Oecologia (Berl) (1981) 49:109–118

*Oecologia*


# Nutrient Relationships in Shallow Water in an African Lake, Lake Naivasha

John J. Gaudet and Francis M. Muthuri
Department of Botany, University of Nairobi, P.O. Box 30197, Nairobi Kenya

**Summary.** In the littoral zone of a shallow, tropical lake (Lake Naivasha, Kenya), average nutrient composition of emergent macrophytes along a permanent transect (0–2m depth) on a dry weight basis was: P 0.23%; N 0.96%; and S 0.11%. In the hydrosoil the average composition was much lower, sediments were: P 0.03%; N 0.24%; and S 0.05%. The water depth varied, with lake edge being exposed during the annual drawdown for a part of the year and subsequently being inundated. Water quality varied considerably during the year (temperature 19–28° C; pH 7.0–8.0; conductivity 282–975 μ $Scm^{-1}$).

Of the three nutrients in the water of the littoral zone, N had the highest mean concentration (4.25 $mg \cdot l^{-1}$) while P was intermediate (1.90) and sulphur had the least (0.99). The distribution of nutrients followed a decreasing gradient from shore to open water. High levels of nutrients were recorded in September following the inundation of drawdown soil and plant material.

The large stock of nutrients generated in the littoral zone helps to replenish nutrients in the open lake where low concentrations are typical.

## Introduction

The littoral zone of a lake represents a transition between terrestrial and aquatic systems. This shallow water, usually dominated by aquatic macrophytes, plays an important role in most lake systems (Gaudet 1974). Many of the lakes of the world are relatively small in area and shallow. As such, the littoral flora constitutes a major source of organic matter that contributes significantly to the productivity of such lakes (Wetzel 1975). In Africa many large shallow lakes exist, for example: Lake George 2.5 m depth (250 $km^2$); Lake Chad 2 m depth (20,000 $Km^2$, Luther and Rzoska 1971); Lake Naivasha 4 m depth (120 $Km^2$ Gaudet 1977a); and Lake Chilwa 3 m depth (700 $Km^2$ Howard-Williams 1972). Such lakes (total area 21,070 $Km^2$) contain extensive areas of littoral zone which provides a diverse habitat for plants and animals, contributes significantly to autotrophic production, and act as a trap for allochthonous and autochthonous materials (Howard-Williams and Lenton 1975).

Lake Naivasha in Kenya (Fig. 1) is typical of African shallow waters. This lake is fringed by papyrus swamps which act as buffers separating the surrounding, intensive farmed, land from the open lake (Gaudet 1977a). The macrophytes in the shallow water communities of this lake will be greatly influenced in the future by farming and recreational activities around the lakeshore, especially if the lake edge flora is cleared. But, because the role of this community is not well understood it is not possible to formulate recommendations about the conservation and management of land and water at the lake edges. Especially important in this respect, is the role of such tropical aquatic communities in nutrient cycling. Of the nutrients, phosphorus, nitrogen and sulphur are the most important in limiting production of fresh water ecosystems especially at the high production rates typical of the tropics. In order to better understand this community, it was decided to: a) determine the total nutrient levels (N, P and S) in one shallow water tropical community, especially, in the macrophyte, water and hydrosoil components; b) investigate nutrient release from macrophyte decomposition and inundation of hydrosoil under laboratory conditions; and to c) outline the general transfer patterns with this macrophyte-water-soil system.

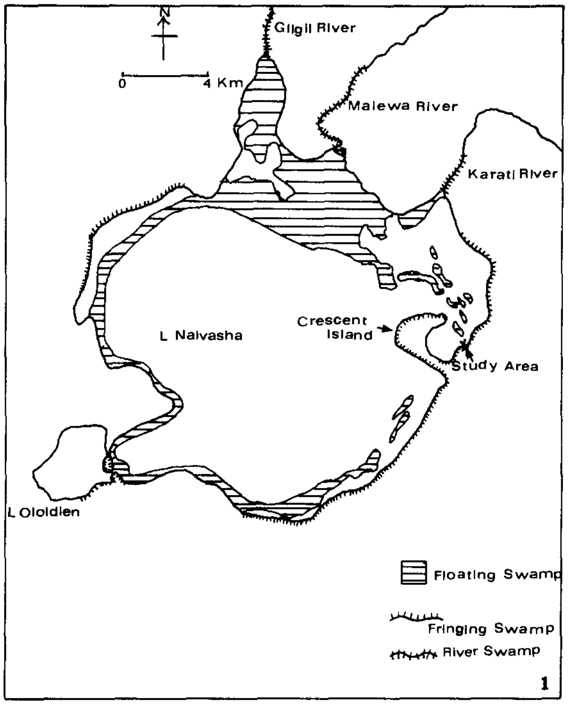


**Fig. 1.** Lake Naivasha in Kenya (after Gaudet 1977a)

## Materials and Methods

### *Study Site*

The area under study is located at the edge of Lake Naivasha (0°45′S and 36°20′E) a closed-basin lake in East Africa (Fig. 1). The flora

0029-8549/81/0049/0109/$02.00

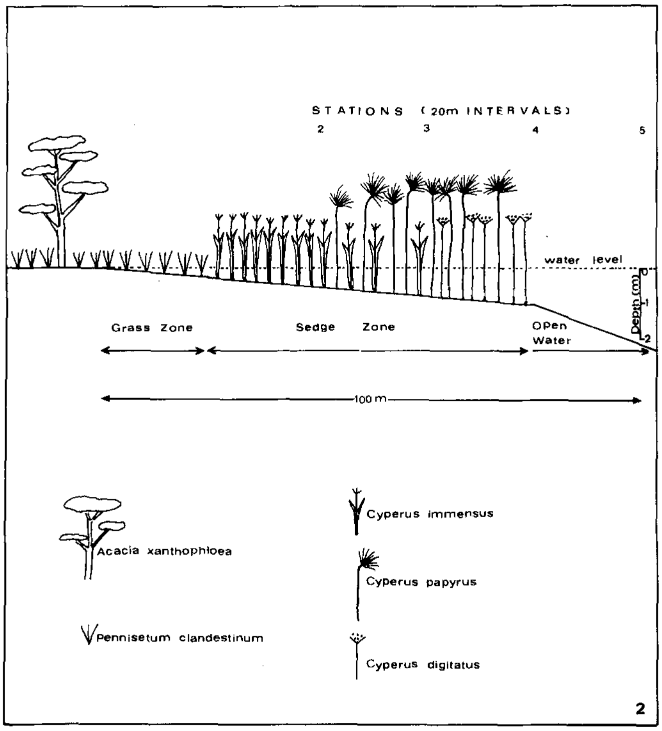


**Fig. 2.** Profile of the study area on the lake shore

and general ecology have been described previously (Gaudet 1977a). One long permanent transect (100 m) was set out from land (*Acacia/Pennisetum* Zone) to the open lake (Fig. 2). Five stations were located along this transect at 20 m intervals including:

*Grass Zone* (Station 1). A 20 m wide zone dominated by Kikuyu grass (*Pennisetum clandestinum* Chiov.). During this study this zone (represented by Station 1) underwent drawdown, a complete cycle of drying followed by inundation. It was occasionally grazed by cattle during the dry period.

