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Nutrient distribution in a papyrus swamp: Lake Naivasha, Kenya

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Abstract

Much of the permanent swamps of tropical Africa consists of monotypic stands of papyrus (*Cyperus papyrus* L.). Papyrus has a high photosynthetic and productive potential due to the presence of C_4 photosynthesis. The objective of this study was to assess the nutrient status in the various compartments of a papyrus swamp which fringes Lake Naivasha, Kenya, in order to identify nutrients most likely to limit primary production. In swamp water, plant-available nitrogen was largely in the form of ammonium ions, phosphorus concentrations were higher than in the open lake water and sulphur was present in only trace amounts. The presence of C_4 photosynthesis in papyrus means that it is more efficient than C_3 species in its use of nitrogen. Plant tissue nutrient analysis suggested that there was a considerable amount of translocation of nutrients from older portions of the plant to new growth. The atomic ratio of 44N:3P:1S in papyrus suggests that sulphur is the nutrient most limiting growth of papyrus in the swamps. Calculations show that removal of large quantities of nutrients following papyrus harvesting may lead to reduced production rates in subsequent regrowth periods.

Keywords: Nitrogen; Phosphorus; Sulphur; *Cyperus papyrus*; Nutrient dynamics

1. Introduction

Although much of the African continent is arid it also supports some of the worlds largest areas of freshwater swamps. The total area of these swamps is difficult to assess because of their seasonality but certainly the area of permanent swamp amounts to hundreds of thousands of square kilometres (Beadle, 1981; Hughes and Hughes, 1992). Large areas of these permanent swamps in Africa consist of monospecific stands of

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papyrus (*Cyperus papyrus* L.). The most extensive papyrus swamps are found around the perimeter of Lake Victoria and in Uganda and Sudan associated with the river Nile basin. In Uganda, the largest papyrus swamps are found in the littoral regions of Lakes Albert, George, Kioga and Victoria as well as other smaller lakes (Beadle, 1981). The bulk of permanent swamps along the Nile lies within the Sudd region of Sudan (Rzóska, 1974). In Kenya and Tanzania, lake, river and valley swamps are common although the total area is not known. Large swamp areas also occur in Zaire where papyrus swamps are best developed in the Upemba region (Thompson et al., 1979; Hughes and Hughes, 1992).

Papyrus has a high photosynthetic and productive potential due to the presence of C_4 photosynthesis, a characteristic shown by many high yielding tropical grasses (Jones, 1986). Under optimum conditions, in hydroponic culture, papyrus has been shown to have very high short-term rates (125 g dry weight m^{-2} day^{-1}) of primary production (Thompson, 1976) and under natural conditions rates of aerial primary production have been shown to be 6607 g m^{-2} y^{-1} (Muthuri et al., 1989). This biomass production presents a potentially enormous economic resource and attempts have already been made to exploit it (Jones, 1983). Several feasibility studies on the exploitation of papyrus have been carried out in Uganda and Sudan and some failed attempts have been made to set up paper and pulp industries in these countries (Thompson, 1976). In recent years, rapid disappearance of fuel-woods in many developing countries have stimulated investigations into the use of papyrus as an alternative source of fuel (Jones, 1983).

The possible, large scale exploitation of papyrus in the future will have significant ecological implications for the swamps and the adjacent wetland systems. A major impact of the papyrus harvesting will be the loss of large quantities of nutrients from the swamps when the vegetation is removed. A possible consequence of the loss of limiting nutrients such as nitrogen, phosphorus and sulphur may be a reduction in the swamp primary production leading to lower sustainable yields of biomass.

The main objective of this work was to assess nutrient levels in the various compartments of a papyrus swamp which fringes Lake Naivasha, in the Rift Valley of Kenya in order to (i) determine the nutrient(s) most likely to be limiting primary production and to (ii) assess the likely impact of biomass harvesting on nutrient availability and its consequences for papyrus primary productivity.

2. Materials and methods

This study was conducted on a papyrus swamp along the shore of Lake Naivasha (0° 45'S, 36° 20'E) in the eastern Rift Valley of Kenya at an altitude of 1890 m asl. The ecology of the study area has been described by several authors (Gaudet, 1977a; Jones and Muthuri, 1985; Muthuri, 1985; Harper et al., 1990). The experimental site was situated at the western shore of the lake in a fringing, floating swamp about 100 m from the shore.

Because the growth rates of papyrus show little change throughout the year (Muthuri et al., 1989) it was assumed that nutrient distribution likewise shows little annual variation. Sampling was therefore carried out on one occasion only.

The nutrient levels in water, sediments and papyrus plant material were analysed in replicate samples as follows. Where appropriate the analyses are presented as means ± one standard deviation.

2.1. Water analysis

Ten water samples were collected in a modified plastic Dussart bottle (Golterman et al., 1978) from the water pools at different locations inside the papyrus canopy. The collected samples were transferred into 1 litre plastic bottles and preserved with a few drops of $CHCl_3$. The preserved samples were taken to the laboratory and analysed as follows:

Orthophosphate — Water samples were filtered through pre-washed 0.45 μm membrane filters (Nuflow Filters, Oxford, London) and orthophosphate was determined spectrophotometrically by the ammonium molybdate–ascorbic acid method of Strickland and Parsons (1977).

