The Ecology of Vascular Hydrophytes on Lake Kariba

by

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INTRODUCTION

The vascular hydrophytes of Lake Kariba have been studied to varying degrees and from various aspects by a number of biologists. The ecology of *Salvinia auriculata* has been investigated by the author (MITCHELL 1960, 1963, 1965, 1967), and the formation of sudd colonies on *Salvinia* mats by BOUGHEY (1963). The development of the shoreline vegetation has received attention from BOUGHEY (1965), MAGADZA (in the press), JARMAN & MITCHELL (in prep.) and JARMAN & P. I. THOMAS (1969). A. J. MCLACHLAN (1968) has made a study of the development of submerged aquatics, particularly on the Sengwa cleared area, while BOWMAKER (1968) has carried out similar observations on *Salvinia* and submerged aquatics at Sinamwenda. BEGG (pers. comm.) and DONNELLY (1968) have made complementary observations to those of BOWMAKER, but over a wider area of the lake.

This paper was prepared for and read at the Symposium on Standing Waters at the 1968 Congress of the Southern African Limnological Society. The results of *Salvinia* research, briefly reported here, are being prepared for more detailed publication elsewhere. Some of the other work is similarly also in preparation for publication and the author wishes to acknowledge his gratitude to those who have allowed him to supplement his own observations with their unpublished information.

Vascular hydrophytes, in the sense used by SCULTHORPE (1967),

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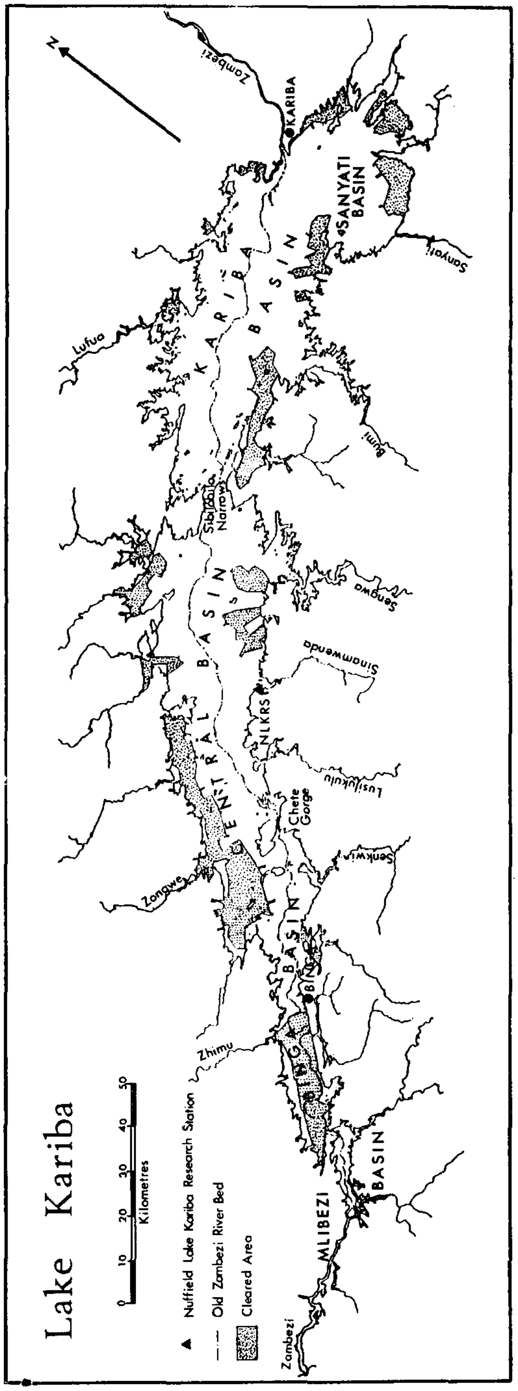
Lake Kariba
0 10 20 30 40 50
Kilometres
Nuffield Lake Kariba Research Station
Old Zambezi River Bed
Cleared Area
Zambezi
MLIBEZI BASIN
BINGA BASIN
BINGA
Zhimu
Zongwe
Senkwi
Chete Gorge
CENTRAL BASIN
NLKRS
Lusitukulu
Sinamwenda
Sengwa
Narrows
KARIBA BASIN
Lufua
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SANYATI BASIN
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that are able to grow either in water, or in water saturated soil, in and around Lake Kariba may be divided simply on the basis of life forms into four groups.

1. Free floating hydrophytes

These occur mainly in areas sheltered from vigorous wave action and are exemplified by *Salvinia auriculata* AUBL. and *Pistia stratiotes* L.

