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Primary Productivity of Papyrus (*Cyperus papyrus*) in a Tropical Swamp; Lake Naivasha, Kenya

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ABSTRACT

Papyrus (Cyperus papyrus) *standing biomass and the primary productivity of undisturbed and previously harvested areas of papyrus was measured in Lake Naivasha swamp, Kenya. Papyrus culm density in undisturbed swamp was estimated to be* $13{\cdot}1 \pm 1{\cdot}9$ *culms* m^{-2} *and aerial biomass was* $3602\ g\ m^{-2}$. *In undisturbed swamp the aerial productivity was* $14{\cdot}1\ g\ m^{-2}\ day^{-1}$ *while the previously harvested swamp reached a peak of* $21{\cdot}0\ g\ m^{-2}\ day^{-1}$ *after 4 months of regrowth and a ceiling aerial biomass of* $2731\ g\ m^{-2}$ *after 6 months. The annual aerial production rate of papyrus in Lake Naivasha was estimated to be* $5150\ g\ m^{-2}\ year^{-1}$. *To sustain yields of regularly harvested papyrus swamps, the harvest intervals should exceed 1 year.*

Key words: papyrus, *Cyperus papyrus*, productivity, biomass energy, tropical swamps.

INTRODUCTION

Emergent macrophytes in swamps and marshes are amongst the most productive plant communities.[1-4] Although they cover only 1% of the continental land surface, they contribute as much as 5% of the total annual primary production.[5] Most of the information available on the

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primary production of emergent macrophytes comes from studies of temperate wetland communities. Among the most intensively studied communities in these regions are those dominated by *Phragmites* and *Typha* species that have been estimated to have productivities as high as between 4000 and 6000 g m^{-2} $year^{-1}$ on fertile sites.[2] Little quantitative data on standing biomass and productivity of tropical swamps have been published, although there is evidence that they are more productive than the temperate swamps.[2,4]

In Africa, most swamps are dominated by papyrus (*Cyperus papyrus* L.) which covers large areas in Uganda and Sudan,[6] the Upemba basin in Zaire and the Okavango delta in Botswana.[7,8] In one of the few estimates of productivity in tropical swamps, Thompson *et al.*,[8] working in Upemba basin, Zaire, found that papyrus productivity ranged from 7·1 to 25·9 g m^{-2} day^{-1}. These values were, however, based on short-term measurements made over only 4 days. Hence, there is a need for more detailed and longer term investigations. Also, more information on the productivity of this papyrus is required at a time when it is being recognized as a resource worthy of exploitation as a biomass fuel.[9] The aim of this study was to estimate over a full year the standing biomass and annual primary productivity of papyrus in a tropical swamp which fringes Lake Naivasha, Kenya.

MATERIALS AND METHODS

Common methods of estimating primary production include measurements of peak biomass,[10] maximum minus minimum biomass,[11] and methods which account for death and decomposition between harvests.[12] These methods are usually applied in communities that are characteristic of temperate ecosystems and undergo seasonal growth patterns with peak biomass occurring at the end of the growing season. Estimating primary production in tropical swamps is more difficult than in temperate regions because plant establishment, growth and mortality occur concurrently throughout the year, so that there is little temporal change in the standing crop.[13] To measure primary production of such communities with a relatively stable biomass requires measurements of population dynamics and the life cycle of individual shoots. In these communities, above-ground biomass and primary productivity can be estimated non-destructively from the relationships between shoot size and dry weight and the pattern of growth of individual plant units.

In the present work, the dry weight of papyrus culm-units (culm + umbel) was estimated from measurements of their girth at the top of the sheathing scale leaves. To establish such a relationship, several culm-units from areas close to the experimental site were cut at rhizome level after girth measurements had been made and were taken to the laboratory and dried to constant weight at 80°C. Using the data from girth and dry weight measurements, the following equation was derived; $\log_{10} W = (2{\cdot}63 \log_{10} G) - 0{\cdot}491$, where W = weight (g) of culm-units and G = girth (cm) of the culm at the top of the scale leaves. This equation was obtained from a linear regression (Fig. 1) fitted to the culm girth and dry weight relationship for a wide range of culm-unit sizes.

