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Fluxes of Carbon and Water in *Cyperus papyrus* L. tropical wetlands.

By

Matthew Saunders

Thesis submitted for degree of Ph.D.

To the University of Dublin, Trinity College

2005

Declaration.

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Summary.

Carbon dioxide (CO_2), water vapour (H_2O) and energy fluxes play important roles in the functioning of vegetative ecosystems and also influence the climate of our planet at both the regional and global scale through important feedback mechanisms.

Tropical wetlands cover a very small proportion of the total continental land mass but because they are highly productive their contribution to global primary production far outweighs their limited distribution. Fluxes of CO_2, H_2O and energy were measured using eddy covariance techniques from a stand of the C4 emergent sedge *Cyperus papyrus* L. at the Kirinya West wetland, Jinja, Uganda and a formerly pristine papyrus wetland, but now dominated by *Colocasia antiquorum* (cocoyam) cultivation at the Nakivubo wetland, Kampala, Uganda. Carbon losses from the papyrus vegetation at night ranged between 20 and 30 μmol CO_2 m^{-1} s^{-1} while peak, midday rates of CO_2 uptake were approximately 40 μmol CO_2 m^{-1} s^{-1}. Numerical integration of the flux data suggest that papyrus wetlands have the potential to sequester approximately 0.48 kg C m^{-2} y^{-1}. Carbon losses from the cocoyam vegetation at night were similar to those from the papyrus vegetation, however peak rates of CO_2 uptake were lower and ranged between 25 and 40 μmol CO_2 m^{-1} s^{-1}. Numerical integration of the flux data show cocoyam wetlands act as a smaller carbon sink than papyrus, sequestering approximately 0.37 kg C m^{-2} y^{-1}.

The average daily flux of water from papyrus canopy evapotranspiration (4.75 kg H_2O m^{-2} d^{-1}) was approximately 24% higher than the calculated daily water loss through evaporation from open water. Average rates of canopy evapotranspiration from the cocoyam vegetation were lower at 3.34 kg H_2O m^{-2} d^{-1}.

The standing biomass and primary productivity of papyrus vegetation was measured at the Kirinya West wetland, Jinja, Uganda. The papyrus culm density was estimated to be 16 culms m^{-2}, and the total standing live biomass was 9.39 kg DM m^{-2}. Below ground biomass (rhizome and fine roots) constituted 75% of the total live biomass, with the aboveground biomass (scale leaves, culm and umbel) accounting for the remaining 25%. The annual aerial productivity of the papyrus vegetation was estimated to be 8.08 kg m^{-2} y^{-1}.

Table of Contents

Chapter 1. General Introduction.

Chapter 2. The Field Study Sites.

Chapter 3. Standing Biomass and Productivity of *C. papyrus*. L dominated Wetlands.

Chapter 4. Fluxes of Carbon, Water and Energy.

List of Tables.

Chapter 3. Standing Biomass and Productivity of *C. papyrus*. L dominated wetlands.

Chapter 4. Fluxes of Carbon, Water and Energy.

List of Figures.

Chapter 1. General Introduction.

Chapter 2. The Field Study Sites.

Chapter 3. Standing Biomass and Productivity of *C. papyrus*. L dominated wetlands.

Chapter 4. Fluxes of Carbon, Water and Energy.

Chapter 1.

General Introduction.

1.1 Climate change and the global carbon cycle.

Much climate change research is focused upon the analysis of the impacts of increasing concentrations of greenhouse gases (GHGs) in the atmosphere. The focus of this study is on the GHGs carbon dioxide (CO_2), water vapour (H_2O) and methane (CH_4) and their exchange with wetland ecosystems. The significance of each gas depends largely upon its relative concentration, rate of release into the atmosphere and the corresponding radiative forcing effect. The absorption and re-emission of infrared radiation by GHG's in the atmosphere is generically termed the greenhouse effect, and can be quantified as greenhouse warming potential (GWP). The GWP of CH_4 for example is 25 greater than that of CO_2 on a mole to mole basis (Lay *et al.* 1996).

Carbon dioxide is one of the most important greenhouse gases, largely due to its rapid increase in atmospheric concentration since the industrial revolution and its lengthy retention time within the atmosphere. Historical data shows that the concentrations of atmospheric CO_2 trapped in ice cores approximately 400 000 years ago ranged from 180–290 μmol mol^{-1} (Schlesinger, 2003). Following the last glacial epoch the concentration of CO_2 varied from 230 to 290 μmol mol^{-1}, and prior to the industrial revolution CO_2 concentrations in the atmosphere remained at this level. The advent of fossil fuel combustion in the last 150 years has lead concentrations to increase to a current approximate level of 360 μmol mol^{-1}, an increase of approximately 24% (Pickering and Owen, 1994). The Intergovernmental Panel on Climate Change (IPCC) (2001) has forecast, based upon predicted rates of fossil fuel usage, an approximate doubling of present CO_2 concentrations within the next 100 years.

Following the last ice age and prior to significant human activities on the planet the carbon cycle was in a close state of equilibrium, whereby the net release of carbon into the atmosphere was balanced by the net sequestration rates of the various biological components. Before the period of rapid industrialisation, GHG emissions were mainly the result of human activities such as agricultural production, the combustion of wood products as fuel for food preparation and heating (Kammen and Marino, 1993), and the exploitation of plant biomass reserves for construction purposes. From this point in time the balance of carbon between the atmosphere and the biosphere was not synchronous and this imbalance was exacerbated further by the industrial revolution. Estimated rates of CO_2 release into the atmosphere range from 6 to 8 Gt C yr^{-1} (Pickering and Owen, 1994; Kammen and Marino, 1993; Schlesinger, 2003), and if fossil fuel consumption continues to follow the present trends of usage this estimate may double.

There are biotic, abiotic and anthropogenic inputs of carbon into the atmosphere. Inputs from key biological components include the release of CO_2 from plants, soils and the oceans. There are however not only inputs but also losses (exports) from the atmosphere as well, thus producing a cyclic effect, and it is the natural balance of the carbon cycle that has been disturbed through human activity. The quantification of the imports and exports of carbon to and from the atmosphere is important in understanding the carbon balance as it stands at present. The inputs of CO_2 from anthropogenic sources are well documented, however the assessment of carbon sources and sinks from globally dominant, natural ecosystems is at present poorly documented. An important area of research therefore is the quantification of potential source or sink strengths for major biological ecosystems, and the role these ecosystems play with regards to regulating rates of CO_2 release. The data produced from these biological studies is of importance to both management practices and land use issues in addition to climate change mitigation procedures.

The IPCC has, since 1990, reviewed at regular intervals the increasing evidence for a relationship between increased carbon emissions, elevated CO_2 concentrations and climate change. The ratification of the United Nations Framework Convention on Climate Change (UNFCCC) also highlighted the necessity for a greater understanding of the carbon cycle and its relationship to the radiative forcing of the Earths climate. The convention proposed that signatory countries should endeavour to stabilise and eventually reduce their emissions of GHG's in an attempt to slow the rate of future climatic change. In order to achieve this it is important to understand the factors that regulate the strengths of natural GHG sources and sinks in addition to the way these fluxes integrate and induce positive climatic feedback effects on a global scale (Fearnside, 2004).

The carbon cycle is a term used to describe the flow of carbon in its various forms through the atmosphere, ocean and terrestrial ecosystems and back to the atmosphere again. Globally, it is estimated that approximately 730 Gt C are stored within the atmosphere, 2000 Gt C are stored within terrestrial ecosystems, of which plants account for 500 Gt C and soils for 1500 Gt C, and 38 000 Gt C are stored in oceanic waters (IPCC, 2001). The amount of CO_2 that is removed from the atmosphere and converted into carbohydrate during photosynthesis is termed Gross Primary Production (GPP), the products of which are then either transformed into new plant tissue during plant growth or are returned to the atmosphere through autotrophic respiration. The difference between photosynthetic gain and respiratory release from vegetation is described as Net Primary Production (NPP), and is quantifiable as a net gain in physical plant biomass over time. The carbon stored through NPP will eventually return to the atmosphere through either heterotrophic respiration or combustion. Net Ecosystem Production (NEP) describes the balance between carbon gained through NPP and carbon loss through heterotrophic respiration, a process governed largely by the temperature and moisture content of soils (Lloyd and Taylor, 1994; Schulze, 2000). The Net Biome Production (NBP) provides a final measure of the total amount of carbon sequestered or stored by an ecosystem having accounted for losses due to erosion and export of dissolved or suspended carbon, and removal of carbon through biomass harvesting, herbivory or fire. If a terrestrial ecosystem is carbon neutral, carbon gain through NPP balances carbon loss through respiration and thus the NBP is zero. NBP changes are induced through natural climate variability, ecological disturbance, anthropogenic influence of land use management and the indirect feedback mechanisms resulting from climate change.

Wetlands are potentially significant sequesters of carbon due to the formation of peat deposits under anaerobic waterlogged conditions. The total global wetland carbon stock is estimated to be 240 Gt C, of which 94% is located in wetland soils (IPCC, 2001). However, these estimates may be on the conservative side because they are based on assumptions that peat deposits do not exceed 1m in depth, although there are observations of peat deposits that are up to 5 m in depth (Jones and Muthuri, 1997). Carbon cycle dynamics have not been extensively quantified in tropical ecosystems and wetlands in particular have been little studied. Wigely and Schimel (2000) estimated that the terrestrial exchange of carbon of all ecosystems in the tropics over a ten year period between 1980 and 1990 resulted in a net release of 3.2 ± 0.2 Gt C yr^{-1} which was largely due to land use changes. This estimate was based on a knowledge of rates of land clearance, biomass inventories and models of forest re-growth, which focused on the Amazonian tropical region. However emission rates for other tropical regions, especially those in Africa have very high levels of uncertainty.

Methane is an important component of both GHG flux estimates and the carbon cycle, particularly in wetlands. There are several sources of methane both natural and anthropogenic and the total estimated release rates of CH_4 range between 400 to 600 Tg yr^{-1} (Bouwman, 1990; Milich, 1999). Wetland areas that experience anoxic conditions are significant sources of CH_4 although there is significant uncertainty about specific release rates (Bazhin, 2003; Ding *et al.* 2002; Makhov and Bazhin, 1999). For example, natural wetland areas are estimated to release between 40 to 160 Tg CH_4 yr^{-1} while rice paddies are estimated to release between 60 to 140 Tg CH_4 yr^{-1}. The accuracy of these estimations can have significant effects on the total GWP of total methane sources, and on the estimation of the carbon balance as a whole.

1.2. The role of wetlands in carbon sequestration.

Approximately 7% of the Earths surface is constituted of wetland ecosystems, and 50% of this global wetland area is located within the tropics, approximately 20°N to 30°S. The influence of wetlands within the context of the global carbon cycle is potentially more significant than the total global wetland area suggests (Neue *et al.* 1997). The tropics are regarded as a region of high net primary productivity (NPP) (Barbosa and Fearnside, 1996) and therefore are potentially an important global carbon sink. Neue *et al.* (1997) estimate that approximately 250 Gt of carbon are stored within tropical wetlands.

Wetland areas are defined as a transitional zone between terrestrial and aquatic ecotones. It is possible to segregate these wetland areas based on hydrological regime, soil type and vegetation cover. Papyrus wetlands show defined vegetative zones and depending on localised hydrological regimes can experience periods of permanent inundation or hydrological draw down. Based on the broad classification scheme suggested by Bartlett and Harriss (1993) papyrus wetlands are described as swamp ecosystems.

Tropical wetlands have been shown to exhibit high rates of primary production, where temperature and insolation are also high (Jones and Humphries, 2002; Muthuri, 1985). Rates of carbon assimilation by the tropical aquatic C4 grass *Echinochloa polystachya* showed peak rates of CO_2 assimilation of 30 and 35 μmol m^{-2} s^{-1} during periods of hydrological draw down and inundation respectively (Morison *et al.* 2000). The estimated NPP of *E. polystachya* inferred from Net Ecosystem Exchange (NEE) measurements was approximately 4 kg C m^{-2} yr^{-1}. A study conducted on a papyrus wetland also showed high rates of NPP, of approximately 2.51 kg C m^{-2} yr^{-1} (Jones and Humphries, 2002). These studies describe some of the highest NPP estimates recorded to date and suggest the importance of tropical wetlands with regards to carbon sequestration. NPP however only describes the process and result of carbon assimilation through photosynthesis and release through autotrophic respiration. The degradation of senescent and decomposing plant material and the subsequent carbon release through heterotrophic respiration alters the balance of the carbon cycle within these wetlands. The flux of carbon into and out of these wetlands is a balance between a series of key factors. Carbon is assimilated and then stored within plant material, during the growth cycle of the plants the net increment of carbon is continuous, this in itself is a balance though between assimilation during the day and respiration at night. However during the senescence stage of the plants life cycle, biological decomposition and degradation acts to release carbon. In such highly productive ecosystems the accumulation of decaying organic matter is significant. The long term sequestration potential of this plant detritus is largely dependent on the physical and environmental characteristics of the wetland. Wetlands that experience permanent inundation have the potential to sequester large amounts of carbon as the presence of floodwater reduces the rate of aerobic decomposition of the detritus. Patterns of inundation however influence the biogeochemistry of both the water column and the underlying sediment. The chemical status of the water depends largely on the floodwater source and the type and relative biomass of the aquatic flora and fauna. Jones and Muthuri (1997) suggested that significant stores of carbon could accumulate beneath the plant rhizome in papyrus wetlands. The size of such carbon sinks depends largely on the depth to which the detritus accumulates, however Jones and Muthuri (1997) estimated that that on average approximately 68 kg C m^{-2} was stored in detrital deposits 1 metre in depth.

Tropical wetlands are therefore highly productive and have the potential to sequester and store large amounts of carbon on a long term basis.

1.3. Introduction to Uganda and Lake Victoria.

Uganda is a land-locked country in East Africa covering an approximate area of 236 580 km^2, between latitudes 3°14'N to 1°29'S and longitudes 29°34'W and 35°01'E (Hughes and Hughes, 1992). The general topographic relief in Uganda consists of low plateau ranging in altitude from 1100 to 1300 metres above sea level. Of the total surface area in Uganda approximately 3 822 530 ha are represented by lakes or open water bodies, and of this figure 3 100 060 ha are comprised by the Ugandan component of Lake Victoria. Forty five percent of the total surface area of Lake Victoria is located within Ugandan borders, comprising a valuable natural resource. The watershed of this lake and the Nile river complex covers the whole of Uganda, however approximately 90% of the water entering the lake is derived from direct precipitation (Carter, 1955). The coastline surrounding the Ugandan section of Lake Victoria is dominated by a series of flat-topped hills and corresponding valleys, these valleys tend to be forested along their sides, leading down to *C. papyrus* L. wetlands covering the lagoon inlets to the lake. Wetlands constitute approximately 13% of the total Ugandan land mass (Ikiara, *pers com*) and papyrus vegetation tends to dominate permanently inundated wetland areas. There are no accurate records of papyrus wetland coverage in the tropics (Jones, 2000) however Jones and Humphries (2002) estimate that papyrus wetlands cover approximately 40 000 km^2 in the East African region.

The Ugandan climate is dominated by three main airstreams, the South East and North East Trade Winds and the South West Monsoon. These winds, and changes in topography dominate precipitation patterns over Uganda, however the highest rates of precipitation are recorded over Lake Victoria (Hughes and Hughes, 1992). Rainfall patterns in the Lake Victoria region lack distinct seasonal trends, however historical data show that rainfall is highest between March and May, and September to November. The mean monthly rainfall data for the Lake Victoria coastline between Kampala and Jinja range from a maximum of 350 mm to a minimum of 125 mm (Department of Ugandan Land Survey, 1967). The maximum precipitation rates are derived largely from heavy thunderstorm periods common to the lakeshore areas.

1.4. The Papyrus Plant.

Cyperus papyrus L. more commonly known as papyrus is an emergent macrophytic sedge belonging to the *Cyperaceae* family, which is made up of approximately 90 genera and 4000 species (Muthuri, 1985). A single papyrus plant unit consists of the rhizome, culm and umbel. The rhizome is covered with inter-nodal scale leaves (Muthuri, 1985) which also cover the lower part of the plant culm. The rhizome is sympodial in nature and has a leading growing point where new aerial shoots are produced through the development of a lateral bud. The rhizome section furthest away from the growing point is still living even though new culms are no longer produced. Between 4 to 8 living culms are present on a rhizome at any point in time (Li and Jones, 1995; Muthuri, 1985). Figure 1.1 shows an entire papyrus plant consisting of individual plant units (culm, umbel, scale leaves and the nodal rhizome supporting the individual culms) and their respective age class. These age classes include juvenile (I-II), mature (III-IV), senescent (V) and dead culm units (VI). The bases of the culms are covered in scale leaves while the culm diameter decreases from the culm base to its tip underneath the umbel. Intercellular air channels extending the length of the culm unit are present within the internal matrix of the papyrus culms (Li and Jones, 1995). These air channels are obstructed at the rhizome–culm, and culm–umbel interface. Intercalary meristems are also present at these junctions. Stomata are present within the epidermis of the culm, with the exception of the area covered by scale leaves. In mature culms the stomatal frequency increases from the base to the tip of the culm, with the maximum stomatal density occurring at approximately two-thirds of the culm height (Li and Jones, 1995). The umbel of the papyrus plant as detailed in Figure 1.2 is located at the apex of the culm unit. The umbel consists of several hundred cylindrical rays to which three to five bracteoles may be attached (Jones and Humphries, 2002; Muthuri, 1985). Mature umbels are normally 40 to 50 cm in diameter and can be either sterile or fertile. Fertile umbels produce both spikes and spikelets while the sterile umbels produce only bracteoles. The sterile umbels form the primary photosynthetic organ of the plant however it has been suggested that the culms also show high rates of photosynthetic activity.

Emergent macrophytes such as papyrus show high rates of net primary productivity and large amounts of biomass accumulation. Muthuri (1985) showed that the culm units constitute 50% of the total biomass of papyrus plants, with the remaining 50% split evenly between the rhizome and root units. Jones and Muthuri (1997) estimated that the rhizome and root component constitutes approximately 58% of the total standing live biomass while the shoot biomass (culm and umbel) comprise the remaining 42%.

1.5. Papyrus Wetlands.

Swamplands cover many hundreds of thousands of square kilometres in tropical Africa and the wetland structure of the littoral regions of East African lakes tend to be dominated by *Cyperus papyrus* L. (Eggeling, 1935; Gaudet, 1979; Lind and Morrison, 1974; Lind and Visser, 1962) however successional trends in species composition can commonly be identified. As described by Carter (1955), these littoral areas can be distinguished into four key habitats. The first zone encountered at the lake shore is the grass swamp; here several plant species are found including *Leersia hexandra* and the area is subject to periods of drought and inundation depending on rates of precipitation and the relative water level of the lake. The papyrus zone is found adjacent to the grass swamp; *Cyperus papyrus* L. continuously dominates this region, however climbing plant species such as *Ipomoea rubens* can also be found in this region. The water depth below

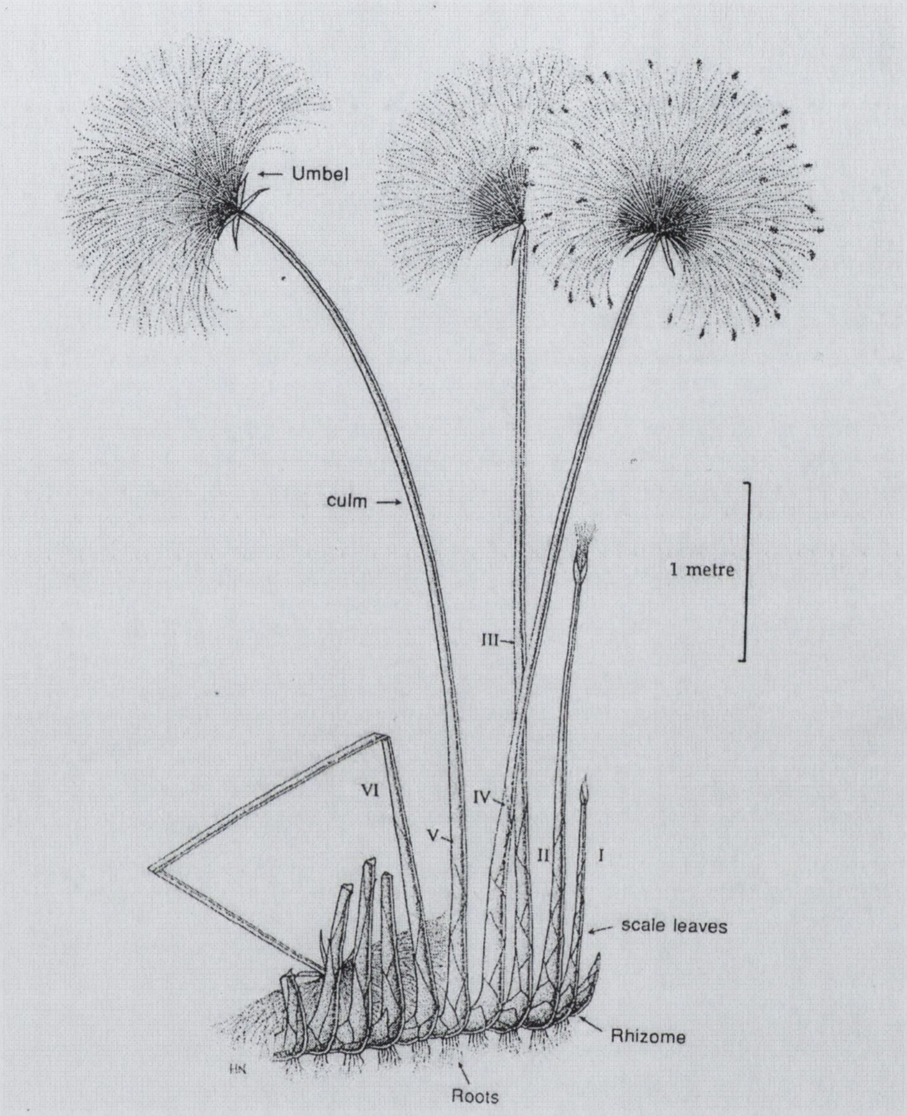

Figure 1.1. An example of a *Cyperus papyrus* L. plant. Showing the rhizome, culm and umbel sections. Also shows the range of age classes of individual plant units ranging from I – VI. (From, Jones and Muthuri, 1997).

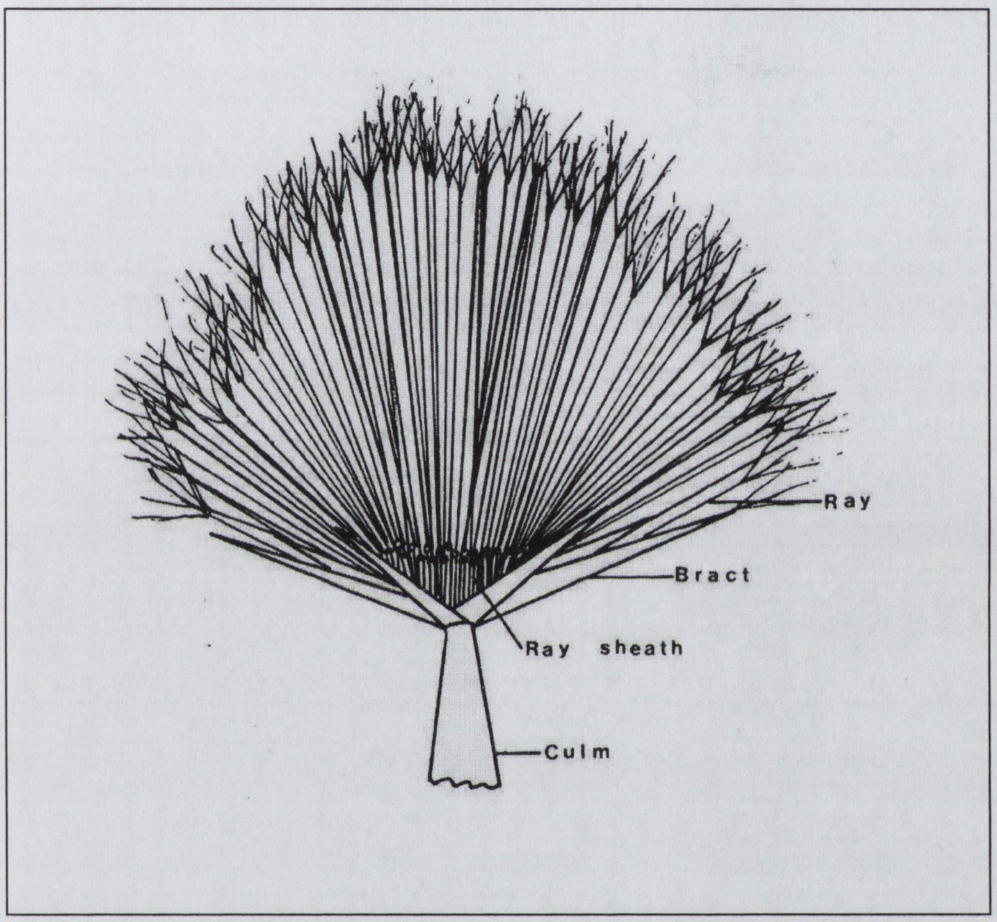

Figure 1. 2. An illustration of a young papyrus umbel, showing the main components of the inflorescence. (From, Muthuri, 1985).

the papyrus can vary from 1.5 to 3 metres and the papyrus forms a floating rhizomatous mat consisting of a series of interlinked individual plant rhizomes. As each plant rhizome consists of up to six living culms and several senesced and dying culms, this can produce a very dense, relatively homogenous canopy the height of which ranges from 4 to 7 metres. The plants produce new culm units from the growing point of the rhizome and thus this solid mat structure continues to grow. The senescing and dead culms are deposited onto the surface of the rhizome mat and from here gradually decompose. The decomposition of plant culms leads to the deposition of an organic detritus layer on the surface of the rhizome mat. This detritus accumulates and gradually moves down through the mat and is deposited into the water body to form organic peat deposits beneath the rhizome. These peat deposits can be relatively extensive and several metres in depth (Jones and Humphries, 2002). Where the papyrus zone is located close to the lake shore, and in areas of fluctuating precipitation, lake draw-down can expose these detritus deposits to the atmosphere releasing carbon through aerobic decomposition.

Beyond the papyrus zone the stability of the wetland decreases as the rhizomatous mat disappears and is replaced by free floating vegetation. The final vegetative zone before the open lake waters is the water lily zone. This area consists of *Nymphaea hendelottii*, *Nymphaea lotus* and *Trapa bispinosa*. These plants can be rooted to the lake floor but have leaves floating on the surface of the water. There is a large amount of open water in this area and the width of this zone depends primarily on the depth of the water body at this point.

1.5.1. Environmental Characteristics of Papyrus Swamps.

Papyrus wetlands are propagated through the expansion of the plant rhizome from the muddy partially submerged waters of the lake shore. Under continued waterlogged conditions the papyrus network will extend to form a floating platform out into the lake. This floating pontoon accumulates a large amount of senescing and dead organic material. This material gathers on the rhizome surface to form a floating layer of organic soil material (Beadle, 1981). The organic detritus gradually moves through the rhizome and will eventually move into the water column below in either dissolved or solid form.

The waterlogged conditions in which the papyrus network first establishes, tend to be highly anoxic. There is little movement and mixing of the water column, and any oxygenation of the water occurs at the water-atmosphere interface and is limited to the top of the water column. These conditions continue out into the lake beneath the papyrus rhizome. The physical presence of large emergent macrophytes such as papyrus and the resulting rhizome network, have two significant impacts on the water column below. The dense canopy of the vegetation shades the rhizome surface, which reduces both the penetration of solar radiation into the water column below and limits the mixing effects associated with wind. Restricted solar radiation penetration limits both floral species competition at the rhizome surface and algal photosynthesis within the water column, directly below the rhizome mat. Restricted algal production reduces the amount of oxygen returned to the water through photosynthesis. At the lakeward fringe of the papyrus swamp the water lily (*Nymphaea*) or open water zone, is described by Beadle (1981) as an area supersaturated with dissolved oxygen. This is due to significant exposure to solar radiation at depth within the water column, promoting intense underwater photosynthesis. The mixing of this highly oxygenated water with the water beneath the papyrus rhizome is dependant largely on lacaustrine seiches, however the rapid aerobic decomposition of organic material will rapidly exhaust any dissolved oxygen within the water column.

Carter (1955) studied trends in the biogeochemistry of the water column associated with papyrus wetlands, covering open water, water lily, papyrus and grass swamp zones. He found a distinct trend of increasing water quality from the lakeshore to the open water zone. The water at the lakeshore was sampled at the grass–papyrus interface and was found to have high concentrations of iron, a feature attributed to the highly lateritic nature of the soil in East Africa. This suggests that the water found in this zone was in part derived by overland flow. The water was found to be highly anoxic with concentrations of dissolved oxygen between 0 to 2 % saturation. The water was slightly acidic in nature with a pH ranging from 6.4 to 7.0 and the redox potential was low but variable ranging from 0 to 350 mV. The water column beneath the papyrus rhizome and associated with the grass swamp zones have been described by Carter (1955) in three distinct sections. These are the surface water immediately above the papyrus mat, the water immediately below the papyrus mat, and the water located beneath the papyrus mat close to the shore where the rhizome mat meets the solid sediment surface. Depending on the depth of submergence of the papyrus rhizome, any water located above the rhizome mat might experience some degree of wind driven mixing with surface waters of the water lily zone. In this case the water might show oxygenation trends ranging from 0 to 50%, pH ranging from 7.0 to 8.0 and a redox potential ranging from + 167 to 425 mV. The water column beneath the rhizome mat showed low values of oxygen saturation at approximately 5%. This value is generally constantly low although it might be altered during heavy rainstorms or lacaustrine seiches resulting in increased mixing of the water column. The pH of the water in this section is slightly less acidic and closer to neutral ranging from 6.6 to7.0, while the redox potential varies significantly ranging from 0 to + 400 mV with the lower values occurring close to the sediment surface.

The penetration of solar radiation to depth in the water lily zone promotes significant underwater photosynthesis within the biological community, leading to high dissolved oxygen concentrations. Stratification of temperature, dissolved oxygen and pH occurs in the water lily zone, where the lowest dissolved oxygen concentrations occur at the papyrus and *Nymphaea* interface and gradually increase through to the open water zone. The open waters of the lake are described as being relatively pure in composition, the waters are well oxygenated with redox potentials ranging from 330 to 410 mV and are slightly alkaline with a pH of 8.6.

Azza *et al.* (unpub) in a recent study compared the physico-chemical conditions of the water column at the papyrus wetland fringe and the bay/open lake boundary to historical data. The study showed that the water column at the wetland fringe is at present, characterised by low levels of dissolved oxygen and a neutral pH, while the water column at the bay/open boundary are characterised by high levels of dissolved oxygen and a strongly alkaline pH.

The large amounts of organic material that accumulate beneath the papyrus rhizome are deposited into a predominantly anaerobic environment. The subsequent anaerobic decomposition of the detritus, consisting largely of carbohydrate material, results in the gaseous formation of carbon dioxide, methane, hydrogen, carbon monoxide and ethylene. The evolution of these gases is not uniform in volume although Beadle

(1981) suggests the composition of such gases would contain 60% methane, 30% carbon dioxide and the remaining 10% consists of hydrogen, carbon monoxide and ethylene. Muthuri (1985) suggests that nitrogen is a major constituent of the gas, and based on the composition of samples taken from Lake Naivasha, papyrus wetlands might evolve gas containing 45% nitrogen, 23% methane, 21% carbon dioxide, 6% oxygen, 4% hydrogen and 1% hydrogen sulphide. The production and subsequent emission of gases such as methane and nitrous oxide, represents an important component of the greenhouse gas budget of papyrus dominated wetlands. In addition the reduction of inorganic sulphates in the water to form hydrogen sulphide, even in small concentrations, would potentially increase the toxicity of this anaerobic environment further.

1.5.2. Disturbance of Papyrus Wetlands.

In areas of high population pressure one of the primary trends of anthropogenic disturbance within papyrus wetlands is the clearing of the area for the cultivation of *Colocasia antiquorum* (cocoyam). This crop is well suited to wetland areas, as it requires a substantial supply of water. The plant is described as having a corm from which a cluster of large leaves grow (Acland, 1971). The leaves may grow to heights of 1.3 metres when fully mature and are attached to the stalks in the middle of the lamina as opposed to the leaf margin. The plant is perennial by nature although it is possible to harvest corms six months after planting.

In wetland areas cocoyams are grown in large monotypic stands where the tall stalk and large leaves create a significant shading effect on the sediment surface reducing competition from other plants. Large holes, approximately 15 to 30 cm deep are dug in the detritus after the papyrus has been cleared, into which the corms are planted. During harvesting the whole plant is exhumed, the leaves are cut away leaving short stalk sections and the corm is cut approximately 5 cm below the stalk interface. The corm and stalk section is then replanted. Figure 1.3 shows an example of a mature cocoyam plant.

1.6. Measuring Greenhouse Gas Fluxes.

The measurement techniques and principles applied to the study of greenhouse gas flux at present, centres around the exchange of gas scalars between the biosphere and the atmosphere. These studies range from analysis of a single leaf to flux estimation over an entire ecosystem or topographic region. Each method or scale of flux estimation is appropriate in its own right, although attempting to scale fluxes from small to large scales or vice versa can produce erroneous flux estimates. This study attempts to investigate the flux of carbon dioxide (CO_2) water vapour (H_2O) and energy at the canopy scale, and fluxes of methane (CH_4) at the plant scale.

1.6.1. Measuring Fluxes of Carbon Dioxide, Water Vapour and Energy.

The Eddy Covariance (EC) technique allows the estimation of fluxes of CO_2 and H_2O at the ecosystem scale. The EC system allows the non-invasive analysis of gas scalars moving into or out of a plant canopy. Gas scalars concentrations are sampled and then related to periods of atmospheric turbulence. The movement of air seldom exhibits laminar flow and thus the turbulent flow of air is measured. Turbulent flow is analysed in three dimensions above the canopy and the average vertical turbulence component is obtained. This vertical turbulence is then correlated to the gas scalars and would in the case of CO_2, for example, detect CO_2 depleted air during periods of photosynthesis and CO_2 enriched air during periods of respiration. This technique is described in detail in Chapter 4.

1.6.2. Measuring Trace Gas Emissions.

When anoxic conditions prevail in wetland sediments, CH_4 is a product of methanogenesis where labile organic matter is readily available and inorganic electron acceptors such as sulphate are negligible (Jones, 2000; Singh *et al.* 2000). Wetland plants both influence CH_4 production through the provision of methanogenic substrate in the form of root exudates but also influence rates CH_4 flux by providing a direct conduit

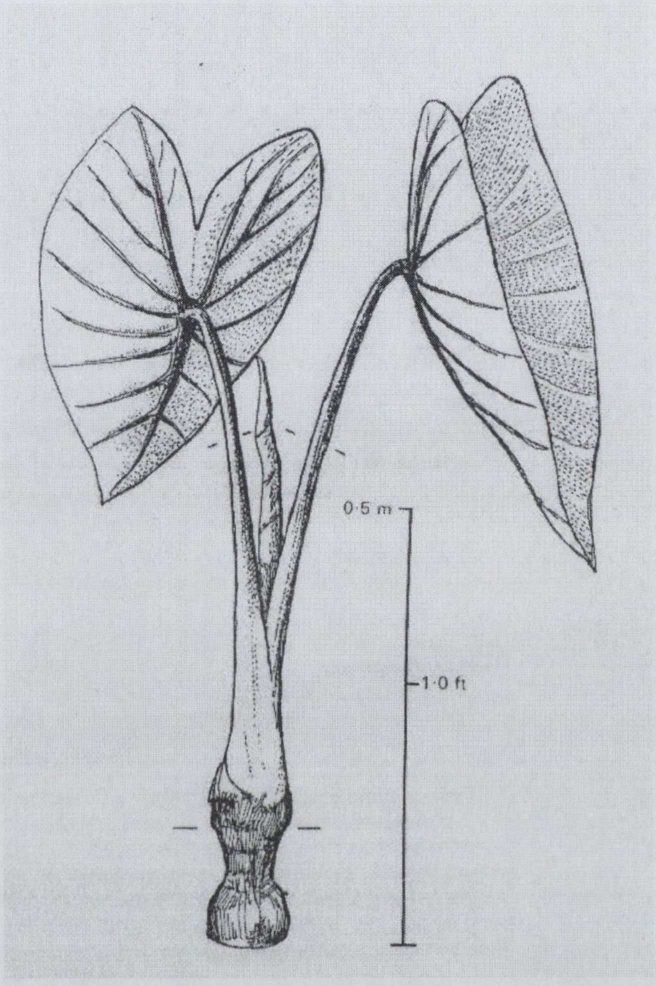

Figure 1.3. *Colocasia antiquorum* (coco yam). An example of an entire plant showing the corm, stalks and leaves. The lines show the point of cutting when preparing the plant for re-planting. (From, Acland, 1971)

between the sediment and the troposphere. CH_4 emission also occurs in un-vegetated wetland areas where CH_4 gas is released in bubble form due to changing partial pressures of dissolved gases in relation to the hydrostatic pressure of the sediment (Singh *et al.* 2000). In this study CH_4 emission was investigated through plant mediated transport only, as the papyrus vegetation formed a homogenous barrier between the sediment, water column and the atmosphere. Emissions of CH_4 through plant mediated transport were determined by collecting gaseous samples using static chamber techniques, which were later analysed using gas chromatography (Chapter 4). Patterns of internal gaseous transport within plants have long been a subject of intense interest (Grosse *et al.* 1996; Li and Jones, 1995) and thus the transport and release of CH_4 through the intercellular cavities of the plant culm was measured.

1.7. Modelling Atmosphere - Biosphere Gaseous Exchange.

Modelling biological processes allows the evaluation of scientific data and contributes to decision-making processes at the experimental, project and government levels (Gaunt *et al.* 1997). Models give decision makers the tools necessary to objectively explore and evaluate spatial problems within a range of contexts. Within ecological studies, process based models offer a valuable insight into ecosystem functioning and relevant management techniques (Fitz *et al.* 1996). Modelling physiological data allows the integration of this information across many orders of magnitude (Harley and Baldocchi, 1995; Lloyd *et al.* 1995). A good example of this is the estimation of canopy scale photosynthesis based on measurements from a single leaf. However the accuracy of modelled gaseous fluxes, over scales ranging many orders of magnitude may vary due to spatial and temporal variability (Derwent *et al.* 1999).

When considering modelling gaseous exchange between the atmosphere and biosphere it is possible to contemplate the processes behind such exchange of gas scalars on three levels of analysis. From the smallest scale there is the process of gas exchange of a single leaf. In order to photosynthesise, the stomata of the leaf open to allow the movement of carbon dioxide across a concentration gradient from the surrounding air into the leaf. This transition occurs between the leaf and the leaf boundary layer, i.e. the air directly surrounding the plant leaf. The next step is to consider an entire canopy of plant leaves undergoing the process of gas exchange but at this point the exchange occurs between the plant canopy as an entire unit and the atmospheric surface boundary layer. Finally there is the exchange of gas scalars between the surface and planetary boundary layer. The measurement of gas exchange at any of these stages is entirely valid, however the utilisation of such data to directly scale flux estimates must be approached with a degree of caution.

The movement of gas scalars such as CO_2 between the biosphere and the atmosphere is of importance with regards to atmospheric composition and the associated issue of climate change. An improved understanding of the processes regulating the fluxes of carbon from the atmosphere and into biological plant material is an important constituent of greenhouse gas and climate change mitigation policy. The adoption of the Kyoto agreement in 1997 and the ratification of this policy by its signatories, has set specific limits on the anthropogenic release of greenhouse gases into the atmosphere. Another facet of this climate change policy is to identify potential source and sinks of greenhouse gases within biological components of the global environment. Process-based measurements of greenhouse gas fluxes have been undertaken on a number of natural ecosystems, including forests (Valentini *et al.* 1996), grasslands (Hunt *et al.* 2002), arable crops and wetlands (Leuning *et al.* 2000; Morison *et al.* 2000). These studies have also been undertaken across the globe to cover many climatic regions. The data produced from these types of investigations are useful to validate "bottom up" approaches to gas flux models, where measurements made on small scale environmental systems are scaled up to produce flux estimates over a larger area or longer period of time. These models are also of importance when investigating the potential impact climate change will have on these natural ecosystems. The influence of climate change can have localised impacts on the climatic variables of a region. These variables might include perturbations in rainfall patterns, temperature and sunlight regimes all of which are of importance to biological systems, and all of which could influence the role in which these ecosystems play in the mitigation of climate change.

1.8. Scope of Study.

1.8.1. Wetlands as Ecosystem Services.

The term ecosystem service refers to the conditions and processes of natural ecosystems and the species composition, which are utilised to sustain and fulfil human life (Chee, 2004). The provision of services by ecological systems, are critical to both the maintenance of all aspects of life on Earth, including the welfare of the human population and the preservation of species diversity (Costanza *et al.* 1997; Lerdau and Slobodkin, 2002). Ecosystems can therefore be assigned an economic value (Creedy and Wurzbacher, 2001) the assessment of which allows the integration of both ecological and economic principles and will in the future help to address the omission of ecosystem service provision within policy decision at both local and regional levels. Ecosystem valuation is a difficult process however as the demand function placed on the ecosystem may be hard to quantify, and the specific demands or needs of all parties involved with or reliant upon the ecosystem might be subject to bias (Opschoor, 1998). Costanza *et al.* (1997) attempted to calculate an economic value of particular ecosystem services for several key biomes, including wetlands. The methodology used in this assessment comprised a synthesis of previous studies, the majority of which were based on the "willingness-to-pay" principle. Based on this principle wetland areas identified as tidal marshes, mangroves, swamps and floodplains, provided ecosystem services worth approximately \$19,580 ha^{-1} y^{-1}.

Wetlands play an important role in the maintenance and conservation of aquatic water bodies. Research to date has focused mainly on European and North American water bodies, however demographic and land use patterns in many developing countries are placing these fundamental ecosystems under threat. East Africa holds many globally important freshwater reserves, such as Lake Victoria the second largest freshwater lake in the world covering an area of 67 850 km^2. This area however also has one on the highest population growth rates in the world between 3-4% per annum (Okeyo-Owuor, 1999). These population pressures have an impact on both the lakes and the surrounding land, reducing the quality of both. The impact on the quality of the water bodies has a direct effect on the local population, as these bodies are the main source of drinking water and dietary protein for the local inhabitants. Wetlands have also been shown to provide a valuable service as a low-cost alternative for the treatment of municipal, industrial and agricultural effluent (Ayaz and Akca, 2001; Geber and Bjorkland, 2002; Nelson *et al.* 2001). In addition these lakes provide secondary sources of income through agricultural development and the provision of building materials, while emergent macrophytes play an important role in localised climate control. In addition, the only outflow from Lake Victoria is the Nile river where the construction of the Owen Falls Dam allows the generation of hydro-electric power. Uganda generates enough power here to meet domestic demand and allows energy to be exported to neighbouring East African countries (Kansiime, *pers comm.*).

Research on the Great Lakes of East Africa have shown a series of changes in both water quality and trophic structure over the past 50 years (Kansiime, 1999). These studies have primarily focused on the reduction of water quality highlighted by the changing phytoplankton abundance and composition leading to increased eutrophication and a reduction in both fish stocks and suitable breeding habitats.

1.8.2. Introduction to the ECOTOOLS Project.

The ECOTOOLS Project is a European Union funded project that is aimed towards the creation of practical management tools for natural resources in East Africa. The project also aims to relate productivity of local ecosystems to sustainable resource use in a local, regional and global context. The project incorporates inputs from several international research institutions; these are listed in Appendix 1. Each research partner is responsible for a specific area of research within the project. The commitment of the Botany Department, Trinity College Dublin, was to determine fluxes of carbon, water and energy between the biosphere and atmosphere over papyrus dominated wetlands.

The multiuse wetland areas of Lake Victoria were chosen as the study sites of the ECOTOOLS project. The Lake Victoria wetlands are a highly productive asset for the East African region and because of this it is important to develop multiuse ecosystem management practices which can adapt to changing economic pressure in this region.

The wetland areas surrounding the shores of Lake Victoria are of importance to the local and regional economic development of the area. The wetlands have a number of uses including fishing, flora harvesting, agriculture, wastewater treatment and tourism. Increased pressure is being placed on these ecosystems through modifications in land use practices, overexploitation of biological resources and changing demographic trends in wetland catchment areas. The direct effect of these pressures results in reduced productivity and degradation of the ecosystem and therefore a reduction in biodiversity. There is therefore a direct conflict between the continued subsistence and development of communities within these areas and the conservation and adaptation of wetlands to facilitate continued demographic changes.

1.8.3. The Role of Wetlands in the Local Environment.

The wetlands surrounding the shores of Lake Victoria provide a number of functions for the local community. Primarily they provide subsistence, as the lake and accompanying lagoons provide food, water and shelter for the local inhabitants. Fish communities supply approximately 70% of the dietary protein of local inhabitants. These fish communities are dominated by three species *Lates niloticus*, (Nile Perch) *Rastrineobola argentea*, (Native Pelagic Minnow) and *Orechromis niloticus*, (Nile Tilapia). The current dominance of these species is due to a reduction in water quality and the introduction of non-native species (Perch and Tilapia), which have the ability to out-compete the less aggressive native species. Estimates of fish yields show that the Nile Perch and Tilapia constitute approximately 90% of the total catch (Mwakubo, *pers comm.*). The aquatic macrophytic flora in the lagoons of Lake Victoria provides an important habitat for the fish species. They provide a refuge for feeding, breeding and protection from predation largely from adult perch species.

The lake is also the primary source of drinking water for the region. However the provision of this is becoming increasingly difficult, as the wetlands are a conduit for municipal, industrial and agricultural wastewater, which is discharged into the lake. The treatment of municipal wastewater in many urbanised areas of less developed countries is limited due to the high capital investment needed for the treatment of wastewater to secondary levels. This can result in the direct discharge of partially or even untreated effluent into the lake, and can lead to the development of water borne diseases such as typhoid and cholera. Wastewater discharge also increases the concentrations of nutrients such as N and P within the lake, the results of which are well documented (Hecky, 1993), and can lead to the eutrophication of the water through algal blooms. Eutrophication decreases dissolved oxygen concentrations within the water and has a significant impact on fish populations. Kansiime and Nalubega (1999) have shown that wetland vegetation such as papyrus could play an important role in the treatment of wastewater through bio-manipulation. It is suggested that emergent aquatic macrophytes such as papyrus can be used as a tertiary measure to remove the excess nutrient load of the wastewater, by percolating effluent through the wetland. This increases the retention time between discharge from source to arrival in the main water body of the lake. Percolation allows increased contact between the wastewater, plants and their associated microbial communities, allowing higher rates of pollutant removal. The process of bio-manipulation of wastewater is of importance around large cities such as Kampala, the capital city of Uganda. The Nakivubo wetland separates Kampala with the Inner Murchison Bay of Lake Victoria. This wetland receives secondary treated effluent from the Bugolobi sewage treatment plant and raw sewage from the Luzira Prison compound. In addition the wetland, which was once a pristine papyrus ecosystem, has been gradually degraded through cocoyam agriculture. The supply of drinking water for the city of Kampala is drawn from an intake at Gaba, located in the Inner Murchison Bay downstream from the discharge of the Nakivubo wetland.

Papyrus wetlands also supply the local community with products of economic importance on both a local and regional scale. The endemic floral communities provide materials for construction, thatching and furniture making, in addition to some medicinal herbaceous species. While in addition the organic material produced through the decomposition of the wetland plants produces relatively fertile land for the production of cocoyam (*Colocasia antiquorum*) and sugar cane (*Saccharum officinarum*). The agricultural production in these wetland border areas is generally conducted on a subsistence scale, although where large populations reside within wetlands areas agricultural processes are undertaken on a much larger scale to the detriment of the indigenous wetland vegetation. Agricultural crop production does however provide additional economic gain, thus leading to the stimulation of socio-economic growth in some densely populated wetland areas.

1.8.4. Aims of Thesis.

The major aims of this study are:

- To quantify fluxes of CO_2, H_2O and energy exchange between the atmosphere and papyrus dominated wetlands.

- To quantify the carbon source or sink strength of papyrus wetlands and to investigate the influence that human encroachment has on the source or sink strength of these wetlands through the cultivation of *Colocasia antiquorum*.

- To use knowledge gained regarding the carbon cycle of papyrus wetlands to identify best management practices that will allow local communities to utilise the resources offered by the wetland in a sustainable manner while conserving the natural biodiversity of the wetland and realising the potential of these wetland areas to sequester large amounts of carbon.

- To utilise the results obtained to provide more detailed information on the carbon cycle within papyrus wetlands, to define future research problems and provide and disseminate the information obtained to both local inhabitants and scientists working on Lake Victoria, and regional policy makers as part of the ECOTOOLS project.

Chapter 2.

The Field Study Sites.

2.1. Introduction.

The Kirinya and Nakivubo wetlands are both examples of tropical perennial swamps found along the northern shores of Lake Victoria, Uganda. Figure 2.1 shows the Ugandan territory of Lake Victoria and the approximate locations of the Nakivubo and Kirinya wetlands. The Nakivubo wetland is of interest due to its close proximity to Kampala, Uganda's capital city, while the Kirinya wetland is situated close to the Owen Falls Dam, the source of the River Nile, the only outflow of Lake Victoria.

2.2. Description of the Kirinya West Wetland.

2.2.1. Location of the Kirinya West Wetland.

The Kirinya West wetland (Figure 2.2; Plate 2.1) is located at 00°24'N and 33°11'E on the northern shore of Lake Victoria, Uganda. The wetland is in close proximity to the town of Jinja, and lies at an altitude of 1175 m above sea level in the East African rift valley complex.

The wetland forms a natural tropical perennial swamp covering an area of 471 100 m^2, (Kansiime and Mwesigye, unpub) and is connected to Lake Victoria via the Napoleon Gulf. A large outcrop approximately 50 m in height borders the eastern fringe of the wetland, where the Kirinya prison and Walukuba housing estate are located (Plate 2.2 and 2.3). The northern part of the wetland is in close proximity to effluent stabilisation ponds coordinated by the National Water and Sewerage Corporation (NWSC), a government based fuel repository and small-scale banana plantation (Plate 2.4).

Figure 2.1. Map showing the Ugandan territory of Lake Victoria. Circles represent the approximate location of the Nakivubo (solid circle) and Kirinya (dashed circle) wetlands (From; http://encarta.msn.com/map_701514012/Victoria_Lake.html).

1 ○ Approximate location of the Nakivubo wetland.

