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UPTAKE, ACCUMULATION, AND LOSS OF NUTRIENTS BY PAPYRUS IN TROPICAL SWAMPS[1]

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Abstract. Analysis of papyrus (*Cyperus papyrus* L.) indicated that N, P, and K are generally found in higher concentrations in juvenile stems while Ca, Mg, Fe, and Mn are found in higher concentrations in mature stems. Iron was found to be concentrated in the roots, while Mn was concentrated in old umbels. Silicate content increased with age. Potassium and Na were easily eluted and leached from stems, while other nutrients required more time. Over 50% of all eight elements are accumulated prior to the attainment of 50% of the biomass. The total amount of nutrients taken up and accumulated by papyrus (per m^2) is higher than most other macrophytes, and this seems to be due to the high biomass of this aquatic sedge. Estimates of losses due to elution, rain, and decomposition accounted for approximately two-thirds of the total nutrient accumulated. The remainder is assumed to be deposited in the swamp as peat.

Key words: Africa; decomposition; elution; macrophytes; nutrient cycling; papyrus; plant nutrients; rain leaching; swamp detritus; tropical swamps.

INTRODUCTION

Papyrus, *Cyperus papyrus* L., is a large aquatic sedge with stems up to 5 m high (Fig. 1). It dominates several large swampy areas in tropical Africa. Although well-known from ancient times (5,000 BC), the ecology of papyrus has not been intensively studied. Papyrus swamps present considerable absorbing surfaces as they spread out over the water at river and lake edges. During formation of floating mats, large amounts of nutrients are incorporated into the plant.

The chemical composition of papyrus was first reported by Lind and Visser (1962), but neither the exact number of portions nor the age of the organs was considered. This early study revealed large differences in nutrient concentrations in different organs. Recently, Gaudet (1975) found a large variation in concentrations in this plant between different sites, but not within sites. Until now, however, no attempt has been made to determine the average amounts of nutrients taken up and accumulated by papyrus swamps. This present paper will quantify differences in nutrient concentrations in papyrus organs, and the average rate of uptake and accumulation in these tropical swamps.

Loss of nutrients from papyrus would be as important as uptake in regard to nutrient cycling in these swamps. Hence, this paper will also consider losses by rain leaching, elution, and decomposition.

MATERIALS AND METHODS

Plants were collected from 10 different sites in Africa representing many of the habitats and geographical regions in which papyrus is found (see Gaudet 1975 for location of all sites).

Plant tissue was obtained from 20 different portions, representing all organs of the plant. Portions were representative of the whole plant in that they were taken from: unelongated culms (upright stems) with closed umbels (Stem Set I); young culms elongate but with umbels just opening (Stem Set II); mature culms with open umbels (Stem Set III); old dead culms (Stem Set IV); the rhizome; and the roots (Fig. 1).

Each plant was dissected in the field and one 10-cm section of culm, one 10-cm section of rhizome, one cluster of 30–40 roots, and one complete umbel were taken from each individual plant. All plant material was rinsed with rainwater or distilled H_2O and blotted or wiped dry. In the laboratory, the roots were scrubbed well with distilled H_2O, and all material was dried overnight at 80°C. It was then ground in a series of laboratory mills to pass a 1-mm sieve, and redried prior to weighing a 400-mg portion, which was digested until clear in 10 cm^3 of a 10:1 mixture of H_2SO_4 and $HClO_4$. Total nitrogen in the digest was determined with a Technicon Auto Analyzer® using method 103–70A (Anon. 1971), which depends on formation of an indophenol complex. Phosphate was determined after adjusting the acidity of the digest using the method of Jackson (1958), with stannous chloride as the reducing agent. Potassium, sodium, calcium, magnesium, iron, and manganese were determined after appropriate dilutions on a spectrophotometer. Standards for each element as well as mixed standards incorporating all of the above elements were used. Lanthanum chloride was added to prevent interference. Silicate was determined on dry plant material from Lake Naivasha using a gravimetric method (Horowitz 1970).

Several experiments were carried out under laboratory conditions to determine nutrient losses. The material used in the rain leaching and decomposition experiments was taken from Lake Naivasha, while that used in the elution experiment was taken from Kabanyolo Swamp. In the rain leaching experiment the upper portion of culms (i.e., mostly umbel) from each stem set was cut under water and transferred to the laboratory where the umbel was sprayed with a coarse spray of 500 cm^3 of distilled deionized water (pH 7.2) from a plastic sprayer for 15 min, covering an area of 625 cm^2. This simulated a rain

