Hydrobiologia **488:** 107–113, 2002.
D.M. Harper, R. Boar, M. Everard & P. Hickley (eds), Lake Naivasha, Kenya.

Impacts of the C_4 sedge *Cyperus papyrus* L. on carbon and water fluxes in an African wetland

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Key words: Africa, *Cyperus papyrus* L., carbon balance, C_4 photosynthesis, evapotranspiration, wetlands

Abstract

Fluxes of CO_2 and H_2O vapour were measured by eddy covariance from a stand of the C_4 emergent sedge *Cyperus papyrus* (papyrus), which formed a fringing swamp on the north-west shore of Lake Naivasha, Kenya. The fluxes of CO_2 and H_2O vapour between the papyrus swamp and the atmosphere were large but variable, depending on the hydrology of the wetland system and the condition of the vegetation. These measurements, combined with simulation modelling of annual fluxes of CO_2, show that papyrus swamps have the potential to sequester large amounts of the carbon ($\sim$1.6 kg C m^{-2} y^{-1}) when detritus accumulates under water in anaerobic conditions, but they are a net source of carbon release to the atmosphere ($\sim$1.0 kg C m^{-2} y^{-1}) when water levels fall to expose detritus and rhizomes to aerobic conditions. Evapotranspiration from papyrus swamps (E) was frequently lower than evaporation from open water surfaces (E_o) and plant factors have a strong influence on the flux of water to the atmosphere. For the period of measurement E/E_o was 0.36.

Introduction

Papyrus (*Cyperus papyrus* L.) forms the dominant emergent vegetation in most permanently flooded wetlands of tropical Africa (Hughes & Hughes, 1992). There are no accurate records of the area covered by papyrus-dominated swamps but one estimate puts it at about 4000 km^2, most of which is in central and east Africa (Thompson & Hamilton, 1983). Papyrus is remarkable because it is one of the largest herbaceous species, with culms growing to a height of 5 m and above-ground standing phytomass which often exceeds of 12.0 t C ha^{-1} (Jones & Muthuri, 1985). The culms are topped by characteristically large, spherically shaped, reproductive umbels that are also the main photosynthetic surface. The umbel is typically about 50 cm in diameter and consists of several hundred cylindrical rays, each of which extends into three to five flattened (leaf-like) bracteoles.

Papyrus, like other productive tropical emergent wetland species such as *Echinochloa polystachya* and *Paspalum repens*, uses the C_4 photosynthetic pathway (Jones, 1987b). The wetland environment appears an unlikely habitat for C_4 species, which are generally assumed to be adapted best to hot and dry locations (Doliner & Joliffe, 1979). However, the high efficiencies of use of radiation, water and nitrogen by C_4 species is hypothesised to have an important impact on the functioning of wetlands dominated by C_4 species such as papyrus (Knapp & Medina, 1999). Two functions of ecosystems which are influenced strongly by the presence of C_4 characteristics are the CO_2 balance between carbon gains in photosynthesis and losses in respiration, and H_2O vapour losses in evapotranspiration.

Living papyrus vegetation often overlies several metres depth of detritus or peat (Jones & Muthuri, 1997). This peat forms in the oxygen depleted environment below established floating rhizome mats as detritus accumulates from the dead and decomposing papyrus vegetation. Few estimates have been made of the amount of peat below papyrus but it is likely that African swamps could form a significant sink for carbon when continuously inundated and carbon gains in photosynthesis exceed carbon losses in respiration (Jones & Muthuri, 1997). Conversely, when the detritus is exposed to the atmosphere, and aerobic conditions, by a hydrological draw-down or drainage then these systems may become a net carbon source for the atmosphere as carbon losses exceed carbon gains.

It is clear that evapotranspiration by emergent vegetation can have a significant impact on the hydrology of wetlands and associated water bodies. However, the question as to whether the presence of aquatic vegetation leads to an increase or decrease in evaporative losses from water bodies has been a topic of debate for many decades, and there still appears to be no clear answer (Idso & Anderson, 1988). Anderson & Idso (1987) conclude that a major factor influencing the rate of evapotranspiration is the height of the vegetation, so that extensive canopies of tall emergent macrophytes such as the grass *Typha latifolia* do tend to increase evaporative loss of water from large water bodies, whereas extensive canopies of short emergent vegetation such as the floating macrophyte *Eichhornia crassipes* tend to reduce evaporative losses from such surfaces. However, these conclusions do not take account of any physiological differences between vegetation types, in that C_4 species have higher water use efficiencies than the C_3 species considered above (Long, 1999). It might be anticipated therefore that evaporative water loss from canopies of C_4 vegetation, like papyrus, would be lower than that from C_3 vegetation of a similar stature. The only previously reported measurements of evapotranspiration from papyrus were made by Rijks (1969), who found that an old stand of papyrus in Uganda lost, on average, 40% less water to the atmosphere than did the open lake.