2 ◌ Approximate location of the Kirinya wetland.

A pipeline connecting the fuel repository to a pontoon in the Napoleon Gulf was laid through the Kirinya wetland prior to this study. The pipeline was laid by cutting a transect through the north-eastern part of the swamp. The western fringe of the wetland borders the Loco housing quarters (Plate 2.5). The periphery of the wetland on all landward borders has been partially encroached by subsistence agriculture of cocoyam and sugar cane.

Access to the wetland has been facilitated by the construction of three transects across the wetland, running in an easterly direction. These transects are only open at the western end to prevent encroachment into the wetland from the population on the eastern side. The construction of these transects does however compromise the stability of the floating rhizome network. In order to provide long-term, stable access to the wetland, wooden walkways have been constructed along the transects. The construction and maintenance of these transects was funded by the Lake Victoria Environmental Management Project (LVEMP).

2.2.2 Geology of the Kirinya Wetland Area.

The underlying geology of the Jinja region is dominated by the Buganda-Toro geological classification. This geology dates back to the Pre-Cambrian era and is one of the most extensive formations in south central and western parts of Uganda. The Kirinya wetland system lies on a granite gneiss base which stretches from the Rwenzori Mountains on the Western Ugandan border through central Uganda to Jinja on the northern shore of Lake Victoria. Sedimentary rock formations such as arenites and argillites are also common in this area. Arenites are similar in composition to shale however they are bound by silica while arenites are a coarse sandstone deposit. Lacaustrine sands, silts and clays dominate the soils of the Kirinya wetland area. The formation of peat deposits beneath tropical wetlands are a common phenomenon, the Kirinya wetland is a lagoon-based swamp beneath which 2 to 3 m of organic material has accumulated.

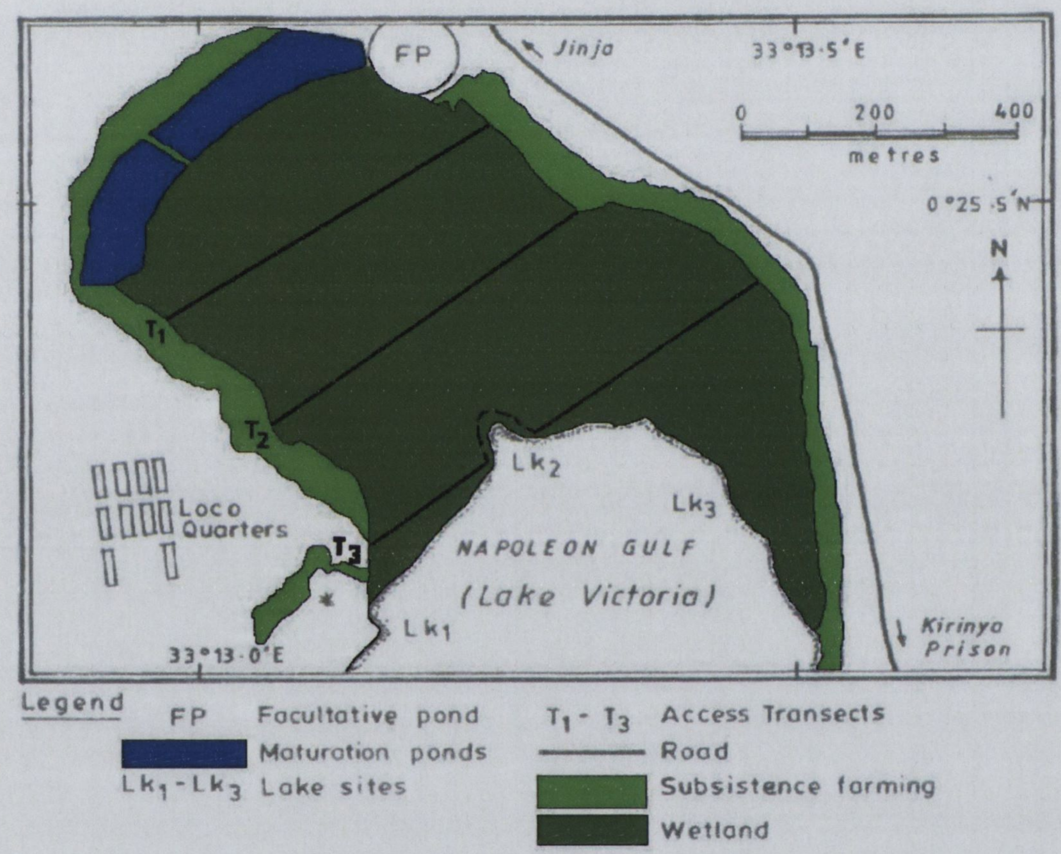

Figure 2.2. Map showing the Kirinya West Wetland. The legend indicates the NWSC stabilisation ponds, the LVEMP access transects and the location of subsistence agriculture along the periphery of the wetland. (Re-drawn from Kansiime and Mwesigye, unpub).

Plate 2.1. The Kirinya West Wetland. Plate shows the Kirinya West Wetland (1), the Kirinya East Wetland (2) and the Napoleon Gulf (3). Picture taken from elevation to the East of the wetland.

Plate 2.2. The Kirinya West Wetland. Photograph taken looking east from the western shore of the wetland. Plate shows part of the elevated outcrop to the east of the wetland. Plate also highlights the zonation of the Kirinya wetland, the foreground shows the grass zone (1), the miscanthidium zone (2) and the papyrus zone (3).

Plate 2.3. The Kirinya West Wetland. Photograph taken from inside the papyrus swamp looking southeast towards the elevated escarpment housing the Kirinya Prison (1). Plate highlights the uniform nature of the papyrus canopy.

Plate 2.4. The Kirinya West Wetland. Photograph taken from inside the papyrus swamp looking northeast. Plate shows the town of Jinja (1), the fuel repository (2) and banana plantations (3).

Plate 2.5. The Kirinya West Wetland. Photograph taken from inside the papyrus swamp, looking southwest. Plate shows the papyrus canopy and the proximately of the local Loco housing quarters (1).

2.2.3. Meteorology of the Kirinya Wetland Area.

This area of Lake Victoria exhibits an equatorial climatic regime. Annual rainfall occurs in two periods with heavier periods of rain falling from March to May and shorter rainfall periods occurring from November through December (Carter, 1955). The rainfall is attributed to a number of factors such as altitude, topography and has been linked to the Inter Tropical Convergence Zone (ITCZ), and the influence the lake has on localised climatic regimes (Kansiime and Nalubega, 1999). Lake Victoria receives 90% of its precipitation from direct rainfall, manifested in the form of heavy localised thunderstorms.

The Jinja region lies within the Lake Victoria hydrological zone. This area is defined by the inland penetration of lake-derived wind, occurring throughout the day. This zone also exhibits defined diurnal temperature regimes, where at the lake shore there is a diurnal temperature variation of approximately 7°C and at the inland limit of the on shore breeze (approximately 30 - 50 kilometres from the lake shore), there is a diurnal temperature variation of approximately 11°C (Department of Ugandan Land Survey, 1967). The Jinja region receives a mean annual rainfall of between 1375 to 1500 mm. Maximum rates of precipitation occur in April and November with approximately 175 mm and 210 mm falling in each month respectively. The driest months occur in January and July, with 75mm and 60mm falling in each month respectively. Water levels within Lake Victoria show only small perturbations throughout the year (≈50cm), resulting in a stable hydrological regime. These factors favour emergent macrophytic species such as papyrus.

There is little variation in air temperature regimes across Uganda except for localities at high altitude. Jinja experiences maximum and minimum air temperatures of approximately 29°C and 16°C respectively. Mean maximum air temperatures remain relatively stable throughout the year, from January through March and September through December the temperatures remain relatively stable at 28-29°C. The months of April through August show a slight decrease in mean maximum air temperature with temperatures ranging from 26–29°C. The mean minimum air temperatures show a similarly stable pattern, with temperatures averaging a constant 16°C, with some variation in March, April, June and July.

2.2.4. Vegetation of the Kirinya West Wetland.

The Kirinya wetland is dominated largely by *Cyperus papyrus* L. with some localised areas of *Miscanthidium violaceum*. These emergent macrophytes are rooted at the northern, western and eastern fringes of the wetland. From the rooted zone the papyrus covers the entire lagoon forming a floating rhizomatous mat. The floating vegetation covers an area of 471 100 m^2 and depth of the water column beneath the rhizome mat varies between 2–3.5 m with a mean depth of 2.3 m

Healthy papyrus plants dominate the wetland where these plants, depending on age class, range from 3–5 m in height, and are topped by large reproductive umbels. The papyrus forms a dense canopy restricting light penetration, however the taller plant culms tend to bend in strong winds allowing light to penetrate to the rhizome base. In these areas opportunistic plants such as scrambling and climbing species are common. Examples of such species include *Ipomoea rubens* and *Enhydra flactuans*. When papyrus monocultures are disturbed through harvesting or burning, the species composition can alter, with opportunistic species tending to flourish (Kansiime and Nalubega, 1999). Prior to this study part of the papyrus monoculture was burnt. A small section located between transects 1 and 2 (Figure 2.2) on the northeastern fringe of the wetland was accidentally burnt by local inhabitants. The resulting re-growth from the fire was dominated by papyrus, and within two months the canopy height and dense structure was re-established. The composition of the papyrus plants in this region did however alter slightly, where the plants tended to be smaller in size with regards to culm girth than plants of a similar height in adjoining, undisturbed areas. The density of plants culms per unit area increased with a higher proportion of smaller plant culms per unit area. Increased plant productivity after periods of disturbance have been measured by Muthuri (1985).

Miscanthidium plants are common around the periphery of the wetland and in small isolated patches within the papyrus stand. These perennial grasses have tall upright stalks between 2–4 m in height, with an inflorescence approximately 25–40 cm long. It has been suggested that these plants are unable to form free-floating mats and are restricted to areas subject to low level flooding (Lind and Visser, 1962). The presence of *Miscanthidium* at the swamp fringe supports this theory, as the plants are rooted to the substrate in these areas and would be subject to small flooding episodes. *Miscanthidium* is however present in small patches within the floating papyrus wetland. This suggests that either the depth of the water column in these regions is lower, or the papyrus rhizome is providing a means of support.

The Kirinya wetland has been encroached on all landward sides through subsistence agriculture. The wetland vegetation in these areas has been cleared and the nutrient rich organic detritus is used to cultivate *Colocasia antiquorum* (cocoyam).

2.2.5. Wetland Function; Wastewater Treatment.

The Kirinya West Wetland is part of an integrated tertiary municipal effluent treatment scheme. The Lake Victoria Environmental Management Project (LVEMP) has established a pilot project, investigating the impacts of municipal effluents on Lake Victoria and the influence of papyrus wetlands on the biological attenuation of this wastewater. The wetland receives secondary treated wastewater from the town of Jinja, and serves a population of 28 000 people, collecting 4 400 m^3 of effluent per day (Kansiime and Mwesigye, unpub). The wastewater is held in a series of stabilisation ponds on the northern fringe of the wetland, and is then released over a large part of the wetland from where it percolates through the vegetation mat finally reaching the Napoleon Gulf. It is theorised that the wetland vegetation will bio-manipulate the wastewater providing a tertiary means of treatment. The attenuation process is enhanced by prolonged contact between the wetland vegetation and the wastewater allowing plant and microbial communities to attenuate both nutrients and bacterial pollutants.

2.3. Description of the Nakivubo Wetland.

2.3.1. Location of the Nakivubo Wetland.

The Nakivubo wetland (Figure 2.3; Plates 2.6 – 2.10) is located between latitudes 00°17’ and 00°19’ N and longitudes 32°37’ and 32°39’ E on the northwestern shore of Lake Victoria, Uganda. The wetland lies at an altitude of 1135 m above sea level and is approximately 5 km outside Kampala, the capital city of Uganda.

The wetland forms a natural tropical perennial swamp covering an area of approximately 2,500,000 m^2. The wetland connects Kampala to Lake Victoria through the Inner Murchison Bay, a small, partially enclosed water body. The shores of the Inner Murchison Bay are dominated by swamp vegetation where the Nakivubo, Wankolokolo, Kansanga and Nakibega swamps all discharge into the bay. In comparison to the Kirinya wetland, the Nakivubo swamp covers a channel as opposed to a bay/lagoon. The Nakivubo channel is approximately 2.3 km in length and was constructed in the mid 1950’s to carry storm water from Kampala into Lake Victoria (Kansiime and Nalubega, 1999). The channel receives precipitation and wastewater from both natural and constructed tributaries, discharging on average approximately 103 000 $m^3\ d^{-1}$ into the Inner Murchison Bay.

The topography of Kampala describes a series of seven hill and valley complexes. The Luzira, Bugolobi and Bukasa ridges on the eastern, northern and western fringes of the swamp enclose the Nakivubo wetland. These ridges range from 50–80 m in height above the wetland. The wetland area surrounding the Bugolobi hill has been developed for housing and subsistence agriculture and there are also substantial tree plantations. The Luzira hill houses the Luzira Maximum Security Prison, where there are a series of six culverts discharging wastewater from the prison into the wetland. The Bukasa ridge has been subject to extensive residential development and small-scale open cast mining, producing hardcore used in road construction. The residential areas surrounding the Nakivubo wetland have placed significant population pressures on the wetland.

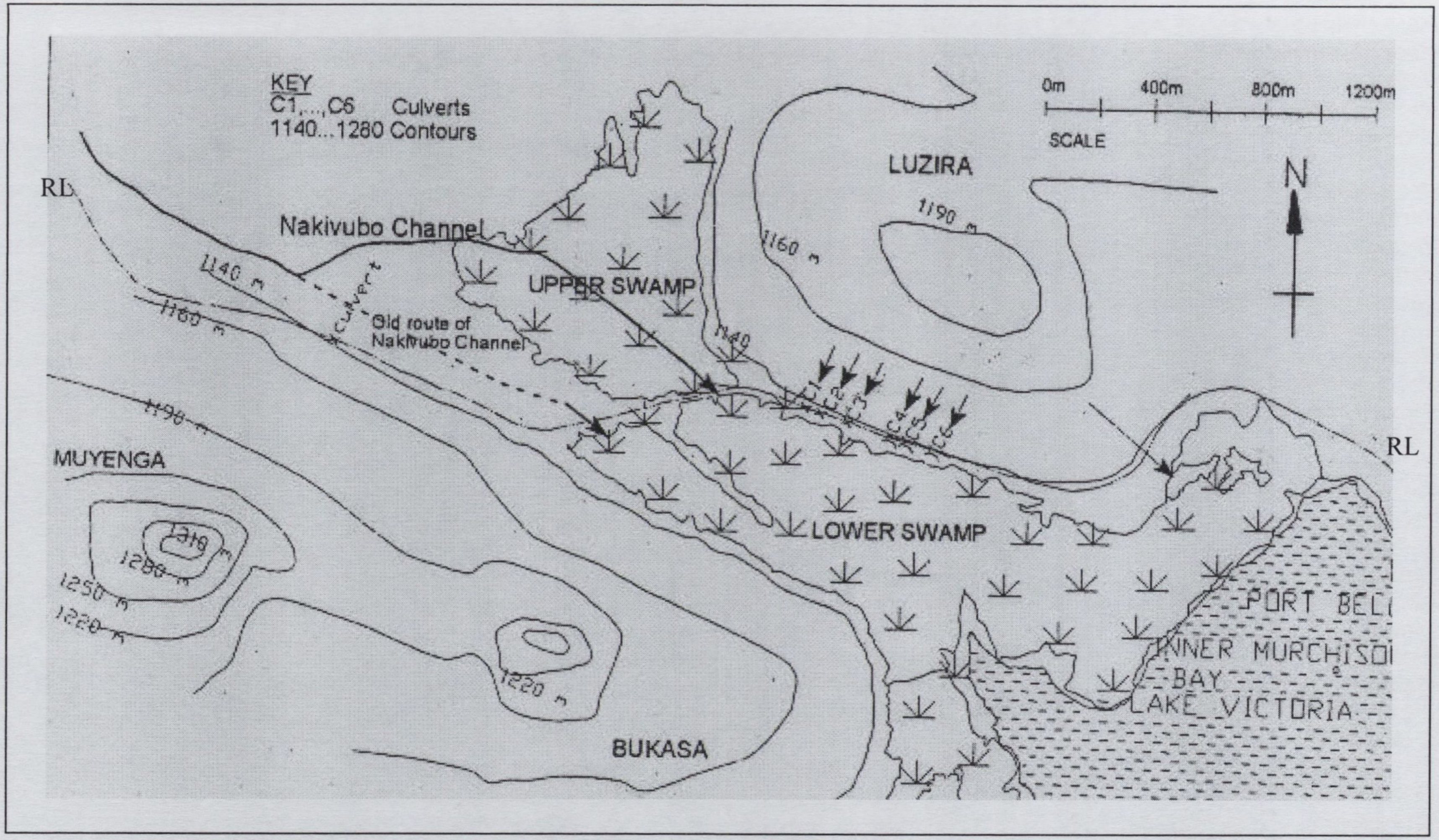

Figure 2.3. Map showing the Nakivubo channel and swamp. The swamp area is divided into upper and lower sections by the railway line (RL). Map shows the old and new Nakivubo channel and the discharge points of culverts from the Luzira Prison (C1 – C6). Map taken from Kansiime and Nalubega (1999).

Plate 2.6. The Nakivubo Wetland. Plate shows the upper section of the wetland (1) and part of the Bukasa residential development (2). Photograph taken from Bukasa Hill.

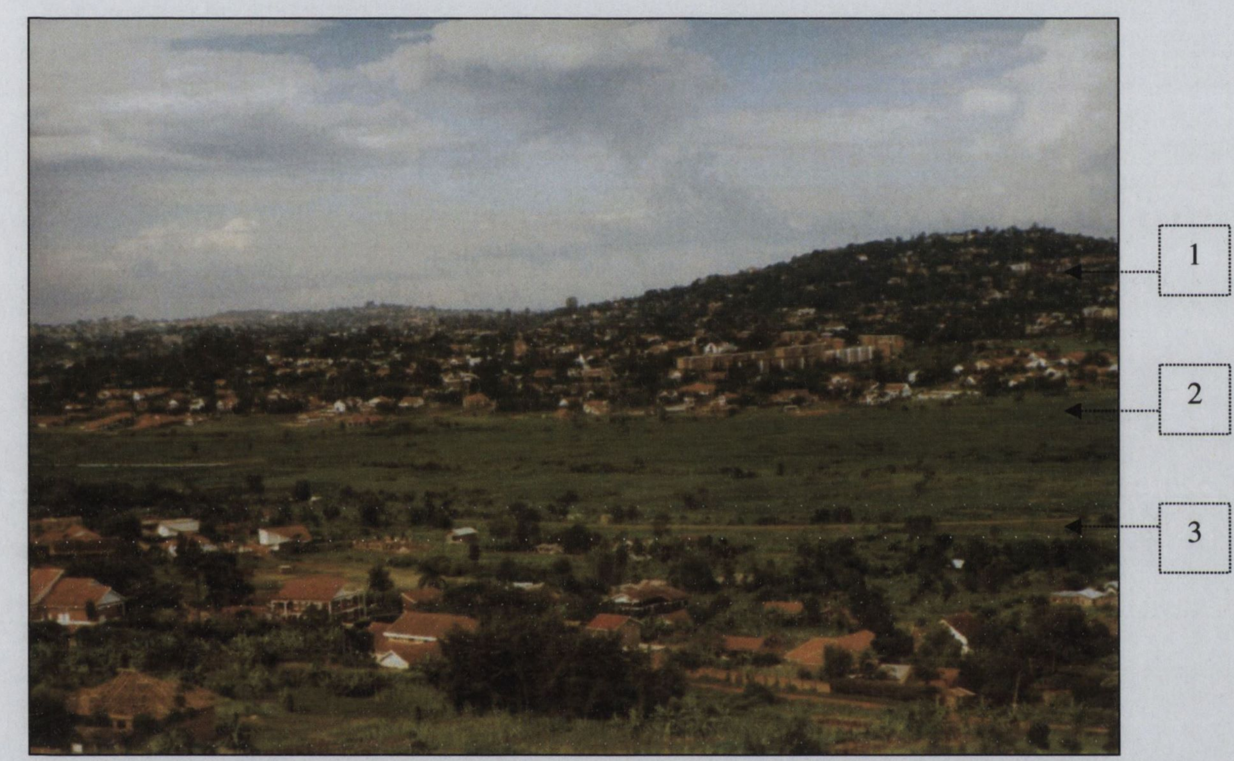

Plate 2.7. The Nakivubo Wetland. Plate shows the Bugolobi Hill (1) the upper section of the swamp (2) and the point at which the railway line moves west to east crossing the wetland (3). Photograph taken from Bukasa Hill.

Plate 2.8. The Nakivubo Wetland. Plate shows the middle section of the wetland where the railway line (1) separates the upper (2) and lower swamp (3). The Bugolobi Hill is pictured in the background. Photograph taken from Bukasa Hill.

Plate 2.9. The Nakivubo Wetland. Plate shows the lower section of the wetland (1) and the railway line (2) running along the northern fringe of the swamp. The Luzira Prison (3) is pictured in the background. Photograph taken from Bukasa Hill.

Plate 2.10. The Nakivubo Wetland. Plate shows the lake-ward fringe of the swamp (1) and the Inner Murchison Bay (2). The Port Bell Dock is visible in the background (3) as is the vegetation of the Wankolokolo swamp (4). Photograph taken from Bukasa Hill.

The encroachment on the wetland through the cultivation of subsistence crops such as *Colocasia antiquorum* has significantly altered the species composition of the wetland.

2.3.2. Geology of the Nakivubo Wetland.

The underlying geology of the Nakivubo wetland area is dominated by high to medium grade gneiss formations. This geological classification dates back to the Pre-Cambrian era, and are extensive throughout northern, central and southern Uganda. Similar to Kirinya, the soils of the Nakivubo wetland are dominated by alluvial and lacaustrine sands, silts and clays. The development of peat deposits at the Nakivubo wetland are not as extensive as those found at the Kirinya wetland. This is due to the high rates of discharge and the flood regime induced by the lake, which exports the organic detritus out into the main body of the lake. The Nakivubo wetland experiences a flushing regime, whereby freshwater seiches from the lake alter the water levels of the wetland, removing swamp water, solid particulate organic material and dissolved nutrients from the wetland (Kansiime and Nalubega, 1999).

2.3.3. Meteorology of the Nakivubo Wetland.

The climatic regime of the Nakivubo wetland exhibits similar trends to the Kirinya wetland near Jinja on the northern shore of the lake. The two wetlands are approximately 50 kilometres apart and experience relatively similar meteorological climes. Kampala receives a mean annual rainfall of between 1250 and 1375 mm; on a monthly basis maximum rates of precipitation fall in April and November with approximately 200 mm and 230 mm falling in each month respectively. The driest months occur in June and July with approximately 50 mm falling in each month respectively. The water levels within the Nakivubo wetland do however experience some perturbations as large volumes of water moving through the wetland are derived from overland flow and direct discharge. Also the movement of water into the wetland through lake induced seiches can alter the height of water levels within the swamp.

Temperature regimes again show little variation throughout the year. Kampala experiences maximum and minimum air temperatures of approximately 28°C and 16°C respectively. Mean maximum air temperatures are highest in January and February at 28°C, temperatures then fall from March through August to approximately 26°C, and then increase from September through December to 27°C. The mean minimum air temperatures show decreasing minimum temperatures from January through to September, where temperatures fall from 18 to 16°C. Minimum temperatures increase to 17 - 18°C through November and December.

2.3.4. Vegetation of the Nakivubo Wetland.

The vegetation of the Nakivubo wetland has been described by Kansiime and Nalubega (1999). This study *circa* 1999 described the vegetation of the Nakivubo wetland as being dominated by two species namely *Cyperus papyrus* L and *Miscanthidium violaceum*. The floristic description of the wetland was however segregated into several broad groups centred on dominant vegetation; the physical condition of the plants and the species associated with the principal vegetation types. The zonation of the major vegetation types of the Lower Nakivubo wetland is shown in Figure 2.4. The vegetative zones were classified as healthy papyrus, stunted papyrus, *Miscanthidium*, papyrus with *Phragmites*, *Ficus* spp., *Colocasia antiquorum* and swamp-lake interface vegetation.

The healthy papyrus zone dominates areas where wastewater flow is highest. The plants in this region range in height from 3-5 m depending on age class, and have characteristically large culm girths. Healthy papyrus form large monocultures and dense canopy structures, which restricts light penetration and reduces species composition at the rhizome mat. In areas where mature plants are dominant, the large reproductive umbel of the plants cause the papyrus to bend and lean especially in strong winds. This allows light penetration and favours opportunistic plant species, such as *Ipomoea rubens*.

Stunted papyrus plants are easily identified by their lower culm height of 2-3 m and light green through yellow culms and umbels. The parts of the Lower Nakivubo wetland covered by stunted papyrus are not generally influenced by wastewater flow, and tend to be inundated only during the wetter months of the year. The plant canopy in this region is much less dense and therefore allows the colonisation by opportunistic plant species.

The *Miscanthidium* zones of the Nakivubo wetland occur in large floating mats in the centre of the swamp. These areas exist due to the physical support of the papyrus rhizome, as *Miscanthidium* generally tends to prefer shallower frequently flooded areas. The *Miscanthidium* forms thick floating mats and tends to out-compete papyrus through the restriction of water and nutrient supply. It is suggested that the presence of *Miscanthidium* in the central part of the wetland is due to the increased water levels in Lake Victoria during the 1960's. Heavy rains at this time raised the level of Lake Victoria by approximately 2.5 m. Prior to this event it is hypothesised that the Nakivubo wetland was a marshland where *Miscanthidium* was more widespread and rooted to the substrate.

The presence of *Phragmites* within the central papyrus zone is again due to the physical support offered by the papyrus rhizome. *Phragmites* plants tend to reach height of approximately 3 m and are restricted to areas where floodwater or open water are not prevalent. In the central area of the wetland there is also a small strip of dense, established vegetation. This area is dominated by *Ficus trichopoda*, but also includes *Alchornea cordifolia*, *Maesa lanceolata* and *Briddelia bridelifolia*.

Large areas of the swamp periphery have been cleared for the cultivation of C*olocasia antiquorum* (Cocoyam). Accessibility of the wetland has largely influenced the areas used for cultivation, with the railway line offering stable access to most parts of the wetland.

The swamp – lake vegetation shows a floristic transition between the lake-ward edge of the papyrus swamp and the open water areas. This zone is dominated by floating aquatic vegetation such as *Vossia cuspidata*. In some areas this floating vegetation is so dense that it provides a stable footing for the papyrus rhizome to extend lakewards.

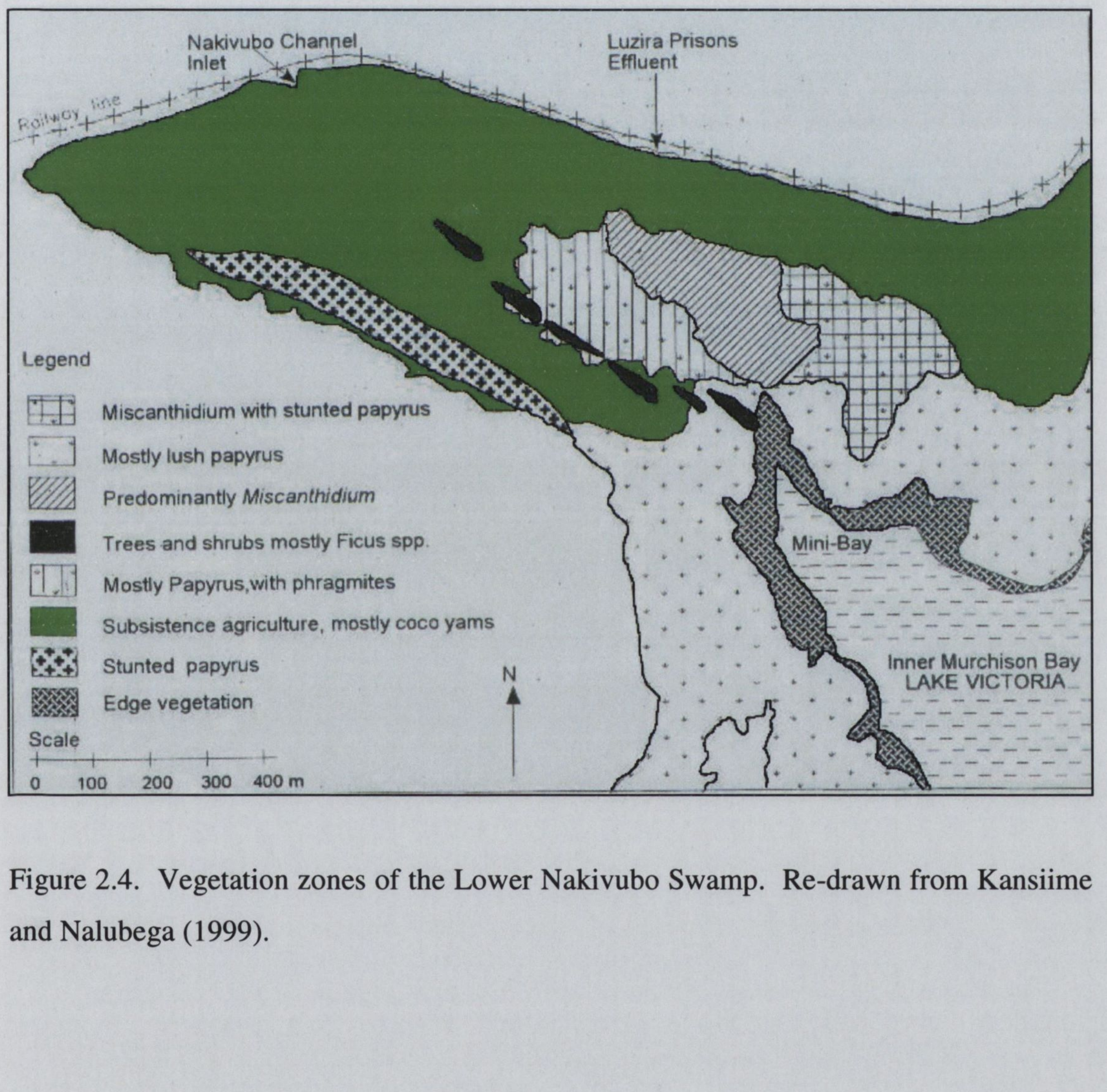

Figure 2.4. Vegetation zones of the Lower Nakivubo Swamp. Re-drawn from Kansiime and Nalubega (1999).

Population pressures and open access to the Nakivubo wetland region have, since 1999, lead to the extensive development of cocoyam agriculture. This study was based in the Lower Nakivubo Wetland from June to October 2004. At this point a large proportion of the healthy / lush papyrus and other zones in the central region of the lake had been cleared and converted to cocoyam plantations (Figure 2.4) with the exceptions of small, isolated outcrops of papyrus, *Miscanthidium* and *Ficus spp*.

2.3.5. Wetland Function.

The Nakivubo wetland has for the past 30 years been the recipient of both wastewater and storm water from the city of Kampala. On average the wetland receives and discharges a volume of approximately 103 000 m^3 d^{-1}. This discharge includes partially treated sewage from Kampala, raw sewage discharge from the Luzira prison, and effluent from the industrial zones surrounding Kampala including soap production, oil depots and abattoirs. The vegetation of the Nakivubo wetland is the only buffering component between discharge at source and release into the Inner Murchison Bay. Due to the flushing and mixing of water in the wetland through lacaustrine seiches, this wastewater discharge rapidly enters the main water body of Lake Victoria. This has direct implications for the city of Kampala as the main extraction point of drinking water for the city's populace is at the Gaba Water Treatment Works, approximately 4 km due south of the Nakivubo wetland.

The Nakivubo wetland is also an important source of raw materials for the local population. Papyrus plants are used for thatching and roofing materials in small basic hut buildings, and are also used to construct traditional African craft items, which can provide an important source of income. The wetland is also of importance for agricultural activities, the organic detritus that accumulates on the rhizome surface is used to cultivate cocoyam crops. The process of yam cultivation results in the clearance of large areas of papyrus, which reduces the physical stability of the rhizome mat. The extent of wetland degradation through cocoyam cultivation in the Nakivubo wetland has significantly increased since the study of Kansiime and Nalubega (1999). At this time agricultural cultivation in the Lower section of the swamp was located primarily around the swamp fringes, however the central body of the papyrus vegetation was gradually being removed (Figure 2.4). By mid 2004 most of the healthy papyrus in this central wetland area had been removed and converted into cocoyam agriculture, with only isolated patches of original vegetation remaining.

Chapter 3.

Standing Biomass and Productivity of *C. papyrus*. L dominated Wetlands.

3.1. Introduction

The primary productivity of ecosystems plays a pivotal role in the carbon cycle as it determines the carbon stocks and flows within an ecosystem. Emergent macrophytes cover only a limited area of the total continental land mass, but because they are highly productive their contribution to global primary production far outweighs their limited distribution (Muthuri *et al.* 1989). Tropical wetlands for example cover approximately 1% of the global land mass but contribute approximately 5% of global net primary production (Jones and Muthuri, 1997). In Uganda alone wetlands constitute 13% of the total land mass (Ikiara, *pers com*) and *Cyperus papyrus* L. tends to dominate permanently inundated African wetlands (Thompson, 1977). The standing biomass of papyrus wetlands is among the highest of all herbaceous (non-woody) plant communities (Jones and Muthuri, 1997). Measurements of plant biomass typically estimate the weight of living material contained within above ground and below ground compartments (Roberts *et al.* 1993). The distinction of plant vegetation into above and below ground components can present difficulties in the case of papyrus wetlands as a large percentage of the plant material constitutes a floating vegetative mat (excluding the perimeter of the wetland) and is therefore not rooted in a solid substrate. The above ground biomass component of papyrus vegetation is comprised of the culm, aerial scale leaves and umbel, while the below ground biomass consists of the rhizome and fine root structures.

Measurements of standing biomass and productivity of emergent macrophytes, have to date largely been focused on temperate wetland ecosystems (Muthuri *et al.* 1989). Definitive estimates of the biomass components and net primary productivity of papyrus dominated wetlands are relatively limited, and there are few published measurements comprised of unrestricted, long-term sampling which employ a standardised methodology (Jones and Muthuri, 1997; Muthuri *et al.* 1989). The current investigation therefore, attempts to quantify both the standing biomass and productivity of *C. papyrus* L. using the methodology described by Jones and Muthuri (1997), Muthuri (1985) and Muthuri *et al*. (1989).

3.2. Materials and Methods.

3.2.1. Study Site.

The study site for this work was the Kirinya West wetland near Jinja, Uganda (Figure 2.2). This site was also used for the EC flux measurements and estimates of biomass and primary productivity were made using quadrats located at random within the EC flux footprint.

3.2.2. Biomass Estimation.

Measurements of plant biomass in the Kirinya West wetland were made by randomly sampling six 3 m × 3 m quadrats, within the footprint used for carbon and water flux measurements. The above ground plant material in these quadrats was harvested and separated into live and dead material and weighed. A representative sub-sample from each quadrat was removed and the relationship between the culm girth and the dry weight of the culm units was determined. The linear regression analysis fitted to the culm girth and dry weight relationship for a range of culm-unit sizes (Figure 3.1) produced the following equation;

$$\text{Log}_{10} W = (2.42 \log_{10} G) - 0.11$$

Where;

W = dry weight (g) of culm units.

G = girth (cm) of the culm at the top of the scale leaves.

From this relationship the dry weight biomass of all the plant culms in the quadrat were calculated (Jones and Muthuri, 1997; Muthuri *et al.* 1989). Below ground biomass was estimated by removing a 1m × 1m section of papyrus rhizome within the original quadrats. The detrital material was removed and the rhizomatous material was divided into live and dead sections based on rhizome colour and the presence of live culm sections. The live rhizome material was separated from the fine root fraction and the fresh weight of all component parts were measured. Representative sub-samples were removed and dried to a constant weight at 80°C dry weights were then calculated for the rhizome sub-sample sections.

3.2.3. Estimation of Net Primary Production.

The Net Primary Productivity (NPP) of the above ground papyrus plant material at Kirinya was estimated using six 3 m × 3 m undisturbed quadrats, which were regularly measured over a period of six months. Tropical wetlands do not experience pronounced seasonal periods if growing, and therefore the recruitment, maturation and senescence of papyrus plants continue throughout the year (Muthuri, 1985). In order to calculate NPP, live culms of all age classes within the quadrats were labelled and the culm girth at the top of the sheathing scale leaves was measured. The quadrats were surveyed monthly and the culm girths of all existing live culms were measured and recorded. At each measurement interval new culm recruits were also labelled and recorded. NPP was estimated from the monthly increment in existing and new biomass, which was calculated using the relationship between the culm girth and the dry weight of the culm units (Figure 3.1).

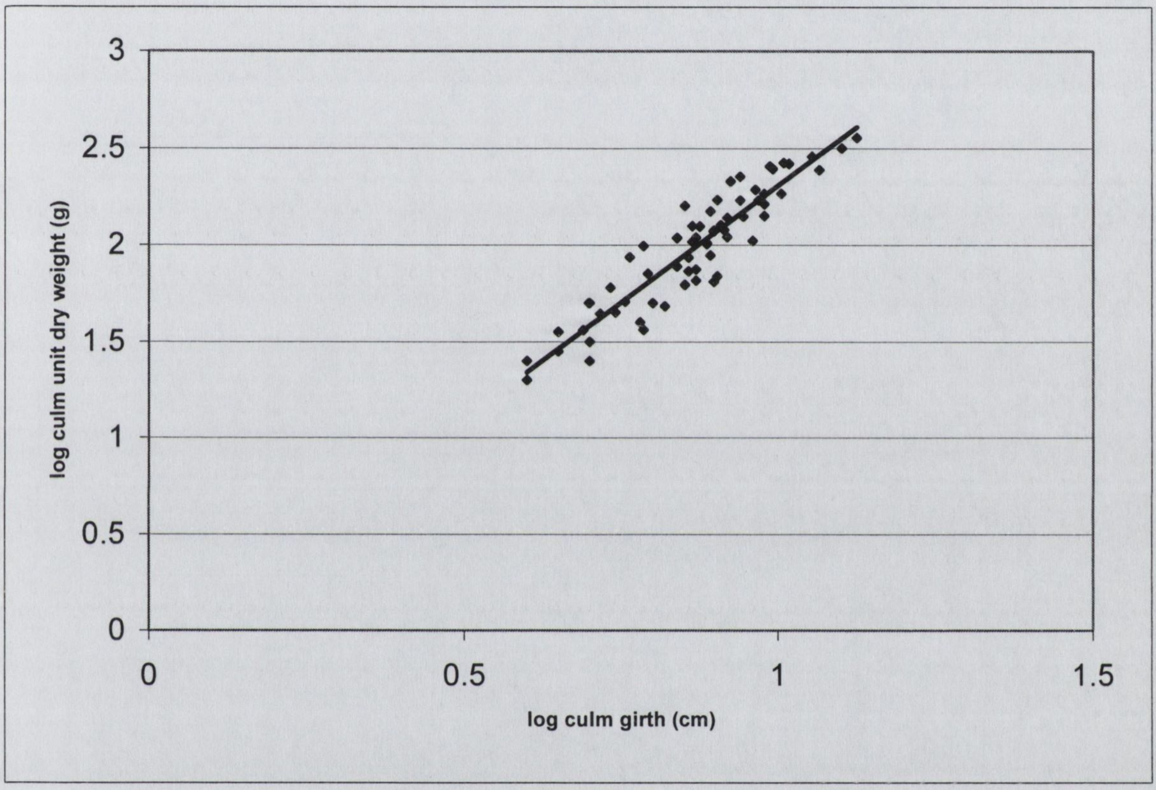

Figure 3.1. Relationship between papyrus culm-unit dry weight and the culm girth at the top of the sheathing scale leaves ($R^2 = 0.86$).

3.3. Results.

3.3.1. Biomass.

Figure 3.2 shows the dry weight of both above and below ground biomass of papyrus vegetation at the Kirinya West wetland. The aboveground biomass of the live papyrus plant units (scale leaves, culm and umbel) was 2.26 ± 0.29 kg DM m^{-2}, while the biomass of dead aerial plant material was 2.19 ± 0.94 kg DM m^{-2}. The below ground biomass component constituted 76% of the total live biomass with the rhizome and fine roots weighing 7.13 ± 1.3 kg DM m^{-2}. The biomass of the detrital deposits at the rhizome surface was 4.13 ± 0.74 kg DM m^{-2}.

These estimates of standing biomass are similar to previously published measurements made on other papyrus wetlands in Uganda, Kenya, Democratic Republic of Congo (DRC) and Rwanda. Figure 3.3 shows a comparison of biomass estimates from this study and previous measurements. These estimates of aerial biomass range from 1.06 kg DM m^{-2} on the Mulenda floodplain, DRC, to 5.17 kg DM m^{-2} at the Upemba Island, DRC (Thompson *et al.* 1979).

The monthly estimates of the mean live culm unit biomass of the papyrus vegetation at the Kirinya wetland are shown in Figure 3.4. The mean culm unit biomass for all the sampled quadrats ranged between 151–165g. The mean culm biomass of the papyrus plants showed little variation over the six month measurement period and suggest that there is little seasonal variation in standing biomass due to continual plant growth. A comparison of the mean culm unit biomass of papyrus vegetation from various sites across East Africa is shown in Figure 3.5. Published estimates of mean unit biomass of papyrus vegetation ranged between 67–367 g with the lower estimates recorded at the Mulenda Floodplain, DRC and the highest estimates recorded at Kampala, Uganda. The mean culm unit biomass of the papyrus vegetation at the Kirinya West wetland was in the lower part of this range at 157 g.

Estimates of culm density of papyrus vegetation at the Kirinya West wetland ranged between 7 and 21 m^{-2}. The mean culm density of the papyrus vegetation at this

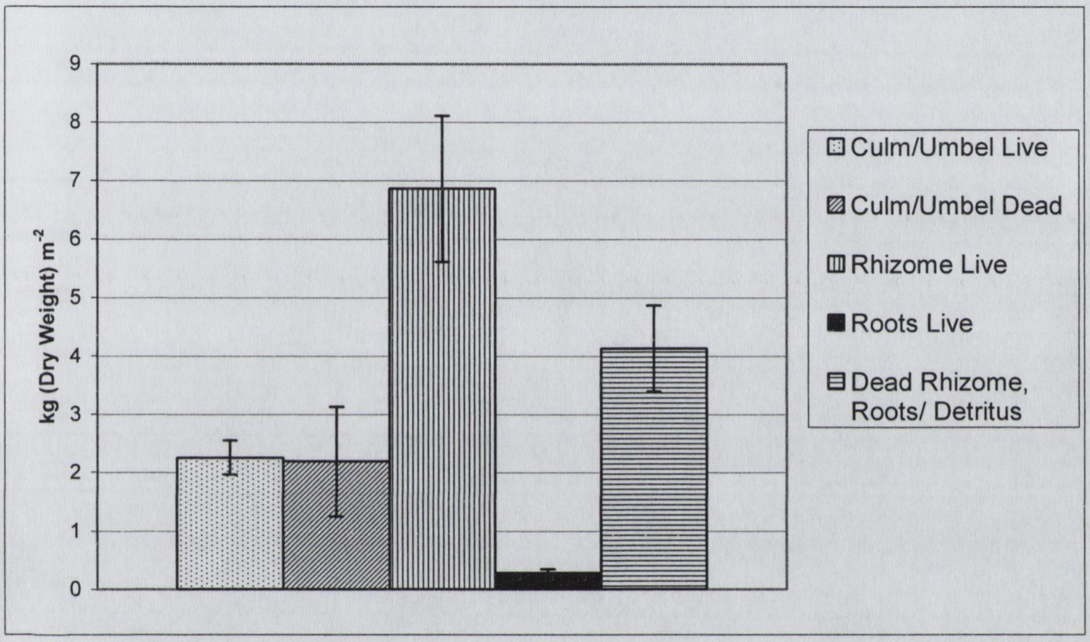

Figure 3.2. Mean biomass distribution of papyrus vegetation. Data represents both living and dead plant material from above and below ground biomass compartments. (Number of Quadrats = 6; Values ± SD)

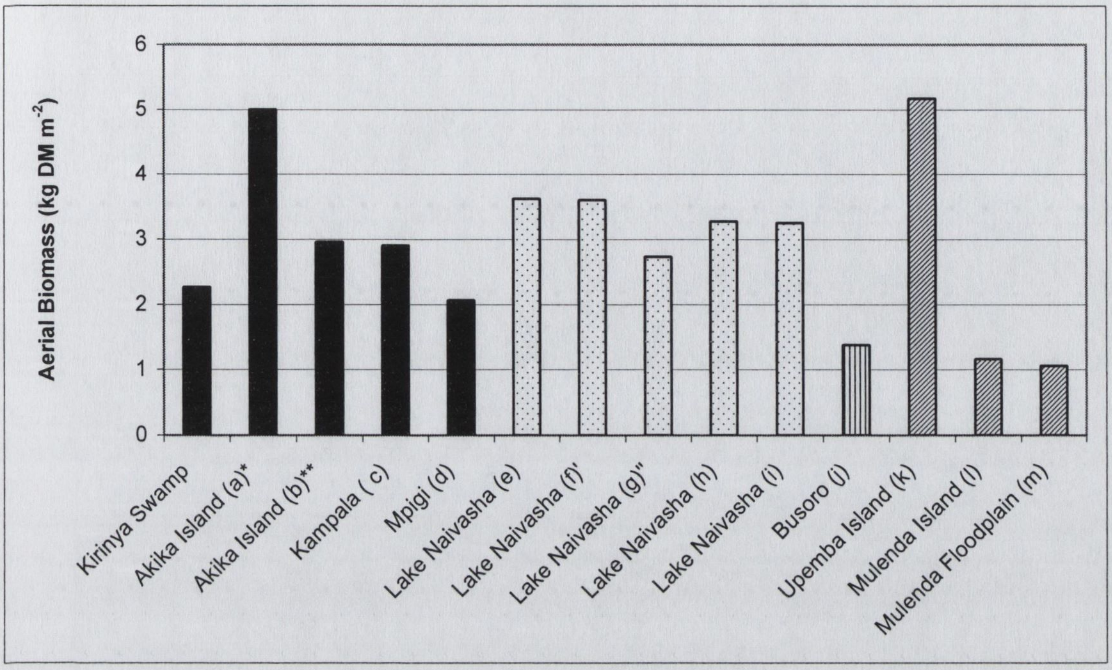

Figure 3.3. Mean estimates of the dry weight aerial biomass from papyrus dominated wetlands in Uganda, Kenya, Rwanda and Democratic Republic of Congo (see legend below).

■ Uganda

░ Kenya

▥ Rwanda

▨ Democratic Republic of Congo

Refs;
(a, b, c, k, l, m, Thompson *et al,* 1979)
(d, h, i, j, Jones and Muthuri, 1997)
(e, Muthuri, 1985)
(f, g, Muthuri *et al,* 1989)
* Measurements made at swamp fringe
** Measurements made at swamp interior
' Measurements made on undisturbed vegetation
" Measurements made on disturbed vegetation

site was 16 m^{-2}. A comparison of culm density estimates of papyrus vegetation at the Kirinya wetland and other African sites are shown in Figure 3.6. Estimates of culm densities in the East African region ranged between 7 and 23 m^{-2}, the lower estimates were recorded near Kampala, Uganda while the highest estimates were recorded on Upemba Island, DRC (Thompson *et al.* 1979). Estimates of culm density at the Kirinya wetland are similar to measurements made at other Ugandan wetlands, Mpigi (Jones and Muthuri, 1997) and Akika Island (Thompson *et al.* 1979).

3.3.2. Net Primary Production.

Estimates of aboveground net primary production (NPP) at the Kirinya West wetland are shown in Figure 3.7. The maximum estimate of NPP was 33.5 g m^{-2} d^{-1} while the minimum estimate was 14.3 g m^{-2} d^{-1}. The mean monthly NPP estimates over the test period ranged between 15.8 and 24.5 g m^{-2} d^{-1}, with an average NPP estimate of 21.2 g m^{-2} d^{-1}. Over the experimental period the papyrus vegetation showed patterns of increasing productivity for the first three months, (NPP increased from 17.4 to 24.5 g m^{-2} d^{-1} between June and August 2003) followed by patterns of decreasing productivity over the last three months. In most cases estimates of papyrus productivity at the end of the experimental period were of similar magnitude to estimates at the beginning of the experiment.

Estimates of aboveground NPP derived from this work and previously published data are shown in Figure 3.8. Rates of daily biomass increment range from 7.1 g m^{-2} d^{-1} measured on the Mulenda floodplain, DRC (Thompson *et al.* 1979) to 35 g m^{-2} d^{-1} at the Kahawa swamp, Kenya (Chale, 1987). The productivity of the Kirinya swamp at 21.2 g m^{-2} d^{-1} is lower than measurements of productivity made on other Ugandan papyrus wetlands.

Thompson *et al.* (1979) suggested that differences in the standing biomass of papyrus stands could be attributed to the prevailing climatic conditions (temperature, relative humidity), which change with altitude. Table 3.1 summarises data on the aerial biomass, productivity and culm density of papyrus wetlands located at a range of

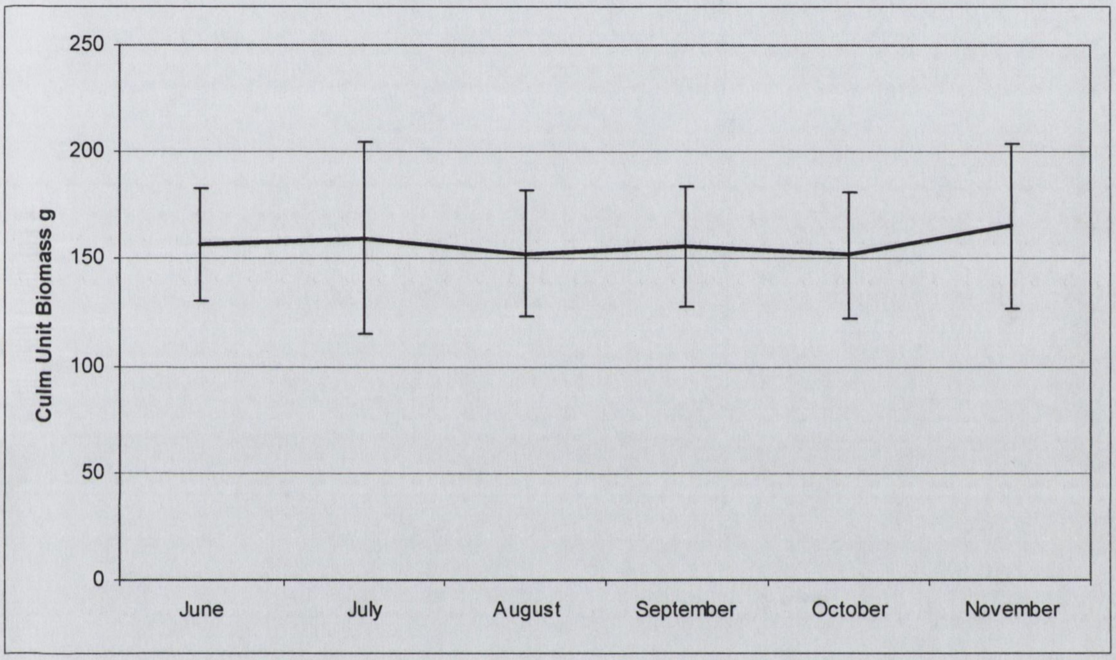

Figure 3.4. Mean monthly culm unit biomass of papyrus vegetation at the Kirinya West wetland, Uganda. Error bars represent ± S.D (n=6).

