WETLANDS OF EAST AFRICA: BIODIVERSITY, EXPLOITATION, AND POLICY PERSPECTIVES

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Abstract

Wetlands are extensively distributed in East Africa and provide many valuable functions (e.g., flood alleviation, ground water recharge, retention and regulation of pollutants and water plant nutrients); products (e.g., fish, fuelwood, timber, crafts, herbal medicines, rich sediments for agriculture); refugia for fish and other fauna; and other attributes (biodiversity, aesthetic beauty for tourists, cultural heritage). Permanent swamps, dominated by papyrus (*Cyperus papyrus*) are inhabited by unique assemblages of plants and animals with extraordinary adaptations to the extreme conditions (low dissolved oxygen, high levels of carbon dioxide, reducing conditions) imposed by the dense swamp environment. Ecotonal areas tend to be richer faunistically than the dense interior of permanent swamps. However, the permanent swamps may still be very important in the maintenance of faunal structure and diversity; and their degradation may precipitate declines in the diversity and richness of swamp taxa through loss of habitat, faunal mixing, and loss of refugia. In East Africa, humans have lived with and within wetlands throughout history. However, since the 1950s, large-scale swamp conversion and population pressure on small wetlands has threatened the integrity of many African wetlands, precipitated local declines in indigenous wetland organisms, and altered ecosystem functions. The overall goal of setting policies by the East African governments is to promote the wise use and conservation of the East African wetlands so that their ecological and socio-economic functions are sustained for the present and future well being of the people. The Government of Uganda, recently launched such a policy, the first of its kind in Africa to have been formulated in accordance with the Ramsar Convention. It encompasses wetlands in protected and non-protected areas and offers a good example in Africa of a strong political will to conserve wetlands and their biodiversity.

Introduction

The term 'biodiversity' is more than just the number of species; it includes the complexity, the richness and abundance of nature at all levels, from the genetic variation to the layout of communities and systems across terrestrial landscapes and within the water (Baskin 1997). The whole concept of conserving biodiversity

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hinges on understanding the structural and functional properties of ecosystems, and the sensitivity of these properties to changes in the underlying taxa.

Wetlands are among the world's most productive environments. They are the cradles of biological diversity, providing the water and primary productivity upon which countless species of plants and animals depend for survival. They support high concentrations of birds, mammals, reptiles, amphibians, fish, and invertebrate species and are critical to the maintenance of adjacent ecosystems through such processes as nutrient flushing, effects on microclimates, and water holding capacity. Wetlands are also important storehouses for plant genetic material. Rice, for example, which is a common wetland plant, is the staple food/diet for more than one-half of humanity.

Wetlands are extensively distributed on the African continent and form a habitat of great ecological importance. The permanent swamps are inhabited by unique assemblages of plants and animals with extraordinary adaptations to the extreme conditions imposed by the dense swamp environment. In East Africa, humans have lived with and within wetlands throughout history using seasonal swamps as grazing lands; harvesting swamp plants for a variety of purposes including materials for roofing, furniture, and fish traps; and exploiting wetlands for fisheries and aquaculture. However, since the 1950s, large-scale swamp conversion and population pressure on small wetlands have threatened the integrity of many African wetlands, precipitated local declines in indigenous wetland organisms, and altered ecosystem functions.

In this chapter, we review the characteristics of East African wetlands as they relate to the richness and diversity of plant and animal taxa. We then focus on the economy of wetlands through their use in such areas as tourism, fisheries, and ethnobotany; and the potential impacts of human exploitation on wetland diversity and function. Finally, we review the current activities and priorities for wetland conservation and development in East Africa.

Dominant Vegetation Types and Limnological Characteristics

We define wetlands following Harper and Mavuti (1996) as temporarily or permanently wet ecosystems dominated by emergent vegetation. Wetlands of East Africa can be divided into two very broad categories: seasonal (temporary) wetlands, and permanent wetlands. Both forms result from impeded drainage and are communities at the edge or ecotone between dry land and open water (Thompson 1976, Bugenyi 1991, Harper and Mavuti 1996), but the first category, seasonal wetlands, is restricted to land that is only periodically inundated. In East Africa, seasonal wetlands are dominated by grasses that are perennial, or swamp forest with tree species such as *Mitragyna stipulosa, Macaranga schweinfurthii,* and the palms *Phoenix reclinata, Raphia monbuttorum*, and *Calamus deeratus* (Thompson 1976). Other less-severely waterlogged soils are characterized by trees such as *Acacia* spp., *Combretum ghasalense*, and *Balanites aegyptica* (Thompson 1976).

Permanent swamps only develop where there is shallow moving water that is perennial and protected. The emergent sedge papyrus *(Cyperus papyrus)* dominates much of the 85,000 km^2 of permanent swamp on the African continent (Beadle and Lind 1960, Beadle 1981, Thompson and Hamilton 1983) and is the major emergent vegetation in most permanently flooded swamps in tropical Africa (Hughes and

Hughes 1992). In tropical East Africa, it is the most common swamp plant (Thompson 1985); and in this region, the most expansive papyrus swamps are found around the perimeter of Lake Victoria (Figure 1). Within Uganda, the most exten

