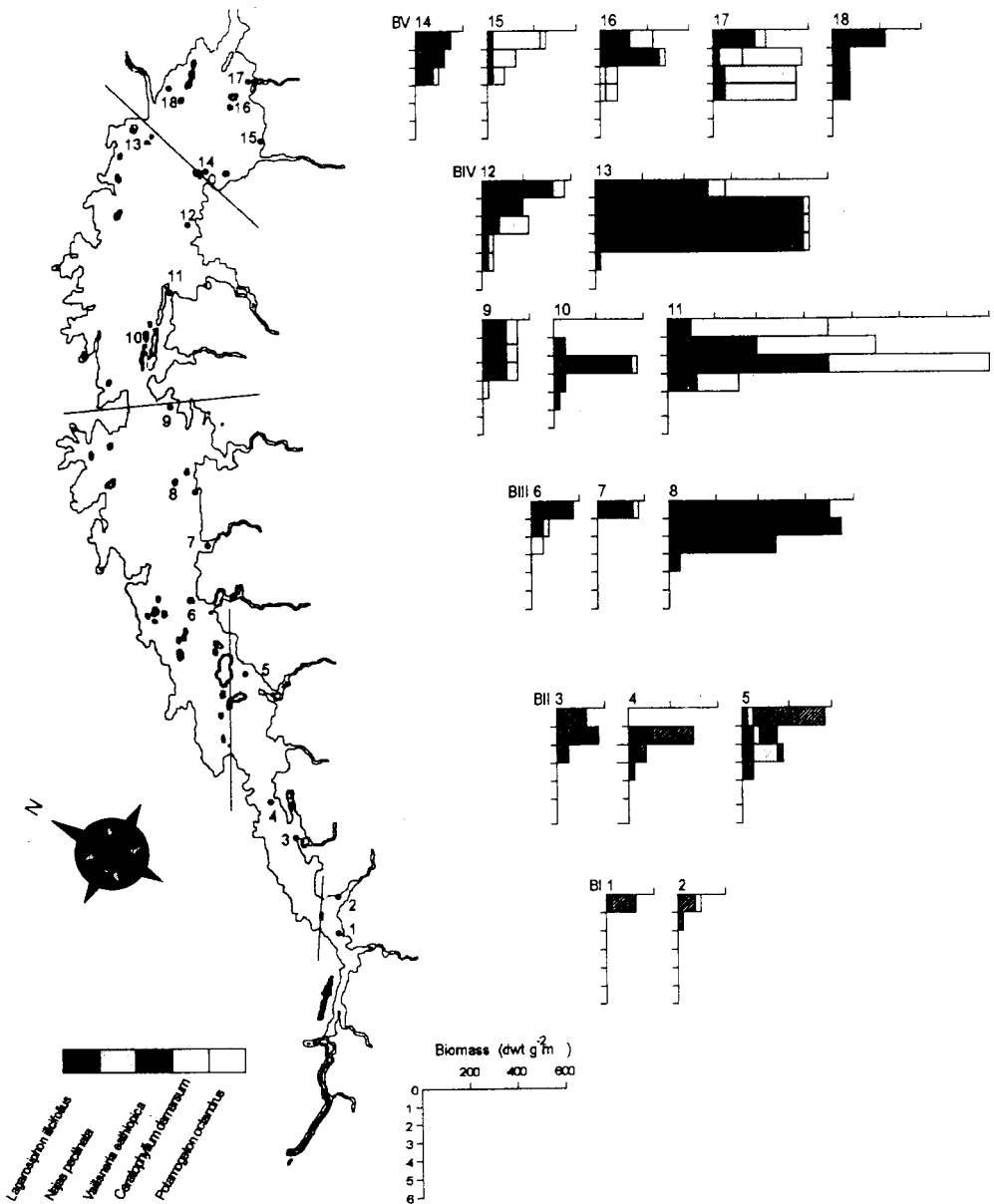
Figure 6.3 Biomass distribution of biomass of aquatic vascular vegetation at different stations (1–18) in Lake Kariba (from Machena and Kautsky 1988)

Plant biomass (g m^2 (dry weight))
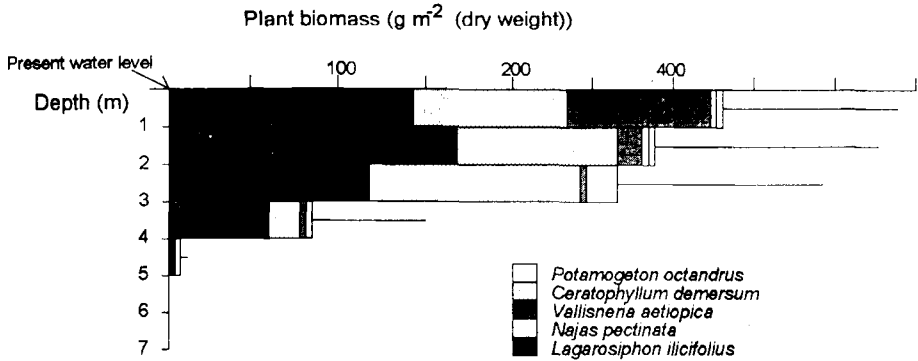
Figure 6.4 Variation with depth in standing stock of submerged macrophytes in Lake Kariba (from Machena and Kautsky 1988)

This discrepancy probably reflects a tropical situation where insolation is high and constant throughout the year with no limiting winter period. Even in Lake Tanganyika, where Secchi disk transparencies of 22 m have been recorded, rooted macrophytes generally do not grow deeper than 10 m (Coulter 1991). In Lake Kariba, there is a general correlation of the depth of angiosperm growth with Secchi disk transparency (Figure 6.5). One notable feature of the distribution of the vegetation is that *Vallisneria* is dominant in the upper reaches of the lake where the other species are very sparse (Figures 6.3 and 6.4).

The macrophyte biomass of 1400 g m^{-2} (dry weight) obtained for Lake Kariba is less than that recorded for other tropical lakes. Clayton (1982) has reported a biomass of 3518 g m^{-2} (dry weight) for *Lagarosiphon major* for Lake Rutoma (New Zealand). Howard-Williams and Allanson (1981) have recorded 1950 g m^{-2} (dry weight) of *Potamogeton pectinatus* in Lake Swartvlei (South Africa). High biomass values are generally consistent with expectation in tropical situations.

Environmental factors controlling the distribution and zonation of the vegetation
The environmental factors patterning the distribution of the vegetation have been revealed (Machena 1987) with the Canonical Correspondence Analysis (CCA) (ter Braak 1986 and 1987) which is a technique for multi-variate direct gradient analysis. In this case, three environmental variables were used, e.g. depth, transparency and slope (Table 6.1, Machena 1987).

