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Responses of a fringing *Cyperus papyrus* L. swamp to changes in water level

Rosalind R. Boar *

School of Environmental Sciences, Centre for Ecology, Evolution and Conservation, University of East Anglia, Norwich NR4 7TJ, UK

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Abstract

Over a 9-year period (1993–2001), the land-water width of a papyrus fringe on the southern shore of Lake Naivasha, Kenya, varied between 40 and 60 m. Increases in width via rhizome spreading into open water followed the 1997/1998 El Niño flood when water depths rose by about 2 m. Germination of papyrus seeds also responded to water depth with a mean ± S.E. rate in experiments of 23 ± 6% after 21 days when water level was 5 cm below the sediment surface. No germination occurred when sediment was flooded or allowed to desiccate. Rhizome spreading from floating mats appeared to be favoured by deep water with seedling spread favoured on newly inundated, low-gradient slopes in shallow water. Although natural regenerative capacity was influenced by water depth, the height, density, biomass and chemical content of papyrus were not. Total average biomass along a land-water transect was 6950 ± 860 g m^{-2} which was large in relation to nutrient and mineral contents. Culms contained 0.47 ± 0.14% N and 0.06 ± 0.05% P and rhizomes 0.71 ± 0.21% and 0.10 ± 0.06%. Sediment underlying the swamp was aerobic and there were small land-water gradients in the BOD of swamp water and sediment. However, chemical gradients were weak compared with wider papyrus swamps elsewhere. Lake and swamp water mixed in the narrow fringe studied and residence times for organic matter may not have been long enough for organic material to mineralise before entering lake water.
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Keywords: African wetland; Lake Naivasha; Tropical swamp; El Niño; Ecotone

1. Introduction

East African swamps are likely to be highly productive (Muthuri et al., 1989; Gaudet, 1992) and biologically diverse (Denny, 1993) with important landscape functions (Junk, 2002) and a high capacity to intercept or transform materials moving from catchments to open waters (Naiman and Décamps, 1990; Denny, 1997; Azza et al., 2000). Where swamps occur as land-water ecotones, they are also likely to be highly dynamic and unstable over varying time scales (Bugenyi, 2001; Attrill and Rundle, 2002). Tropical wetlands are often subject to substantial fluctuations in water level (Denny, 1985; Thompson, 1985; Lehman, 1998; Talling and Lemoalle, 1998). The surface area of Lake Naivasha in Kenya (ca. 150 km^2), for example, fluctuates by 30% between periods of high (939 mm) and of low (442 mm) annual rainfall. In the longer term, the lake level has varied by at least 9 m since 1910 (Becht and Harper, 2002) and Maasai history, which is consistent with sedimentological evidence from Verschuren (1999), tells that the lake basin was dry towards the end of the 19th century.

Lake Naivasha is one of the most important freshwater resources in Kenya and its hydrology and biological community have been studied for at least the last 30 years (Harper et al., 2002). Most of the shoreline is covered by a narrow fringe of the tall sedge, *Cyperus papyrus* L. (Boar et al., 1999; Boar and Harper, 2002). One of these fringing swamps has been visited at intervals over a 9-year period (1993–2001) in which both low and very high water levels occurred. The aim of the work has been two-fold (i) to quantify swamp size and regenerative capacity in relation to fluctuations in water level and (ii) to discover if plant performance and swamp physicochemistry vary spatially in relation to water depth.

2. Methods

2.1. Study sites

A mature papyrus fringe on the southeast shoreline of Lake Naivasha was visited in late July and August at yearly or 2-yearly

* Tel.: +44 1603 593103; fax: +44 1603 591327.
E-mail address: R.Boar@uea.ac.uk.

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intervals between 1993 and 2001. At the beginning of the study, the swamp was rooted in peaty soil at its landward edge with a root mat that rested on unconsolidated lake sediment for most of its shoreward length. The root mat was floating on lake water at its lakeward edge. Sampling was carried out along one 80 m transect that had a fixed origin on privately owned dry land (UTM grid co-ordinates: 37N 201394 mE 9909581 mN) and ran perpendicular to the shore along a land-water gradient through the papyrus to the open lake. The slope of the shore was 0.54% so the fixed transect corresponded to a water depth gradient. Other parts of the lake's shoreline had steeper gradients with 4.33 and 3.81% slopes in south-western and the north-western areas (Weterings, 1999). Swamps in these other areas were visited in 1993 and 1995. A bathymetric map of the lake is given in Hickley et al. (2002).