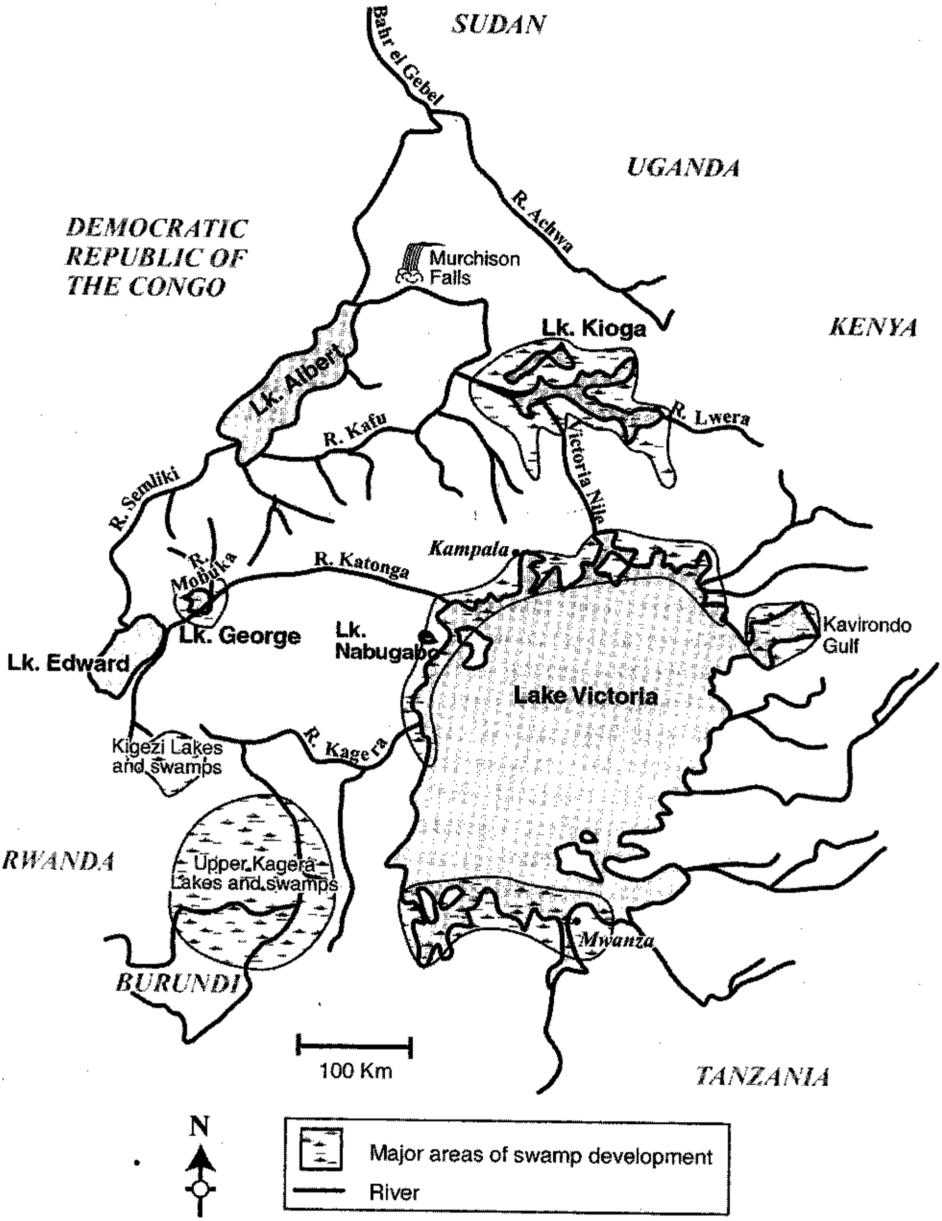

Fig. 1. Map of the Lake Victoria/White Nile catchments illustrating the major areas of permanent swamps (redrawn after Thompson 1976).

sive papyrus swamps are found in the littoral regions of several larger lakes including Victoria, Albert, Kyoga, and George as well as numerous smaller lakes (Beadle 1981). In Kenya, a fringing belt of papyrus is more or less continuous along the Lake Victoria shoreline, and large stretches of papyrus also occupy an area of about 160 km^2 in the contiguous Yala Swamp of lakes Kanyaboli and Saru (Britton 1978). In Tanzania, lake, river, and valley papyrus swamps are also common (Muthuri and Jones 1997). Elsewhere in Africa, large papyrus swamps occur in the Upemba region of the Democratic Republic of the Congo (Muthuri et al. 1989, Hughes and Hughes 1992) and the Okavango Delta in Botswana (Muthuri et al. 1989).

Denny (1985) classifies papyrus swamps into three major categories. Lacustrine swamps are typically floating mats that develop only under stable hydrological regimes at the edges of lakes. Valley swamps occur in river valleys with good hydraulic gradients, and the papyrus is usually rooted in the soil. These valley swamps are extensive, often choking river valleys for several kilometers (Carter 1955). Riverine and floodplain swamps are those that fringe rivers with small amplitudes and spread into floodplains (Denny 1985). The lakeside swamps are limited in their lakeward growth by winds and water currents that frequently tear off islands. These floating islands are a familiar feature in lakes Victoria and Kyoga, and can form significant navigational hazards when they block bays or other water routes.

Papyrus is the largest sedge in the world, normally attaining heights of 3-4 meters, and typically comprising over 95% of the plant biomass of the swamp (Thompson 1976, Thompson et al. 1979, Ellery et al. 1995). It is a rhizomatous perennial plant, and unusual amongst emergent wetland vegetation in having the C_4 pathway of photosynthesis (Jones and Milburn 1978, Jones and Muthuri 1997). Its establishment requires an almost continuously waterlogged substrate. The dense canopy of papyrus limits both mixing of the water column and light, intercepting over 90% of the incoming radiation (Jones and Mithuri 1985, Thompson et al. 1979). In combination with high rates of organic matter decomposition, these conditions result in extremely low oxygen levels in the water beneath the swamp canopy (Carter 1955, Beadle and Lind 1960, Chapman and Liem 1995, Chapman et al. 1998). In Kibale National Park, Uganda, valley papyrus swamps are common and can extend for tens of kilometers. In the Rwembaita Swamp of Kibale, a 6.5 kilometer stretch of papyrus, dissolved oxygen levels in pools and channels within the dense swamp interior averaged only 1.61 ± 0.27 mg L^{-1} (SE, based on monthly samples at several microsites within the swamp, Figure 2). Peak values were observed during seasonal flooding when levels were often greater than 3 mg L^{-1} (Figure 2). The dissolved oxyen levels in the Rwembaita Swamp are not unusually low for papyrus swamps. Carter (1955) studied the limnological characters of the water along a transition gradient between the open lake water, through the fringing papyrus, to the seasonally inundated grasslands along the shores. He also presented data for papyrus and grassland valley swamps, a small lake, and runoff water. Carter (1955) reported oxygen values averaging less than 0.1 mg L^{-1} for the shore regions of littoral papyrus swamps in Lake Victoria, and average values of 2.5 mg L^{-1} for the outer areas of the papyrus zone where papyrus interacts with the waters of the main lake (Figure 3). Carter found that the distance from the edge of the papyrus in Lake Victoria and the anoxic-oxic boundary increased during seasonal