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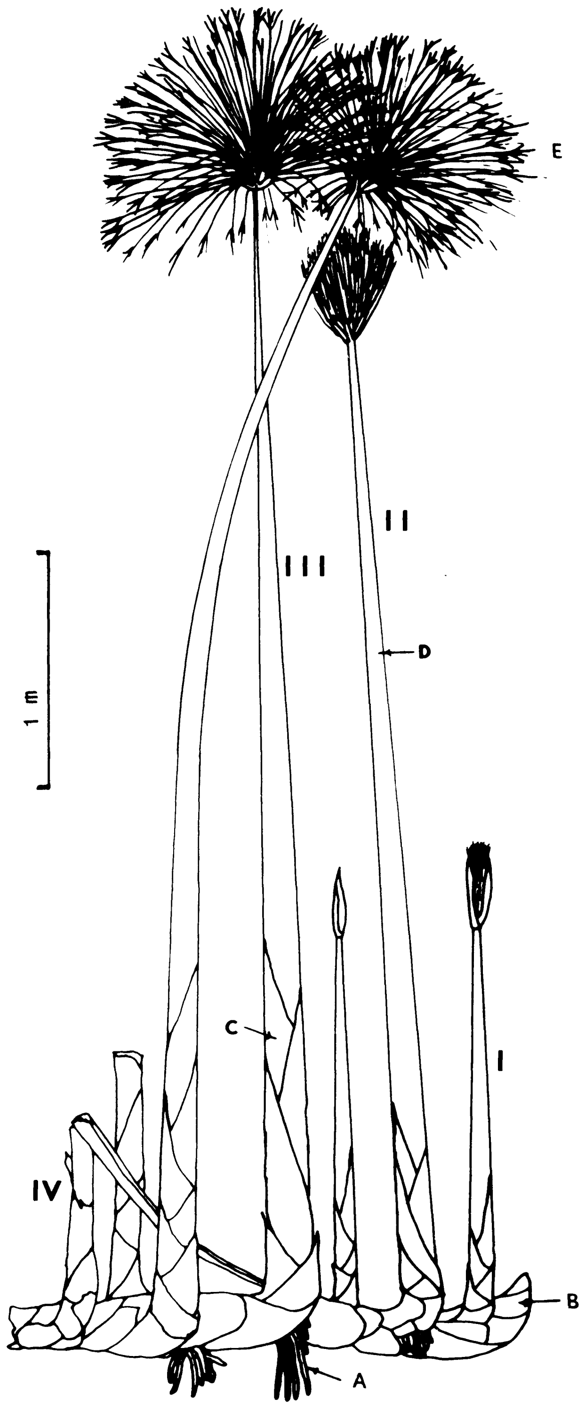

FIG. 1. *Cyperus papyrus* L. showing roots (A), rhizome (B), scale leaves (C), culm (D), and umbel (E). Stem Sets (I, II, III, and IV) consist of scale leaves, culms, and umbels.

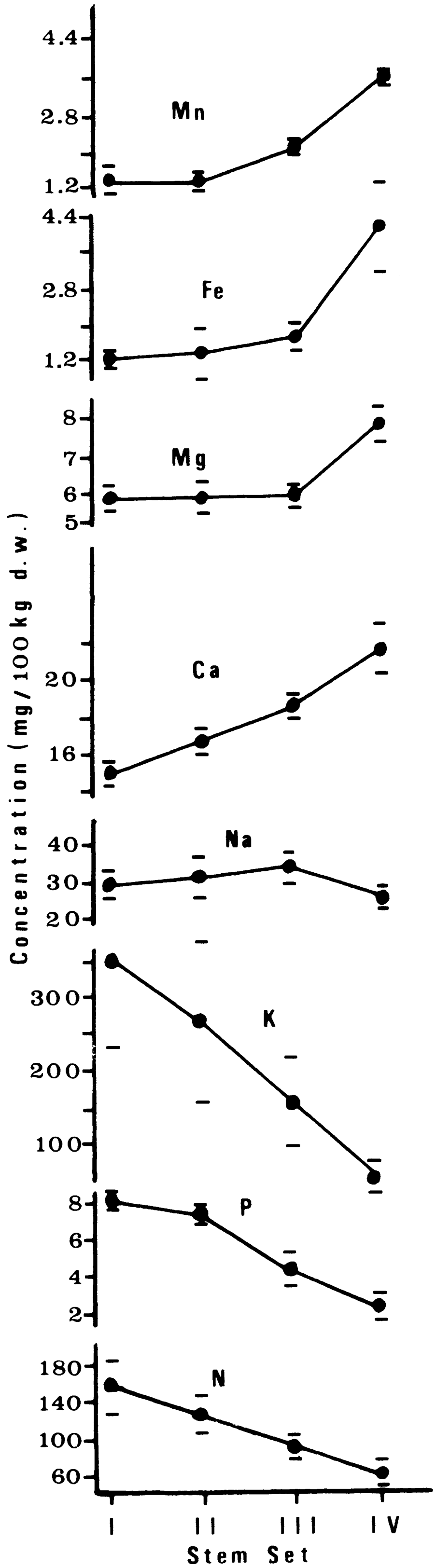

FIG. 2. Mean nutrient concentration in different Stem Sets (n = 40, bar indicates ± SD).