*Sedge Zone* (Stations 2, 3, and 4). A 60 m wide zone dominated by *Cyperus immensus* C.B.Cl. Other sedges included *Cyperus papyrus* L. and *Cyperus digitatus* Roxb. There was evidence of occasional grazing by coypus (*Myocastor coypus* Molina) in this zone.

*Open Water* (Station 5). Located 20 m offshore away from the edge of the Sedge Zone, this station reflected open water conditions. Here sampling was conducted from May to December, 1978, during which period the area underwent a fall and rise in water level of 0.5 m.

### *Sampling and Analytical Techniques*

Samples of the dominant plant species, soil and water were taken periodically. Water samples were analysed for total nitrogen, dissolved and particulate phosphorous as described previously by Gaudet (1979). Total sulphur was determined on a 20 ml aliquot of unfiltered water mixed with $NaHCO_3$ and evaporated to dryness. All sulphur in the residue was reduced to $H_2S$ by refluxing in a mixture of HI, HCOOH and $H_3PO_2$ using $N_2$ as carrier gas. Sulphur (as $H_2S$ absorbed in NaOH) was determined titrimetrically using mercuric chloride and dithizone (Anon. 1968).

Ten composite samples (culm, rhizome and root) of each of the 4 most common species along the transect were dried at 80° C, ground to pass 1 mm, dried to constant weight and analyzed as follows:

*Phosphorus.* 100 mg was ashed at 500° C with $Mg(NO_3)_2$. The residue was then digested and phosphorus determined colorimetrically (Gaudet 1979).

*Nitrogen.* 200 mg was digested in 5 ml $H_2SO_4$, diluted to 50 ml and a 10 ml aliquot used for micro-distillation (Gaudet 1979).

*Sulphur.* 200 mg was ashed at 500° C with $NaHCO_3$. All sulphur in the residue was then reduced to $H_2S$ and determined as above.

Ten soil samples (2 at each station) were dried at 105° C, ground in a mortar to pass 1 mm sieve and dried to constant weight prior to analysis, and phosphorus, nitrogen and sulphur determined as in the plant material.

In order to investigate *in situ* decomposition of plant material, litter bags were set up in Lake Naivasha, using the dominant plant in this area, *Cyperus immensus* C.B.Cl. Culms were collected along the transect, cut into 10 cm pieces, dried randomly mixed and known weights (10 g) were placed in nylon litter bags of 0.5–1.0 mm mesh. The litter bags were submerged in water in the Sedge Zone at a depth of 0.5 m with the help of floats and anchors. Two litter bags were retrieved after 0, 7, 14, 21, 28, 48, 79, 157 and 181 days and the contents dried, weighed and analysed for nitrogen, phosphorus and sulphur as above.

Release of nutrients during decomposition of plant material was investigated in the laboratory by setting up glass jars of lake water (1 l) into which 10 g of dried *Cyperus immensus* culms were placed. The water in two replicate jars and a control were analysed for nutrients, pH and conductivity after 6, 12 and 24 h, 2, 7, 21, 28 and 60 days.

During the low water period (June, July and August) the whole of the transect dried out and exposed sediment from the hydrosoil was collected from among the base of the macrophytes, placed in a plastic tank exposed to sunlight. When the soil had further dried to a constant weight, it was flooded with lake water (5 l) to a depth of 0.2 m (average water depth along the transect). Occasional stirring of the water layer was done to simulate crayfish and wave action. Samples from the tank were analysed for pH, conductivity and nutrients after 6 and 24 h, 2, 3, 7, 14, 21, 28 and 50 days.

## Results

### *Water Quality Along the Transect*

As expected, the mean annual conductance and temperature decreased while pH increased going out from shore as water depth increased (Fig. 3A). Seasonal changes in pH and conductance were fairly constant during the drawdown period when Station 1 dried out from June through August (Fig. 3B). With the later increase in water level in September conductance rose steeply with pH following thereafter. Both decreased later during high water conditions. Temperature sharply decreased during drawdown due to the low air temperatures prevalent during this period, but it rose again to the 23–25° C range.

### *Nutrient Levels in Water*

Total P was generally higher during drawdown (June–July) decreasing later in the year in December (Fig. 4A). The concentration of particulate P was greater than dissolved P throughout the year, however, late in the year, in December, when total P was low, dissolved P exceeded particulate. The ratio of the

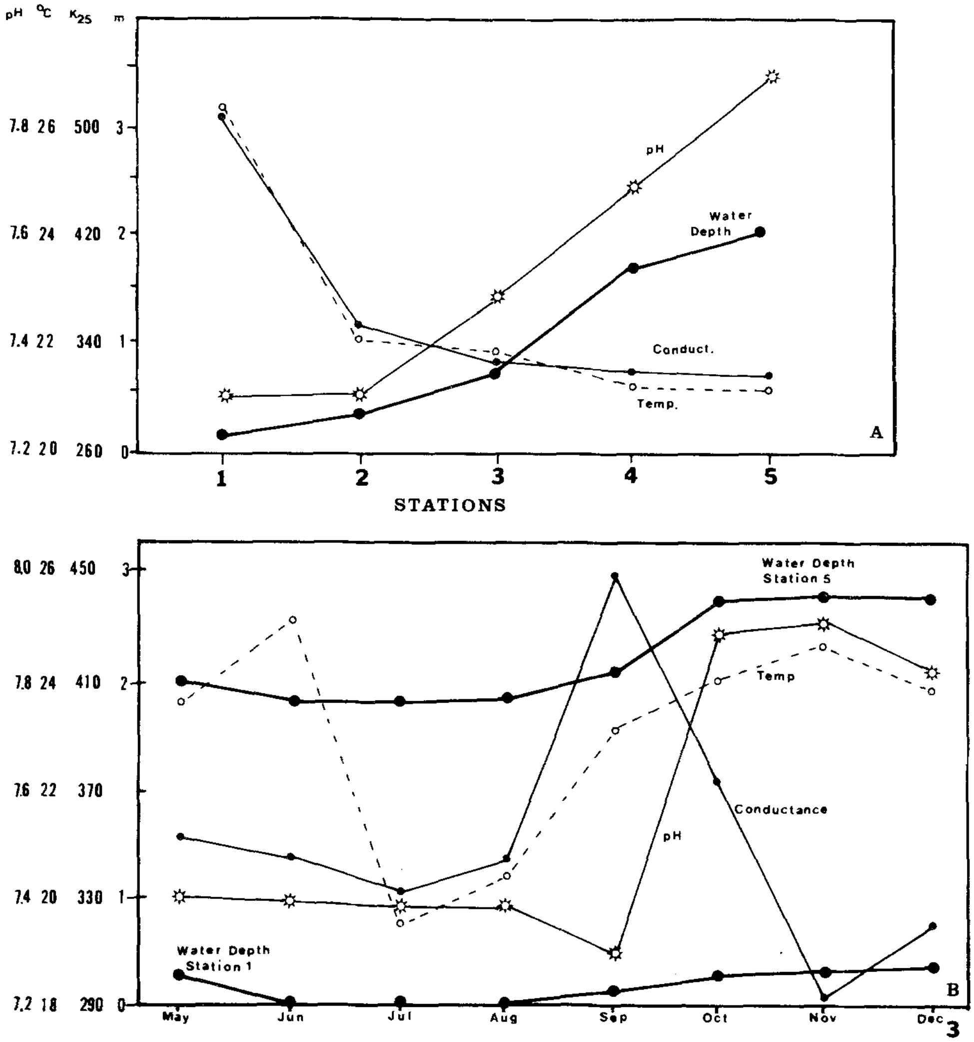


**Fig. 3.** **A** Annual mean values for temperature, conductance pH and water depth along the transect. **B** The seasonal changes in parameters

two forms of P differed from zone to zone. The average ratio of particulate to dissolved was 2:1 in the Grass Zone, 6:1 in the Sedge Zone and almost 1:1 in the open water. Following inundation at Station 1 in September high concentrations of (7.4 mg $l^{-1}$ total – P were found. This fell sharply within one month as the water level rose. Mean values for total – P followed a decreasing trend along the transect from the Grass Zone (1.90 mg $l^{-1}$) to the open water.