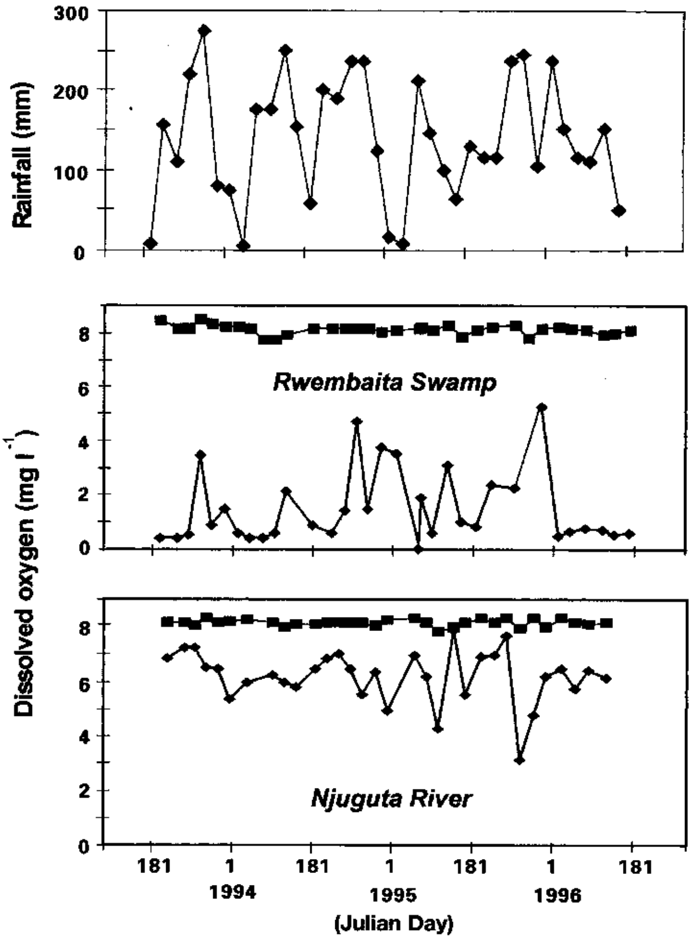

Fig. 2. Mean dissolved oxygen concentrations (mg L^{-1}) for two sites in Kibale National Park, Uganda: a papyrus swamp (Rwembaita Swamp) and an everflowing river (Njuguta River). Each value represents the mean of duplicate samples at a series of microsites within each system. Saturation values for each site are indicated based on the average temperature of the site for each sampling period. Monthly rainfall data are presented in the top panel based on data collected at the Makerere University Biological Field Station located approximately 3 km from the Rwembaita Swamp.

rains, and reported an increase in oxygen values in surface waters from <0.5 mg L^{-1} in the dry season to 1.4 mg L^{-1} during the rainy period. Similarly, in the dense papyrus at the mouth of the Chambura River in Uganda, Beadle (1932) found no detectable oxygen within a few centimeters of the surface.

The water under these swamp conditions is slightly acid, and the pH of papyrus swamp water is usually between 6 and 6.5. In lakeside papyrus, one again finds a transition from the acid waters of the shoreline papyrus to basic waters of the open lake (Figure 3, Balirwa 1998). The low pH is most likely due to the high levels of dissolved carbon dioxide and humic acids formed from organic matter decomposition. Carbon dioxide can reach very high levels in the dense swamp interior (Figure 3). Milburn