Table 6.1 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

Axis	Coefficients		Correlations	
	1	*2*	*1*	*2*
Eigen value	0.66	0.38		
Depth	8.05	2.25	0.85	0.67
Slope	−2.86	4.92	0.01	0.88
Transparency	6.82	0.87	0.83	0.38
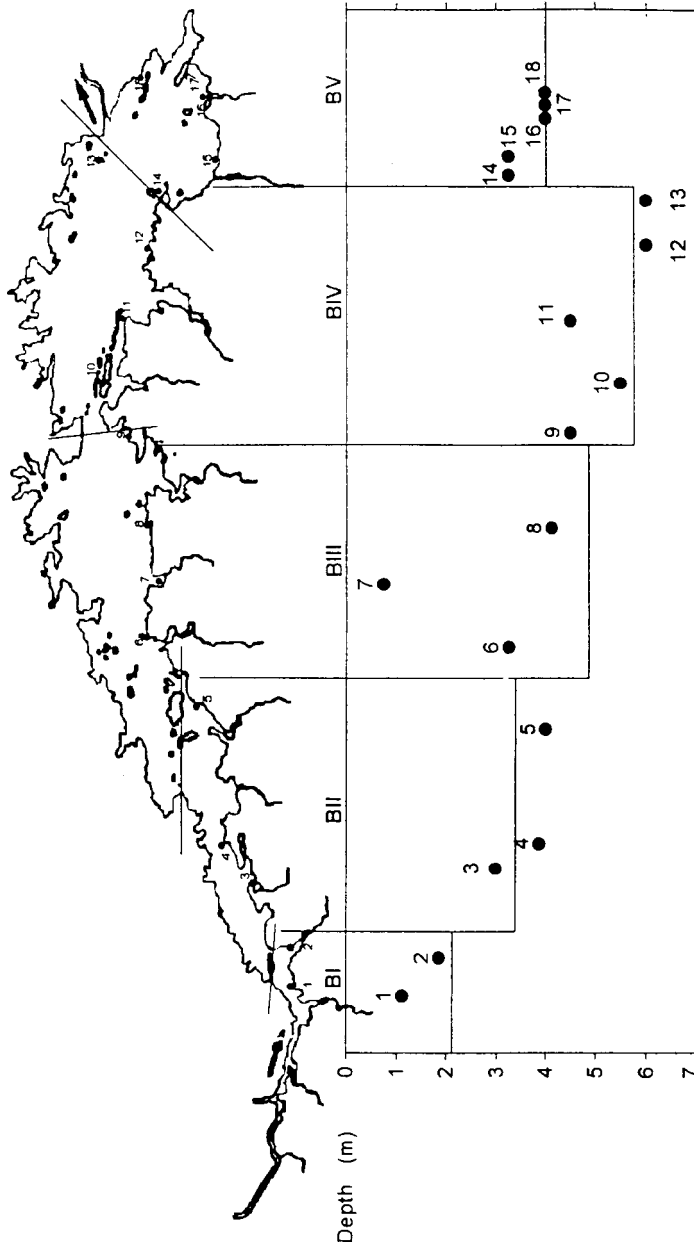
Figure 6.5 Lower limit of vegetation growth at the different sampling stations plotted together with annual mean Secchi depth values for the different basins. Horizontal bars: Secchi data from Begg (1970) for the different basins B1 to B5 (from Machena and Kautsky 1988)

The result of the CCA analysis is shown in both Table 6.1, and Figure 6.6 which represents only axes I and II. In Table 6.1 axis I represents the depth and transparency gradients and explains 66.5% of the extracted variation in the distribution of the vegetation. Axis II relates to slope and explains 20% of the extracted variation.

Community structure

The community structure of the vegetation has been revealed with the use of the computer programs TWINSPAN (Hill 1979) for classification and Canonical Correspondence Analysis for ordination and correlation with environmental variables as explained above.

The TWINSPAN classification revealed groupings of monospecific and mixed communities of species (Figure 6.7). Each of the major species formed an indicator. *V. aethiopica* formed the most monospecific groups indicating little inclination for mixing with other species. *P. octandrus* did not mix with *C. demersum* and *N. pectinata*. *L. ilicifolius* formed more mixed groupings than other species and in fact mixed with all other species.

Furthermore ordination revealed zonation along a depth gradient with *Potamogeton* and *Vallisneria* occuring in shallow and turbid water and weightith *Najas* and *Ceratophyllum* occuring in deep water. *Lagarosiphon* occupied an intermediate position (Figures 6.6, 6.7 and 6.8).

In the ordination diagram (Figure 6.6), the arrows indicate the direction of the gradient and rate of change along this gradient. The "centres" of species distribution are marked by letters which indicate the sites where particular species have their respective optima along the environmental gradient. Hence, the abundance and probability of occurence of a species decreases with distance from its centre in the plot.

The different positions of the centres along the depth gradient reflect the zonation. Between these centres, there is a varying degree of mixing between species. The *Lagarosiphon* community occurs at the centre of gravity in the community composition. This indicates that *Lagarosiphon* is the most abundant species and has the ability to mix with other species, whereas *Vallisneria, Potamogeton, Ceratophyllum* and *Najas* are found towards the extremes of the environmental gradient measured. Peripheral species along the axes indicate narrow distributions and stronger indicator potential (Hill 1973, Gauch *et al.* 1977). *Vallisneria, Potamogeton, Ceratophyllum* and *Najas* are, therefore, species with restricted niches with respect to the environmental variable measured here.

The community structure as obtained in the TWINSPAN classification, already appeared in the CCA ordination.

Vegetation stratification is summarized in Figure 6.8, pointing out competitive exclusion along the depth gradient. Competitive exclusion is characteristic where gradients are marked (Grace and Wetzel 1981, Keddy 1984, Rydin 1985, Rorslett 1987). Where gradients are not strong, Goldberg and Werner (1983) argue for an equivalence of competition among species within a community.