Total nitrogen concentrations were higher than either phosphorus or sulphur with the highest mean annual concentration (4.25 mg $l^{-1}$) in the Sedge Zone, and the least concentration in the open water (Fig. 4B). This differed from phosphorus and sulphur where highest mean levels (1.90 and 0.99 mg $l^{-1}$, respectively) were generally found in the Grass Zone at Station 1 (Fig. 5).

Of the three nutrients total sulphur was generally at the lowest overall concentration (Figs. 4C and 5). Otherwise, the pattern of distribution was similar to that of phosphorus.

*Nutrient Levels in Plants and Soil*

There was little significant difference between nutrient levels of the species (Table 1) with the exception of the generally low levels of S in the sedges. The mean levels in the macrophytes, fell within the ranges found for the other African macrophytes

**Table 1.** Nutrient composition plant and soil material, % dry weight with ±std. deviation in brackets, $N=10$

| | Nitrogen | Phosphorus | Sulphur |
|---|---|---|---|
| *Pennisetum clandestinum* | 1.05 | 0.24 | 0.23 |
| | (0.12) | (0.09) | (0.08) |
| *Cyperus immensus* | 1.17 | 0.32 | 0.13 |
| | (0.30) | (0.18) | (0.07) |
| *Cyperus papyrus* | 0.70 | 0.13 | 0.04 |
| | (0.30) | (0.05) | (0.02) |
| *Cyperus digitatus* | 0.90 | 0.23 | 0.05 |
| | (0.09) | (0.08) | (0.09) |
| *Soil* | 0.24 | 0.03 | 0.05 |
| | (0.08) | (0.00) | (0.01) |

(Howard-Williams 1977; Gaudet, 1975 and 1976; and Lind and Visser 1962). Nitrogen was always present at the highest level in the macrophyte component while sulphur was present at the lowest level. The N: P: S ratio for the macrophytes was 9:2:1.

The mean nutrient values for soil were lower than those for macrophytes (Table 1). There was 4 times more N, 8 times more P, and 2 times more S in the macrophytes than in the soil. The N:P:S ratio of nutrients in soil was 8:1:2.

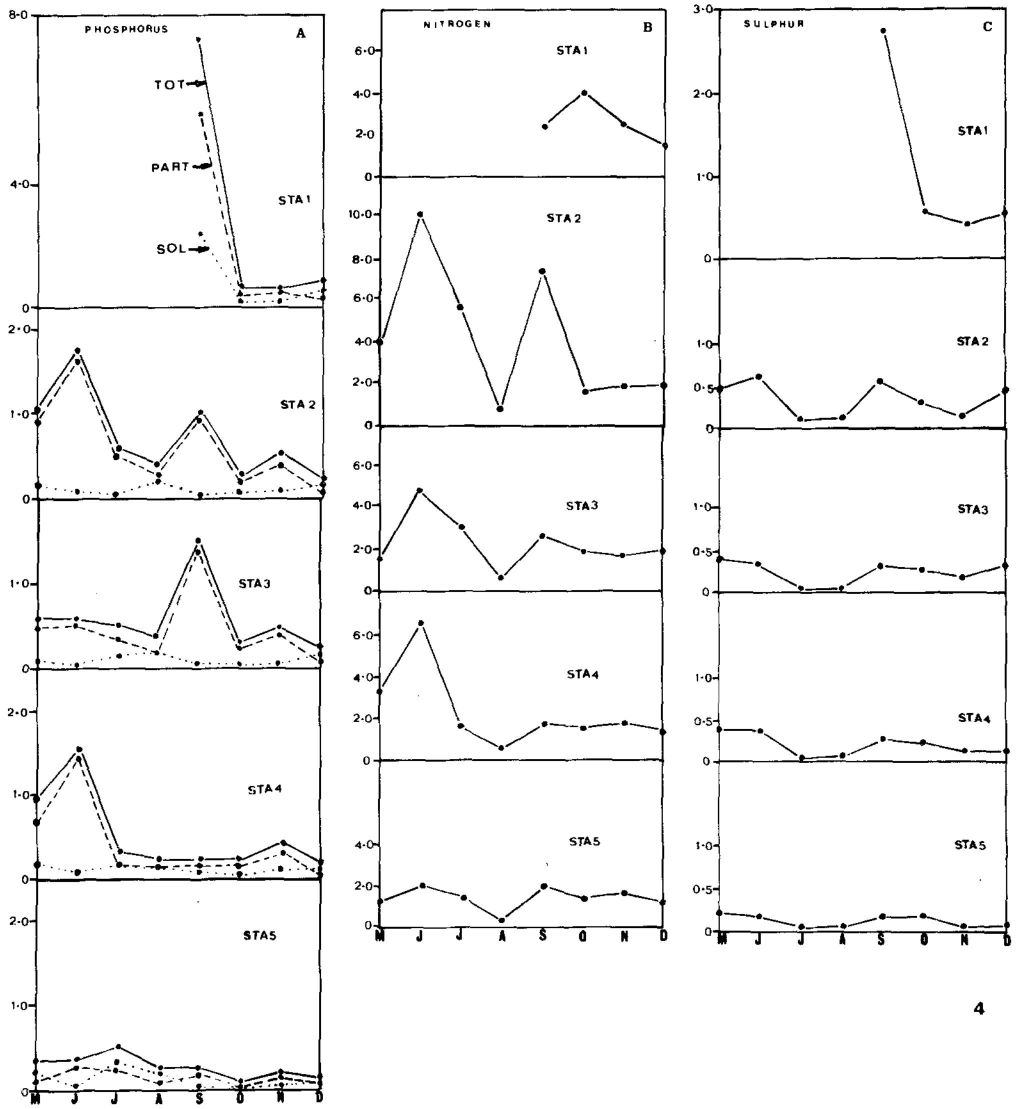


**Fig. 4A–C.** Seasonal variations in nutrients at the 5 stations: **A** phosphorous; **B** total nitrogen; and **C** total sulphur

*Nutrient Release During Decomposition*

The litter bags showed a rapid weight loss during the first month (Fig. 6) after which the rate slowed so that 30% of the original dry matter still remained after 6 months. Over half the dry matter was lost within the first 130 days.

Phosphorus levels showed an initial loss over the first 30 days. The loss (35% within 7 days) was followed by a slight increase. There was a similar but less dramatic loss of sulphur. Nitrogen decreased sharply (12% within 21 days) followed by a very large increase in the litter so that after 6 months nitrogen levels had risen to 34% over the original levels.