The experimental site was a lake-fringing swamp consisting of a virtual monoculture of papyrus and located on the western side of Lake Naivasha, Kenya (0° 45′S, 36° 20′E), in the Eastern Rift Valley at an altitude of 1890 m. The floating papyrus mat extended about 1 km into the lake but it was grounded at the lake margin. The flora and ecology of the lake has been described by Gaudet[14] and some aspects of the climate have been described by Jones & Muthuri[15] and Muthuri.[16] Figure 2 shows the 12-year monthly means of mean daily temperature and solar radiation for Lake Naivasha basin from Meteorological Station No. 90.36/281 (0° 44′S, 36° 27′E) of the Meteorological Department,

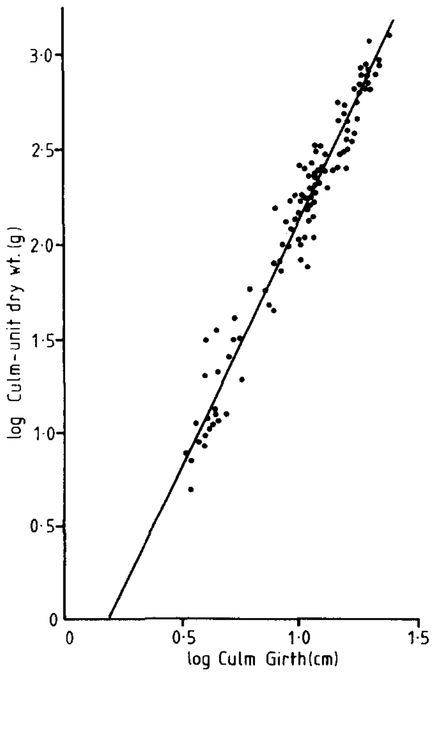

Fig. 1. Relationship between papyrus culm-unit dry weight and the culm girth at its base: $Y = -0{\cdot}491 + 2{\cdot}63X$, $r^2 = 0{\cdot}980$, $P = <0{\cdot}001$, $n = 131$.

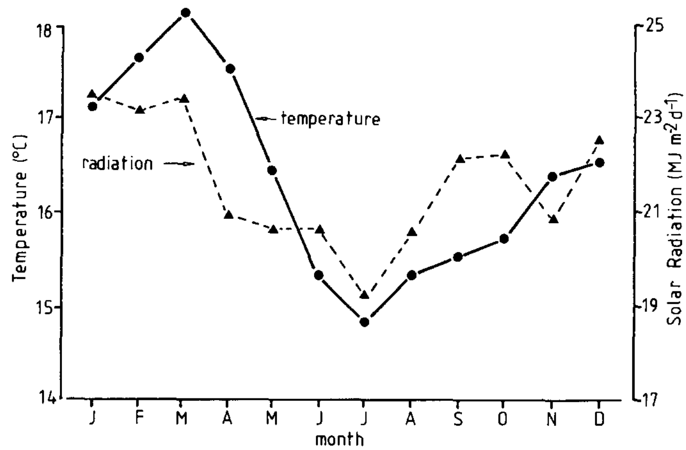

Fig. 2. The annual cycle of mean air temperature (●) and solar radiation (▲) based on a 12-year mean from 1970 to 1982 recorded at Naivasha Meteorological Station No. 90.36/281 (0° 44'S, 36° 27'E and 1936 m above sea level). (By kind permission of the Meteorological Department, Ministry of Transport and Communications, Kenya.)

Ministry of Transport and Communications, Kenya. This station is situated about 20 km from the study site at an altitude of 1936 m. The annual range in mean temperature is small, between 3 and 4°C but the diurnal range is greater at approximately 16°C.