shower delivering 8 mm of rain. The results from a control spray (in which no plant material was used) were subtracted from the readings obtained after water analysis. In the elution experiment, pieces of culm (10 cm) from one stem (Stem Set III) were left in a glass container through which water from Lake Victoria

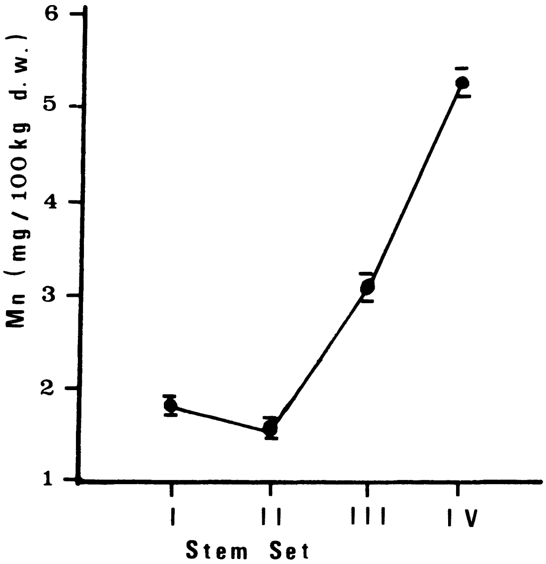

FIG. 3. Mean manganese concentration in umbel from different Stem Sets (n = 10, bar indicates ± SD).

was allowed to flow in a slow stream. Periodically two pieces were removed and analysed. Nutrient loss due to decomposition was determined by incubating dried papyrus tissue (ground to pass a 1-mm sieve) in nylon mesh bags in water from Lake Naivasha. These cultures were inoculated with decomposing bacteria (*Pseudomonas syringae* van Hall and *Bacillus cereus* var. *mycoides* Flugg) and kept at 30°C. An estimate of bacterial density was obtained every 4 days by streaking on nutrient agar. Four samples were used (umbel, culm, root, and rhizome) which had been eluted in lake water for 20 days prior to being ground and incubated. Incubation was terminated after 26 days, when the biomass of the four samples had decreased by approximately one-third. They were then washed in distilled

TABLE 2. Silicate determinations on mature and old culms (% dry wt)

Stem set	Portion	$\bar{X}$	SiO_2 (%) range
III	Leaf sheath	0.37	0.29–0.45
	Culm base	4.04	3.10–4.98
	Culm top	6.25	5.01–7.49
	Umbel	22.06	18.92–25.20
IV	Leaf sheath	26.47	20.03–32.91
	Culm base	8.45	6.24–10.66
	Culm top	18.40	13.04–23.76
	Umbel	40.89	32.92–48.86

deionized H_2O (at the same pH as lake water, 7.8) until they were virtually bacteria-free. The difference in nutrient composition before and after incubation is expressed as average percent decomposition loss. All three experiments were replicated once and the results averaged.

RESULTS

Differences in nutrient concentrations in organs.—The nutrient levels vary significantly between organs in papyrus (Table 1). In addition, the nutrient composition varies from the tip to the base of each stem (Fig. 2). The present analysis of papyrus organs agrees well with the early work reported by Lind and Visser (1962). Their means generally fall within the range determined here for most elements. They noted that Mn was most abundant in the umbel; this high concentration is confirmed by the present study (Table 1) which also showed this to be a function of age (Fig. 3). Iron is also concentrated, but at the base of the plant in the roots (Table 1). Silica is concentrated not in one organ as with Fe and Mn, but in the epidermis of the culm and umbel which contain silicate crystals. A large disparity exists between silicate in portions of a mature culm in Stem Set III,

TABLE 1. Composition (% dry wt) of papyrus organs and whole plant based on different portions representing all ages from 10 different sites (± SD in parentheses). Letter 'a' indicates a signicant difference (P = .01) when this organ is compared to the root using Least Significant Difference; 'b' = the rhizome; 'c' = the culm; and 'd' = the umbel