2. Hydrophytes attached to the substrate

Emergent: growing on constantly submerged soils or on wet exposed soils of the so called "soak zone" along the lake shore. Examples of the first type are *Phragmites mauritianus* KUNTH, *Typha latifolia* L. subsp. *capensis* ROHRB., while the second type is exemplified by many cyperaceous species such as *Cyperus articulatus* L., *C. difformis* L., *C. flabelliformis* ROTTB., *C. imbricatus* RETZ., *Pycreus patens* (VAHL) CHERM., *P. pelophilus* (RIDL.) C.B.CL. and *P. polystachyos* (ROTTB.) BEAUV. An important variant of the first type is the so called "sudd", which grows rooted in stable floating mats of *Salvinia.* Here *Scirpus cubensis* (POEPP. and KUNTH) and *Ludwigia stolonifera* (GUILL. and PERR.) RAVEN are common.

Floating Leaved: growing on submerged soils in depths of up to about three metres, e.g. *Nymphaea sp., Nymphoides indica* (L.) KUNTZE and *Potamogeton schweinfurthii* A. BENN, which has both floating and submerged leaves.

Submerged: growing on submerged soils in depths of up to about ten metres, e.g. *Potamogeton pusillus* L., *Ceratophyllum demersum* L. and *Lagerosiphon ilicifolius* OBERM. Portions of these plants frequently break free from the substrate and drift about just below the surface of the water.

FREE FLOATING HYDROPHYTES

The first report of aquatic plants on the newly forming Lake Kariba was received in May, 1959, five months after water impoundment commenced. COCKROFT, the District Commissioner from Binga, collected three plant constituents of an estimated fifty acre mat of vegetation floating in the lake near the Chete Gorge (see map). These were identified as *Utricularia inflexa* FORSK. var. *inflexa, Pistia stratiotes* and *Salvinia auriculata.* At about this time *Lemna sp.* was also reported to occur in large numbers and subsequently *Utricularia inflexa* var. *stellaris* (L.F.) P. TAYL. was also identified from the lake (SCHELPE 1961).

The *Utricularia spp.* evidently underwent a spectacular population growth during these early months but this was noted to have become completely arrested by October, 1959. The plant had certainly become comparatively rare on the lake by 1961. By contrast *Salvinia*, and to a lesser extent *Pistia*, continued to occupy increasingly larger areas of water.

Salvinia auriculata was first recorded from the Zambezi River System in 1948, when it was collected above Victoria Falls. In Lake Kariba, the plant was confined initially to the middle reaches of the lake between Chete Gorge and Sibilobilo Narrows, whereas *Pistia* was more widespread. However, due to the action of the prevailing easterly and north-easterly winds, *Salvinia* rapidly extended its distribution up the lake and was recorded as reaching Binga, about twenty-five miles above Chete, on the 29th September, 1959 (CHILD pers. comm.). In contrast by April, 1960, the plant had only just become established in the Bumi River about the same distance in the opposite direction below Sibilobilo Narrows.

In January, 1960 the author visited the lake and in a report to the former Federal Government of Rhodesia and Nyasaland, subsequently published in the Federal Science Teachers Journal (MITCHELL, 1960), described the susceptibility of *Salvinia* to wind and wave action. This meant that the plant could only become permanently established in sheltered areas of calm water, in inlets and among the partially submerged woodland then lining much of the lake shore. Three morphological forms of the plant were described, the distinction being drawn between a mat form, an open water form and a primary colonising form. Only the first of these forms was found to produce sporocarps. This form, destined to become by far the most common on the lake, is also the most difficult to kill with contact herbicides (HATTINGH 1962).

In April, 1960, the area was visited by SCHELPE, who in addition to touring the lake by boat, carried out the first aerial survey of the extent of *Salvinia* on the lake (SCHELPE 1961).

Subsequently, further research (MITCHELL 1963, 1965 and 1967) has indicated inter alia that *Salvinia auriculata* produces sterile spores so that reproduction is entirely vegetative. This supposition has been confirmed by recent cytogenetical work in India (LOYAL & GREWAL 1966).

Experiments indicate that on Lake Kariba the nutrient that appears to limit the growth of the fern is nitrate nitrogen. It has also been shown that following invasion of an area by the plant there is a period of slow build-up until about 10% of the area is occupied. Under favourable conditions the mat then undergoes an exponential growth phase leading to a rapid colonisation of the rest of the available area.