Measurements of standing biomass and above-ground productivity were made in quadrats of 3 m × 3 m which were marked out at random at distances greater than 25 m from the landward edge of the swamp. Measurements were initiated on three undisturbed quadrats and three quadrats from which all aerial material had been harvested immediately before the start of the measurements (cut quadrats). Unfortunately, a month after the start of the experiment one quadrat from each treatment was damaged by fire and was therefore excluded from the measurements. Measurements on the remaining duplicate quadrats from each treatment were made at monthly intervals from July 1981 to June 1982. All culms with bases in the quadrats were identified by number and new recruits were added to the list every month. Culms were divided into three age classes: (i) juvenile, with unopened umbels; (ii) mature, with opened green umbels; and (iii) senescent, with more than half of the umbel brown (achlorophyllous) and clear evidence of senescence of the culm. The girths of all living culms in the quadrats were measured each month and used to estimate total living aerial biomass. The monthly increments in aerial biomass (net aerial primary productivity) could be determined from these estimates combined with changes in culm density.

Measurements of rhizome and root biomass in the papyrus swamp are very difficult to make. This is because the live and dead rhizomes and roots form a very compact floating mat which can be more than 1 m thick and from which we have, as yet, been unable to remove intact and defined areas. This floating mat appears to consist of a high proportion of dead and slowly decomposing rhizomes. In order to obtain a more reliable estimate of five root biomass, papyrus plants were grown in five large, circular tanks which were lined with polythene and located on the University of Nairobi campus. Each tank had a surface area of 0·25 m^2 and a capacity of 100 litres. Before use the tanks were well washed with detergent, rinsed and then filled with tap water. Stock nutrient solutions were added to each tank to make up a concentration of 0.1 full-strength Hoagland's solution. This solution was changed every week. Rhizomes of papyrus collected from Lake Naivasha were introduced into the tanks and plants were harvested after 6 months when all the papyrus age classes, i.e. juvenile, mature and senescent culms were represented. The distribution of biomass in the various organs of the papyrus was determined on mature plants. The plants were separated into roots, rhizomes, scale leaves, culms and umbels and dried to a constant weight at 80°C.

RESULTS

Total culm-unit density in the undisturbed quadrats remained between 13 and 16 culms m^{-2} throughout the year. There was no evidence of a seasonal cycle in production of new culms and the relative number of juvenile, mature and senescent culms-units was virtually constant (Fig. 3(a)). In the cut quadrats the number of culms increased from the time of the harvest in July to reach a peak density of 19 m^{-2} in December. Thereafter the total culm density declined to about 15 m^{-2} and remained stable for the final 2 months of the experimental year (Fig. 3(b)). The density of mature culm-units in the cut treatment reached a similar value to the density in the undisturbed quadrats within 7 months of the harvest and the subsequent decline in total culm number was due to the decline in numbers of juvenile culms (Fig. 3(b)).

The standing aerial biomass of the undisturbed quadrats ranged from 3123 to 3794 g m^{-2} throughout the year and there was no evidence of any seasonal cycle in aerial biomass (Fig. 4(a)). The mature culm-units contributed about 75% to the aerial biomass and the juvenile culm-units contributed less than 10%, the balance being made up by the senescent culm-units (Fig. 4(a)). In the cut quadrats the growth curve of standing aerial biomass showed a distinct lag phase, followed by a linear period of growth and a ceiling yield from 6 months after the harvest and onwards.

The peak in aerial biomass in the cut treatment was 2741 g m^{-2} in January 1982 (Fig. 3(b)). The contribution of juvenile culm-units to the aerial biomass was high for the first 4 months after the harvest but after 6 months the mature culm-units were contributing a very similar proportion to that in the undisturbed treatment (Fig. 4(b)).

An estimate of the contribution made by the aerial biomass to the total standing biomass of papyrus can be made from the results of the harvest of plants growing in tanks and then divided into the component parts (Fig. 5). It can be seen that live rhizomes and roots contributed approximately 10% each to the total standing biomass. Of the aerial biomass the culms contributed in excess of 65%, the balance being the umbels on top of the culms and the scale leaves which surround the base of the culms.