Vallisneria, Potamogeton, Ceratophyllum and *Najas* which grow at the extremes of the environmental gradients probably have lower growth rates than *Lagarosiphon* (Mueller-Dombois and Ellenberg 1974, Grime 1983) and have been pushed from their physiologically optimum habitats.
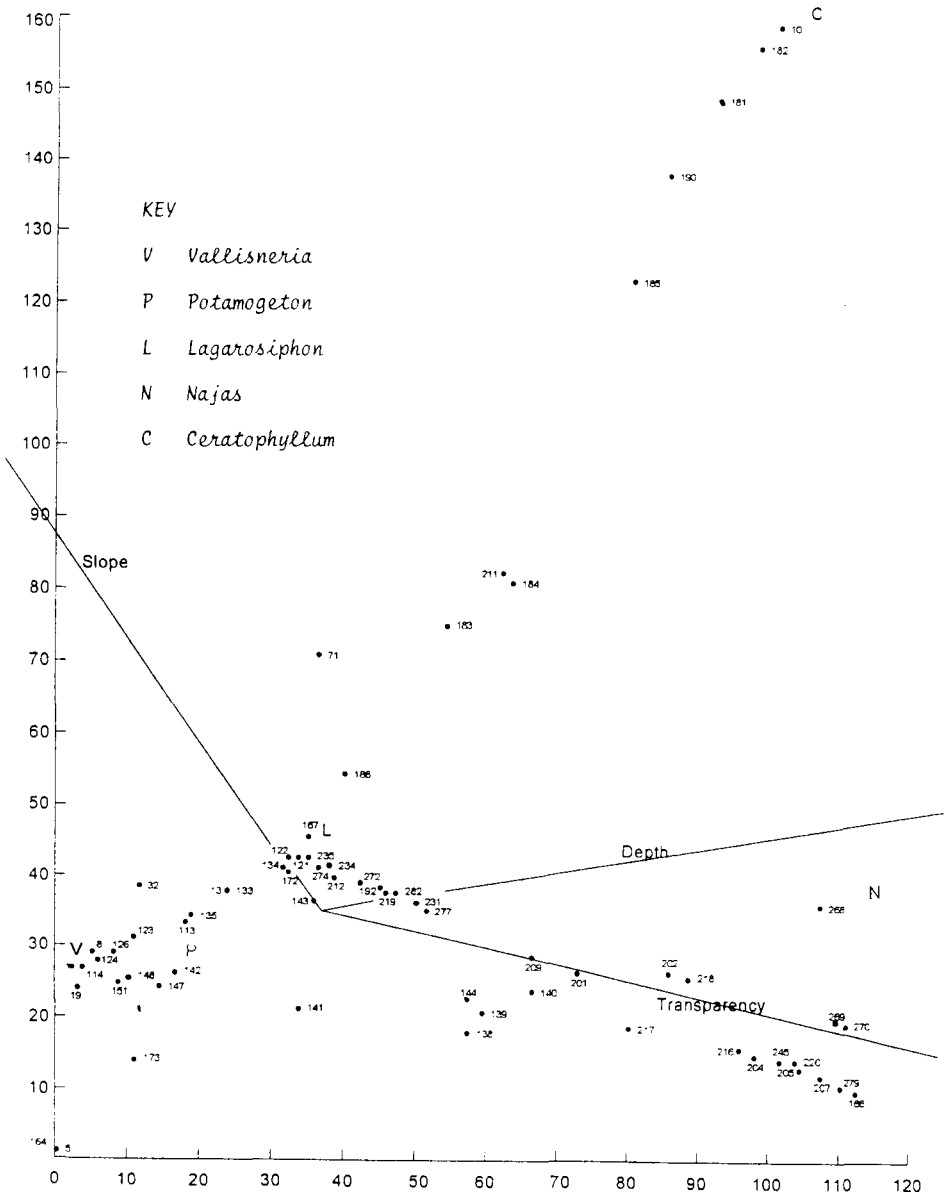
Figure 6.6 CCA ordination diagram of submerged vascular vegetation of Lake Kariba with plant species (letters), environnemental variables (Arrows) and plot numbers

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

No. of
quadrats

3	Vall 1/Cer 1
1	Vall 1/Naj 1
66	Vall 1
1	Vall 2/Pot 1
24	Vall 2
25	Vall 3
3	Vall 3/Lag 1/Naj 1
5	Vall 3/Lag 1/Naj 1
3	Vall 2/Lag 1
2	Vall 1/Lag 1
4	Vall 2/Lag 2
2	Vall 2/Naj 2/Lag 2
29	Lag 2
31	Lag 3
4	Cer 2/Lag 2/Naj 1
12	Lag 2/Naj 2
13	Lag 1/Naj 1
3	Naj 2/Lag 1/Cer 1
11	Naj 3/Lag 1
5	Naj 3
3	Cer 2/Lag 1
3	Cer 3/Lag 1
5	Cer 1
1	Pot 3/Lag 1
1	Pot 1/Lag 1
1	Pot 2
7	Pot 1
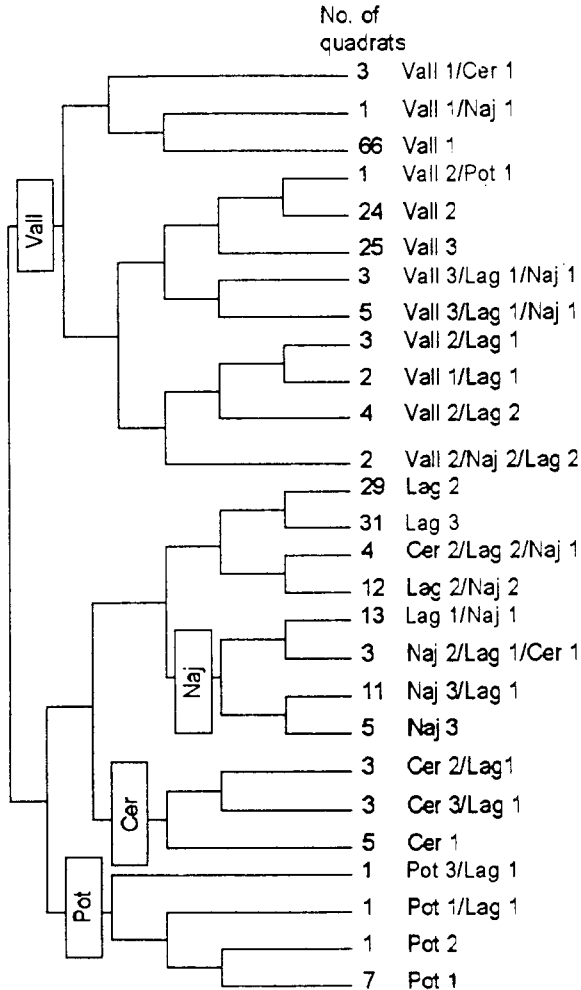
Figure 6.7 TWINSPAN dendrogram of 279 samples from 18 diving transects along the Zimbabwe shore of Lake Kariba. Similar samples are joined at a low level in the dendrogram. Dissimilar samples are not joined until higher levels. Each species served as an indicator species and the respective levels are shown
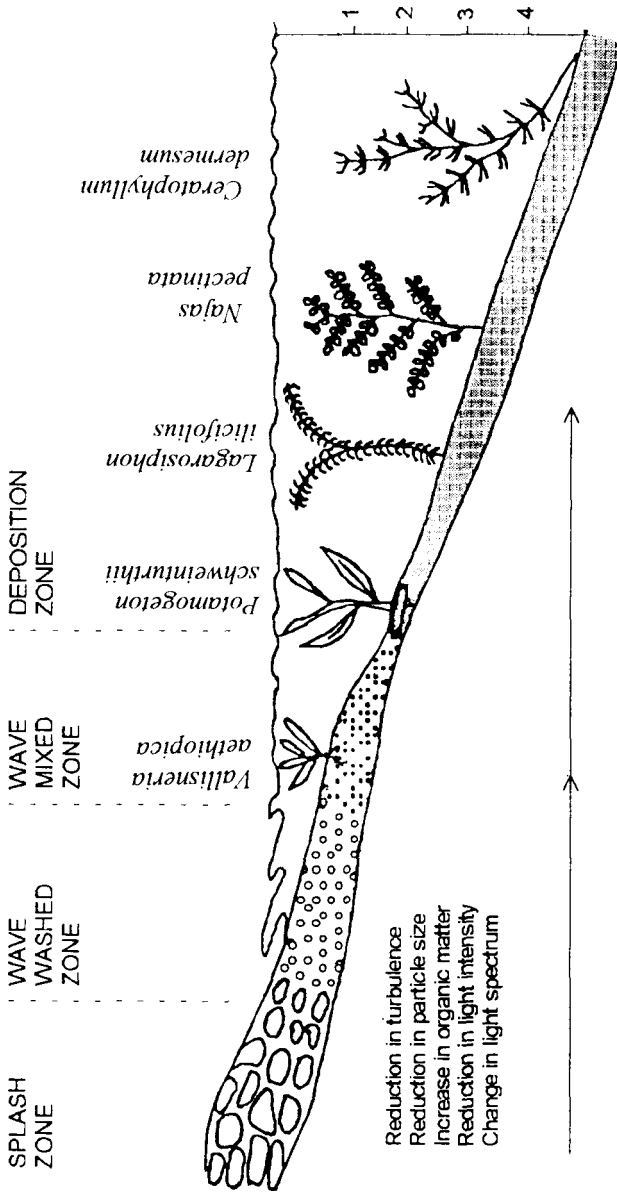
Figure 6.8 A diagram showing the influence of waves on the sediments of wind exposed lake shores and representation of the main aquatic plant growth-forms as influenced by the depth gradient in Lake Kariba (adapted from Denny 1985)