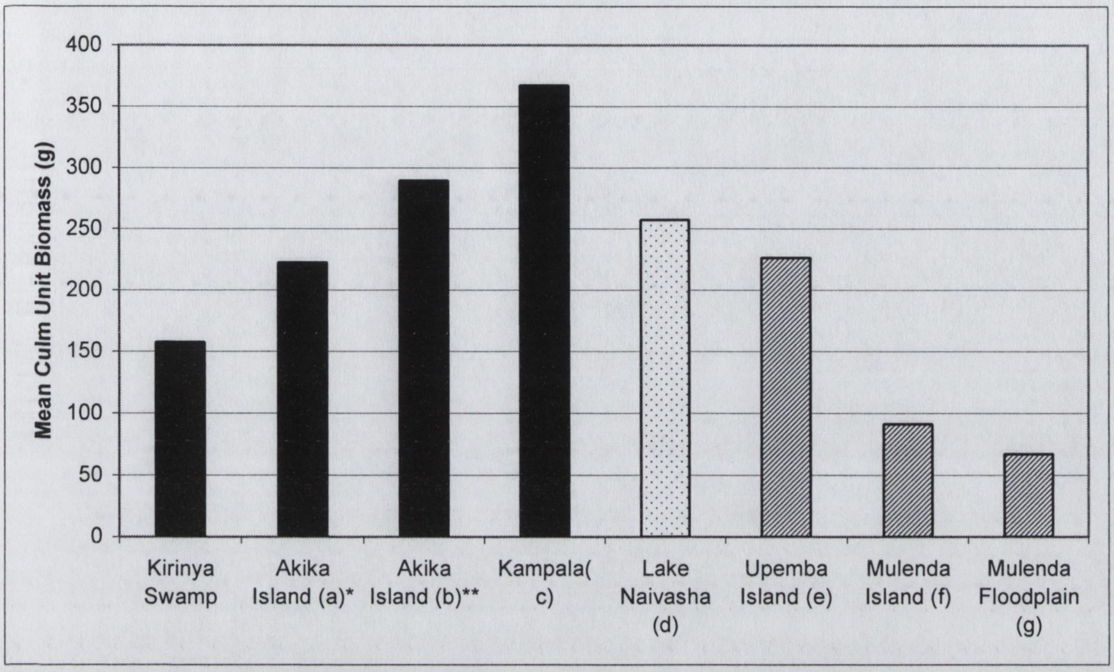

Figure 3.5. Mean culm biomass of papyrus vegetation at wetland sites in Uganda, Kenya and Democratic Republic of Congo (see legend below).

■ Uganda

⁘ Kenya

▨ Democratic Republic of Congo

Refs;

(a, b, c, e, f, g, Thompson *et al*, 1979)

(d, Muthuri, 1985)

* Measurements made at swamp fringe.

** Measurements made at swamp interior.

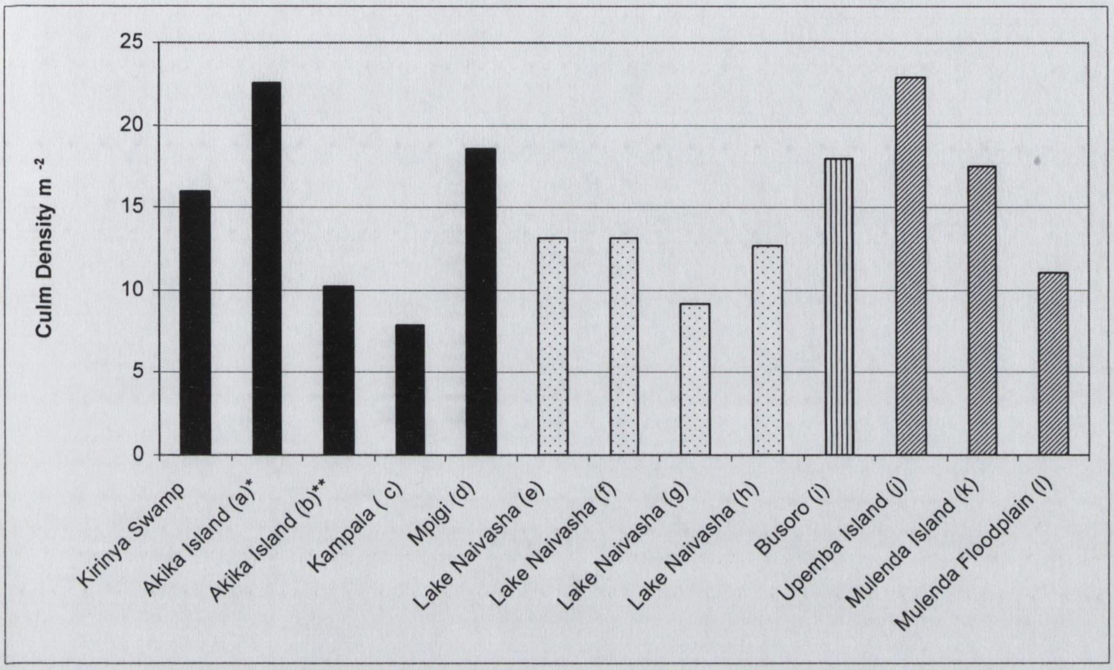

Figure 3.6. A comparison of mean culm densities of papyrus vegetation at wetland sites in Uganda, Kenya, Rwanda and Democratic Republic of Congo (see legend below).

■ Uganda

⁘ Kenya

▥ Rwanda

▨ Democratic Republic of Congo

Refs;

(a, b, c, j, k, l, Thompson *et al*, 1979)

(d, h, i, Jones and Muthuri, 1997)

(e, Muthuri, 1985)

(f, Muthuri *et al*, 1989)

* Measurements made at swamp fringe

** Measurements made at swamp interior

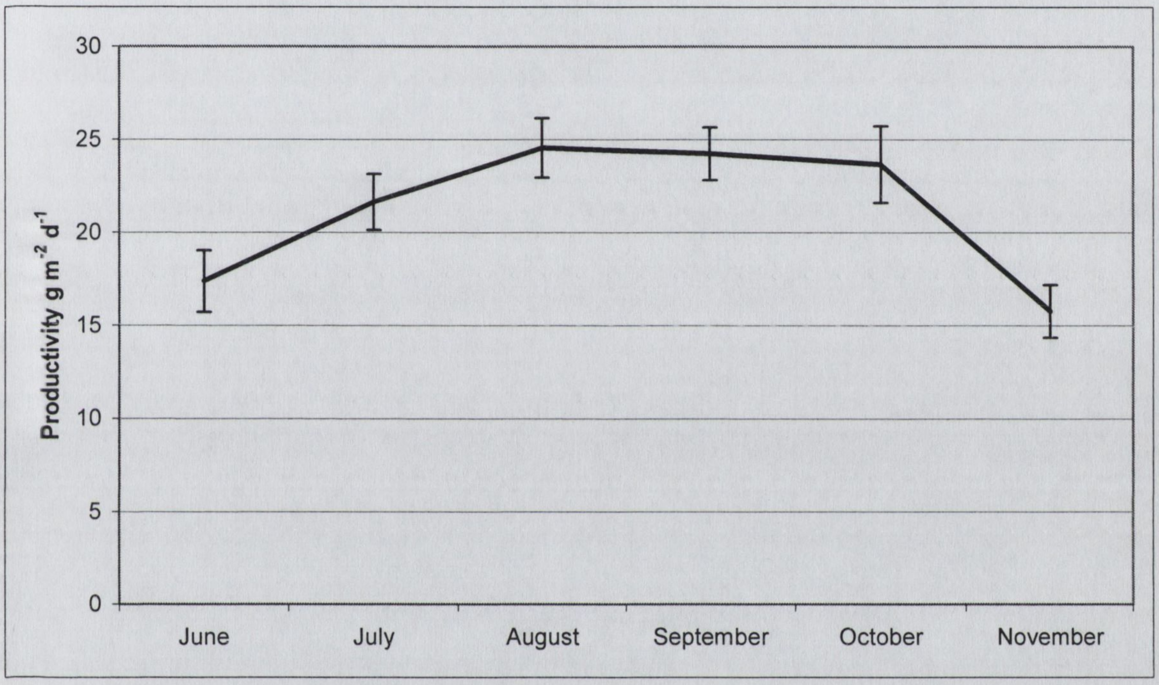

Figure 3.7. Mean net primary productivity of papyrus vegetation at the Kirinya West wetland, Uganda. Error bars represent ± SD (n=6).

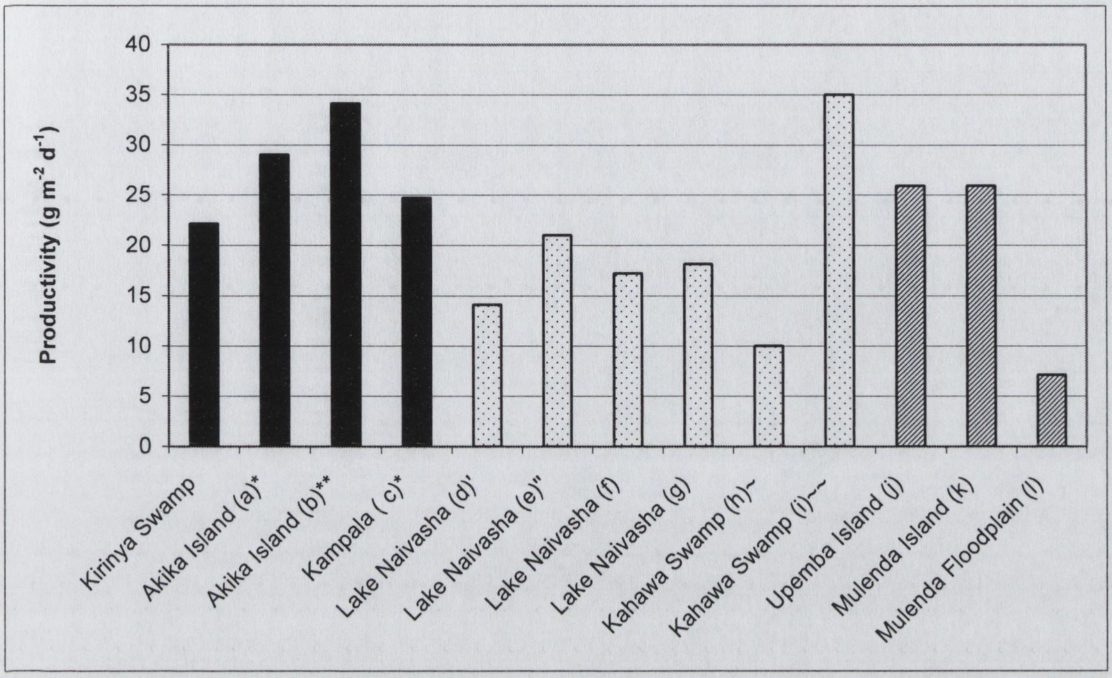

Figure 3.8. Mean productivity of papyrus vegetation at wetland sites in Uganda, Kenya and Democratic Republic of Congo (see legend below).

■ Uganda

⬚ Kenya

▨ Democratic Republic of Congo

Refs;

(a, b, c, j, k, l, Thompson *et al*, 1979)

(d, e, Muthuri *et al*, 1989)

(f, Jones and Muthuri, 1997)

(g, Muthuri, 1985)

(h, i, Chale, 1987)

* Measurements made on swamp interior

** Measurements made on swamp fringe

‘ Measurements made on undisturbed vegetation

“ Measurements made on disturbed vegetation

~ Lower estimate

~~ Upper estimate

Table 3.1. Standing biomass, net productivity and culm density of papyrus stands at sites in Uganda and Kenya.

Site Name	Country	Altitude m asl	Aerial Biomass kg m^{-2}	Productivity g m^{-2} d^{-1}	Culm Density (Culms m^{-2})
Kirinya Swamp	Uganda	1175	2.26	22.14	22.14
Kampala	Uganda	1135	2.9	24.7	7.9
Mpigi	Uganda	1134	2.06	N.D	18.6
Kahawa Swamp	Kenya	1605	4.96	17.5	N.D
Lake Naivasha	Kenya	1890	3.27	17.2	9.2
Lake Naivasha	Kenya	1890	3.60	13.1	14.1
Lake Naivasha	Kenya	1890	3.62	18.1	13.1

altitudes in Uganda and Kenya. The data confirms that there is a general trend of increasing aerial biomass but decreasing productivity with increasing altitude.

3.4. Discussion.

The combined above and below ground live papyrus biomass at the Kirinya wetland was 9.39 kg DM m^{-2}. A value of 7.8 kg DM m^{-2} was recorded for a papyrus swamp located on Lake Naivasha, Kenya (Jones and Muthuri, 1997). Previous measurements of standing biomass of other macrophytic species have included *Phragmites communis* at 2.2-9.5 kg DM m^{-2} (Muthuri, 1985) and *Echinochloa polystachya* at 7.64 kg DM m^{-2} (Morison *et al.* 2000). The combined live biomass of papyrus at the Kirinya wetland is high for herbaceous vegetation, however Jones and Muthuri (1997) suggests that detrital deposits one metre in depth contain approximately twenty times the live standing biomass. The estimates of mean culm unit biomass at the Kirinya wetland (Figure 3.4) varied little throughout the six month measurement period. Papyrus wetlands do not exhibit annual growth cycles (Muthuri *et al.* 1989) and the recruitment, maturity and death of papyrus culm units occurs continually throughout the year.

Previous measurements of NPP on emergent macrophytes have shown wetlands to be highly productive ecosystems (Jones and Muthuri, 1997). The NPP of the Kirinya wetland was estimated to be 8.08 kg m^{-2} y^{-1}, this value is higher than measurements made on a papyrus wetland, Lake Naivasha, Kenya, where a NPP of 6.28 kg m^{-2} y^{-1} was measured (Jones and Muthuri, 1997). However previous measurements of the NPP of papyrus wetlands have utilised different methodologies, producing varied and potentially unreliable estimates (Figure 3.8). This study used the methodology standardised by Jones and Muthuri (1997), Muthuri (1985) and Muthuri *et al.* (1989), in an attempt to produce a comparable measurement of NPP. Other tropical emergent macrophytes such as *Echinochloa polystachya,* a C4 macrophytic floating grass found extensively in the Amazonian floodplains, has shown NPP estimates as high as 10 kg m^{-2} y^{-1} (Morison *et al.* 2000). The high rates of annual NPP reported for tropical emergent macrophytes are largely due to the sustained daily productivity of the plants throughout the year. Tropical regions experience little seasonal variation in the climate, for example the papyrus vegetation at the Kirinya wetland experience high rates of solar insolation, high temperatures and permanent inundation all year round. The papyrus vegetation has several attributes that maintain high rates of NPP, which include the utilisation of the C4 photosynthetic pathway, high nutrient efficiency, a closed canopy structure ensuring the interception of approximately 90% of incident PAR and the permanent inundation of the wetland results in low rates of water stress. The monthly mean NPP estimates of the papyrus vegetation at the Kirinya West wetland (Figure 3.7) showed a period of increased productivity between July and October. Statistical analysis of this data using a two-way analysis of variance (ANOVA) and the Scheffe post-hoc test showed that there was a significant difference in rates of NPP ($p \leq 0.05$). This suggests therefore that papyrus dominated wetlands may exhibit periods of elevated productivity, under relatively stable meteorological conditions.

The allocation of biomass production between above and below ground components showed a large proportion, approximately 76%, allocated to the rhizome and fine roots. High rhizome to shoot ratios are typical of perennial emergent macrophytes such as *Typha latifolia* and *Phragmites communis* (Muthuri, 1985), and the value reported here is higher than those reported by Jones and Muthuri (1997) where 58% of the total standing papyrus biomass was allocated to the belowground component. The estimate of biomass allocation reported also conflicts with estimates made by Muthuri (1985) where 78% of the total biomass was reported to be concentrated in the above ground components of the scale leaves, culm and umbel, with the remaining 22% allocated to the belowground biomass component.

The mean culm unit biomass of papyrus vegetation gives an indication of both plant stature and the prevailing environmental conditions, where the plants exhibit larger culm unit biomass under favourable growth conditions (Muthuri, 1985; Thompson *et al.* 1979). Figure 3.4 shows the mean monthly culm unit biomass for the papyrus vegetation at the Kirinya West wetland. Statistical analysis of this data using two-way ANOVA and Scheffe post-hoc test showed that there was no significant difference in the average standing culm biomass over time. The continual recruitment theory (Muthuri, 1985) suggests that the average live culm biomass per unit area of papyrus wetlands remains stable due to the continual turnover of plant material, i.e. as mature plants start to senesce juvenile plants start to emerge. The culm biomass measurements made at the Kirinya wetland supports this theory.

Figure 3.5 shows the mean culm unit biomass for a range of papyrus wetlands in Uganda, Kenya and DRC. The mean culm unit biomass of the papyrus vegetation at the Kirinya wetland was 157 ± 2.1 g, this value falls below the range reported by Thompson *et al.* (1979) for Ugandan papyrus wetlands of 222–367g, and below measurements made on Lake Naivasha, Kenya of 257g (Muthuri, 1985). Considering the relationship between culm stature and nutrient availability as suggested by Muthuri (1985) and Thompson *et al.* (1979) the Kirinya West wetland appears, in part to be a relatively nutrient poor wetland. However, the Kirinya wetland would be expected to have a high nutrient status as the wetland receives secondary treated wastewater from the town of Jinja. It is possible that the relationship between nutrient status and culm stature is not represented in the Kirinya wetland data due to sampling error, a product of both the limited quadrat size and specific sample location within the EC footprint.

Figure 3.3 shows measured differences in the standing biomass of papyrus vegetation from various wetland sites in Uganda, Kenya, Rwanda and DRC. The differences have been attributed to the localised climatic conditions associated with wetland altitude (Muthuri, 1985; Muthuri *et al.* 1989; Thompson *et al.* 1979), and these authors suggest that there is a climatically determined optimum for papyrus biomass at specific altitude. Table 3.1 suggests a general trend of increasing biomass but decreasing productivity in relation to increasing altitude based on a selection of papyrus wetlands across Kenya and Uganda, due largely to differences in temperature regimes.

Chapter 4.

Fluxes of Carbon, Water and Energy.

4.1. Introduction.

The importance of carbon, water and energy fluxes for the functioning of vegetative ecosystems is highlighted within a large body of research on this topic (Ehman *et al.* 2002; Grace *et al.* 1996; Hunt *et al.* 2002; Jones and Humphries, 2002; Morison *et al.* 2000; Nieveen *et al.* 2005; Wang *et al.* 2004). Carbon dioxide, water vapour and solar radiation play an integral role in both the biology and climate of our planet. The presence of carbon dioxide and water vapour in the atmosphere has a direct effect on the Earths' climate at both the regional and global scale, through the absorption and re-emission of infrared energy (Baldocchi *et al.* 1996). The dramatic increases in measured CO_2 concentrations within the atmosphere over the past 150 years can have both beneficial and adverse impacts on the source to sink relationship of C within ecosystems. For example increased concentrations of CO_2 contribute to the "Greenhouse Effect" facilitating increases in global temperatures and changes to climatic regimes on both a local and global scale. The resulting changes in temperature and moisture regimes can have a direct impact on plant systems, as habitat ranges could alter or competition factors might allow the introduction of invasive plant species into a previously stable habitat. In addition, elevated levels of CO_2 within the atmosphere might stimulate increased rates of photosynthesis, which in theory would increase the rate of carbon sequestration and thus strengthen carbon sink potential. However increased photosynthesis can also lead to increased water loss through evapotranspiration, which influences the canopy water balance and localised climatic conditions.

Wetlands form a biological ecotone between aquatic and terrestrial ecosystems, and cover between 900 to 1024 million hectares, or approximately 5 to 7 % of the Earths surface. Wetland ecosystems also exhibit significant biological diversity and are highly productive when exploited as agricultural areas (Neue *et al.* 1997). In addition wetlands are potentially significant reservoirs of carbon as a result of the formation of peat deposits under anaerobic waterlogged conditions. The total global wetland C stock is estimated to be 240 PgC, of which 94% is located in wetland soils and detritus and the remaining 6% is located in the plant biomass (IPCC, 2001). However these estimates may be on the conservative side because they are based on assumptions that carbon deposits do not exceed 1m in depth. Although there are many observations of peat deposits that are at least 5 to 10m deep (Jones and Muthuri, 1997).

The hydrological cycle plays an important role in maintaining the physical structure and function of wetland areas (Kansiime and Nalubega, 1999). In the Lake Victoria basin precipitation is the primary hydrological input, as approximately 90% of the water entering the lake is derived from direct precipitation (Carter, 1955). The influence exerted by emergent macrophytic vegetation on the hydrological cycle is manifested through evapotranspiration, the exchange of water vapour between the plant canopy and the atmosphere. Although very large amounts of water are lost from wetlands through evapotranspiration there is a good deal of uncertainty surrounding the relative contribution of evaporation and evapotranspiration made to the hydrological cycle (Busch, 2000; Idso and Anderson 1988; Humphries, 2003; Jones and Humphries, 2002; Linacre, 1976; Linacre, 1993; Rijks, 1969; Sanchez-Carrillo *et al.* 2004). The exchange of water vapour between plant canopies and the atmosphere is a topic of significant importance where emergent macrophytic plants are perceived to be a source of competition for freshwater, especially in areas where water resources are in short supply (Humphries, 2003).

The process of transpiration is a consequence of a plants requirement to absorb CO_2 in order to photosynthesise. The diffusion of CO_2 through the stomata exposes large areas of moist cell walls to the atmosphere creating a water potential gradient between the plant and the atmosphere, across which water is lost from the plant (Sutcliffe, 1979). There are several environmental factors that regulate the rate of water loss from plants, including light intensity, relative humidity, temperature and wind speed. Plants do however have the ability to control transpiration, through the regulation of stomatal conductance (Mackay *et al.* 2003).

The atmospheric concentration of water vapour responds to changing temperature, physical processes and atmospheric circulation (IPCC, 2001a). The loss of water vapour from plant canopies through evapotranspiration has potential feedback implications in long-term climate variability, through changes in the emission of outgoing long-wave radiation and changes in atmospheric temperatures.

4.2. Eddy Covariance Technique.

4.2.1. Eddy Covariance Theory.

The eddy covariance (EC) technique has been comprehensively described by Aubinet *et al*. (2000) and Moncrieff *et al.* (1997). The EC system measures the fluxes of gas scalars into or out of a plant ecosystem associated with the turbulent diffusion of air over the plant canopy. This technique measures the three dimensional components associated with the turbulent movement of air and combines this information with the analysis of gas scalar concentrations, to produce "real time" flux estimates. As described by Moncrieff *et al.* (1997) the flux of any gaseous scalar can be described as;

$$F_c = \overline{w p_c} \qquad (1)$$

Where, F_c describes the flux density of the gas scalar ($_c$), w represents the vertical wind speed and p_c describes the concentration of the gas scalar ($_c$). The overall mean product of the sampling period is then described, and is detailed by the overbar in Eq. (1). The parameters of wind speed, temperature and gas scalar concentration all exhibit uneven form over time, and thus should be expressed according to Reynolds decomposition whereby such variables are considered to be fluctuating and thus are represented as the sum of a mean value. Primes are therefore used to incorporate the fluctuation around a mean value. By including these primes, the EC equation can be expressed as Eq. (2),

$$F_c = \overline{w}\ \overline{p_c} + \overline{w'p_c'} \qquad (2)$$

In theory the numeric values of the primes w' and p_c' will be equal to zero however in practice the mean product of fluctuating parameters will seldom be equal to zero. Because of this correction terms are introduced into the EC equation to produce Eq. (3),

$$Fc = \overline{w'pc'} + \text{correction terms} \qquad (3)$$

The EC system can be operated in one of two ways. Either the instrumentation is measuring the three dimensional components of wind and the concentrations of gas scalars in real time, which are analysed to produced block averaged flux estimates. Or the system collects the relevant data in its raw format, facilitating analysis and flux estimations at a later time.

There are two basic components to an EC system, a three dimensional sonic anemometer and an infrared gas analyser. The sonic anemometer collects information regarding the turbulent movement of air in the three dimensional planes (u, v, w,) based on the time-of-flight principal. Sonic pulses are emitted from the transducer heads, the reciprocal transducer registers the arrival of the sonic signal and the transit times recorded allow the calculation of parameters such as orthogonal wind speed and the virtual air temperature. The covariance between the vertical wind speed and temperature fluctuations allows the calculation of sensible heat. The infrared gas analysers used in EC studies operate in either open or closed path modes. The open pathway gas analyser utilises an infrared optical bench that is exposed to the atmosphere, and turbulent fluxes are able to passively move through the infrared beam. The closed pathway analyser, operates using an optical bench closed to the atmosphere and housed within the analyser. In this case a mass flow controller is used to draw gas samples from the atmosphere into the optical bench. Both analysers operate based on the principal that molecules of CO_2 and H_2O are absorbed by infrared light at different wavelengths. Separate detectors are used to measure CO_2 and H_2O concentrations within the air. These detectors use optical interference filters set to 4.26 μm with a bandwidth of 0.15 μm in the case of CO_2 detection and 2.59 μm with a bandwidth of 0.15 μm in the case of H_2O detection.

The alternative types of analyser used in EC studies present their own particular disadvantages for data collection. EC measurements conducted using a closed pathway analyser incur several problems in simply moving the gas sample from source to the optical bench. This system dictates that the air parcel to be analysed is drawn from the atmosphere close to the sonic anemometer, in order to ensure its association with the turbulent process measured. The sample is pump-drawn through a length of Dekabon™ tubing into the optical bench. The length of tube used in this system has little influence on the scalar sample, however the tube diameter can influence the flow rate and thus the lag time of the sample between atmosphere and analyser. In addition the diameter of the tube can dictate whether the air sample flows through the tube in laminar or turbulent fashion. The lag times of samples are of importance when calculating flux estimates, as the scalar concentrations have to be aligned to specific turbulent episodes. Mass flow controllers are used to control the flow rate of sample gas being pumped through the optical bench. Pushing air through a closed cell creates a pressure differential between the optical bench and the surrounding atmosphere. The formation of such a pressure differential can alter CO_2 concentrations within the optical bench and can also lead to the condensation of water vapour within the sample tube.

The optical bench of the open pathway infrared gas analyser is exposed to the atmosphere and therefore eliminates the problems associated with moving a gaseous sample from source to the point of analysis, as occurs with the closed path system. There are however a number of drawbacks in using an open path sensor, these include the need to continually measure the simultaneous fluxes of latent and sensible heat in order to apply density corrections, significant diurnal temperature variation can cause instability in instrument calibration and the exposure of the optical bench to the atmosphere allows the accumulation of water and particulate debris on the lenses which can distort the infra-red beam (Leuning and Judd, 1996). Water in particular is a problem, as it tends to refract the infrared beam while the build up of dirt gradually reduces the intensity of the beam to a point whereby adequate detection is no longer possible. Due to the open nature of the analyser the infrared beam is also subject to disturbance by insects for example, which creates gaps within the data stream.

There are two particular sets of problems that arise when calculating fluxes measured by EC techniques, and these relate to the correction terms presented in Eq. 3. Fluctuations in gas scalar concentrations are produced through the transfer of both latent and sensible heat. Corrections are then applied to the data, which relate changes in the temperature and partial pressure of sample gas within the optical bench of an infrared gas analyser to the scalar concentration of the sample (Webb *et al.* 1980). The data is normalised to take account of the differences between the density of the gas scalar in atmospheric air and the sample within the optical bench. The formation of a pressure gradient between the optical bench of the open path analyser and the surrounding atmosphere seldom occur, however it is important to correct latent heat fluxes considering the partial density of CO_2 and H_2O in air (Moncrieff *et al.* 1997; Webb *et al.* 1980).

Additional correction functions have to be applied to accommodate the influence the instrumentation has on the data produced. The frequency response time of the EC equipment dictates that there will always be a lag between scalar source and detection, and regardless of instrument response time it is nearly impossible for the sonic anemometer and gas analyser to sample the same parcel of air.

Co-spectral models are utilised to relate both the normalised and natural frequencies of scalar detection to the horizontal wind speed and zero plane displacement, for both stable and unstable atmospheric conditions. The model equations cited by Moncrieff *et al.* (1997) are adapted from Kaimal *et al.* (1972) and Moore (1986). These co-spectral functions highlight the problems encountered in sampling scalar flux densities associated with turbulent episodes of varying frequency, and the importance of the sampling height above the zero-plane displacement. High wind speeds and low sampling heights favour the formation of high frequency eddies of which accurate sampling can be difficult, especially with closed pathway EC systems. Lower wind speeds and higher sampling heights produce the formation of lower frequency eddies which can underestimate the signal strength of a gas scalar by up to 20%. It is important therefore when deploying EC equipment in the field to consider the relationship between sampling height, average wind speeds and atmospheric stability, and the influence these factors can have on the data produced. These factors are then corrected for at each particular site through the application of co-spectral correction functions during the post-processing phase of EC data collection.

4.2.2. Eddy Covariance Site Selection.

The location of an eddy covariance system within an experimental field site is important when considering the representation of fluxes from an entire ecosystem. In order to quantify the source or sink potential of a particular ecosystem it is necessary to ensure that the flux source originates within this system and is covered by the fetch footprint of the EC system. Ideal EC sites should be both uniform with regards to vegetation cover and terrain, however if flux measurements are made over inhomogeneous terrain consideration pertaining to the selection and layout of sample sites and instrumentation is needed in order to comply with standards of footprint fetch and site homogeneity (Horst and Weil, 1992; Schmid, 1997). The footprint of an EC system describes the area over which the equipment measures and essentially allows the estimation of the flux source in relation to the frequency of the flux eddy. This footprint area changes in relation to the sampling height of the equipment, the wind speed, the frequency of eddy formation and the direction in which the wind is travelling, and can be determined using numerous analytical footprint models (Haenel and Grunhage, 1999; Hsieh *et al.* 2000). Essentially the higher the sampling point is above the zero plane displacement the larger the fetch footprint becomes. This however has implications with regards to the validity of the flux data as the flux source might originate from outside the sample site. The frequency of the eddy formation also influences the flux data, as high frequency eddies are related to more turbulent atmospheric periods and are associated with flux sources at distance within the fetch footprint, and low frequency eddies are associated with periods of atmospheric stability and produce flux estimates where the source originates adjacent to the EC equipment.

It is necessary for EC equipment to be suspended above the plant canopy in order to estimate flux transfer between the vegetation and the atmosphere, and this determines the extent to which these fluxes are representative of the ecosystem as a whole. The canopy structure of a plant species has a direct effect on the movement of air across it, as wind profiles within plant canopies are specific to each canopy type. For example, in mature forests canopies the majority of turbulent momentum will be absorbed in the upper part of the canopy where most of the leaves are situated (Arya, 2001). The roughness parameter describes the influence imposed on the flow of air by a plant, for example as air moves across the plant its movement is restricted by the aerodynamic resistance of the leaves. The degree of resistance present can then alter the frequency of the eddy or the height of the surface boundary layer above the plant canopy. The aerodynamic resistance of a plant canopy requires consideration when deploying EC equipment due to the alteration of aerodynamic turbulence within the surface boundary layer. The roughness length describes the influence the aerodynamic resistance of the plant canopy has on turbulent momentum, and is estimated to be approximately 10% of the height of the plant canopy. The point at which all turbulent momentum has been absorbed and the wind speed is effectively zero is described as the plane of zero displacement. The interface between a bare soil surface and the atmosphere is considered to act as the ultimate sink for turbulent momentum, however where plants are present they influence this relationship by effectively raising the plane of zero displacement to a point in the plant canopy where the wind speed is effectively zero (Grace, 1981). Where plants are present the zero plane displacement will be raised by approximately 65% of the height of the plant canopy.

The underlying topography and vegetation of an EC site can influence the overall estimation of scalar flux. Where the fetch footprint includes topographic features such as hills in forested areas, large proportions of the flux can be lost during stable atmospheric conditions and low frequency eddy formation. These conditions generally tend to occur during the night where high concentrations of scalar flux can accumulate beneath the plant canopy and can be missed by the EC system due to flux advection. However as atmospheric turbulence increases during the early hours of the day, where fluxes are not lost to advection "spikes" of high scalar concentration are recorded by the EC system.

It is also important to ensure that at least 95% of the flux footprint area is contained within a region of homogeneous plant canopy. Schuepp *et al.* (1990), describes an analytical simulation that allows the determination of the flux footprint of an EC system in relation to roughness length, zero plane displacement and relative wind speed. It is important to consider the flux footprint for both daytime and night time fluxes as the turbulence frequency will vary significantly, influencing the flux footprint further.

4.2.3. Post Processing and Gap Filling Eddy Covariance Data.

Data from EC studies are reported in averaged blocks ranging from 15 to 60 min in length, these data blocks are then accumulated over days, months and years. It is however not viable to accept EC data without critical analysis, as instrument malfunction, extreme weather and changes to the micrometeorological assumption adopted will require the rejection of certain data points (Falge *et al.* 2001; Massman and Lee, 2002). Long term EC data sets provide more accurate assumptions of total scalar flux, however typically only 65% of the data collected over a year will be useable after systems downtime and data rejection (Aubinet *et al.* 2000; Goulden *et al.* 1996). Therefore gaps in the EC data stream have to be filled in order to complete the data set and allow the estimation of total scalar flux over a long period of time. However, in order to make EC data sets comparable from different sites it is preferable to standardise gap filling procedures. Realistically, the procedures used are a function of the flux tower specifications, the physical conditions at the site and the expected end use for the data. The EUROFLUX methodology as described by Aubinet *et al.* (2000) details the basic quality control tests associated with EC data. According to the EUROFLUX methodology, prior to processing and analysis, raw flux data should be filtered in order to identify flaws within the data caused by instrument errors. Simple algorithms can be used to detect random spikes within the data caused by electrical interference with the instrumentation. After spike removal the flux data is subject to stationarity tests whereby the block averaged flux is divided into equal intervals and the covariance of the measured signal is determined. This is then compared with the covariance of the entire flux period. If the difference between the dispersion of the fluxes is less than 30% then the fluxes are assumed to be stationary, and the data is taken to be of high quality. Flux data with dispersion differences ranging from 30 to 60 % are assumed to be of acceptable quality. Having tested the stationarity of the fluxes the integral turbulence of the flux is then analysed. The EC system uses micrometeorological assumptions to determine the movement of wind in the vertical axis. There are however, certain parameters that influence this calculation, such as changes in turbulent velocity, temperature and changes to the depth of the surface boundary layer. The quality of the flux data is considered to be high if the difference between the integral characteristics of the vertical flux of wind as determined by the micrometeorological assumptions and the calculated value as determined in the field measurements differs by no more than 20 to 30%. It is also possible from the analysis of turbulent components to correlate the development of turbulent fluctuations in relation to the effects induced by non-homogenous terrain or mechanical obstacles.

It is possible to verify the plausibility of a filtered data set by attempting to close the energy balance at the test site (Aubinet *et al.* 2000). Accordingly the movement and conservation of energy within an ecosystem must adhere to the first law of thermodynamics. Therefore the sum of turbulent heat flux can be directly compared with the available energy flux within the ecosystem as a whole. The relationship between the incoming net radiation minus the storage heat flux and the sum of latent and sensible heat fluxes should produce a 1:1 relationship, if the energy balance is to be closed perfectly. However, in practice, specific meteorological conditions can produce errors within radiation fluxes and heat storage parameters. Unclosed energy budgets do not necessarily suggest that there are errors within the flux data, however they may indicate the presence of non-vertical turbulent fluxes, which result in the loss of night time fluxes especially through the process of subsidence and advection.

The process of data filtration and equipment downtime results in gaps within the data stream. The gaps in the data vary in duration, however they need to be filled in order to produce continuous long term data streams. Falge *et al.* (2001a; 2001b) have reviewed several gap filling strategies for defensible estimations of NEE based on long term EC flux data sets. At present gap filling strategies within the EC flux community are not standardised, which again introduces problems when making inter-site comparisons of NEE. However certain parties within the flux community such as the

CarboEurope IP initiative are attempting to standardise gap-filling methodologies. The three major gap filling methodologies as described by Falge *et al.* (2001a) include Mean Diurnal Variation (MDV) of prescribed flux periods, Look Up Tables (LUT) based on associated environmental conditions and patterns of Non-linear Regression between NEE flux components and associated factors controlling the flux period. The various gap filling techniques were applied to estimates of CO_2 and H_2O exchange across forests, grasslands and croplands sites that are a part of the EUROFLUX and AmeriFlux networks.

The MDV technique replaces missing data with an averaged flux value for the particular time stamp, based on flux data collected prior to and after the missing observation. In order to produce the MDV tables, the diurnal patterns of carbon flux are averaged in their half hourly form to produce a mean flux estimate for each time stamp in a diurnal curve. The data "window" used to create this mean estimate are taken from between 7 and 14 days prior to and after the missing data point. Two types of data window are discussed and are described as having either an independent or gliding window. The period of data used to create the MDV table using the independent window technique, is dictated by the size of the missing data gap. The MDV tables created using the gliding techniques, use data from a prescribed window size around the gaps in the data.

The LUT and non-linear regression gap filling techniques are both examples of semi-empirical gap filling methods, i.e. whereby the response of the flux data to parameters such as Photon Flux Density (PFD) and temperature are preserved. The LUT method predicts missing values of Net Ecosystem Exchange (NEE) based on the environmental parameters associated with the period of missing flux data. In Falge *et al.* (2001a) these tables were created for four periods throughout the year, to take account of seasonal environmental changes, and each seasonal category was divided into photon flux and temperature classes. The relationship between light response and carbon flux was analysed for a series of temperature regimes. These light response curves, as expected, showed a high degree of scatter within the projected data. This factor highlights the need to consider site specific conditions when using environmental data to predict potential flux estimates. Such conditions include time of day, water use efficiency and homogeneity of the flux footprint from which the data was derived.

Non-linear regression analysis utilises the relationship between NEE and driving parameters in order to estimate missing flux data. This method segregates data into seasonal periods and separates the data stream into daytime and night time blocks. The daytime data gaps can be filled using light response functions, such as the Michaelis-Menten or Misterlich functions. The driving parameters for these regression analyses were classified into three groups; the temperature range for a given time period; allocation of temperature grades based on a 4°C range; and a combination of flux response to both PFD and temperature. Gaps in the night time data stream can be filled using a series of different temperature response equations according to; Lloyd and Taylor; Arrhenius; and Van't Hoff (Falge *et al.* 2001a; 2001b). The contribution of night time carbon flux through leaf, bole and soil respiration can be estimated using the relationship between night time flux and localised air and soil temperatures.

4.2.4. Additional measurements associated with EC studies.

Eddy covariance measurements require the support of meteorological measurements in order to aid the gap filling process where data has been lost or rejected, and essentially to help understand the driving environmental parameters behind patterns of NEE. These measurements should be recorded at the time intervals as the EC data in order to facilitate accurate alignment between meteorological conditions and scalar flux. Depending on the ecosystem over which EC flux measurements are to take place, additional meteorological measurements should include; Net Radiation, Photosynthetic Photon Flux Density, Air and Soil Temperature, Ground Heat Flux Density, Precipitation, Relative Humidity, Soil Moisture Content and Atmospheric Pressure.

4.3. Fluxes of Carbon, Water and Energy over *Cyperus papyrus* L. dominated wetlands.

4.3.1. Introduction

Papyrus wetlands constitute the dominant aquatic ecosystem in East Africa, conservative estimates suggest that these wetlands cover approximately 40 000 km^2 (Jones and Humphries, 2002). The tropical climate, coupled with the C4 photosynthetic characteristics of papyrus, lead to the formation of highly productive, monotypic vegetative ecosystems. The EC technique allows the non-invasive measurement of GHG scalar flux, from inhospitable environments, over long periods of time. Previous research into the source and sink strength of greenhouse gases from papyrus dominated wetlands has been published by Jones and Humphries (2002). Their work focused on the fluxes of carbon, water and energy over a papyrus wetland on Lake Naivasha, Kenya, during periods of hydrological inundation and drawdown. The EC data collected during the investigation of Jones and Humphries (2003) and Humphries (2003) was the first known attempt to describe fluxes of carbon over wetland vegetation in Africa. The micrometeorological data collected from Lake Naivasha in these investigations was collected over a relatively short research campaign, and constitutes a continuous data set of 21 days. The current investigation is therefore one of the first attempts to characterise carbon fluxes from tropical wetlands using EC analyses on a long term basis.

4.3.2. Materials and Methods

4.3.2.1. Site Description

The EC measurements were made over a relatively pristine papyrus wetland at the Kirinya West wetland, near Jinja, on the northern shore of Lake Victoria, Uganda. As stated by Humphries (2003) it is difficult to construct and develop a safe, secure, long term experimental site due to the remote nature of the papyrus vegetation and political instability within the East African region. The site at Kirinya was selected and maintained with the help of Dr. F. Kansiime and Mr. B. Twesigye, of the Institute of the Environment and Natural Resources, Makerere University, Kampala, Uganda (MUIENR). The Kirinya West wetland is at present used by MUIENR for a long term European Union funded project (LVEMP) focused on the attenuation by papyrus wetlands of secondary treated wastewater. The continued use of this wetland area by MUIENR made the process of erecting the EC flux tower close to the local community relatively less problematic. The Kirinya West wetland is located close to the town of Jinja, however the Loco housing quarters (Figure 2.2) are within 200 m of the western shore of the wetland. In order to facilitate the help of the local community MUIENR employ several men to maintain the access transects across the wetland. As the EC equipment would be visible above the papyrus canopy, several individuals from the nearby housing quarters were included in constructing and maintaining the EC tower.

4.3.2.2. Field Measurements

Eddy Covariance

The EC tower was erected in December 2002, after a preliminary visit to Uganda was undertaken in order to select a suitable papyrus wetland over which EC measurements could be made. Initially the Nakivubo wetland outside Kampala was suggested by Dr. Kansiime and his team due to its proximity to Kampala and Makerere University, however the papyrus stand at this site had been severely disturbed since the conclusion of Dr. Kansiime's research (Kansiime and Nalubega, 1999). The Kirinya West wetland was suggested because the homogeneity of the papyrus stand made it ideal for EC measurements. The Kirinya West wetland covers an area of 471,000 m^2 of which papyrus is the dominant, monotypic vegetation. *Miscanthidium* constitutes small sections of the wetland fringe while on the northern shore there is some wetland encroachment through the cultivation of cocoyam (*Colocasia antiquorum*). The location of the EC flux tower is shown in Figure 4.1. Prior to the tower construction the dominant wind direction was determined through discussion with locals and Dr. Kansiime, as well as short term monitoring. Knowledge of dominant wind direction allowed an approximate estimation of the flux footprint measured from the tower, and ensured that the EC measurements would be made over a homogenous papyrus canopy. The tower was designed and constructed in Kampala with the help of the Department of Engineering, Makerere University, Kampala. The tower was then transported in its component parts to Kirinya where it was erected within the wetland. The depth of the water column beneath the papyrus rhizome was an issue when designing the tower. The steel framed tower stood four metres above the papyrus rhizome. In order to secure the tower, four legs were submerged beneath the tower and extended a further three metres into the sediment below. The EC equipment was clamped to a vertical pole, approximately 5 cm in diameter, which was secured using a two clamp cross sections bolted to the top of the tower and again a metre lower down. A series of four guy ropes were then attached to the top of the tower and then sunk through the papyrus rhizomes into the sediment below using four 3 m long steel poles. Two large steel padlocked boxes were also constructed and bolted to the tower. These housed and protected the datalogger and EC transducer boxes as well as the batteries used to power the system. Plate 4.1 is a photograph of the tower *in situ*.

The EC equipment consisted of a LI-COR 7500 open path infrared gas analyser (LI-COR, Lincoln, Nebraska, USA), and a CSAT-3 three-dimensional Sonic Anemometer, (Campbell Scientific Ltd., Leicestershire, England). The additional meteorological equipment installed is described in the following section. The EC data collected were block averaged into 15-minute intervals and stored on a Campbell Scientific datalogger, CR 23x (Campbell Scientific, Leicestershire, England). The gas analyser and sonic anemometer were suspended at a height of 6.5 m from water level and approximately 1.5 m above the height of the tallest papyrus culms within the plant canopy. This sampling height ensured that 95 % of the flux footprint sampled by the EC tower, based on calculations by Scheupp *et al.* (1990), would arise from the homogeneous papyrus plant canopy. The flux footprint generated during the measurement campaign over the Kirinya West wetland is shown in Appendix 2, and was constructed based on the calculations by Scheupp *et al.* (1990). The EC equipment was installed in June 2003 and remained at the site until May 2004, with an aim to collect a

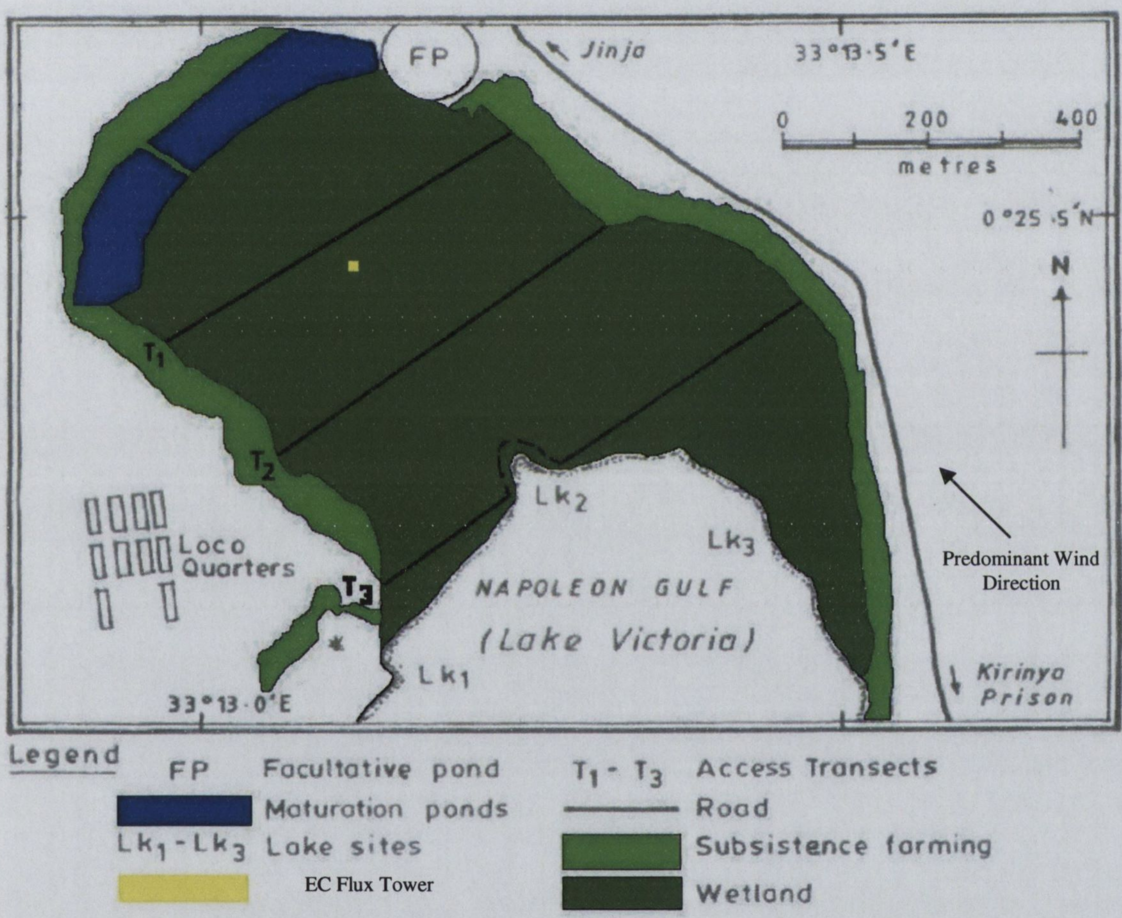

Figure 4.1. Map of the Kirinya West wetland, detailing the predominant wind direction and the location of the EC flux tower 🟨. Redrawn from Kansiime and Mwesigye (Unpub).

Plate 4.1. The EC Tower located at the Kirinya West wetland, near Jinja, Uganda.

continuous data stream from the papyrus wetland. Data loss occurred through equipment downtime and data rejection, in addition to the repeated theft of the batteries used to power the EC system. The battery theft created a three week data gap in November and an eight week gap from the end of December 2003 to the end of February 2004. The battery theft was attributed to the local inhabitants of the Kirinya wetland, and the resulting hostilities between the locals and the research team from MUIENR made the continuation of the EC flux study beyond problematic. However, 126 days of EC data were successfully collected between July and December 2003. Data downloads took place at weekly intervals and AGC (Automatic Gain Control) inspection and CO_2 calibration and span were also performed at this time.

Analysis of the EC data

The EC data were collected on a weekly basis and were segregated into weekly and monthly data blocks. The climate of the Jinja area, being equatorial shows little seasonal variation and therefore the data could be analysed consecutively. The CR23X datalogger does not have the capacity to store all the raw data points collected during EC measurements. Consequently the logger program ensured that the all the raw data points were stored in the short term logger memory before block averaging into 15 minute intervals. The weekly data sets consisted of a 7 day data stream with the data block averaged into 15 minute segments over this period. The flux data were tested for turbulence and stationarity and friction velocity (u^*) criteria were established. Rejected data points were subsequently removed and the data were divided into day and night sections. The night and day intervals were defined by daily trends in PPFD, but on average daybreak occurred at 07:00 hours and dusk occurred at 19:00 hours throughout the test period. The gaps in data sets produced by both data rejection and equipment downtime were then filled. Gaps in the daytime data stream were filled using the Michaelis-Menton function (Falge *et al.* 2001). The weekly analysis of flux data included potential climatic influence, such as rainfall and temperature, which might influence rates of carbon flux through photosynthetic assimilation or respiration. The night time flux data was more problematic to gap fill, as there was little correlation between the process based parameters such as temperature, known to drive night time flux release through respiration. In many temperate ecosystem studies, night time trends of carbon release through respiration have been correlated to air temperature, soil temperature and soil moisture content (Aubinet *et al.* 2000). The tropical, equatorial climate experienced at Kirinya showed very stable night temperatures, and working on a permanently inundated wetland meant that moisture availability would not prove to be a limiting factor. When the night time flux data was plotted against air temperature it was apparent that the relative range of air temperatures made it difficult to establish a relationship between the two parameters. When u^* was introduced on a third axis it became clear that as expected, increasing turbulence would increase the measured flux release.