Monthly values of aerial net primary production in both undisturbed and previously harvested quadrats are shown in Fig. 6. Aerial productivity of undisturbed quadrats varied between 12·4 and 15·9 g m^{-2} day^{-1} with a mean (12 months) productivity of 14·1 g m^{-2} day^{-1}. The aerial

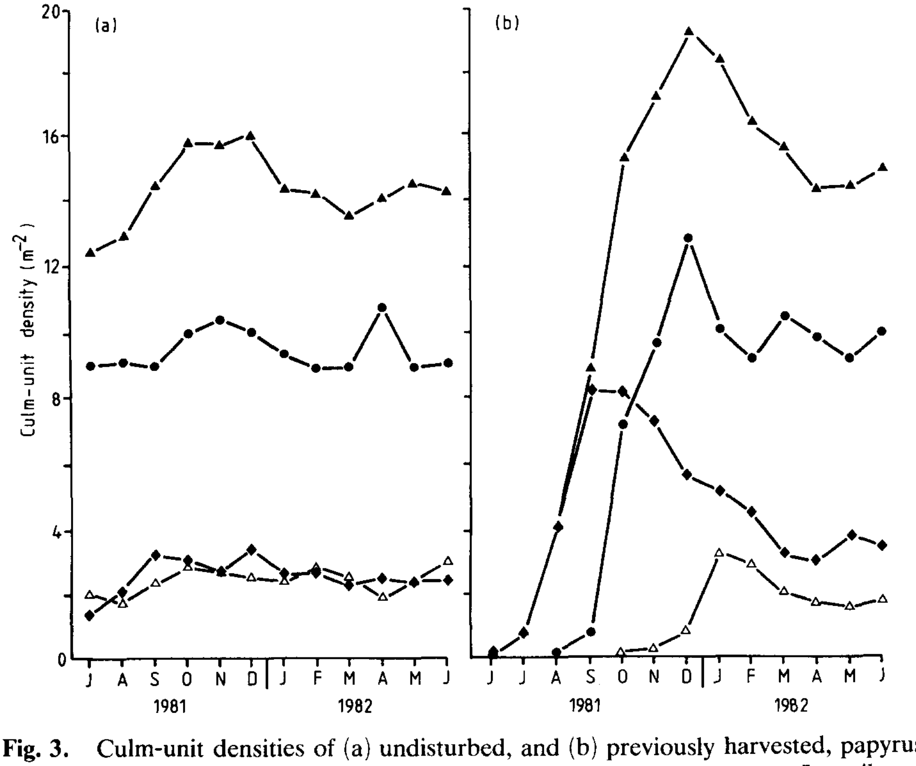

Fig. 3. Culm-unit densities of (a) undisturbed, and (b) previously harvested, papyrus stands. Each value is the mean of measurements from two quadrats. ◆, Juvenile; ●, mature; △, senescent and ▲, total number.

productivity of the previously harvested quadrats rose rapidly from 0·61 g m^{-2} day^{-1} in July 1981 to a peak of 21·0 g m^{-2} day^{-1} in October 1981, 4 months after harvesting. Subsequently, the aerial productivity in the harvested quadrats declined to levels similar to those of the undisturbed quadrats (Fig. 6).