Two possible reasons for the explosive growth of *Salvinia* on Lake Kariba were (a) the creation of calm still conditions from the original flowing river waters of the Middle Zambezi Valley, and (b) the initial nutrient rich status of the water, consequent upon the flooding of previously unsubmerged, poorly leached soils and the death and decay of large quantities of plants and animals drowned by the progressively rising waters of the newly forming Kariba Lake. An increase in chemical content of the water at this time is indicated by the increase in specific conductivity of the water from values of 35 to 45 micro-mhos/sq cm for the Zambezi River to values of 90 to 120 in the newly formed lake (latter figures taken from HARDING 1966). Chemical analyses for nutrient ions such as NO_3^- and PO_4^{3-} showed that these were not present in significantly larger quantities and it is therefore postulated that in the then prevailing ideal conditions for plant growth all available nutrient ions were rapidly absorbed into the primary trophic levels of the ecosystem, which must therefore be considered as important traps of these nutrients. In this respect *Salvinia* was and is especially significant as it is generally distributed by the wind away from the dam wall and the outlets from the lake, thus preventing the loss of these nutrients from Kariba. The general eutrophic conditions during the early years of the lake's formation were also indicated by the frequent blooms of *Microcystis* at this time.

The variations in the overall extent of *Salvinia* on Lake Kariba are summarised graphically in Figures 1 and 2. The areas shown are calculated from the regular aerial surveys initiated by SCHELPE. At first the surveys showed a steady increase in the area colonised by the fern culminating during 1962 in an area measured on the 23rd May to be of the order of 1,000 sq kilometres, or 21.5% of the lake's surface. The 1962/63 floods resulted in a rise of the lake to 487.8 metres above sea level in July, at which level the shoreline provided fewer sheltered areas suitable for the growth of *Salvinia*. Concurrently there developed longer stretches of uninterrupted water. The wind blowing over these increased fetches caused the more frequent formation of large waves. These were responsible for the elimination of most of the free-floating mats which, up to that time, had been a conspicuous feature of the open lake. Furthermore the largest of these waves were able to break up the mats among the partially submerged woodland which had hitherto provided sufficient protection. Thus, with a few exceptions, two of the most important habitats for the fern were eliminated during that year.

In the early part of 1964 spilling of water through the sluice gates resulted in the first rapid drop in lake level. This had a marked effect on the *Salvinia* mats against the shoreline. As the waters retreated, vast quantities of the weed were left stranded out of the water, soon to be killed by desiccation in the hot sun. There was thus yet another reduction in the total amount of *Salvinia* on the lake.

Since 1964 the area has fluctuated between approximately 600 and 850 square kilometres and there is no indication of any marked permanent change in the situation.

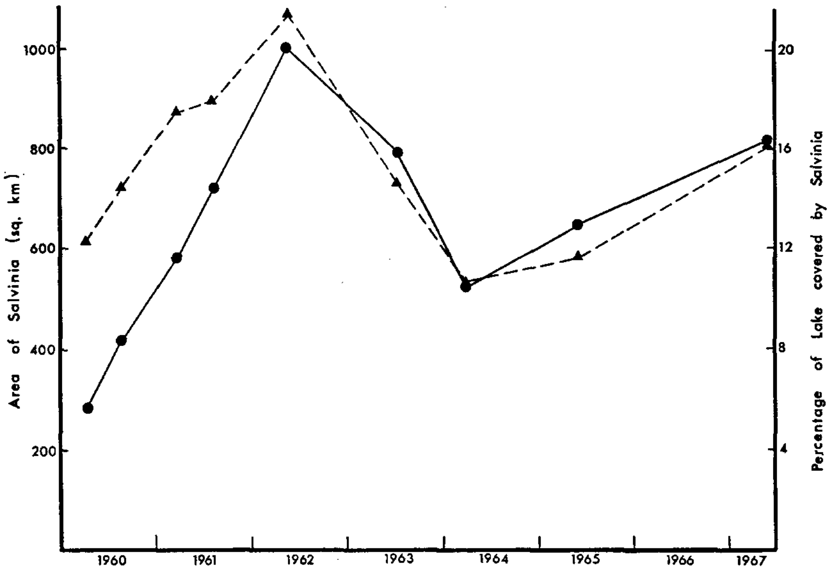

Fig. 1. Graph of the total areas of *Salvinia auriculata* on Lake Kariba (continuous line) and the corresponding percentages of lake covered by the plant (interrupted line). The areas are estimated from aerial surveys of the lake.

It is also obvious that the plant has become increasingly confined to the river inlets and therefore the behaviour of the plant in these areas is of some importance. A stable weed mat in a river inlet is normally upset by the seasonal flooding of the rivers which, particularly when assisted by wind, may have one of two effects:

a) all the *Salvinia* is flushed out and the cycle is then repeated;

b) the *Salvinia* in the upper reaches is forced down the river. If the movement of the mat is impeded in some way, such as by partially submerged trees, or a bend in the river, the plants are compressed to form a block of weed on the surface, and the flood waters begin to flow underneath it. Sometimes the *Salvinia* in the upper part of the inlet will be supplemented by masses of dry weed washed off the shore by the flood waters. The bruising treatment the weed receives during the formation of such a weed block has the effect of damaging large quantities of *Salvinia* so that many of the plants are killed. The