2.2. *Papyrus biometrics*

On every visit to the fixed transect, water depth, culm density and individual culm heights were measured in 0.5 m × 0.5 m quadrats placed at 10 m intervals along the fixed transect. Water depth was also measured at the lakeward edge of the swamp. In two years, water depth was measured on the edges of an additional 13 (in 1993) and 11 (in 1995) areas of papyrus swamp elsewhere around the lake. Swamp widths from land to open water in these locations were measured from aerial photographs using the method given in Boar et al. (1999).

Biomass was measured in July 2000. For this, all emergent material was removed from single 0.5 m × 0.5 m quadrats placed at 10 m intervals. All roots and rhizomes below the quadrat were removed. Samples were divided into dead material; living culms, umbels (bracts and peduncles), seeds, rhizomes, primary roots and the much finer adventitious roots that are produced from primary roots. Roots and rhizomes were washed to remove sediment and roots that appeared dead were discarded. Materials were cut into approximately 2 cm pieces and air dried on nylon mesh racks for 10 days and then oven dried at ca. 60 °C with daily weighing until material reached constant weight on four consecutive days. Weights were recorded to a precision of 25 g for bulk samples weighing 1000 g or more and to a precision of 5 g for smaller samples. Dry material was reserved for chemical analysis.

2.3. *Germination experiment*

Papyrus seeds were separated from a single seed-bearing panicle in July 2000. For ease of handling, sets of 20 intact seeds were placed on lakeshore sediment contained in 10 individual 200 ml plastic pots, giving a sowing density of 5846 seeds per m^2. Ten pots were placed to their brim in larger outer basins that also contained shoreline sediment. Four replicate basins (200 seeds in each) were allocated to each of four treatments: 'flooded' where water level was maintained at 5 cm above sediment with seeds contained within 6 cm high plastic collars secured around the 200 ml pots; 'surface' where water losses to evaporation were replaced to maintain surface saturation; 'below surface' where level was maintained at 5 cm below the surface and 'drying' where losses to evaporation were replaced only by rainfall. Below-surface water level was monitored via an empty and perforated plastic pot that was placed in the centre of each basin and water level in the wetted treatments was maintained by additions of lake water. An additional basin for each water level contained 10 pots without seeds and a final basin contained 10 pots of sediment in which measurements of temperature, pH, oxygen and electrical conductivity were made over the course of the 30-day experiment. Basins were maintained outdoors and their perimeter protected with nylon mesh. Seedlings inside all pots were counted at intervals over the 30 days. Rain fell on day 2 (0.5 mm), day 3 (2 mm), day 22 (0.5 mm) and day 25 (0.5 mm). Seedling density was also counted on the lakeshore in three randomly placed 0.25 m^2 quadrats, where water depth corresponded with the depths in the experimental treatments. After seedlings from the germination experiment had been counted, sediment temperature, pH, oxygen concentration and conductivity were measured in the quadrats at 10 random positions.

2.4. *Chemical analyses*

Sediment used in the germination experiment and biomass from quadrat samples from 20 m intervals along the transect were analysed for chemical content. In the UK, 50 g sub-samples of the materials were oven dried at 60 °C for 36 h and ground through the 1 mm and then 0.25 mm screens of an electric hammer mill. Three sub-samples of approximately 1 mg each (±0.0005 mg) of the 0.25 mm fraction were analysed by gas chromatography for total nitrogen, carbon and sulphur contents to an accuracy of within 3% using a CHNO-S elemental analyser. Sub-samples of 1–2 g were analysed for phosphorus, potassium, calcium and magnesium by ICP-OES (inductively coupled plasma-optical emission spectroscopy) after digestion of samples in hydrochloric acid. Sediment was digested in mixed hydrochloric and nitric acids. Accuracy was within 5% for ICP analyses and machine precision was better than 2%. On one occasion in 1999, concentrations of sulphate and reduced iron and manganese in swamp water were measured colormetrically using a Hach DR 2010 spectrophotometer.

2.5. *Swamp physico-chemistry*

On every sampling visit, electrical conductivity (using a Hanna HI 8633 conductivity meter), water and air temperature were measured at intervals along the transect. For swamp water, measurements were made amongst papyrus culms at ca. 3 cm below the water surface. In 1999 only, dissolved oxygen concentration (using a Hanna HI 9143 m) and pH were recorded.

2.6. *Biological oxygen demand*

The biological oxygen demand (BOD) of sediment, swamp water and papyrus culms decomposing in swamp water was measured at 10 m intervals along the transect during July 1999.