Under laboratory conditions there were large changes in water quality within 24 h after *Cyperus* culms were immersed in water. The colour of water changed from clear to brown, pH decreased sharply from 7.5 to 6.3 (Fig. 7A) and rose again gradually to7.2 after 2 days. Concuctivity values rose more than 600 $uScm^{-1}$ within the first 24 h followed by a slower rate of increase.

This pattern, that is, a rapid initial release followed by a slower release rate, was also exhibited by P, N and S. Phosphorus exhibited a higher release rate than either N or S, where concentrations of P increased in the supernatant water from 0.1 to 11.5 $mg\ l^{-1}$ during the first 2 days (Fig. 7B). This rapid rate of release was followed by a gradual increase to a maximum until after 21 days, when values decreased slightly. Nitrogen like P underwent a rapid release into the water during the first 2 days followed by a more gradual but still rapid release, so that over 20 $mg \cdot l^{-1}$ of total N were found.

Levels of S were always lower than those of either P or nitrogen, but the release pattern was similar.

*Nutrient Release During Soil Inundation*

Within 2 days after inundation of dry, cracked hydrosoil, the pH of the over lying water increased, thereafter remaining more or less constant at 7.9 over a 50 day period (Fig. 8A). Conductivity in the water decreased initially and then rose steadily, increasing from 392 to 742 $uScm^{-1}$ within 50 days.

Generally there was a rapid leaching of nutrients from soil to water followed by a slower release rate. The pattern of release

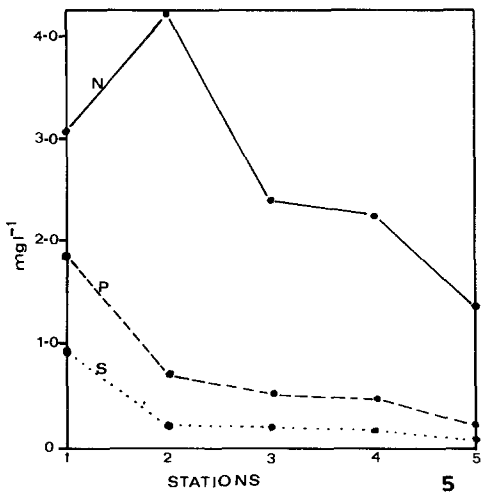


**Fig. 5.** Annual mean total values for nutrients in shallow water of Lake Naivasha

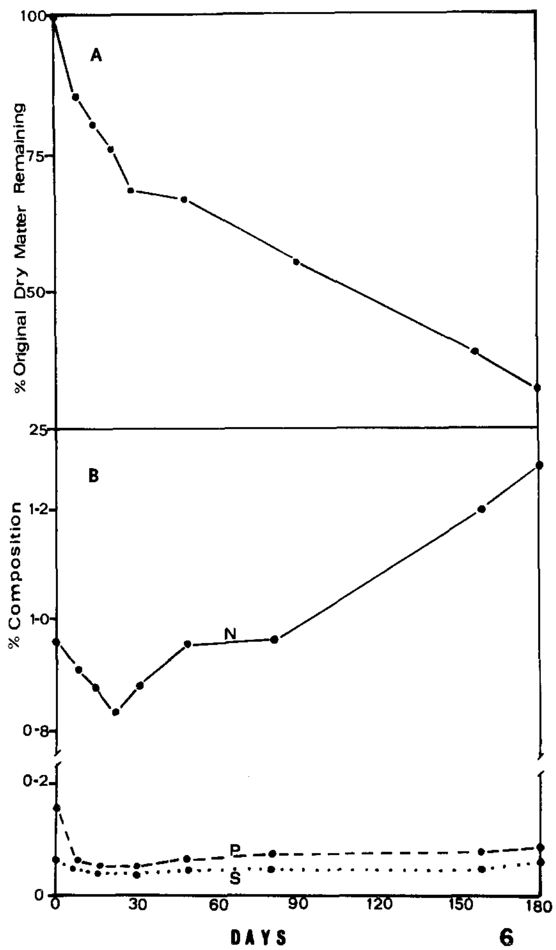


**Fig. 6 A, B.** Changes in **A** dry weight and **B** nutrient content of *Cyperus immensus* during decompostion in Lake Naivasha

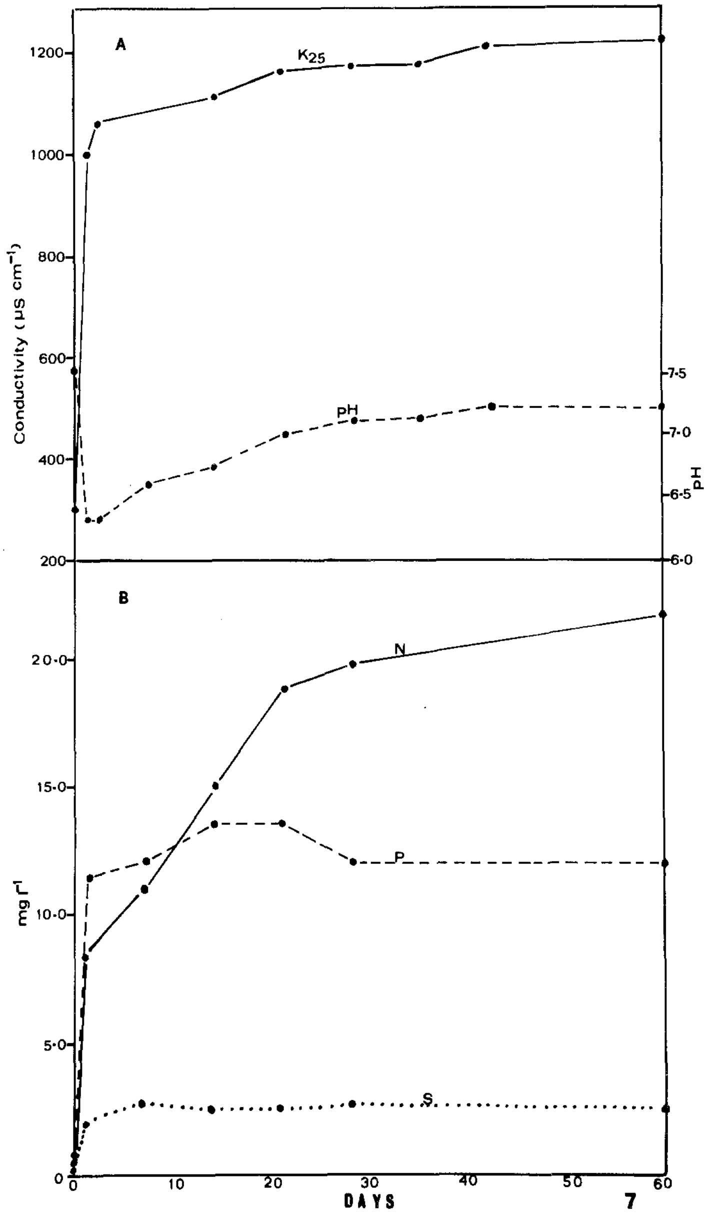


**Fig. 7 A, B.** Changes in water quality during decomposition of *Cyperus immensus* under laboratory conditions. **A** Changes in pH and conductance; **B** changes in nutrients in the overlying water

for P and N were similar, with N exhibiting higher values than P (Fig. 8 B). During the 50 day period N increased by about 3 times from 0.75 to 3.00 $mgl^{-1}$ while P increased by 20 times from 0.05 to 1.08 mg $l^{-1}$. The amount of S released to the water was much larger (66 times) than in the case of either P or N. For example, S concentrations increased from 0.15 to 9.9 mg $l^{-1}$ within the first 7 days. At the end of 50 days the concentration of S in the water was quite high, four times the concentration of N and ten times that of phosphorus.