The MDV gap filling strategy, as documented by Falge *et al.* (2001), was adopted to fill the gaps in the night time data. Data windows, 14 days in length were created around significant gaps in the data, and the mean diurnal flux average per 15 minute time interval was estimated. After gap filling the relevant data sections, a continuous 7 day data stream was produced, and from this data the average diurnal CO_2 flux for the week-long period was estimated. In addition, at this point in the analyses an estimation of the total carbon flux was made. This was done by converting the sum of the 7 day data stream from μmol CO_2 m^{-2} s^{-1} into an estimate of g C m^{-2} over this weekly test period. These weekly estimates of carbon flux were then combined and extrapolated to produce a yearly carbon flux estimate. This investigation aimed to adopt a long term sampling strategy in order to produce an accurate annual carbon flux budget. However due to the logistical problems as previously discussed it was necessary to interpolate the weekly carbon flux estimates to produce an annual sum.

Fluxes of water vapour were subject to the same screening criteria as fluxes of carbon dioxide. Where data had been rejected or lost, gap filling strategies were focused on the relationships between net H_2O flux and both relative air temperature and PPFD.

The water use efficiency of photosynthesis (WUE_{PH}) was calculated for each weekly data set (F/E; where F = mmol CO_2 and E = mol H_2O) using the methodology described by Morrison *et al.* (2000). Air VPD was used to calculate an adjusted ratio (F*VPD/E) and WUE_{PH} estimates were then determined where PFD > 150 μmol m^{-2} s^{-1}.

Meteorological

The meteorological instrumentation on the EC flux tower consisted of a NR Lite Net Radiometer (Kipp and Zonen, Delft, Netherlands), R M Young Wind Monitor (Supplied by Campbell Scientific, Leicestershire, England), HMP45C Vaisala Temperature and Relative Humidity Probe (Supplied by Campbell Scientific, Leicestershire, England), SKP215 Quantum Sensor (Skye Instruments, Llandrindod, Wales) HFP01, Soil Heat Flux Plates (Supplied by Campbell Scientific, Leicestershire, England). Rainfall data was provided by Dr. R Kaggwa, from a meteorological station located on the eastern shore of the Kirinya West wetland. The climatic data collected from the EC flux tower was stored on the CR23X datalogger (Supplied by Campbell Scientific, Leicestershire, England) over 15 minute intervals, and was aligned with the EC data collected.

Detritus Respiration

Measurements of detritus respiration were made using an ADC LCA-4 portable gas analyser (ADC Hoddeston, England) with an attached soil respiration chamber. Measurements were made between 09:00 and 17:00 hours, at random sites within the EC flux footprint. Before each measurement the area was cleared of any living or senescing plant material and the soil respiration chamber was pushed firmly into the detritus, so that the chamber was firmly sealed. To avoid the influence of increased pressure when sealing the chamber, enough time was given to ensure pressure equibrilation before the measurements were initiated. During the measurements the temperature of the detritus was measured at the surface and at a depth of 5 centimetres.

Respiration of Papyrus Plant material.

The contribution to carbon release through the dark respiration of plant material was also assessed. In theory the most effective method of analysing carbon flux from the entire plant would necessitate a chamber large enough to enclose an entire plant unit. In practice this is not logistically possible as the plant units are 5 metres tall in some cases. In order to assess carbon efflux of small sections of the plant, culms were cut and placed in a sealed soil chamber of the ADC LCA-4 portable gas analyser (ADC Bio-Sciences Hoddeston, England). The material for analysis was placed on a board to which the respiration chamber was sealed using modelling clay. The transparent chamber was then covered in order to simulate darkness and the respiration measurements were undertaken. Similar to the study of Jones and Humphries (2002) replicate sections of plant culm and rhizome material were cut from plant material of varying age class. To avoid possible high rates of CO_2 efflux associated with plant wounding (Humphries, 2003) the plant material were cut and left for approximately 5 minutes before analysis.

Total Carbon and Nitrogen.

The total carbon and nitrogen content of papyrus culm and umbel samples were determined from replicate samples of plant material from the lower, middle and upper sections of the culm and umbel material collected from the Kirinya West wetland. Plant material was collected from juvenile, mature and senescent papyrus plants from random locations within the EC flux footprint. The plant material was removed from the field site and sun dried, before being force dried to a constant weight, at 80°C, allowed to cool in a desiccator and then ground using a Cyclotec 1093 Sample Mill (Rose Scientific Ltd, Edmonton, Alberta, Canada). A sub sample of the ground material was weighed to approximately 0.1 g, with an accuracy of 3 S.F. Control samples consisting of EDTA (41.10 % C, 9.59 % N) were also weighed to the same mass and accuracy. The weighed plant samples and controls were wrapped inside foil casings and then analysed on a LECO CNS-1000 elemental analyser (St. Joseph, MI, USA).

Dissolved Organic Carbon.

The dissolved organic carbon content within water associated with the papyrus wetlands was determined. Replicate samples were collected from the water outflow of the second maturation pond where the wastewater enters the papyrus wetland. Samples were also collected from the water column beneath the papyrus rhizome, at random sites within the EC flux footprint. A small auger was used to create a hole in the rhizome mat, and a hand pump was used to fill sample bottles from the water column below. A papyrus culm was used to force the water intake tube through the hole in the rhizome mat and into the water column below. Samples were collected approximately 5 minutes after the intake pipe had been forced through the rhizome mat to reduce the effect of disturbance. The water was crudely filtered by the pump unit, to remove particulate matter from the samples, and then packed into a cool box and refrigerated during transport back to the laboratory in Trinity College Dublin, Ireland. The samples were prepared for analysis by filtering through Whatman GF/C filters, and analysed using a TOC–5000A analyser, (Shimadzu Corporation, Australia). Calibration standards were made using Potassium Hydrogen Phthalate, traceable to the Standard Reference Material of National Institute of Standards and Technology (USA).

Methane Efflux through Plant Mediated Transport.

The emission of methane (CH_4) from the lower culm sections was determined using static perspex chambers. The chambers were constructed from transparent perspex tubing, and were 50 cm in height with a diameter of 5.4 cm and a thickness of 0.3 cm. Suba seals were fixed using silicon sealant into holes drilled 10 cm from the top of each tube. The tubes had a PAR transmission of approximately 90% and were placed over the umbels of the plant and located around the lower culm sections, above the scale leaves of the plants. The chambers were sealed at the top and bottom around the plant culm using modelling clay.

Measurements were conducted at 09:00 hrs, 13:00hrs and 17:00 hrs on three replicate plants consisting of three age classes; juvenile, mature and senescent. The chambers were sealed and left for a period of 60 minutes, and replicate samples were taken at T_0 (initial samples collected after the chambers were sealed) and T_{60} (samples collected after 60 min). The samples were collected using gas tight syringes, and stored in evacuated vials. When removing a sample the air within the chamber was mixed using a 50 ml gas tight syringe. An initial sample was removed and then expelled to reduce possible contamination within the syringe. The evacuated vials used to store the samples were 5 ml in volume, and 10 ml samples were taken at each sampling and bled through the vial leaving a positive pressure to reduce potential sample contamination by ambient air. The vials were then capped with a mouldable adhesive and then secured with tape.

The samples were analysed on a GOW-MAC Series 750 Gas Chromatograph, equipped with a Flame Ionisation Detector. The GC was connected to a GOW-Mac Model 70-700 Strip Chart Recorder. The GC column temperature was set to 70°C while the detector temperature operated at 120°C. Gaseous flow rates through the GC were set as, nitrogen 20 ml min^{-1}, hydrogen 20 ml min^{-1} and compressed air 200 ml min^{-1}. The GC was calibrated using a CryoService (Worcester, England) calibration standard comprising of 1.00% methane in nitrogen mix with a tolerance rating of 5.00%.

4.3.3. Results.

Weather.

Meteorological data were collected *in situ* from the EC flux tower situated within the Kirinya West Wetland, Jinja, Uganda, with the exception of rainfall fall data, collected by Dr. R. Kaggwa at the LVEMP finger-pond site on the perimeter of the Kirinya East Wetland. An additional climate station is located 2 km from the Kirinya wetland, and has previously provided historical climatic data. Unfortunately this station has not been operational since 1999.

Meteorological data were collected from the EC site at 15 minute intervals and expressed on a weekly basis. Rainfall data were collected on a daily basis and monthly totals and means were calculated. Weekly summaries of air temperature above the papyrus canopy are shown in Table 4.1. Maximum temperatures ranged between 28°C and 32°C with the highest temperatures recorded in December 2003. Minimum temperatures ranged from 14°C to 18°C with the lowest temperatures occurring in August 2003. Mean temperatures showed relatively little variation and fluctuated within a 2°C range. However, on average, cooler temperatures were recorded in July and August 2003, with a trend of increasing air temperature through October, November and

December 2003. Weekly air temperature data were then combined into monthly data blocks and diurnal patterns of air temperature, based on these monthly data sets, were produced. Figure 4.2 shows average diurnal patterns of air temperature based on monthly data sets, above a homogenous papyrus canopy. Air temperatures remained relatively stable in the early hours of the morning from 00:00hrs to 07:00 hrs with temperatures fluctuating between 18 and 20°C. After sunrise (approx 07:00 hrs, Figure 4.3) air temperatures steadily increased to a maximum of 27.8°C at approximately 14:30 hrs. Temperatures then tended to fall relatively rapidly between 15:00 and 19:00 hrs with a decrease of approximately 6°C over this period. The rate of decrease then slowed with temperatures falling a further 2°C between 19:00 and 00:00 hrs to approximately 18°C. Patterns of monthly diurnal air temperatures were similar throughout the measurement period, with lower temperatures in the early morning and late evening, and higher temperatures from mid morning through mid afternoon. There was little variation between months with temperatures at any given point in time varying within a 3°C range. Maximum daytime temperatures were higher in the months of October, November and December 2003, while the lowest night time temperatures were recorded in August 2003.

The weekly measured patterns of Photosynthetically Active Radiation flux (PAR, 400–700 nm) received by the papyrus canopy are presented in Table 4.2. Maximum flux ranged from 1800 to 2200 μmol m^{-2} s^{-1} with the highest levels received between mid August and early September. The weekly mean values ranged between 300 and 500 μmol m^{-2} s^{-1}, and showed a fluctuating but increasing trend from July through December 2003. Diurnal patterns of PAR flux incident on a papyrus canopy, based on monthly data sets are shown in Figure 4.3. Patterns of PAR flux increase from daybreak at approximately 07:00 hrs to peak flux at approximately 13:00 hrs then decreasing through the afternoon to dusk at approximately 19:00 hrs. The highest flux values were recorded in September with a peak of 1800 μmol m^{-2} s^{-1} while lowest peak flux values were recorded in August at 1400 μmol m^{-2} s^{-1}. The diurnal PAR cycles recorded indicate an approximate twelve hour flux period between sunrise and sunset, an expected pattern given the equatorial location of the field site. Weekly cumulative PAR values ranged from 220-331 mol PAR m^{-2}.

Month	Week	Maximum °C	Minimum °C	Mean °C
July	3	28.07	15.83	21.53
July	4	28.34	18.31	21.56
August	1	28.64	14.36	21.34
August	2	25.50	15.28	21.82
August	3	30.07	15.47	21.31
August	4	29.20	16.36	21.30
August	5	28.53	16.65	21.63
September	1	29.12	15.96	21.93
September	2	30.05	16.55	22.13
September	3			
September	4	30.15	16.68	22.90
October	1	29.52	15.98	22.17
October	2	30.18	18.24	23.07
October	3	30.22	17.10	22.87
October	4	31.14	17.67	23.35
October	5			
November	1			
November	2			
November	3			
November	4	29.44	17.51	22.56
December	1	29.44	16.47	22.31
December	2	30.51	15.03	23.00
December	3	32.06	15.82	23.25

Table 4.1. Weekly maximum, minimum and mean values of air temperature over a *C. papyrus* L. canopy at the Kirinya West wetland (July – December, 2003). Blank boxes indicate missing data due to battery theft.

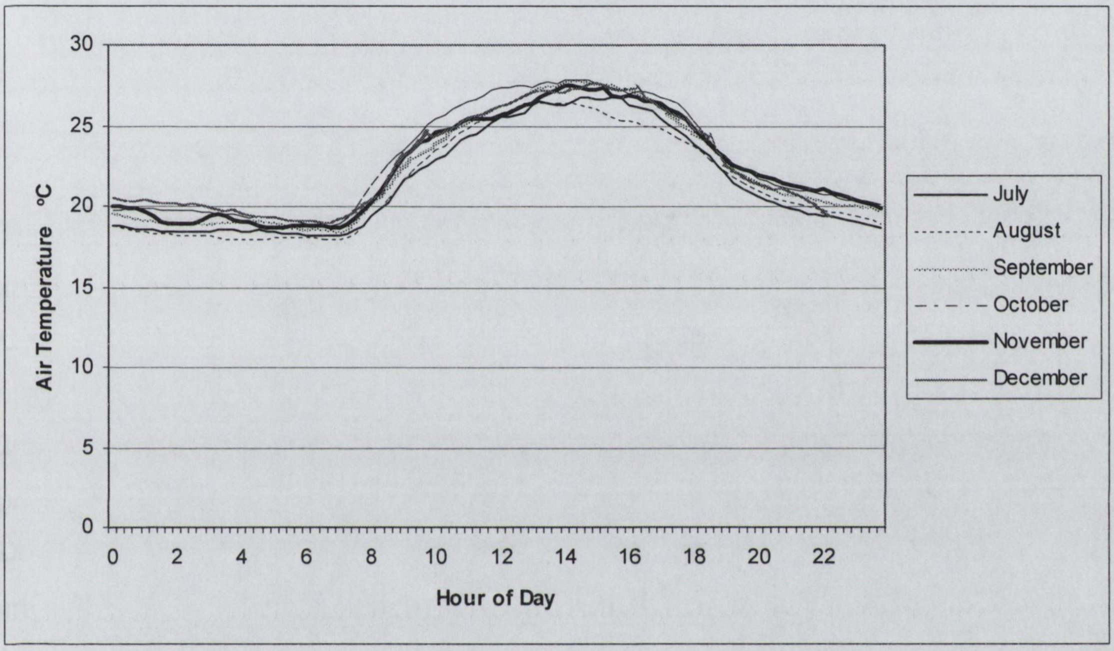

Figure 4.2. Average monthly diurnal air temperatures over a homogenous *C. papyrus*. L canopy. At the Kirinya West wetland. Data collected from July to December 2003.

Weekly mean values of relative humidity (RH) recorded above the papyrus canopy are described in Table 4.3. Maximum estimates of RH were relatively constant ranging from 93 to 96% with the highest values recorded in late July and early August 2003. Minimum RH estimates ranged from 75 to 83% with the upper values in this range occurring in August 2003 and the lower estimates occurring in December 2003. Mean RH values were also relatively stable with values ranging from 73 to 83%, the higher values occurring between July and August 2003, while the lower values were recorded in December 2003. Diurnal patterns of RH showed high, stable night time values ranging from 85 to 92% while daytime patterns of RH showed decreasing trends concurrent with increasing daytime temperature.

The monthly total rainfall values for the Kirinya Wetland are shown in Figure 4.4. There are two pronounced periods of rainfall, between November 2003 to February 2004 and March to May 2004. This data loosely follows the historical patterns described by Carter (1955), with the rainfall between November and February being of a higher intensity. Peak rates of precipitation occurred in the months of November 2003 and May 2004, with 192.5 mm and 196.5 mm falling in each respective month. Rates of precipitation over the test period showed highest values in November 192.5 mm, December 125 mm and September 94.6 mm. Lowest rainfall was recorded in July 2003 and February 2004. The total annual rainfall for the period July 2003 to June 2004 was 1079.7 mm. This value is below the annual range of 1375 to 1500 mm reported by Department of Ugandan Land Survey (1967).

Month	Week	Maximum $\mu mol\ m^{-2}\ s^{-1}$	Mean $\mu mol\ m^{-2}\ s^{-1}$	Cumulative PAR $mol\ m^{-2}$
July	3	1884.9	409.89	275.46
July	4	2029.0	440.20	295.82
August	1	1761.7	328.53	220.79
August	2	1989.6	402.69	270.63
August	3	1874.7	356.13	239.33
August	4	2251.7	394.85	265.37
August	5	2198.0	378.09	254.14
September	1	2153.6	437.21	293.83
September	2	2234.0	469.20	315.31
September	3			
September	4	2074.5	440.09	295.76
October	1	2116.3	394.02	264.80
October	2	2110.3	493.16	331.42
October	3	2111.9	427.89	308.51
October	4	2053.5	496.37	319.81
October	5			
November	1			
November	2			
November	3			
November	4	1941.9	413.81	279.78
December	1	2057.7	465.32	295.03
December	2	1933.9	482.70	296.88
December	3	2084.8	507.82	236.38

Table 4.2. Weekly maximum, mean and cumulative Photosynthetically Active Radiation (400 - 700 nm) over a *C. papyrus* L. canopy at the Kirinya West wetland (July – December, 2003). Blank boxes indicate missing data due to downtime as a result of battery theft.

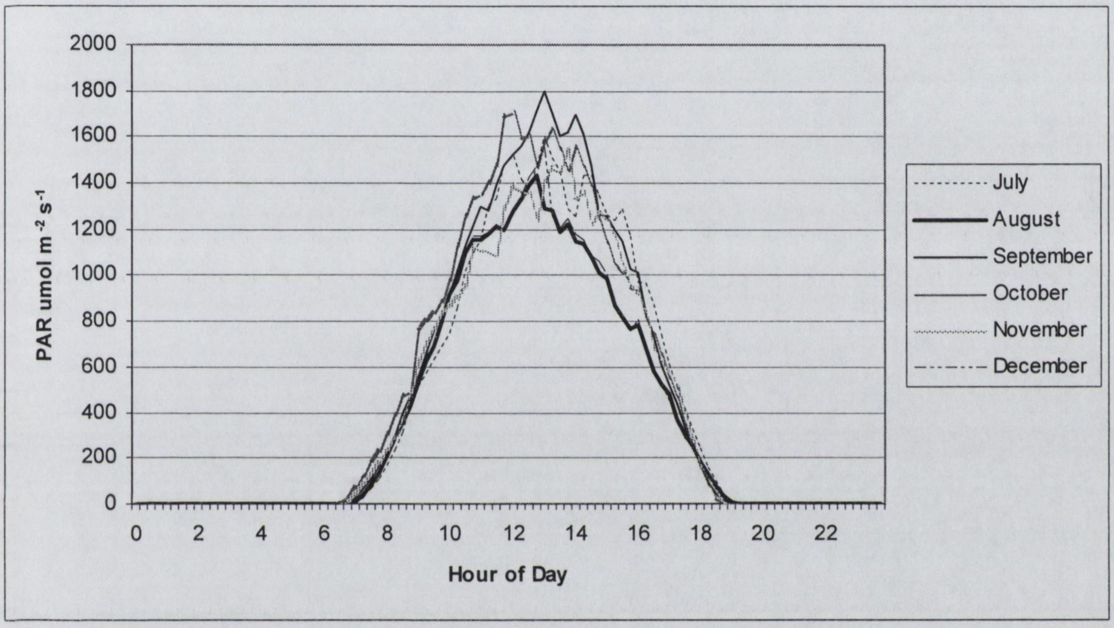

Figure 4.3. Average monthly diurnal variation in PAR (400–700 nm) over a homogenous stand of *C. papyrus* L. at the Kirinya West wetland. Data collected from July to December 2003.

Month	Week	Maximum %	Minimum %	Mean %
July	3	95.60	48.80	80.36
July	4	96.18	46.96	79.87
August	1	96.10	47.96	81.15
August	2	95.63	46.77	78.55
August	3	95.80	48.61	81.52
August	4	95.56	53.68	83.28
August	5	95.40	51.91	81.25
September	1	95.55	47.28	80.08
September	2	94.48	48.14	80.09
September	3			
September	4	95.02	45.60	77.16
October	1	95.00	46.69	78.66
October	2	93.67	48.09	76.81
October	3	94.53	48.69	78.92
October	4	94.69	46.79	73.95
October	5			
November	1			
November	2			
November	3			
November	4	94.78	48.49	78.97
December	1	94.67	41.83	78.66
December	2	95.32	37.74	74.19
December	3	94.43	34.42	75.82

Table 4.3. Weekly maximum, minimum and mean values of relative humidity over a *C. papyrus* L. canopy at the Kirinya West wetland (July–December, 2003). Blank boxes indicate missing data due to downtime as a result of battery theft.

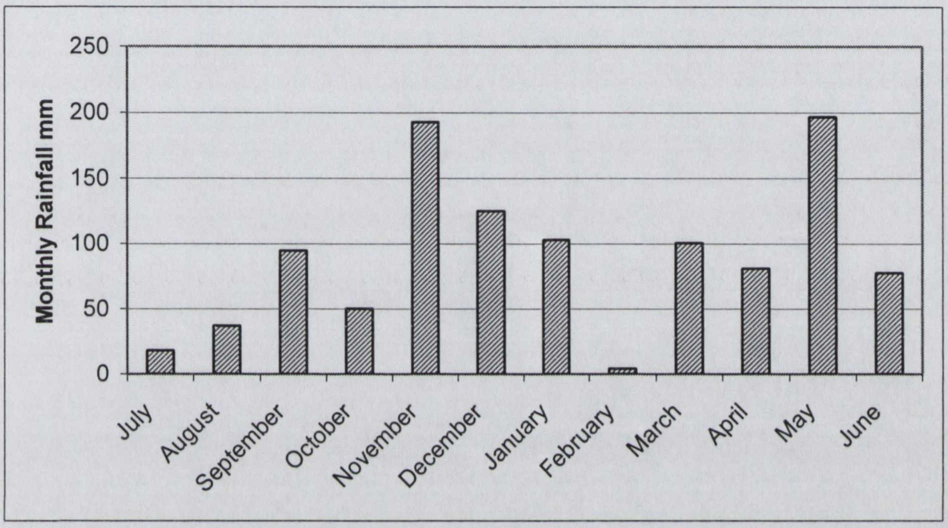

Figure 4.4. Monthly total rainfall data from the Kirinya East Wetland, Jinja, Uganda. Data collected by Dr. R. Kaggwa, National Water and Sewerage Corporation, Kampala, Uganda, between July 2003 and June 2004.

Eddy Covariance.

Energy Budget.

The closure of the energy balance is a suggested criterion for the representation of a scalar flux in relation to vertical turbulence parameters (Aubinet *et al.* 2000). Energy balance closure compares the sum of turbulent heat flux with the sum of available energy within the ecosystem and if these parameters balance then the flux data is assumed to be of good quality. There are however problems with this assumption as specific climatic circumstances such as freezing events can lead to the erroneous estimation of energy balance components. Consequently, certain flux communities such as the CarboEurope-IP initiative have reduced the dependence on energy balance closure to assess the plausibility of EC flux data (Foken, *pers comm*). The energy balance closure is however a useful tool in identifying non-vertical turbulent fluxes.

The relationship between turbulent and available energy flux was analysed for each weekly EC data set. Figure 4.5 shows an example of the relationship between turbulent and available energy fluxes over the homogenous papyrus canopy at the Kirinya West wetland from the 21st to 27th July 2003. The degree of energy balance closure in this example is described by a slope of 0.98 and an R^2 value of 0.91, suggesting a very good agreement between turbulent and available fluxes throughout the energy flux range, with a larger degree of scatter in the upper flux range (600–800 W m^{-2}). Table 4.4 describes the slope and R^2 values associated with the energy balance closure on a weekly basis for the entire data set. All data sets produced similar energy flux relationships. The agreement of these relationships does not fully assess the credibility of the data sets, however it gives a good indication that the turbulent fluxes were not subject to either advection or subsidence. The energy balance closure for the entire data set had Slope and R^2 values ranging from 0.88 to 1.01 and 0.89 to 0.96 respectively.

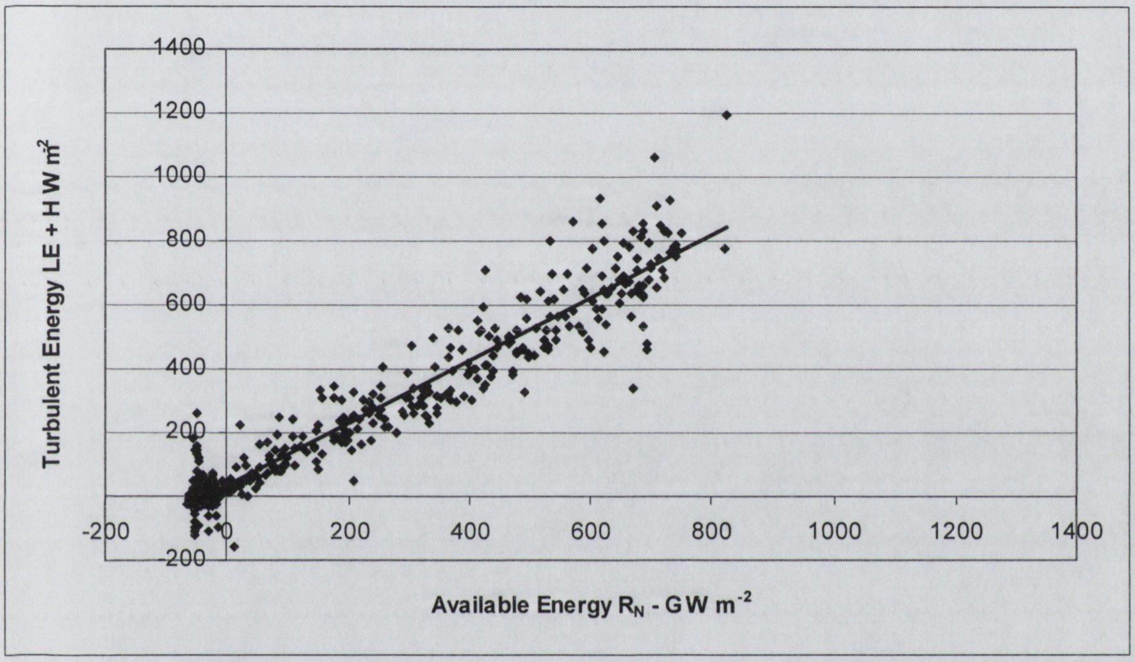

Figure 4.5. Scatter diagram and regression line representing the relationship between turbulent and available energy, over a homogeneous papyrus canopy at the Kirinya West wetland. Data collected between the 21st-27th July 2003. (Slope = 0.982 $R^2 = 0.91$)

Month	**Week**	**Slope**	**R^2**
July	3	0.996	0.91
July	4	0.982	0.94
August	1	1.018	0.93
August	2	0.909	0.95
August	3	0.987	0.93
August	4	0.950	0.91
August	5	0.916	0.92
September	1	0.883	0.91
September	2	0.889	0.94
September	3		
September	4	0.968	0.96
October	1	0.962	0.94
October	2	0.937	0.96
October	3	0.985	0.94
October	4	0.912	0.90
October	5		
November	1		
November	2		
November	3		
November	4	0.939	0.94
December	1	0.895	0.93
December	2	0.955	0.93
December	3	0.949	0.89

Table 4.4. Linear regression analysis of energy balance components. Data collected over a homogenous papyrus canopy at the Kirinya West wetland from July–December, 2003. Blank boxes indicate missing data due to downtime as a result of battery theft.

The energy balance parameters were also divided into their component parts and averaged into mean diurnal energy fluxes, based on a seven day data set. Figure 4.6 shows mean diurnal values of the energy balance parameters over the homogeneous papyrus canopy. The partitioning of energy balance components showed similar trends throughout the flux measurement period. Peak radiative fluxes were experienced at approximately midday, with approximately 60% partitioned into λE and 40% partitioned into H at this point. Ground heat fluxes were negligible at all times, highlighting the effective shading capacity of the papyrus canopy.

Ecosystem Carbon Flux

Net Ecosystem Exchange (NEE) of CO_2 as measured by the EC system for the duration of the test period is shown in Figure 4.7(i)-Figure 4.7(iv). The EC system was deployed at the Kirinya field site for a period of 11 months, although the theft of the power supply for the system led to two extended gaps within the data stream. The positive flux values indicate periods of net ecosystem loss of CO_2 from the system, while negative values indicate a net gain of CO_2 by the ecosystem. On average, daily maximum rates of CO_2 release from the system fell within a range of 20 to 30 μmol CO_2 m^{-2} s^{-1}, with peak losses of approximately 40 μmol CO_2 m^{-2} s^{-1}. Peak rates of CO_2 uptake were on average higher than losses, with peaks of approximately 40 μmol CO_2 m^{-2} s^{-1} commonplace. Figure 4.8 illustrates the typical diurnal patterns of CO_2 flux observed during the measurement period (July-December 2003). Night time respiratory losses ranged between 20 to 30 μmol CO_2 m^{-2} s^{-1}, and after sunrise which occurs at approximately 07:00 hrs (Figure 4.3) the ecosystem switches from a net source to a net sink of CO_2. The switch between source to sink CO_2 efflux patterns occurs at approximately 08.30 hrs, approximately 1.5 hours after daybreak. Maximum CO_2 uptake by the system of 37 μmol CO_2 m^{-2} s^{-1} occurred at approximately 13.15 hrs and was associated with peaks in both air temperature and PAR flux. As PAR flux decreases throughout the afternoon, rates of CO_2 uptake also decrease, and the system switches again from a net sink to a net source of CO_2 at approximately 200 μmol m^{-2} s^{-1}. Remarkably uniform patterns of night time

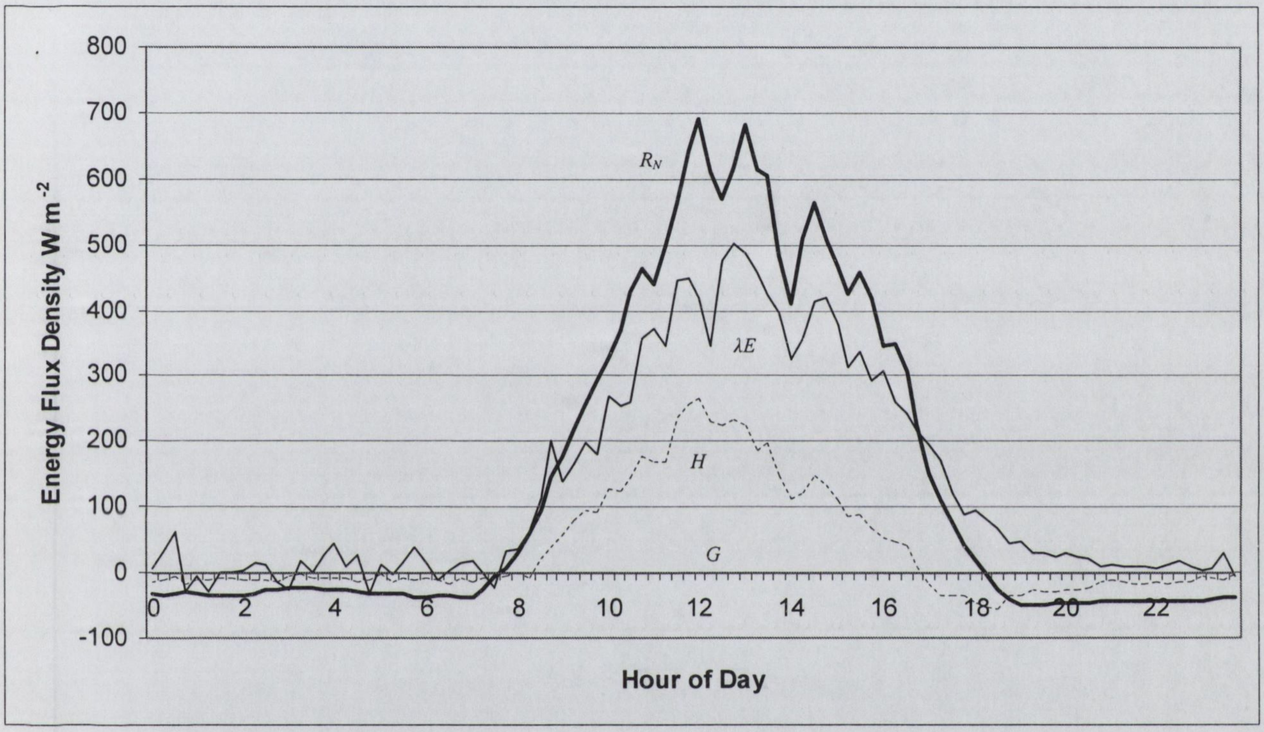

Figure 4.6. Mean diurnal components of energy balance flux over a homogenous papyrus canopy at the Kirinya West wetland from the 21st to 27th July 2003. Diurnal fluxes were averaged on a fifteen-minute basis derived from a seven day data set. Energy balance components are flux densities of net radiation (R_N, thick line), latent heat (λE, thin line), sensible heat (H, dashed line), and ground heat flux (G, dotted line, unseen as fluxes are negligible).

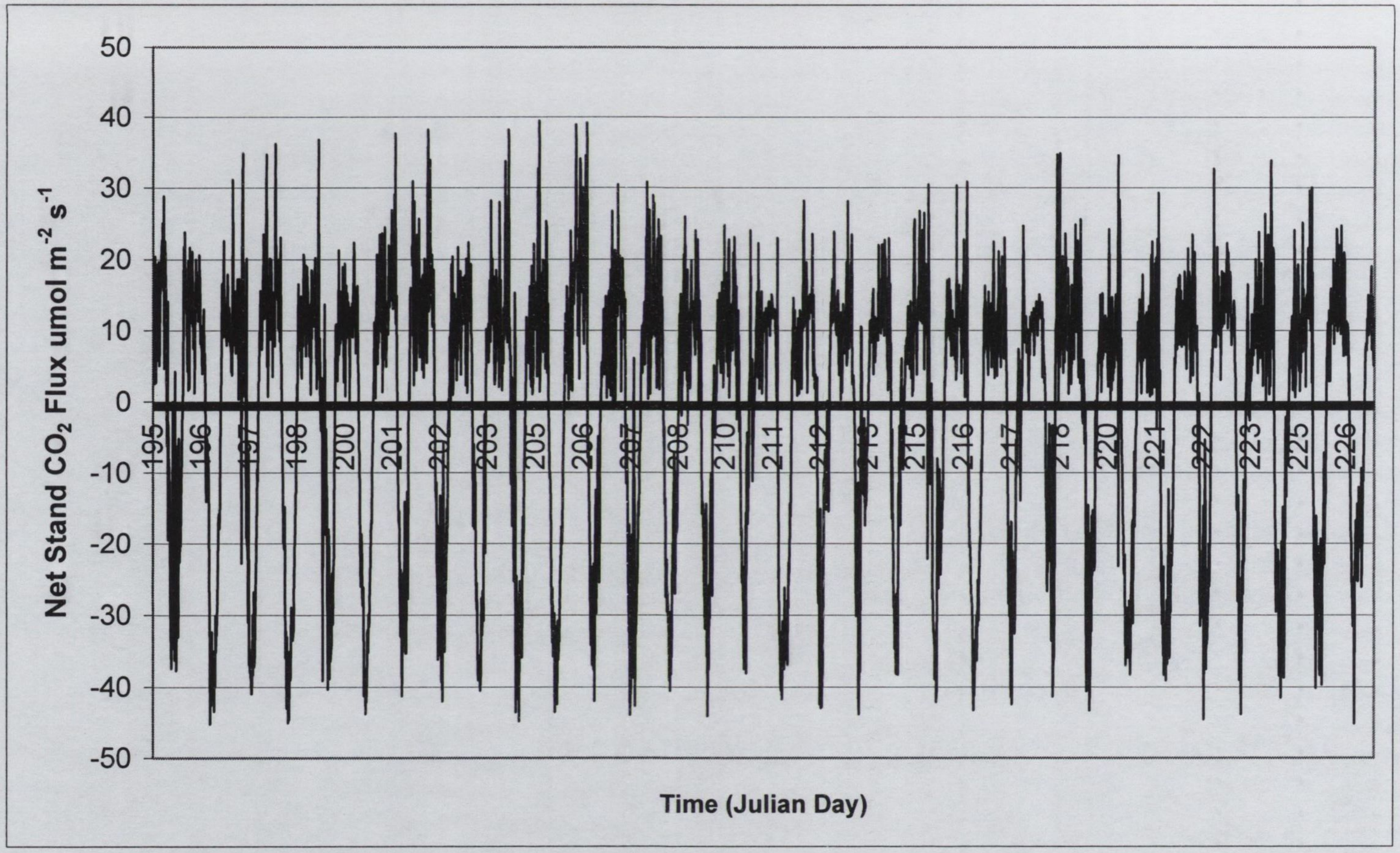

Figure 4.7 (i). Net stand CO_2 flux measured above a homogenous *Cyperus papyrus L.*canopy at the Kirinya West wetland. Data collected from 14th July–14th August 2003. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

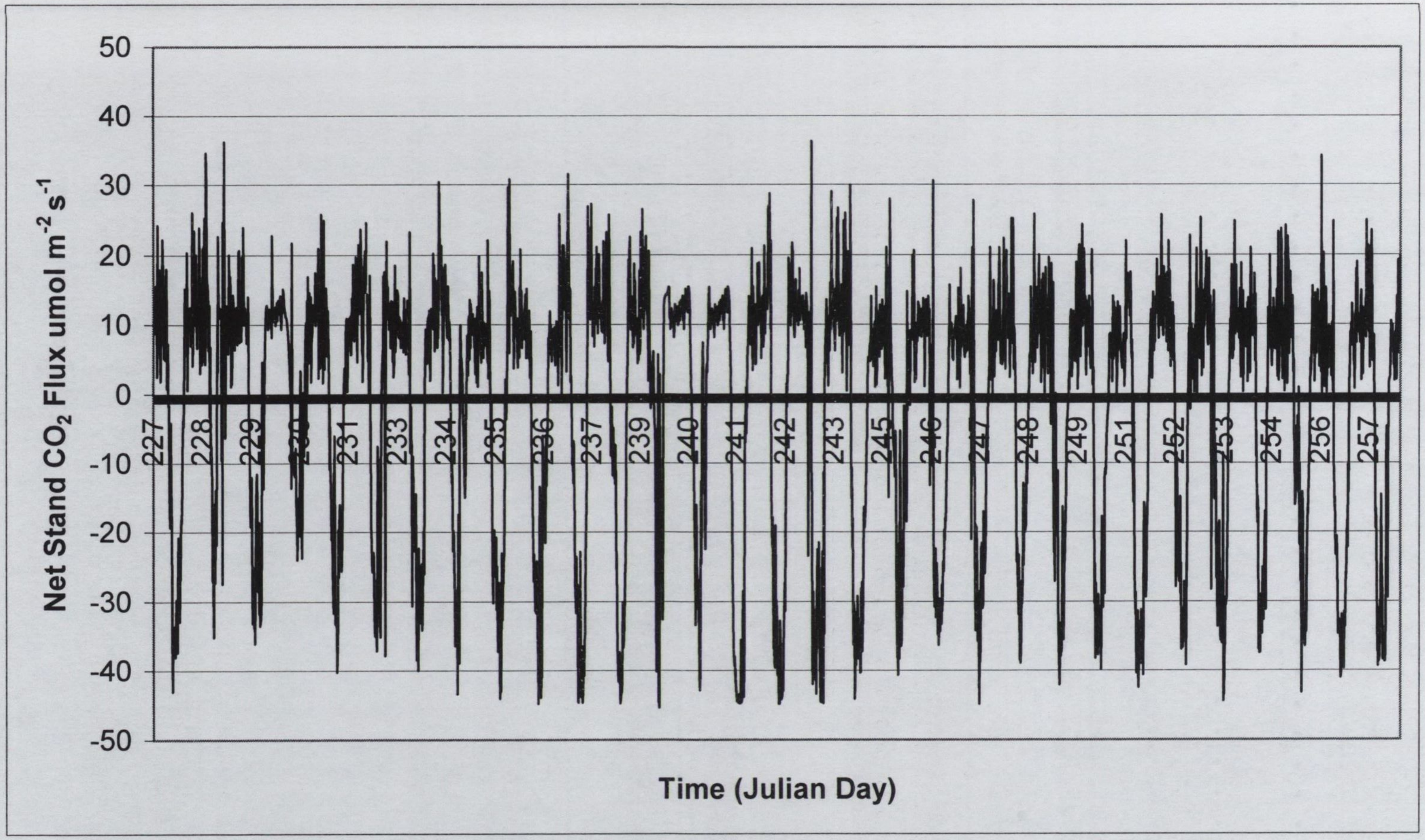

Figure 4.7 (ii). Net stand CO_2 flux measured above a homogenous *Cyperus papyrus L.*canopy at the Kirinya West wetland. Data collected from 15th August–14th September 2003. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

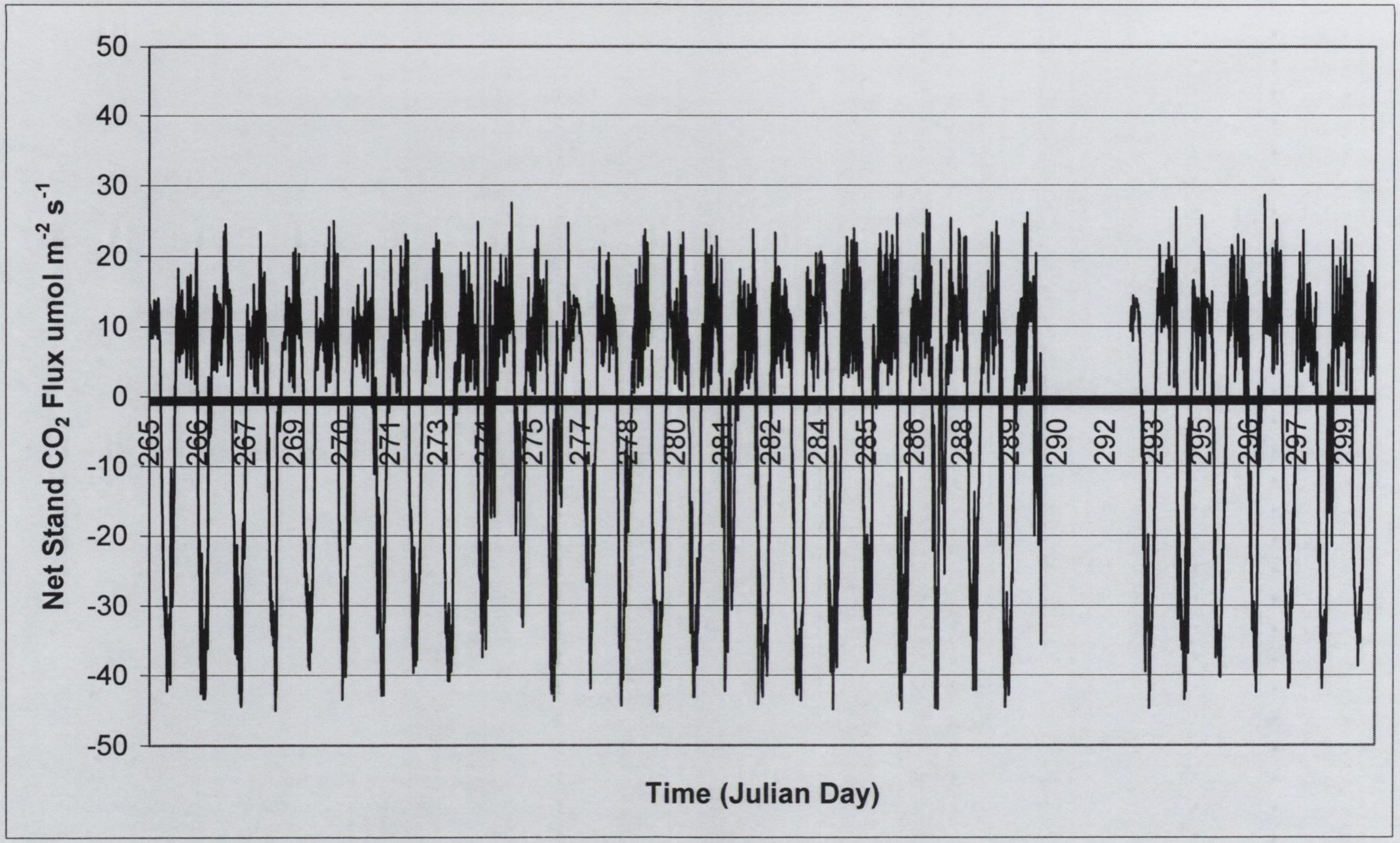

Figure 4.7 (iii). Net stand CO_2 flux measured above a homogenous *Cyperus papyrus L.*canopy at the Kirinya West wetland. Data collected from 22nd September–26th October 2003. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

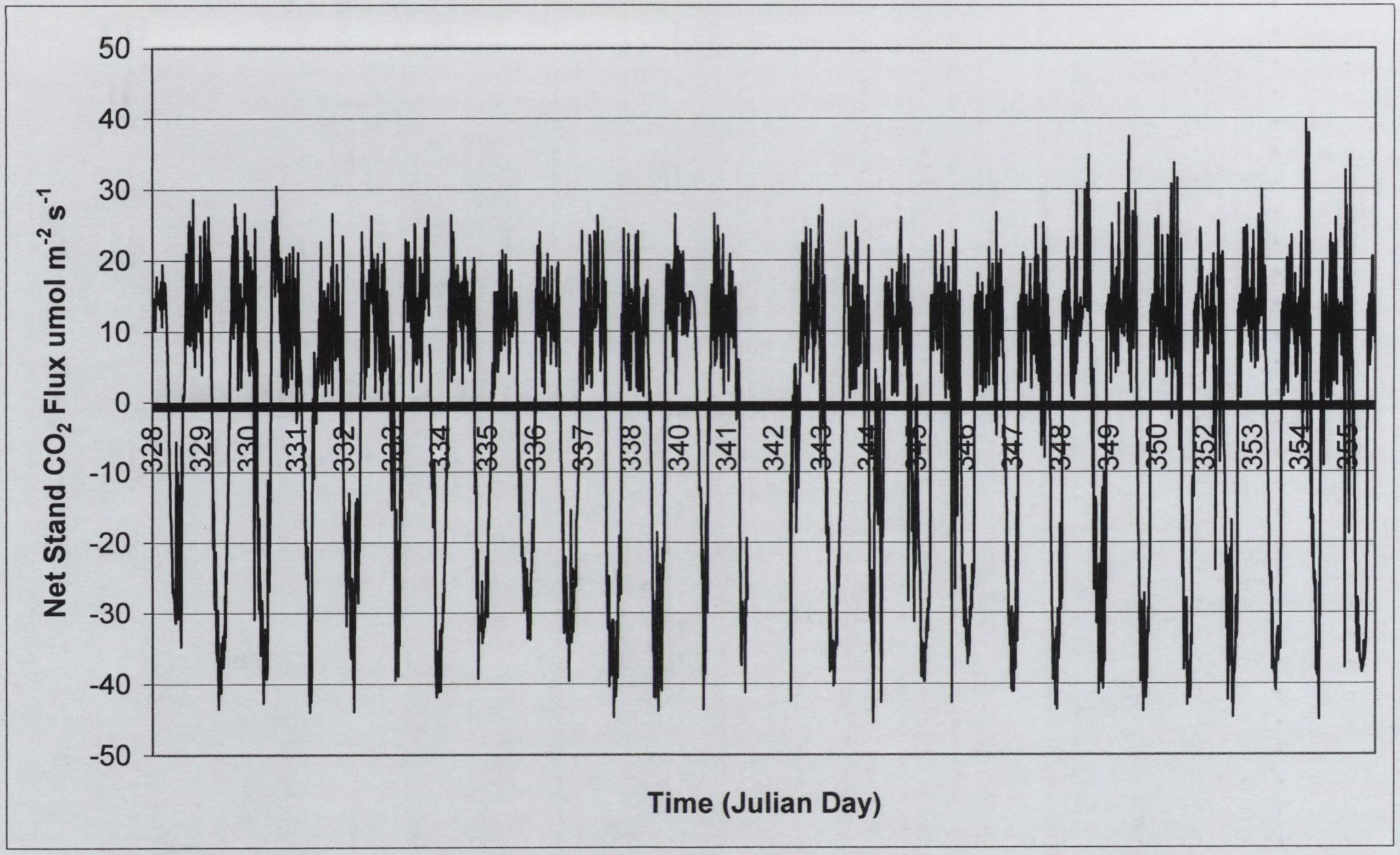

Figure 4.7 (iv). Net stand CO_2 flux measured above a homogenous *Cyperus papyrus L.*canopy at the Kirinya West wetland. Data collected from 24th November–21st December 2003. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

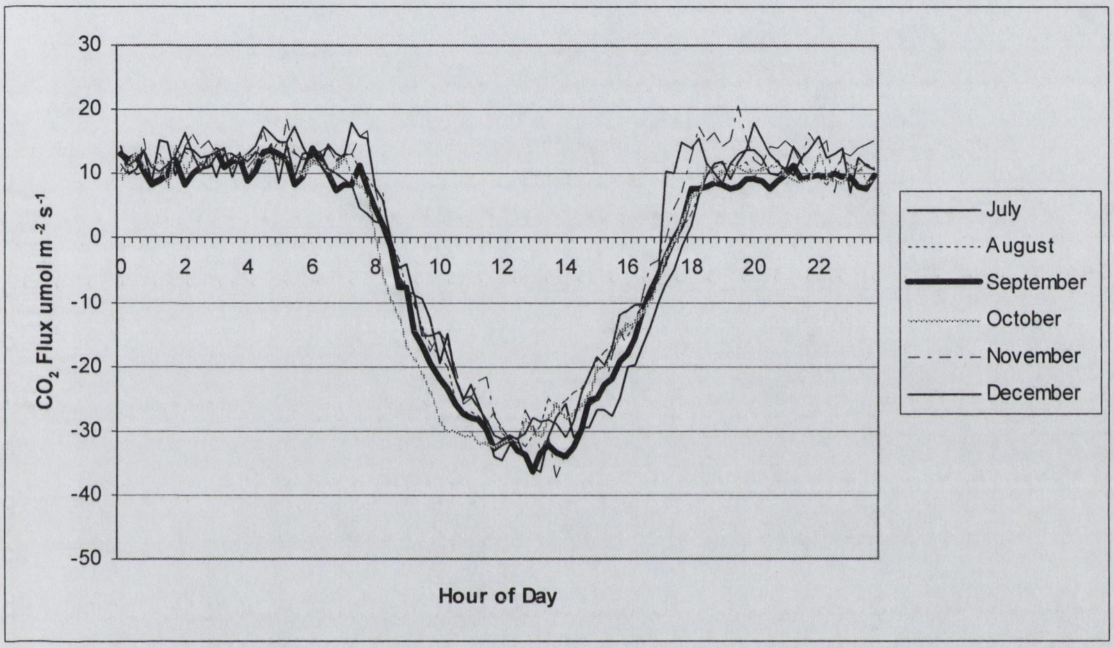

Figure 4.8. Average diurnal cycle of ecosystem CO_2 flux, based on EC data collected between July and December, 2003 over a homogenous papyrus canopy at the Kirinya West wetland. Positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system.

carbon loss and daytime carbon uptake were exhibited throughout the measurement period.