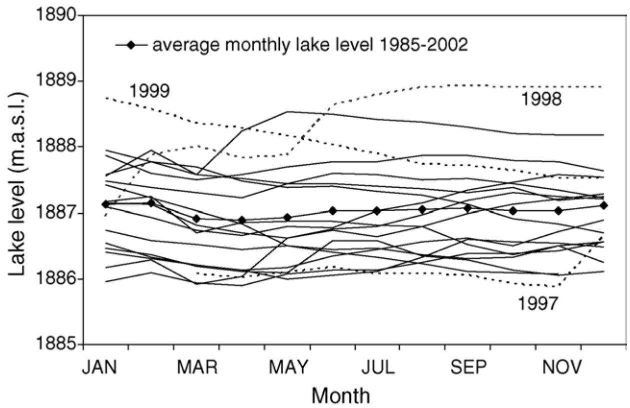

Fig. 1. Average monthly lake levels in Lake Naivasha for each year from 1985 to 2002 and the 18-year average. Dotted lines indicate levels over an El Niño period (1997–1999). Data are from the Lake Naivasha Riparian Association, P.O. Box 1011, Nairobi.

Fluid sediment was withdrawn from near or below rooting depth using 1 cm diameter tubing and a hand-suction pump. Swamp water, 10 ml samples of sediment or 10 cm^2 of papyrus was enclosed in five replicate 125 ml 'dark' gas-tight bottles. Bottles containing sediment or papyrus were filled with lake water and replaced in the swamp. Dissolved oxygen in initial lake and swamp water was fixed with Winkler reagents and after 4 h incubation, the oxygen in incubated bottles was fixed and the oxygen concentration in all bottles was analysed by titration against thiosulphate. After titration, culm material was removed from bottles, dried and weighed. The mean ± S.E. dry weight of 10 cm^2 portions of culms was 0.448 ± 0.008 g. Twenty replicate 10 ml samples of sediment were oven dried at ca. 45 °C for 24 h, weighed and the mean ± S.E. dry weight of 4.502 ± 0.028 g was used to convert oxygen uptake by sediment to mg $O_2\, l^{-1}\, g^{-1}$ sediment h^{-1}.