## Discussion

### *Nutrient Generation from Decomposition*

Wetlands are typically detritus-based systems (Odum 1971) and therefore the process of decomposition is of paramount importance. Decomposition of litter and resultant release of nutrients involves several processes including leaching, weathering and biological action (Mason 1977). Decomposition can be viewed as a community level process. It involves many species populations from many phyla operating across trophic levels and results

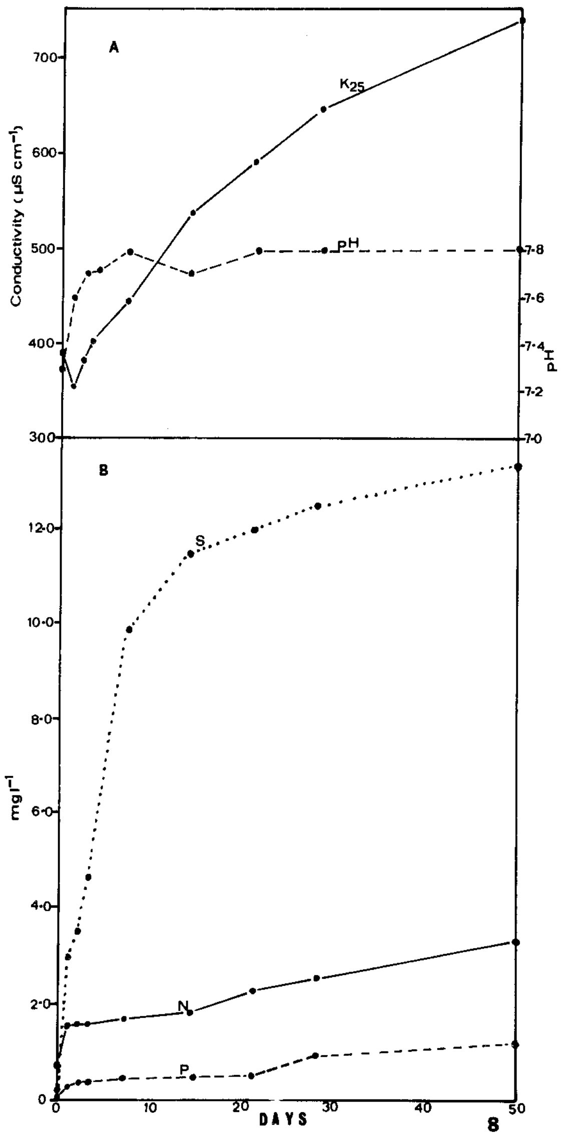


**Fig. 8A, B.** Changes in water quality during inundation of hydrosoil under laboratory conditions, **A** and **B** as above

in the breakdown of detritus with conversion to animal biomass and mineralization (Reice 1974). Decomposition occurs faster in animal than plant material (Mason 1977). But among plant species, floating plants decompose faster than submerged plants which in turn decompose faster than emergent macrophytes (Godschalk and Wetzel 1978). This has large consequences for any shallow water community dominated by emergents such as the present one.

The decomposition curve in our study consists of a rapid decomposition phase followed by a slower second phase a typical curve often seen in decomposition studies (Boyd 1970; de la Cruz and Gabriel 1974; Howard-Williams and Howard-Williams 1978; Howard-Williams and Junk 1976; Godschalk and Wetzel 1978; and Mason and Bryant 1975). The initial rapid loss in weight is more or less a passive process attributed to leaching, solubilization and fragmentation of plant material (Boyd 1970; and Visser 1964).

Although the decomposition curve for *Cypersus immensus* has a similar shape to curves for other emergent macrophytes, the actual rate is different. For comparison the rate of decomposition has been expressed as half life for decay (i.e. the time required for 50% of the original weight to be lost). For *C. immensus* in Lake Naivasha this was 130 days. This rate is slower than the rate found for *Typha domingensis* (100 days in Lake Chilwa swamp; Howard-Williams 1973). Rates of decomposition reported for other emergent macrophytes in temperate lakes for example, *Phragmites communis,* and *Typha angustifolia,* are much slower being 210 and 370 days, respectively (Mason and Bryant 1975).

There is also an initial rapid loss in nutrient composition of the tissue of *C. immensus,* that is attributed to leaching, solubilization and fragmentation of plant tissue. This rapid loss in nutrients takes only a few days. This is also true of the nutrient release into shallow water during decomposition under laboratory conditions. We assume this is due to the well-known process of nutrient release by leaching which involves a pulse-like release of both inorganic and organic constituents of plant tissue and lasts for 1–3 days (Howard-Williams and Howard-Williams 1978).

Following the initial rapid loss in nutrients from the plant litter the level in the litter rose again. This phenomenon has been reported by many other investigators. De la Cruz and Gabriel (1974) found that percentage N and P was higher in plant material undergoing decay than in the living or newly-dead leaves from which the decaying tissue was derived. Boyd (1970) showed that there was an increase in N in *Typha latifolia* litter to a level some 20% higher than at the start of the experiment. In this present study N increased by 34% over the original levels in *C. immensus,* similar to the results reported by other workers (Mathews and Kowalczewski 1969; Mason and Bryant 1975; and Reice 1974). The increase in nutrients in the decomposing litter is largely due to the activity of microorganisms impregnanting the plant tissue (de la Cruz and Gabriel 1974; and Boyd 1970). Mason (1977) attributes nitrogen increase in litter to nitrogen fixation by microorganisms that use the litter as a carbohydrate source.

Because of this increase in nutrient content, decomposing plant detritus is often a better (more nutritious) food for the decomposers than the living plant from which it was derived (Mason 1977 and Odum 1971). The significance then, of detritus in ecosystems such as the shallow water zone of Lake Naivasha, lies mostly in nutrient generation and recycling.