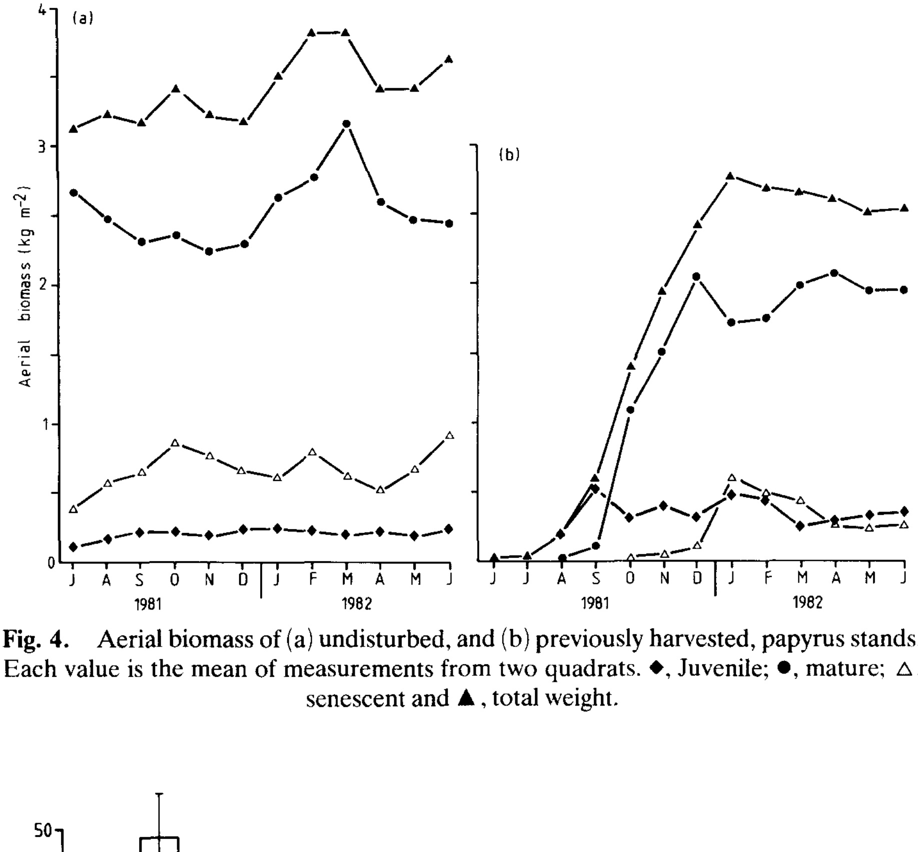

Fig. 4. Aerial biomass of (a) undisturbed, and (b) previously harvested, papyrus stands. Each value is the mean of measurements from two quadrats. ◆, Juvenile; ●, mature; △, senescent and ▲, total weight.

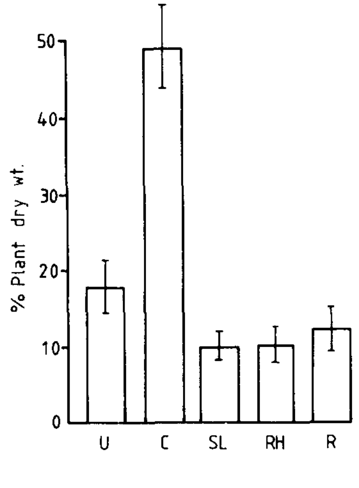

Fig. 5. The distribution of biomass amongst organs of mature papyrus culm-units grown in tanks in the open. U, Umbel; C, culm; SL, scale leaves; RH, rhizome; R, root. Vertical bars represent ± SD, $n = 23$.

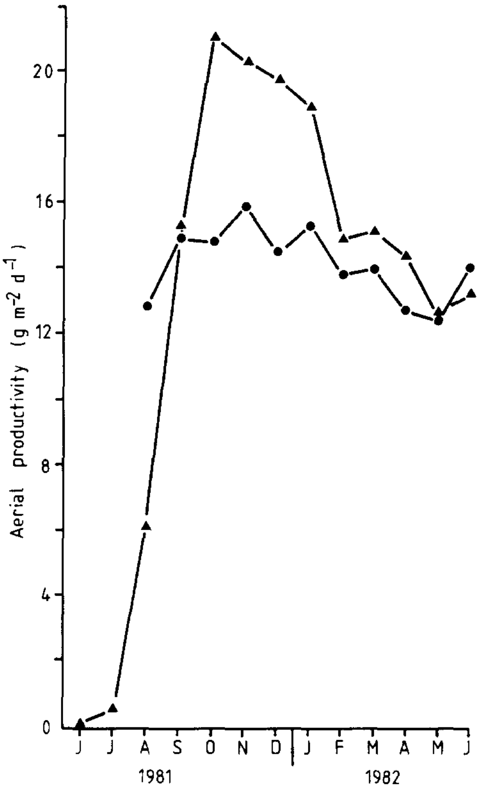

Fig. 6. The mean daily productivities of undisturbed (●) and previously harvested (▲) papyrus stands. Each value is the mean of measurements from two quadrats.

DISCUSSION

Values of culm-unit density recorded in undisturbed swamp in Lake Naivasha fall within the ranges previously reported by Thompson *et al.*[8] in Ugandan swamps (7·9–22·5 m^{-2}). Harvesting the papyrus appeared to stimulate a rapid production of new culms during the re-growth and in only 4 months the culm-unit density in the previously harvested quadrats had exceeded that of the undisturbed quadrats. Peak culm-unit density was attained after 6 months and thereafter the fall in culm-unit density to the levels similar to the undisturbed quadrats is most likely attributed to density dependent mortality. The decline was due primarily to the reduction in numbers of juvenile culm-units. Density-dependent mortality, also referred to as self-thinning, applies in overcrowded populations and has been described in many plant stands,[17-19] although Hutchings[20] has shown that clonal plants like papyrus do not strictly comply with the self-thinning rules.