The aim of the present study was to quantify the effect of papyrus vegetation on two important ecosystem functions viz. carbon balance and evaporation. These processes were measured using the Eddy Covariance (EC) technique and the data were used in conjunction with a 'bottom-up' model of canopy gas exchange which could predict annual cycles of carbon dioxide and water vapour exchange. The measurements enabled us to calculate the strength of papyrus swamps as net sinks for carbon when inundated with water and net sources for carbon when experiencing a draw-down of water levels. The evaporation measurements aimed to provide an answer to the question "does the presence of emergent aquatic vegetation tend to increase or decrease evaporative water losses from water bodies?" (Idso & Anderson, 1988).

Materials and methods

Site description

The experimental work was carried out on a lake-fringing papyrus swamp on the N-W shore of Lake Naivasha, Kenya (0° 45′ S, 36° 20′ E) at an altitude of 1890 m in the Eastern Rift Valley of Africa. The flora and ecology of the lake edge have been described by Gaudet (1977). The papyrus mat at the study site extended 500 m into the lake where it was floating, but it was grounded at the lake margin. During the period of measurements (1995–96), the lake was going through one of its natural draw-downs (Gaudet, 1977; Becht & Harper, 2002). The effect of this was to expose an increasing amount of the rhizome mat and associated detritus to the atmosphere, although the root systems remained continuously waterlogged.

Climate

The equatorial climate at Lake Naivasha is marked by two rainy season peaks in April//May and November, although irregularities from this pattern are common, since rainfall is quite erratic. The average annual rainfall is 620 mm. Ten year, monthly mean records of maximum, mean and minimum temperatures and solar radiation were obtained from a weather station located 5 km from the study site. These have been reported by Muthuri (1985) and Muthuri et al. (1989). Shorter term meteorological measurements were made using an automated weather station (AWS), and data logger (Campbell Scientific Ltd., Leicestershire, U.K.). The weather station was situated on an open site about 50 m from the landward edge of the papyrus and approximately 600 m from the location of the Eddy Convariance (EC) tower. The data average recording interval was set to 15 minutes to coincide with the EC measurements.

Evaporation rates from the lake open water and evapotranspiration from the papyrus canopy were calculated using the Penman formula (Penman, 1948). Meteorological data, collected by the AWS, were used to calculate 15 min averages throughout the day.

CO_2 and H_2O ecosystem measurements

Ecosystem fluxes of CO_2 and H_2O were measured using the EC technique (Moncrieff et al., 1997a, b). The observations were taken over a 4 week period in August 1995 and a 1 week period in March 1996. These periods corresponded with, respectively, the coolest (mean monthly temperature of 15.0 °C) and warmest (mean monthly temperature of 17.9 °C) times of the year. The main components of the EC system were a three-axis symmetrical sonic anemometer (Solent A1012r, Gill Instruments, Lymington, U.K.), an infrared gas analyzer (IRGA) (Li-6262, Li-COR, Lincoln, Nebraska, U.S.A.) in closed path mode and custom written software (Eddy Sol, University of Edinburgh, U.K.) which calculated the fluxes in real time. A full description of the equipment and Eddy Sol software is given by Grace et al. (1995) and Moncrieff et al. (1997a, b).

EC measurements were made by sampling from a mast at a height of 7 m above ground level with air samples drawn down at 6 l min^{-1} down to the IRGA. The adjustable mast was located on a concrete base at a distance of 150 m from the landward edge of the papyrus swamp. The sampling point was 2–3 m above the tallest papyrus culms and gave a flux footprint in which 95% of the footprint area was contained within the region of homogenous papyrus canopy (Schuepp et al., 1990). Averaged fluxes were recorded at 15 min intervals. Span calibration of the CO_2 and H_2O channels of the IRGA was performed at a maximum of 3 day intervals using chemical absorption columns for zero values and a compressed gas source of CO_2 at 600 ± 10 μmol mol^{-1} (Linde Gas, U.K.) and a portable dewpoint generator (Li-610, Li-COR) for span values.