### *Nutrient Cycling*

In shallow African lakes such as Lake Chilwa in Malawi there is a seasonal flushing of the littoral zone which definitely has a large influence on the water quality of the lake (Howard-Williams and Lenton 1975). In Zimbambwe, MacLachlan (1971) has shown that significant levels of mineral ions were released from lakeside grass and dung during the water level rise in the man-made Lake Kariba; e.g., 1 $m^2$ of grass released 9.78 g $K^+$ after 24 h submersion. In Kenya, Gaudet (1977a) has suggested that flooding of exposed mud and dead plants in the drawdown area of Lake Naivasha should result in increased offshore levels of nutrient with a subsequent increase in primary production. The main source of plant nutrients in the drawndown zone of Lake Naivasha would seem to be the interstitial water filling the space among the solid particles of the hydrosoil. In the drawdown this interstial water occupies the hydrosoil only down to about 0.2 m. Below this level the hydrosoil becomes a compact clay which is not permeated by plant roots and, although it is still quite, wet with seepage water, it does not contain the easily-drained soil water (i.e. interstital water) of

**Table 2.** Estimated rates of total nutrient release into overlying water ($g\ m^{-2}\ yr^{-1}$) in shallow water of Lake Naivasha based on data from Figs 6, 7 and 8

| Nutrient | Release from plant by leaching | Release from plant by decomposition | Release from submerged soil | Total theoretical release from leaching, decomposition and sediments |
|---|---|---|---|---|
| Phosphorus | 13.0 | 2.0 | 0.4 | 15.4 |
| Nitrogen | 21.4 | 10.4 | 0.9 | 32.7 |
| Sulphur | 2.6 | 0.7 | 6.4 | 9.7 |

the upper 0.2 m layer. This division roughly corresponds with Gaudet's (1977a) 'AO' drawdown soil, that is, the hydrosoil at the mud surface which is an organic silt soil lying over deeper more impervious clay 'A' layer.

Macrophytes rooted in the hydrosoil (AO layer) function as nutrient pumps transferring nutrients from the interstitial water into the littoral (Dykyjova and Kvet 1978). The general idea of a nutrient pump depends on the fact that mineral nutrients taken up are accumulated in the plant tissue. If these emergent macrophytes are subsequently inundated they generally die back and eventually release their nutrients back into the overlying water during leaching and decomposition of the dead or dying plant material (Table 2).

Owing to the decomposition and mineralization of organic matter in the littoral of Lake Naivasha the Grass and Sedge Zones should be richer in nutrients than the open lake. This was the general observation made by Planter (1970) in European, and Howard-Williams (1972) in African shallow waters. Decomposition and mineralization probably are also responsible for the low pH and high conductivity values found in the vegetated zones when compared to the open lake. Low pH values have also been reported for the large papyrus swamp in the north of Lake Naivasha (Gaudet 1979). Low pH values here are said to be due to an increase in $CO_2$ and humic acids. The low pH values in temperate waters, e.g. those reported for English marshes, similarly have been attributed to a release of hydrogen ions in stagnant water during the process of decomposition (Gorham 1953).

Water level fluctuations are quite important in nutrient regeneration from mud. The mud in the shallow water of Lake Naivasha has a large reserve of nutrients that are released to the overlying water during high water levels. During the dry season the hydrosoil in the drawdown area of the lake edge is exposed, resulting in dried, cracked and aerated soil. This soil is enriched by dung deposited by cattle and hippos grazing and trampling the drawdown flora. When the water level rises and this zone is inundated, the submerged flora, dung and previously oxidized, aerated soils release large amounts of nutrients. In Africa, this phenomenon has been previously reported for Lake Chilwa by Howard-Williams (1972) and the shore of Lake Kariba by MacLachlan (1971). A similar nutrient release has been reported for Czechoslovakian fish ponds where, following drainage, oxidation and mineralization of organic matter takes place in sediments. Afterwards, during the process of re-filling, a large load of nutrients is released into the overlying water (Dykyjova and Kvet 1978).

Mineral elements such as P, N and S often occur in micromolar quantities and frequently limit the rate of production in lakes. Hutchinson (1975) and Wetzel (1975) have pointed to the fact that P deficiency is more likely to limit production of lakes than any other nutrient because of its major role in biological metabolism and the relatively small amounts being recycled in the biosphere. Evidence suggests that P is in low supply in Lake Naivasha. Rapid turnover rates for $^{32}p\text{-}PO_4$ and extremely low concentrations of soluble reactive P have previously suggested that orthophosphate was a limiting factor for phytoplankton production in Lake Naivasha (Peters and MacIntyre 1976). Enrichment of lake water samples under laboratory conditions also suggested a P limitation in this lake (Anon. 1978). Very recent evidence suggests that P remains one of the major controlling factors because the algal biomass (Chl. *a*) and total P relationship is the same as that of P-limited temperate lakes during the summer season (J. Kalff, pers. comm.).

Although N is quite abundant in temperate lakes, it is thought to be a limiting factor in a number of tropical lakes (Golterman 1975). In Africa, Fish (1956) concluded that, based on algal culture experiments, $NO_3$-N was a limiting factor for algal growth in Lake Victoria. Recent experiments with enrichment of lake water samples under laboratory conditions suggest that N is one of the limiting factors in Lake Naivasha and in fact it may be as often limiting as P (Anon. 1978).

In most fresh waters, S is abundant because the sulphate ion is second or third most abundant, being exceeded only by bicarbonate and in some cases silicate (Hutchinson 1975). However, if we consider only the sulphur portion of the sulphate ion and look at concentrations in African fresh waters, values are low, ranging from less than 0.17 to 0.97 mg $l^{-1}$. They are so low that S has been reported as a minor or trace element in African waters (Beauchamp 1953). Shortage of S in these lakes has been attributed to the low concentrations of sulphate in the inflowing streams and the fact that the balance of biological processes acts in such a way that $SO_4$-S in solution is utilized and adsorbed faster than soluble S can be released by decomposition of organic matter (Beauchamp 1953). Culture experiments reveal that a shortage of S could limit production in Lake Victoria and in fact values of $SO_4$-S below 0.17 mg $l^{-1}$ were considered to be the minimum necessary for algal growth (Fish 1956). If the above results are applicable to Lake Naivasha we would also expect low levels in this lake. Gaudet (1979) reported levels of $SO_4$-S to be 3.8 mg $l^{-1}$ (an 11-month mean, from 1975–1976) in the main influent river (Malewa), versus 0.7 mg $l^{-1}$ (with a range of 0.00–1.32) in the open lake. In the present study, 20 m offshore the concentration of total S in the lake was 0.13 mg $l^{-1}$. Gaudet ascribes the steep river-to-lake gradient (from 3.8 to 0.7) to an uptake by the papyrus swamps through which the river flows. In the swamp both adsorption and uptake by papyrus plants would take sulphate out of the throughflow resulting in low levels in the open lake.

In the present study the flooded sediments released more S than either N or P. Yet, the average concentrations of this element (as S) is still lower than either N or P in the shallow water (Grass and Sedge Zones). This suggests that there is a large potential for S input from the muds. However, the subsequent low concentration found in the shallow water imply that a great demand exists for the S throughout the Lake Naivasha ecosystem, in both shallow and open water areas.

The above account for P, N, and S in this lake shows that all three nutrients are generally at low levels in the lake. Potentially, the lake edge would have a large stock of nutrients that could replenish open water low concentrations. This would be apparent during periods when the open water mixes with the shallow water, an exchange that is certainly facilitated by winds and fauna and floral migrations. Active exchange of nutrients occurs during cattle and hippo wading at the lake edge, a daily and nightly phenomenon, respectively. Migration of mature fish into the shallow areas for spawning, would facilitate exchange which could also occur during the movement of schools of juvenile fish from shallow zone to the open lake. This last is especially evident during periods of high water levels. Crayfish taken from littoral regions by birds and large fish also facilitate the exchange of nutrients from the littoral to the open lake. In addition, the crayfish themselves are very active in burrowing and stirring up mud and water at the edge of Lake Naivasha.