The fluxes were then numerically integrated to produce a weekly estimate of carbon gain or release. Table 4.5 illustrates patterns of gross primary production, total ecosystem respiration and corresponding patterns of carbon gain or release, based on weekly EC data sets over the measurement period. Rates of carbon uptake by the papyrus vegetation ranged from 5-23 g C m^{-2} wk^{-1}, while rates of carbon release ranged from 1-3 g C m^{-2} wk^{-1}. Although the diurnal patterns of net carbon uptake and release as illustrated in Figure 4.8 were in general remarkably similar throughout the measurement period, the differences in carbon gained or released, as shown in Table 4.5 were quite large. During the measurement period four of the weekly data sets showed the wetland to be a net source of carbon, whilst in the remaining weeks the wetland acted as a net sink of carbon. Figure 4.9 shows the diurnal carbon flux patterns described by the data collected in the fourth week of November 2003 (a period of net carbon release) and the first week of December 2003 (a period of net carbon uptake). While the patterns of diurnal CO_2 flux appear similar over the two periods, the integrated NEE of carbon was quite different. Based on the EC flux data, the papyrus wetland acted as a net source of carbon between the 24th to 30th of November 2003, releasing approximately 3.54 g C m^{-2} during this period. However between the 1st to 7th of December 2003 the wetland became a net sink of carbon, sequestering approximately 7.75 g C m^{-2}. In Figure 4.9, both periods show similar patterns of night time CO_2 efflux, with rates varying between 10-20 μmol CO_2 m^{-2} s^{-1}. Both periods also show similar patterns when switching between net stand respiration and net stand photosynthesis, with the compensation point for the net change occurring just after 08:00 hrs in both periods. The data collected during both periods show high rates of maximum CO_2 uptake, ranging between 33-37 μmol CO_2 m^{-2}. The most significant difference between the two periods occurs in the data collected between 24th to 30th of November 2003, where a rapid decrease in the rate of CO_2 uptake occurs between 15:00 and 17:00 hrs.

Month	Week	NEE g C m^{-2}	GPP g C m^{-2}	R_{eco} g C m^{-2}
July	3	-5.22	-26.24	21.03
July	4	-9.07	-31.15	22.08
August	1	1.73	-20.10	21.83
August	2	-5.12	-31.96	26.84
August	3	3.95	-17.67	21.62
August	4	-5.01	-23.72	18.71
August	5	-16.49	-44.12	27.63
September	1	-17.07	-37.39	20.32
September	2	-18.02	-42.47	24.45
September	3			
September	4	-23.04	-40.17	17.13
October	1	-10.38	-28.97	18.59
October	2	-24.57	-43.50	18.93
October	3	-7.90	-35.76	27.86
October	4	-17.53	-40.34	22.81
October	5			
November	1			
November	2			
November	3			
November	4	3.54	-18.07	21.61
December	1	-7.75	-24.91	17.16
December	2	-10.11	-25.57	15.46
December	3	1.71	-14.74	16.45

Table 4.5. Weekly carbon flux over *Cyperus papyrus* L. vegetation at the Kirinya West wetland, Jinja, Uganda. Values represent grams of carbon flux per square metre. Data collected from July–December 2003 (blank boxes indicate data loss through battery theft). Negative values indicate carbon uptake positive values indicate carbon release.

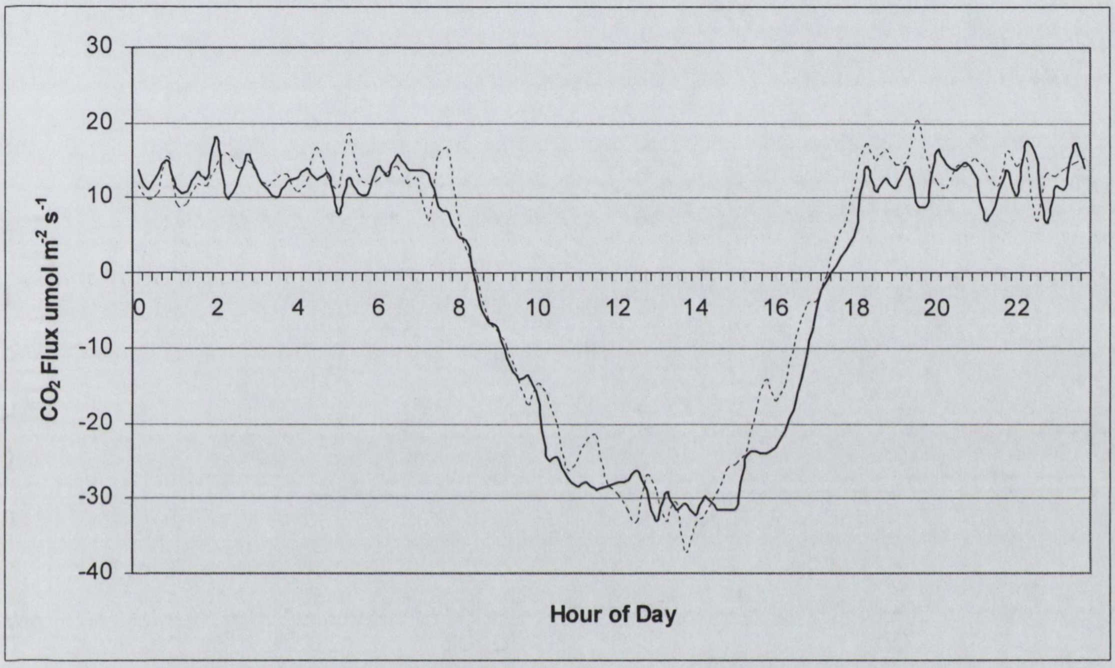

Figure 4.9. Average diurnal cycle of ecosystem CO_2 flux, based on EC data collected from 24th–30th November, 2003 (Dashed Line), and from 1st–7th December, 2003 (Solid Line). EC data collected over a homogenous papyrus canopy at the Kirinya West wetland, positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system.

Rates of carbon assimilation are a function of incoming photosynthetic active radiation (PAR). The relationship between net stand CO_2 flux and PAR for the periods 24th to 30th November 2003 and 1st to 7th December 2003 are shown in Figures 4.10 and 4.11 respectively. Both periods showed similar magnitudes of CO_2 uptake (negative values) with maximum rates of CO_2 assimilation ranging between 40-44 μmol CO_2 m^{-2} s^{-1}. The magnitude of CO_2 release (positive values) were also similar with values ranging between 20-30 μmol CO_2 m^{-2} s^{-1}. Net respiratory carbon flux (carbon release) accounted for a higher percentage, approximately 34% of the total data set for the period 24th to 30th November 2003, while the net respiratory carbon flux accounted for approximately 28% of the data collected between 1st to 7th December 2003.

The average diurnal patterns of PAR flux over both time periods are shown in Figure 4.12. The peak instantaneous irradiance received by the papyrus canopy between 1st to 7th December 2003 was approximately 1640 μmol m^{-2} s^{-1}, while for the period between 24th to 30th November 2003 peak recorded irradiance was approximately 1500 μmol m^{-2} s^{-1}. In addition, the integrated daily irradiance between 24th to 30th November 2003 and 1st to 7th December 2003 were approximately 39.19 mmol m^{-2} d^{-1} and 44.37 mmol m^{-2} d^{-1} respectively.

Water Vapour Fluxes

The average daily fluxes of water vapour measured by the EC system over the duration of the test period are shown in Figure 4.13. The highest daily rates of water loss based on seven day EC flux data sets, occurred in October with maximum losses averaging approximately 6.14 kg H_2O m^{-2} d^{-1}. The lowest rates of water loss were experienced in late August with average losses of approximately 3.03 kg H_2O m^{-2} d^{-1}. Typical monthly diurnal flux patterns of water vapour exchange over a homogenous papyrus canopy are illustrated in Figure 4.14. The flux of water was very low at night but rates during the day rose to approximately 12 mmol H_2O m^{-2} s^{-1} with the peak losses occurring in conjunction with peak air temperatures, low relative humidity, peak PAR flux and high rates of CO_2 assimilation.

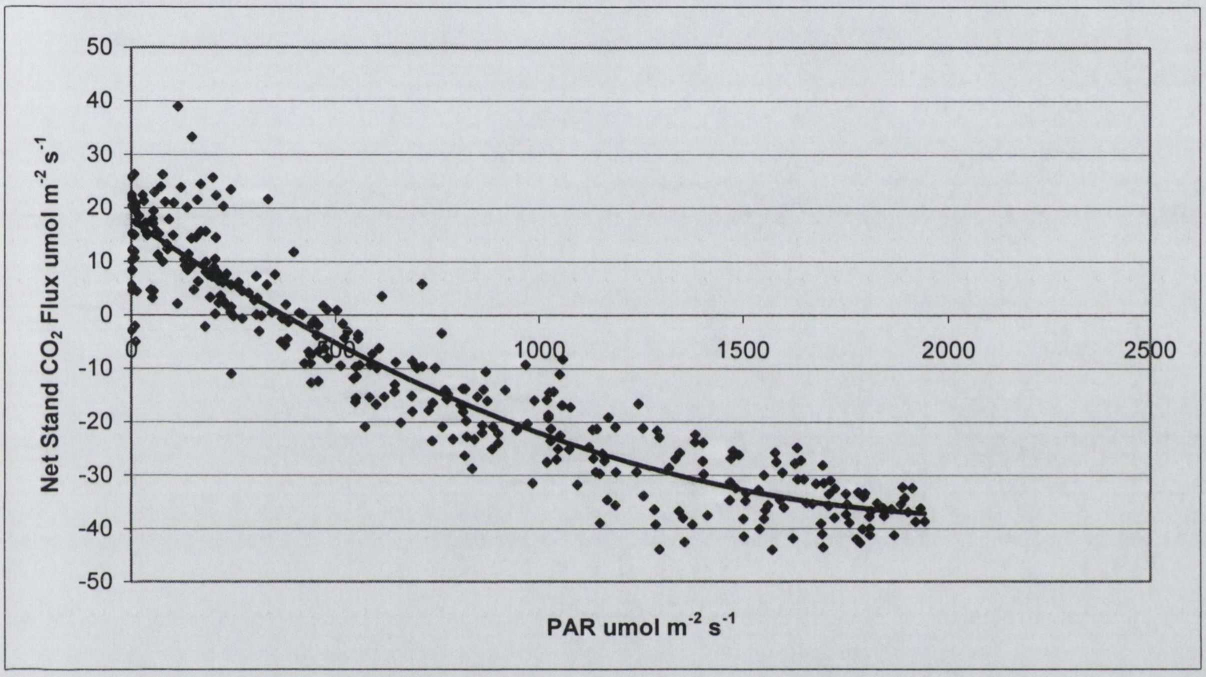

Figure 4.10. Relationship between net stand CO_2 flux and incident PAR for a homogenous papyrus stand at the Kirinya West wetland, Jinja, Uganda. Data collected from the 24th to 30th of November 2003. Positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system, ($R^2 = 0.88$).

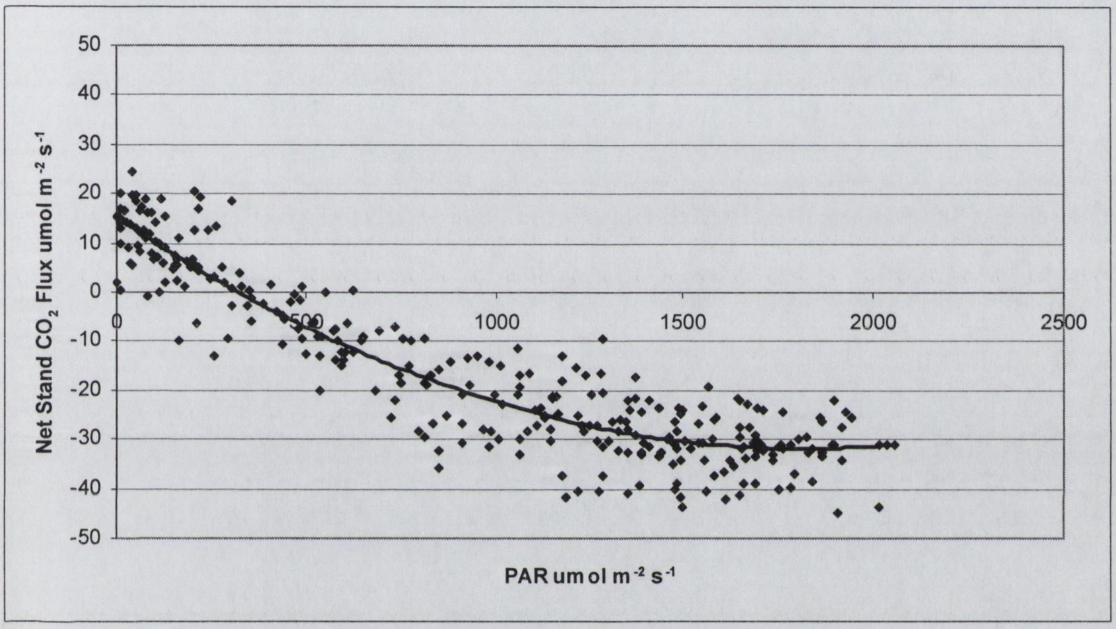

Figure 4.11. Relationship between net stand CO_2 flux and incident PAR for a homogenous papyrus stand at the Kirinya West wetland, Jinja, Uganda. Data collected from the 1st to 7th of December 2003. Positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system ($R^2 = 0.90$).

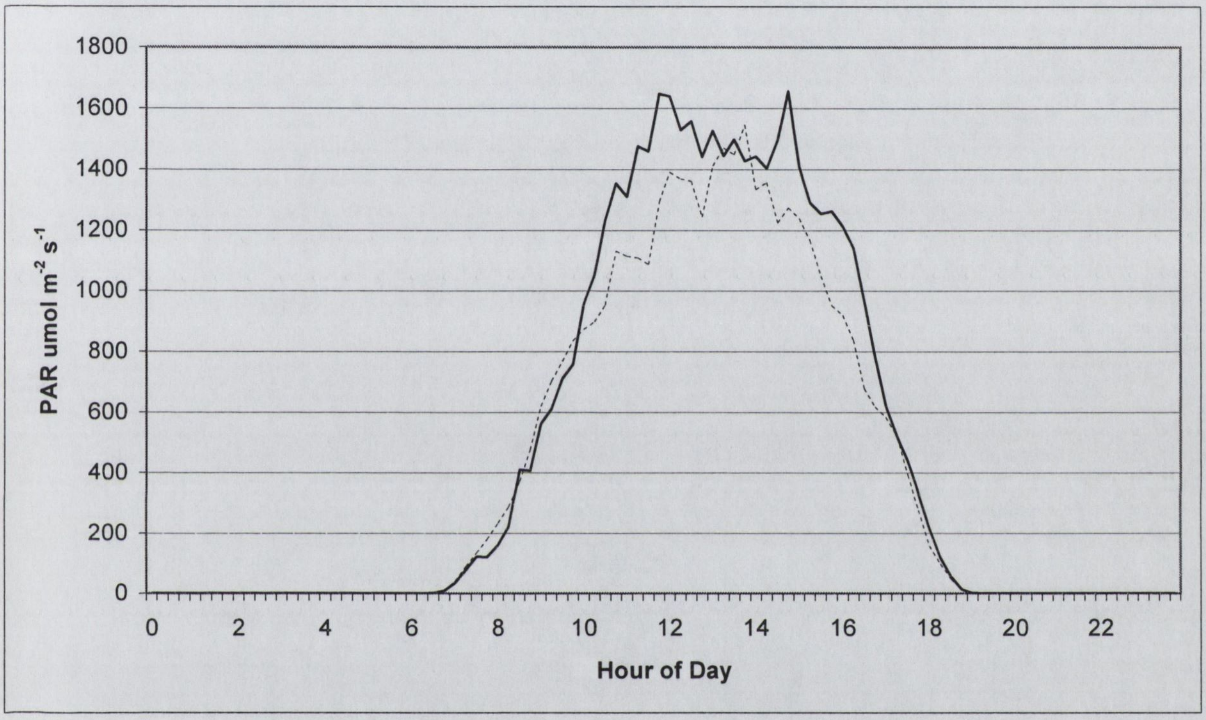

Figure 4.12. Average diurnal flux of photosynthetic active radiation (PAR), based on meteorological data collected over a homogenous papyrus canopy at the Kirinya West wetland Jinja, Uganda. Data collected from 24th – 30th November, 2003 (Dashed Line), and from 1st – 7th December, 2003 (Solid Line).

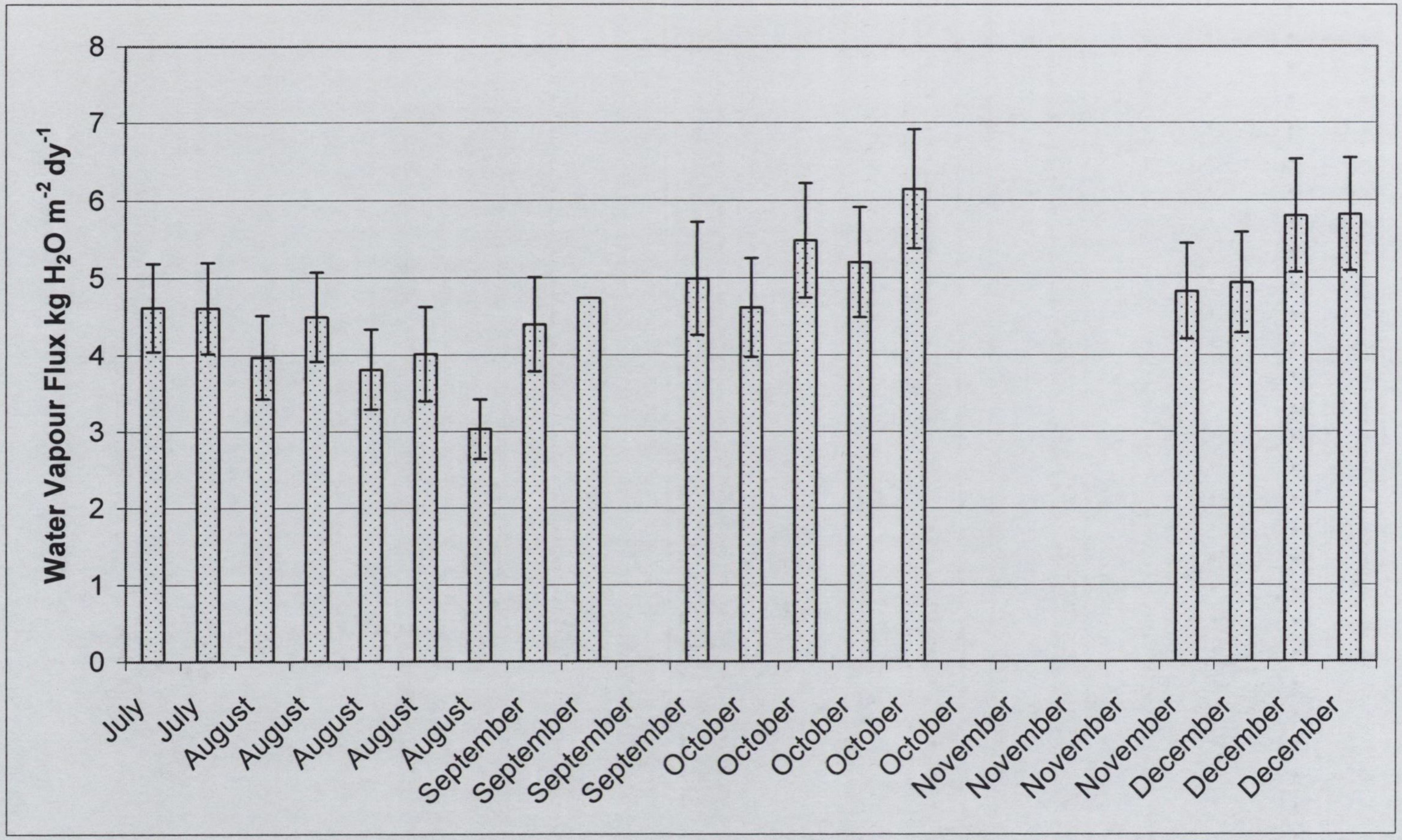

Figure 4.13. Average water vapour fluxes measured above a homogenous *Cyperus papyrus* L. canopy, based on seven day EC flux data sets. Data collected from July to December 2003 at the Kirinya West wetland, and are expressed in kg H_2O m^{-2} d^{-1} (gaps in data represent data loss through battery theft).

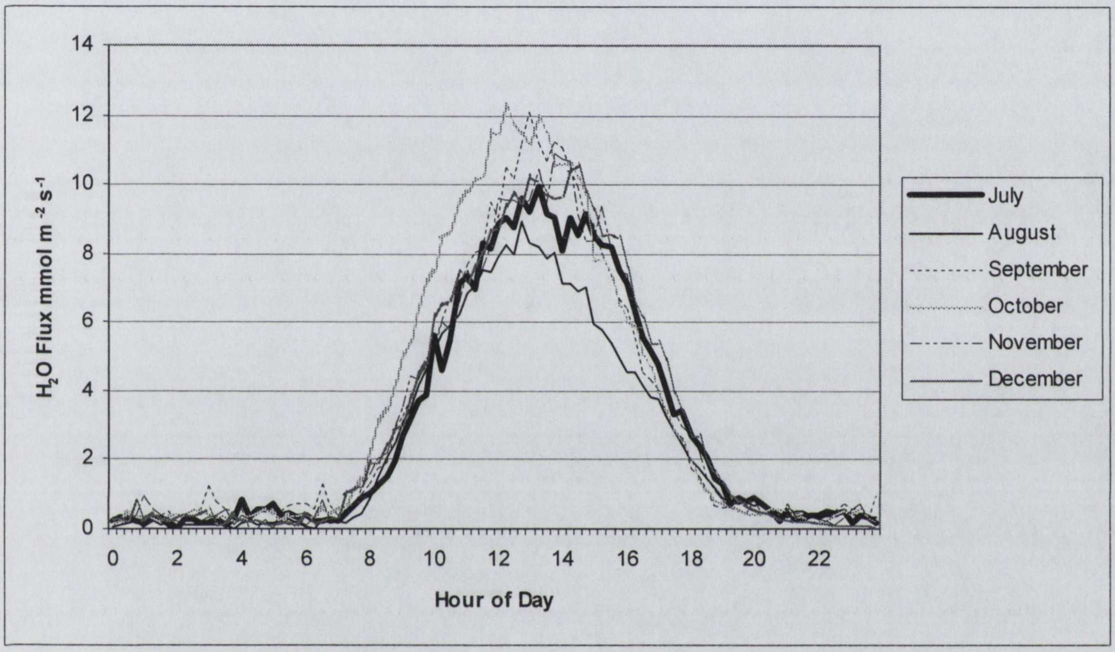

Figure 4.14. Average diurnal water vapour flux based on EC data collected from July-December 2003, over a homogenous papyrus canopy at the Kirinya West wetland, Jinja, Uganda.

Water Use Efficiency of Photosynthesis (WUE_{Ph}) based on EC data describe the stand-level ratio of CO_2 uptake in relation to water vapour release. Estimates of WUE_{PH} for each weekly EC data set, and the linear relationship between water vapour flux and incident photon flux density (R^2) are shown in Table 4.6. Estimates of WUE_{PH} (normalised to VPD and averaged where PFD > 500 μmol m^{-2} s^{-1}) ranged between 2.99-6.05 mmol CO_2. [mol $H_2O]^{-1}$. The average WUE_{PH} for the entire measurement period was 3.78 ± 0.16 (SE) mmol CO_2. [mol $H_2O]^{-1}$. Figure 4.15 shows the WUE_{PH} of the homogenous papyrus canopy at the Kirinya West wetland when water vapour fluxes through evapotranspiration were lowest (25th to 31st August 2003).

Measurements of Net Primary Productivity (NPP) undertaken at the Kirinya West Wetland (Chapter 3), allowed the calculation of WUE_P, which describes the relationship between water vapour loss and dry matter production. Monthly estimates of WUE_P are listed in Table 4.7 and ranged between 4.42-6.36 g DM . [kg $H_2O]^{-1}$. The mean WUE_P over the entire measurement period was 5.16 ± 0.43 (SE) g DM . [kg $H_2O]^{-1}$.

Month	**Week**	**WUE_{Ph}** (mmol CO_2 . [mol $H_2O]^{-1}$)	**R^2**
July	3	3.74	0.87
July	4	3.90	0.89
August	1	3.09	0.89
August	2	3.72	0.91
August	3	3.38	0.87
August	4	2.99	0.88
August	5	6.05	0.76
September	1	3.85	0.87
September	2	3.81	0.85
September	3		
September	4	4.26	0.91
October	1	3.18	0.90
October	2	4.23	0.90
October	3	3.60	0.89
October	4	3.92	0.85
October	5		
November	1		
November	2		
November	3		
November	4	3.25	0.90
December	1	3.63	0.92
December	2	3.48	0.91
December	3	4.00	0.87

Table 4.6. Estimations of average daily WUE_{Ph} based on weekly EC flux data collected between July–December 2003, over a homogenous papyrus canopy at the Kirinya West wetland. WUE_{Ph} values represent the ratio of mmol of CO_2 assimilated through photosynthesis per mol of H_2O lost through transpiration. R^2 values represent the linear relationship between water vapour loss and incident PFD. Blank boxes indicate missing data due to equipment downtime as a result of battery theft.

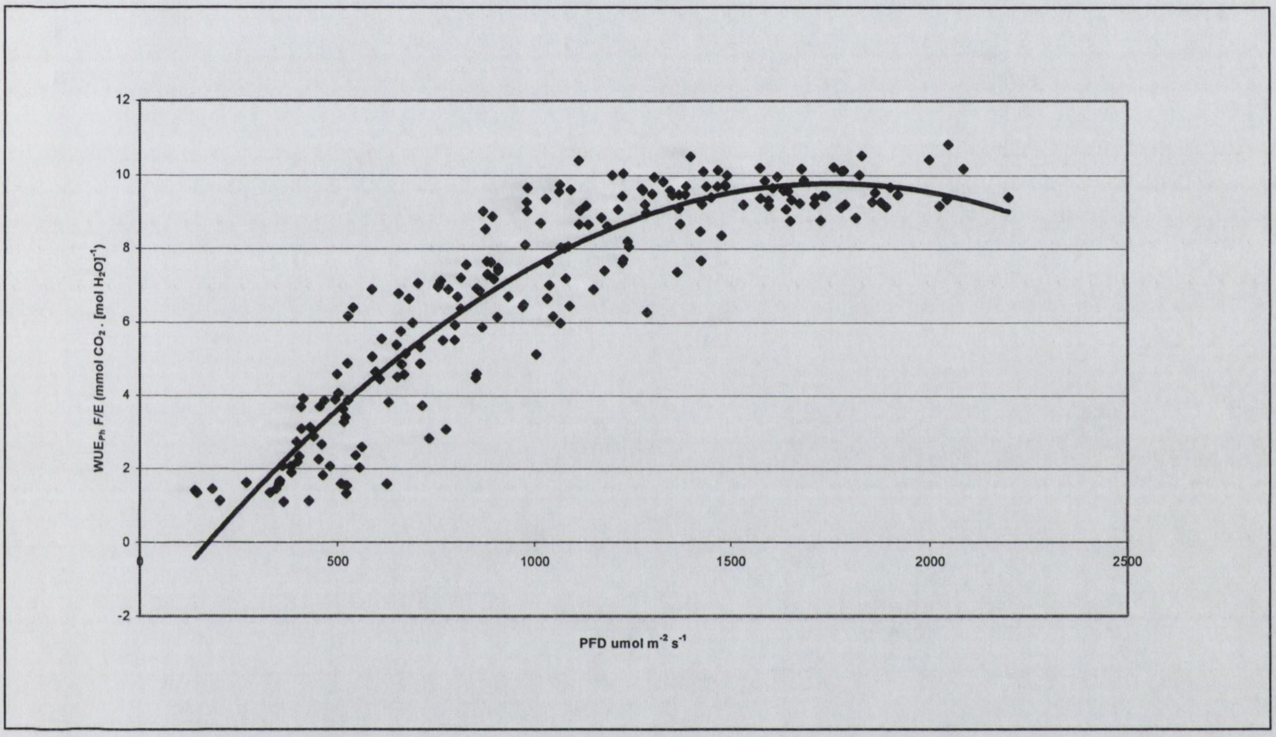

Figure 4.15. Relationship between WUE$_{Ph}$ and incident PFD for a homogenous stand of *C. papyrus* L. based on EC flux data collected from the 25th – 31st August 2003 ($R^2 = 0.86$). Data collected at the Kirinya West wetland, Jinja, Uganda. WUE$_{Ph}$ data were normalised to VPD and values selected when PFD >150 μmol m^{-2} s^{-1}.

Table 4.7. Average WUE_P based on monthly EC flux data collected at the Kirinya wetland between July–October 2003, and average NPP data collected over the same time period (Chapter 3). WUE_P values represent grams of dry matter produced through carbon assimilation in relation to kilograms of water vapour lost through transpiration.

Month	**WUE_P** (g DM . [kg H_2O]$^{-1}$)
July	4.70
August	6.36
September	5.15
October	4.42

Respiration of Detrital Material.

The respiration rate of detrital material located at the surface of the papyrus rhizome was estimated at 12 locations within the EC flux footprint. Figure 4.16 illustrates the mean respiration rate at each site (n = 3). Estimates of carbon flux through respiration ranged from 0.13–0.49 g C m^{-2} hr^{-1}, with a mean rate of respiration of 0.26 ± 0.07 (SE) g C m^{-2} hr^{-1}. The temperature of the detritus at both the surface and a depth of 5 cm were relatively stable. The temperature at the detritus surface ranged from 22-24°C while the temperature of the detritus at a depth of 5 cm was approximately 20°C at each site. The moisture content of the detritus was not estimated, however the Kirinya West wetland is subject to permanent inundation and it is assumed that detrital moisture content would not limit rates of respiration.

Statistical analyses of the detrital respiration data were conducted using a one-way ANOVA and Bonferroni's Multiple Comparison test (Appendix 4). This analysis showed that there were significant differences between site 2 and sites 1, 4, 5, 6, 7, 12 ($p \leq 0.05$) and site 11and sites 1, 4, 6 ($p \leq 0.05$).

Respiration of Plant Material.

The rate of CO_2 efflux through dark respiration of papyrus plant material is shown in Figure 4.17. Respiration rates were calculated as the loss of carbon per gram of carbon of the sample material analysed. Respiration rates were highest in juvenile plant culms, at 0.31 ± 0.02 (SE) mg C g^{-1} C hr^{-1}, followed by mature and senescent culms at 0.21 ± 0.03 (SE) and 0.11 ± 0.03 (SE) mg C g^{-1} C hr^{-1} respectively. The respiration rate of the rhizome and fine root fraction was on average lower than carbon losses from the plant culm material at 0.18 ± 0.04 (SE) mg C g^{-1} C hr^{-1}. Temperatures within the respiration chamber during analysis were close to constant at approximately 25°C.

Statistical analyses of the mitochondrial respiration data, conducted using a one-way ANOVA and Bonferroni's Multiple Comparison test (Appendix 5), showed that there were no significant differences in rates of mitochondrial respiration between age classes ($p \geq 0.05$).

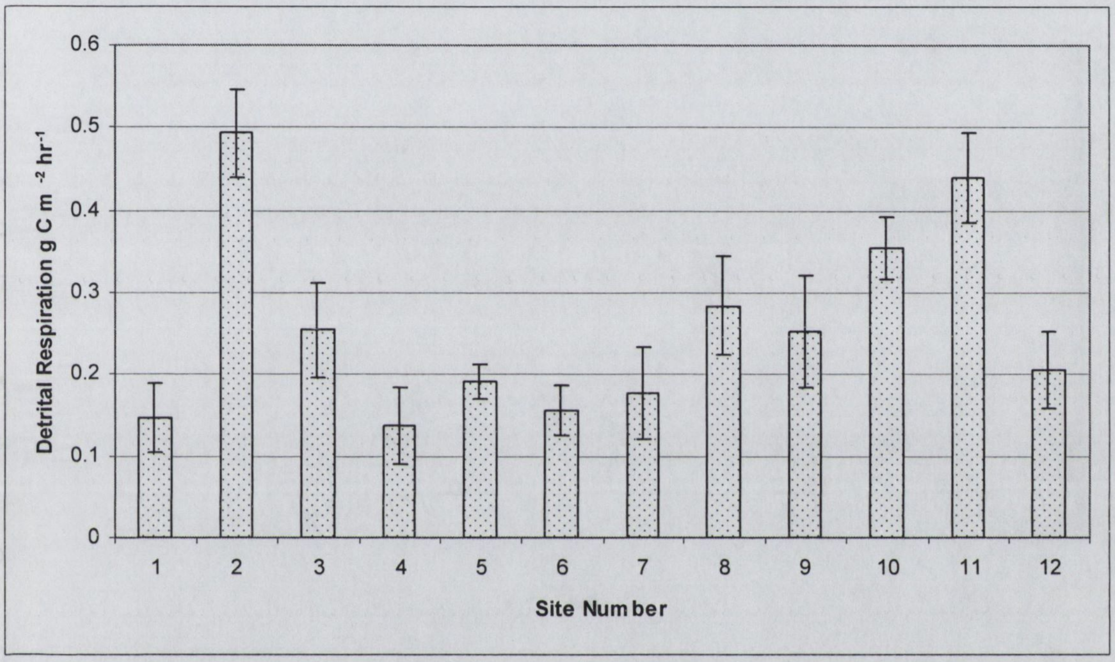

Figure 4.16. Average respiration rate of detrital material located on the surface of the papyrus rhizome. (Number of samples per site = 3; Error bars represent ± SD)

Total Carbon and Nitrogen.

The Total Carbon (TC) content of papyrus culms and umbel material for a range of age classes are shown in Figure 4.18. TC contents ranged from 36.4–41.7% for the culm material and 40.3–41.5% for the umbel material. The lower plant culm sections in all age classes had lower TC contents than the middle and upper culm sections. There was little distinction in TC between the middle and upper culm sections within the respective age classes. The juvenile and mature culms exhibited the lowest TC irrespective of culm section, with little difference between the two age classes. The senescent culms showed the highest TC content being 3-4% higher in all culm sample positions. The papyrus umbels showed high TC values with little variation between age class, the juvenile plants had the lowest TC of 40.3%, while the senescent plants maintained the highest TC at 41.5%.

Statistical analyses of the total carbon data were conducted using one-way ANOVA and Scheffe Post Hoc Test (Appendix 6). This analysis showed that there were significant differences in carbon content between juvenile and senescent and mature and senescent culms ($p \leq 0.001$). There were also significant differences between the lower plant culm and the middle, upper and umbel plant sections ($p \leq 0.05$).

The nitrogen content of the papyrus plants fell within a range of 0.34–2.18% (Figure 4.19). In both the plant culm and umbel samples the highest nitrogen content were found in the juvenile plants and the lowest in the senescent plants. There was little difference between the nitrogen content of the lower middle and upper plant culm sections within respective age classes. The juvenile plants had the highest nitrogen contents of the culm samples with 1.43%, 1.25% and 1.26% in the lower, middle and upper culm sections respectively. The mature culms had nitrogen contents of 0.77%, 0.68% and 0.76% in the lower, middle and upper culm sections respectively. The senescent culms had the lowest nitrogen contents with 0.34% in both the lower and middle culm sections and 0.44% in the upper culm sections. The juvenile papyrus umbels had the highest nitrogen content, with values of 2.18%, while the mature and senescent umbels had nitrogen contents of 2.09% and 1.20% respectively.

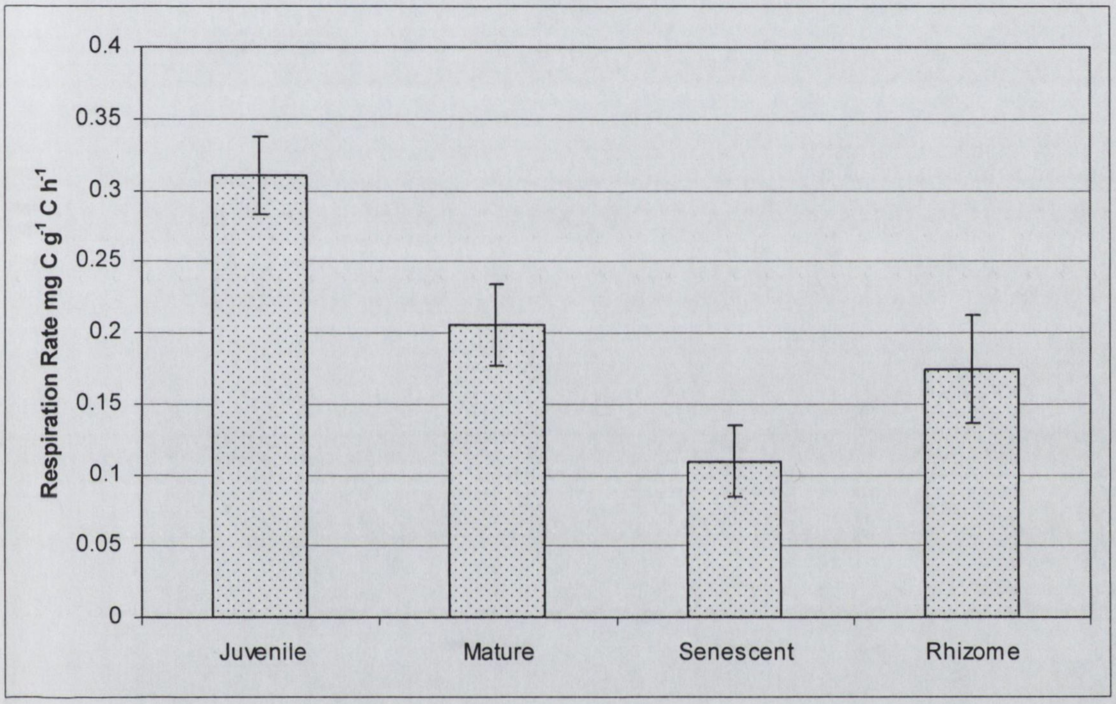

Figure 4.17. Average rate of mitochondrial respiration from papyrus culm and rhizome plant material at the Kirinya West wetland. Measurements were conducted on juvenile, mature and senescent plant culms and rhizome material with fine roots attached. Error bars indicate ± SD.

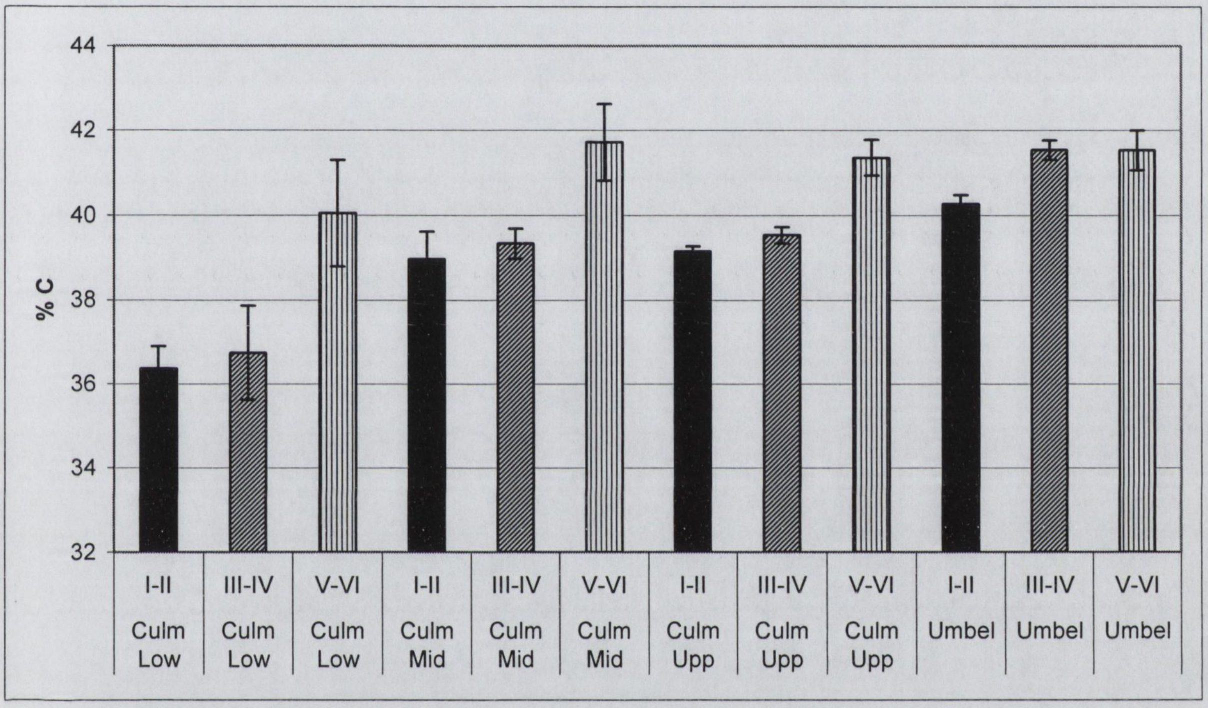

Figure 4.18. Total Carbon (TC) content of *C. papyrus*. L plant material. Estimates of TC were made on lower, middle and upper culm sections and umbel material for a range of age classes. The age classes represent juvenile (I-II), mature (III-IV) and senescent (V-VI) plant material. (Error bars indicate ± SE).

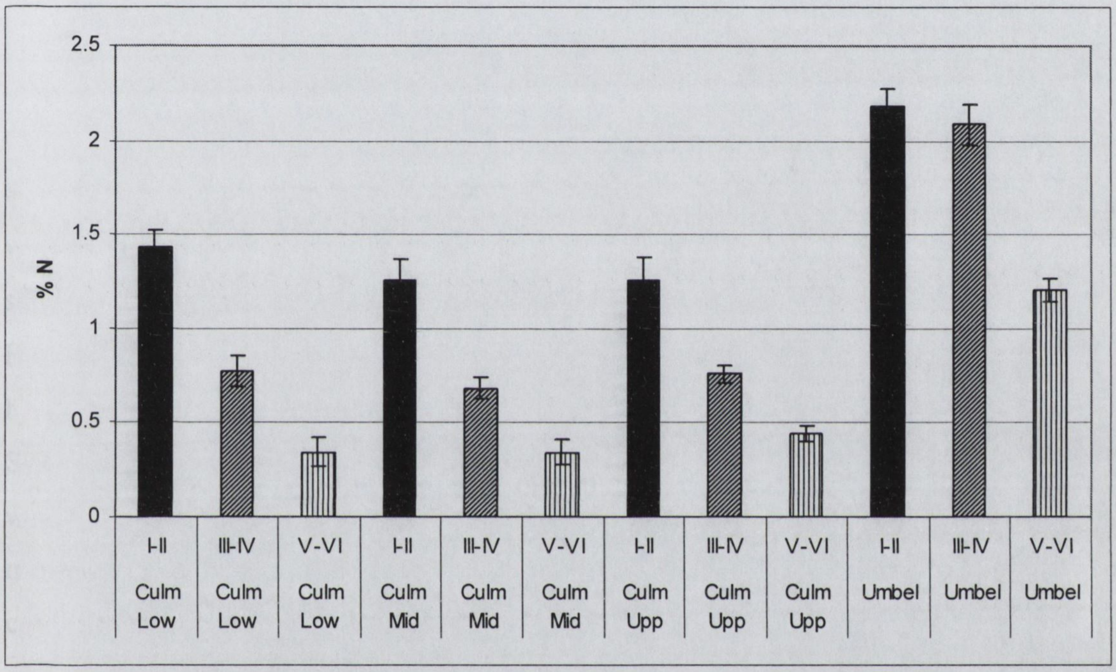

Figure 4.19. Total nitrogen content of *C. papyrus*. L plant material at the Kirinya West wetland. Estimates were made on lower, middle and upper culm sections and umbel material for a range of age classes. The age classes represent juvenile (I-II), mature (III-IV) and senescent (V-VI) plant material. (Error bars indicate ± SE).

Statistical analyses of the total carbon data were conducted using one-way ANOVA and Scheffe Post Hoc Test (Appendix 7). This analysis showed that there were significant differences between the TN content of the juvenile, mature and senescent plant culms ($p \leq 0.001$). There were also significant differences in the TN content of the juvenile and senescent and mature and senescent papyrus umbels ($p \leq 0.001$)

Dissolved Organic Carbon.

The water flowing into the Kirinya West Wetland from the waste water treatment maturation ponds had high concentrations of Dissolved Organic Carbon (DOC) compared to samples taken within the swamp and in the lake. The DOC concentration of the wastewater effluent entering the wetland was 13.78 ± 0.2 (SE) mg l^{-1}. While the water samples collected from the free-standing water beneath the papyrus rhizome within the EC flux footprint had DOC ranging from 5.97 ± 0.22 (SE) mg l^{-1} to 10.98 ± 0.23 (SE) mg l^{-1} (Figure 4.20). The lowest DOC concentrations were recorded in samples collected at Site 3, which was located along Transect 1 in the middle of the wetland (Figure 4.1). The water column at this point was the deepest of all sites sampled at approximately 3–4 metres. The lowest DOC concentration sampled was from that of the lake water collected from the open water body in the Napoleon Gulf. The DOC of the lake water was approximately 4.99 ± 0.53 (SE) mg l^{-1}.

Statistical analyses of the DOC data were conducted using a one-way ANOVA and Bonferroni's Multiple Comparison test (Appendix 8). The analyses showed significant differences between the effluent and wetland samples ($p \leq 0.001$), the effluent and lake samples ($p \leq 0.001$), between the wetland sites 1, 2, 4, 5, and 3 ($p \leq 0.001$), and between wetland sites 1, 2, 4, 5, and the lake samples ($p \leq 0.001$).

Methane Efflux.

The plant mediated emission of methane from papyrus was measured from juvenile, mature and senescent plant culms at three points over a 24h hour period. Rates of emission were estimated at 09:00 hrs (Figure 4.21), 12:00 hrs (Figure 4.22) and 17:00

hrs (Figure 4.23). Methane fluxes were highest from the mature culms, they were low from juvenile culms and were negligible form senescent culms. The juvenile papyrus culms had mean rates of methane emission of 0.046 ± 0.009 μg CH_4 cm^{-2} hr^{-1}, at 09:00 hrs, and 0.101 ± 0.01μg CH_4 cm^{-2} hr^{-1} at both 12:00hrs and 17:00hrs. The mature culms showed the highest mean rates of methane emission with 0.08 ± 0.007 μg CH_4 cm^{-2} hr^{-1} at 09:00 hrs, 0.28 ± 0.03 μg CH_4 cm^{-2} hr^{-1} at 12:00 hrs and 0.12 ± 0.019 μg CH_4 cm^{-2} hr^{-1} at 17:00 hrs. Senescent culms showed constantly low rates of methane emission over all time periods with mean flux rates of 0.05 ± 0.009 μg CH_4 cm^{-2} hr^{-1} at 09:00 hrs, 0.03 ± 0.01 μg CH_4 cm^{-2} hr^{-1} at 12:00 hrs and 0.03 ± 0.008 μg CH_4 cm^{-2} hr^{-1} at 17:00 hrs.

Statistical analyses of the CH_4 efflux data were conducted using one-way ANOVA and Scheffe Post Hoc Test (Appendix 9). These analyses showed no significant differences between the time of day and rate of CH_4 efflux ($p \geq 0.05$), however there were significant differences between the rate of CH_4 efflux from juvenile and senescent and mature and senescent plant culms ($p \leq 0.05$).

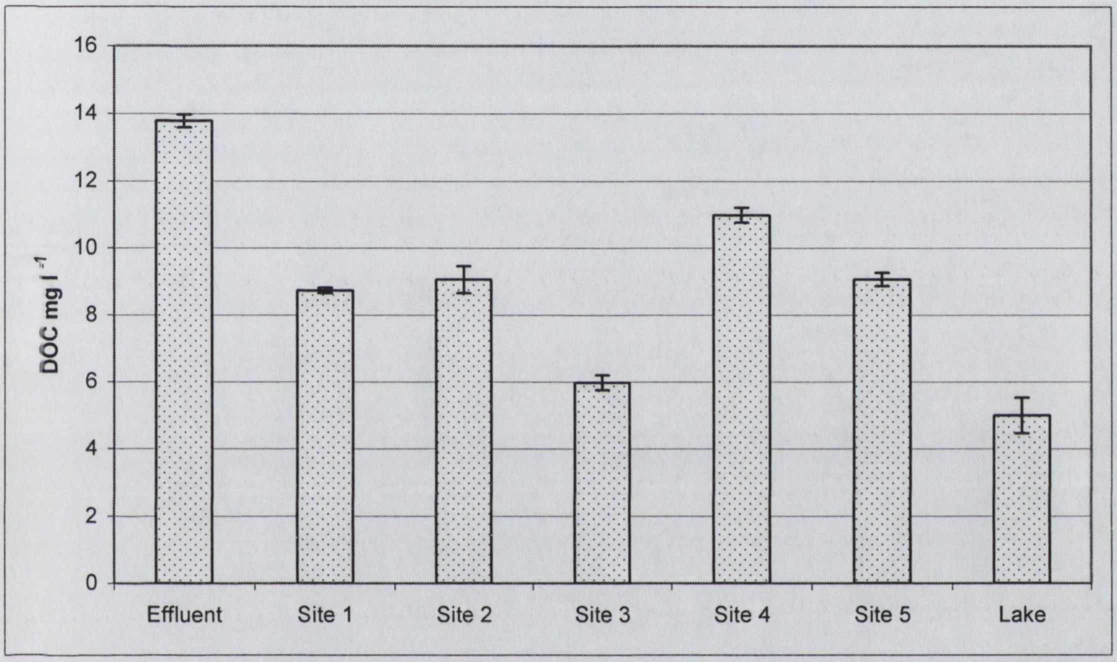

Figure 4.20. Dissolved Organic Carbon content of water samples taken from the Kirinya West Wetland. Samples collected from wastewater treatment ponds at point of entry into the wetland (Effluent), from the free standing water column beneath the papyrus rhizome (Sites 1 –5 , selected at random within the EC flux footprint) and from the open water within the Napoleon Gulf. (Number of samples 3; Error bars indicate ± SE).