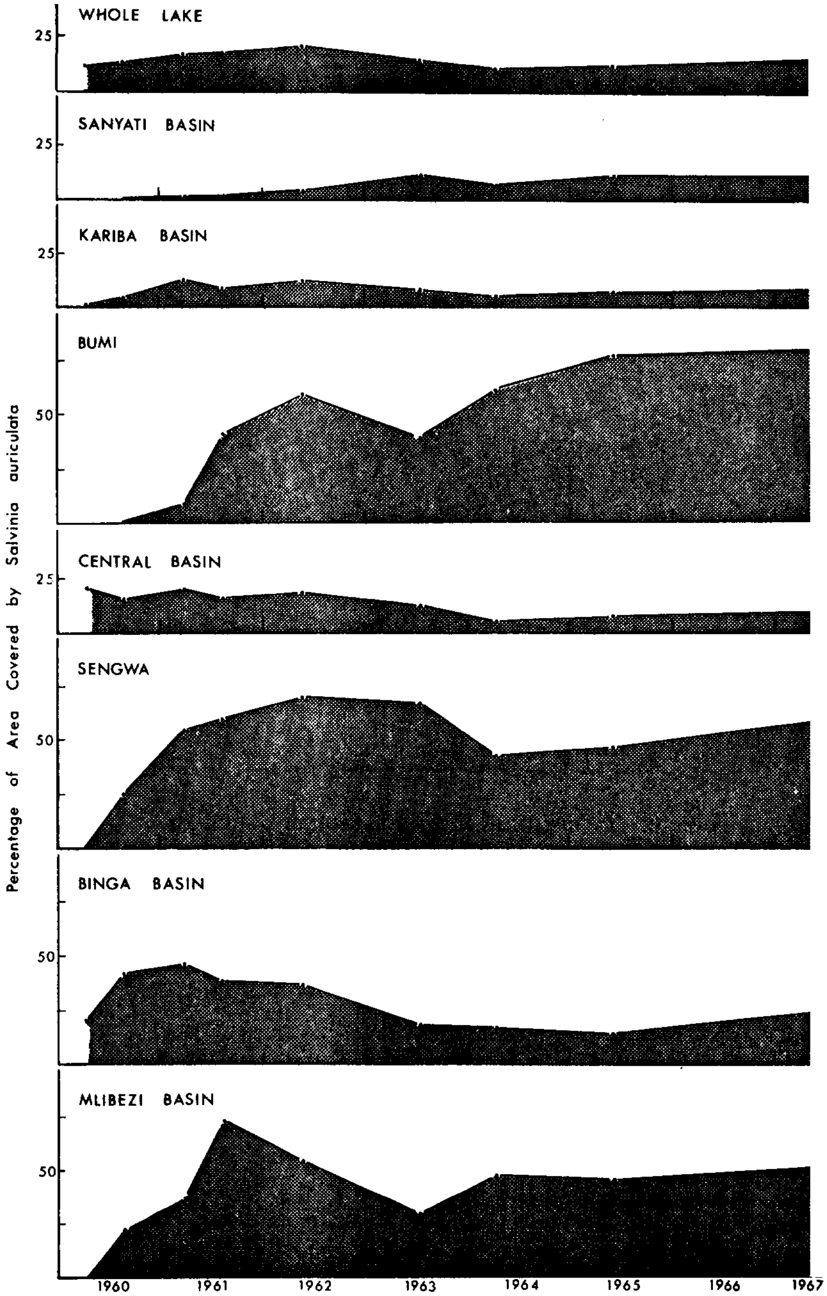

Fig. 2. Graphs of the percentages of different areas of Lake Kariba covered by *Salvinia auriculata*. The values are calculated from the estimates of areas of *Salvinia* made from aerial surveys of the lake.

decay of freshly killed and old dried *Salvinia* material releases nutrients that stimulate the growth of the surviving plants and as a result the area of water cleared by the flood action is rapidly colonised once more.

A well established, stable *Salvinia* carpet covering the surface of an inlet has a characteristic effect on the water beneath it. By comparison with adjacent water, not covered by the fern, the light penetration is nil, the oxygen concentration is decreased, the carbon dioxide concentration is increased, the pH lowered and the conductivity of the water is increased. Differences in the concentration of nutrient ions may depend upon the age of the mat. By comparison with surface waters from the open lake there are generally less nutrients in water from a vigorously growing, newly established *Salvinia* mat but there may be considerably more when there are quantities of dead *Salvinia* in the mat. The results of the chemical analyses of three water samples taken on the same day from the Sinamwenda River are quoted in Table I as an example.