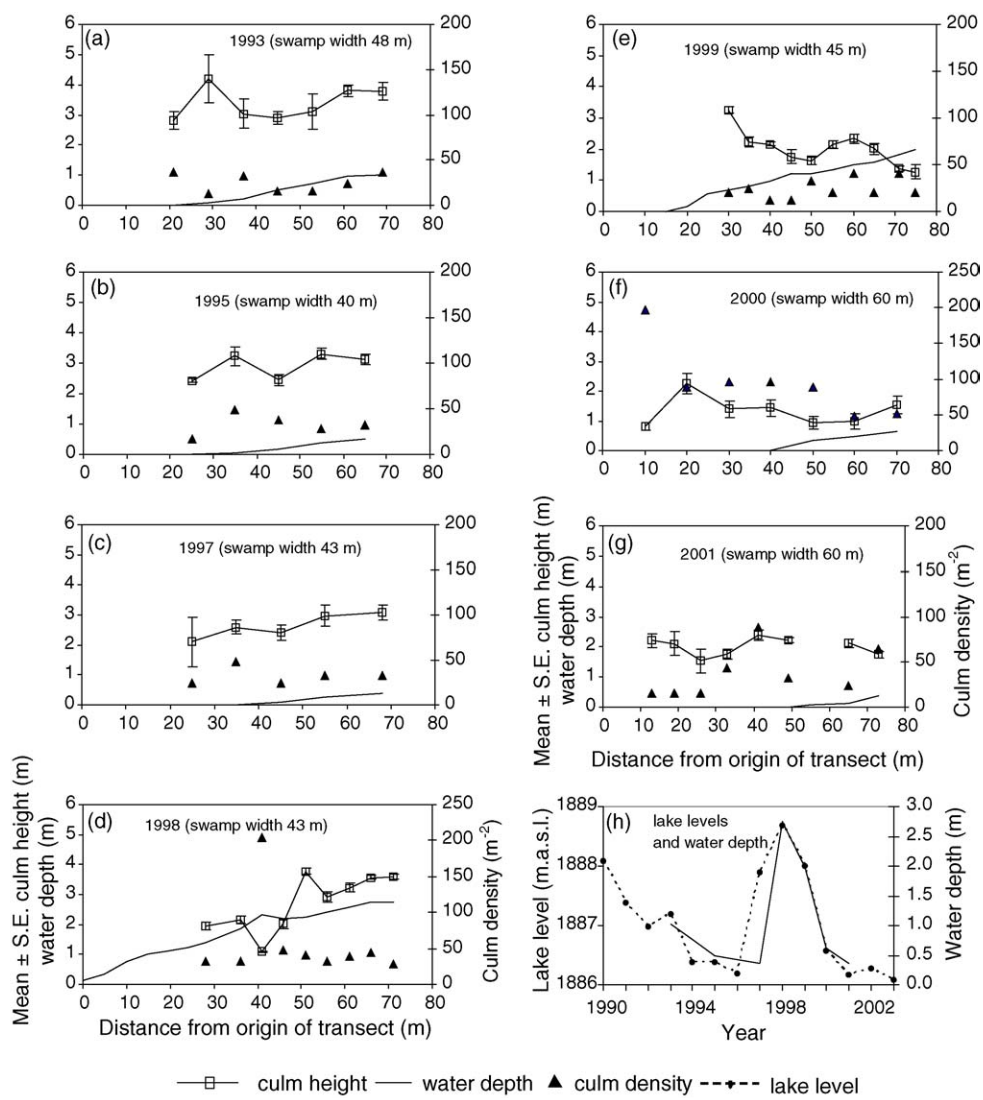

Fig. 2. (a)–(g) Height and density of papyrus (*Cyperus papyrus*) culms and water depths measured in July/August over the period 1993–2001 at intervals along a fixed land-water transect and (h) lake level and water depth at the lakeward edge of the transect.

3. Results

3.1. Water level and plant performance

There was little evidence of seasonal changes in lake level but changes between years were large (Fig. 1). The sampling period included an El Niño event when lake level changed by 3.06 m between November 1997 and September 1998. Water depth measured at the lake edge of the study swamp in July/August varied by 2.38 m between the sampling years (Fig. 2). In 1993 when the study began, the water line was 28 m from the transect datum. In the driest year (2001), the water line was 53 m away and in the wettest year (1998), the datum was submerged in a lagoon that had formed on the landward side of the swamp. At around 40 m, the papyrus fringe was narrowest in 1995 and 1997, which were dry years but within 2 years of the 1997/1998 El Niño flood, it had expanded to 60 m. Width of the study swamp varied with water depth 2 years earlier ($r^2 = 0.86$, $y = 38 + 9.8x$, $P < 0.02$). Direct correlations between swamp widths around the lake and water depth at the edge of the swamps (1993: $R = 0.86$, $P < 0.001$, $n = 13$; 1995: $R = 0.77$, $P < 0.01$, $n = 11$) showed that spatial relationships between water depth and swamp width occurred elsewhere in the lake.

Annual mean height of culms did not vary with water depth at the lakeward edge ($R = -0.12$) of the fixed transect although there were differences in culm height between years ($P < 0.001$). Mean ± S.E. culm height varied between 4.20 ± 0.22 m and 1.02 ± 0.25 m in all quadrats ($n = 51$) sampled in all years with a grand mean of 2.18 ± 0.29 m. Height increased towards open water in 1998, the wettest year ($R = 0.60$, $P < 0.02$) but decreased in 1999 ($R = -0.73$, $P < 0.02$) with the onset of drying. In general, short culms tended to be more frequent at the landward end of the transect. The percentages of standing dead culms in the swamp's landward and lakeward edges (46 ± 8% and 17 ± 5%) were always high compared with the mean proportion in the rest of the swamp (9 ± 1%). With the exception of 2000 ($R = -0.82$, $P < 0.05$), there was little evidence of change in culm density along the land-water gradient with density variations within the swamp greater than any differences in density between years.

In the year that biomass was measured, total biomass was the same irrespective of position on the transect although the biomass of primary roots decreased towards the lake ($R = 0.98$, $P < 0.05$), Table 1. Mean total biomass in the swamp was 6945 ± 859 g dry weight m^{-2}.

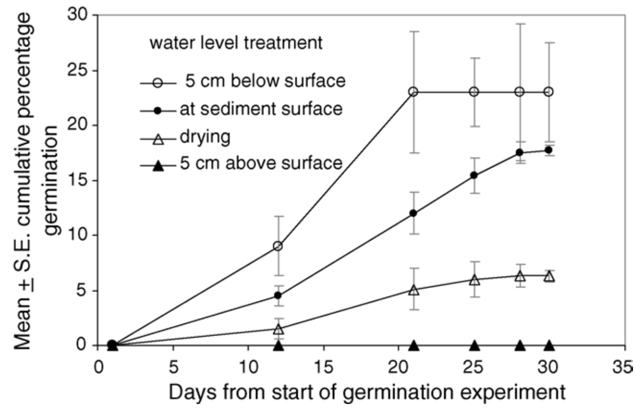

Fig. 3. Germination of papyrus (*Cyperus papyrus*) seeds over 30 days in outdoor pot experiments where water level was varied.