Nutrient	Root	Rhizome	Culm	Umbel	Whole plant
	n = 10	n = 30	n = 120	n = 40	n = 200
N (mean)	1.12 (0.12) b,c,d	1.29 (0.17) a,c,d	0.73 (0.32) a,b,d	1.74 (0.28) a,b,c	1.22 (0.29)
(range)	0.48–1.69	0.28–2.50	0.01–3.63	0.38–3.43	
P	0.052 (.01) b,c,d	0.066 (.012) a,c,d	0.042 (.011) a,b,d	0.074 (.01) a,b,c	0.059 (.001)
	0.016–0.083	0.006–0.140	0.001–0.150	0.004–0.140	
K	2.48 (0.59) c,d	2.81 (0.65) c,d	1.56 (0.85) a,b	1.36 (0.22) a,b	2.05 (0.72)
	1.60–4.40	0.80–6.40	0.10–9.80	0.10–3.10	
Na	0.37 (.01) b,c,d	0.27 (.01) a,c,d	0.30 (.02) a,b,d	0.21 (.02) a,b,c	0.29 (.02)
	0.18–0.52	0.10–0.65	0.05–1.00	0.10–0.38	
Ca	0.20 (.01) b,c,d	0.13 (.01) a,c,d	0.18 (.01) a,b,d	0.16 (.01) a,b,c	0.17 (.01)
	0.13–0.30	0.07–0.22	0.07–0.33	0.07–0.41	
Mg	0.092 (.007) b,c,d	0.041 (.005) a,c,d	0.064 (.002) a,b,d	0.101 (.002) a,b,c	0.075 (.003)
	0.041–0.310	0.013–0.160	0.002–0.280	0.003–0.282	
Fe	0.2138 (.0605) b,c,d	0.0158 (.0003) a,c,d	0.0289 (.0002) a,b,d	0.0181 (.0091) a,b,c	0.0692 (.0135)
	0.0390–0.7500	0.0026–0.1250	0.0013–0.6250	0.0033–0.1263	
Mn	0.0099 (.001) b,c,d	0.0068 (.0002) a,c,d	0.0195 (.0007) a,b,d	0.0294 (.0006) a,b,c	0.0164 (.0006)
	0.0026–0.0263	0.0008–0.0207	0.0013–0.1155	0.0025–0.1630	
SiO_2	6.41 (1.59) b,c,d	3.60 (.80) a,c,d	15.40 (11.41) a,b,d	24.87 (6.32) a,b,c	12.57 (3.86)
	3.72–8.10	1.01–4.53	0.29–32.91	11.70–48.86	

where a very steep gradient occurred from culm base to umbel (Table 2). This gradient changed with death, since old, dead culms (Stem Set IV) had a higher silicate content. This is especially true in the leaf sheath of Stem Set IV, which typically had already undergone some decomposition.

Uptake and accumulation of nutrients in papyrus swamps

In order to calculate the net uptake and accumulation of nutrients in any emergent macrophyte the rate of biomass production must be known. In temperate areas this can be determined by cropping a given area in a marsh or swamp and recording the incremental increase in dry weight. But in a tropical swamp there is no period of intense spring-summer growth followed by maturity and death with onset of winter. Instead, there is continuous production which cannot be sampled by usual cropping techniques. For example, in a very productive site on Lake George (see Gaudet 1975 for location) ≈ 17 living culms are found per m². Of these, at least 4 are very young culms comparable to Stem Set I and ≈ 4 are intermediate, i.e., comparable to Stem Set II. The remainder are all in some phase of maturation and are comparable to Stem Set III. Since the turnover time at this site is 147 days (Thompson 1976), this means that 1 culm dies every 8.5 days and is replaced by a new culm. Thus, during the 147-day turnover period ≈ 17 culms are in a continual process of growth. If we consider that ≈ 4 Stem Set I and ≈ 4 Stem Set II culms are present per m² at any given time, we can assume that they will in turn each be replacing ≈ 4 mature culms. The net uptake and accumulation of nutrients by such a theoretical population of 4 cohorts is shown in Table 3. In the calculations the "stem unit" is used as defined by Thompson, which includes one upright culm, that portion of the rhizome at the base of this culm, and roots on the rhizome.

TABLE 3. Uptake and accumulation of nutrients in papyrus in one swamp on Lake George which supports a total of 17.2 culms/m² (including juveniles) and a biomass of 5.00 kg/m². Figures in parentheses represent four theoretical culms of Stem Set III (cohorts of younger Stem Sets)

Stem set	I	II	(III)	III	Totals
Stem set age (days)	30	50	(100)	100	
No. of culms/m²	4	4	(4)	9	17
Dry wt g/stem unit	150	250	(380)	380	
Biomass (g dry wt/m²)	600	1,000	(1,520)	3,420	5,020
Nutrient					
N (% dry wt)	1.76	1.48	(1.06)	1.06	
(accum., g/m²)	10.56	14.80	(16.11)	36.25	61.61
(net accum., g/m²)	10.56	4.24	(1.21)		
(rate, g/m²/day)	0.35	0.21	(0.02)		
P	0.105	0.117	(0.106)	0.106	
	0.630	1.170	(1.611)	3.625	5.43
	0.630	0.540	(0.441)		
	0.021	0.027	(0.009)		
K	3.88	2.73	(1.54)	1.54	
	23.28	27.30	(23.41)	52.67	103.25
	23.28	4.02	(−3.89)		
	0.78	0.20	(−0.08)		
Na	0.390	0.386	(0.430)	0.430	
	2.340	3.860	(6.536)	14.706	20.91
	2.340	1.520	(2.676)		
	0.078	0.076	(0.054)		
Ca	0.146	0.150	(0.178)	0.178	
	0.876	1.500	(2.707)	6.088	8.46
	0.876	0.624	(1.207)		
	0.029	0.031	(0.024)		
Mg	0.0752	0.0603	(0.0771)	0.0771	
	0.4512	0.6030	(1.1719)	2.6368	3.69
	0.4512	0.1518	(0.5689)		
	0.0150	0.0076	(0.0113)		
Fe	0.0245	0.0237	(0.0253)	0.0253	
	0.1470	0.2370	(0.3846)	0.8653	1.25
	0.1470	0.0900	(0.1476)		
	0.0049	0.0045	(0.0029)		
Mn	0.0070	0.0053	(0.0099)	0.0099	
	0.0420	0.0530	(0.1505)	0.3386	0.43
	0.0420	0.0110	(0.0975)		
	0.0014	0.0006	(0.0019)		