Dissolved phosphorus — Water samples were filtered as above and digested with concentrated H_2SO_4 and neutralized with NaOH. The hydrolysed phosphorus was then determined as above.

Total phosphorus — Unfiltered water samples were analysed as for the dissolved phosphorus.

Ammonium nitrogen — Determined spectrophotometrically on filtered water samples using the indophenol blue method (Golterman et al., 1978).

Nitrite nitrogen — Determined spectrophotometrically on filtered water samples by the sulphanilamide–naphthylamine hydrochloride method (Golterman et al., 1978).

Nitrate nitrogen — Determined by the sulphanilamide–napthalamine hydrochloride method following cadmium-copper reduction of NO_3–N to NO_2–N (Golterman et al., 1978).

Total nitrogen — Determined on unfiltered water by the micro-Kjeldahl distillation technique after digestion with concentrated H_2SO_4 (Golterman et al., 1978). The distillate was collected in boric acid and titrated with 0.02 M H_2SO_4 to a faint pink colour.

Total organic nitrogen — Determined on unfiltered water samples as in the total nitrogen and corrected by substracting NH_3–N values determined above.

Dissolved organic nitrogen — Determined on filtered water samples as in total nitrogen and corrected by substracting NH_3–N values determined above.

Particulate organic nitrogen — Calculated as the difference between the total organic nitrogen and the dissolved organic nitrogen.

Total sulphur — 20 ml aliquots of unfiltered water were mixed with 1 g $NaHCO_3$ and evaporated to dryness. 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 a carrier gas. Sulphur (as H_2S absorbed in NaOH) was then determined titrimetrially using mercuric chloride and dithizone (Beaton et al., 1968).

Dissolved sulphur — Determined on filtered water samples as outlined above.

Sulphate sulphur — Attempts were made to estimate SO_4–S by precipitation of sulphate with barium chloride and measuring the turbidity with a spectrophotometer at 400 nm (Golterman et al., 1978). However, SO_4–S of the water samples was below the limits of detection (0.5 mg l^{-1}) for the above technique.

2.2. Sediment analysis

Fourteen samples of sediment (detritus) were collected from among the roots of the papyrus plants at different locations in the study site and dried at 105°C. The dried samples were ground in a mortar and pestle, sieved through a 1 mm sieve and dried again prior to nutrient analysis. These samples were analysed according to Allen et al. (1974) and Beaton et al. (1968) as follows:

Nitrogen — 200 mg of detritus sample was digested in 5 ml concentrated H_2SO_4, diluted to 50 ml and 10 ml aliquots were used for the micro-Kjeldahl distillation as outlined above.

Phosphorus — 100 mg of detritus sample was digested in 5 ml concentrated H_2SO_4, neutralised with NaOH, and diluted to make 1 litre. 100 ml aliquots were used for phosphorus determination using the spectrophotometric method described above.

Sulphur — 200 mg of detritus sample was mixed with $NaHCO_3$ and ashed at 500°C for 3 hours. Sulphur was then reduced to H_2S and determined as above.

2.3. Plant analysis

The rhizomes of papyrus are sympodial, as each shoot apex initially adds to the length of the rhizome but then turns sharply upwards to become an aerial shoot referred to as a culm. The culm has two intercalary meristems, one at the culm base and one at the base of the umbel. There are typically 4–7 living culms on a rhizome at any one time (Fig. 1) and each culm survives for approximately 180 days (Muthuri et al., 1989). Six age classes of culm were identified for the present analysis as indicated by Roman numerals in Fig. 1; (I) young elongating culm with closed umbel, (II) elongated culm with umbel just opening, (III) fully elongated culm and fully expanded umbel, (IV) similar to III but older, (V) senescing culm ($>$ 10% achlorophyllous), (VI) dead culm ($>$ 80% achlorophyllous).

Nutrient analysis of papyrus plant material was carried out on representative whole plant samples and plant organs of all ages (Fig. 1). Sixteen whole plants were harvested and were washed under running tap water and rinsed with distilled water. Each whole plant was cut vertically into four equal sections. One quarter, consisting of all papyrus organs i.e. umbel, scale leaves, rhizomes and roots, was used for whole plant analysis and another quarter was divided into the respective organs.

Each sample was cut into small pieces, mixed and dried at 80°C. The dry material was ground in a mill (Glen Creston, Stanmore, England) to pass a 1 mm sieve. The ground plant samples were analysed for nutrients as for the soil samples above. The results of nutrient analysis were expressed as a percentage of dry weight.