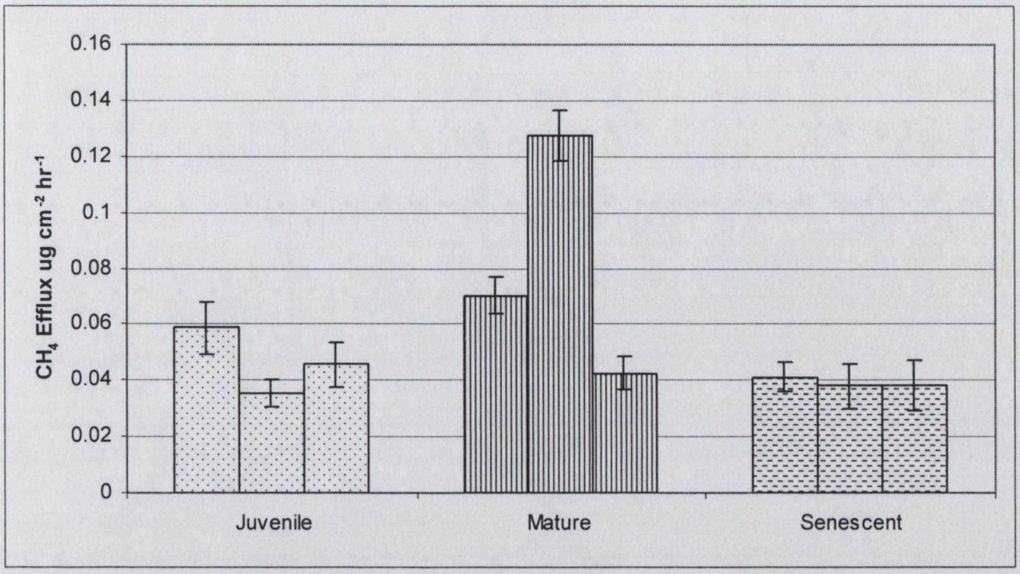

Figure 4.21. Average efflux of methane (μg CH_4 cm^{-2} hr^{-1}) from juvenile, mature and senescent *C. papyrus* L. culms at the Kirinya West wetland. Data shows rate of efflux estimated at 09:00 hrs. (N = 3; Error bars indicate ± SE).

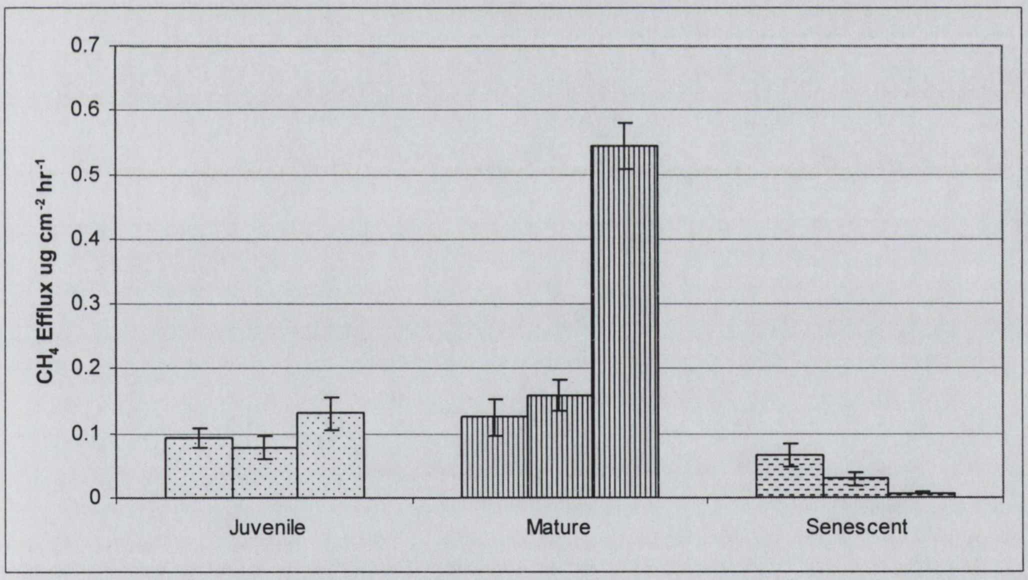

Figure 4.22. Average efflux of methane (μg CH_4 cm^{-2} hr^{-1}) from juvenile, mature and senescent *C. papyrus* L. culms at the Kirinya West wetland. Data shows rate of efflux estimated at 12:00 hrs. (N= 3; Error bars indicate ± SE).

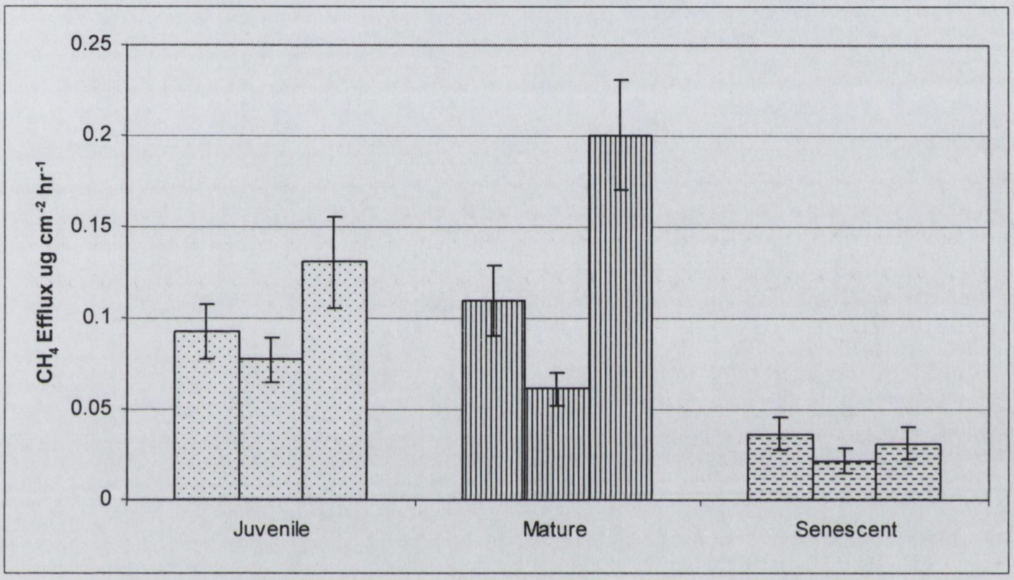

Figure 4.23. Average efflux of methane (μg CH_4 cm^{-2} hr^{-1}) from juvenile, mature and senescent *C. papyrus* L. culms at the Kirinya West wetland. Data shows rate of efflux estimated at 17:00 hrs. (N= 3; Error bars indicate ± SE).

4.4. Fluxes of Carbon, Water and Energy over cocoyam (*Colocasia antiquorum*) cultivated wetland.

4.4.1. Introduction.

Wetland areas in the Lake Victoria basin are subject to increasing human population pressures. One key manifestation of such pressure is the increase in wetland area being used for agricultural production. The Nakivubo wetland connects Kampala, the capital city of Uganda to Lake Victoria, and is a good example of the pressures agricultural production can place on the biological diversity of such wetland areas. The encroachment of agricultural development on wetlands originates on a small scale and in general these areas tend to expand from the landward edge of the wetland. The natural papyrus vegetation at the Nakivubo has largely been removed and the cultivation of *Colocasia antiquorum* (cocoyam) now dominates (Figure 2.4). The Nakivubo wetland therefore exhibits agricultural disturbance characteristics and also provides a large homogenous stand of *C. antiquorum* on which to undertake EC flux measurements.

The Nakivubo wetland because of its location receives secondary treated wastewater and industrial effluent from the city of Kampala. The tertiary bio-attenuation of wastewater through the Nakivubo wetland has occurred since the 1970's (Kansiime, 1999), however the reduction in natural vegetation cover consisting mainly of papyrus through wetland reclamation for agricultural purposes may reduce the ability of the wetland to effectively treat the wastewater. The alteration of the vegetation cover of the Nakivubo wetland may also have a direct impact on the biogeochemical cycles associated with the wetland ecosystem. This might influence the carbon source or sink strength of the wetland, the dissipation of solar radiation and energy fluxes within the local environment and water losses through evapotranspiration. Because of the large wetland area associated with the Lake Victoria basin, such factors may have a significant impact on the regulation and governance of local climatic feedback mechanisms.

The encroachment of agriculture on papyrus-dominated wetlands also influences the physical conformity of the wetland. The rhizomatous nature of papyrus wetlands allows the formation of a relatively solid floating platform. The clearance of this vegetation for agricultural development therefore diminishes the physical stability of the wetland.

4.4.2. Materials and Methods.

4.4.2.1. Site Description

As described in Chapter 2, the Nakivubo wetland was selected, as it represents a good example of wetland disturbance through agricultural encroachment. The encroachment of cocoyam agriculture has replaced most of the papyrus stand as documented by Kansiime and Nalubega (1999), and it provides a large, relatively homogenous stand of *C. antiquorum* over which to perform EC flux measurements. The site was selected and maintained with the assistance of Dr. F. Kansiime and Mr. B. Twesigye from MUIENR. Due to the open nature of the wetland and the close proximity of heavily populated areas the security of the EC flux tower was provided through the assistance of the Ministry of Water, Lands and Environment, and the Luzira maximum security prison.

The lower section of the Nakivubo wetland was selected for the EC campaign due to the large stand of *C. antiquorum* available, and because the remaining papyrus rhizome structure was more solid and stable. The railway line crossing the wetland is situated on a weir structure, which helps to retain water in the upper Nakivubo wetland and allows a prolonged period of bio-attenuation of wastewater. The increased water depth and reduced stability of the wetland structure deemed the upper Nakivubo wetland too dangerous to attempt to site the EC flux tower. MUIENR utilise both sections of the Nakivubo wetland for research purposes, this allowed the integration of the EC flux tower within the agricultural areas used by the local community.

4.4.2.2. Field Measurements.

Eddy Covariance.

The EC flux tower was constructed in the lower Nakivubo wetland in June 2004. The Nakivubo wetland covers an area of 2,500,000 m^2, the vegetation of which is largely covered by cocoyams grown as a subsistence crop. Small areas of stunted papyrus and tree plantations are also present. The location of the EC flux tower is shown in Figure 4.24. The location of the EC flux tower was determined through historical and short term monitoring of the prevailing wind direction. This ensured the flux footprint of the EC tower would predominantly cover the *C. antiquorum* vegetation. The stability of the wetland rhizome and the depth of the water column restricted access and penetration into the wetland. The EC tower stood one metre above the wetland rhizome and was secured by submerging the tower legs into the sediment below. The tower was constructed in a location best suited to both high quality flux measurements and personal safety.

The EC equipment, described in section 4.3.2.2, was erected at a height of 2 metres above the wetland rhizome, approximately 0.5 to 1 metre above the height of the tallest plants. This measurement height ensured that 95 % of the flux footprint sampled by the EC tower, based on calculations by Scheupp *et al.* (1990), would arise from the homogeneous cocoyam plant canopy. The flux footprint generated during the measurement campaign over the Nakivubo wetland is shown in Appendix 3, and was constructed based on the calculations by Scheupp *et al.* (1990). Apart from the usual data loss through equipment downtime and data rejection, rates of collection were good with a total of 147 days of EC data collected between June and October 2004. Data downloads took place at weekly intervals and AGU inspection and CO_2 calibration and span were also performed at this time. The EC flux analysis procedures used are described in section 4.3.2.2

Meteorological.

The meteorological equipment used and measurements taken are described in section 4.3.2.2.

Detrital Respiration

Measurements of carbon loss through detrital respiration were made at the Nakivubo wetland within the EC flux footprint using the ADC LCA-4 portable gas analyser (ADC Bio-Sciences, Hoddeston, England). Replicate measurements were made between 09:00 and 17:00 hrs and rates of CO_2 release were measured at 30 second intervals over 15–30 minute periods. During the measurements the temperature of the detritus was measured at the surface and at a depth of 5 centimetres.

4.3.3. Results.

Weather.

Meteorological data were collected *in situ* from the EC flux tower situated within the Nakivubo wetland. The data were collected at 15 minute intervals and the daily values were averaged on a weekly basis. Weekly estimates of air temperature over the Nakivubo wetland vegetation are shown in Table 4.8. Daily maximum temperatures ranged between 25°C and 31°C, with the highest temperatures recorded in October 2004. On average maximum air temperatures were lower during June and July 2004 and gradually increased through August to October. Daily minimum air temperatures ranged from 10°C to 18°C with the lowest temperatures occurring in July 2004. Mean air temperatures showed relatively little variation with daily means fluctuating between 19°C and 22°C. The air temperatures were similar to data previously recorded at the same site by Kansiime and Nalubega (1999), where average maximum, minimum and mean temperatures of 29°C, 15°C and 21°C were respectively recorded. The average diurnal patterns of air temperature based on monthly data sets, above the cocoyam canopy at Nakivubo are shown in Figure 4.25. Night time air temperatures remained relatively stable, fluctuating between 16 and 19°C in the early hours of the morning 00:00 hrs to 07:30 hrs. After sunrise (approximately 07:00 hrs, Figure 4.26) air temperatures steadily increase to a maximum of 26°C at approximately 12.15 hrs. The air temperature then tended to stay relatively stable remaining above 25°C between 12:00 hrs and 15:00 hrs (June–August, 2004) and between 12:00 hrs and 17:00 hrs (September–October, 2004). Temperatures then tended to decrease between 15:00 hrs and 20:00 hrs by 5-6°C. There was little inter-month variation with values fluctuating within a 3°C range at any given point over the 24 hour time course. The lowest night time temperatures were recorded in July where early morning temperatures (00:00 hrs to 07:30 hrs) remained relatively stable at approximately 16°C and there was little monthly variation between peak temperatures, with values ranging from 25.5–26.4°C.

The mean weekly patterns of PAR (400–700 nm) received by the *C. antiquorum* canopy are described in Table 4.9. The maximum influx ranged from 1760–2272 μmol m^{-2} s^{-1} with the highest levels received during September to October 2004 when maximum influx of PAR was consistently above 2000 μmol m^{-2} s^{-1}. The mean weekly estimates ranged from 329–507 μmol m^{-2} s^{-1}. Diurnal patterns of PAR flux above a *C. antiquorum* canopy, based on monthly data sets are shown in Figure 4.26. The highest flux values occurred in June with peaks of approximate 1657 μmol m^{-2} s^{-1}, and the diurnal PAR patterns were similar from July through October with peak fluxes averaging approximately 1400 μmol m^{-2} s^{-1}. Weekly cumulative PAR values ranged from 225-341 mol PAR m^{-2}.

Weekly means of relative humidity (RH) recorded over the *C. antiquorum* vegetation are listed in Table 4.10, with mean RH values ranging between 75–81%.

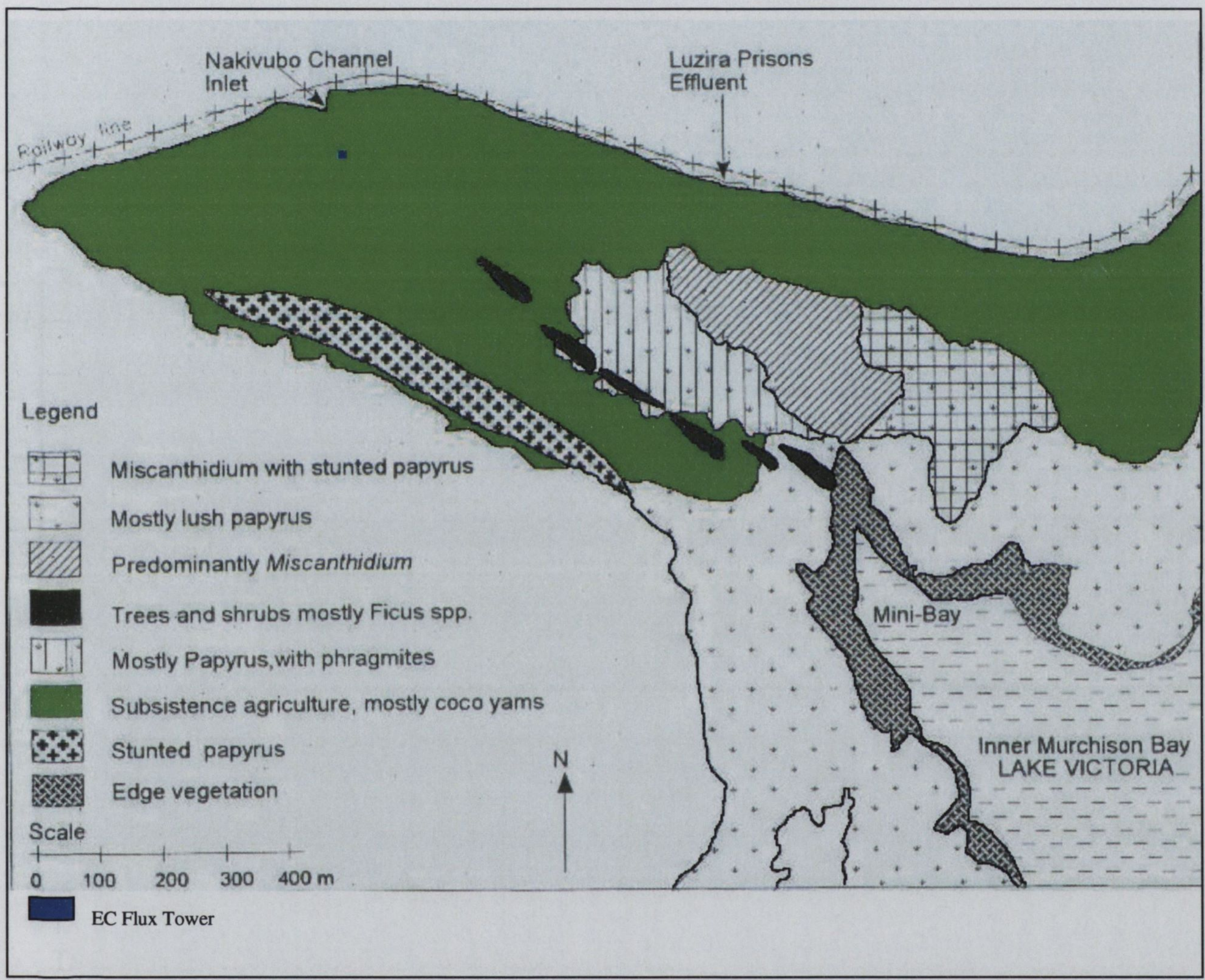

Figure 4.24. Map showing the Lower Nakivubo wetland vegetation and the location of the EC flux tower 🟦. (Re-drawn from Kansiime and Nalubega, 1999).

Month	**Week**	**Maximum °C**	**Minimum °C**	**Mean °C**
June	2	25.89	14.24	21.05
June	3	28.18	15.52	20.95
June	4	26.55	16.40	21.20
June	5	26.09	13.84	20.44
July	1	26.56	10.87	19.40
July	2	27.45	12.65	20.59
July	3	27.74	15.34	20.67
July	4	28.65	12.99	20.77
August	1	28.27	15.07	20.96
August	2	28.34	14.95	21.08
August	3	28.35	13.32	20.16
August	4	29.39	15.38	21.15
September	1	29.89	13.84	20.78
September	2	28.29	15.69	21.24
September	3	29.28	15.92	21.67
September	4	28.14	16.31	21.28
September	5	29.97	16.17	20.90
October	1	31.89	16.17	22.25
October	2	31.50	16.90	22.26
October	3	28.15	18.06	21.68
October	4	29.23	15.85	21.58

Table 4.8. Weekly maximum, minimum and mean values of air temperature over a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from June to October 2004.

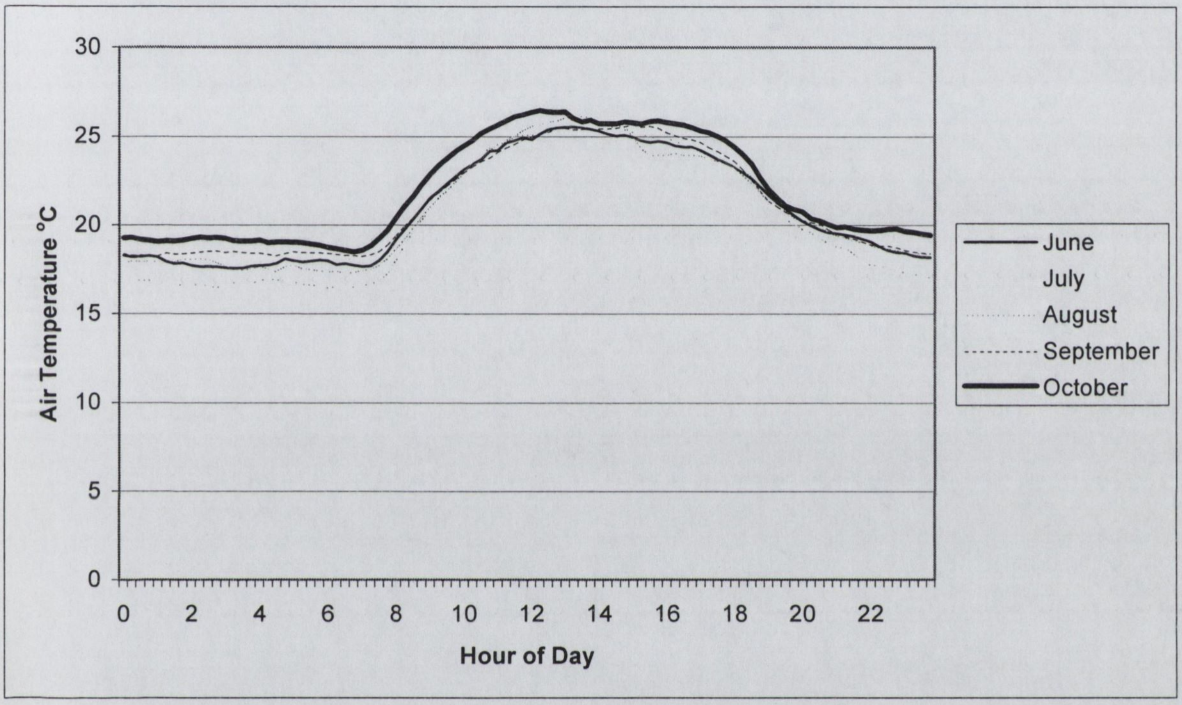

Figure 4.25. Monthly average diurnal air temperatures over a *C .antiquorum* canopy at the Nakivubo wetland. Data collected from June to October 2004.

Month	**Week**	**Maximum** μ**mol m^{-2} s^{-1}**	**Mean** μ**mol m^{-2} s^{-1}**	**Cumulative PAR mol m^{-2}**
June	2	2079	406.5	320.19
June	3	2151.7	396.91	266.73
June	4	1944.4	397.71	248.48
June	5	1877.5	507.97	341.37
July	1	1790.2	447.33	300.64
July	2	1760.6	418.29	281.10
July	3	2046.9	358.55	240.96
July	4	1947.4	407.82	274.06
August	1	2129.3	335.62	225.88
August	2	2231	395.94	251.75
August	3	1839.6	329.92	246.95
August	4	2081.7	449.13	301.83
September	1	2124.9	416.11	279.63
September	2	1971.6	448.31	301.28
September	3	2199	459.37	308.71
September	4	2175.3	389.10	261.50
September	5	2099.1	347.90	233.81
October	1	2078	503.88	338.64
October	2	2120.8	434.23	291.83
October	3	2272.4	324.84	230.15
October	4	2026.6	359.87	241.87

Table 4.9. Weekly maximum, mean and cumulative Photosynthetically Active Radiation (400-700 nm) over a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from June to October 2004.

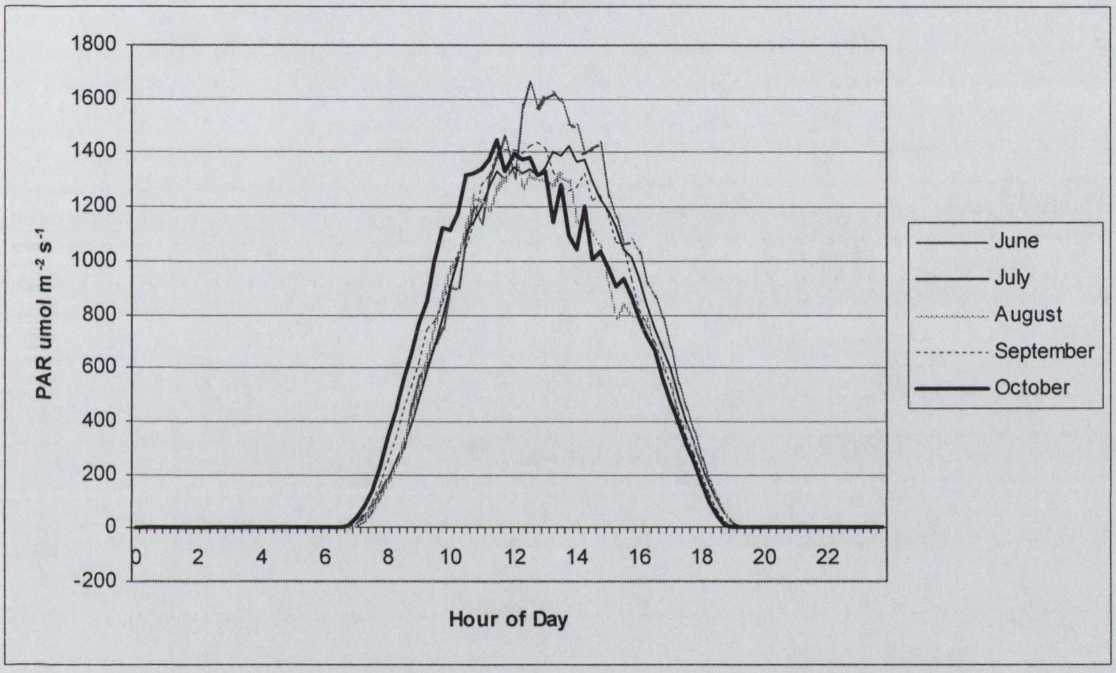

Figure 4.26. Average monthly diurnal variation in PAR (400 – 700 nm) over a stand of *C. antiquorum* at the Nakivubo wetland. Data collected from June to October 2004.

Month	Week	Maximum %	Minimum %	Mean %
June	2	93.49	60.32	77.35
June	3	93.90	48.27	80.85
June	4	93.05	55.56	80.10
June	5	94.00	50.72	77.07
July	1	93.96	51.16	75.53
July	2	94.13	51.58	78.25
July	3	93.52	45.54	80.14
July	4	93.94	40.60	76.35
August	1	93.80	45.87	79.38
August	2	93.60	45.16	78.94
August	3	93.36	45.55	80.25
August	4	93.64	42.51	78.91
September	1	93.89	42.14	78.88
September	2	93.62	50.40	80.16
September	3	93.15	48.03	77.66
September	4	93.31	50.40	79.99
September	5	93.36	47.02	81.65
October	1	93.65	40.32	77.43
October	2	92.93	42.59	78.15
October	3	93.01	54.00	81.85
October	4	93.38	40.03	80.76

Table 4.10. Weekly maximum, minimum and mean values of relative humidity over a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from June to October 2004.

Eddy Covariance.

Energy Budget.

The relationship between turbulent and available energy fluxes were analysed for each weekly data set. Figure 4.27 shows the relationship between turbulent and available energy fluxes over the *C. antiquorum* canopy at the Nakivubo wetland, from the 21st to 27th July 2004. The degree of energy balance closure in this example is described by a slope of 0.59 and an R^2 value of 0.87. This suggests only weak agreement between turbulent and available fluxes throughout the energy flux range. Table 4.11 shows the slope and R^2 values associated with the energy balance closure for the entire data set. The energy balance closure for the entire data set had slope and R^2 values of 0.59 to 0.77 and 0.76 to 0.89 respectively.

An example of the component fluxes of the energy budget above a *C. antiquorum* canopy at the Nakivubo wetland are shown in partitioned form in Figure 4.28. At midday 60% of the radiative fluxes were partitioned into λE and 16% partitioned into H at this point. Ground heat fluxes were negligible at all times, highlighting the effective shading capacity of the *C. antiquorum* vegetation. Approximately 24% of the energy entering the wetland at this point was either lost or undetected by the EC system.

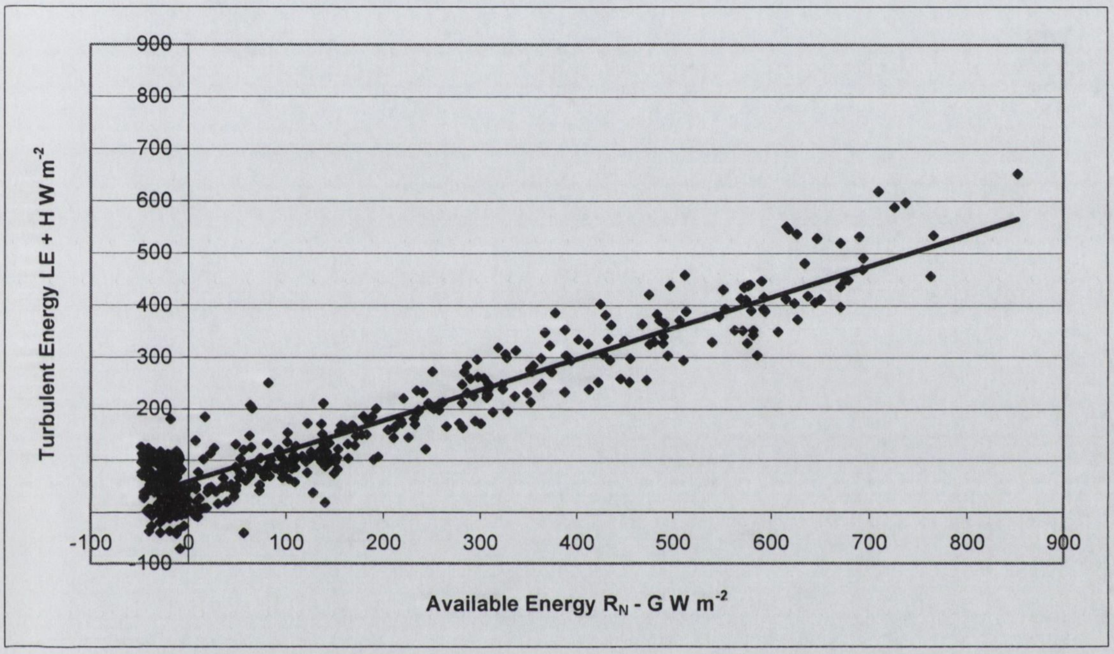

Figure 4.27. Scatter diagram and regression line representing the relationship between turbulent and available energy, over a *C. antiquorum* canopy. Data collected from 2nd to 8th August 2004, at the Nakivubo wetland. (Slope = 0.59 $R^2 = 0.87$)

Month	Week	Slope	R^2
June	2	0.676	0.89
June	3	0.668	0.89
June	4	0.644	0.88
June	5	0.606	0.88
July	1	0.647	0.88
July	2	0.654	0.88
July	3	0.651	0.87
July	4	0.664	0.87
August	1	0.594	0.87
August	2	0.613	0.89
August	3	0.692	0.85
August	4	0.661	0.87
September	1	0.667	0.86
September	2	0.672	0.85
September	3	0.705	0.87
September	4	0.696	0.84
September	5	0.622	0.84
October	1	0.770	0.85
October	2	0.755	0.83
October	3	0.645	0.76
October	4	0.674	0.85

Table 4.11. The slope and R^2 values of the linear regression of energy balance components. Data collected over a *C. antiquorum* canopy at the Nakivubo wetland from June to October 2004.

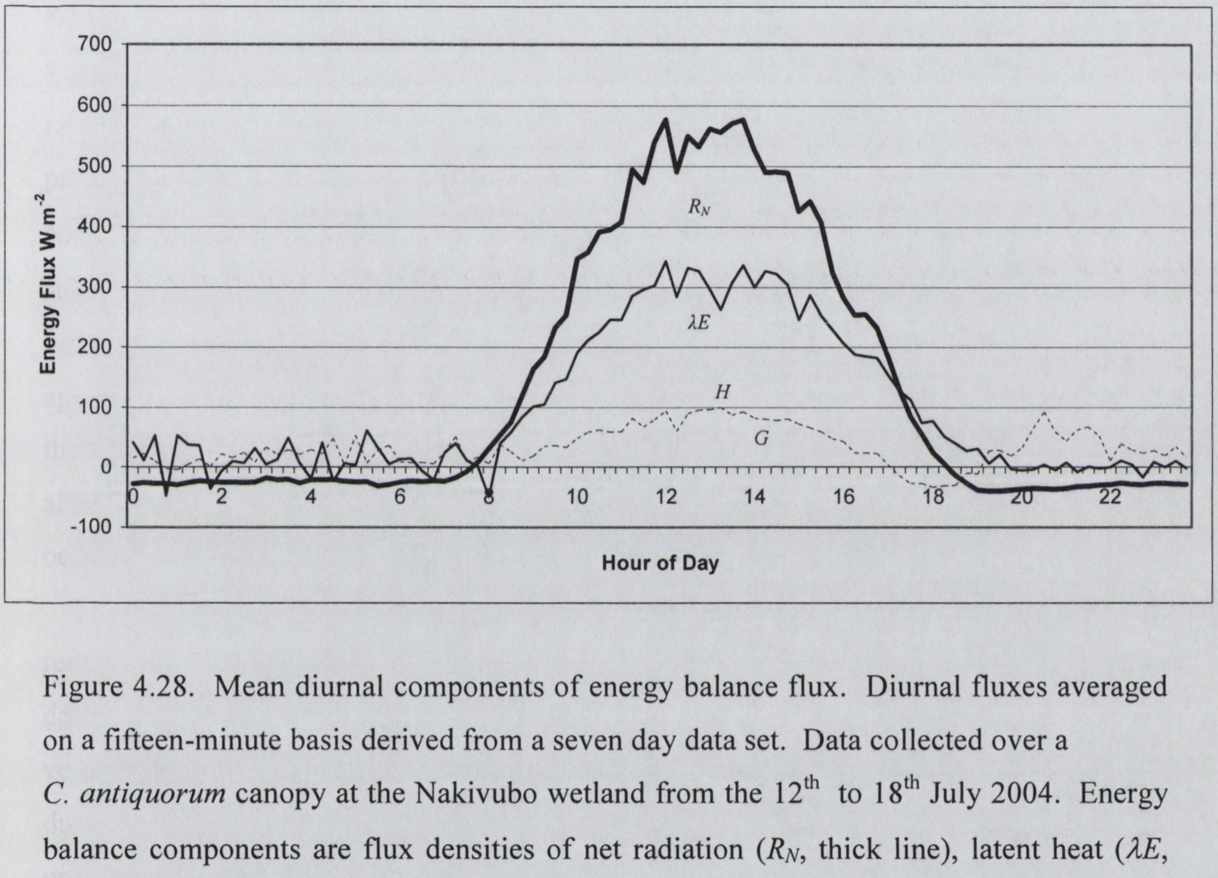

Figure 4.28. Mean diurnal components of energy balance flux. Diurnal fluxes averaged on a fifteen-minute basis derived from a seven day data set. Data collected over a *C. antiquorum* canopy at the Nakivubo wetland from the 12th to 18th July 2004. Energy balance components are flux densities of net radiation (R_N, thick line), latent heat (λE, thin line), sensible heat (H, dashed line), and ground heat flux (G, dotted line, unseen as fluxes are negligible).

Ecosystem Carbon Flux

Net Ecosystem Exchange (NEE) of CO_2 as measured by the EC system for the duration of the test period, is shown in Figure 4.29(i) and Figure 4.29(ii). The EC system was deployed at the Nakivubo wetland for a period of five months, during which there were only small gaps in the data stream due to equipment downtime. The positive flux values indicate periods of net ecosystem loss of CO_2 from the system, while the negative values indicate a net gain of CO_2 by the ecosystem. Peak rates of CO_2 release from the system ranged between 20 and 30 μmol CO_2 m^{-2} s^{-1}, while peak rates of CO_2 uptake ranged between 25 and 40 μmol CO_2 m^{-2} s^{-1}. Figure 4.30 illustrates the typical diurnal patterns of CO_2 flux observed during the measurement period (June-October, 2004). Night time respiratory losses ranged between 5 and 12 μmol CO_2 m^{-2} s^{-1}, and after sunrise the ecosystem switches from a net source to a net sink of CO_2. The switch between source and sink CO_2 efflux patterns occurred at approximately 08.00 hrs, approximately one hour after daybreak (Figure 4.26). As PAR influx decreases throughout the afternoon the rate of CO_2 assimilation by the *C. antiquorum* vegetation also decreases, and the system reverts back to acting as a carbon source. This change occurs at approximately 18:15 hrs, before sunset.

Table 4.12 illustrates patterns of gross primary production, total ecosystem respiration and corresponding patterns of carbon gain or release, based on weekly EC data sets over the measurement period. Rates of carbon uptake by the cocoyam vegetation ranged up to 21 g C m^{-2} wk^{-1}, while approximately 3 g C m^{-2} wk^{-1} were lost during the period of net carbon release. Although the diurnal patterns of net carbon uptake and release were similar throughout the test period, the data in Table 4.12 illustrates that contrasting patterns of net carbon uptake or release occurred. During the measurement period only one of the weekly data sets showed the wetland to be a net source of carbon. Figure 4.31 shows the diurnal carbon flux pattern for data collected in the first week of September 2004 (a period of net carbon release) and the second week in September 2004 (a period of net carbon uptake). Both periods show similar patterns of nigh time CO_2 efflux, with rates varying 5-15 μmol CO_2 m^{-2} s^{-1}. The data collected between 6th to 12th September 2004 showed peak rates of CO_2 uptake of approximately

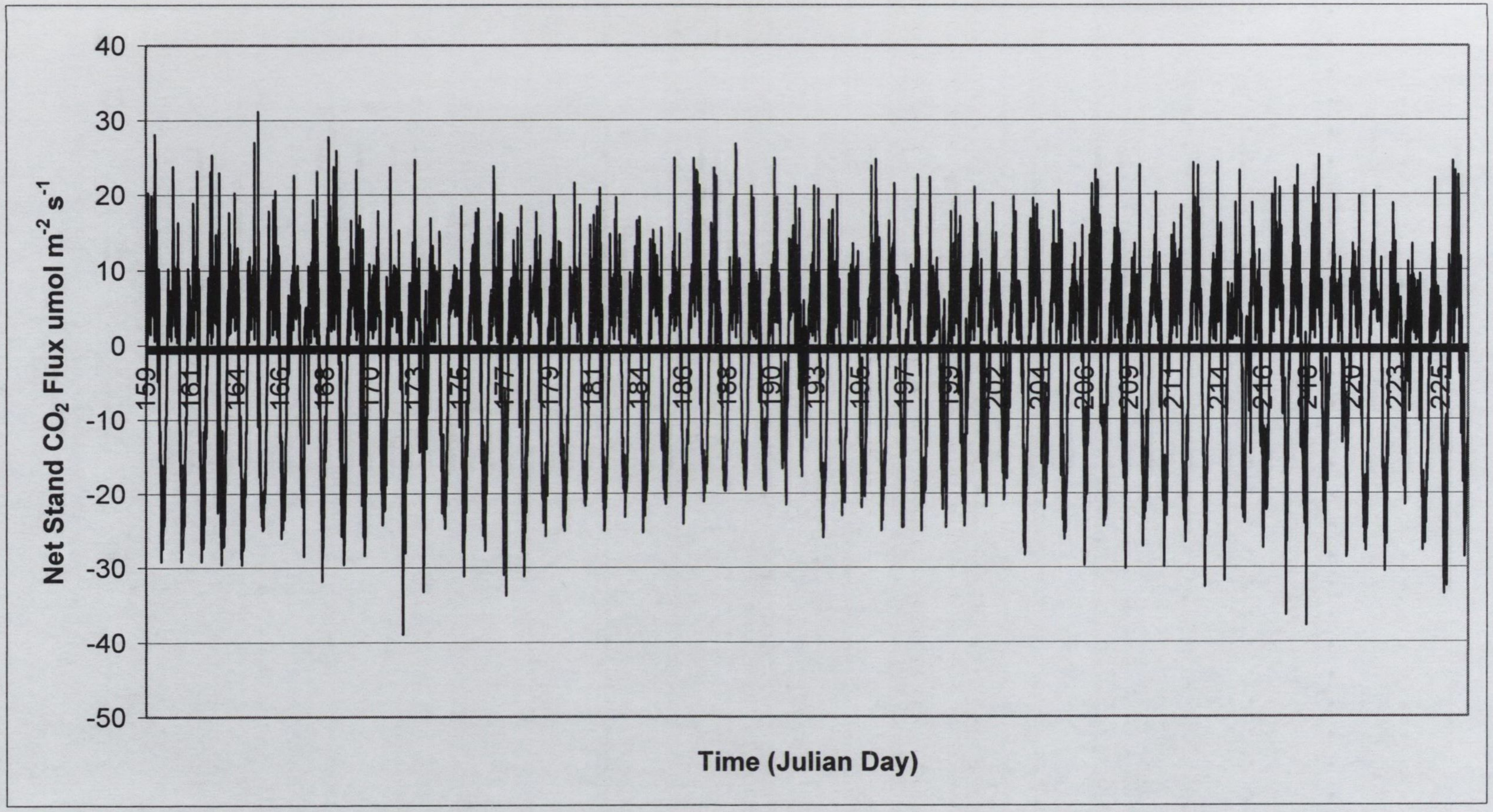

Figure 4.29(i). Net stand CO_2 flux measured above a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from 8th June to 14th August 2004. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

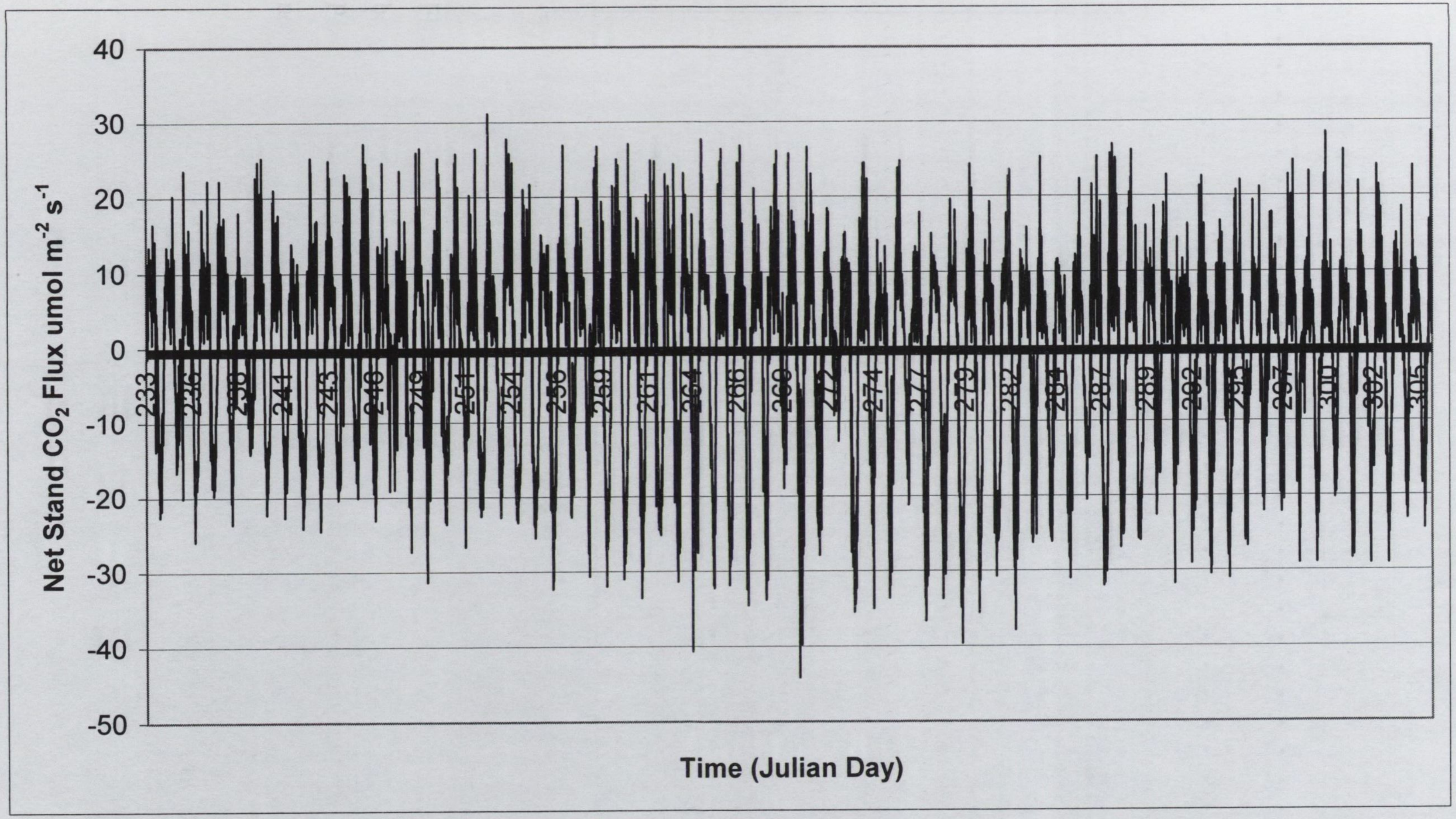

Figure 4.29(ii). Net stand CO_2 flux measured above a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from 21st August to 1st November 2004. Negative values indicate a net gain of CO_2 by the ecosystem, positive values indicate a net loss of CO_2 from the ecosystem.

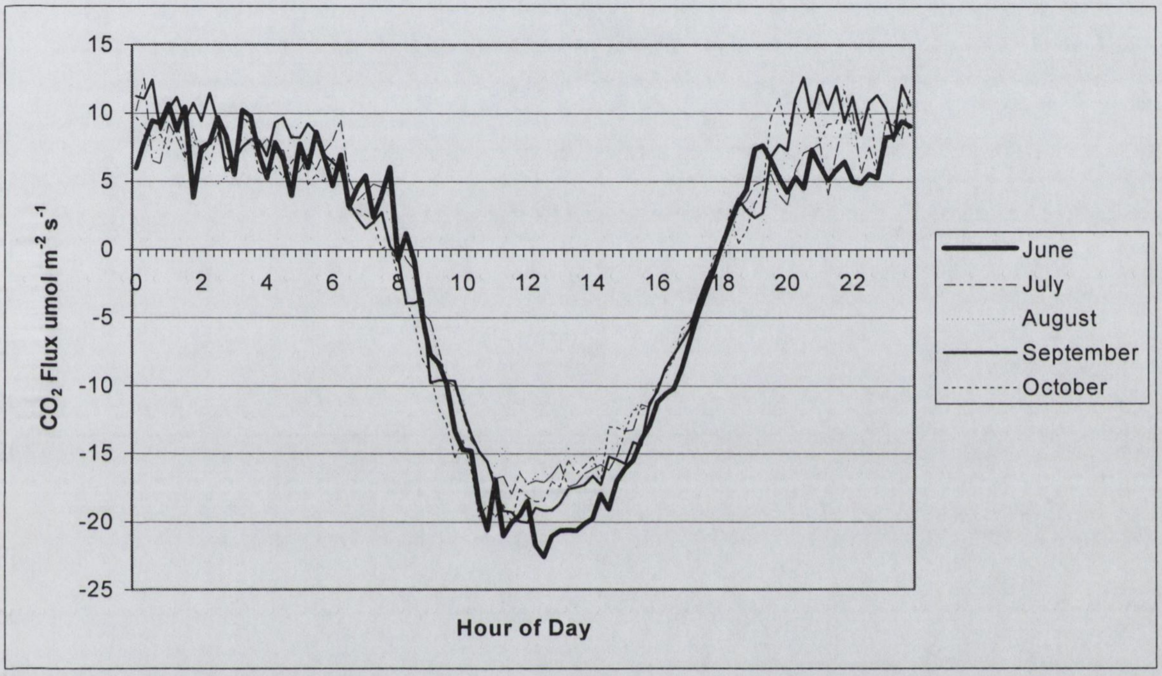

Figure 4.30. Average diurnal cycle of ecosystem CO_2 flux based on EC data collected between June and October, 2004 over a *C. antiquorum* canopy at the Nakivubo wetland. Positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system.

19 μmol CO_2 m^{-2} s^{-1}, in comparison peak rates of CO_2 uptake between 30th August to 5th September were approximately 15% lower. In addition, rates of CO_2 uptake between 15:30 hrs and 17:00 hrs were approximately 40-70% lower in flux data collected between 30th August to 5th September 2004 when compared to flux data collected between 6th to 12th September 2004.

Rates of carbon assimilation are a function of incoming photosynthetic active radiation (PAR). The relationship between net stand CO_2 flux and PAR for the periods 30th August to 5th September 2004 and 6th to 12th September 2004 are shown in Figures 4.32 and 4.33 respectively. Both periods show similar magnitudes of CO_2 uptake (negative values) with maximum rates of CO_2 assimilation ranging between 25-27 μmol CO_2 m^{-2} s^{-1}. The magnitude of CO_2 release (positive values) were also similar with values ranging between 11-17 μmol CO_2 m^{-2} s^{-1}. Net respiratory carbon flux (carbon release) accounted for a higher percentage, approximately 27% of the total data set for the period 30th August to 5th September 2004, while the net respiratory carbon flux accounted for approximately 17% of the data collected between 6th to 12th September 2004.

The average diurnal patterns of PAR flux over both time periods are shown in Figure 4.34. The peak instantaneous irradiance received by the cocoyam canopy for both periods was approximately 1500 μmol CO_2 m^{-2} s^{-1}. The integrated daily irradiance for the period 30th August to 5th September 2004 was approximately 39.96 mmol m^{-2} d^{-1}, while the integrated daily irradiance for the period 6th to 12th September 2004 was approximately 43.04 mmol m^{-2} d^{-1}.

Water Vapour Fluxes.