Nutrient losses in papyrus

Nutrient loss in papyrus occurs from rain leaching (Table 4), especially from old culms. A simulated rain shower, delivering 8 mm, leaches out an initial maximum level with much less coming out in subsequent rains. For example, in the old umbels (Stem Set IV) the first rain resulted in a leachate containing 14.2 mg Na/l, the second rain after drying the umbels contained 6.2 mg Na/l, and the third and subsequent rains contained ≈ 3.0 mg Na/l.

Most substances leached from aboveground parts by rainfall on terrestrial plants are probably reabsorbed by the roots of the same or adjacent plants (Tukey 1970). In a papyrus swamp this reabsorption is facilitated because the plant grows up in a stagnant mass of water and detritus which does not allow for much movement of materials away from the parent plant. Losses to runoff, for example, would be minimal. Thus, in a papyrus swamp a single rain shower falling on living culms (Stem Sets I, II, and III) carries down large amounts of nutrients (Table 4), but most of this is offset by the uptake of minerals which accompanies the course of transpiration. Old dead culms are less likely to take up nutrients, thus rain leaching from Stem Set IV culms was considered here to be a loss that is not compensated for by uptake. In the leachate, P and Fe were only detectable at trace levels. A slight amount of N was leached from Stem Set II almost exclusively as reduced N (NH_4^+). This may have originated from the light coating of sticky sap quite often found on the young umbels, possibly as a result of insect feeding or guttation. Potassium and Na came out in large quantities with Na predominating. This is expected, because Na is known to be more readily lost than K during rain leaching of forage crops (Clement et al. 1972). Also, Mn is lost from old papyrus umbels in quantities which must be considered large for a mi-

TABLE 4. Loss of nutrients during one artificial rain shower (8 mm) falling on umbels from each Stem Set under laboratory conditions. Each set of umbels received 0.5 l distilled H_2O as rain, and the results (averages of 2 sets) are expressed on that basis. Only standing dead culms are included in the calculation of annual loss, which was calculated on a cumulative basis of 100% of the Stem Set IV loss during the first 8-mm rain, 50% during the second 8-mm rain, and thereafter 30% for a total of 1,000 mm

Stem set	I	II	III	IV	Annual
No. of culms/m^2	4	4	9	13	cumulated loss
Nutrient	Loss from living stems			Loss from dead stems	(g/m^2)
N (μg/0.5 l)	0.1	7.2	1.7	1.2	
($\mu g/m^2$ loss)	0.4	28.8	15.3	15.6	0
P (as above)	0.1	0.3	0.0	0.0	
	0.4	1.2	0.0	0.0	0
K (mg/0.5 l)	1.0	2.6	1.6	5.0	
(mg/m^2 loss)	4.0	10.4	14.4	65.0	2.50
Na	0.2	1.1	2.0	11.7	
	0.8	4.4	18.0	152.1	5.84
Ca	0.0	0.25	0.62	2.00	
	0.0	1.00	5.58	26.00	1.00
Mg	0.0	0.01	1.08	2.64	
	0.0	0.04	9.72	34.26	1.32
Fe	.02	0.01	0.00	0.00	
	.08	0.04	0.00	0.00	0
Mn	.033	0.066	0.252	0.538	
	.066	0.262	2.264	6.988	0.27

cronutrient, but apparently Mn along with Na are readily leached from leaves (Tukey 1970), and papyrus is no exception.

Regarding elution and decomposition losses, it should be pointed out that in swamp plants elution is a comparatively fast process of solution of nutrients in dead tissue when it falls into the swamp water. On the other hand, decomposition depletes nutrients from dead tissue over a longer period of time and involves mineralization of nutrients immobilized within organic components such as cellulose, lignin, etc. Although it is realized that elution and decomposition go on simultaneously, they are treated below as separate processes. During the 20-day elution experiment, decomposition was held to a minimum by using flowing water, large pieces of tissue, and a cool temperature (19–21°C). During this experiment K and Na showed the highest decrease (Table 5). Iron, Mn, N, P, Ca, and Mg are lost at lower levels. In most cases the rate of loss was highest within the first 20 days, which is arbitrarily considered here to be the elution period. After this a slow loss continues for a long time; this last phase is considered part of the decomposition period referred to below.