TABLE I

The results of chemical analyses of three surface water samples from the Sinamwenda river, Lake Kariba, 23rd September, 1963.
(all values given in mg/l)

	PO_4^{3-}	NO_3^-	NO_2^-	Na^+	K^+	Ca^{++}	Mg^{++}
Open water	< 0.02	0.011	< 0.002	4.2	0.75	8.4	2.9
Young *Salvinia* mat	0.03	0.005	0.002	3.9	1.00	10.3	4.4
Patch of dead *Salvinia*	0.12	0.025	0.004	5.8	2.70	10.3	3.2

After *Salvinia*, the most important free floating hydrophyte on Lake Kariba is *Pistia stratiotes*. During the early history of the lake this plant colonised quite large areas of calm water. In April, 1960, it was reported to form "almost pure colonies among half submerged trees along the shore" in the Binga area (SCHELPE 1961). The aerial survey carried out in August, 1961, recorded pure colonies of the plant to be occupying areas totalling 21.8 sq kilometres both among partially submerged woodland and over cleared areas in the Sanyati Basin at the southeast end of the lake. At this time it was also commonly found in large numbers in newly established weed mats.

However, *Pistia* was unable to compete successfully with *Salvinia* and was more or less eliminated from areas in which the latter was able to form stable colonies. In only one recorded instance was this situation reversed. In the Zongwe River Inlet in August, 1962, the *Salvinia* mat was replaced by a mixed community of *Pistia* and *Salvinia*, which was dominated for a while by the former.

The aquatic grass *Vossia cuspidata* (ROXB.) GRIFF. is another free floating hydrophyte that has been considered a potential weed on Lake Kariba. First recorded in April, 1960, as free floating colonies in mid-lake above Binga (SCHELPE 1961), it is now more frequently encountered in association with *Salvinia* mats, though BOUGHEY (1963) has reported that it is the only sudd plant that is apparently able to survive independently of these mats. Up to the present there is no indication that it will become troublesome on the Lake.

EMERGENT HYDROPHYTES OF THE "SUDD"

Stable *Salvinia* mats provide a suitable substratum for the growth of certain other vascular plants and the term "sudd" has been used for the floating colonies of plants that result from this process of colonisation. Many sudd species reproduce vegetatively by means of horizontal stems, or stolons, and these bind the *Salvinia* plants on which they are growing into floating islands of varying sizes thereby contributing to the stability of the whole weed mat. There are practical difficulties in obtaining undisturbed water samples from underneath these sudd islands but it is nevertheless apparent that the effects described previously for *Salvinia* mats are magnified. There is no record of complete deoxygenation, but oxygen concentrations of 58% have been recorded (HARDING in litt.).

In the river inlets the sudd plants may sometimes knit the mat into a cohesive whole that is not easily moved by floods, thus ensuring a prolonged infestation of that area by weed, as has been observed to have occurred in the Zhimu (Chimene), Lusilukulu, Senkwi and Sinamwenda Rivers at various times. A drop in lake level preceeding seasonal flooding of the rivers will enhance this effect whereas a rise in level will loosen the weed mat between the sudd islands so that it is more likely to be flushed out of the river inlet.

The colonisation of stable *Salvinia* mats by other vascular plants was reported to have started during 1960, and possibly 1959. (MITCHELL 1960, SCHELPE 1961, BOUGHEY 1963). The most widespread constituent of these early sudd colonies was the sedge, *Scirpus cubensis*. Another important species at this time was *Ludwigia stolonifera* (*L. adscendens* (L.) HARA), and in certain river inlets was the only sudd plant present. SCHELPE (1961) also records *L. leptocarpa*, (NUTT.) HARA, *Polygonum senegalense* MEISN. and the grasses *Panicum repens* L. and *Echinochloa pyramidalis* (LAM.) HITCHC. & CHASE, as invading stable *Salvinia* mats in April, 1960.

BOUGHEY (1963) lists 40 species of plants which he recorded growing as sudd plants up to the end of 1961, and which he assigns to two groups, "those of semi-aquatic habit and ruderals of open ground generally". Among the former he lists species of *Ludwigia*, *Polygonum*, *Cyperus* and *Scirpus cubensis*, *Typha latifolia* and *Phragmites mauritianus*; while the ruderals are exemplified by *Eclipta alba* L., *Alternanthera nodiflora* R. BR. and *Commelina diffusa* BURM. F. It was suggested that the source of diaspores for the semi-aquatic sudd species were plants that were growing around fresh water springs of the valley, or in the Zambezi River and/or its tributaries. The source of the diaspores of the ruderal sudd species seemed to be the temporary vegetation which formed on the lake's soak zone during the earlier years of its formation (BOUGHEY 1963).

BOUGHEY (1963) also stressed the importance of the wind both in distributing sudd colonies and in destroying them when they are separated from the support and protection of the *Salvinia* mat.