Lagarosiphon must have the physiological ability to maximise its biomass production (Chambers 1987, Chambers and Kalff 1985). Plants that are pushed to the extremes of environmental gradients do not necessarily prefer those extreme conditions; alternatively, they may be able to survive because they have greater ecological tolerances for those environmental conditions (Mueller-Dombois and Ellenberg 1974).

Distribution along a depth gradient, plant growth-form, and vegetative strategies
The various gradients at play (changes in the wave induced turbulence, light profile, sediment particle size, and sediment nutrient levels) along a depth profile are described above (Introduction, this volume). Their implication in relation to plant growth are briefly outlined below (see Figure 6.8).

Close to the shore, plants are subjected to high light intensity and low sediment nutrient levels and to disturbance from wave scouring and water level fluctuations. Depending on the level and frequency of the turbulence and simultaneous disturbance, plants could either colonize or fail to colonize this environment and those that succeeded could either be ruderals or stress-tolerators (*sensu* Grime 1979, Kautsky 1988). At the other end of the depth gradient, there is little disturbance by waves and low light intensity is the main stress factor. Sediment nutrient levels are high from deposition. Plants that survive in this environment are stress tolerators in relation to low light intensity. Operational factors characterising the middle part of the depth gradient are different. Sediment nutrient and light levels are high and disturbance is low, making the environment conducive to rapid plant growth. Plants colonizing this environment are often fast growing and would be characterized as competitors (*sensu* Grime 1979).

It seems that the rooted macrophytes in Lake Kariba have responded to the various environmental stresses through various adaptations. The various types of shores in Lake Kariba have been colonized by plants of different growth-forms and with different strategies (Figure 6.8). Some of the exposed sandy shores are colonized by *Panicum repens*, a largely terrestrial but amphibious grass. *Phragmites mauritianus* which also occupies the exposed sandy shores has been observed at very few places. It is one of the early colonizing species of the lake and its population has not expanded very much. Some exposed sandy and rocky shores can not be colonized by plants. The short-stemmed and rhizoid *Vallisneria aethiopica* occupies shore areas with sandy to fine sediments. *Vallisneria* may not be limited by nutrient poor substrates, as it has leaves well adapted for nutrient absorption from the water medium (Denny 1985). However, most of the areas colonized by *Vallisneria* are characterized by shallow and turbid water (with low light intensities); hence, this species is mainly restricted to the western end of the lake subjected to heavy turbidity from the Zambezi River (Machena 1987). As *Vallisneria* in these areas is subjected to both stress and high disturbance, its production is low and this species contributes to only 11% of the biomass of macrophytes in the lake (Machena and Kautsky 1988). *Potamogeton* spp. are also rhizoid but, because they have tall stems, they are susceptible to wave activity, and hence are restricted to protected shores. Consequently, they contribute to only 0.5% of the total macrophyte biomass in this type of environment. Thus architecture and life history constraints have a large effect on species distribution (Duarte and Rolff 1991).

L. ilicifolius is the dominant species contributing up to 52% of the total macrophyte biomass. It occupies the middle part of the depth gradient with high sediment nutrient content and light levels, and low disturbance (Machena 1987). Well rooted and fast growing, it is an effective competitor, exploiting the rich environment and forming a canopy at the surface preventing light to reach the bottom. *N. pectinata* is restricted to deep water characterized by reduced light. *Najas* is well rooted and has the second highest biomass: 33% of the total. This high biomass indicates that *Najas* is not stressed but its limitation to deep water is probably due to the competitive influence of *Lagarosiphon*. *C. demersum* is rootless and cannot benefit from the relatively high nutrient levels in the sediments, and is mostly restricted to deep water and steep slopes (Machena 1987). It contributes to only 3% of the total biomass (Machena and Kautsky 1988). *Ceratophyllum* is tolerant of low light and can be found at the limits of the euphotic zone (Denny 1985).

Four functional growth-forms have been identified amongst macrophytes in Lake Kariba (Machena 1987):

•   rooted and erect (*Lagarosiphon* and *Najas*);
•   erect but not rooted (*Ceratophyllum*);
•   rhizoid and short-stemmed (*Vallisneria*);
•   and rhizoid and erect (*Potamogeton*).

The four functional growth-forms combine with two adaptive strategies. *L.* and *Najas* are competitors and together contribute up to 85% of the total macrophyte biomass. *Vallisneria*, *Ceratophyllum*, and *Potamogeton* are stress tolerators and together make up the remaining 15% of the biomass.

Three life strategies are described by Grime (1979) for terrestrial plants: ruderal, competitive and stress tolerant. Kautsky (1988) has identified four life strategies of aquatic soft bottom macrophytes: ruderal, competitive, stunted and biomass storer. Stunted and biomass storer strategies are variants of the stress-tolerant strategy. Growth-form and strategy type and life-form are important and are used to characterize evolutionary response of plant species to their environment (Pigott 1980, van der Maarel 1980).

The environmental factors mentioned above i.e. depth, transparency (light), slope, or wave exposure, and competition, interact and the extent of this interaction influences the distribution and pattern of vegetation at a particular location. In the zone influenced by waves, the wave action/sediment-type interaction exerts the control whereas, below the wave mixed zone, quantity and spectral quality of light are important (Spence 1982).