3.2. Germination experiment

Papyrus seeds germinated within 12 days, Fig. 3, but none germinated in standing water. The maximum germination rate of 45% (mean ± S.E., 23 ± 6%) occurred at 21 days where the water level was 5 cm below the surface but after 21 days, seedling mortality began to occur. Where water level was maintained at the surface, seeds continued to germinate and by day 30, all seedlings had survived and reached a density of 1022 ± 99 m^{-2}. In sediment allowed to desiccate, the few seedlings that had germinated died. On day 30, seedlings in surface-saturated sediment were 12.5 ± 1.2 mm tall (median = 6 mm) with heights similar to seedlings where water was 5 cm below the surface. Maximum heights in the two treatments were 57 and 89 mm and in the tallest seedlings, the first stage of rhizome development had begun. Densities of seedlings on the lakeshore varied between zero in standing water and desiccated sediment, 48 ± 17 m^{-2} in surface saturated sediment and 184 ± 34 m^{-2} in sediment saturated at ca. 5 cm below the surface. Densities in pots were up to six times higher than this.

Environmental conditions in the culture pots were similar to growing conditions at equivalent water depths on the lakeshore. Daytime air temperature varied between 15.6 and 32.2 °C and sediment temperature 15.2 and 27.4 °C with no difference between pots and the lakeshore. Similarly, sediment at 5 cm below the surface was anoxic in both lake sediment and in pots. Conductivities in pore water tended to be higher in basins (day 30: 587 ± 25 μS cm^{-1}) than in lake sediment (day 30: 242 ± 69 μS cm^{-1}, $P < 0.01$). Lakeshore sediment contained:

Table 1
Biomass, standing dead mass and root to shoot ratio of papyrus (*Cyperus papyrus*) measured in August 2000 at intervals along a fixed land-water transect

Distance	Umbels	Culms	Fine root	Root	Rhizome	Total biomass	Standing dead	R:S
Dry mass (g m^{-2})								
10 m	420	3000	300	520	2340	6580	180	1.61
30 m	980	3940	640	300	2140	8000	40	1.06
50 m	560	2320	400	240	1160	4680	700	1.03
70 m	620	2580	2020	100	3200	8520	1600	2.66

Table 2
Mean ± S.E. chemical contents of papyrus (*Cyperus papyrus*) during August 2000

	Carbon	Nitrogen	Phosphorus	Potassium	Sulphur	Calcium	Magnesium
Concentration (% dry weight)							
Seeds	45.1	2.19	0.34	1.42	0.23	0.38	0.17
Umbels	41.5 ± 2	1.15 ± 0.27^{12345}	0.13 ± 0.12	1.01 ± 0.54^{1}	0.11 ± 0.03^{1}	0.44 ± 0.12^{12345}	0.11 ± 0.04
Culms	41.7 ± 0.4	0.47 ± 0.14^{1}	0.06 ± 0.05	1.93 ± 0.20^{12}	0.05 ± 0.03^{123}	0.32 ± 0.05^{4}	0.08 ± 0.02^{12}
Fine root	39.3 ± 1	0.79 ± 0.04^{2}	0.06 ± 0.01	0.24 ± 0.04^{23}	0.12 ± 0.03^{2}	0.98 ± 0.07^{146}	0.18 ± 0.04^{13}
Root	41.5 ± 3	0.61 ± 0.31^{13}	0.05 ± 0.03	0.74 ± 0.45	0.10 ± 0.06	0.82 ± 0.12^{247}	0.18 ± 0.09^{24}
Rhizome	41.8 ± 3	0.71 ± 0.21^{4}	0.10 ± 0.06	1.67 ± 0.60^{3}	0.16 ± 0.06^{3}	0.22 ± 0.06^{3567}	0.10 ± 0.02^{34}
Dead culms	52.3 ± 16	0.55 ± 0.29^{5}	0.05 ± 0.05	1.55 ± 1.46	0.08 ± 0.02	0.49 ± 0.41	0.11 ± 0.04

Seeds were present in one sample only. Plant parts sharing the same number have different ($P < 0.05$) concentrations (Tukey's test).

4.6% carbon; 0.44% nitrogen; 0.04% phosphorus; 0.62% potassium; 0.65% calcium; 0.36% magnesium and 0.01% sulphur giving C:N:P and N:P:S ratios by weight of 107:10:1 and 44:4:1.

3.3. Plant chemistry

The elemental content of papyrus sampled from the fixed transect did not vary with its position on the water depth gradient so Table 2 gives mean values for all quadrats together. Nutrients appeared to be concentrated in seeds, sulphur was least concentrated in culms and calcium and magnesium were generally concentrated in roots ($P \leq 0.05$). Mean ± S.E. nitrogen content was low at $0.47 \pm 0.14\%$ in culms and $0.71 \pm 0.21\%$ in rhizomes. Phosphorus content was generally very low with the highest concentration of $0.10 \pm 0.06\%$ in rhizomes where potassium ($1.67 \pm 0.60\%$) was also concentrated. In relation to other tissues, fine roots contained high proportions of nitrogen and sulphur. Ratios of nitrogen and phosphorus to sulphur were 9:1:1 in culms, 7:0.5:1 in adventitious roots, 6:0.5:1 in primary roots and 6:0.5:1 in rhizomes. The C:N in living culms was 89:1 and 94:1 in standing dead culms. The N:P:S ratio in dead culms was 1:0.6:1.