TABLE 5. Nutrient loss by elution from culms and estimated loss by elution from a papyrus swamp. Dead material calculations based on an average composition from Lake George, where dead material lying in the water consisted of 32 dead culms/m^2 along with old rhizome and root material with a total dry wt of 4.48 kg/m^2. Loss from culms based on average of 2 analyses

Day	N	P	K	Na	Ca	Mg	Fe	Mn
			Nutrients (% dry wt)					
0	0.950	0.054	2.40	0.120	0.160	0.0213	0.0026	0.0157
10	0.630	0.034	0.80	0.140	0.160	0.0274	0.0019	0.0120
15	0.640	0.030	0.30	0.075	0.173	0.0283	0.0016	0.0120
20	0.630	0.038	0.19	0.050	0.150	0.0201	0.0016	0.0120
% loss after 20 days	34	30	92	58	6	6	39	24

Nutrient	Nutrient content of dead material (g/m^2)	Loss from dead material by elution (g/m^2)
N	33.21	11.3
P	1.54	0.5
K	43.46	40.0
Na	12.10	7.0
Ca	8.96	0.5
Mg	3.14	0.2
Fe	3.14	1.2
Mn	1.25	0.3

TABLE 6. Nutrient loss due to decomposition of different organs after 26-day incubation of eluted material. Results are averages of 2 sets of cultures and are expressed as % dry wt

Nutrient	Root	Rhizome	Culm	Umbel	Average loss (%)
N Day 0	0.90	0.83	0.52	0.75	26
Day 26	0.54	0.43	0.50	0.64	
P	0.022	0.056	0.012	0.040	84
	0.004	0.008	0.002	0.006	
K	0.36	0.21	0.20	0.18	53
	0.15	0.11	0.09	0.10	
Na	0.065	0.063	0.071	0.039	52
	0.031	0.030	0.030	0.024	
Ca	0.101	0.076	0.175	0.140	39
	0.082	0.034	0.138	0.047	
Mg	0.078	0.062	0.038	0.069	37
	0.068	0.046	0.012	0.030	
Fe	0.0101	0.0100	0.0070	0.0083	32
	0.0065	0.0075	0.0050	0.0050	
Mn	0.0067	0.0033	0.0034	0.0048	31
	0.0038	0.0025	0.0028	0.0035	

In a papyrus swamp which has not been burnt or cut over for some time, a large number of dead culms are present, ≈ 3 for every 1 green culm. Some of these dead culms remain standing, held up by neighbouring culms, whereas many others are found lying about in and out of the water. Eventually most of these dead culms settle into the water. Since the composition of dead aerial culms (i.e., Stem Set IV) is known, and since the composition of culms after lying in the water is known (Table 5), it is possible to calculate the approximate elution loss. The losses are shown in Table 5 as percentage loss (i.e., the amount lost from the total level of that element in culms lying down in 1 m^2 of swamp).

Gaudet (1976) estimated that one-third of the biomass of papyrus was lost during decomposition inside papyrus swamps. In order to simulate this decomposition under optimum conditions several techniques were employed (tissue ground to a fine particulate size, inoculation with pure cultures of decomposing bacteria, and increased incubation temperature). This procedure brought about a one-third loss in biomass in 26 days. The biomass loss for the aerial organs, umbel and culm, was only 29% and 31% as opposed to that of the storage organs, the root and rhizome at 37% and 38%, respectively. After this rapid decomposition the tissue was washed to remove all soluble components as well as bacteria, so that the results presented in Table 6 represent only those nutrients remaining after decomposition, not those due to enrichment by the bacteria themselves or to decomposition products. Also, the tissue had been eluted for 20 days previously, therefore elution losses are not included in the results.

As a result of decomposition the levels of K and Na are decreased even further (Table 6). Phosphorus, Ca, and Mg are depleted to much lower levels than during elution, and Fe and Mn are lost at about the same level as the elution loss.

Discussion and Conclusions

Taken individually, the general pattern of distribution of nutrients in papyrus is not unusual when compared to other emergent aquatic macrophytes, such as *Phragmites communis* (Kvét 1973). In both plants, N and P seem to reach high levels in young tissue and are depleted in older portions. This is to be expected because young tissue is the most active in metabolism and N and P are mobile nutrients. Potassium (and to some extent Na) decreases in older portions, most likely because of leaching by rain especially in the umbels. A similar distribution for K was found by Kvét in *Phragmites*. The very high level of K at the base of the juvenile culm in papyrus occurs along with high levels of P and N. This is in the region of the intercalary meristem where cell divison (and later cell expansion) proceeds at a maximum rate. Calcium and Mg show very little difference in level from culm to culm, possibly because these two elements are relatively immobile. Manganese and Fe were definitely higher in older culms and both were concentrated in certain organs. Maximum concentrations of Mn occurred in older umbels, while Fe was most abundant in roots. Iron accumulation in roots is a phenomenon seen in other aquatic macrophytes such as *Saururus* (Boyd and Walley 1972). Oborn (1960) also found high levels of Fe in the roots of aquatic macrophytes. The possibility existed that in the present study the high levels of Fe were caused by iron bacteria or detritus adhering to the roots. The ordinary technique used for all root samples in this and previous work (Gaudet 1975) was to scrub them well with water. This technique was as effective as vigorous washing with detergent or Fe-free glycerol. The most vigorous technique, 5% HC1, causes a dramatic decrease in Fe and all other elements. Thus, the high Fe content of the roots is due to concentration within cellular compartments as well as external contamination. The latter was removed by ordinary scrubbing, and is thus not included in the present results.