Respiration measurements

Tissue respiration of papyrus was estimated from measurements of respiration rates of material from each of the culm age classes which included juvenile, mature, senescent and standing dead (Muthuri & Jones, 1997). Respiration rates were determined by modifying a 100 mm diameter soil respiration chamber (SRC-1, PP Systems, Hertfordshire, U.K.), used in conjunction with an IRGA (CIRAS, PP Systems), by fixing an air-tight plate to the base of the chamber. This allowed the insertion and sealing of cut culm sections into the chamber and determination of respiration rate by monitoring the rate of increase of CO_2 within the chamber (Parkinson, 1981). Respiration on a dry matter basis was calculated after oven-drying the samples to constant weight.

The respiration rate of papyrus detritus was determined on a ground area basis using the PP Systems soil respiration chamber. Dry and dead papyrus umbels and culms were first cleared from the sampling area and the chamber was pushed firmly down approximately 10 mm into the detritus so that the stainless steel perimeter ring was partially embedded to ensure an airtight seal. Measurements were made at 20 locations around the study site and they were repeated three times at each location. Detritus temperature, measured with a mercury in glass thermometer, was 18 °C at the time of the respiration measurements which were made in the middle to late afternoon. It should be noted that because the detritus contained living root and rhizome material, the measurements made using the chamber included respiration from both detritus and root/rhizome fractions.

Simulation modelling

WIMOVAC (Windows Intuitive Model of Vegetation response to Atmosphere and Climate) is a process-based model of leaf physiology and canopy structure (Humphries & Long, 1995), details of which can be found at the internet site http://www.life.uiuc.edu/plantbio/wimovac/model.htm. This 'bottom-up' model has been modified and parameterised to predict the CO_2 and H_2O exchange of the papyrus canopy (Humphries et al., submitted). This has been done by incorporating the C_4 characteristics of papyrus bracteole photosynthesis and modelling radiation distribution in the papyrus canopy. The model was run to simulate annual cycles of CO_2 exchange under (i) the prevailing climatic conditions during the EC measurements, when the swamp was experiencing a slow draw-down in lake level of about 2 m over about 7 years, which would expose rhizomes and detritus to the atmosphere, and (ii) conditions when the rhizomes and detritus were inundated with water.

Results

Carbon dioxide flux

Eddy Covariance data for 21 days during the periods 4–21 August 1995 and 11–17 March 1996, when continuous EC and meteorological data were collected at 15 min intervals throughout the whole diurnal cycle, were used in the following analysis. The averaged diurnal flux for the whole 21 days is shown in Figure 1(i). Shown also are flux measurements predicted using the WIMOVAC 'bottom-up' model parameterised for papyrus (Humphries et al., submitted). Model CO_2 flux predictions show a close conformity

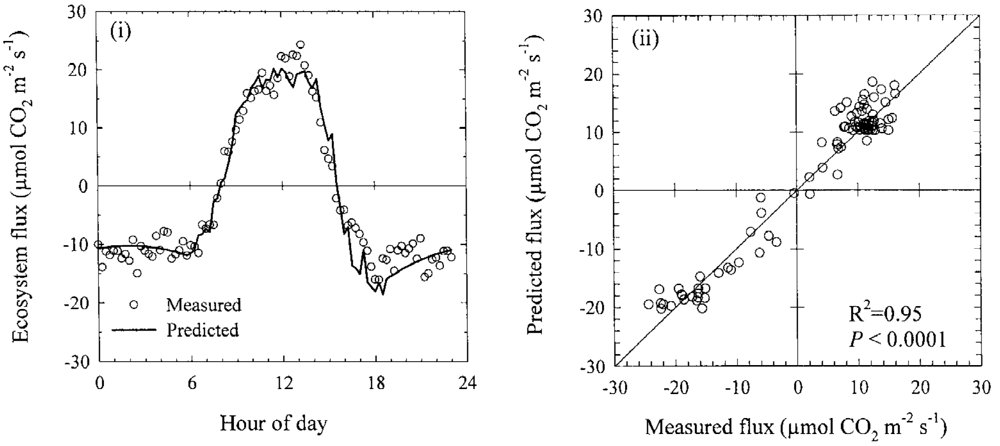


Figure 1. (i) Averaged diurnal cycle of ecosystem CO_2 fluxes from 21 days of Eddy Covariance measurements and predicted (modelled) ecosystem CO_2 fluxes for a stand of papyrus vegetation at Lake Naivasha and (ii) relationship between measured and predicted flux values ($r^2 = 0.95$ $p < 0.0001$). The continuous line shows a 1:1 relationship.