3. Results

3.1. Nutrient concentrations in swamp water

Nutrient levels are expressed as mass of nutrients per unit volume of water. Of the three forms of inorganic nitrogen (NO_3–N, NO_2–N and NH_3–N) ammonium nitrogen

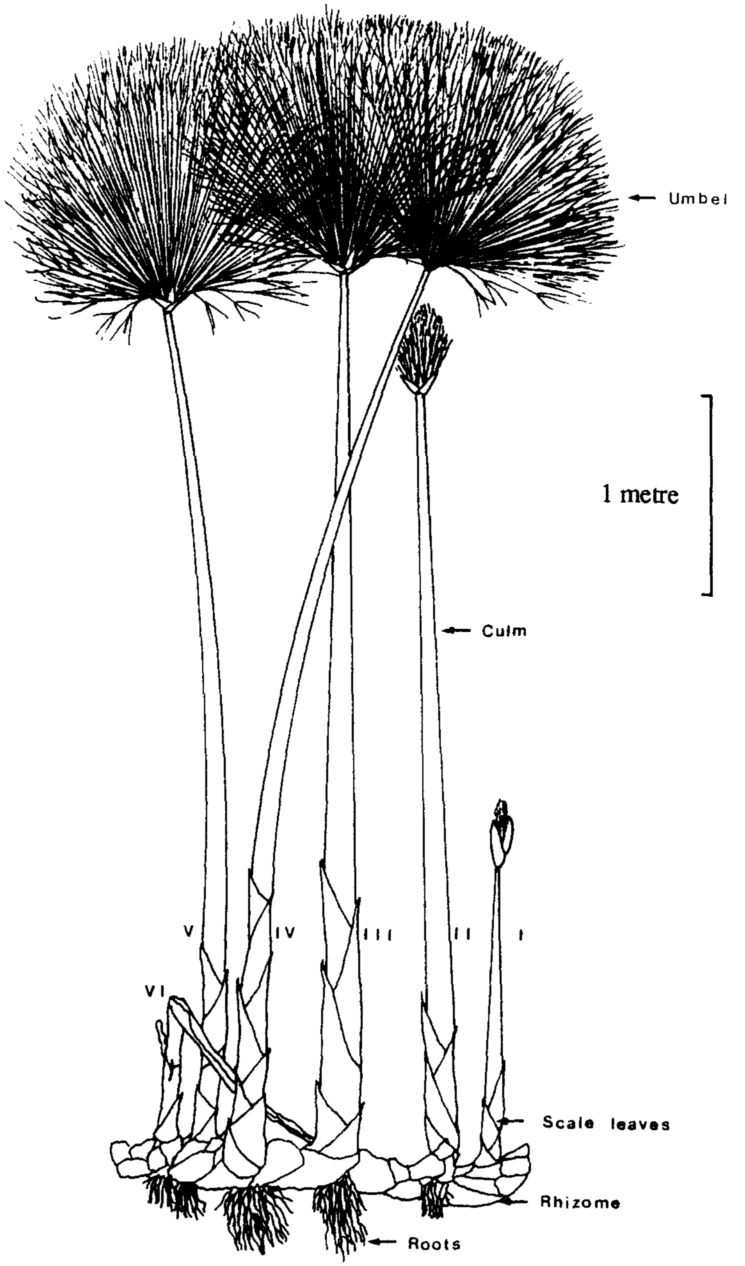

Fig. 1. A *Cyperus papyrus* plant showing the age classes of organs from the youngest (culm-unit I) to the oldest (culm-unit, VI).

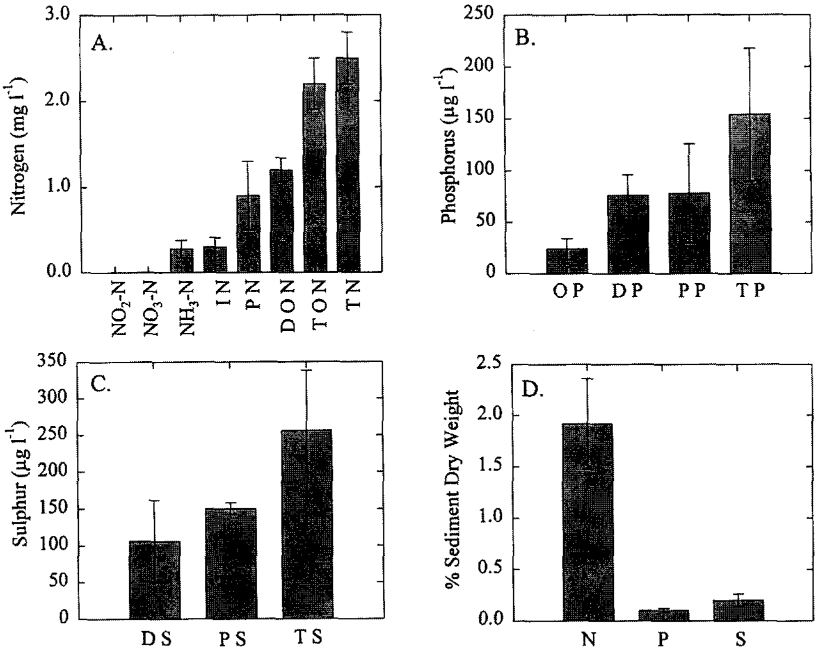

Fig. 2. Nutrient concentrations in papyrus swamp water. (a) Nitrogen, where IN is inorganic nitrogen, PN is particulate nitrogen, DON is dissolved organic nitrogen, TON is total organic nitrogen and TN is total nitrogen. Bars represent ± one standard deviation ($n = 10$). (b) Phosphorus, where OP is orthophosphate, DP is dissolved phosphorus, PP is particulate phosphorus and TP is total phosphorus. Bars represent ± one standard deviation ($n = 10$). (c) Sulphur, where DS is dissolved sulphur, PS is particulate sulphur and TS is total sulphur. Bars represent ± one standard deviation ($n = 10$). (d) Nutrient levels in papyrus swamp sediment (detritus). Bars represent ± one standard deviation ($n = 14$).

had the highest concentration in swamp water, with a mean of 280 ± 100 $\mu g\ l^{-1}$ (Fig. 2a). In total, inorganic nitrogen had a mean value of 300 ± 100 $\mu g\ l^{-1}$. The concentration of nitrate nitrogen was higher than nitrite nitrogen although both were only present in trace amounts. The former had mean of 6 ± 3 $\mu g\ l^{-1}$ while the latter had a mean of 1.1 ± 0.4 $\mu g\ l^{-1}$.