The weekly average water vapour fluxes as measured by the EC system are shown in Figure 4.35. Average losses ranged between 2–5 kg H_2O m^{-2} d^{-1}, the highest occurring in October 2004, averaging 5.44 kg H_2O m^{-2} d^{-1}, the lowest rates of water loss were experienced in August where losses were approximately 2.26 kg H_2O m^{-2} d^{-1}. Typical monthly diurnal flux patterns of water vapour exchange over a *C. antiquorum*

Month	**Week**	**NEE g C m^{-2}**	**GPP g C m^{-2}**	**Reco g C m^{-2}**
June	2	-14.24	-29.02	14.24
June	3	-10.15	-27.78	17.63
June	4	-8.21	-20.26	12.05
June	5	-13.10	-25.68	12.58
July	1	-2.94	-13.31	10.37
July	2	-8.62	-13.98	5.36
July	3	-4.73	-14.83	10.10
July	4	-8.43	-19.38	10.95
August	1	-5.83	-13.92	8.09
August	2	-10.34	-16.29	5.95
August	3	-2.49	-9.42	6.93
August	4	-2.57	-12.07	9.50
September	1	3.11	-5.45	8.56
September	2	-3.51	-12.38	8.87
September	3	-5.86	-17.33	11.47
September	4	-8.21	-17.96	9.75
September	5	-7.84	-13.70	5.86
October	1	-21.13	-30.46	9.33
October	2	-6.40	-16.53	10.13
October	3	-4.46	-10.47	6.01
October	4	-5.44	-15.95	10.51

Table 4.12. Weekly carbon flux over a *Colocasia antiquorum* dominated wetland. Values represent grams of carbon flux per square metre. Data collected from June to October 2004 at the Nakivubo wetland, Kampala, Uganda. Negative values indicate carbon uptake positive values indicate carbon release.

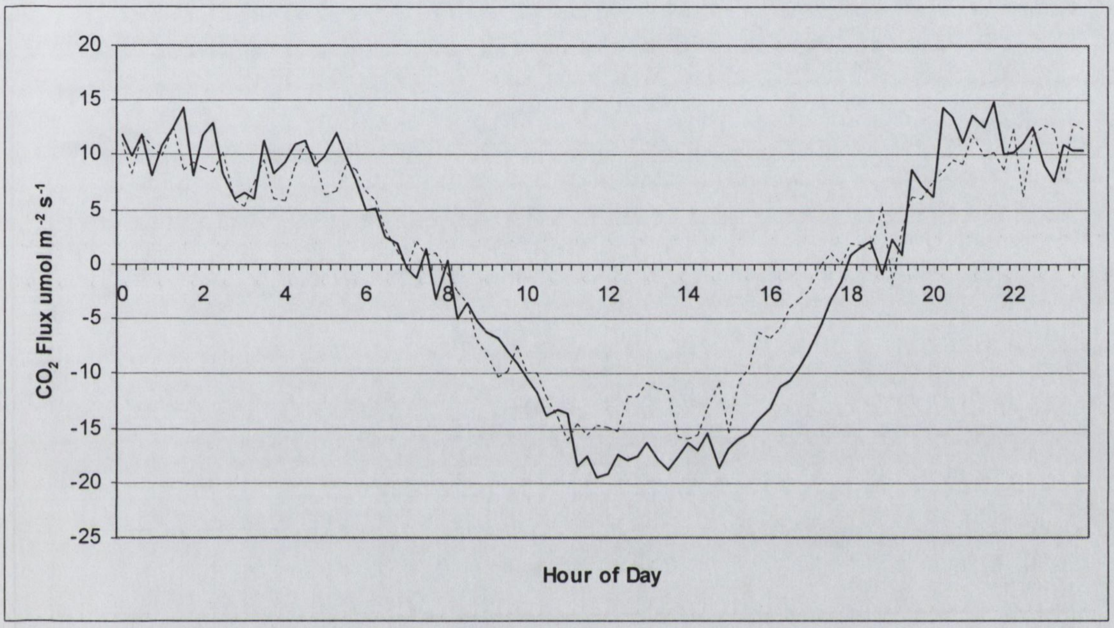

Figure 4.31. Average diurnal cycle of ecosystem CO_2 flux, based on EC data collected from 30th August to 5th September 2004 (Dashed Line), and from 6th to 12th September 2004 (Solid Line). EC data collected over a *C. antiquorum* canopy at the Nakivubo wetland. Positive values indicate net loss of CO_2 from the system while negative values indicate net uptake of CO_2 by the system.

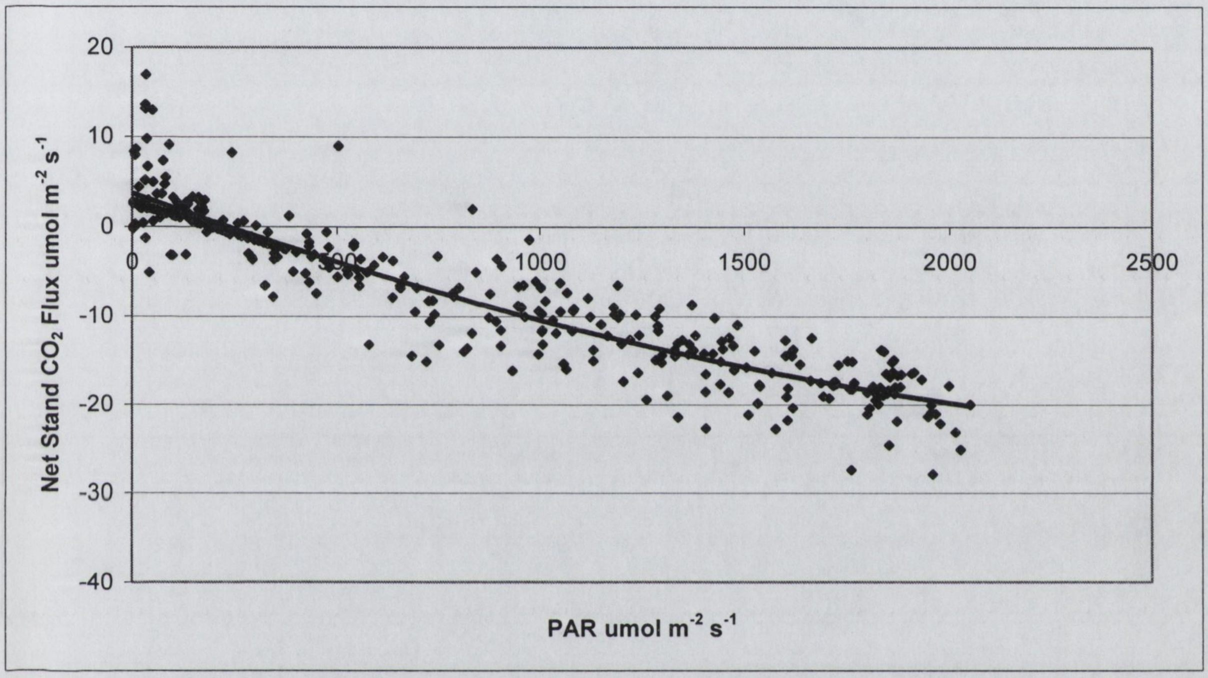

Figure 4.32. Relationship between net stand CO_2 flux and incident PAR over a *C. antiquorum* canopy. Data collected at the Nakivubo wetland, between the 30th August and 5th September 2004. ($R^2 = 0.86$).

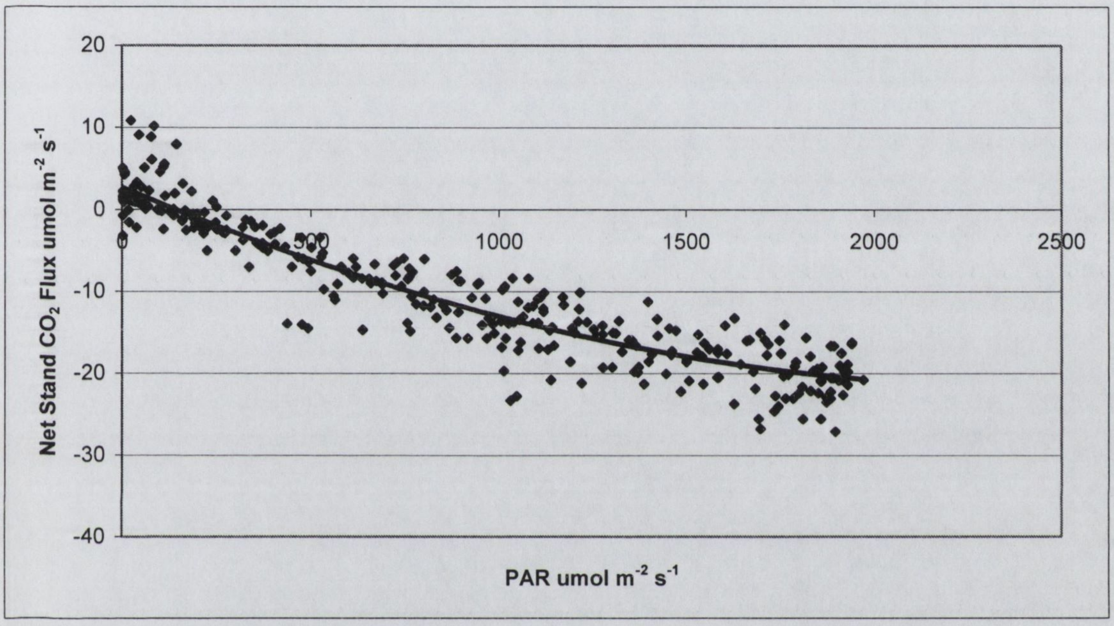

Figure 4.33. Relationship between net stand CO_2 flux and incident PAR over a *C. antiquorum* canopy. Data collected at the Nakivubo wetland, between the 6th and 12th September 2004. ($R^2 = 0.89$).

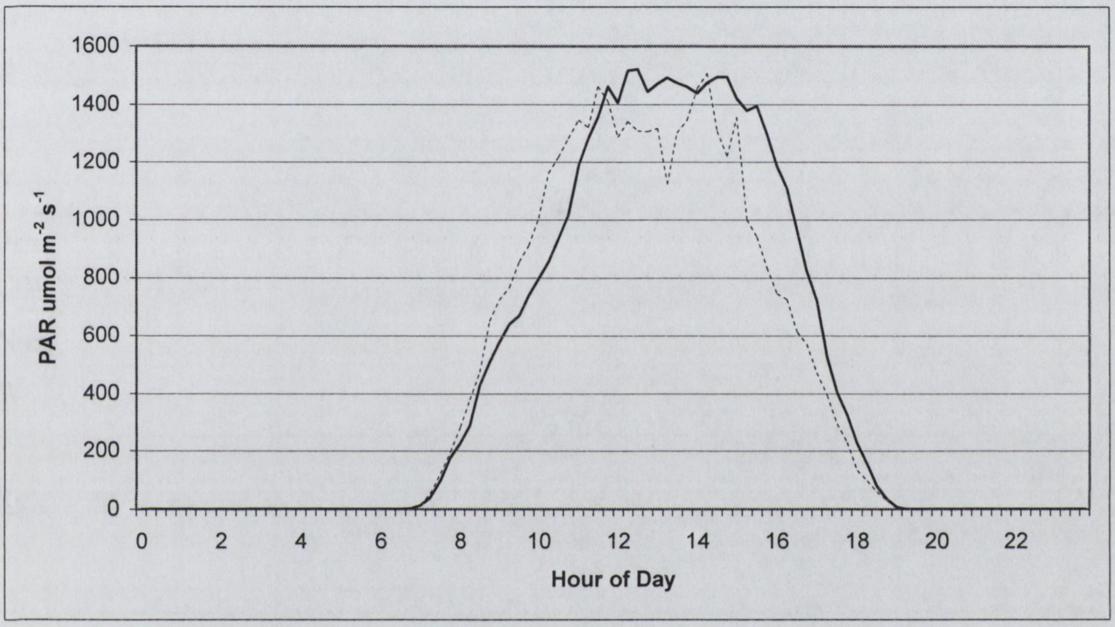

Figure 4.34. Average diurnal flux of photosynthetic active radiation (PAR), based on meteorological data collected over a *C. antiquorum* canopy at the Nakivubo wetland. Data collected from 30th August to 5th September 2004 (Dashed Line), and 6th to 12th September 2004 (Solid Line).

canopy are illustrated in Figure 4.36. The flux data indicate little loss of water through evapotranspiration at night. Rates of evapotranspiration increased steadily from sunrise to a maximum of approximately 8.5 mmol H_2O m^{-2} s^{-1}. Peak water losses through evapotranspiration occurred in conjunction with high air temperatures, low relative humidity, high PAR intensities and maximum rates of CO_2 assimilation.

Estimates of Water Use Efficiency of Photosynthesis (WUE_{PH}) have been calculated (Section 4.3.2.2) and normalised to VPD for each weekly EC data set, and are shown in Table 4.13. In addition Table 4.13 shows the linear relationship between water vapour fluxes and incident photon flux density (R^2). Estimates of WUE_{PH} (normalised to VPD and averaged where PFD > 500 μmol m^{-2} s^{-1}) ranged between 2.27-3.52 mmol CO_2. [mol H_2O]$^{-1}$. The average WUE_{PH} for the entire measurement period was 2.79 mmol CO_2. [mol H_2O]$^{-1}$. Figure 4.37 shows the WUE_{PH} of the *C. antiquorum* vegetation at the Nakivubo wetland for the data collected between 21st and 27th June 2004, the average WUE_{PH} for this period was 2.76 mmol CO_2. [mol H_2O]$^{-1}$.

Respiration of Detrital Material.

The respiration of detrital material located at the wetland surface was estimated at nine sites selected at random within the EC flux footprint. Figure 4.38 illustrates the mean rate of respiration based on measurements taken at each site (n=3). Estimates of carbon loss through respiration ranged from 0.06–0.22 g C m^{-2} hr^{-1}, with a mean rate of respiration of 0.12 ± 0.002 g C m^{-2} hr^{-1}. The temperatures of the detritus at both the surface and a depth of 5 cm during the measurement period were remarkably stable, ranging from 22-25°C.

Statistical analyses of the detrital respiration data were conducted using a one-way ANOVA and Bonferroni's Multiple Comparison test (Appendix 10). The analyses showed that there were significant differences between all sample sites ($p \leq 0.001$) except for sites 1 and 5, 1 and 6, 3 and 4, 5 and 6, 8 and 9 ($p \geq 0.05$).

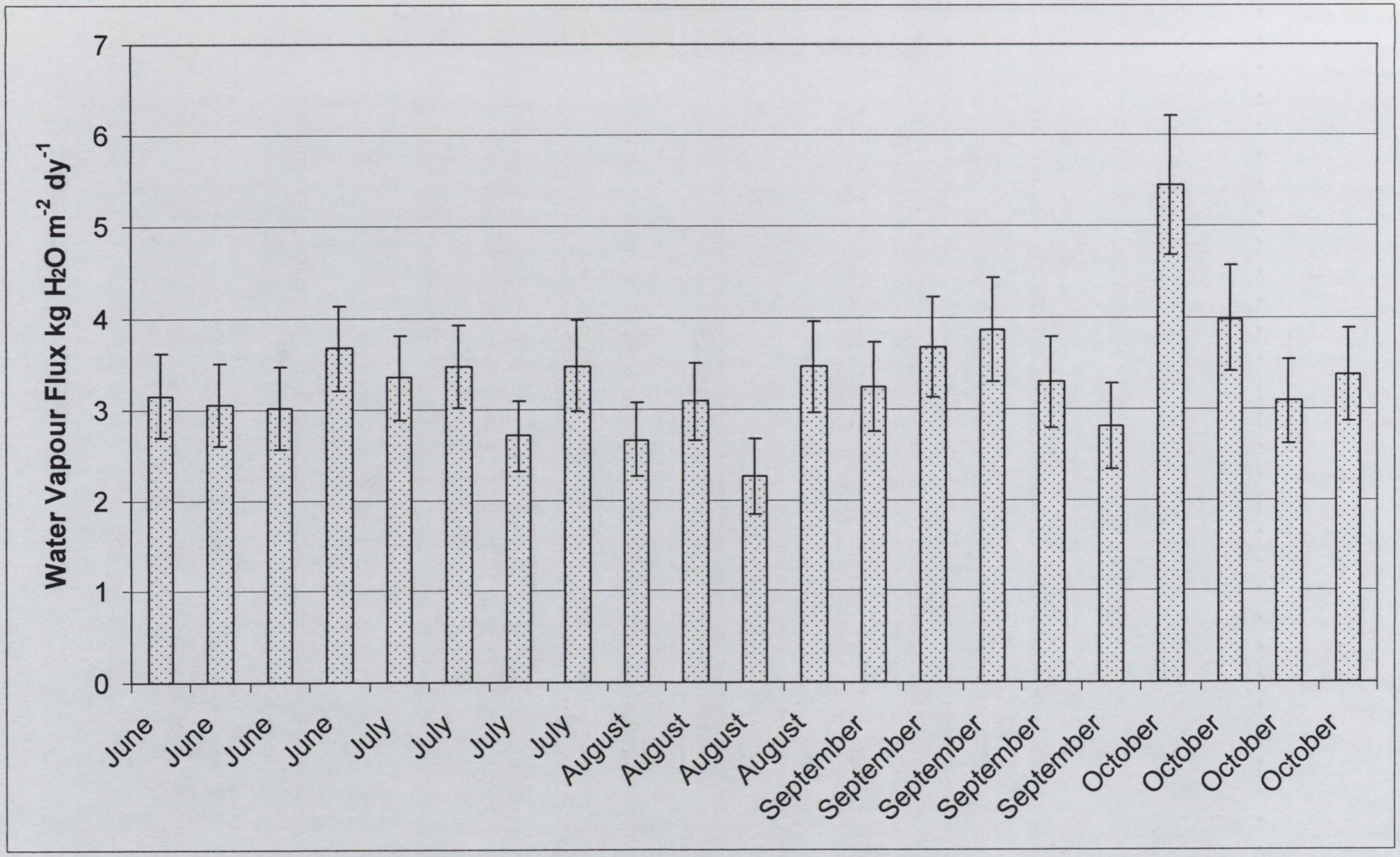

Figure 4.35. Average water vapour fluxes measured above a homogenous *C. antiquorum* canopy, based on seven day EC flux data sets. Data collected from June to October 2004 at the Nakivubo wetland, and are expressed in kg H_2O m^{-2} d^{-1}.

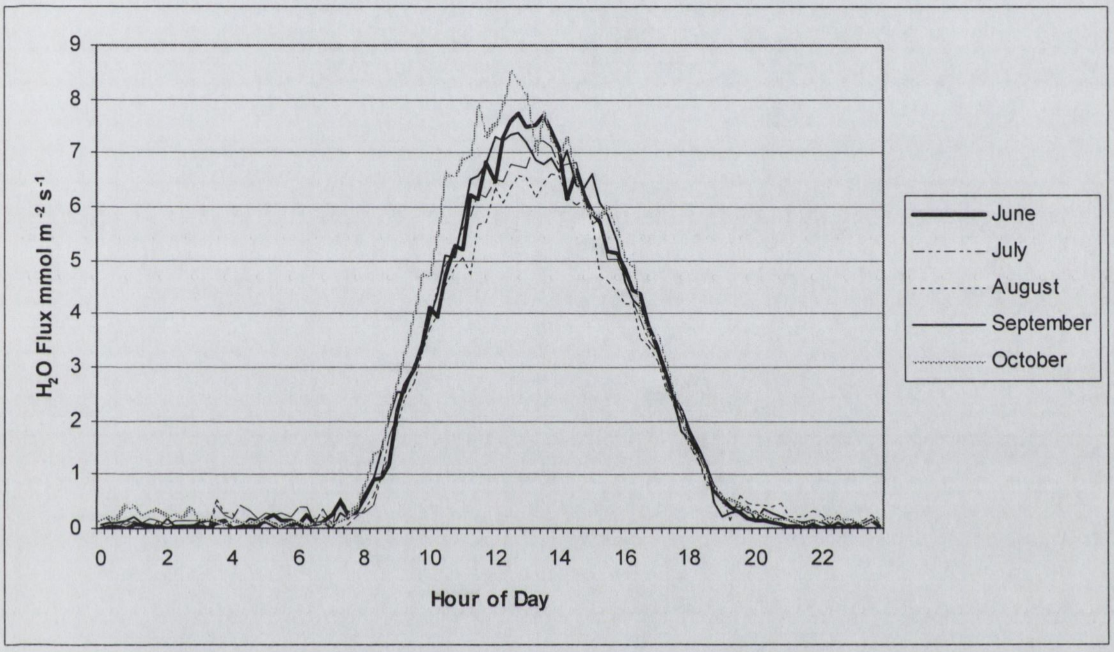

Figure 4.36. Average diurnal water vapour flux based EC data collected from June-October 2004, over a *C. antiquorum* canopy at the Nakivubo wetland, Kampala, Uganda.

Month	**Week**	**WUE_{Ph}** **(mmol CO_2 . [mol H_2O]$^{-1}$)**	**R^2**
June	2	3.23	0.95
June	3	2.92	0.94
June	4	2.95	0.92
June	5	2.76	0.94
July	1	2.56	0.91
July	2	2.75	0.92
July	3	2.83	0.91
July	4	3.38	0.89
August	1	3.52	0.91
August	2	2.95	0.91
August	3	2.86	0.87
August	4	2.32	0.90
September	1	2.27	0.90
September	2	2.30	0.92
September	3	2.84	0.90
September	4	3.24	0.88
September	5	2.78	0.85
October	1	3.02	0.89
October	2	2.54	0.88
October	3	2.30	0.85
October	4	2.29	0.86

Table 4.13. Estimations of average WUE_{Ph} based on weekly EC flux data collected between June – October 2004, over *C. antiquorum* canopy. WUE_{Ph} values represent the ratio of mmol of CO_2 assimilated through photosynthesis per mol of H_2O lost through transpiration. R^2 values describe the linear relationship between water vapour loss and incident PFD.

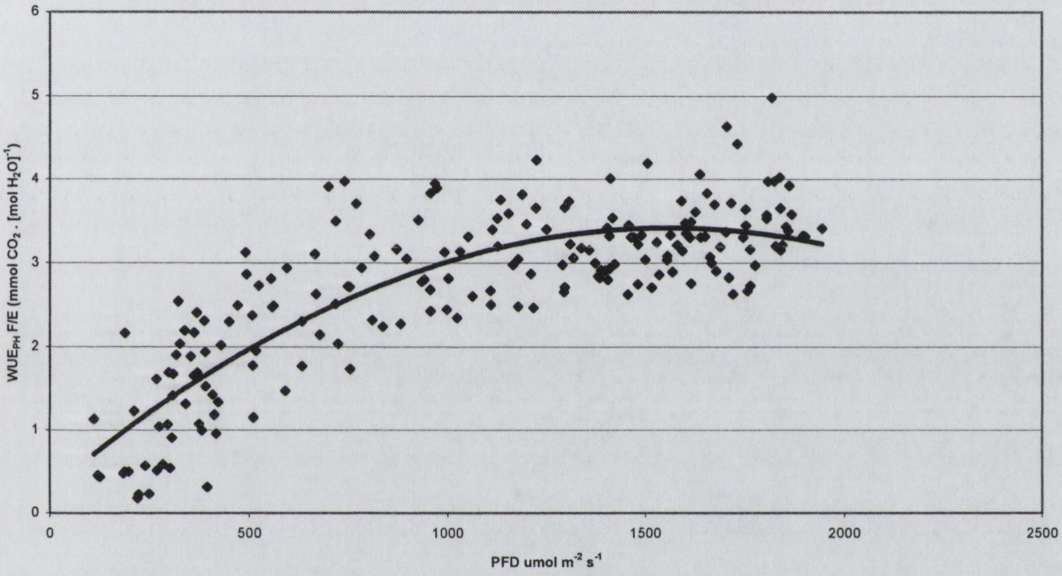

Figure 4.37. Relationship between WUE_{Ph} and incident PFD for a stand of *C. antiquorum* based on EC flux data collected between 21st and 27th June 2004 at the Nakivubo wetland, Kampala, Uganda. WUE_{Ph} data were normalised to VPD and values selected when PFD >150 μmol m^{-2} s^{-1}. Dashed line indicates mean WUE_{Ph} where PFD >500 μmol m^{-2} s^{-1}. ($R^2 = 0.70$).

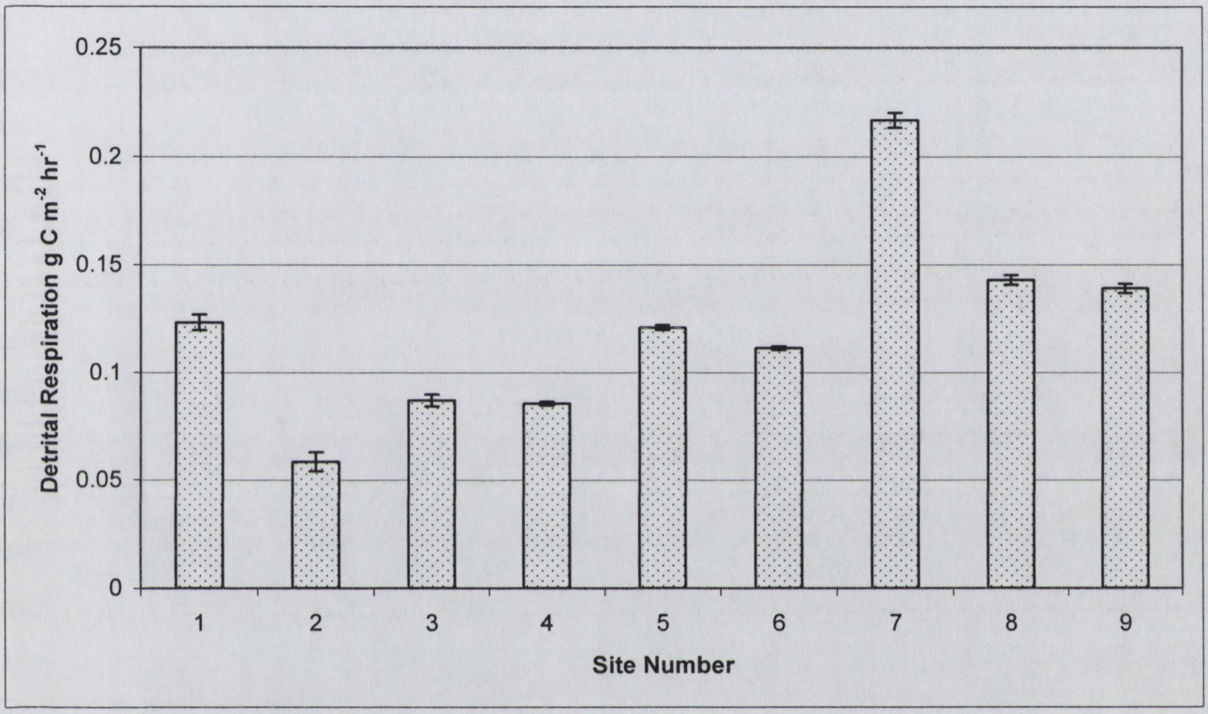

Figure 4.38. Average respiration rate of detrital material located on the surface of the *C. antiquorum* rhizome at the Nakivubo wetland. (Number of samples per site = 3; Error bars represent ± SD).

4.5. Discussion.

The wetland areas of the Lake Victoria basin are characterised by highly productive emergent macrophytic plant communities (Jones and Humphries 2002; Jones and Muthuri, 1997; Muthuri *et al*. 1989) where *Cyperus papyrus* L. forms the permanent monotypic vegetation in many of the permanently flooded areas. The wetland areas utilised for this study compared both the physical and physiological characteristics of wetlands under pristine and disturbed conditions. The Kirinya West wetland contains papyrus vegetation in a relatively pristine, undisturbed state forming a monotypic, lagoon based floating pontoon within the Napoleon Gulf, Lake Victoria, Uganda. The Nakivubo wetland however, is an example of the impact that agricultural encroachment can have on formerly papyrus-dominated wetlands.

The influence that disturbance has on the functioning of these wetlands is of environmental importance with regards to carbon sequestration, greenhouse gas emission and the regulation of local climate. The balance between human interaction and the biological integrity of these wetlands is becoming increasingly important due to increasing population pressures and industrial development in these areas. These wetlands are utilised by local communities for agricultural production, building and craft making materials, energy generation and wastewater treatment (Kansiime and Nalubega, 1999; Moore, 1980). The services provided to local inhabitants by these wetlands are undisputedly of economic importance, however increasing development in these areas may directly result in a reduction of the environmental quality of these wetlands.

One of the fundamental differences between these two wetlands is their physical structure. The Kirinya wetland forms a floating pontoon of predominantly monotypic papyrus vegetation covering a small lagoon of the Napoleon Gulf of Lake Victoria. The Nakivubo wetland however forms a valley-based swamp covering the main discharge channel from the city of Kampala into Lake Victoria. Kampala and the surrounding area is densely populated, placing pressure on the wetland through the need for municipal and industrial wastewater attenuation and the development of subsistence agriculture primarily by individuals of low income. The changing vegetative composition of the Nakivubo wetland documented by Kansiime and Nalubega (1999) was largely due to agricultural encroachment of the lower swamp section and the development of timber plantations in areas of the upper swamp. What was formerly papyrus vegetation in the lower Nakivubo wetland (Kansiime and Nalubega, 1999) is now dominated by *Colocasia antiquorum* cultivation.

There is little difference between the meteorological regimes of the two wetlands, which are approximately 50 km apart. Historical data illustrates these similarities as both regions have similar temperature and precipitation regimes (Department of Ugandan Land Survey, 1967). Rainfall is marginally higher in the Jinja region, however both areas experience bi-modal patterns of precipitation where maximum precipitation occurs in April and November and minimum precipitation occurs in July. Both wetland areas are also permanently inundated, suggesting that water availability will not significantly influence the physiological function of the wetland vegetation. However, water levels within the Nakivubo wetland do periodically fluctuate, as the volume of water held within and discharged through the wetland varies. On average this wetland discharges approximately 103,000 m^3 d^{-1} composed of overland, subsurface, storm water and wastewater discharges and is subject to approximately 11 lacaustrine seiches per day (Kansiime and Nalubega, 1999).

Meteorological patterns, notably solar radiation, temperature and relative humidity exhibited pronounced diurnal periodicity at both wetland sites. The rate of maximum instantaneous solar radiation received, were similar at both sites. Patterns of air temperature were directly correlated to the influx of solar radiation, night-time temperatures ranged between 16-19°C at the Nakivubo wetland and 17-20°C at the Kirinya wetland. Maximum daytime temperatures at the Nakivubo and Kirinya wetlands were 26°C and 27°C respectively.

Maximum rates of PAR influx received by the papyrus vegetation varied between 1761.7 – 2251.7 μmol m^{-2} s^{-1} and 1760.6 – 2272.4 μmol m^{-2} s^{-1} above the *C. antiquorum* canopy. The average PAR intensity during periods of net stand photosynthesis was approximately 956.1 μmol m^{-2} s^{-1} above the papyrus canopy and 947.8 μmol m^{-2} s^{-1} above the *C. antiquorum* canopy.

Cyperus papyrus L. exhibits the C4 photosynthetic pathway (Jones, 1987; Jones and Humphries, 2002; Jones and Milburn, 1978). At their respective temperature optima

C4 plants exhibit higher rates of carbon assimilation than C3 species (Edwards and Walker, 1983) as rates of photosynthesis do not saturate in high light intensities, and can be maintained at low sub-stomatal CO_2 concentrations (Lawlor, 1993). C4 plants also exhibit more rapid growth rates and higher dry matter yields than C3 plant species and also tend to have lower nitrogen requirements. The characteristics exhibited by C4 species are advantageous where temperatures are high and water resources might be limited. Therefore the global distributions of C4 plant species are concentrated in areas that experience warm and dry climatic conditions. It is therefore, something of an anomaly that a C4 plant species such as papyrus should dominate the permanently inundated wetland regions of East Africa.

Taber Hand (1975) described papyrus swamps as "tropical rainforests in miniature" and suggested that undisturbed papyrus wetlands have the potential to form "climax communities" due to the lack of seasonal fluctuation and continual plant growth and recruitment. The development of papyrus plants along a single rhizome dictates that the plant units (culm and umbel) located on the rhizome will differ in age class and stature. The continual presence of mature plants maintains a homogeneous plant canopy. The homogeneity of *C. antiquorum* vegetation depends largely on the scale and regime under which the plants are cultivated. Agricultural development is usually undertaken at a subsistence scale, with harvesting and re-planting a continual process due to vegetative propagation from existing corms. Due to the large scale agricultural development at the Nakivubo wetland the crop stand remains relatively homogeneous.

Eddy covariance measurements were made over papyrus vegetation at the Kirinya West wetland between June 2003 and May 2004. Large amounts of downtime were experienced due to the repeated theft of the batteries used to power the EC equipment. These logistical problems resulted in the EC tower being out of commission for approximately 60% of its time in the field. However, during periods of successful data capture only about 19% of the data collected was lost due to the rejection criteria associated with stable atmospheric conditions experienced at night, spike removal and routine calibration and maintenance. The EC campaign at the Nakivubo wetland over cocoyam vegetation was undertaken between June and October 2004. Approximately 25% of the data collected was either rejected due to stable night-time atmospheric conditions or lost through spike removal, equipment downtime or sensor calibration. The total duration of EC flux measurements documented in this study represents the longest EC flux campaign over tropical wetlands of this type, collecting approximately 266 days of data from both wetland sites.

The closure of the energy balance during EC flux measurements provides a method through which turbulent and available energy fluxes (net radiation, ground heat flux, latent and sensible heat) can be accounted for (Aubinet *et al.* 2000; Wilson *et al.* 2002). The statistical regression of latent and sensible heat fluxes in relation to available energy within the ecosystem (all other sources and sinks of energy) at the Kirinya West wetland showed agreement ranging between 0.88 and full closure. The maximum imbalance of the energy budget at this site was 12%, a value which is lower than the mean deviation in energy balance closures reported at FLUXNET sites (Wilson *et al.* 2002). The partitioning of energy balance parameters at Kirinya showed that evapotranspiration (including any evaporative fluxes from the surface detrital component) constituted approximately 60% of the total energy flux. Fluxes of latent heat are indicative of water availability within an ecosystem and low partitioning to evapotranspiration indicates limitations in availability of water to ecosystems (Bernhofer *et al.* 2003; Hunt *et al.* 2002). This suggests that the papyrus plants at the Kirinya wetland are not water limited, and thus have continual access to the water column through the rhizome and fine root network. The loss of available heat flux through the papyrus rhizome, as measured by the heat flux plates, was negligible throughout the flux measurements. This highlights the closed nature of papyrus canopy and efficiency with which this plant canopy shades the rhizome surface below.

The energy balance measured over the *C. antiquorum* vegetation at the Nakivubo wetland showed lower closure than the papyrus vegetation. The agreement of latent and sensible heat fluxes with the total available energy within the ecosystem ranged between 0.59-0.77. The upper range of energy balance agreement is within the range reported by Aubinet *et al.* (2000) where energy balance closure at EUROFLUX sites ranged from 70% to full energy balance closure. The partitioning of energy balance components at the Nakivubo wetland showed that fluxes of latent heat constituted 60% of the available energy flux, while sensible heat components constituted a further 16%. The high rates of latent heat flux suggest that the *C. antiquorum* vegetation is also not limited by the availability of water. Based on energy balance closure, approximately 23-41% of the available energy within this ecosystem is unaccounted for by the EC measurements. The apparent loss of energy from the ecosystem suggests the systematic underestimation of energy sinks within the wetland. The reason for this is unclear but it may be linked to the structure of the *C. antiquorum* vegetation, which exhibits a more open stand structure than the papyrus vegetation, suggesting that a higher proportion of the available energy might be incident at the rhizome surface. While the location of the heat flux plates were selected at random they were restricted by cable length. As a result the plates may have been in constant shade from the large cocoyam leaves so that the ground heat flux of the energy balance components was underestimated. In addition the available energy absorbed by the large leaf structures of the cocoyam vegetation might represent an undetermined sink for available energy. An additional source of error relates to the fact that the source areas of the instruments measuring energy components differ considerably (Aubinet *et al*. 2003). While the area measured by the net radiometer constitutes a circle of limited diameter determined by sensor height, which is constant over time, the flux footprint generated by the eddy covariance system varies significantly over time, and it is dependent on both wind speed and direction. As a result it is often possible to identify differences between measurements of radiation and turbulent fluxes even in extremely homogenous sites (Schmid, 1997). Furthermore the amount of available energy absorbed by the flux tower itself could be a contributory factor in the potential underestimation of sensible heat flux over the *C. antiquorum* vegetation. The metal framed tower was exposed above the plant canopy at the Nakivubo wetland, whereas the tower was shaded by the dense papyrus canopy at the Kirinya wetland. The area measured by the net radiometer was close to the EC tower, and because the tower was in contact with the water column and sediment beneath the wetland, any available heat energy absorbed by the tower would be dissipated into the water column below.

Net Ecosystem Exchange (NEE) represents the balance between the gross uptake of carbon (GPP) and the combined respiratory flux components of autotrophic (R_A) and heterotrophic (R_H) respiration which constitute the total ecosystem respiratory flux (R_{eco}) (Granier *et al*. 2003). Rates of night time carbon release through detrital respiration are closely controlled by the hydrological regime and temperature (Matteucci *et al.* 2000), while rates of carbon uptake during the day are dependent largely upon the metabolic pathway utilised by different plant species for the assimilation of carbon for example C3, C4 and CAM (Edwards and Walker, 1983; Lawlor, 1993) and the duration, intensity and interception of available PAR (Hanan *et* al. 2002; Tirone *et al.* 2003). Peak rates of night time CO_2 release from the Kirinya wetland ranged between 10 and 20 μmol CO_2 m^{-2} s^{-1} over the papyrus canopy (Figure 4.8). After daybreak, as the intensity of photosynthetically active radiation (PAR) increases, so does photosynthesis, which switches the system as a whole from a net source to a net sink for CO_2. Peak rates of CO_2 uptake over the papyrus canopy occurred at slightly after midday and were associated with maximum values of PAR and air temperatures. Maximum rates of CO_2 uptake during this period ranged between 35 and 37 μmol CO_2 m^{-2} s^{-1}. These flux rates are similar to those previously measured over *Echinochloa polystachya*, a C4 macrophytic floating grass found extensively in the Amazonian floodplains, where maximum rates of photosynthetic uptake were 40 μmol CO_2 m^{-2} s^{-1} (Morison *et al.* 2000). Peak rates of CO_2 uptake over the Kirinya wetland are however, higher than previously found for papyrus swamps where a maximum CO_2 gain of 24.7 μmol CO_2 m^{-2} s^{-1} was measured over a papyrus swamp on Lake Naivasha, Kenya (Jones and Humphries, 2002).

Diurnal patterns of CO_2 flux over the papyrus vegetation were different during periods when the wetland system acted as either a net source or sink of carbon (Figure 4.9). There was a strong relationship between net stand CO_2 uptake and PAR at the Kirinya West wetland (Figures 4.10-4.11) and both periods had high rates of maximum net carbon assimilation, at approximately 40 μmol CO_2 m^{-2} s^{-1}, with photosynthetic saturation occurring at light intensities > 1500 μmol m^{-2} s^{-1}. However the main difference in CO_2 fluxes between the two periods, was the higher respiratory fluxes during the period of net carbon release (Figure 4.10). Rates of carbon release through heterotrophic and autotrophic respiration are extremely sensitive to temperature (Ceulemans *et al.* 2003) but in this case night time temperatures were remarkably similar between both periods. It was found that the average horizontal night time wind speeds were low during the period of net carbon uptake but they were approximately 70-100% higher during the period of net carbon release. This may have resulted in an underestimation of night time respiratory fluxes by EC systems during stable atmospheric conditions.

The NEE measurements made over the papyrus wetland show that both high rates of instantaneous and integrated daily irradiance allow the efficient C4 papyrus plants to maintain high rates of carbon assimilation and thus the wetland can act as a very active carbon sink. These measurements also showed that estimates of NEE varied over the measurement period (Table 4.5) ranging from rates of carbon uptake of 23 g C m^{-2} to carbon release of 3 g C m^{-2}. As shown in Table 4.5 rates of gross primary productivity (GPP) showed similar weekly variation while rates of ecosystem respiration (R_{eco}) remained relatively stable. Periods of low instantaneous irradiance reduce rates of CO_2 assimilation, and carbon uptake falls below the overall respiratory carbon release (R_A + R_H), consequently the wetland becomes a net carbon source.

The decomposition of organic detritus through respiration is primarily controlled by moisture content, the extent of waterlogging and temperature (Lloyd and Taylor, 1994; Schulze, 2000). The Kirinya wetland remains permanently inundated with only small fluctuations in water levels throughout the year. Water levels are always high enough to ensure that the papyrus rhizome system is continually waterlogged and largely anaerobic, thus preventing aerobic decomposition of the underlying peat deposits. Temperature patterns show diurnal trends (Figure 4.2), with night time temperatures remaining relatively stable at approximately 20-22°C, while during the day the maximum air temperatures reach approximately 28-30°C. Measured daytime detrital temperatures at a depth of 5 cm remained remarkably stable at 20°C throughout the measurement period, due to the dense canopy shading of the detritus. Therefore the rate of detrital decomposition is expected to remain relatively constant.

Measurements of R_A (Figure 4.17) indicated decreasing rates of R_A with increasing culm age, however statistical analyses using a one-way ANOVA and Bonferroni's Multiple Comparison test (Appendix 5), showed that there were no significant differences in rates of mitochondrial respiration between age classes ($p \geq 0.05$). The mean estimate of culm respiration, at 0.21 ± 0.01 mg C g^{-1} C h^{-1} was somewhat lower than measurements made on Lake Naivasha, Kenya, where rates of culm respiration were 0.59 mg C g^{-1} C h^{-1} (Jones and Humphries, 2002).

The mean values of R_H of detrital deposits at the rhizome surface (Figure 4.16) were estimated to be 0.26 g C m^{-2} h^{-1}. These values are similar to those measured by Jones and Humphries (2002) who recorded detrital respiration measurements of 0.23 g C m^{-2} h^{-1}. Although the Kirinya wetland is subject to permanent inundation the saturation of the detritus at the rhizome surface varies depending on the physical conformity of the rhizome. Saturated or waterlogged detrital deposits are likely to exhibit lower rates of respiration due to reduced gaseous diffusivity and limited available oxygen. The temperature at the detritus surface and at a depth of 5 cm remained stable throughout the duration of the experiment, however should temperature regimes change, through the removal of the shade offered by the papyrus canopy, then respiration rates are likely to increase. For example, rates of soil carbon efflux from inundated sugarcane plantations in Brazil, showed a significant difference in the amplitude of soil carbon efflux in relation to changing soil temperature, with flux estimates ranging from 0.38-0.76 kg C m^{-2} y^{-1} over a temperature range of 20-28°C (Da Rocha *et al.* 2000).

The overall balance of carbon exchange with the atmosphere is controlled by the relationship between the decomposition of organic material and the gross productivity of the wetland vegetation (Law *et al.* 2002). The NEE of carbon over the experimental period at the Kirinya wetland when summed over a whole year, showed an approximate carbon sequestration rate of 0.48 kg C m^{-2} y^{-1}. Papyrus vegetation on Lake Naivasha, Kenya showed changeable patterns of NEE dependant on the hydrological regime. During periods of inundation it was estimated that the wetland sequestered approximately 1.6 kg C m^{-2} y^{-1} while during periods of hydrological drawdown the wetland released approximately 1.0 kg C m^{-2} y^{-1} (Jones and Humphries, 2002). Another tropical C4 species, *Saccharum officinarum* showed rates of carbon sequestration during the growth cycle of the crop of 0.55 to 3.65 kg C m^{-2} y^{-1}. However after the harvest the ecosystem became a net source of carbon, releasing on average 0.58 kg C m^{-2} y^{-1} (Da Rocha *et al.* 2000).

Estimates of carbon content of the papyrus culm and umbel material at the Kirinya West wetland, Uganda ranged from 36.4 to 41.7% (Figure 4.18). These values are similar to those reported by Jones and Muthuri (1997) where the carbon content of papyrus plant material on Lake Naivasha, Kenya ranged from 44 to 47%. There were significant differences in the TC content between the juvenile and mature and senescent papyrus plant material at the Kirinya wetland ($p \leq 0.001$). The lowest TC content was recorded in the juvenile plant material and carbon content increased with plant age. There were also significant differences in TC content of the plant material sampled from the lower, middle and upper culm sections ($p \leq 0.05$) where the lowest carbon content was measured in the base of the papyrus culms. The carbon content of mid and upper culm sections were similar across the age classes and the umbels showed the highest carbon content of all the plant material sampled.

Aquatic plants growing in a nutrient rich environment normally exhibit high levels of nutrients within their tissue (Azza *et al.* 2000; Chale, 1987; Kyambadde *et al.* 2004; Muthuri and Jones, 1997). The discharge of wastewater into papyrus wetlands will increase the nutrient status of the wetland and a corresponding increase in the nutrient content of the papyrus plants is expected. The total nitrogen (N) content of the papyrus culm and umbel material ranged from 0.34 to 2.18% (Figure 4.19). The average N concentrations of the culm and umbel plant organs were 0.9% and 1.8% respectively. These values are lower than measurements made by Chale (1987), where average N concentrations of papyrus plant material (culm 4.8%; umbel 6.2%) from a highly eutrophic papyrus wetland were measured. There were significant differences in the TN content of the juvenile, mature, senescent plant culms and umbels ($p \leq 0.001$). The highest N contents in the papyrus material at the Kirinya wetland were recorded in the juvenile plants, and nitrogen content then decreased with age. The higher N concentration of the younger plant material suggests that high rates of N uptake are associated with rapid plant development in the early stages of growth (Kansiime and Nalubega, 1999). The lower N content of the older senescent plant material suggests the translocation of mobile nutrients such as N to the younger, metabolically active plant tissue (Muthuri, 1985). The umbel material showed the highest N content, as this structure represents both the inflorescence and the primary photosynthetic organ of the papyrus plant. The N content of plant material at the Kirinya wetland were very similar to those reported by Muthuri and Jones (1997). The average N content of papyrus material from Lake Naivasha, Kenya, ranged between 0.3% (plant culm) to 2.4% (umbel) and also showed patterns of decreasing N content with age.

As part of the carbon transformation within the papyrus ecosystem, senescent plant material accumulated at the rhizome surface is subject to partial aerobic decomposition, although significant detrital deposits remain. Over time the carbon within this detrital pool moves through the rhizome mat and eventually into the water column below which is largely anaerobic. The most calcitrant carbon eventually enters the water column in suspension and forms peat deposits beneath the papyrus rhizome. Carbon is also lost from detrital deposits in dissolved organic form, and highly productive emergent macrophytes are considered to be a major source of DOC within wetland ecosystems (Mann and Wetzel, 1996). The export of DOC from aquatic ecosystems may also represent a significant component of regional carbon budgets (Clair *et al.* 2002; Mayorga *et al.* 2005). The magnitude of carbon losses in suspended or dissolved form depends largely on the rates of water flow beneath the papyrus rhizome, which can flush this material into the main body of the lake. In this study there were significant differences in DOC concentrations across the wetland ($p \leq 0.001$) where the highest DOC concentrations were found in the secondary treated wastewater discharged into the Kirinya wetland (13.78 ± 0.2 mg l^{-1}) (Figure 4.20). Concentrations beneath the papyrus rhizome were lower than the effluent where average concentrations were approximately 8.76 ± 0.8 mg l^{-1}. The lowest DOC concentrations (4.99 ± 0.53 mg l^{-1}) were found in the lake water adjacent to the papyrus wetland. The decreasing DOC concentration across the wetland represent a gradient across which carbon flows, and can be continually added through plant and detrital leaching. Decreasing DOC concentrations have however been measured across a constructed wetland subject to wastewater effluent, due to the removal of DOC through the biological degradation and oxidisation of the labile organic fraction (Pinney *et al.* 2000). Laboratory studies also showed that approximately 80% of the total DOC was removed over a 4 hour period, and that the growth efficiencies of bacterial population are higher on DOC from plant leachate than on particulate plant detritus (Mann and Wetzel, 1996).

Estimates of detrital mass beneath papyrus dominated wetlands are limited, however Jones and Muthuri (1997) estimate that detrital deposits contain approximately 20 times the biomass of the live plant components and under stable hydrological conditions might exceed 5 m in depth. The movement of water beneath the papyrus rhizome will however influence the rate of relocation of detrital material from beneath the root and rhizome mat into the main body of the lake. Kansiime and Nalubega (1999) describe how water is exchanged between these wetland areas and the main body of the lake through oscillations in water levels caused by storm surges or submerged tectonic activity. The number, period and amplitude of the lacaustrine seiches is dependent on the dimensions of the wetland basin and the force applied to create the seiche. However it appears that water tends to be continually recycled in a piston motion and therefore much of the same water re-enters the swamp. The loss of suspended detrital material from beneath the root and rhizome mat was not measured in this study, however a study by Gichuki *et al.* (2005) measured the movement of organic matter through papyrus dominated wetland using stable isotope techniques. The isotopic signal was measured from sediment samples taken from the river discharging into the wetland, from beneath the papyrus vegetation and from the open water lake region. The isotopic signatures of the river and lake sediment samples were composed largely of C3 plant material and phytoplankton, while the signature of sediment from beneath the wetland was predominantly C4 due to the papyrus vegetation. This suggests therefore that losses of detrital material accumulated beneath papyrus wetlands through hydraulic flushing are minimal. However if carbon is not lost from the system through flushing a large proportion must be lost *in situ* through oxidisation and decomposition in the form of CO_2 and CH_4.

The NEP of an ecosystem represents the balance between carbon assimilation and heterotrophic respiration, excluding carbon losses through harvest or combustion. The values of annual NEP for tropical ecosystems vary widely but tropical forests are normally assumed to be the most productive ecosystems with NEP ranging between 0.7 – 5.9 Mg C ha^{-1} y^{-1} (IPCC, 2001). NEE measurements made at the Kirinya wetland show higher rates of carbon uptake per unit area than tropical forests, however rates of R_H are also higher resulting in similar estimates of net carbon gain. Estimates of NEP at Kirinya based on NEE measurements fall within the range documented for tropical forests. Under current climatic conditions and assuming that detrital deposits accumulated beneath the papyrus rhizome are retained by the ecosystem, the NBP of the Kirinya papyrus wetland which is subject to minimal natural and anthropogenic disturbance will remain positive and therefore a prolonged carbon sink.