Large amounts of carbon were stored in papyrus biomass, Table 3. Rhizomes contained the major part of the standing stock of nitrogen, phosphorus and sulphur whereas culms contained the major share of potassium, calcium and magnesium. The ratios of total C:N:P in papyrus mass were 565:8:1, of N:P:S were 8:1:1 and the carbon to nitrogen ratio was 67:1.

3.4. Environmental measures

The conductivity of swamp water did not vary along the land-water transect in any of the sampling years although there were differences between years in the range of conductivities measured. During 1998, swamp water appeared to be diluted to a concentration similar to lake water ($192 \pm 0.88\ \mu S\ cm^{-1}$); the conductivity of water in the lagoon that formed behind the swamp was $201 \pm 0.5\ \mu S\ cm^{-1}$. Swamp water was less concentrated than lake water ($P < 0.02$) in the drier years of 1995 and 1997. Pair wise comparison for all years showed that overall there was no difference ($P = 0.15$) between conduc- tivity within the swamp ($278 \pm 22\ \mu S\ cm^{-1}$, 1993–2001) and in the middle of the lake ($298 \pm 31\ \mu S\ cm^{-1}$, 1993–2001). There was, however, a small pH gradient through the swamp. The pH of swamp water in the most landward papyrus was 8.10, which increased ($R = -0.87$, $P < 0.01, n = 8$) to 8.32 in papyrus at the edge of the open lake. At the time, the pH of water in the open lake was 8.37. Mean oxygen concentration in swamp water was $6.6 \pm 0.2\ mg\ l^{-1}$ ($89 \pm 3\%$ saturation) and there was a gradient through the swamp with the shallow water at the landward edge ($R = 0.89$, $P < 0.01$) containing about $1\ mg\ l^{-1}$ less dissolved oxygen. The oxygen concentration in surface lake water about 10 m lakeward of the swamp was $7.6 \pm 0.4\ mg\ l^{-1}$ ($86 \pm 4\%$ saturation) with a mean temperature of $21.7 \pm 0.64\ ^{\circ}C$. Although on average swamp water contained less oxygen than lake water ($P < 0.001$), there was no difference in the percent saturations. Sulphate was detectable at $1\ mg\ SO_4\ S\ l^{-1}$ at only two of the nine sampling points and the concentrations of total iron and of manganese in water were 0.11 and $0.08\ mg\ l^{-1}$ at the landward end of the transect and 0.05 and $0.06\ mg\ l^{-1}$ nearest to the lake.

Table 3
Mean ± S.E. standing stocks of carbon, nutrients and minerals in papyrus (*Cyperus papyrus*) sampled during August 2000

	Carbon	Nitrogen	Phosphorus	Potassium	Sulphur	Calcium	Magnesium
Standing mass ($g\ m^{-2}$)							
Umbels	271 ± 71	7.4 ± 2	0.81 ± 0.21	6.5 ± 1.7	0.73 ± 0.19	2.8 ±0.7	0.68 ± 0.18
Culms	1233 ± 210	13.9 ± 2.4	1.8 ± 0.3	57 ± 10	1.6 ± 0.3	9.5 ±1.6	2.3 ± 0.4
Fine root	326 ± 220	6.6 ± 4.5	0.48 ± 0.32	2.02 ± 1.36	1.0 ± 0.7	8.2 ±5.6	1.5 ± 1.0
Root	123 ± 52	1.3 ± 0.6	0.10 ± 0.04	0.46 ± 0.20	0.22 ± 0.10	1.5 ± 0.7	0.31 ± 0.13
Rhizome	941 ± 253	15.7 ± 4.2	2.2 ± 0.6	37 ± 10	3.6 ± 1.0	4.9 ± 1.3	2.2 ± 0.6
Dead culms	329 ± 262	3.5 ± 2.8	0.29 ± 0.23	9.8 ± 7.8	0.48 ± 0.38	3.1 ± 2.5	0.69 ± 0.55
Total	3223 ± 617	48 ± 10	5.7 ± 1.2	113 ± 18	7.6 ± 1.8	30 ± 8	7.6 ± 1.8