In regard to plant migrations here we are dealing especially with *Salvinia,* a free-floating aquatic fern, now considered to be a major weed on the lake (Gaudet 1976). During any prevailing on-shore wind, large mats of *Salvinia* pile up in the shallow water and significant amounts of nutrients must be absorbed and adsorbed during this period. Later when the wind direction changes, as it does practically every day, the *Salvinia* mats float out onto the open water. Some of the absorbed nutrients must be released to the 'nutrient poor' open lake during these changes in location of aquatic weed mats as they represent 20 $km^2$ of coverage (estimate R. Mennell 1979).

Nutrient exchange between shallow water and open lake will be affected by all these activities. We would expect then that the level of primary production in this lake would be correlated with changes in water level. Melack (1976) found such a correlation. He showed that as the lake edge is submerged, offshore primary production generally increased. Recently it has been found that zooplankton (biomass and numbers) also increase during high water periods when the lake edge is inundated (Mavuti, pers. comm.). Thus the lake edge behaves like a 'nutrient kitchen' for the lake. It recycles, processes and regenerates nutrients from plants, animal and sediments. The released nutrients are eventually transferred to the open lake where they enter the open water food webs resulting in an increased production during and following periods of high water level.

*Nutrient Dynamics*

The processes involved in generation or re-cycling of nutrients are complex and as yet little understood, consequently, they are not considered in this study. However, it would be of great help to workers involved in lake management to at least know the approximate size of nutrient standing stocks in the various components of the Lake Naivasha shallow water ecosystem. Also the rate of flux among the major components and the potential annual input of nutrients into the lake from shallow water and other sources would be of help in predicting production levels in the lake.

In order to do this, nutrient standing stocks in the hydrosoil were calculated based on the nutrient content of the upper 0.2 m of soil (nutrients are only easily available down to this depth). Nutrient standing stocks in the overlying water were calculated with the assumption that the average water depth in the shallow zone was 1 m. Nutrient standing stocks in the drawdown flora were calculated based on previous biomass data of Gaudet 1977a.

By far the largest standing stocks of all the nutrients were in the sediments (Fig. 9). This component has a large influence on the overlying water when the exposed hydrosoil is submerged as discussed above. In addition, the emergent macrophytes derive their nutrients from this substrate and hence its importance as a basic source of nutrients in nutrient cycling. The plant component is the next largest pool, while the overlying water contains the lowest standing stock of nutrients. A similar distribution of nutrient standing stocks for only N and P has been reported

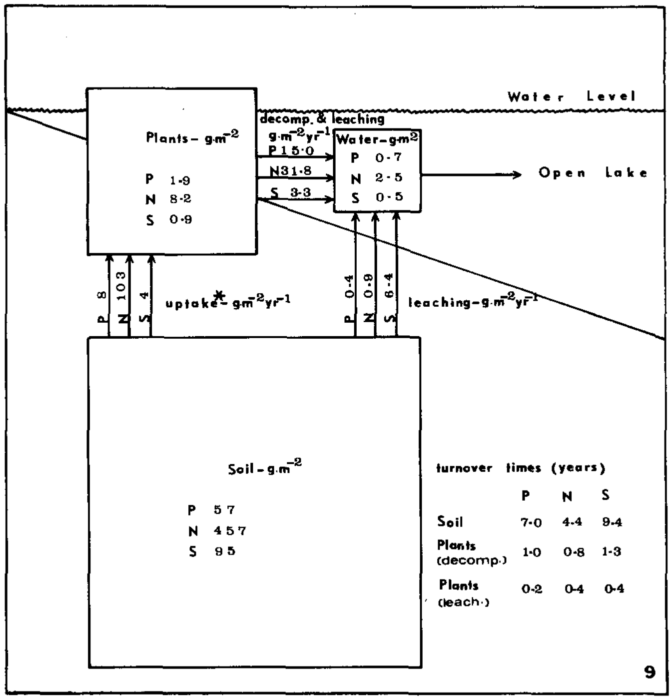


**Fig. 9.** General relationships of P, N and S in the shallow water of an African lake. (* = uptake rates estimated using data from *Cyperus papyrus*; Gaudet, 1977b)

for Swartvlei Lake in South Africa (Howard-Williams 1977), but in the Swartvlei study no mention was made of S.

In Lake Naivasha, N dominates all three components, and P is at a higher level than S in both the plant component and the water, but a lower level of P occurs in the sediments.

Transfer rates were calculated on the basis of present data especially for *Cyperus immensus,* except for macrophyte uptake rates which were estimated from Gaudet (1977b) for *Cyperus papyrus.* Transfer rates from sediments to macrophytes are higher than transfer rates from macrophyte to the water; in other words the rate of uptake is greater than the release rate, a general phenomenon reported by Odum (1971). The combined release of P from macrophytes through leaching and decomposition (15.0 g $m^{-2}$ $yr^{-1}$) does not seem to appreciably affect the level of P in the overlying water because here the nutrient stock is quite low (0.7 g $m^{-2}$). Perhaps this is because of the ability of the hydrosoil to adsorb $PO_4$-P. For example, in another Rift Valley lake, Lake Nakuru, MacIntyre (1975) found an uptake of $PO_4$-P of at least 17.5 g $m^{-2}$ $yr^{-1}$. Adsorption by the sediments could also affect N (as $NH_3$) and S (as $SO_4$). In addition, the lake biota (in general) and phytoplankton (in particular) would be active in taking up P, N and S. This would also contribute to the low level of nutrients in the overlying water.

Nitrogen and P dominate the transfer along the soil-plant-water pathway (Table 2 and Fig. 8), but the flush of S from the soil indicates that more S is transferred along the soil-water pathway than the direct uptake and release from plants. The nutrient transfer from macrophytes to water by leaching occurs over a short interval while decomposition occurs over longer periods of time. Thus the plant-water transfer is probably an overestimate because it is based on the combined rate of leaching and decomposition. Difference in turnover times is even more obvious if the calculation of turnover time is based only on decompostion compared to leaching alone. In any event, the turnover times for hydrosoil are longer than the turnover times

**Table 3.** Estimated open lake nutrient standing stocks and the estimated inputs from the drawdown area and Malewa River

| | L. Naivasha standing stocks in 1974 (tons)[a] | Theoretical annual input from the drawdown (tons)[b] | Percentage input from drawdown (%) | Annual input from Malewa River 1976 (tons)[c] | Percentage input from the river (%) | Percentage derived from other sources (recycle, rain, seepage, etc) (%) |
|---|---|---|---|---|---|---|
| Phosphorus | 77 | 16 | 21 | 5 | 6 | 73 |
| Nitrogen | 84[d] | 33 | 39 | 29 | 35 | 26 |
| Sulphur | 242[d] | 10 | 4 | 1,399 | 578 | – |

[a] Lake Naivasha standing stocks = Lake volume (1974) × average total nutrient concentration during low water period
[b] Drawdown input = 1974 water volume of drawndown × average nutrient concentration during the high water period
[c] Malewa River input = annual discharge (1976) × average nutrient concentration of river water (Gaudet, 1979)
[d] Estimate of total $SO_4$–S in the northern open lake based on Gaudet (1979)

for plants. The shortest turnover times occur for N and the longest for S in both the soil and plant compartments.