GROWTH AND PRODUCTION OF *LAGAROSIPHON ILICIFOLIUS*

Growth and production values have been determined for *Lagarosiphon* only (Machena *et al.* 1990). In order to get some indication of the magnitude of production of submerged vascular vegetation, Machena *et al.* (1990) assumed that the values for *Lagarosiphon* could be extrapolated to other macrophyte species. This assumption was made while recognising that there is zonation of submerged vegetation in Lake Kariba and that each species is probably subjected to different radiant flux densities.

Both growth rates and production rates of *L. ilicifolius* have been estimated through following the development of individually marked plants that grew from fragmented shoots (Machena *et al.* 1990). In addition to this, Machena *et al.* (1989) also assessed the metabolism of the *Lagarosiphon* and sediment communities (bare patch of sediment). Metabolism (community production and respiration) was calculated using diurnal oxygen curves monitored in plexiglass enclosures incubated for up to 40 hours. The *in situ* enclosure experiments were performed during different seasons (Table 6.2) to cover variations in environmental conditions and changes in the development phases of *Lagarosiphon.*

Table 6.2 *Lagarosiphon ilicifolius Lag.* community metabolism in plexiglass enclosures. Carbon equivalents of production and respiration values are given in parentheses

	Period of study	Lag. in cylinder g (dry weight)	Gross* production P $mgO_2 g^{-1} d^{-1}$		Areal** gross production P $gO_2 m^{-2} d^{-1}$	$g C m^{-2} d^{-1}$
A	23–25/11/85	5.9	19.9	(7.5)	1.78	0.67
B	26–28/01/86	7.3	30.9	(11.6)	3.40	1.30
C	15–17/02/86	9.0	31.7	(11.9)	4.31	1.60
D	10–12/05/86	2.9	29.6	(11.1)	1.30	0.49
E	07–09/06/86	3.8	24.7	(9.3)	1.19	0.44
F	26–28/07/86	8.7	29.9	(8.6)	3.02	1.11
G	15–17/03/88	8.7	9.5	(3.6)	1.24	0.47

	Period of study	Areal** community respiration R $gO_2 m^{-2} d^{-1}$		Net community production PN $mg C g^{-1} d^{-1}$	Community respiration R $mgO_2 g^{-1} d^{-1}$		$\frac{P}{R}$
A	23–25/11/85	1.55	(0.58)	0.98	17.31	(6.51)	1.15
B	26–28/01/86	3.10	(1.20)	0.90	28.40	(10.70)	1.09
C	15–17/02/86	6.10	(2.30)	-4.90	44.90	(16.80)	0.71
D	10–12/05/86	1.80	(0.41)	4.86	16.66	(6.27)	1.20
E	07–09/06/86	0.96	(0.37)	3.10	16.68	(6.20)	1.24
F	26–28/07/86	1.70	(0.60)	3.60	13.09	(4.92)	1.77
G	15–17/03/88	1.33	(0.50)	-0.24	10.12	(3.80)	0.93

*Production or respiration values per unit weight of plant obtained by dividing changes in oxygen levels in the encolosure by the weight of plant harvested in the enclosure
**Areal values of production and respiration obtained by extrapolating total values within the enclosure to m²

Diurnal changes in pH, photosynthetic active radiation (PAR), turbidity, temperature, conductivity and dissolved oxygen were also monitored in the enclosures and these are presented in Figures 6.9A–F. As expected, values for temperature, pH and oxygen were lowest in the early morning and peaked in the late afternoon. The total temperature range covered during the study by Machena *et al.* (1990) was 22–33 °C, showing fairly high temperatures through out the study.
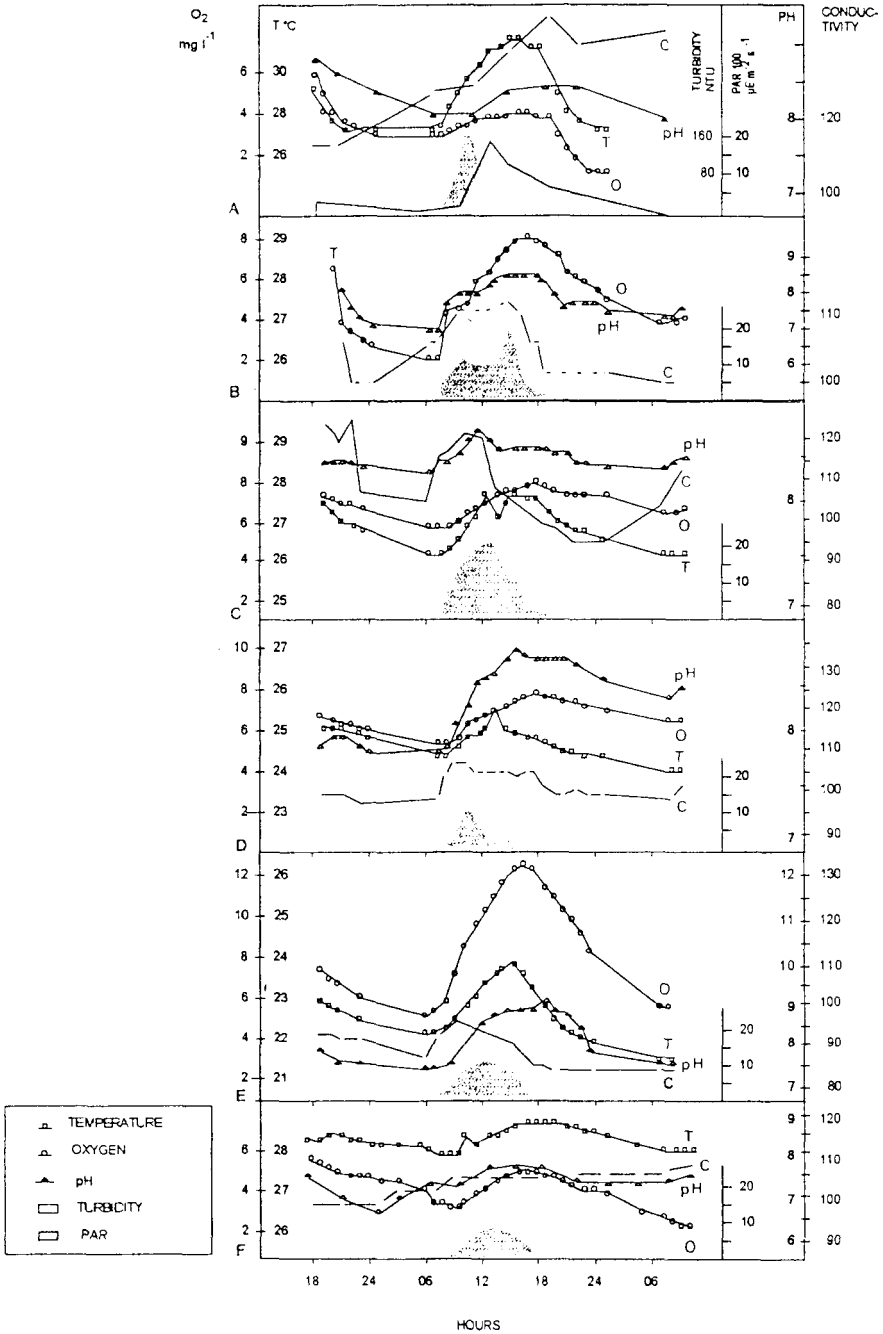
Figure 6.9 Diurnal variations of dissolved oxygen, pH, temperature and conductivity within the enclosure and of photosynthetic active radiation (PAR) and turbidity adjacent to the enclosure during different experiments from top to bottom: A: 23–25/11/85; B: 26–28/01/86; C: 10–12/05/86; D: 7–9/06/86; E: 26–28/07/86; F: 15–17/03/87 .