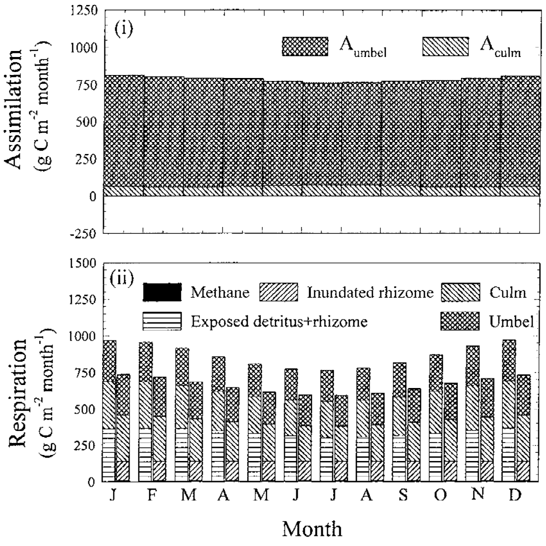


Figure 2. (i) Monthly values of umbel gross assimilation (A_{umbel}) and culm gross assimilation (A_{culm}) for a stand of papyrus vegetation at Lake Naivasha and (ii) monthly total culm, umbel and detritus respiration under conditions of hydrological draw-down exposing detritus to the air (left bar) and water inundation (right bar). Methane emissions under water inundation are also shown.

with measured values (R^2 = 0.95), correctly predicting both the magnitude and dynamics of the CO_2 flux (Fig. 1(ii)). Maximum CO_2 gain (24.3 μmol m^{-2} s^{-1}) occurred at approximately 13.00 h and was associated with the highest light intensity and slightly below maximum air temperature. Maximum CO_2 loss (-16 μmol m^{-2} s^{-1}) occurred at 18.00 h and was associated with the low light intensity and high temperatures occurring shortly before sunset (Figure 1(i)).

Table 1. Papyrus ecosystem dry matter distribution and respiration rates

Papyrus ecosystem component	Dry matter (g C m^{-2})	Specific respiration (mg C g^{-1} h^{-1})	Ground area based respiration (g C m^{-2} h^{-1})
Culm	720	0.59	0.424 ± 0.04
Umbel	323	1.28	0.412 ± n.a.
Rhizome & root	1480	0.10	0.146 ± 0.01
Detritus	64000	n.a.	0.233 ± 0.02

Using monthly mean meteorological data, the WIMOVAC model of canopy photosynthesis was used to predict monthly gross carbon gain in photosynthetic assimilation (A) (Fig. 2(i)). Carbon loss in respiration was derived from measurements of specific respiration of culms, umbels and rhizomes combined with detritus respiration measurements calculated on a ground area basis (Table 1). Specific respiration rates were scaled to canopy values and expressed on a ground area basis from a knowledge of dry matter distribution in the canopy (Muthuri et al., 1989). Monthly values of carbon loss in respiration from culms, umbels and detritus and methanogenesis from detritus (see Jones & Muthuri, 1997) are shown in Figure 2(ii). This was done assuming contrasting conditions of inundation of the rhizomes and detritus by water. The first was when the rhizomes and detritus were partly exposed to the atmosphere, as in the case of the field measurements reported here, when there was a net ecosystem loss of carbon. The second was when the rhizomes and detritus are assumed to be inundated with water. Under these conditions, which rapidly become anaerobic, detritus respiration is strongly inhibited and there is a net ecosystem gain of carbon.

Water vapour fluxes

Eddy Covariance measurements of water vapour flux from the papyrus swamp indicate little loss of water through evaporation at night. During the day, evapotranspiration rose to a peak of about 5.8 mmol H_2O m^{-2} s^{-1} during the early afternoon (Fig. 3). Modelled estimates of canopy evapotranspiration using the Penman equation including stomatal and boundary layer resistance terms gave a close agreement with the measured values, although they tended to underestimate measured values in the morning and overestimate measured values around midday (Fig. 3). The pattern of evaporation from the open lake, calculated using the Penman Equation, showed a similar pattern to the papyrus canopy evapotranspiration (Fig. 3) although there was evaporation of about 2 mmol H_2O m^{-2} s^{-1} throughout the night and evaporation in the middle of the day and into the afternoon exceeded canopy evapotranspiration by as much as 4 mmol H_2O m^{-2} s^{-1}. The averaged total daily flux of papyrus canopy evapotranspiration (E) was 2.4 kg H_2O m^{-2} dy^{-1} while open water evaporation (E_o) was 6.6 kg H_2O m^{-2} d^{-1} so that the ratio of transpiration to evaporation (E/E_o) was 0.36.