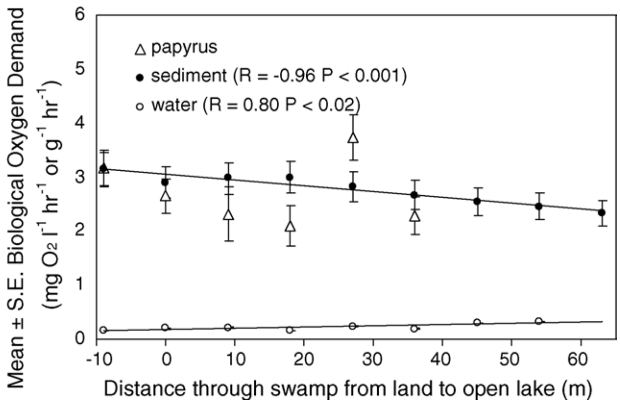

Fig. 4. Biological oxygen demand of interstitial water, underlying sediment and decomposing papyrus (*Cyperus papyrus*) measured during August 1999.

Concentrations of iron decreased toward the lake ($P < 0.05$) but the absolute change was small.

3.5. Biological oxygen demand

The oxygen demand of swamp water was measured in 1999, a wet year when landward papyrus was flooded by 0.7 m water. The BOD of swamp water increased from 0.17 ± 0.004 mg $O_2\,l^{-1}\,h^{-1}$ at the landward edge of the swamp to 0.33 ± 0.08 mg $O_2\,l^{-1}\,h^{-1}$ ($R = 0.80$, $P < 0.02$) in papyrus at the edge of open water (Fig. 4). The BOD of sediment and decomposing culms was much higher than water and decomposing culms set up a maximum of 3.74 ± 0.93 mg $O_2\,g^{-1}\,h^{-1}$. The BOD of dead culms did not change with their position along the land-water transect. There was a decrease in sediment BOD ($R = -0.96$, $P < 0.001$) from land to open water with values changing from 3.14 ± 0.70 mg $O_2\,l^{-1}\,h^{-1}$ to 2.34 ± 0.52 mg O_2 g sediment^{-1} h^{-1}.

4. Discussion

Spreading and recession of papyrus swamp coincided with changes in lake level. Changes in lake level did not follow the seasonal pattern described by Vincent et al. (1979) but were instead dominated by between-year variation and sequences of extreme flooding or drying (Becht and Harper, 2002) that corresponded with El Niño–La Niña cycles (Viles and Goudie, 2003). Over the 2 years after the 1997/1998 flood, the littoral papyrus margin extended into open water by around 40% of its former width. Extension was by rhizome spreading from the floating mat; no seedlings were recorded on any sampling occasion. Germination experiments suggested that sudden rises in lake level associated with El Niño flooding and the extreme drying of La Niña offer poor opportunities for papyrus regeneration by seedlings. Seeds germinated and survived best in pot experiments when sediment was saturated or water level was just below the surface, poorly in sediment that was drying and seeds did not germinate at all when sediment was flooded. Results were consistent with the origination of the study swamp since its papyrus dated from one large germination event in June 1988 (Root, personal communication) when lake levels were rising gradually after the extremely low levels of 1987. Observations from both the field and the germination trials suggest that papyrus seeds germinate quickly in rewetted sediment but that new swamps will form only on shallow gradient shores or when water level is rising slowly enough for seedling growth to keep pace with water level. Episodic germination events suggest that papyrus has a persistent seed bank adapted to take rapid advantage of gaps created unpredictably by El Niño-scale fluctuations in lake level. Transient seed banks are better adapted to predictable fluctuations that are usually seasonal (Thompson and Grime, 1979). Around 20% of the papyrus seeds sown at the most favourable water levels germinated which is high for wetland plants (Grime et al., 1981; Van der Valk and Rosburg, 1997). The exacting water level requirement for germination may explain why newly germinated papyrus forms reefs that lie parallel to the shore (Gaudet, 1977). In contrast to regeneration by seed, sudden rises in lake level coincided with rhizome spreading from the lakeward edge of floating mats but widespread mortality also occurs where swamps are rooted in bottom sediment for all of their width or portions of broken mat submerge. Results suggest that the dynamic relationship between papyrus cover and water depth will allow the periodic expansion of floating swamp, but only where floating rhizome mats remain intact and can act as focal areas for growth.