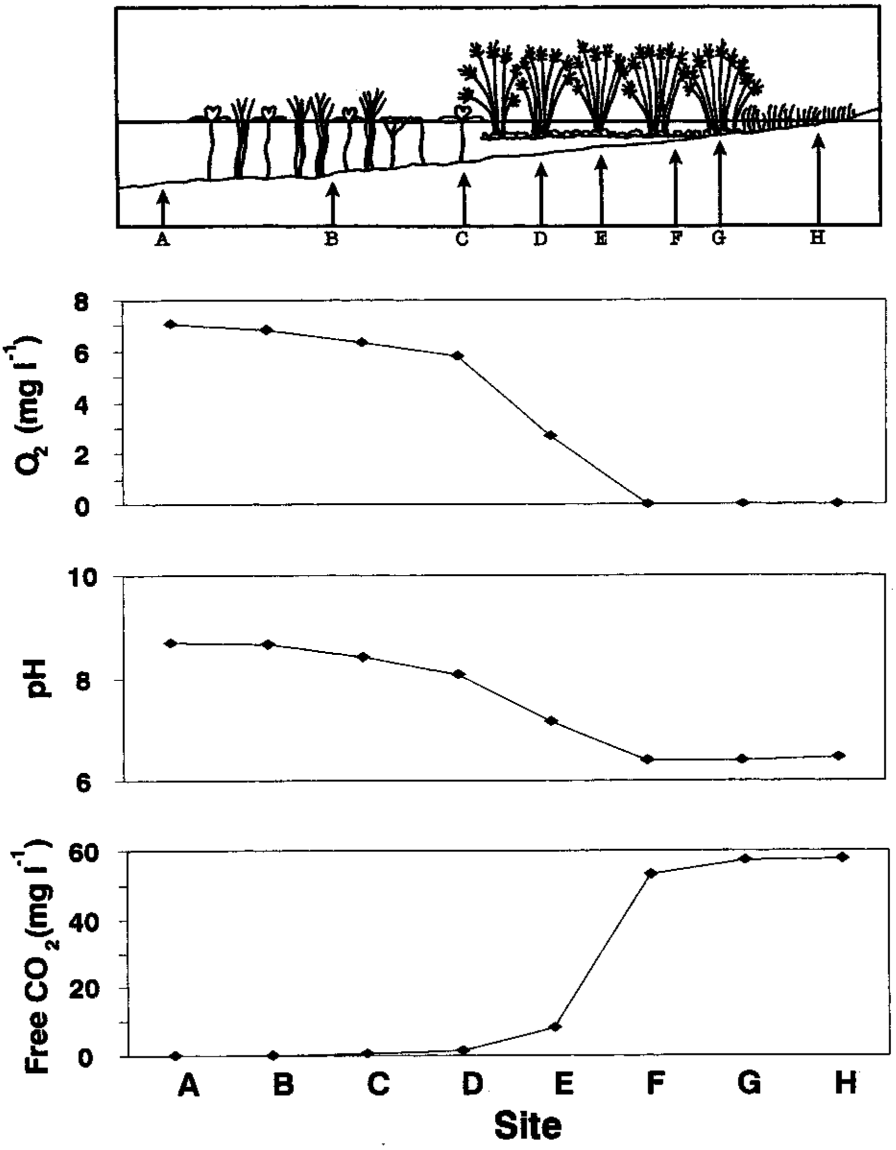

Fig. 3. Gradients of dissolved oxygen concentration (mg L^{-1}), pH, and free carbon dioxide (mg L^{-1}) in the surface waters (dry seasons conditions) between the open water of Lake Victoria through the fringing papyrus to the grass swamp along the shore. Data were obtained from Carter (1955) for his Bugangu site. Top illustration adapted from Carter (1955).
A – open water outside the lily zone
B – water in the center of the lily zone
C – water in the lily zone within approximately 0.9 m of papyrus
D – water in the papyrus zone, approximately 7.7 m from the lily zone
E – water in the papyrus zone, approximately 16.5 m from the lily zone
F – water in the papyrus zone, approximately 7.7 m from the shore edge
G – water in the papyrus zone, approximately 3.3 m from the shore edge
H – water in the grass swamp on the shore side of the papyrus zone

and Beadle (1960) reported concentrations of 148 mg L^{-1} of carbon dioxide (dissolved plus bound as HCO_3) in a Ugandan papyrus swamp at the end of a very long dry spell. Using the data set presented by Carter (1955) we quantified the relationship between the concentration of free CO_2 and dissolved oxygen (% saturation). Eighty-one percent of the variance in dissolved oxygen concentration among sites was explained by the concentration of free CO_2. Therefore, the most hypoxic areas of the swamps tend to be characterized by the highest levels of carbon dioxide, and this may impose severe respiratory constraints on water-breathing organisms.

Because the organic materials in the swamp are mainly carbohydrates with little protein, the gaseous end product of organic decomposition is methane (Beadle 1981). Hydrogen sulphide is usually not detected (Beadle 1981, Howard-Williams and Gaudet 1985). The composition of the gases evolved from decomposing anaerobic and waterlogged papyrus stems was reported by Visser (1963) as 60% methane, 30% carbon dioxide, and 10% hydrogen, carbon monoxide, and ethylene. In the deep waters of some lakes, H_2S is produced and accumulates in sufficient quantities to be potentially toxic to some aquatic organisms (Beadle 1963, Beadle 1981). Beadle (1981) points out that apart from carbon dioxide, there is no evidence that the gases listed above accumulate in sufficient concentrations in African swamps to seriously impact animals. However, the methane is still a problem for humans; and may account for marsh gas explosions on streamers passing through such areas (Lake Kyoga as reported in Beadle 1981; Nile Sudd as reported by Rzoska 1974).

Papyrus has a very high photosynthetic and productive potential. In Lake Naivasha in Kenya, the harvestable standing biomass has been estimated at 32 t per ha, and the plant can probably regain its original biomass in less than 12 months (Jones 1983). Thus, the annual production of the most productive papyrus swamps compares favorably with forests as a biomass source (Jones 1983). The high productivity and success of papyrus in the wetlands of East and Central Africa may be due to the presence of C_4 photosynthesis, a characteristic of many highly productive tropical grasses (Muthuri and Jones 1997). Jones (1987) hypothesizes that the net assimilation of papyrus is likely to be limited by available nitrogen. He postulates that because C_4 photosynthesis facilitates more efficient use of nitrogen, C_4 species should have a higher net productivity in wetlands and therefore, be more competitive than C_3 species.

Papyrus swamps have been characterized as detritus-based ecosystems (Howard-Williams and Gaudet 1985). The detritus is produced from the decomposing plants, and the decomposition of the detritus is rather slow because of the largely anaerobic conditions in the swamp. Chapman et al. (in press) found that dissolved oxygen concentration in the Rwembaita Swamp, Uganda, was positively correlated with rainfall; however, there was evidence of a lag effect (Figure 2). The only significant predictor of oxygen availability was rainfall over the 2-month period prior to the oxygen measurement. This lag effect on the temporal dynamics of dissolved oxygen may be related to the extensive lateral expansion of the swamp in the early stages of seasonal flooding that retards the anticipated increase in water flow. A second factor that may retard seasonal oxygen peaks is the resuspension of oxygen-demanding materials. Rainwater contributes very little to nutrient loading (~1 to 2%) in papyrus swamps (Gaudet 1979). However, below the papyrus mat, and interspersed within the mat, is an accumulation of decomposing plant material (peat, Gaudet 1976). Below this on the swamp bottom fine organic material accumulates and is referred to as sludge (Gaudet 1976). The detritus fraction within papyrus swamps deposited as sludge contains the bulk of the nutrients. Seasonal flushing is typical of African swamps (Gaudet 1979), and it is likely that sludge is transported downstream during seasonal rains. Resuspension of the reducing materials may limit the oxygen-producing effects of pulses of oxygenated water that enter with rainfall.