The total organic nitrogen in swamp water had a mean concentration of 2.20 ± 0.30 mg l^{-1} (Fig. 2a). Of the two forms of organic nitrogen, the dissolved organic nitrogen had a greater concentration than particulate organic nitrogen. The dissolved organic nitrogen had a mean concentration of 1.29 ± 0.14 mg l^{-1} while particulate nitrogen concentration was 0.91 ± 0.38 mg l^{-1}. The total nitrogen concentration of the swamp water was 2.51 ± 0.30 mg l^{-1} (Fig. 2a).

The distribution of various forms of phosphorus in the swamp water is shown in Fig. 2b. Mean orthophosphate concentration was 24.0 ± 12.0 $\mu g\ l^{-1}$. The mean concentration of dissolved and particulate phosphorus were similar with values of 76.8 ± 19.5 and 76.5 ± 47.8 $\mu g\ l^{-1}$ respectively. The total phosphorus had an mean value of 153.3 ± 63.3 $\mu g\ l^{-1}$.

The concentration of dissolved sulphur in swamp water was 105 ± 57 $\mu g\ l^{-1}$ (Fig.

2c). The concentration of particulate sulphur (151 ± 51 $\mu g\ l^{-1}$) exceeded that of dissolved sulphur, while the total sulphur had a mean concentration of 256 ± 82 $\mu g\ l^{-1}$.

3.2. Nutrient concentrations in swamp sediments

Nutrient concentrations in swamp sediments (detritus), calculated on a mass per unit mass basis and expressed as percentage values, are shown in Fig. 2d. The highest nutrient level in the swamp sediments was for nitrogen followed by sulphur while the phosphorus level ($0.104 \pm 0.009\%$) was the lowest among the three nutrients.

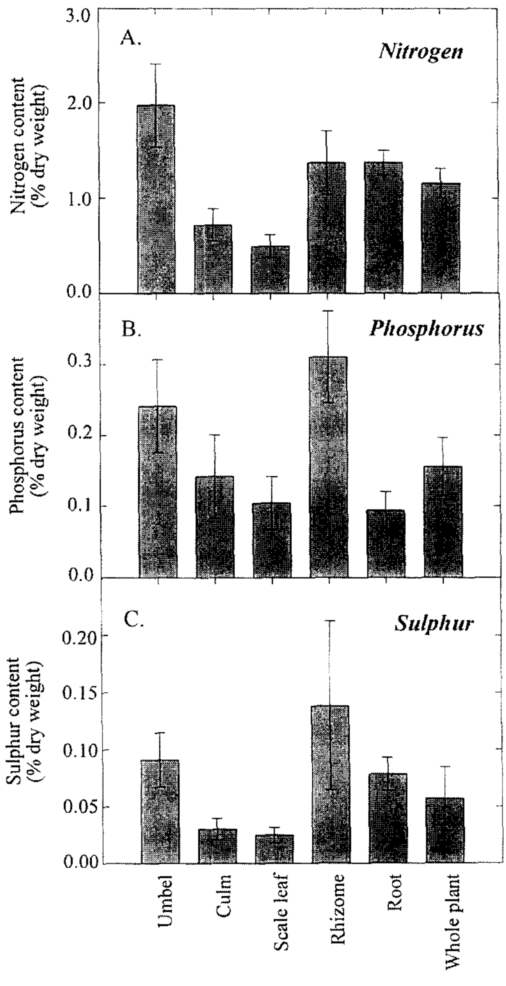

Fig. 3. (a) Nitrogen, (b) phosphorus and (c) sulphur content of papyrus organs. Values are means of all living culm-units (I–V). Bars represent ± one standard deviation ($n = 16$).

3.3. Nutrient concentrations in papyrus plant material

Nutrient concentrations were calculated on a mass per unit mass dry weight basis and are expressed as percentage values. Highest concentrations of nitrogen in plant material, at an average of almost 2% of dry weight, occurred in the umbels (Fig. 3a). Nitrogen content of the culms was considerably lower at 0.72 ± 0.17%, while scale leaves had the lowest level of nitrogen (0.50 ± 0.12%) in the aerial material. The roots and rhizomes had relatively high and very similar nitrogen concentrations (about 1.4%). Whole plant samples had a mean nitrogen content of 1.16 ± 0.15% (Fig. 3a). These values are the means of all living culm-units (I–V).