It is interesting to note that BOUGHEY's list does not include *Panicum repens*, which was recorded by SCHELPE and has recently been reported on *Salvinia* mats by DONNELLY (pers. comm.), as this species has recently become important on the shoreline.

BOUGHEY postulates that *Salvinia* mats are a necessary prerequisite for the formation of sudd colonies, but in the case of certain semi-aquatic species, floating mats of vegetation have been observed in calm conditions independent of *Salvinia*. Two such colonies of *Ludwigia stolonifera* persisted for over a year in the Lufua River before this was invaded by *Salvinia*. During this period these colonies, which were anchored in separate partially submerged tree tops, became associated with increasing quantities of floating debris which were bound into a single mass by the roots arising at the nodes of the horizontal stems of the plants.

Individual sudd colonies do not appear to be permanent. Tensions caused within the weed mat by floods, changes in lake level, or movement of boats, have the effect of breaking the colonies, usually at places where the plants are old or moribund. This would seem to be an important factor in limiting the succession of plants that might otherwise occur in this situation.

EMERGENT HYDROPHYTES OF THE SHORELINE

The creation of Lake Kariba provides a unique opportunity to study the development of the flora of a fresh water lake shore in tropical conditions. However, there are several characteristics of Kariba shores, which serve to distinguish them from those of natural African lakes.

Firstly, the shore is subject to considerable annual fluctuations in lake level as a result of the Central African Power Corporation's present policy of dropping the lake level during the latter part of the summer in preparation for the expected Zambezi floods in April, May and June.

Secondly, the substratum of the shoreline was originally composed of flooded soils of the Middle Zambezi Valley and Escarpment. Over a period of time wave action has modified these in various ways, the degree of modification depending on the degree of exposure, the steepness of the shore and the geological rock type. In exposed sandstone areas the normal modification has been to remove the soil particles from between the rocks so that a sterile boulder armoured coastline results. In areas of shale where the rock is more readily eroded by water, the resulting shore is one of fine sand, other soil particles having been washed away and apparently deposited in deeper water off the shore (BOND 1965).

The general effect of wave action on the lake shore is to limit the vegetation to those areas in which there is some degree of protection. However, it is also in these areas that the dry *Salvinia* mat left by the falling lake level is most frequent, and this appears to have an inhibitory effect on the germination of other plants (MAGADZA, in the press JARMAN & MITCHELL in prep.).

At least three physical factors which possibly limit the growth of littoral plants have been suggested: (a) wave action resulting in armoured shores or sterile sandy beaches; (b) the presence of *Salvinia* mats; and (c) the restriction of area available on steep shores (MAGADZA, in the press).

Another important general feature of the lake shoreline is the luxuriant growth of grasses that usually takes place during the rains on previously submerged shores, particularly where these have a gentle slope. These grasses attract fairly large numbers of grazing game animals and when these areas are resubmerged considerable quantities of nutrients are released into the water from both animal droppings and decaying grasses and other herbaceous plants (S. M. MCLACHLAN unpublished, A. J. MCLACHLAN 1968).

The only true hydrophytes to be found on the shoreline are encountered on the "Soak zone" along the margin of the lake. But, due to changes in lake level which may be quite rapid at certain times of the year, these plants have so far not formed permanent colonies. Only those species which are able to withstand periods of submergence interspersed with periods of exposure will be likely to survive. In this respect the recently increased occurrence of *Panicum repens* in this habitat is of interest. This grass is able to grow in water as well as on emergent soils, in which its subsurface stolons derive some degree of protection from desiccation. It is therefore well adapted to the conditions prevailing along the lake shore at the present time and it is possible that it could lead to a stabilisation of this habitat (MAGADZA in the press, MITCHELL & JARMAN in prep.). A second plant that may succeed here is *Ludwigia stolonifera* which, by virtue of its ability to grow out over an open water surface and its ability to exist in relatively dry conditions in a very reduced growth form, at least for some time, is able to survive changes in lake level provided these are not too rapid.

Zonation in the vegetation of the shoreline can sometimes be detected. When present, this can usually be related to prior fluctuations in lake level. Where the lake has dropped slowly over some months, there is often a well developed zone of plants which germinated in the soak zone during that time. Many of the species that are able to survive the drop in lake level are common ruderals of the area, which were also observed by BOUGHEY (1965) to grow in the annual soak zones of succeeding lake levels as the lake rose progressively from 1959 to 1963. In the summer of 1966/67 three vegetation zones could be identified: (1) an upper "Gramineae" zone; (2) a narrow middle "*Laggera*" zone established on the soak zone of July to December 1965; and (3) a lower "*Ludwigia*" zone of shore recently exposed by falling lake level (MAGADZA in the press).