In the Njuguta River, a fast-flowing river into which the Rwembaita Swamp flows, Chapman et al. (in press) found a negative relationship between rainfall (2 days, 2 weeks, and 1 month prior to the oxygen measurements) and dissolved oxygen concentration. In this river, it is likely that depressed oxygen associated with seasonal rainfall is associated with the inflow of large volumes of deoxygenated water from the Rwembaita and Njuguta Swamps during seasonal flushing of the swamp waters. Gaudet (1976) found that swamp sludge is physically exported at lake and river edges and lies in a "fan" in front of the swamp face. He further reported that phosphorus trapped in the detritus within the swamp becomes more available after export because of decomposition under aerobic conditions. The combination of inflow of hypoxic swamp waters and an influx or resuspension of oxygen demanding materials may lower dissolved oxygen content during flood events downstream of papyrus swamps.

After papyrus, the most common swamp plant in East Africa is probably *Miscanthidium violaceum*, a grass which tends to be found in rather acidic conditions. *Miscanthidum* swamps are typical of low-nutrient sites, which seem to be too acidic for other reeds and floodplain grasses (Beadle and Lind 1960). These wetlands are usually dry enough to support *Sphagnum* species and other fen bryophytes (Thompson and Hamilton 1983). *Miscanthidium violaceum* is sometimes mixed with papyrus; but at several sites in East Africa, for example some of the valley swamps flowing into Lake Victoria, it is the dominant plant. Dissolved oxygen concentration is also very low in *Miscanthidium* swamps, although growth of periphyton can lead to diurnal peaks in small open pools within the mats. In the dense interior of the *Miscanthidium* swamp surrounding Lake Nabugabo (Lwamunda Swamp), Chapman and Chapman (unpubl. data) found that dissolved oxygen levels averaged 0.7 mg L^{-1} in the early morning, but increased to 3.3 mg L^{-1} in the midday period of a dry season day. The water under the *Sphagnum* is often very acid and its salt content extremely low. In the Lwamunda Swamp, Chapman and Chapman (unpubl. data) recorded an average pH of 5.7 and a conductivity level of 16.4 $\mu S\ cm^{-1}$ (dry season day).

Permanent swamps in East Africa are populated by several other species of plants. In fact, the tall structural complexity afforded by live papyrus and fallen stems provides a habitat for the growth of numerous vines. For example, Lind and Morrison (1974, Table 1) reported 34 species of plants in a papyrus zone in the fringing wetlands of Lake Victoria, and 36 species in the *Miscanthidium violaceum* zone of the same region. There are however, clear floristic differences between the acid habitat of *M. violaceum* communities and papyrus swamps, and among papyrus swamps. Denny (1985) found that *Miscanthidium* communities had twice the number of sedges and grasses than papyrus swamps and that the two habitats shared only 15 to 20% of their plant assemblage (Table 1). It is also clear that the floristic assemblages of papyrus swamps differ among sites and between valley and lakeside forms. For example, the valley swamps of Kibale Forest, Uganda, harbor 36 species of plants (McWalter, Otto, and Crisman, unpubl. data), but share only four species with a lakeside papyrus swamp in Lake Victoria (Table 1).

Non-indigenous wetland plants are also common in East Africa, and one of the most invasive species has been the water hyacinth, *Eichhornia crassipes*. It is native to Amazoina, but has naturally spread to other areas in South America (Harley 1990). During the last century, it has colonized large parts of the tropical zones. On the African continent, water hyacinth was first introduced to Egypt between 1879 and 1892 (Gopal and Sharma 1981), then South Africa in 1910, and Democratic Republic of Congo in 1952 (Gopal 1987). It has also infested River Pangani in Tanzania, the Kafue River in Zambia, the Upper Nile, and is found in Lake Mariut in Egypt (Njuguna 1992). Water hyacinth appeared in Lake Naivasha in Kenya in 1982 and in Lake Kyoga in Uganda in 1988. It was first reported in 1990 in Tanzania and in the Ugandan waters of Lake Victoria in 1988 (Twongo et al. 1995). The weed is now firmly established in Lakes Victoria, Naivasha, Kyoga, Albert, and along the River Nile.

The weed is distributed into two distinct forms, as stationary fringes along shorelines and as mobile mats. In Lake Victoria, the weed has established at an average fringe width of 10 to 15 m since 1995. In some shorelines parts *Vossia cuspidata* (hippo grass) dominates the water hyacinth, thus reducing the area of stationary water hyacinth fringe (Twongo and Balirwa 1996). Water hyacinth is a free-floating macrophyte, which normally floats on the water surface and its distribution is largely dependent on wind and water movements (Muthuri 1992). This group of aquatic macrophytes includes members of Lemnaceae (duckweeds), such as *Lemna, Spirodela*, and *Wolffia*, as well as the aquatic weeds *Eichhornia crassipes, Salvinia molesta*, and *Pistia stratiotes*. These last three floating aquatic weeds have infested the wetlands of Kenya at different times and with varying degrees of spatial extent; and all three have infested Lake Naivasha (Njuguna 1992). Water hyacinth has also spread around Lake Naivasha sharing the littoral areas with *Salvinia*.