In addition to the differences between papyrus organs in nitrogen content, nitrogen levels also varied with organ age (Fig. 4). Nitrogen content was highest in juvenile plants and decreased with increasing age. The most pronounced nitrogen gradient occurred in the umbels so that young umbels (culm-unit II) had a nitrogen content of 2.44 ± 0.15% but it dropped to a concentration of 0.78 ± 0.19% in the dead umbels (culm-unit VI). Other papyrus organs and whole plant samples followed a similar trend

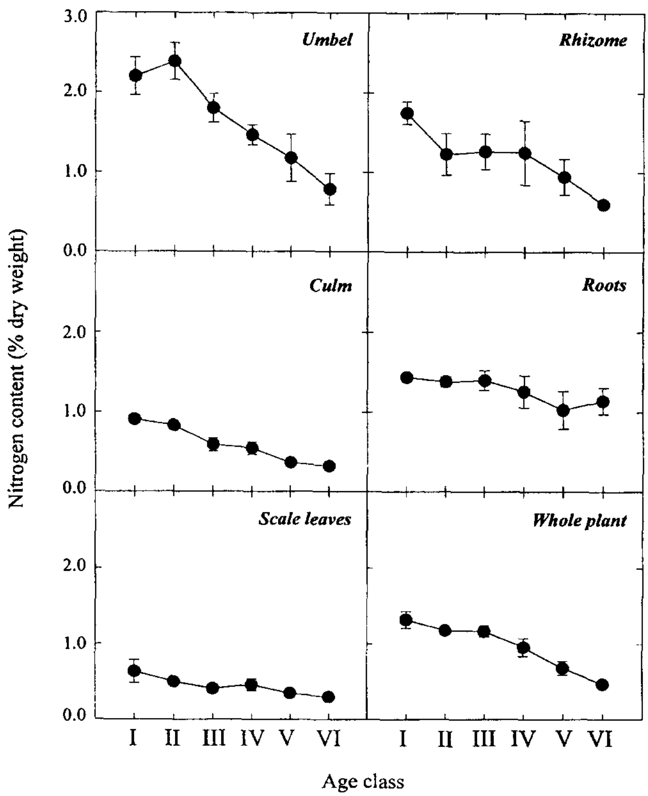

Fig. 4. The nitrogen content of papyrus organs in age classes I–VI. See Fig. 1 for age classes. Values are means ± one standard deviation ($n = 4$).

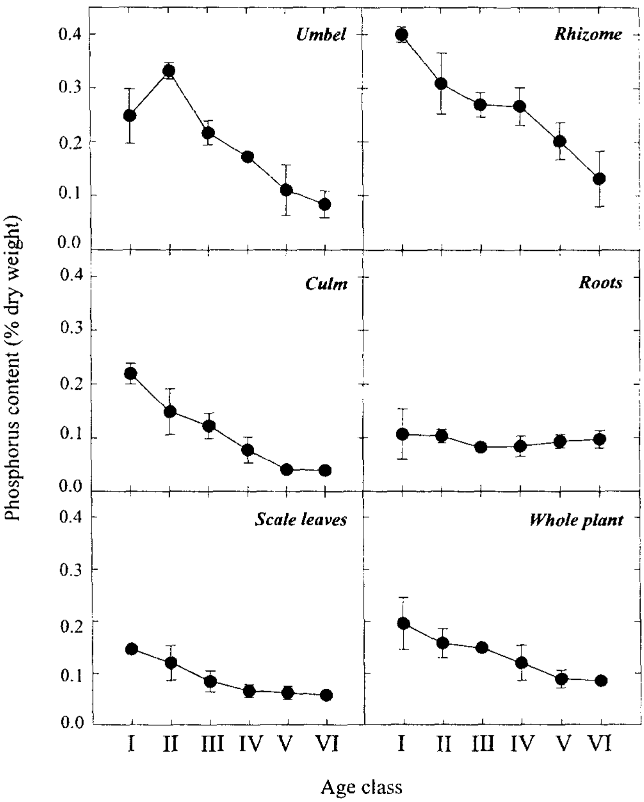

Fig. 5. The phosphorus content of papyrus organs in age classes I–VI. See Fig. 1 for age classes. Values are means ± one standard deviation ($n = 4$).

but there was a smaller decline, particularly between young and older scale leaves and roots (Fig. 4).

Highest levels of phosphorus (0.31 ± 0.07%) occurred in the rhizome and not in the umbel as with nitrogen (Fig. 3b). Averaged phosphorus content of the umbels of all ages was 0.24 ± 0.07% while the culms and scale leaves had phosphorus levels of 0.14 ± 0.06% and 0.11 ± 0.04% respectively (Fig. 3b). Although the roots had a relatively high concentration of nitrogen, this organ contained the lowest concentration (0.09 ± 0.03%) of phosphorus. Whole plant samples had a mean phosphorus content of 0.16 ± 0.04%.

As with nitrogen, phosphorus concentration decreased with increasing age of the plants (Fig. 5). The steepest gradient was found in the rhizomes where the juvenile rhizomes (culm-unit I) had a phosphorus content of 0.405 ± 0.010% while the oldest rhizomes (culm-unit VI) had the lowest (0.132 ± 0.051%) phosphorus content. Other papyrus organs and whole plant samples had similar phosphorus concentration gradients although the roots, as with nitrogen, showed little difference in phosphorus content between the young and the oldest roots.