Wali et al. (1972) concluded that the high productivity of aquatic macrophytes in Marion Lake, Canada, may be attributed to the higher nutrient content of the sediments, but they also pointed out that high nutrient levels in the macrophytes seemed related to the depletion of nutrients in the hydrosoil. This would suggest that high rates of production and nutrient accumulation go hand in hand. Several authors have come to this general conclusion. For example, Caines (1965) felt that a greater accumulation of nutrient ions in aquatic macrophytes was correlated with periods of increased growth. Boyd and Hess (1970) showed standing crop to be the most important factor determining quantities of nutrients per m^2 in the cattail, *Typha*. Boyd (1970*a*) noted that maximum nutrient uptake and accumulation generally occurred prior to the attainment of maximum standing crop in emergent macrophytes. In many species studied by him more than 50% of most nutrients were taken up prior to the point where 50% of the dry weight standing crop had been reached. It would be a mistake to view this as a simple correlation, since Boyd (1971) indicated that nutrient uptake in aquatics is not just a function of dry matter production but is a physiological characteristic of the species. For example, some species of aquatic macrophytes (especially floating-leaved and submerged) are characterized as having a low standing crop but contain high percentage composition of nutrients, while species with high standing crops (esp. emergents) invariably have low percentage compositions. This relationship was demonstrated for N by Polisini and Boyd (1972), who found standing crop for 16 species in one impoundment was positively correlated with total quantity of N per m^2, while inversely correlated with N composition. It is interesting to speculate that whatever adaptations result in increased production in species such as papyrus, also result in a decreased percent nutrient composition.

Table 7. Comparison of annual uptake of nutrients by emergent macrophytes. Uptake for *Typha latifolia* and *Scirpus americanus* calculated from data of Boyd 1970*a*

Species	Annual uptake ($g \cdot m^{-2} \cdot yr^{-1}$)					
	N	P	K	Na	Ca	Mg
Cyperus papyrus	103.3	7.8	129.9	28.1	19.2	6.0
*Typha latifolia**	59.4	6.9	121.6	14.2	58.9	12.3
*Scirpus americanus**	12.6	1.9	21.5	5.8	13.5	6.6

*Maximum rates, calculated by multiplying the highest daily rate in Table 3, Boyd 1970*a* by 365.

Regarding the annual uptake of nutrients by papyrus, it is difficult to compare it to other emergents because the few studies that have been done concern temperate macrophytes with growth limited to the spring and summer seasons. If temperate emergents such as *Typha latifolia* and *Scirpus americanus* were grown on a year-round basis, the maximum annual uptake could be estimated (Table 7). On a dry weight basis, the estimated average uptake of most nutrients by papyrus is still higher than the maximum estimated

TABLE 8. Estimated nutrients in a papyrus swamp (g/m²)

	Standing crop			Annual losses				Balance
Nutrient	Present in live tissue	Present in dead tissue	Total uptake and accumulation	Elution leaching	Rain leaching	Offtake (0.5%)	Decom-position	Nutrients left in standing crop (accumulates in swamp as peat)
N	61.61	41.69	103.3	11.3	0	0.5	26.9	64.6
P	5.43	2.41	7.8	0.5	0	0	6.6	0.7
K	103.25	26.61	129.9	40.0	2.5	6.5	68.9	12.1
Na	20.91	7.17	28.1	7.0	5.8	0.1	14.6	0.6
Ca	8.46	10.77	19.2	0.5	1.0	0.1	7.5	10.1
Mg	3.69	2.26	6.0	0.2	1.3	0	2.2	2.3
Fe	1.25	1.27	2.5	1.2	0	0	0.8	0.5
Mn	0.43	0.96	1.4	0.3	0.3	0	0.4	0.4

uptake of other emergents. If the average (or seasonal) annual uptake by temperate emergents is used for comparison, papyrus would far exceed the rates of uptake by these emergents. But, although the rate of uptake is higher the pattern of uptake is similar to emergents such as *Typha* (Boyd 1970*a*). In papyrus during the arbitrary 100-day period, while the four culms are maturing, over 50% of all eight nutrients are taken up and accumulate, and this occurs prior to the attainment of 50% of the biomass for these four cohorts. The net rate of uptake and accumulation declines with age except in the case of Mn.