The overall impact of the shallow water zone on nutrient loading is best seen by comparison with other major sources of nutrients. If we compare the lake nutrient standing stocks, annual inputs from the shallow water zone (via drawdown), and the Malewa River input (Table 3) we see that there must be a large portion (73%) of lake P that is recycled (or is derived from rainfall, seepage, etc). In calculating the Malewa River input of P into the lake an 'open system' was assumed, i.e., all nutrients brought into the basin by the river would end up in the lake directly. But we also know that the North Swamp must have a large effect on the P content of the inflow river water (Gaudet 1978).

The standing stock of N in the lake is larger than the input, it is also higher than the level of P. This is probably due to other inputs such as seepage and nitrogen fixation in the North Swamp.

The input of S from the river is quite large and this source alone could in one year theoretically contribute more than 5 times the amount of S in the lake. However, in the open water during this study only low concentrations of this element were present. Gaudet (1979) also showed low values, and at times dissolved S was undetectable for some months of the year in the open lake. This illustrates the fact that not all incoming $SO_4$-S enters the lake, it is also assumed that large quantities of $SO_4$-S must be adsorbed or precipitated in the North Swamp even before reaching the main lake, and even upon reaching open water $SO_4$-S adsorbed to particles would be excluded from analysis, because dissolved S is here taken to be total S after 0.45 μm filtration.

The shallow water drawdown area contributes more N and P than the estimated river inputs. However, it must be pointed out that the drawdown estimate is most likely a maximum estimate. Also the estimate is only based on data collected over a short period of time. More work especially on nutrient generation in shallow water over longer periods of time would be required before reliable nutrient budgets can be derived for this lake. The present study is therefore considered preliminary in respect to the whole lake, but, hopefully, this present work will provide some basic ideas for future research, management and conservation on Lake Naivasha.

## References


Anon 1968 Determination of sulphur in soils and Plant Material. Technical Bulletin No. 14. The Sulphur Institute, 1725 K Street, NW, Washington, DC 20006

Anon 1978 Limnological investigation of lakes in Kenya 1976–1977. Technical Report No. 6. Water Quality and Pollution Control Section, Ministry of Water Development, Kenya

Boyd CE, 1970 Losses of mineral nutrients by decomposition of *Typha latifolia*. Arch Hydrobiol 66:511–517

Beauchamp RSA, 1953 Sulphate in African inland waters. Nature 171:769–771

de la Cruz AA, and Gabriel BC, 1974 Caloric, elemental and nutritive changes in decomposing *Juncus roemerianus* leaves. Ecology 55:881–886

Dykyjova D, and Kvet J, 1978 Pond Littoral Ecosystems. Berlin Heidelberg New York, Springer Ecological Studies 28

Fish GR, 1956 Chemical factors limiting growth of phytoplankton in Lake Victoria. E Afri Agric J 21:152–158

Gaudet JJ, 1974 The normal role of vegetation in water. In: D Mitchell (Editor), Aquatic Vegetation and Its Use and Control. UNESCO, Paris p 24–37

Gaudet JJ, 1975 Mineral concentrations in papyrus in various African swamps. J Ecol 63:483–491

Gaudet JJ, 1976 *Salvinia* infestation on Lake Naivasha, Kenya. In: Varshney and Rzoska Aquatic Weeds in S.E. Asia, Junk Publ The Hague p 193–209

Gaudet JJ, 1977a Natural drawdown on Lake Naivasha (Kenya) and the origin of papyrus swamps. Aquatic Botany 3:1–47

Gaudet JJ, 1977b Uptake, accumulation, and loss of nutrients by papyrus in tropical swamps. Ecology 58:415–422

Gaudet JJ, 1979 Seasonal changes in nutrients in a tropical swamp. North Swamp, Lake Naivasha, Kenya. J Ecol 67:953–981

Godschalk GL, Wetzel RW, 1978 Decomposition in aquatic angiosperms. I. Dissoved components. II. Particulate components. III. *Zostera marina* L. and a conceptual model of decomposition. Aquatic Botany 5:281–384

Golterman H, 1975 Physiological Limnology. An Approach to the Physiology of Lake Ecosystems. Elsevier Amsterdam

Gorham E, 1953 Chemical studies on the soils and vegetation of waterlogged habitats of the English Lake district. J Ecol 41:435–460

Howard-Williams C, 1972 Limnological studies in an African swamp: Seasonal and spatial changes in the swamps of Lake Chilwa (Malawi). Arch Hydrobiol 70:379–391

Howard-Williams C, 1973 Vegetation and environment in the marginal areas of a tropical African lake (Lake Chilwa, Malawi). Ph D thesis, University of London

Howard-Williams C , 1977 The distribution of nutrients in Swartvlei, a Southern Cape Coastal Lake. Reprinted from Water SA, Vol 3 No 4, Oct

Howard-Williams C, Howard-Williams W, 1978 Nutrient leaching from the swamp vegetation of Lake chilwa, a shallow African lake. Aquatic Botany 4:257–267

Howard-Williams C, Junk WJ, 1976 The decomposition of aquatic macrophytes in the floating meadows of an Amazonian varzea lake. In: P. Muller (Editor) Neotropische Okosysteme. Biogeographica 7:115–123

Howard-Williams C, Lenton G, 1975 The role of littoral zone in the functioning of a shallow tropical lake ecosystem. Freshwater Biol 5:445–459

Hutchinson GE, 1975 A Treatise on Limnology Vol 1, Part 2 – Chemistry of Lakes. John Wiley and Sons

Lind E, Visser S, 1962 A study of a swamp at the north end of Lake Victoria. J Ecol 50:599–613

Luther H, Rzoska J Project Aqua A source book of inland waters proposed for conservation. International Biological Programme Handbook No 21

MacIntyre S, 1975 Ortho-phosphate concentrations in Kenyan lakes. (Abst.) 38th Annual Meeting of the American Society of Limnology and Oceanography, Halifax, Nova Scotia

MacLachlan S, 1971 The rate of nutrient release from grass and dung following immersion in lake water. Hydrobiologia 37:521–530

Mason CF 1977 Decompsotition. Studies in Biology No 74, E Arnold Pub Ltd London p 58

Mason CF, Bryant RJ, 1975 Production, mineral content and decomposition of *Phragmites communis* Trin. and *Typha angustifolia* L J Ecol 63:71–95

Mathews CP, Kowalczewski A, 1969 The disappearance of leaf litter and its contribution to production in the River Thames. J Ecol 57:543–552

Melack J M, 1976 Limnology and dynamics of phytoplankton in equatorial African lakes. Ph D Thesis, Dept of Zoology, Duke University, Durham NC

Odum EP, 1971 Fundamentals of Ecology. WB Saunders Company

Peters RH, and MacIntyre S, 1976 Ortho-phosphate turnover in East African lakes. Oecologia (Berl) 25:313–319

Planter M, 1970 Elution of mineral components out of dead reed, *Phragmites communis* Trin Pol Arch Hydrobiol 17:357–362

Reice SR, 1974 Environmental patchiness and the breakdown of leaf litter in a woodland stream. Ecology 55:1271–1282

Visser SA, 1964 A study of the decomposition of Cyperus papyrus in the swamps of Uganda, in natural peat deposits, as well as in the presence of various additives. Eas Afri Agric For J 29:268–287

Wetzel GR 1975 Limnology. WB Saunders Company Philadelphia

Received September 5, 1980