Of the three nutrients analysed, sulphur had the lowest average concentration in papyrus plant material (Fig. 3c). As with phosphorus, the highest concentrations of

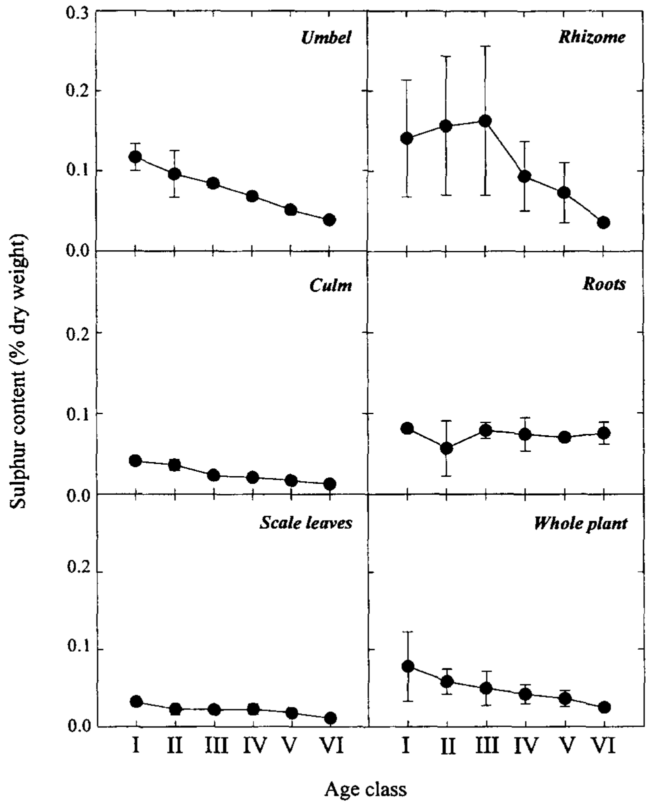

Fig. 6. The sulphur content of papyrus organs in age classes I–VI. See Fig. 1 for age classes. Values are means ± one standard deviation ($n = 4$).

sulphur (0.14 ± 0.07%) occurred in the rhizomes. Sulphur content of the umbel and roots was 0.09 ± 0.02% and 0.08 ± 0.02% respectively while the culms and scale leaves each had a sulphur content of 0.03 ± 0.01%. Whole plant samples had a sulphur concentration of 0.06 ± 0.03%. Similar to other nutrients, sulphur in plant tissue decreased with increasing age of the plant (Fig. 6). The steepest gradient was found in the rhizomes where from a high sulphur content of 0.168 ± 0.024% in juvenile rhizomes, the values dropped to 0.036 ± 0.002% in the oldest rhizomes. Other organs and whole samples had similar sulphur distribution although only a small variation in sulphur content occurred between the young and older roots.

4. Discussion

A comparison of levels of inorganic nitrogen in the swamp water show that the concentration of ammonium nitrogen measured in the Lake Naivasha swamp is much higher than either the nitrite or nitrate. A similar situation has been reported for Kawaga

Swamp in Uganda, which is also dominated by papyrus, where concentrations of ammonium and nitrate were 860 and 0.4 $\mu g\ l^{-1}$ respectively (Gaudet, 1976). High levels of ammonium nitrogen as compared to other forms of inorganic nitrogen are mainly due to anaerobic conditions prevailing in the swamps when the normal denitrification pathway is switched to one producing ammonia (Sprent, 1987). The concentration of total inorganic nitrogen in the swamp water (0.30 mg l^{-1}) was much lower than the concentration of total organic nitrogen (2.2 mg l^{-1}). Of the two forms of organic nitrogen, the dissolved organic nitrogen contributed 59%, while particulate nitrogen was 41%. Dissolved organic nitrogen mostly occurs in forms resistant to rapid bacterial degradation and has been reported to represent more than 50% of total dissolved nitrogen in other lakes (Wetzel, 1975).

Total nitrogen concentration in the papyrus swamp water of Lake Naivasha (2.51 ± 0.30 mg l^{-1}) was higher than total nitrogen (1.6 mg l^{-1}) reported by Kalff (1983) in the open lake. This is probably due to the presence of large quantities of organic matter undergoing decomposition. Nichols and Keeny (1973) have observed that large quantities of organic nitrogen are released during decomposition of aquatic vascular plants. Nitrogenous organic compounds are also secreted by the larger aquatic plants and in situations where the littoral zone is well developed, these secretions can form a major source of organic nitrogen to the lake (Wetzel and Manny, 1972). The nitrogen available for plant uptake in this ecosystem is probably largely in the form of ammonium ions. It is therefore the concentration of this form of nitrogen which is important in determining whether growth is limited by nitrogen. However, the unknown rate of conversion of organic forms of nitrogen to inorganic forms is also important in considerations of nitrogen limitation.