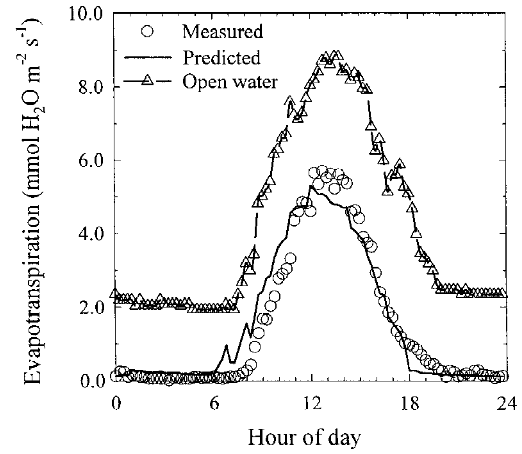
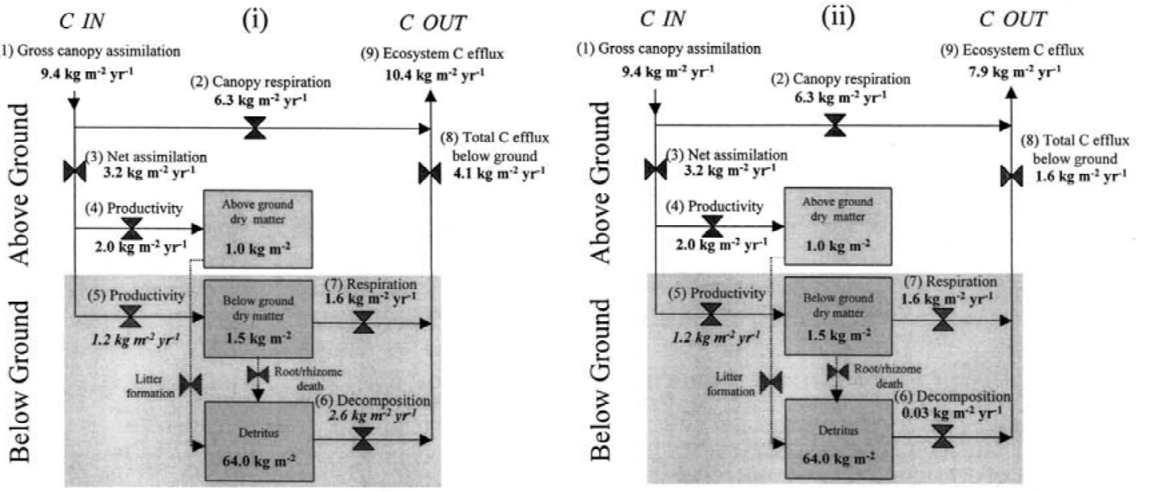


Figure 3. Averaged diurnal cycle from 21 days of Eddy Covariance measurements (circles) and predicted (modelled) values (continuous line) of evapotranspiration for a stand of papyrus vegetation at Lake Naivasha, and open water Penman evaporation (triangles).