Wetland Faunas: Diverse Adaptations to Environmental Challenges

The rather extreme conditions of the dense swamp environment in East Africa (low dissolved oxygen, high levels of carbon dioxide, reducing conditions, detritus availability) affect aquatic organisms and determine, in part, the unique assemblages that characterize these habitats. The richness of animal life in the dense interior of papyrus and *Miscanthidium* swamps tends to be lower than in the ecotonal wetlands where interaction with the main lake waters raises dissolved oxygen levels and lowers carbon dioxide content. However, there are several aquatic taxa that possess adaptations facilitating survival in the dense swamp interior.

There are numerous micro-organisms found in the swamp mat and mud responsible for anaerobic decomposition; and these organisms are independent of molecular oxygen (Visser 1963, Beadle 1981). However, extreme hypoxia obviously poses a challenge to non-air-breathing multicellular animals. Aquatic macroinvertebrates exhibit an impressive diversity of respiratory adaptations. These adaptations have associated costs and benefits that vary with the ecological background and affect their ability to use or disperse through hypoxic or anoxic waters. Aquatic macroinvertebrates can be divided into two basic categories: aeropneustic and hydropneustic. Taxa belonging to the first group primarily use oxygen from the atmosphere, whereas those belonging to the second group extract dissolved oxygen from the water.

Several air-breathing aquatic snails inhabit the dense interior of papyrus East African swamps. Two common taxa are *Pila ovata* and *Biomphalaria* spp, some of which are vectors of human intestinal parasite *Schistosomiasis* (Beadle and Lind 1960, Beadle 1981). The snail becomes infected only when the water is contaminated with human feces that contain the eggs of the schistosome, so the main sources of infection are sites where people habitually come to the water such as pools at the edge of the swamp or transport channels (Beadle and Lind 1960). Therefore, many of the areas within the dense interior of East African swamps harbor abundant populations of the snail vectors, but are in fact, not a source of the disease (Beadle and Lind 1960).

Interestingly, there are some swamps in East Africa where molluscs (air-breathing snails and clams) are extremely rare. For example, in Lake Nabugabo, Uganda *Schistosomiasis* seems to be absent due to the paucity of intermediate gastropod hosts. Conductivity is generally low in waters throughout the Lake Nabugabo area due to the insoluble rocks of the catchment and flow through the extensive Lwamunda swamp where ions are removed through absorption and accumulation by the swamp vegetation (Figure 4). In the Jinja area of Lake Victoria, Balirwa (1998) reported an average mollusc density of 136 individuals per m^2 at the wetland ecotone, 1054 ind. m^{-2} 20 m off of the wetland ecotone, and 300 ind.m^{-2} in open water stations, a dramatic contrast to an average density of 35 ind. m^{-2} in the inshore areas of Lake Nabugabo (Jackson 1998) and the absence of molluscs in open water stations. The low conductivity (low level of ions) in Lake Nabugabo may be responsible for the low number of molluscs and absence of crustaceans which, with their calcareous shells and exo-skeleton, have great need for the ions especially calcium (Beadle 1981).

The swamp worm *Alma emini* is very abundant in the upper layer of papyrus mud and plays an important role in the decomposition of plant material in the swamps (Beadle and Lind 1960, Beadle 1981). The worm obtains atmospheric oxygen by exposing its hind end above the mud whereby a dorsal groove richly supplied with blood vessels absorbs oxygen from the air. The groove is then folded to form a tube to the air and the hind end is withdrawn into the mud leaving behind the opening to the "temporary lung" (Beadle and Lind 1960, Beadle 1981).

Several other atmospheric breathers have respiratory siphons that allow the organism to pierce the surface film (Ward 1992). These siphons are tube-like structures that allow the insects to breathe without having to surface and are characteristic of nepids (Nepidae, Hemiptera, water scorpions), which are common inhabitants in many papyrus swamps.

Mosquito larvae (Diptera: Culicidae) are also air breathers; about 80 species breed in East African swamps, and 40 of these are found in permanent valley swamps where hypoxia is very extreme (Goma 1960, 1961a). However, the vast majority of the swamp-dwelling mosquito larvae do not carry malaria (Beadle and Lind 1960). The principle vectors in East Africa, *Anopheles gambiae* and *A. funestus*,

Table 1. A comparision of the plant species composition among a papyrus and *Miscanthidium* zone of a lake-edge swamp of Lake Victoria (retabulated after Thompson (1985, original data from Lind and Morrison 1974) and a valley papyrus swamp of Kibale Forest, Uganda (McWalter, Otto, and Crisman, unpublished data).

Family ***Species***	**Papyrus**		***Miscanthidium***
	Lake Victoria	**Kibale Nat'l Park**	**Lake Victoria**
Alismataceae			
Limnophyton obtusifolium	present		
Asclepiadaceae			
Pergularia daemia		present	
Asteraceae			
Adenostemma perrottetii		present	
Crassocephalum picridifolium		present	
cynura scandens		present	
Melanthera scandens	present	present	
Senecio syringifolius		present	
Vernonia sp.		present	
Balsaminaceae			
Impatiens burtonii		present	
Impatiens irvingii	present		
Basellaceae			
Basela alba		present	
Bryophyta			
Sphagnum spp.			present
Capparaceae			
Euadenia sp.		present	
Caryophyllaceae			
Drymaria cordata		present	
Commelinaceae			
Commelina africana		present	
Compositae			
Melanthera scandens	present		
Mikania cordata	present	present	present
Convolvulaceae			
Ipomoea rubens	present		
Lepistemon owariense		present	
Cucurbitaceae			
Lagenaria sphaerica		present	
Zehneria scabra		present	
Cyperaceae			
Acriulus greigiffolia	present		present
Cyperus denudatus	present		present
Cyperus haspan			present
Cyperus papyrus	present	present	
Cyperus sp.		present	
Fimbristylis pilosa			present
Fuirena umbellata			present
Pycreus nitidus	present		present
Pycreus polystachyos	present		present
Rhynchospora subquadrata			present
Schleria nyassensis			present
Schleria nutans			present
Dennstadtiaceae			
Microlepia speluncea		present	

Table 1. (Continued).