In most lake ecosystems, phosphorus is generally considered to be the element most likely to be deficient and therefore its availability will limit productivity (Hutchinson, 1957). The only significant form of inorganic phosphorus in the swamp water of Lake Naivasha is orthophosphate and the mean concentration of 24 $\mu g\ l^{-1}$ found for the papyrus swamp water was much higher than the 3 $\mu g\ l^{-1}$ reported by Peters and MacIntyre (1976) for the open lake. The concentrations of dissolved phosphorus (76.6 $\mu g\ l^{-1}$) and particulate phosphorus (76.6 $\mu g\ l^{-1}$) found in the swamp water are also higher than levels of dissolved phosphorus (29.6 $\mu g\ l^{-1}$) and particulate phosphorus (26.1 $\mu g\ l^{-1}$) reported for the open lake (Njuguna, 1982). The high levels of phosphorus in swamp water as compared to the open lake are attributed to the mineralization of the large amounts of organic matter present in the swamp. The relatively high concentations of available phosphorus in the papyrus swamp suggests that this nutrient does not limit growth under normal conditions when organic material is available for mineralisation.

Although the predominant form of sulphur in natural waters is normally in the oxidized state as sulphate (Wetzel, 1975) the concentration in Naivasha swamp water was very low (< 0.05 mg l^{-1}) presumably because of the anoxic, and therefore reduced state, of the swamp water (Jones and Muthuri, 1985). Average concentrations of sulphate sulphur in open temperate lakes have been estimated to be between 1 and 10 mg l^{-1} (Hutchinson, 1957), but Beauchamp (1953) pointed out that the waters of Lake Victoria were apparently deficient in sulphur. Subsequent water culture experiments confirmed this and showed that values of sulphate sulphur below 0.17 mg l^{-1} were too low for algal growth (Fish, 1956). Hesse (1957) also reported low values of sulphur in Lake Victoria; concentrations of sulphate sulphur and total sulphur were 0.18 and 0.38 mg l^{-1} respectively.

The mean levels of dissolved and particulate sulphur in the swamp water were higher than sulphate at 0.11 and 0.15 mg l^{-1} respectively. These levels of sulphur are lower than those reported by Gaudet (1979) for the Malewa River, the major inflow of Lake Naivasha, but higher than those of the open lake. Gaudet and Muthuri (1981) have reported concentration of total sulphur in the open lake, 20 m offshore, to be 0.13 mg l^{-1}. Although the dynamic processes involved in generation and recycling of sulphur have not been investigated in this study, it is evident from the low concentrations in swamp water that this element is likely to be limiting plant production in the papyrus swamps, especially in the presence of an apparently adequate supply of phosphorus and nitrogen.

Sediment nutrient levels reported in this study fell within the ranges found in other tropical swamp sediments (Gaudet, 1976 and 1979; Gaudet and Muthuri, 1981; Hesse, 1957 and 1958). It is important to note that although the mud sediments contained appreciable amounts of sulphur, the water in contact with these sediments contained only trace amounts of this element. For example, sulphate sulphur extracted with Morgan's reagent from Lake Victoria surface mud showed a concentration of 60 mg l^{-1} SO_4–S and yet the lake water filtered from that mud contained less than 1 mg l^{-1} SO_4–S (Hesse, 1957). This implies that sulphates are adsorbed on the mud and are therefore not available to the overlying water. Hesse (1958) confirmed that the sorption of sulphates does occur and was mainly due to the presence of calcium and silica compounds in mud sediments. The absorption of sulphates by the mud is therefore likely to lead to low levels of sulphates available for plant growth and possibly limits primary production.

Results of plant tissue analysis showed gradients in the distribution of major nutrients in the various papyrus organs. Similar observations for papyrus have also been made by Lind and Visser (1962) and Gaudet (1977b). Polisini and Boyd (1972) found that on average, nitrogen content of the leaves (3.66%) and inflorescences (2.89%) was twice the average amount (1.61%) in the petioles of the aquatic macrophytes, *Pontederia cordata*, *Orontium aquaticum* and *Nelumbo lutea*. Tissue analyses of the reed, *Phragmites communis* has shown that the leaves have a higher nitrogen content (3.53%) than stems (0.86%), roots (0.99%) and rhizomes (0.92%) while the rhizomes have higher phosphorus content (0.41%) than stems (0.22%), leaves (0.30%) and roots (0.31%) (Úlehlová et al., 1973). In *Juncus effusus*, Boyd (1971) has reported levels of phosphorus (0.36%) and sulphur (0.29%) in the inflorescences to be higher than phosphorus (0.19%) and sulphur (0.20%) concentrations in the samples of the whole plant.

From the above account, the photosynthetic organs (leaves) and the inflorescences generally have higher nutrient content than other organs. Confirming this for papyrus, highest concentration of nitrogen, phosphorus and sulphur were found in the umbel which serves as both a photosynthetic organ and an inflorescence. The high levels of nutrients in the rhizome are also expected because of its storage function. High levels of nitrogen found in papyrus roots are possibly associated with nitrogen fixation. The root

Table 1
Nutrient composition (% dry weight) of emergent macrophytes (average values for the whole plant)