Nutrient loss due to rain in papyrus swamps must be largely dependent on local rain patterns. For example, in East Africa papyrus swamps in eastern Kenya receive only a few rain showers per year (500 mm), while those in western Uganda receive many (2,000 mm). In calculating the annual cumulative loss from a papyrus population (in Table 4), the value of 1,000 mm was arbitrarily selected as intermediate. Also, only dead culms were included as it is assumed that the loss from such material is not compensated for by uptake by dead culms, since such culms are no longer functional. The pH of rainwater may have a large effect on the rate of rain leaching, thus in the above experiment the pH of the 'rain' was kept at 7.2. This is an intermediate pH, since East African rain varies from 5.7 to 9.8 (at Kampala, Uganda, Visser 1964).

Emergent aquatic macrophytes lose nutrients rapidly upon death and decomposition, especially when the dead or dying material falls into the water. Boyd (1970*b*) found bags of *Typha* leaves lost 95% and 93% of the total original leaf K and Na after 20-days submergence. After 200 days, losses were: Mg 90%, Ca 75%, P 50%, and N 40%. Planter (1970) found most nutrients were quickly lost from *Phragmites communis* stems and leaves. Similar results were obtained by Mason and Bryant (1975) for *Typha* and *Phragmites*. The initial rapid disappearance of nutrients from emergent macrophytes is felt by Boyd (1971) to be associated with losses of soluble constituents (elution) and a breakdown of delicate tissue such as pith. This first phase of nutrient loss may start before the plant organ falls into the swamp water. The second phase of decay involves microbial decomposition of fiber. Loss of nutrients in papyrus follows a similar pattern to *Typha* and *Phragmites*, but the amount of time involved in recycling one organ is considerably shortened in tropical swamps. Thus, the turnover time for papyrus is 4 mo (Thompson 1976), whereas in a typical temperate emergent, *Typha*, only 50% of all components are lost during 4 mo (Boyd 1971). Also, one nutrient, silica, does not follow this general pattern of loss by solution or mineralization. In grasses and sedges it is mostly concentrated in the epidermis as intercellular inclusions called, 'silicophytoliths' (Bertoldi de Pomar 1975). Death and decomposition allow an increase in silicate because of a decrease in cellular components in addition to degradation of the cell walls. This process would leave silicate behind, as it would not be decomposed quickly (Bertoldi de Pomar 1975). This results in a high silicate level in the peat found in papyrus swamps (Gaudet 1976).

Considering nutrient uptake, accumulation, and loss, papyrus can be characterized in the following way. Because of a high rate of production, one of the highest rates among the emergent macrophytes (35 g · m^{-2} · day^{-1}, Thompson 1976), the young portions must take up nutrients at a high rate compared to other emergents, resulting in a very large standing crop of nutrients (e.g., 103 g potassium per m²). As each culm on the plant approaches death, certain elements such as K and Na are lost by rainwater leaching and by elution if the culm falls into the swamp. Nitrogen and P are not as easily leached and their dramatic decrease in the older culms most likely is due to translocation. Nutrient losses also occur during decomposition. In a papyrus swamp there is a large amount of dead material consisting of old stems (and rhizomes and roots) which decompose when they finally reach the water in the swamp and are then broken down to peat. But, as the peat sinks into the anaerobic atmosphere under the floating mass of papyrus, decomposition slows and peat accumulates. Eventually the peat becomes water-logged and sinks to the swamp bottom where it is liable to be flushed out into surrounding rivers or lakes by incoming river water (Gaudet 1976). The bulk of decomposition then, is confined to that period between death and peat formation. During this decomposition period, nutrients are lost to the swamp water or are incorporated directly by microbes. It has been estimated (Gaudet 1976) that almost one-third of the nutrients originally present in the standing crop are lost each year during this process. This loss is estimated in Table 8. In addition to decomposition, the nutrients in the standing crop also are subjected to offtake by animals, disease, etc., which has been estimated at 0.5% of the total biomass (Thompson 1976). This also is shown in Table 8. Thus, the pattern of uptake, accumulation, and loss may be looked at in terms of the nutrient balance (Table 8) where the losses are arranged according to several types: elution and rain losses which are readily soluble; offtake and decomposition where the losses may be either readily soluble or require some time to become soluble (e.g., ammonia N in aphid excreta which is quite soluble compared to N in old stem tissue, which may not completely solubilize until after a year or more); and lastly, a certain amount of each element is left in the material which is not decomposed, leached, eaten, or eluted, but becomes peat within the swamp. From the point of view of nutrient cycling this peat must be examined in some detail before nutrient pathways in papyrus swamps can be worked out satisfactorily.

In the above study the estimated losses could be more finely 'tuned', e.g., rain leaching could be closely adjusted to simulate the actual case in a given swamp. Also, the decomposition loss could be more accurately adjusted depending on average monthly air and water temperatures for a given swamp. Most likely a model so tuned would show that an increase in rain leaching (because of increased annual rainfall) may be accompanied by a decrease in decomposition, because cooler temperatures might accompany increased rainfall. In other words, the effect of one might compensate for the other. More information is needed on papyrus swamps before realistic models can be constructed, especially lacking is a more complete analysis of the detritus-mud-water relationships.

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