Family **Species**	**Papyrus**		***Miscanthidium***
	Lake Victoria	**Kibale Nat'l Park**	**Lake Victoria**
Euphorbiaceae			
Bridelia micrantha	present	present	
Flacourtiaceae			
Scolopia rhamniphylla		present	
Graminae			
Andropogon canaliculatus			present
Digitaria scalarum			present
Eragrostis mildbraedii			present
Hyparrhenia diplandra	present		
Leersia hexandra	present		present
Loudetia phragmitoides			present
Miscanthidium violaceum			present
Panicum parvifolium	present		present
Panicum subalbidum			present
Paspalum commersonii			present
Guttiferae			
Hypericum lalandii			present
Labiatae			
Hyptis lanceolata	present		
Neohyptis paniculata	present		
Leguminosae			
Cassia kirkii			present
Desmodium salicifolium		present	
Eriosema glomeratum			present
Mimosa pigra			present
Smithia elliotii			present
Vigna luteola	present		
Vigna sp.		present	
Lentibulariaceae			
Utricularia gibba			present
Malvaceae			
Hibiscus diversifolius	present		
Melastomataceae			
Dissotis brazzei			present
Dissotis rotundifolia	present		
Melastomastrum segregatum	present		
Tristemma incompletum	present		present
Menispermaceae			
Cissampelos mucronata	present		
Stephania abyssinica		present	
Tinospora caffra		present	
Ochnaceae			
Sauvagesia erecta			present
Onagraceae			
Ludwigia leptocarpa	present		
Oxalidaceae			
Biophytum petersianum			present
Moraceae			
Ficus verruculosa	present		present
Passifloraceae			
Adenia schweinfurtii		present	
Poaceae			
Oplismenus sp.		present	

Table 1. (Continued).

Family **Species**	**Papyrus**		***Miscanthidium***
	Lake Victoria	**Kibale Nat'l Park**	**Lake Victoria**
Dennstadtiaceae			
Polygonaceae			
Polygonum pulchrum	present		present
Polygonum strigosum	present	present	present
Polygonum salicifolium	present	present	
Pteridophyta			
Thelypteris confluens			present
Thelypteris striata	present		
Thelypterus sp.		present	
Rosaceae			
Rubus apetalus		present	
Rubiaceae			
Hallea rubrostipulata		present	
Oldenlandia affinis		present	
Oldenlandia goreensis	present		
Pentodon pentandius	present		
Scrophulariaceae			
Torenia thouarsii	present		present
Sterculiaceae			
Melochia bracteosa	present		
Tiliaceae			
Triiumfeta macrophylla	present		
Umbelliferae			
Hydrocotyle mannii		present	
Oenanthe procumbens		present	
Urticaceae			
Laportea ovalifolia		present	
Vitaceae			
Cyphostemma adenocaule	present		

do not breed inside the dense interior of papyrus swamps, but can be found in open pools at the edges (Beadle and Lind 1960, Beadle 1981). Papyrus swamp reclamation or conversion by drainage can actually create favorable habitat for malaria vectors in the pools and ditches created in the process (Garnham et al. 1948, Steyn 1948, Goma 1961b).

Clams of the genus *Sphaerium* are also common in papyrus swamps. Use of the respiratory pigment hemocyanin may permit them to exploit hypoxic swamps. Hypoxic conditions, though, may come at a cost by greatly reducing their metabolic rate. In their study of two sphaerid species (*Pisidium amnicum and Sphaerium corneum*), Holopainene and Penttinen (1993) found that the clams suppressed their metabolic rate to 7.5% of their active level in anoxic water. The cost may be offset by competitive advantages. These invertebrates are filter feeders and/or deposit feeders and selecting these hypoxic habitats may reduce competition from other invertebrates that use these resources. For example, ephemeropterans (mayflies) are abundant in well-oxygenated streams and rivers, but extremely rare in the swamp sites, which may reduce competitive effects for clams in the swamp.

Because of the extreme conditions in the dense swamp interior, the macroinvertebrate assemblage differs from open-water systems. For example, in Kibale

National Park, Uganda, the macroinvertebrate community of the dense papyrus is dominated by air-breathing snails, nepids, and clams; whereas the communities of a nearby stream and river sites are dominated by tracheal air breathers like odonates (dragonfly and damselfly nymphs) and ephemeropterans (Figure 4).

There are a myriad of adaptations (physiological, morphological, and behavioral) in fishes to the respiratory challenges imposed by oxygen scarce waters. Permanent swamps tend to be inhabited by a very specialized fish fauna adapted for life in deoxygenated waters. The development of air-breathing organs is more common in tropical fresh waters than anywhere else (Roberts 1975), and in Africa one finds air-breathing representatives in at least 12 of the families of freshwater fishes. The few accounts of papyrus and *Miscanthidium* swamp fish faunas include many air breathers *(Protopterus aethiopicus, Clarias* species, *Ctenopoma muriei, Polypterus senegalus;* Carter 1955, Welcomme 1970, Beadle 1981, Chapman 1995, Chapman and Liem 1995, Chapman et al. 1996a,b, Table 2). Unlike gills that seem to be evolutionarily homologous among species, air-breathing organs show remarkable diversity in their structural morphology and their origins. These include such innovations as diverticula of the branchial chambers (e.g., *Clarias, Ctenopoma*) and modification of the air bladder (e.g., *Polypterus, Protopterus*). Air-breathing fishes combine the use of dissolved and atmospheric oxygen; however, there is great variation in the degree of dependence on atmospheric air and in the degree of the development of gills and air-breathing organs (Carter 1957). Some species like the lungfishes (*Protopterus* sp.), are obligatory air-breathers and will die without access to the surface. Other species, including the air-breathing *Clarias,* have well-developed gills and can meet their oxygen requirements using water breathing at higher oxygen levels.