In order to record the long term development of the shoreline vegetation, a number of permanent quadrats have been established with student assistance in the vicinity of the Nuffield Lake Kariba Research Station at Sinamwenda. These have been set up on shores that vary in relation to exposure to wave action, soil type, slope, adjacent woodland vegetation, etc. A number of comparative quadrats have also been established in woodland vegetation away from the lake. The vegetation in these permanently demarcated areas which measure 20 metres by 50 metres will be resurveyed at periodic intervals and the changes recorded.

ATTACHED HYDROPHYTES WITH FLOATING LEAVES

Plants with this growth form are uncommon in Lake Kariba, probably because of the fluctuations in lake level. On the Sengwa cleared area *Nymphoides indica* and *Nymphaea sp.* have been recorded growing in ephemeral pools which, when inundated by rising lake water become part of the lake, though these plants do not survive long after these inundations (MCLACHLAN 1968).

Within the last eighteen months *Potamogeton schweinfurthii*, which produces both submerged and floating leaves, has been recorded from near the Sinamwenda River by the writer and from the Sengwa and Sanyati East cleared areas by BEGG & DONNELLY (pers. comm.).

SUBMERGED HYDROPHYTES

To the biologist an important characteristic of Lake Kariba is the relative paucity of aquatic niches for animal life. At present by far the largest surface area of habitat available to aquatic invertebrates is provided by floating mats of *Salvinia*, a foreign plant from Central and South America, and the consequent value of these mats in the general biology of the lake has been pointed out by BOWMAKER (1968). The importance in this respect of the development of a permanent sub-littoral vegetation of indigenous aquatic plants has been demonstrated by MCLACHLAN (1968) and DONNELLY (1968), and the establishment of a permanent shoreline vegetation of semi-aquatic plants native to the area is thought to be similarly important (BOWMAKER 1968). However, the presence of *Salvinia* mats in many of the areas that would be favourable for the growth of these native plants, is retarding their development. The inhibitory effect of dried *Salvinia* mats on the establishment of shoreline vegetation has already been pointed out. By excluding light from the lower layers of the lake and by taking up the plant nutrients as they become available, floating mats of living *Salvinia* are also inhibiting the establishment of submerged aquatic plants. It is significant that most of the development of these plants has taken place in areas where, for one reason or another, *Salvinia* does not form permanent mats. For example the cleared areas, though sometimes partially protected, do not provide anything on which the *Salvinia* plants can become anchored and they are blown away from the area by very light winds.

Ceratophyllum demersum has always been present in Lake Kariba. It was recorded in 1960 by SCHELPE (1961) and the writer has observed the plant frequently, particularly in river inlets. JUNOR (pers. comm.) reported that in November, 1959, during "Operation Noah",* the Bumi River was almost impenetrable because of these plants. MCLACHLAN (1968) recorded the plant on the Sengwa cleared area in 1965 as rooting in a rocky substratum at a depth of about 10 metres. DONNELLY (1968) also recorded it at about the same depth in the Sanyati cleared area.

By contrast *Potamogeton pusillus* did not make an appearance on

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*The game rescue exercise in which large numbers of animals were removed from islands in Lake Kariba before these were submerged by the progressively rising lake waters.

the Sengwa cleared area until September 1964, but within a few months had occupied almost the entire area to a depth of four metres (McLachlan 1968). This situation has become general throughout the lake where the substratum has proved suitable for colonisation by this species, and there is some indication that it is more able to tolerate wave action than the other submerged aquatics.

During the summer of 1966 *Lagerosiphon ilicifolius* began to appear in the lake usually in fairly deep sheltered areas such as the District Commissioner's Harbour at Binga, and the harbour of the Nuffield Lake Kariba Research Station at Sinamwenda. This species has subsequently considerably increased its range of distribution and, according to Donelly (1968), may be replacing *Potamogeton pusillus* in the more sheltered areas.

The aquatic invertebrate fauna living in the habitats provided by *Ceratophyllum demersum*, *Potamogeton pusillus* and *Lagerosiphon ilicifolius* has been stated to be spectacularly rich by comparison with *Salvinia* mats in terms of both biomass and species (Bowmaker 1968). The permanent beds of these plants are therefore very significant in the overall productivity of Lake Kariba.

Recently *Vallisneria aethiopica* Fenzl has been collected from the Sanyati basin (Begg & Donelly pers. comm.), and *Ottelia ulvifolia* (Planch.) Walp. from the Sanyati River (Begg pers. comm.). Enrichment of the submerged flora by these plants, and by *Potamogeton schweinfurthii*, is likely to have a further beneficial effect on the lake's productivity.

A non-vascular plant *Chara sp.* may also be important in this habitat. It is common in rivers such as the Sinamwenda and is recorded by Donnelly (1968) from the Sanyati East cleared area.