Papyrus in Lake Naivasha invests about half of its biomass in roots and rhizomes (Boar et al., 1999). The landward edge of the study swamp was rooted to a depth of about 1 m below the sediment surface and its deep roots would have given considerable resilience to desiccation over periods of low lake level, but only on a shallow gradient shoreline. Growing on a slope of 0.54%, landward papyrus rooted to a depth of 1 m would be robust to a 185 m recession in the wetted shoreline. This is larger than the 120 m recession that occurred at the study site between 1993 and in April 2003 (after the end of the study) when the wetted shoreline had receded a further 46 m from its 2001 position. A trade-off exists: papyrus on shorelines with shallow slopes may well be more resilient to drying but it is also more exposed to wild herbivores and to grazing livestock. At times of draw down, grazers may damage or remove all above ground biomass but regenerative capacity remains intact via the seed bank and the rhizome stock. Papyrus does not, however, regenerate after its reclamation in favour of horticulture or cultivation, which together explain the progressive loss (irrespective of water level) in the area of papyrus around the lake (Boar et al., 1999; Hickley et al., 2004). The ways that temperate swamp responds to water depth are, in some respects, similar to papyrus. Depending on the bathymetry of the stand, *Phragmites* area also decreases with increasing duration of low water levels (Bodensteiner and Gabriel, 2003) but the reasons for loss are more likely to involve exposure to low winter temperatures than exposure to herbivores.

The biomass, size and density of culms were measured in 2000 when half of land-water transect was flooded. At around 7000 ± 850 g m^{-2}, total biomass was broadly similar to the range reported by other authors (Muthuri et al., 1989; Jones and Muthuri, 1997; Kipkemboi et al., 2002). There were, however, no consistent relationships between water depth and papyrus biomass, size, or density along the land-water transect and no annual variations (1993–2001) in the average size or density of culms in relation to lake level at the time of sampling. The conclusion from this is that although water depth appears to influence areal cover by papyrus swamp, changes in water depth along land-water gradients do not necessarily influence its performance within swamps.

There were no land-water gradients in the chemical contents of papyrus. Keddy (2000) has observed that fertility gradients in wetlands tend to be large-scale, spanning eroding and depositional environments. Such gradients may be in the order of several hundred metres. On smaller scales, perhaps in the order of tens of metres or within a single type of vegetation, plant content and environmental concentrations tend not to correspond well. Nutrient and mineral contents were, with the exception of calcium and magnesium, similar to papyrus in Lake Victoria (Lind and Visser, 1962), probably higher than averages found in the Sudd (Gaudet, 1979a) and slightly lower than measured in the deeper water of the western part of Lake Naivasha (Muthuri and Jones, 1997). With the exception of seeds, papyrus biomass was nutrient deficient in relation to plant averages (Ellis and Mellor, 1995) and despite nitrogen fixation in the root zone (Mwara and Widdowson, 1992), nitrogen concentration in papyrus was less than in temperate wetland plants (Güsewell and Koerselman, 2002). Phosphorus concentrations were very low given the eutrophic status of the lake (Kitaka et al., 2002). With an overall C:N:P ratio of 565:8:1, papyrus appeared to be very nutrient efficient (*sensu* Grubb, 1989). Papyrus nonetheless assimilates a large absolute mass of nutrients, minerals and carbon, which enters pathways of decomposition with a proportion of the dissolved or particulate products entering the open lake system.

An overall pattern of seasonal flow-through of water, solutes and particulate material is typical of African swamps (Carter, 1955; Howard-Williams and Howard-Williams, 1977) including the vast papyrus swamps of the Sudd where ions in swamp water are diluted on passage of river water in wet periods and accumulate in the swamp during dry periods (Mefit-Babtie, 1983). Gaudet (1979b) described flows of material into lake water through a former 4000 m wide papyrus swamp in the north of Lake Naivasha. He found strong seasonal land-water gradients in dissolved oxygen, conductivity and some nutrients. During wet seasons, bottom water was flushed out of the swamp carrying a plume of swamp detritus, chemically reduced nutrients and mineral ions into the open lake. Gradients in swamp chemistry then re-established. The narrow study swamp differed from wider swamps in that exchanges between swamp and lake water through inflow, wind mixing or baroclinic circulation (Mnaya and Wolanski, 2002) were most probably continuous in years with average or near average water levels and certainly continuous during El Niño periods. Some chemical gradients from land to open water existed but were small even though sampling was carried out at a time of year when gradients in wide swamps would be strong. Vertical gradients in pH, conductivity and temperature were unlikely given exchanges with lake water and were not found by Azza et al. (2000). Conductivities of swamp and lake water were similar and despite land-water gradients in BOD, decomposition processes in the study swamp were aerobic. Both of these observations are consistent with continuous rather than seasonal mixing with lake water. This implies that in narrow fringes of papyrus, organic matter is not retained for long enough for completion of the redox-sensitive nutrient transformations that contribute to nutrient buffering (Naiman and Décamps, 1990). If a case for papyrus conservation were to rest upon only its role as a nutrient buffer, or as a barrier to soil particles (Boar and Harper, 2002), then swamps need to be much wider than the minimum of 50 m that has been set in the management plan for the lake (LNRA, 1999).

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