Discussion

Emergent macrophytes in swamps, marshes and floodplains form some of the most productive plant communities (Jones, 1987a). We have previously shown, from measurements of plant biomass dynamics, that papyrus on Lake Naivasha has an above-ground net primary production (NPP) of 2.51 kg C m^{-2} yr^{-1} (Muthuri et al., 1989) and Piedade et al. (1991) found that the grass *Echinochloa polystacha*, in the central Amazon region, has a productivity of 3.97 kg C m^{-2} yr^{-1}. It is probably no coincidence that both these species have C_4 photosynthesis as their NPPs are amongst the highest ever recorded for natural communities. These observations suggest that under conditions where water and nutrients are non-limiting, communities of C_4 species have the potential to fix some of the largest amounts of carbon on a ground area basis. Unlike *E. polystacha*, papyrus does not show a marked seasonal pattern of growth, and in fact the standing biomass is remarkably stable at approximately 1.5 kg C m^{-2}, but it has a high annual aerial turnover rate of ~1.7 (NPP divided by standing biomass). The fluxes of carbon in the papyrus swamp at Naivasha, calculated on the basis of the EC measurements and model simulations, are shown in Figure 4. The fluxes are presented for two conditions. In the first case, they show carbon fluxes when the detritus in the swamp is exposed at a time of draw-down (Fig. 4(i)). This was the state of the swamp during the measurements reported here. In the second case, the rhizome and root system is inundated with water (Fig. 4(ii)). Under these circumstances, an oxygen-depleted environment develops rapidly in the water and rates of CO_2 release from detritus decomposition are very low. Measurements of gaseous release by ebullition show that total C release (CO_2 and CH_4) is 0.062 kg C m^{-2} y^{-1} (Jones & Muthuri, 1997) whereas the exposed detritus flux under aerobic conditions is 4.12 kg C m^{-2} y^{-1}. Papyrus wetlands therefore have the potential to be carbon sources or carbon sinks, depending on the hydrological status of the wetlands. The potential strength of the papyrus wetlands carbon sink in Africa is particularly important in relation to the identification and quantification of carbon sinks in the tropics (Schimel, 1995).

The question of whether the presence of emergent aquatic vegetation tends to increase or decrease evap-



Exposed: Net C loss of 1.0 kg m^{-2} y^{-1}

Inundated: Net C gain of 1.5 kg m^{-2} y^{-1}

Figure 4. Pools and fluxes of carbon for a papyrus ecosystem (i) when detritus and rhizomes are exposed to the atmosphere under conditions of a hydrological draw-down and (ii) when detritus and rhizomes are inundated by water. Rectangles represent quantities, valve symbols represent flows. Values are expressed in terms of carbon mass on a ground area basis. *Notes*: (1) Gross canopy assimilation predicted by the WIMOVAC model. (2) Canopy respiration predicted by scaling measured values. (3) Net assimilation is predicted from gross assimilation minus canopy respiration. (4) Measured above ground productivity is from Muthuri et al. (1989). (5) Below ground productivity is net assimilation minus above ground productivity. (6) Detritus decomposition in (i) is total detritus carbon flux minus measured and scaled rhizome respiration and in (ii) is measured efflux of CO_2 and CH_4 from Jones & Muthuri (1997). (7) Respiration is scaled measurement of rhizome respiration. (8) Total efflux is below ground respiration plus decomposition. (9) Ecosystem efflux is canopy respiration plus below ground efflux.

orative water loss from wetland areas has been a topic of intense debate for many decades (Idso & Anderson, 1988). However, Idso (1981) pointed out that most data suggestive of a vegetation-induced evaporation increase had been derived from experiments with identical pairs of small-water tanks (with or without vegetation) exposed to the open air. Decreases in evapotranspiration, on the other hand, were suggested by similar experiments which placed the tanks of plants within an extensive natural stand of the vegetation. Relatively few measurements appear to have been made using micrometeorological methods, but those that have generally confirm that swamp evaporation is less than lake evaporation (Rijks, 1969; Linacre et al., 1970). The fact that papyrus is a C_4 species is also of relevance in relation to evapotranspiration. Hasegawa (1977) demonstrated that, in general, the transpiration rate of C_3 plants was higher than C_4 plants and O'Toole & Tomar (1982) supported this view when they demonstrated that, when grown under identical conditions and at a similar leaf area index, C_4 *Echinochloa crus-galli* L. (barnyard grass) transpired about half as much water as C_3 *Oryza sativa* L. (rice).

In conclusion, we have demonstrated that the presence of papyrus with its C_4 characteristics has a major impact on the functioning of tropical wetland ecosystems. The high rates of CO_2 fixation and primary production result in large fluxes of CO_2 which can lead, under suitable hydrological conditions, to correspondingly high rates of carbon sequestration. The C_4 characteristics of papyrus mean that high rates of CO_2 assimilation can occur while, relative to C_3 vegetation, evapotranspiration is comparatively low. Under these circumstances, water loss by evaporation from papyrus vegetation is considerably less than from corresponding area of open water.

Acknowledgements

We thank Dr John Moncrieff for assistance in construction and deployment of the Eddy Covariance system and the Eddy Sol software used in this study. Mr Frances Kariuki is thanked for his assistance with the field measurements. We are grateful to Mr R. Hopcraft for kindly allowing us access to the field site at Loldia Farm, Naivasha. Financial support for this work was received from the EU STD3 R&D Programme under contract no. TS3*-CT92-0149.

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