Unlike temperate swamps, tropical papyrus swamps do not show an annual cycle of growth with a period of intense spring/summer growth followed by maturity and death with the onset of winter. Instead, the recruitment, growth and death of papyrus culm-units occurs concurrently throughout the year. Hence there is little annual change in culm-unit density or in the aerial biomass of the swamp when it is undisturbed. The aerial biomass of the undisturbed Lake Naivasha papyrus swamp is higher than estimates reported by Thompson *et al.*[8] for interior swamps in Upemba basin in Zaire (1061–1163 g m^{-2}) and Uganda (1900–2950 g m^{-2}) but is lower than the biomass of the apparently more vigorous sites (fringe zones) of Upemba island (5173 g m^{-2}) and Akika island of Lake George, Uganda (5000 g m^{-2}). Differences in aerial biomass of papyrus in various sites have been attributed to prevailing climatic conditions by Thompson *et al.*[8] These authors noted an increase in standing biomass of papyrus swamp with increase in altitude and suggested that there is a climatically determined optimum biomass for papyrus swamp at a particular altitude. The biomass values from the present study, and other aerial biomass values reported by Thompson *et al.*[8] for Uganda and Zaire swamps fit the proposed trend. Lake Naivasha swamp, at an altitude of 1890 m, has an aerial biomass in the region of 3500 g m^{-2} whereas two Uganda sites situated at 913 and 1130 m have lower values of 2900 and 2950 g m^{-2}, respectively. In addition, Upemba interior swamps at 545 m had the lowest biomass (115–1163 g m^{-2}). However, more swamps need to be sampled in order to justify this proposal as Jones & Muthuri[15] have reported a lower aerial biomass (1384 g m^{-2}) in Busoro swamp in Rwanda although it is situated at higher altitude (1495 m) than the Ugandan sites.

Papyrus aerial organs (umbel, culm and scale leaves) contribute approximately 75% of the total plant biomass. Because of the difficulty of sampling rhizomes and roots from papyrus swamps, this estimate is based upon measurements made on plants growing in containers. The high aerial proportion of total plant biomass in papyrus is unlike many other perennial emergent macrophytes such as *Typha latifolia, Typha angustifolia, Scirpus lacustris* and *Phragmites communis* that have large proportions (often two to five times) of their biomass in the form of roots and rhizomes, even at the time of maximum seasonal standing crop of green shoots.[21,22]

The harvesting of papyrus, and monitoring its re-growth, was carried out with the aim of obtaining information that will be of use to planners involved in future papyrus swamp utilization and management. Although harvesting papyrus increased the culm-unit density to higher levels than those of normal papyrus stands, the final (ceiling) aerial biomass after 1 year was lower than any value of aerial biomass recorded during the year in the undisturbed stand. Other workers have made similar observations. Gaudet[23] found that harvesting papyrus reduced the standing crop although culm density increased dramatically after 4 months of regrowth. In addition, papyrus height was reduced from 4·7 to 0·8 m in stands cropped twice at 2-month intervals. Similarly, Mochnacka-Lawacz[24] working in a *Phragmites communis* swamp found that the aerial biomass of uncut *Phragmites* at 1406 g m^{-2} was three times that of the sum total aerial biomass of *Phragmites* cut three times during the season. These results suggest that if high and sustainable yields of papyrus are to be obtained from continued cropping then there should be long intervals (more than 1 year) between harvests.

Continuous cropping of papyrus could have important ecological effects on the swamps. Most significant in this respect will probably be the loss of large quantities of nutrients removed with the harvested biomass that would otherwise be recycled in the swamp. For example, with a papyrus above-ground biomass of 36 t ha^{-1} it is estimated that completely harvesting Lake Naivasha swamp (200 ha) would remove 72 000 t of papyrus biomass. Using the papyrus nutrient composition data from Muthuri[16] (N 1·16%, P 0·16% and S 0·06%) it can be calculated that harvesting the above swamp will remove 836 t of nitrogen, 115 t of phosphorus and 43 t of sulphur. The removal of such large quantities of nutrients following papyrus cropping would probably eventually affect the rates of production in this ecosystem.