The net stand CO_2 exchange of the *C. antiquorum* vegetation at the Nakivubo wetland showed peak rates of night time CO_2 release ranging between 5 and 13 μmol CO_2 m^{-2} s^{-1} and peak rates of CO_2 uptake of approximately 25 μmol CO_2 m^{-2} s^{-1} (Figure 4.30). In fact, the maximum rate of carbon uptake by the *C. antiquorum* vegetation was approximately 25-50% lower than measured over the papyrus canopy. The relationship between net stand CO_2 flux and PAR of the cocoyam vegetation (Figures 4.32-4.33) when compared to same relationship over the papyrus vegetation (Figures 4.10-4.11) showed lower maximum rates of photosynthetic carbon assimilation at high light intensity. Interestingly, the light response curves produced over the C4 papyrus vegetation showed photosynthetic saturation at high light intensity, while the light response curves produced over the C3 cocoyam vegetation appeared relatively linear and showed low photosynthetic saturation at high light intensity. This is largely due to the different canopy architecture of both the papyrus and cocoyam vegetation. The papyrus vegetation exhibits a closed canopy structure while the bracteoles of the papyrus plant exhibit erectophile, plagiophile and planophile inclination, thus allowing the plant to capture sunlight over a range of zenith angles. In comparison, the cocoyam vegetation exhibits an open canopy structure, while the large leaves of the cocoyam plant tend to be vertically inclined and therefore absorb light at a more oblique angle.

In the case of these tropical wetlands the rate of CO_2 uptake and the amount of carbon sequestered depends largely on the instantaneous and integrated daily irradiance at the plant canopy (Figure 4.31 and Figure 4.34). The NEE dynamics during periods of high PAR intensity are dominated by the photosynthetic assimilation of CO_2 and therefore represent periods of net carbon uptake. The influence of cloud cover and precipitation events for example on the incident PAR at the plant canopy results in a net loss of carbon from the ecosystem as the balance between carbon uptake and net carbon release (R_A + R_H) is dominated by the respiratory component. The release of carbon through the organic decomposition of detritus (R_H) will remain relatively constant as the temperature both above the *C. antiquorum* canopy and at depth within the detritus remained relatively stable throughout the measurement period, and the hydrological regime of the wetland dictates that root and rhizome mat will remain permanently waterlogged. The average rate of heterotrophic respiration of the detrital deposits at the rhizome surface (Figure 4.38) was approximately 0.12 ± 0.002 g C m^{-2} hr^{-1}. The detrital temperature at a depth of 5 cm ranged between 20 to 24°C, the higher estimates of detrital respiration illustrated in Figure 4.38 correspond to measurements made at higher detrital temperatures. This pattern highlights the impact potential changes in the temperature regime may have on the amplitude of detrital carbon efflux. Measurements of R_H at the Nakivubo wetland were approximately 50% lower than measurements made at the Kirinya wetland. The rhizomatous network of the Nakivubo wetland was much less solid than at the Kirinya wetland and the penetration of water from beneath the wetland led to the complete saturation of detrital deposits. Measurements of detrital respiration at the Nakivubo wetland were made at locations beneath mature *C. antiquorum* plants, consistent with the vegetation stand over which the EC flux measurements were undertaken. The harvesting and re-planting of *C. antiquorum* crops is a continual process, which can be undertaken at 6 month intervals. The corms are exhumed, the leaves are cut and discarded and the plant crown is replanted. The crowns may not be re-planted in existing holes, leading to detrital disturbance, and the discarded leaves will be subject to aerobic decomposition. The contribution to the total ecosystem respiratory flux through R_H might therefore increase during periods of crop harvest. The continuous inundation of the Nakivubo wetland has the potential to induce anaerobic conditions beneath the rhizome mat, allowing the development of underlying peat deposits. The high rates of water discharge through the wetland and the continual flushing through lacaustrine seiches might serve to re-oxygenate the water column thus promoting the aerobic decomposition of detrital deposits, and may physically relocate detrital material into the main body of the lake. Such carbon losses may however be relatively small, as the lacaustrine seiches tend to recycle the water within the wetland (Kansiime and Nalubega, 1999).

Based on the weekly flux dynamics, the NEE over the experimental period at the Nakivubo wetland, showed an approximate carbon sequestration rate of 0.37 kg C m^{-2} y^{-1}, which falls within the range measured in tropical forests and is approximately 30% lower than the estimated NEE of the Kirinya wetland. Therefore the influence that disturbance has on papyrus wetlands through the cultivation of *C. antiquorum* is manifested in lower rates of carbon sequestration under certain PAR and hydrological regimes.

The Kirinya wetland under current environmental conditions and management practices will maintain a positive NBP, and will therefore act as a prolonged carbon sink. At present carbon losses through biomass removal and herbivory are minimal, however if local population densities increase wetland disturbance through agricultural encroachment may also increase. In addition a more accurate estimation of carbon losses through the export of DOC and suspended solid material from the wetland is needed in order to elucidate NBP estimates.

The NBP of the Nakivubo wetland is harder to quantify as the *C. antiquorum* crop is subject to periodic biomass removal through harvesting and detrital disturbance through re-planting. The EC measurements suggest that under the present environmental and floral status, the Nakivubo wetland also maintains a positive NBP. However, the decomposition of harvested leaves and increased heterotrophic respiration of detritus through aerobic disturbance may increase carbon losses from the wetland in the short term prior to the establishment of mature plants. The total standing biomass of cocoyam crops at the Nakivubo wetland were estimated to be approximately 6.5 kg DM m^{-2} (Kansiime *et al.* 2005). Assuming 70% of the total biomass is stored in the cocoyam tuber it is estimated that approximately 1.95 kg C m^{-2} will be removed from the wetland during plant harvest, and approximately 0.65 kg C m^{-2} will be returned to the atmosphere through the aerobic decomposition of the discarded yam leaves. It was not possible to determine the impact that harvesting has on carbon sequestration during this study. However it is expected that areas subject to harvest and re-planting of corms will exhibit lower rates of carbon sequestration and may potentially act as a net carbon source.

Estimates of the production and emission of CH_4 from tropical wetlands vary considerably with measurements ranging between 25-60% of the total global wetland CH_4 flux (Bartlett and Harriss, 1993; Melack *et al.* 2004). The limited representation of precise ground-based measurements at the regional scale is largely responsible for the uncertainty surrounding CH_4 fluxes (Frankenberg, 2005, Melack *et al.* 2004).

Methane production is the terminal stage in the degradation of labile organic matter under anaerobic conditions and represents a chain of successive oxydo-reductive reactions involving the initial hydrolysis by facultative anaerobes of organic polymers into simpler monomer compounds such as fatty and amino acids. These monomer compounds are then subject to acidogenesis under characteristically low redox potentials (Eh < -200 mV) to produce acetate, which along with hydrogen and carbon dioxide are utilised by methanogens to produce methane (Bouwman, 1990; Conrad, 1989; Le Mer and Roger 2001). The emission of methane from productive ecosystems is a balance between microbial production, gas transport and eventual degradation. The dominant processes resulting in the transportation of gas from the site of production into the atmosphere include molecular diffusion, ebullition and plant mediated transport. The molecular diffusion of methane across the sediment–water and the water–atmosphere interface accounts for a relatively small proportion of the total efflux in papyrus wetlands. The largest proportion of the methane flux emitted from the papyrus vegetation is through the process of ebullition. This is a function of the sum of the partial hydrostatic pressure of the dissolved gas in relation to the relative pressure of the sediment (Singh *et al.* 2000). Of the gas emitted through ebullition, methane constitutes between 50-90% of the total. Ebullition emissions of methane and other gas scalars produced during the anaerobic decomposition of detritus can accumulate beneath the floating rhizome network, which forms a barrier between the water–atmosphere interface.

Emergent macrophytic vascular plants also form conduits (aerenchyma) allowing the movement of gas between the soil or detritus and the atmosphere. This allows methane produced in anoxic regions to move directly into the atmosphere while bypassing oxic horizons, thus reducing the potential for degradation through oxidation within the soil horizon (Joabsson *et al.* 1999; Potter *et al.* 1996). The aerenchyma is comprised of a series of thin-walled cells that enclose large functional intercellular air cavities (Li and Jones, 1995). The aerenchymous network connects the above ground plant stems with the embedded or floating root and rhizome system and creates a pathway along which several gases can move. This includes CO_2, accumulated during root respiration, and which can be transported into the aerial plant section and re-assimilated into the plant through the photosynthetic pathway. The aerenchyma is also used to supply the respiring roots and rhizomes with oxygen (Jesperson, *et al.* 1998).

The measured fluxes of methane through plant mediated transport (PMT) from the Kirinya papyrus wetland were low (Figures 4.21-4.23), and accounted for a net loss of carbon through PMT of 0.006 kg C m^{-2} y^{-1}. Rates of methane emission through gaseous ebullition constitute between 20-70% of the total wetland CH_4 efflux (Jones, 2000), with the lower rates of ebullition occurring over open water and the higher rates from mats of floating grasses (Bartlett and Harriss, 1993). Jones and Muthuri (1997) reported total carbon release through the gaseous ebullition of CH_4 from papyrus wetlands in Kenya of 0.03 kg C m^{-2} y^{-1}.

Higher rates of plant mediated gas transport are expected in mature plants due to the more extensive development of aerenchyma, which may increase the volume and concentration of gas transported (Jones, 2000). In this study significant plant mediated fluxes of CH_4 were measured from mature plant culms ($p \leq 0.05$), where maximum fluxes of 0.54 μg CH_4 cm^{-2} h^{-1} were recorded in the middle of the day, a time of high incident PAR influx, high air temperatures and periods of high photosynthetic carbon assimilation. It is likely therefore that the high CH_4 fluxes are associated with periods when the stomata are open and this suggests that there is some degree of stomatal control of CH_4 release during night time periods.

The degradation of labile organic matter under anaerobic conditions occurring beneath the papyrus wetland has the potential to produce large quantities of methane. Rates of CH_4 efflux through PMT were low however because the papyrus vegetation is predominantly only rooted to the substrate at the wetland perimeter and thus the majority of the papyrus plants forms a free floating mat. Bartlett and Harriss (1993) suggest that rates of methane efflux through ebullition are higher over mats of free floating vegetation however the papyrus vegetation may act as a physical barrier limiting the emission of methane from the water column to the atmosphere.

The production and emission of trace gases such as methane from papyrus wetlands has the potential to significantly alter the overall greenhouse gas budget of these wetlands. This investigation into plant mediated emission of methane showed that rates of CH_4 efflux from the papyrus vegetation were low, however much higher rates might be expected due to diffusion of CH_4 through the papyrus rhizome or through pools of open water within the wetland structure.

In addition to methane, nitrous oxide (N_2O) is an important greenhouse gas due to its high radiative warming potential, and can be produced in large quantities from nutrient rich aquatic environments (Huttunen *et al.* 2003; Pihlatie *et al.* 2005). The Kirinya West wetland acts as a buffer for secondary treated wastewater and exhibits elevated nutrient status (Kansiime and Nalubega, 1999), although measurements of plant mediated N_2O efflux were not made during this investigation, such N_2O emissions may significantly alter the greenhouse gas budget of these wetlands.

There is a good deal of uncertainty surrounding the relative contribution of evaporation and transpiration to rates of water loss from wetlands (Busch, 2000; Idso and Anderson 1988; Humphries, 2003; Jones and Humphries, 2002; Linacre, 1976; Linacre, 1993; Rijks, 1969; Sanchez-Carrillo *et al.* 2004). Previous studies suggest that rates of water loss through wetland evapotranspiration are lower than rates of evaporation from open water bodies (Humphries, 2003; Jones and Humphries, 2002; Linacre *et al.* 1970). Rates of transpiration are influenced by environmental parameters such as air temperature and vapour pressure deficit (Farquhar and Sharkey, 1982; Losch and Tenhunen, 1981), which are both linked to the influx and partitioning of global radiation budgets. The leaf area index of a plant canopy and the relative aerodynamic resistance characteristics of the leaves, influence the exchange of water, carbon and heat between the plant canopy and the atmosphere, and the amount of relative extractable water available to a plant will also influence rates of transpiration (Dolman *et al.* 2003; Grainier *et al.* 2003).

Patterns of evapotranspiration tend to exhibit a diurnal periodicity closely linked to the intensity of incoming solar radiation (Sutcliffe, 1969). Rates of evapotranspiration over the papyrus canopy at Kirinya followed this pattern (Figure 4.14), with rates of evapotranspiration rising to approximately 12.5 mmol $H_2O\ m^{-2}\ s^{-1}$, in the early afternoon coincided with peak air temperatures. Stomatal closure tends to occur as vapour pressure deficits (VPD) in the surrounding air increase (Dolman *et al.* 2003). However rates of evapotranspiration from the papyrus canopy will tend to increase as VPD of the air increase, suggesting that the C4 characteristics of papyrus plants allows stomatal opening at high VPD in order to facilitate photosynthesis. The average rate of canopy water loss through evapotranspiration at the Kirinya wetland (4.75 ± 0.23 kg $H_2O\ m^{-2}\ d^{-1}$) was approximately twice the value reported by Jones and Humphries (2002) over a papyrus stand on Lake Naivasha, Kenya (2.4 kg H_2O m^{-2} d^{-1}), and was also higher than estimates made over a stand of *Echinochloa polystachya* under similar hydrological conditions (3.04 kg H_2O m^{-2} d^{-1} Morison *et al.* 2000).

There is an intrinsic relationship between CO_2 uptake and H_2O loss, where the stomata allow the passage of water from the leaf interior to the atmosphere during CO_2 assimilation (Larcher, 1995). EC flux data can be used to describe the instantaneous water use efficiency of the plant canopy, by calculating the relationship between photosynthesis and transpiration (F/E). This is expressed as the water use efficiency of photosynthesis (WUE_{PH}) and was calculated and normalised to VPD, and mean estimates were calculated where PFD >500 µmol m^{-2} s^{-1}. Mean measurements of WUE_{PH} over the papyrus canopy were 3.78 ± 0.16 mmol CO_2 mol^{-1} H_2O. The papyrus plant utilises the C4 photosynthetic pathway and was therefore expected to be efficient with regards to water usage in relation to carbon fixation. A study on the C4 aquatic grass *Echinochloa polystachya* (Morison *et al.* 2000) reported WUE_{Ph} (normalised to VPD) of 5.76 mmol CO_2 mol^{-1} H_2O during inundated periods on the Amazon, which is similar to estimates from the Kirinya West papyrus wetland under similar hydrological conditions.

An alternative method of analysing the relationship between carbon uptake and water loss during the growth cycle of a plant is to consider the relationship between dry matter production and water consumption (Larcher, 1995). This relationship is expressed as the water use efficiency of productivity (WUE_P). The WUE_P was calculated for the papyrus site where NPP data was available (Table 4.7), describing the cumulative increase in dry matter and the water consumption on a monthly basis over the entire measurement period. The average WUE_P for the papyrus stand was 5.16 ± 0.43 (SE) g DM. [kg $H_2O]^{-1}$. This value is slightly higher, but similar to estimates reported by Larcher (1995) where C4 plants are reported to have WUE_P ranging from 3-5 g DM. [kg^{-1} $H_2O]^{-1}$.

The Nakivubo wetland, dominated by *C. antiquorum*, showed low losses of water at night, while peak rates of evapotranspiration rose to approximately 8.9 mmol H_2O m^{-2} s^{1} (Figure 4.36), this peak occurred in conjunction with maximum air temperatures and high PAR intensity and vapour pressure deficits. The integration of the EC flux data collected at Nakivubo show that the average daily flux of water from the *C. antiquorum* canopy was 3.34 ± 0.14 kg H_2O m^{-2} d^{-1}. This estimate of water loss is similar to estimates of water loss from semiarid tropical mangroves, 2.80 kg H_2O m^{-2} d^{-1}, but is lower than estimates for floating plants which range between 7.78 – 18.68 kg H_2O m^{-2} d^{-1} (Larcher, 1995).

The mean WUE_{PH} for the *C. antiquorum* canopy was 2.79 ± 0.08 mmol CO_2 mol^{-1} H_2O (± SE) normalised to VPD where PFD >500 μmol m^{-2} s^{-1} and was approximately 27% lower than the mean WUE_{PH} estimate for the papyrus canopy. The micrometeorological measurements of evapotranspiration have shown that the C4 papyrus vegetation uses more water than the cocoyam vegetation, but uses water more efficiently. In terms of instantaneous carbon fixation, the papyrus vegetation fixed an additional 0.99 mmol of CO_2 per mole of H_2O transpired when compared to the cocoyam vegetation.

Wetlands containing emergent macrophytes such as papyrus have previously been shown to have lower rates of water loss than open water. Jones and Humphries (2002) reported an average total daily flux of papyrus canopy evapotranspiration of 2.4 kg H_2O m^{-2} d^{-1}, compared to 6.6 kg H_2O m^{-2} d^{-1} lost due to open water evaporation. Estimates of water loss through evaporation from the open water body of Lake Victoria were made using the Penman-Monteith equation (Grace, 1981; Landsberg, 1981; Sumner and Jacobs, 2005). Using meteorological data collected at both the Kirinya and Nakivubo wetlands the daily loss of water from the open body of the lake due to evaporation, was estimated to be 3.6 kg H_2O m^{-2} d^{-1}. The average daily flux of water from papyrus canopy evapotranspiration (4.75 kg H_2O m^{-2} d^{-1}) was approximately 24% higher than the calculated daily water loss through evaporation from open water. The high rates of water loss from papyrus are related directly to the high rates of carbon assimilation, whereby the open stomata act as a conduit for water to pass through the wetland and into the atmosphere. The average daily flux of water from the cocoyam vegetation (3.34 kg H_2O m^{-2} d^{-1}) was lower than calculated daily water losses through evaporation.

These wetlands are ecologically important as they play a direct role in the processes and regulation of water loss from these lacaustrine bodies. The impacts of disturbance on papyrus wetlands through the cultivation of cocoyam, has the potential to reduce water losses through evapotranspiration. However the benefits associated with the conservation of freshwater are diminished by the reduced ability of the wetland to sequester carbon, especially when considered in terms of climate change feedback processes.

Chapter 5.

General Discussion.

Increasing concentrations of greenhouse gases (GHG) in the Earth's atmosphere and the influence these gases have on the radiative forcing of the global climate has prompted intense scientific and political interest in both the cycles of these gas scalars and the anthropogenic influence on the source or sink strength of GHG flux from natural ecosystems. Over the past fifteen years the evolution of the United Nations Framework Convention on Climate Change (UNFCCC) and the Kyoto Protocol has highlighted the need for a more detailed quantitative assessment of GHG budgets and has also lead to the development of a series of potential mitigation strategies aimed at reducing GHG emissions. Article 3.3 of the 1997 Kyoto Protocol to the UN Framework Convention on Climate Change addresses the issue of measuring verifiable carbon stocks and associated changes through net greenhouse gas emissions resulting from anthropogenic land use change and related forestry activities (Kyoto Protocol, 1997). Article 3.4 of the Protocol suggests that activities relating to agricultural soils, land use change and forestry not included under Article 3.3 could also be used to meet greenhouse gas emission targets (Smith, 2001). These articles of the Kyoto Protocol are designed for compliance by Annex I countries (defined as industrialised countries and member of the OECD in 1992 or countries undergoing economic transition) and describe how signatory countries may meet quantified greenhouse gas limitation or reduction commitments by utilising biospheric carbon sinks. Article 3.3 refers to forestry activities including afforestation, reforestation and deforestation processes that have taken place since 1990 and are accountable under the first commitment period 2008 to 2012. Article 3.4 holds to no defined commitment period, but includes anthropogenic inputs to greenhouse gas emission accounts from activities related to agricultural productivity, land use change and forestry. The production of greenhouse gas emission inventories as outlined by the IPCC may be undertaken by two methods, the measurement of carbon stocks within the ecosystem at the beginning and end of the commitment period, or the measurement of fluxes of carbon into and out of a given ecosystem over the commitment period. Within the Kyoto protocol, Uganda is listed as a Non-Annex I Country, defined as a developing country but recognised by the convention as a country that is extremely vulnerable to the adverse effects of climate change through processes such as desertification and drought, and the potential impact such climate change factors may have on economic development. The Ugandan government has signed and ratified both the United Nations Framework on Climate Change (UNFCCC) and the Kyoto Protocol. The Initial National Communication of Uganda (2002) as presented to the Conference of Parties to the UNFCCC was the product of the "Enabling Uganda Project" and was developed and published by the Ministry of Water, Lands and Environment. This report attempted to create both an inventory of sources and sinks of greenhouse gases in Uganda and an assessment of the vulnerability and potential adaptation of the country to climate change. The GHG emission categories included in the Ugandan national report included energy, industrial processes, agriculture, solvents, land use change, forestry, and waste production and management. The GHG's addressed in the inventory included carbon dioxide, methane, nitrous oxide, nitrogen oxides, sulphur dioxide and non-methane volatile organic compounds. The GHG inventory was produced using the methodology as outlined by the IPCC-1995 guidelines, with the exception of the agricultural category where default emission factors were used in most cases. The National report addresses both natural ecosystems (forests, woodlands, savannah, wetlands and aquatic) and modified ecosystems (agro-systems, forest plantations, urban systems and irrigation schemes). The report suggests that wetland ecosystems such as those along the shores of Lake Victoria are extremely sensitive to climate change, detailing the floods of 1960-1962 where the water levels within lakes Victoria, Kyoga and Albert rose dramatically. The impacts of climate change are however measured purely on an economic basis, as approximately 40% of the Ugandan population derives considerable economic benefits in the form of fishing, water supplies, transport links, hydroelectric energy production and tourism. This purely economic approach is reflected in the GHG inventory as the source or sink strengths of fossil fuel consumption, industrial processes, agriculture and savannah burning and land use change and forestry are calculated, while the sink strengths of natural ecosystems such as wetlands have otherwise been neglected. GHG mitigation options are strongly influenced by socio–economic benefits and are identified as the minimisation of losses in production, the improvement in production and utilisation efficiency, the improvement of health due to a reduction of pollution and the creation of additional opportunities for the creation of wealth. Although improvements in these areas may well mitigate GHG emissions the only reference to the enhancement of natural CO_2 sinks is the Forest Action Plan, aimed at increasing forest cover and ensuring sustainable management practices. The National Wetlands Policy, also included in the National Communication to the UNFCCC is aimed at maintaining the biological diversity within the natural community of plants and animals and promoting the optimal socio-economic functions of wetland areas. However the potential impact wetland areas such as those dominated by *Cyperus papyrus* L. might have in enhancing CO_2 sinks is not considered within the National Communication. This investigation has therefore attempted to verify the potential source or sink strength of papyrus dominated wetlands, through the measurement of carbon fluxes both into and out of the wetland, as outlined by IPCC methodology.

This investigation utilised eddy covariance techniques to measure the exchange of carbon dioxide, water vapour and energy fluxes from *Cyperus papyrus* L. dominated wetland ecosystems. Papyrus wetlands are highly productive ecosystems and when found in pristine, undisturbed condition have the potential to assimilate large quantities of carbon from the atmosphere (Jones and Muthuri, 1997). In the equatorial lagoons of the Kirinya and Nakivubo wetlands, environmental parameters such as temperature and relative humidity showed little variation through the measurement period of this investigation. In addition water levels showed little fluctuation and both the papyrus and cocoyam vegetation were subject to permanent inundation. Under such stable environmental conditions large amounts of carbon are assimilated through photosynthesis and stored in short, medium and long term reservoirs. Short term carbon pools describe the carbon stored within the above and below ground living plant biomass, medium term carbon pools refer to the detrital deposits which develop at the plant rhizome surface as the papyrus plants senesce and are decomposed, while the long-term carbon pools describe the accumulation of the most calcitrant carbon at the sediment surface beneath the floating papyrus rhizome. This study attempted to determine and quantify the relevant carbon pools within these pristine papyrus wetlands, and to investigate how agricultural encroachment changes the dynamics of the carbon cycle and whether this anthropogenic impact alters the source or sink strength of the wetlands with regards to carbon sequestration.

The EC measurements at the Kirinya and Nakivubo wetlands show that both undisturbed, homogenous papyrus vegetation and wetlands cleared for agricultural production of cocoyam act as carbon sinks, under present climatic conditions and management practices. Based on the EC flux measurements made at the Kirinya wetland it is estimated that the magnitude of carbon uptake by pristine papyrus vegetation is approximately 480 g C m^{-2} y^{-1}, while based on EC flux measurements carbon uptake by cocoyam vegetation at the Nakivubo wetland is approximately 370 g C m^{-2} y^{-1}. Both values of carbon uptake fall within the range reported by Valentini *et al.* (2003) where the magnitude of carbon uptake from a range of ecosystems including tropical and temperate forests, grasslands and agricultural crops ranged from near zero to 700 g C m^{-2} y^{-1}.

Current observations indicate that changes in climate such as increased temperature or hydrological conditions such as wetland inundation, will influence the carbon sink strength of these papyrus based wetlands. The flux measurements clearly show that wetland disturbance through cocoyam cultivation reduces the carbon sink potential of these wetland areas, although *C. antiquorum* vegetation is also shown to reduce rates of water loss through transpiration. These wetland areas during measurement periods acted predominantly as carbon sinks, maintaining a positive Net Biome Productivity (NBP) due to the significant detrital and peat deposits accumulated at the rhizome and sediment surface, and minimal losses through the export of aboveground biomass (Jones and Muthuri, 1997). Under submerged, anaerobic conditions the rates of carbon loss from these long term carbon stores through heterotrophic respiration are low. However, changing hydrological conditions resulting in periods of draw-down could leave these carbon pools exposed to the atmosphere and the resulting enhanced aerobic decomposition would emit large amounts of carbon dioxide into the atmosphere. In addition, the rate of carbon loss from peat deposits through hydrological flushing and lacaustrine seiches will influence, and most likely reduce the NBP of the wetlands. It is clear that the carbon balance of these wetland ecosystems is extremely sensitive to changes in the hydrological regime and thus they are vulnerable to any reduction in water input to the system.

Rates of carbon gain through Gross Primary Production (GPP) were shown to be largely dependant on levels of instantaneous and integrated daily PAR, while rates of carbon loss through heterotrophic respiration (R_H) of the detrital deposits at the rhizome surface are largely controlled by the hydrological regime (moisture content) and temperature (Hyvonen *et al.* 2005; La Scala *et al.* 2003; Reichstein *et al.* 2000; Schulze, 2000). Both the Kirinya and Nakivubo wetlands are subject to permanent inundation and therefore the moisture content of the detritus in both wetlands was considered to be a limiting factor for R_H, while the high, night time temperatures were responsible for the high, stable observed rates of CO_2 release through R_A and R_H at night. Future increases in temperature have the potential therefore to increase carbon losses through R_H and thus lower the NBP of these wetlands. Further assessment of the carbon budget of these wetlands is required to improve our understanding of the impacts that future climate changes will have on rates of carbon sequestration and release, as well as localised climatic feedbacks processes resulting, for example, in changes to the regional hydrological cycle.

The change in management practice investigated here showed that the degradation of papyrus vegetation in favour of an agricultural crop resulted in a reduced rate of carbon sequestration. The removal of papyrus vegetation and development of cocoyam agriculture also reduces the physical stability of the wetland rhizome platform and exposes a larger area of the rhizomatous detrital deposits to the atmosphere, again potentially influencing carbon sink strengths. The manner in which cocoyam crops are cultivated also influences the carbon sink strength of these wetlands, as cocoyams are planted within the detritus, further exposing these carbon deposits to the atmosphere and leading to increasing rates of R_H. When the plants are harvested the corms are exhumed, the large leaves are discarded and the corm crown is replanted. This disturbs the detritus but the practice also leaves large amounts of discarded plant material, which is then subject to aerobic decomposition. The EC measurements at the Nakivubo wetland were made over a maturing crop and therefore carbon losses during harvest were not measured. It is likely that the NEE measurements during harvest periods would show a reduction in the overall rate of carbon sequestration due to a low leaf area index, and the removal of the cocoyam crop will significantly lower the NBP of the wetland. At present the management practices employed within *C. antiquorum* wetlands are directed towards the optimisation of crop yields. Any future attempts to develop these wetland areas as carbon sinks will probably lead to a conflict between the production of food crops for the local population, and the maintenance of carbon sequestration as an ecosystem service.

The micrometeorological measurements of evapotranspiration from the wetlands showed greater long term losses from the C4 papyrus vegetation than the C3 cocoyam vegetation. This is despite the fact that C4 plant species have shown lower transpiration rates per unit leaf area than C3 plant species (Larcher, 1995). The reason for this unexpected result is that the transpiring area of papyrus plants was much greater than that of the cocoyam vegetation. The C4 plant species was however more efficient with regards to instantaneous carbon fixation, reflected in the observation that an additional 0.99 mmol of CO_2 were fixed per mole of H_2O transpired compared to the C3 plant species. Rates of water loss through transpiration of emergent macrophytes such as papyrus on Lake Naivasha, Kenya, have previously been shown to be lower when compared to evaporation from open water bodies (Jones and Humphries, 2002), where the average total daily flux of papyrus canopy evapotranspiration was approximately 2.4 kg H_2O m^{-2} d^{-1}, compared to 6.6 kg H_2O m^{-2} d^{-1} lost due to open water evaporation. Estimates of canopy evapotranspiration from the papyrus vegetation at the Kirinya wetland (4.75 kg H_2O m^{-2} d^{-1}) were higher than previously measured by Jones and Humphries (2002) from a papyrus wetland on Lake Naivasha, Kenya. The higher rate of evapotranspiration at the Kirinya wetland reflects the availability of water afforded by the permanent inundation of the wetland and also highlights the conduit formed by the papyrus vegetation linking the aquatic, biospheric and atmospheric systems. Measurements of evapotranspiration at Lake Naivasha were made on a papyrus wetland subject to periodic hydrological drawdown, suggesting that the vegetation suffered episodic water stress and would therefore probably have lower rates of evapotranspiration. The stomatal control of water loss at the Lake Naivasha papyrus wetland is also reflected in measurements of CO_2 assimilation, where average peak rates of assimilation were approximately 10 μmol m^{-2} s^{-1} lower than recorded at the Kirinya papyrus wetland. The differences in rates of water loss through evaporation of open water at the Kirinya/Nakivubo and Lake Naivasha sites (3.6 kg H_2O m^{-2} d^{-1} and 6.6 kg H_2O m^{-2} d^{-1} respectively) reflect the differences in environmental conditions at each site (temperature, relative humidity, VPD), due to differing altitudes (Humphries, 2003).

Water losses from the cocoyam vegetation through evapotranspiration were lower when compared to the papyrus vegetation. Mature cocoyam vegetation therefore demonstrates an important ecological function through the partial regulation of water loss from these lacaustrine bodies. The impact of disturbance on papyrus wetlands through the cultivation of cocoyam has the potential to reduce water losses through evapotranspiration. However the benefits associated with potential conservation of freshwater are diminished by the reduced ability of the wetland to sequester carbon.

Some of the ecosystem services provided by papyrus wetlands to surrounding communities include building and craft making materials and a source of combustible fuel (Kansiime and Nalubega, 1999). The high rates of NPP and biomass increment associated with papyrus wetlands highlights the potential of these wetlands with regards to both commercial exploitation and carbon sequestration, as the removal of papyrus for construction or craft materials ensures a long term store of carbon in the materials produced. The utilisation of papyrus vegetation as a fuel source would however lower the NBP of papyrus wetland systems towards being carbon neutral, as the carbon stored in the plant biomass will be returned directly to the atmosphere as a product of combustion. In order to be commercially viable a structured harvesting regime of papyrus vegetation is needed to ensure the maximum yields from the wetland, this may however reduce the flow of carbon between the short and long-term carbon pools (plant biomass-peat deposits) as the papyrus vegetation would be harvested before senescence. Over time therefore the carbon stored within the peat deposits at the sediment surface will gradually be reduced, as carbon is lost through the export of suspended and re-suspended organic material into the main body of the lake and little carbon will be introduced through the decomposition of dead plant material located at the rhizome surface.

When papyrus vegetation is harvested the subsequent re-growth of papyrus produces higher culm densities per unit area, however the aboveground biomass of new culms is generally lower when compared to undisturbed plots (Muthuri, 1985). This reduction in aboveground biomass is manifested in shorter papyrus culms with smaller basal diameters. The removal of papyrus vegetation on a bi-monthly basis resulted in an 83% reduction in culm height (Muthuri *et al.* 1989). Increased culm densities are maintained for the first 4-6 months after harvest, after which a reduction in the recruitment of juvenile culms occurs and through density dependant mortality the peak culm unit densities fall to levels similar to those associated with undisturbed plots (Muthuri *et al.* 1989).

The continuous removal of papyrus could also have important ecological consequences on the long term productivity of these wetlands through the loss of nutrients such as N, P and S from the ecosystem (Muthuri *et al.* 1989). However plant uptake of such nutrients from wastewater discharged into these swamps is both ecologically and environmentally important as a means of reducing the eutrophic impact of nutrient enriched waters and providing a tertiary means of wastewater attenuation (Kansiime and Nalubega, 1999). Therefore, a suitable harvesting regime should provide a sustainable management option for the long-term removal of nutrients from the system. Research has suggested that in order to maintain a sustainable yield from papyrus wetlands and to preserve rates of carbon sequestration and wastewater attenuation, papyrus harvesting should occur at intervals of 9-12 months (Kansiime and Nalubega, 1999; Muthuri *et al.* 1989).

Papyrus vegetation also forms a dense canopy structure, the removal of which might alter the microclimate at the rhizome surface through changing light and temperature regimes. Increased light levels at the rhizome surface will encourage the growth of other species and will increase inter-specific competition, which may reduce the productivity of papyrus (Muthuri *et al.* 1989). Also, increasing the temperature of detrital deposits at the rhizome surface might significantly influence the carbon cycle of these wetlands, through the increased heterotrophic respiration of the detritus.

It is important when devising management strategies for these wetlands to consider the needs of the local population surrounding these wetland areas, as they are amongst some of the poorest inhabitants in Uganda. The NEE measurements of both papyrus and cocoyam wetlands have shown their potential as carbon sinks, however the cocoyam wetland will have a much lower NBP as the yam corms are removed from the wetland during harvest and therefore carbon is lost from the system. On the other hand cocoyam agriculture produces a crop of both economic and subsistence value. If the local populace are to be allowed to utilise the wetland in order to cultivate agricultural crops a suitable solution might be to develop a system whereby the perimeter of the crop could be used to cultivate cocoyam for example and the interior of the wetland would then remain dominated by papyrus vegetation. This situation would allow the maintenance of a positive NBP of the wetland with regards to carbon sequestration but still allow the local population to generate a source of food and additional income. In addition this arrangement would be of benefit to those wetland areas which are utilised to attenuate partially treated wastewater before release into the main body of the lake. The attenuation of wastewater by emergent macrophytes is an important tool for the Ugandan population as Lake Victoria is a key source of potable water. If the wastewater were to be directed through the central section of the wetland, where the papyrus vegetation dominates, then the uptake of excess nutrients such as N and P, heavy metals and faecal coliforms would be limited to the papyrus vegetation and might reduce potential bioaccumulation within the agricultural crops. If the papyrus vegetation were to be harvested at regular, sustainable intervals and utilised to make construction or craft materials then these products would serve to remove and store large amounts of carbon, maintaining a positive NBP, and would remove excess nutrients from the waters of the wetland and the main body of the lake, thus reducing the potential impacts of eutrophication.

Although both the papyrus and cocoyam wetlands have been shown to act as a net sink of carbon, if the wetlands are considered in terms of their overall GHG budget to include CO_2, CH_4 and N_2O, it is probable that these wetlands will act as a net source of GHG's. The accumulation and subsequent anaerobic decomposition of organic material accumulated beneath the wetland rhizome is a significant source of CH_4, this study has shown that plant mediated emissions of CH_4 are relatively low, however rates of CH_4 emission through ebullition may be significantly higher. In addition significant rates of

N_2O emission from aquatic macrophytes have been documented from nutrient enriched wetland ecosystems (Huttunen *et al.* 2003; Pihlatie *et al.* 2005). Papyrus wetlands along the Ugandan coastline of Lake Victoria are therefore a potentially significant source of N_20 as they are utilised for the tertiary treatment of both municipal and industrial wastewater (Kansiime and Nalubega, 1999).

The research conducted as part of the ECOTOOLS project was aimed at the creation of practical tools for natural resource management that relate ecosystem productivity to sustainable resource use on local, regional and global environmental scales. The multiuse wetland areas of East Africa, in particular Lake Victoria represent highly productive global ecosystems, which are integral to both local and regional socio-economic development. However changing demographic patterns are placing increased pressure on these wetland areas, resulting in the modification and over exploitation of this resource base. The results of the ECOTOOLS project focused on providing regional wetland managers, and policy and decision makers with a broad overview of both individual wetland systems and Lake Victoria as a whole, and how such research can be implemented within the management structure of such complex ecological, socio-economic and political systems. Currently the wetlands found along the Ugandan shoreline of Lake Victoria are poorly managed while at the same time are becoming overexploited by local inhabitants who have little formal education. The best strategy is to redistribute the responsibility of managing and controlling an ecosystem downwards to locally acting resource managers who in a self-sufficient manner will control the water and matter cycles and internalise subsistence functions (Ripl, 2003). The implementation of such resource management at the local level is however difficult, as the maintenance of a highly productive food source is of greater importance to the local inhabitants than the preservation of papyrus dominated wetlands as greenhouse gas sinks.

The work described in this study has successfully addressed the key aims of the thesis through the long term quantification of carbon dioxide, water vapour and energy exchange between the atmosphere and papyrus dominated wetlands. The micrometeorological measurements have highlighted the potential of both papyrus and cocoyam dominated wetlands as significant carbon sinks. The development of the carbon model provided a better understanding of the key carbon pools within papyrus wetlands and the specific interactions between these pools. In addition the close conformity of the model predictions with the integrated EC flux measurements will allow the further development and application of this model to other papyrus wetlands in the East African region. This work also highlighted the susceptibility of the carbon sink potential of these wetlands to changing climatic conditions such as increasing temperature and changing hydrological regime. The information obtained during this study has been incorporated with all other research conducted as part of the ECOTOOLS project and been compiled within a publication entitled "Tools for Wetland Ecosystem Resource Management in Eastern Africa". The results, presented both in this thesis and within the ECOTOOLS book, were disseminated at two meetings held in Kampala, Uganda and Kisumu, Kenya.

An important conclusion of the work is that future research on the carbon cycle dynamics of papyrus dominated wetlands requires a better understanding of the impact hydrological drawdown has on the carbon sink potential of wetlands and how temperature sensitivity might influence rates of both autotrophic and heterotrophic respiration. In addition a more detailed understanding of the transport and fate of both particulate and dissolved organic matter accumulated beneath the papyrus rhizome, will provide a more accurate estimation of the NBP of tropical wetlands. Further research into the overall greenhouse gas balance of these wetlands is also needed, including a more comprehensive assessment of CH_4 and N_20 emissions through both plant mediated efflux and ebullition.

Chapter 6.

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Appendix 1. Research Partners involved with the ECOTOOLS Project.

CSGI. University of Siena, Department of Chemical and Bio-system Sciences, Siena, Italy

KIPPRA. Kenyan Institute for Public Policy Research and Analysis, Nairobi, Kenya.

IHE-UNESCO. International Institute for Infrastructural Hydraulic and Environmental Engineering, Delft, Netherlands.

Trinity College Dublin, Department of Botany, Dublin Ireland.

Makerere University, Uganda. Institute of Environment and Natural Resources, Kampala, Uganda.

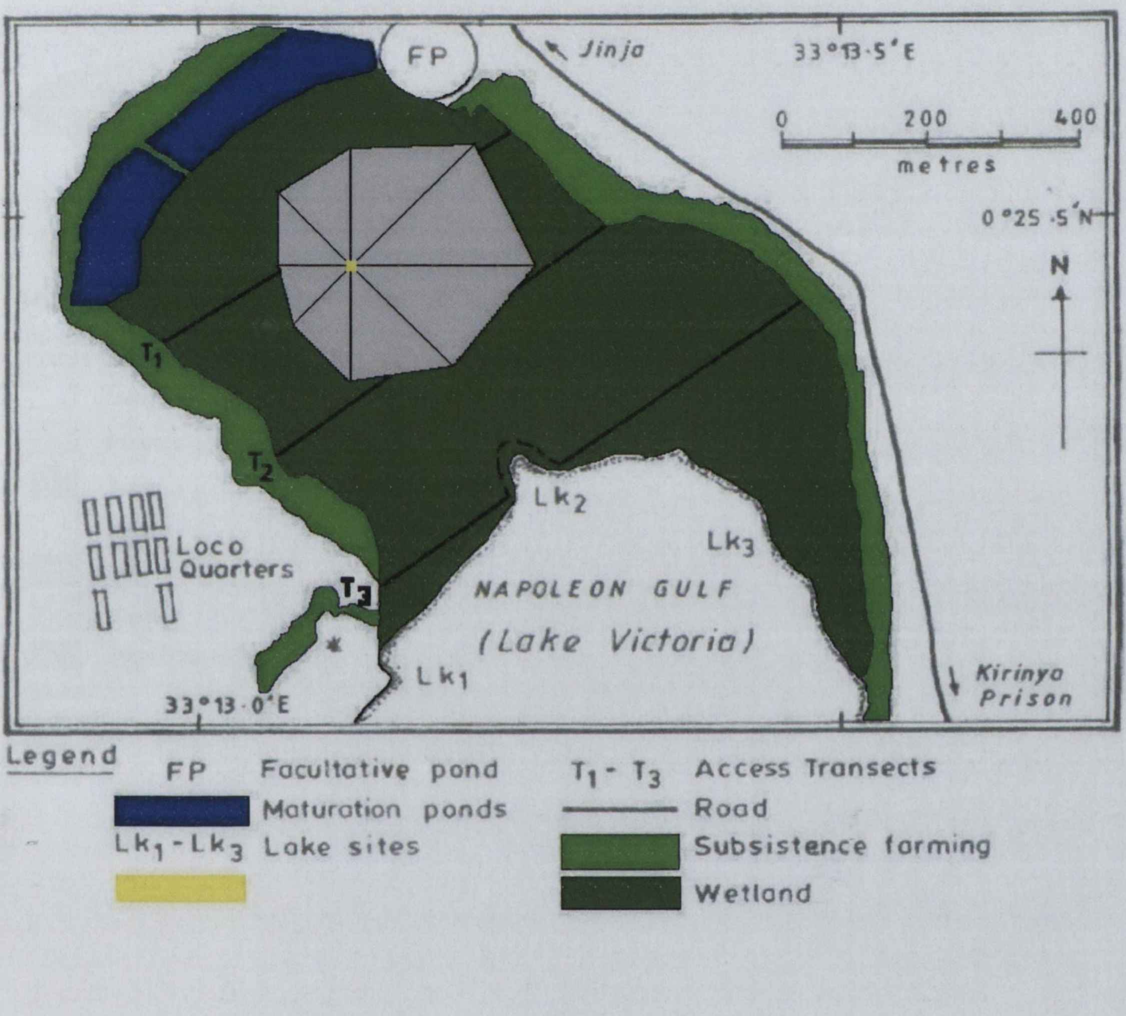
Ugandan Ministry of Water, Lands and Environment. Department of Planning and Quality Assurance, Kampala, Uganda.

University of York. Department of the Environment, York, England.

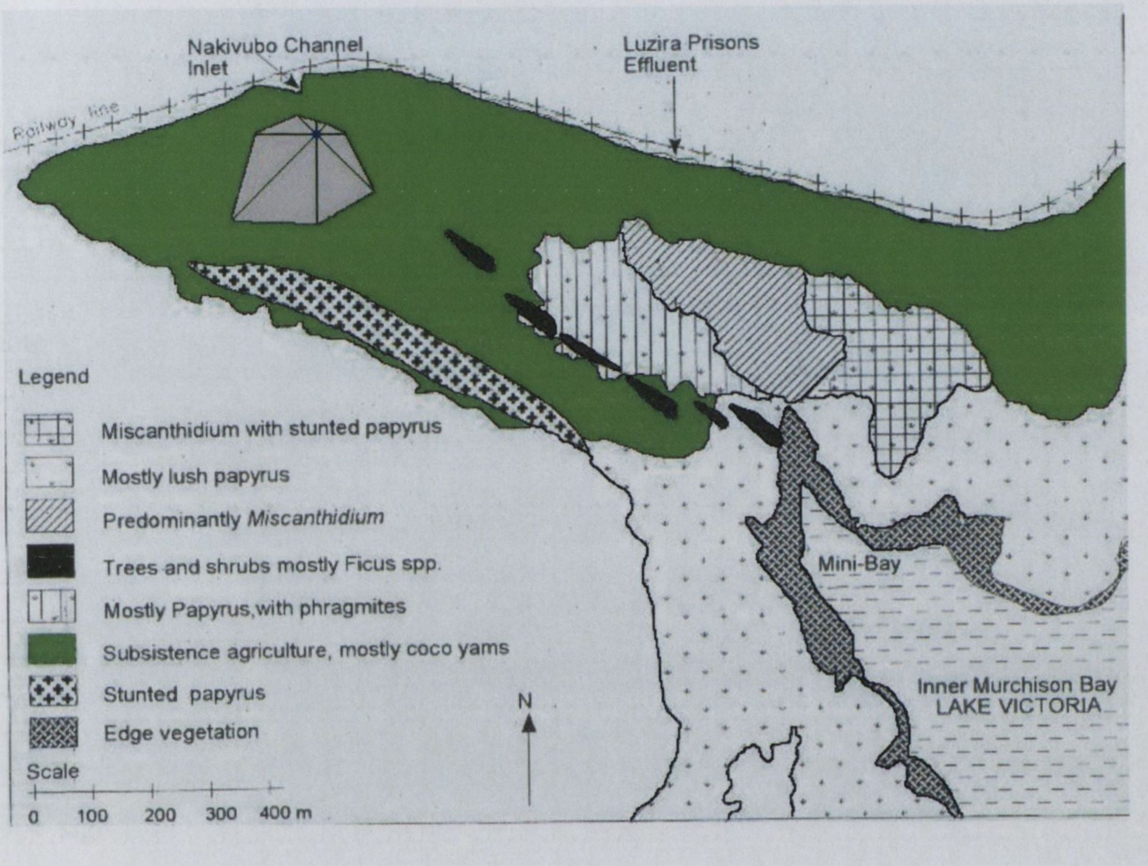
University of Roma Tre. Department of Biology, Rome, Italy.

Wageningen University. Aquatic Ecology and Water Quality Management Group, Wageningen, Germany.

Appendix 2. Flux Footprint over the Kirinya West Wetland, Jinja, Uganda.



Appendix 3. Flux Footprint over the Nakivubo Wetland, Kampala, Uganda.



Appendix 4. Analysis of Variance and Bonferroni's Multiple Comparison test for detrital respiration data from the Kirinya West wetland.

Source	df	Sum of Squares	Mean Square	F-ratio	Probability
Treatment (site)	11	0.449	0.041	5.49	0.0002

Site	1	2	3	4	5	6	7	8	9	10	11	12
1		X									X	
2	X			X	X	X	X					X
3												
4		X									X	
5		X										
6		X									X	
7		X										
8												
9												
10												
11	X			X		X						
12		X										

(X = significant difference $p \leq 0.05$).

Appendix 5. Analysis of Variance and Bonferroni's Multiple Comparison test for mitochondrial respiration data from the Kirinya West wetland.

Source	df	Sum of Squares	Mean Square	F-ratio	Probability
Treatment (age)	3	0.063	0.02	3.94	0.054

Appendix 6. Analysis of Variance and Scheffe Post Hoc test for total carbon data from the Kirinya West wetland..

```
Analysis of Variance For     TC
No Selector

Source      df   Sums of Squares      Mean Square     F-ratio        Prob
Const        1   56762.3              56762.3         42999         ≤ 0.0001
Psn          3      54.877               18.2923         13.857        0.0003
Age          2      39.9521              19.976          15.132        0.0005
Psn*Age      6       9.51015              1.58502         1.2007       0.3694
Plt          2       4.64041              2.3202          1.7576       0.2141
Psn*Plt      6      11.7946               1.96577         1.4891       0.2620
Age*Plt      4       3.87221              0.968053        0.73332      0.5866
Error       12      15.8411               1.32009
Total       35     140.488
```

Appendix 7. Analysis of Variance and Scheffe Post Hoc test for total nitrogen data from the Kirinya West wetland..

```
Analysis of Variance For     TC
No Selector

Source      df   Sums of Squares      Mean Square     F-ratio        Prob
Const        1   40.6364              40.6364         1270.9        ≤ 0.0001
Psn          3    7.00061              2.33354          72.98       ≤ 0.0001
Age          2    5.40235              2.70118          84.478      ≤ 0.0001
Plt          2    0.0397764            0.0198882         0.62199      0.5441
Error       28    0.8953               0.031975
Total       35   13.338
```

Appendix 8. Analysis of Variance and Bonferroni's Multiple Comparison test for dissolved organic carbon data from the Kirinya West wetland.

Source	df	Sum of Squares	Mean Square	F-ratio	Probability
Treatment (site)	3	0.063	0.02	3.94	0.054

Site	Effluent	1	2	3	4	5	Lake
Effluent		X	X	X	X	X	X
1	X			X	X		X
2	X			X	X		X
3	X	X	X		X	X	
4	X	X	X	X		X	X
5	X			X	X		X
Lake	X	X	X		X	X	

(X = significant difference $p \leq 0.001$).

Appendix 9. Analysis of Variance and Scheffe Post Hoc test for methane efflux data from the Kirinya West wetland.

```
Analysis of Variance For    LCH4
No Selector

Source      df     Sums of Squares     Mean Square     F-ratio     Prob
Const       1      38.0356             38.0356         504.15      ≤ 0.0001
Tim         2       0.187946            0.093973         1.2456       0.3381
Age         2       1.69934             0.849671        11.262        0.0047
Tim*Age     4       0.460291            0.115073         1.5252       0.2829
Plt         2       0.0469643           0.0234822        0.31125      0.7410
Tim*Plt     4       0.138821            0.0347052        0.46         0.7637
Age*Plt     4       0.298003            0.0745007        0.98748      0.4664
Error       8       0.603565            0.0754457
Total       26      3.43493
```

Appendix 10. Analysis of Variance and Bonferroni's Multiple Comparison test for detrital respiration data from the Nakivubo wetland.

Source	df	Sum of Squares	Mean Square	F-ratio	Probability
Treatment (site)	7	0.018	0.003	129.7	0.001

Site	1	2	3	4	5	6	7	8
1		X	X	X			X	X
2	X		X	X	X	X	X	X
3	X	X			X	X	X	X
4	X	X			X	X	X	X
5		X	X	X			X	X
6		X	X	X			X	X
7	X	X	X	X	X	X		
8	X	X	X	X	X	X		

(X = significant difference $p \leq 0.001$).