Growth and phenology

The growth curve (dry weight) and phenology of individual shoots of *Lagarosiphon* are shown in Figures 6.10 and 6.11. *Lagarosiphon* is rooted and grows vertically with little branching until it reaches close to the water surface where it branches extensively, thereby increasing its photoreceptive surface area. Length of *Lagarosiphon* varied from a few centimetres on unproductive sites to about 4 m in deep and sheltered areas of the lake (Machena and Kautsky 1988)
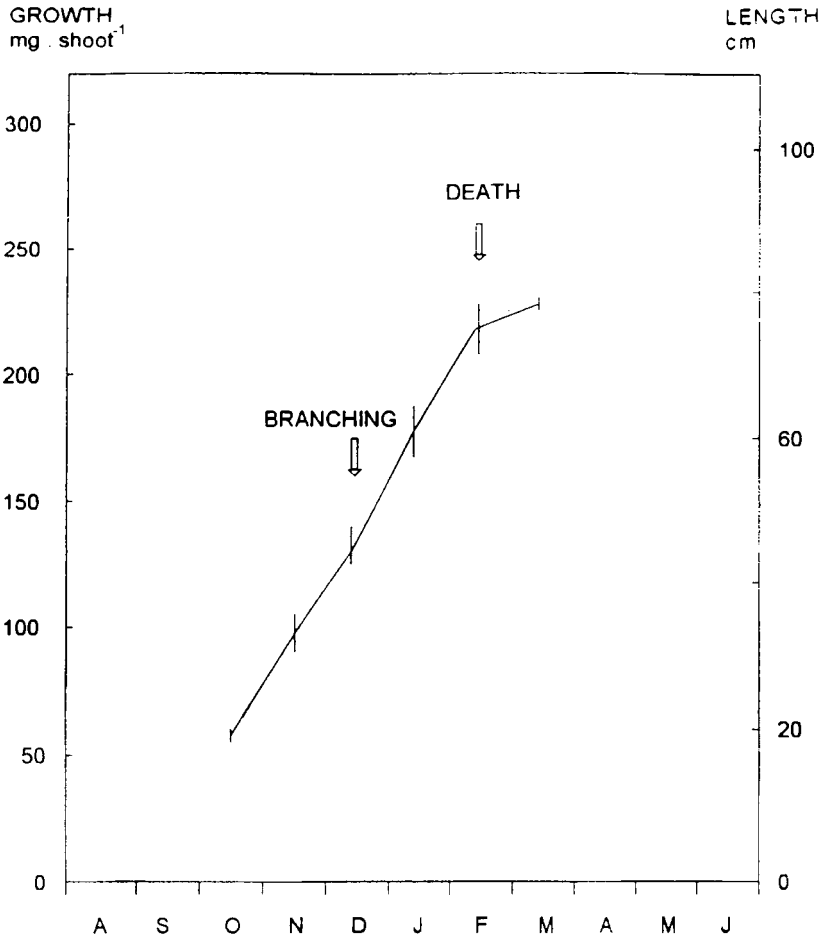
Figure 6.10 Growth of *L. ilicifolius* in Lake Kariba; onset of branching and death are indicated. Vertical bars are S.E. of means (Machena *et al.* 1990)

L. ilicifolius populations in the lake are perennial. The growth period of each cohort is about 5 months, and this gives a turnover rate of 2.4 for overall annual net production. Growth is luxuriant during summer (November–April). Cohorts that develop during summer branch extensively, forming a canopy, at the end of their growth period. Canopy formation prevents light to reach the bottom and this

probably initiates the rotting of the stems from the bottom. Rotting will continue until the branches fragment, and these drift as entangled mats constituting the major reproductive modules. At this stage, the plant fragments have already started to develop roots which enable a rapid establishment after contact with the substratum is made. These plant fragments either continue drifting, or sink and establish.

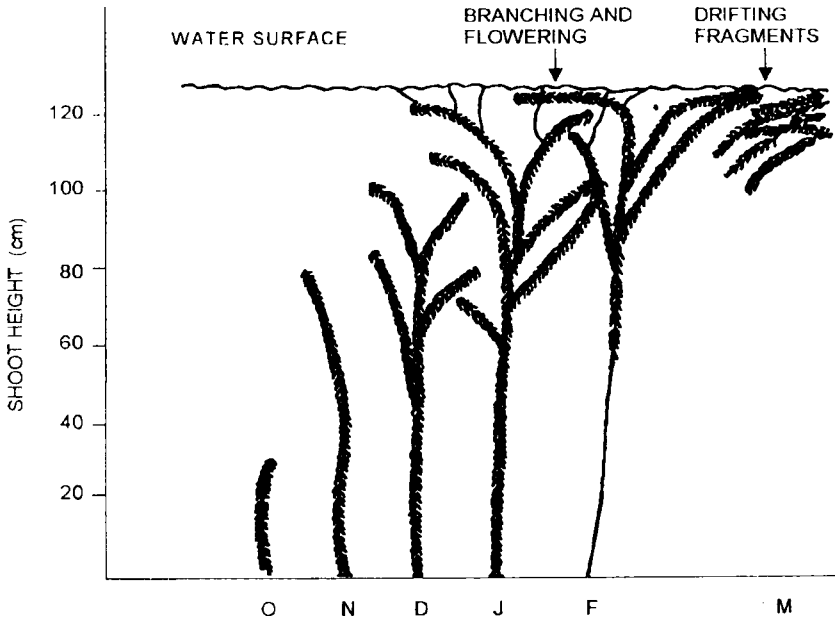Figure 6.11 The growth cycle of *L. ilicifolius* in Lake Kariba (from Machena *et al.* 1990) showing a marked density of mature shoots on the water surface (Machena *et al.* 1990)

The average annual water fluctuation in the lake is about 3 m, and terrestrial vegetation is inundated when the lake level rises following the summer rains. It has been observed that those plant fragments which drift to the shore with the currents are trapped in the flooded vegetation and sink to the bottom where they establish new plants (Machena *et al.* 1990). By the time the flooded vegetation disintegrates (3–4 months), a population of *Lagarosiphon* has already been established.