In addition to the loss of large quantities of nutrients, harvesting papyrus will alter the canopy structure and modify the light and temperature microclimate of the swamp. The loss of papyrus canopy will allow more radiation to reach water level and this will stimulate the growth of other macrophytes. As a consequence there may be an increase in interspecific competition that could reduce papyrus production. The increased radiation at water level, following papyrus harvest, will also raise the temperature of the swamp sediments and papyrus underground organs. The effect of these higher temperatures on the growth of papyrus requires further investigation.

There have been several suggestions that papyrus swamps can sustain one of the highest primary production rates of any known plant community. Indeed, in hydroponic culture it attained growth rates of 125 g m^{-2} day^{-1} while under natural conditions, 41 g m^{-2} day^{-1} has been reported for fertile sites.[2] However, in Lake Naivasha swamp in this study, aerial productivity for the undisturbed stand was estimated to be considerably less at 14·1 g m^{-2} day^{-1}. Total productivity, including root and rhizome, could not, however, be estimated. The aerial productivity of Lake Naivasha swamp determined here falls within values reported for the Upemba papyrus swamps (7·1–25·9 g m^{-2} day^{-1}) in Zaire but is lower than the productivity for the Ugandan swamps (24·7–34·1 g m^{-2} day^{-1}).[8] The productivity of Lake Naivasha papyrus is also within the ranges reported for other emergent macrophytes. van der Valk & Davis,[25] working in glacial prairie marshes, have reported daily production rates for a range of species varying from 4 to 23 g m^{-2} day^{-1}. Productivity of *Typha elephantina* during the growing season in India ranged from 4·7 to 9·4 g m^{-2} day^{-1},[26] while *Typha latifolia* has been reported to have productivities of 19 g m^{-2} day^{-1} in South Carolina and 53 g m^{-2} day^{-1} in Oklahoma.[27]

There is clearly, therefore, no evidence that the short-term productivity of papyrus is significantly greater than any other wetland species. However, unlike papyrus swamps, most of the previous measurements have been in temperate wetland communities where growth is not sustained throughout the year but is confined largely to spring and summer seasons. Since growth occurs throughout the year in tropical wetlands the annual production of papyrus would be expected to exceed that of similar temperate wetland communities.

In general, the most productive of temperate communities appear to be fertile reed swamps which can produce around 1500–3000 g m^{-2} $year^{-1}$.[3] Keefe[28] reported annual productivity values of between 150 and 3000 g m^{-2} $year^{-1}$ for the north temperate freshwater and saltwater wetland macrophytes while production rates of freshwater macrophytes in tidal wetlands of the middle Atlantic coast ranged from 489 to 3500 g m^{-2} $year^{-1}$.[29] The annual production of papyrus in Lake Naivasha swamp is higher because of its continuous year-round growth. From the daily production rates it is estimated to be 5110 g m^{-2} $year^{-1}$.

Clearly, this large primary production of papyrus swamps must have tremendous impact on the adjacent water bodies. Swamps are basically detritus-based ecosystems where the biomass produced in papyrus swamps is turned into detritus during the process of decomposition. The detritus accumulates in the swamp to form peat below the surface of the papyrus mat and sludge at the bottom of the lake. However, some of the sludge is physically exported to the interace between the swamp and open lake,[30] and this becomes a source of nutrients which accounts, in part, for the increased production reported for the edge of papyrus swamps.[31]

Although papyrus swamps under natural conditions are highly productive it is also clear than their exploitation for biomass fuel will have profound ecological effects on the ecosystem. In order to maintain high yields and good quality culms for continued harvesting, suitable management programmes must be evolved which can successfully regulate the harvest intervals to achieve sustainable yields. These must be based on a clear understanding of the ecology of the papyrus swamps, under defined management regimes. Although this work has addressed some of these problems, more studies are required before papyrus swamps can be exploited without fear of causing permanent deterioration of this fragile ecosystem.

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