Plant species	Location	% N	% P	% S	N:P:S ratio (atomic)	Source
Typha latifolia	S. Carolina (USA)	1.21	0.17	0.14	20:1:1	Boyd (1970a)
Justicia americana	Alabama (USA)	2.04	0.13	0.19	35:1:1	Boyd (1969)
Glyceria maxima	England	1.57	0.19	–	–	Buttery et al. (1965)
Pontederia cordata	S. Carolina (USA)	1.40	0.24	0.22	15:1:1	Boyd (1978)
Scirpus americanus	S. Carolina (USA)	1.46	0.18	0.60	18:1:5	Boyd (1970a)
Carex lacustris	New York (USA)	1.70	0.17	–	–	Bernard and Solsky (1976)
Alternanthera philoxeroides	Alabama (USA)	2.88	0.36	0.30	22:1:1	Boyd (1969)
Juncus effusus	Southeastern (USA)	1.14	0.13	0.18	19:1:1	Boyd (1971)
Sagittaria latifolia	S. Carolina (USA)	–	0.30	0.15	–	Boyd (1970b)
Phragmites communis	England	1.56	0.14	–	–	Buttery et al. (1965)
Panicum hemitomon	S. Carolina (USA)	1.50	0.14	0.23	25:1:2	Boyd (1978)
Hydrocotyle umbellata	S. Carolina (USA)	2.56	0.18	0.16	37:1:1	Boyd (1978)
Eleocharis quadrangulata	S. Carolina (USA)	1.01	0.10	0.15	24:1:1	Boyd (1978)
Cyperus papyrus	L. Victoria (Uganda)	1.23	–	0.08	–	Hesse (1957)
Cyperus papyrus	L. George (Uganda)	1.34	0.11	–	–	Gaudet (1977b)
Cyperus papyrus	L. Naivasha (Kenya)	1.16	0.16	0.06	44:3:1	Present Study

rhizosphere of *Cyperus papyrus* has been shown to be well colonized by the N_2-fixing bacteria and high rates of nitrogen fixation (acetylene reduction activity) have been recorded in intact root system of papyrus (Mwaura, 1981).

As shown by Gaudet (1977b), nutrient concentration in papyrus decreased from the youngest to the oldest plant tissues. This is also common with other emergent macrophytes. For example, young plants of *Phragmites communis* were shown to have the highest content of nitrogen, phosphorus and potassium, which decreased as the plants aged (Úlehlová et al., 1973). Differences in nutrient composition between the young tissue and the older plant portions are likely to be largely due to translocation. Boyd (1969) suggested that nutrients stored by the plants are translocated to the metabolically active sites when environmental conditions are optimal for growth. By so doing papyrus partly recycles nutrients from the old portions to new growth.

Examples of nutrient composition of emergence macrophytes from various sites are presented in Table 1. It is evident that nitrogen and phosphorus levels of papyrus are within limits reported for other emergent macrophytes from a range of sites. However, sulphur content is lower than values reported for other macrophytes. The N:P:S atomic ratios were quite variable but on the whole the macrophytes other than papyrus had a mean N:P:S ratio of 24:1:1 while the ratio for papyrus in this study was 44:3:1. If the N:P:S ratio of 24:1:1 is taken to be typical for emergent macrophytes then it can be concluded that, relative to nitrogen and phosphorus, sulphur is likely to be the limiting nutrient for growth of papyrus at this location. Also, the presence of C_4 photosynthesis in papyrus means that it has a lower demand for nitrogen in its photosynthetic tissues (Brown, 1978) and as a result nitrogen is less likely to be limiting for growth.

In some respects the foregoing analysis of nutrient relations is inadequate because not all forms of nutrients are taken up by the plants in their elemental form. Nitrogen, phosphorus and sulphur are mostly taken up by plants in form of NO_3–N and NH_4–N, PO_4–P and SO_4–S respectively. Therefore it is the availability of these soluble inorganic nutrients that are most crucial to the plants. The dynamic processes involved in the release of inorganic nutrients from swamp sediments in interstitial water, the water overlying the sediments and the subsequent uptake by the macrophytes system are in a state of flux and therefore it is not possible to state conclusively from mere sample analyses that a certain nutrient is limiting before critical nutrient levels in plant tissue have been determined. However, evidence from nitrogen and phosphorus concentrations in the swamp water, sediments and plant tissue and the N:P ratios of papyrus in comparison to other emergent macrophytes suggest that these nutrients are not limiting in Lake Naivasha papyrus swamp. The low sulphur concentration in swamp water and papyrus tissue and the high N:S atomic ratios in comparison to other macrophytes indicate that sulphur is most likely to be limiting in this ecosystem.

The above account of nutrient dynamics pertain to a natural functioning swamp with minimal human interference. This is likely to change if past feasibility studies (Jones, 1983; Moore, 1980) lead to the exploitation of papyrus by regular harvesting. Based on the papyrus above-ground biomass of 36 t ha^{-1} (Muthuri, 1985) it is estimated that a complete harvest of Naivasha Swamp (2000 ha) would remove 72,000 t of papyrus biomass. This represents a significant loss of nutrients from the swamp especially if, as proposed, the papyrus is cropped at least annually. Using the average aerial papyrus nutrient levels (N, 1.16%; P, 0.16% and S, 0.06%) it is estimated that harvesting of Naivasha papyrus would remove 836 t of nitrogen, 115 t of phosphorus and 43 t of sulphur annually. Removal of such large quantities of nutrients following papyrus cropping will certainly affect the normal functioning of the swamp ecosystem including the possible reduction in production rates if any of these nutrients, particularly sulphur, are limiting for growth. It is hoped, however, that the data generated in this study will help in the formulation of suitable cropping strategies in order to maintain sustainable papyrus yields.

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