The rapid annual growth, canopy formation at the water surface and the massive vegetative reproduction by stem fragments are competitive strategies (*sensu* Grime 1979 and Kautsky 1988), and these would account for the dominance of *Lagarosiphon* over other submerged macrophyte species in the lake (Machena 1987).

According to Machena *et al.* (1990), it appears that cohorts which develop in summer invest considerable energy in vegetative propagation. During the other seasons, little branching and flowering were evident although different cohorts

still went through a similar cycle. The macrophyte community therefore presents a dynamic flux comprising phases of building up, high maintenance and die-off.

The growth pattern of *Lagarosiphon* in Lake Kariba is similar to that of *Potamogeton pectinatus* in Lake Swartvlei, South Africa (Howard-Williams 1978). Both species have perennial populations with cohorts in different stages of development more or less during the whole year. Maximum production of *Potamogeton* occurs in summer followed by a massive die-off of shoots and, like *Lagarosiphon* in Lake Kariba, growth and decay continue all year round. In Lake Kariba, the biomass ratio of mature to young shoots is high between February and October.

All plants seem to grow from fragmented shoots. Machena *et al.* (1990) saw no evidence of plants developing from seeds although much flowering was observed between November and March (summer). This situation has been observed in other studies. In some cases, sexual reproduction does not seem to play an important role in the maintenance of submerged macrophyte populations (Sculthorpe 1967, Haag 1983, Riemer 1984, Kautsky 1987, Stevensson 1988), although seeds may be important to ensure survival in the event of disaster (van Wijk 1983, Riemer 1984). Mitchell (1969) also found that *Salvinia molesta* in Lake Kariba produces sterile spores and reproduces vegetatively. In terrestrial communities, vegetative propagation is efficient for maintenance and new establishment around established plants (Grime 1979). In the case of *Lagarosiphon*, vegetative propagation is important for colonization of new areas and this might have reduced the need for seeds.

Production rates

From measurement of individual shoots of *L. ilicifolius*, a mean net production rate of 7.5 mg C g^{-1} (dry weight) d^{-1} was obtained for November–March (Machena *et al.* 1990).

From plexiglass enclosures, the net community production rate varied between –4.9 and 4.6 mg C g^{-1} d^{-1} over the period of measurement (Table 6.2) with a mean value of 1.16 mg C g^{-1} d^{-1} (Table 6.2).

Gross production in the sediment enclosures amounted to 13% of gross production in the *Lagarosiphon* community. At the same time, respiration in the sediment community varied between 28% and 42% of that of the *Lagarosiphon* community. The average contribution of the sediment community to daily *Lagarosiphon* community production (13%) is primarily from epibenthic algae. Although this figure represented a diurnal period, it is within the range of 3 to 14% that Murray and Wetzel (1987) found as the contribution of sediments to the annual primary production of both *Zostera marina* and *Ruppia maritima* communities in Chesapeake Bay (U.S.A.).

Lagarosiphon and its attached algae comprise the major producers. In some cases, the epiphytic algae can be more productive than the plants on which they are attached (Cattaneo and Kalff 1980, Morgan and Kitting 1984), but no attempt was made for Lake Kariba to break down the producers into separate components. In the lake, microalgae living on the bottom and various substrates (mean biomass of 60 g dry weight m^{-2} in the 0–5 m depth zone, Ramberg *et al.* 1987) grow mainly on the macrophytes *Lagarosiphon* and *Najas pectinata*. *Gleotrichia* sp. is

the dominant periphyton species, followed by a number of *Oscillatoria* spp. and *Lyngbya* spp. (Ramberg *et al.* 1987).

Sediment respiration (28-42 of total respiration in the *Lagarosiphon* community) indicates a high level and seasonal variation of heterotrophic activity (Hargrave 1969, Murray and Wetzel 1987) in the lake. High sediment respiration values have been recorded in other studies, for example, Murray and Wetzel (1987) reported sediment respiration to contribute 58% of the total respiration of *Zostera marina* communities. According to Sozska (1975) cited by Cattaneo and Kalff (1980), macrophytes are not grazed directly but contribute significantly to herbivores and detrivores only when they die. In some cases, e.g., Hargrave 1969, bacteria alone may contribute to 30-40% of sediment respiration. In Lake Kariba, the mussel population is abundant (Machena and Kautsky 1988) and these must also contribute significantly to sediment respiration (see Kautsky and Kilbus this volume).

The mean production rate of *Lagarosiphon* derived from the enclosure experiments of 1.16 mg C g⁻¹ (dry weight) d⁻¹ was 6.5 times lower than the rate of 7.5 mg C g⁻¹ (dry weight) d⁻¹ calculated from growth studies of marked plants. The large difference is due to the fact that the two techniques show different aspects of production (Machena *et al.* 1990). Both results complement to give an enhanced understanding of community processes (Kemp *et al.* 1986). In the enclosure experiments, the net primary production is highly influenced by the total respiration of the community.

Also, from an ecosystem point of view, the measurement of community metabolism is attractive because it reflects the production of the entire system as well as its successional states. Moreover, intermittent measurements of growth increments or harvesting give an integrated measure (over time) of the net production reflected as plant biomass. Growth increments or harvesting techniques though, will not take into account losses due to fragmentation and exudation. The large differences in the results from the two techniques could also be explained by the fact that the short-term measurements in the enclosures did not reflect the continuously changing environmental conditions in the open system, and that the direct growth measurements were performed during the period of maximum production of *L. ilicifolius*.

If calculated from enclosures measurements, the production rate of *Lagarosiphon* in Lake Kariba is rather low compared to literature data for other macrophyte species. Conversely, if the data from growth measurements are used, it falls well within the range of production values presented by Westlake (1975) who concluded that optimum production rates for a great variety of species are usually between 2 and 10 mg C g⁻¹ d⁻¹ with a mean value of about 4.

The growth rate value of 16.4 mg g⁻¹ dry weight d⁻¹ for *Lagarosiphon* is also lower than the value of 25.7 mg g⁻¹ d⁻¹ for *Potamogeton thunbergii* calculated from the value of 0.18 g⁻¹ week⁻¹ given by Denny (1985). Denny also gives a growth rate of 0.46 g⁻¹ week⁻¹ (65.7 mg g⁻¹ d⁻¹) for *P. schweinfurthii*. The values of Denny (1985) for *P. thunbergii* and *P. schweinfurthii* indicate high production rates which are consistent with the growth of tropical species. However, these plants were grown in ponds under ideal conditions. Furthermore the values incorporate changes in weight of shoots, rhizomes and roots. Contrary to this,

growth changes of *Lagarosiphon* in Lake Kariba were followed at 4 m depth and light could have been a limiting factor as maximum biomass of *Lagarosiphon* in Kariba occurs between 2 and 3 m depths (Machena and Kautsky 1988)

Total annual dry organic matter production of *Lagarosiphon* in Lake Kariba ranges from 12.8 to 861.3 g (dry weight) m^{-2} yr^{-1} (mean of 492.8 g (dry weight) m^{-2}). with a *Lagarosiphon* biomass in the lake ranging from 2.6 to 174.8 g m^{-2} (Machena and Kautsky 1988). The within lake variability of macrophyte standing crop and production per unit area are about two orders of magnitude, which is similar to findings in other lakes (Carpenter and Lodge 1986).