Chronological review

The separate events described above may be related to one another by briefly reviewing them in the chronological order in which they occurred during the continuing development of Lake Kariba.

The Kariba Gorge was dammed in December, 1958. The natal year of the lake (1959) was marked by flushes of plant growth. *Microcystis* streaked the water with its characteristic blue-green colour and reports of floating rafts of *Salvinia*, *Pistia*, *Utricularia* and *Lemna* were received. By the end of the year the quantity of *Salvinia* was such as to cause apprehension among those who, in designing a dam for hydro-electricity, had not taken into account the biological disturbances this might cause. This realisation reinforced by the well publicised game rescue exercise, "Operation Noah", had the result of drawing the attention of administrators, engineers, and indeed the general public to the biological consequences of creating man-made lakes with, in the author's view, some benefit to subsequent similar schemes.

During 1960 the sudd began to develop and *Ceratophyllum* was regularly observed. This year also saw the first development of an emergent hydrophyte shoreline vegetation on the soak zone that formed while the water level was more or less constant.

There was little change in the general pattern of events in 1961 and 1962, but in 1963 the lake reached its highest level at which a number of previously important *Salvinia* habitats were eliminated. The rapid and considerable drop in lake level early in 1964 destroyed further quantities of *Salvinia*, but came too late in the rainy season to allow the full development of other vegetation on the exposed lake shore. Towards the end of 1964 colonies of the submerged aquatic *Potamogeton pusillus* became established in suitable areas and their development has continued ever since.

The rains which fell in the summer of 1964/65 promoted the growth of grasses, sedges and herbs on the exposed shores in such quantity as to attract game animals to graze and fertilise these areas. By this time the *Salvinia* and sudd colonies had achieved a measure of stability which has changed relatively little since.

The period from 1965 to 1968 has not been marked by the same spectacular, rapid biological changes which had characterised Lake Kariba up to that time. However, the vascular hydrophyte flora of the lake still continued to develop with the appearance of plants such as *Lagerosiphon ilicifolius* and *Potamogeton schweinfurthii*, which had not been recorded previously from the lake.

So far the cichlid fish, *Tilapia melanopluera* DUMERIL, does not seem to have inhibited the development of the submerged hydrophytes as it appears to have done in other Rhodesian water bodies (JUNOR 1968), but this possibility should not be discounted altogether and should be borne in mind as a factor in future investigations.

Therefore it would appear that the hydrophyte flora of Lake Kariba is still undergoing significant new developments and, at the present stage, it is not yet possible to predict the eventual outcome.

SUMMARY

The main events in the development of the vascular hydrophyte flora of Lake Kariba are reviewed on the basis of the growth forms present in the Lake.

The habitats occupied by free floating plants are still dominated by *Salvinia auriculata* and here the situation appears to have reached a measure of stability.

The colonies of sudd plants on *Salvinia* mats have similarly reached an apparently stable state.

The emergent vegetation of the shores of the lake is shown to be affected by a number of factors, the most important probably being the fluctuations in lake level.

Attached hydrophytes with floating leaves are present in such small quantity as to be a relatively unimportant constituent of the present vascular hydrophyte flora of Lake Kariba.

The significance to the productivity of Lake Kariba of the establishment of indigenous aquatic and semi-aquatic plants is stated. The detrimental effect of *Salvinia* mats in retarding the establishment of these plants is pointed out.

The development of the submerged aquatic flora is briefly described.

Finally these separate events are reviewed in the chronological order in which they occurred.

RÉSUMÉ

Les principaux stages dans le développement de la flore vasculaire hydrophyte du Lac Kariba sont examinés selon l'échelle de croissance des plantes qui se rencontrent actuellement dans le lac.

Les habitats des plantes flottantes sans attache sont toujours dominés par la *Salvinia auriculata*; dans ces aires la situation semble avoir atteint, dans une certaine mesure, un état stable.

Les colonies de plantes su sedd sur les radeaux de *Salvinia* paraissent aussi avoir atteint un état stable.

Preuve est fournie que la végétation émergeant sur les rives du lac est influencée par un certain nombre de facteurs, dont les plus importants sont les variations dans le niveau du lac.

Les hydrophytes à pédoncule et à feuilles flottantes se rencontrent en quantité tellement réduite qu'elles ne constituent qu'un élément relativement sans importance de la flore vasculaire hydrophyte actuelle du Lac Kariba.

En termes de productivité du Lac Kariba, les conséquences de l'établissement de plantes aquatiques ou semi-aquatiques est mise en lumière. L'effet préjudiciable des radeaux de *Salvinia* en tant qu'ils retardent l'établissement de ces plantes est souligné.

Le développement de la flore aquatique submergée est esquissé.

Finalement ces événements indépendants sont passés en revue dans l'ordre chronologique de leur apparition.

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