Extrapolating the *Lagarosiphon* production to cover all rooted submerged vegetation

The biomass of all macrophyte species combined for the colonizable zone of 0–5 m depth ranges from 3.7 to 329.2 g dry weight m^{-2} with an average of 191.9 g dry weight m^{-2} (Machena and Kautsky 1988). Calculations using the biomass of all macrophytes give biomass production values ranging from 0.06 to 5.4 g m^{-2} d^{-1} with an average of 3.2 g m^{-2} d^{-1} These values give a mean annual production of 1149 g m^{-2} yr^{-1} (528 g C m^{-2} yr^{-1}).

Annual production of submerged plants can have maximal values of up to 900 g m^{-2} yr^{-1} in temperate regions and up to 2,300 g m^{-2} yr^{-1} in the tropics (Westlake 1975). Thus, annual production for Lake Kariba is high if all the submerged macrophyte biomass is included in the calculations and is comparable to that reported for productive lakes (see Stevensson 1988)

If the assumptions made are valid, the mean annual macrophyte production for the entire Lake Kariba would be 5.975 million tonnes (dry weight) equivalent to 2.746 million tonnes carbon within the colonized zone of 0–5 m depth and an average bottom area of 105.22 km^2 m^{-1} between 0 and 5 m.

Planktonic algal production for Lake Kariba has been evaluated by Cronberg (this volume) from field measurements in March 1988. It was estimated as 0.42 g C m^{-2} d^{-1} equivalent to 765,000 tonnes C yr^{-1} Hence on a lake basis, macrophytic production contributes 78% to the total primary production. This reflects the fact that this macrophyte production can be regarded as abundant when compared with similar data (see Westlake 1975, Stevensson 1988) and that the littoral area is 10% of the total surface area of the lake which is a high value for such a large water body. In addition, as the littoral component also includes epiphytic and benthic algal growth, the total littoral primary production would be higher. For some shallow lakes including Lake Swartvlei (Howard-Williams 1978) and Lake Chad (Lévêque *et al.* 1983) littoral plant production exceeds planktonic algal production.

The bio-energetics pattern of the *Lagarosiphon* community

The bio-energetics trend of the community is indicated by the month to month P/R ratios (Table 6.2). The P/R ratio for January is 1.09 and indicates a system close to steady-state. Maintenance metabolism is significant and equals the gross primary production. This ratio coincides with flowering and extensive branching of plants. In February, the community progresses to heterotrophy with a P/R ratio of less than one. The excess of consumption over production is indicative of the declining state of the plants at this time of the year when there is a large-scale die-off of

shoots. The situation is reversed after May when the system becomes autotrophic. The P/R ratios are similar to those recorded in other studies e.g. Hannan and Dorris (1970). Murray and Wetzel (1987) give an account of similar processes in the sea grass (*Zostera marina* and *Ruppia maritima*) communities in Chesapeake Bay. U.S.A.

Summing up the gross production and respiration of the *Lagarosiphon* community given in Machena *et al.* (1990) gives an average ratio of 1.16. This indicates a high degree of self-maintenance over a large part of the year. As the plants are the major producers of the community, this indicates that a large proportion of the community production is stored up in plant tissues that are not readily utilised by herbivores. This is consistent with the observation that there is little grazing on *Lagarosiphon* and on other plants as well, which will be confirmed by the general approach of the trophic relationships in Lake Kariba (Moreau *et al.* this volume).

CONCLUSION

This study has revealed the organization of macrophyte communities in Lake Kariba. One of the advantage of studying the ecology of the whole lake has been the elucidation of operative factors underlying the organization of the macrophyte communities in the system. As many animals (secondary producers) are in various ways dependent on the vegetation, their abundance and distribution would be dependent on the organization of the vegetation and ultimately on the operative physical factors. The large difference in the production values between the community taken as a whole and individual plants reflect in a large way the role other components of the ecosystem play in the metabolism of the community. Of particular interest is the high sediment respiration rate. In a way, the two sets of production values are not comparable though they are complementary in increasing our understanding of the community processes.

This study of the ecology of macrophyte communities is by no means exhaustive. In order to increase our knowledge of the interactions within the communities, further studies could be carried out:

- to elucidate the nature of interactions between snails and the particular plant species with which they are associated; this could also be important for the mapping of bilharzia around the lake.
- to study the light responses of each macrophyte species, to determine if this is an important factor of the zonation.
- to carry out *in situ* competition experiments in pots with different macrophyte combinations;
- to correlate the biomass and species distribution of inshore fish with the vegetation in order to determine the extent to which fish populations are regulated by the organization of the vegetation.

SUMMARY

This contribution deals with the present organization of macrophyte communities, the operative physical factors underlying their organization, their production and the role of these communities in Lake Kariba.

Seven species of submerged macrophytes have been recorded in the lake. This low species diversity might come from the annual lake level fluctuations creating a physically unstable habitat and from the competitive interference by *L. ilicifolius* Oberm, the main species.

The present biomass distribution of submerged vascular vegetation was investigated by diving and found to be well correlated with the transparency of the water. Maximum biomass (1.400 g dry weight m^{-2}) and a depth penetration of 6 m were found in areas poorly influenced by river inflow, while these were only 110 g dry weight m^{-2} and 2 m respectively in the basin receiving water from the Zambezi River. The total biomass for the lake was 101.000 tonnes (dry weight) of rooted vegetation composed of *L. ilicifolius* Oberm. (52%), *N. pectinata* Parl Magnus (33%), *I. aethiopica* Frenzy (11%), *C. demersum* L. (3%) and *P. octadrus* (0.5%). Average plant biomass for the potentially colonizable 0–12 m zone and for the whole lake amounted to 79.9 g m^{-2} and 18.8 g m^{-2} respectively.

Growth and production values have been determined for *Lagarosiphon*. The mean net production rate from growth measurements is equivalent to 7.5 mg C g^{-1} d^{-1}. The average community P/R ratio of 1.16 indicates that the community is operating close to steady state and shows a high degree of self maintenance. *Lagarosiphon* has a turn-over rate of 2.4 but the populations are perennial, i.e. grow all year round.

An average contribution of the sediment community to daily *Lagarosiphon* community production of 13% is primarily from epibenthic algae.

The biomass of all macrophyte species combined for the colonizable zone of 0–5 m depth ranges from 3.7 to 329.2 g m^{-2} with an average of 191.9 g m^{-2} and the mean annual production is 1149 g dry weight m^{-2} yr^{-1}, for example, 528 g C m^{-2} yr^{-1}. For the whole lake, this is equivalent to to 2.746 million tonnes carbon which is 78% of the total lake primary production.

Institute of
Development Studies