Although air-breathing fishes are common in dense East African swamps, there are also several non-air-breathing fishes that cohabit these extremely hypoxic habitats. For example, Chapman and Liem (1995) found that the small cyprinid *Barbus neumayeri* inhabits the dense interior of papyrus swamps in Uganda. Large gills, the use of aquatic respiration at the air-water interface (aquatic surface respiration, ASR, Kramer and Mehegan 1981) where diffusion produces an oxygen rich layer of surface water, and selection of microhabitats with higher oxygen availability permit *B. neumayeri* to survive in the hypoxic swamp waters (Chapman and Liem 1995, Olowo and Chapman 1996, Chapman et al. 1999). In addition, Chapman et al. (1996b) discovered remnant populations of a small mormyrid, *Petrocephalus catostoma* in wetland lagoons surrounding Lake Nabugabo, Uganda after its population had been extirpated from the main lake associated with the introduction of Nile perch *(Lates niloticus).* This tiny electric fish survives by virtue of a low metabolism, a low critical oxygen tension, large gill surface area, and inverted swimming during ASR to expose its subterminal mouth to the surface layer (Chapman and Chapman 1998). Welcomme (1970) reported several non-air-breathing fishes in the wetland lagoons that were produced between 1961 and 1964 behind the fringing swamps of Lake Victoria when water levels increased abruptly (Table 2). Welcomme found that the more isolated lagoons were characterized by lower species richness. It is likely that the fringing swamp acts much like a biological filter limiting colonization and survival. For lagoons that are very isolated from the main lake, recolonization may be limited to much longer term climatic fluctuations leading to extreme flood cycles resulting in short-term availability of both dissolved oxygen and pathways for dispersal.Non-air-breathers

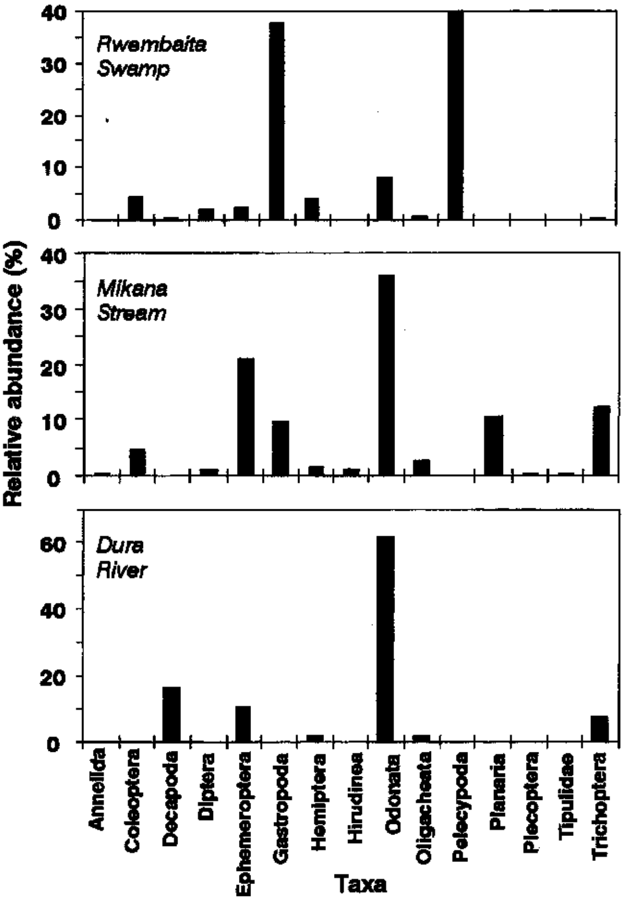

Fig. 4. The relative abundance (%) of aquatic benthic macroinvertebrate taxa found in (a) the dense interior of the Rwembaita Swamp (papyrus), (b) Mikana Stream (a small intermittent stream), and (b) an well-oxygenated, everflowing section of the Dura River in Kibale National Park, Uganda. Data were obtained from a series of scoop net samples over a 2-year sampling period (June 1995 to June 1997).

are also common in ecotonal areas between wetlands and the open water of lakes or rivers where oxygen levels are higher (Chapman et al. 1996a,b, Rosenberger and Chapman 1999). However, many of these species do not penetrate the dense swamp interior producing a sharp transition in species composition that corresponds to a sharp transition in physicochemical conditions in wetland ecotones (Rosenberger and Chapman 1999). Balirwa (1998) identified 30 species from wetland-dominated interfaces in Lake Victoria in contrast to 10 species from deeper (4 to 8 m) open-water habitats.

Despite the limited diversity of fishes in papyrus swamps, these habitats may contribute to the maintenance of faunal diversity in East Africa. For some air-breathing fishes, papyrus swamps are important habitats that are used throughout the year or seasonally as breeding grounds. Within the Lake Victoria Basin, for

Table 2. Fish assemblages in a series of East African wetlands. Data for the wetland lagoons in the fringing *Miscanthidium violaceum* swamp surrounding Lake Nabugabo, Uganda; the papyrus choked Juma River (~200 upstream from the mouth); and the deep interior of the *Miscanthidium*/papyrus swamp surrounding Lake Manywa, Uganda were abridged from Chapman et al. (1996a), Rosenberger and Chapman (1999), and Chapman and Chapman (unpublished data). Data for a series of wetland lagoons created behind the fringing swamp of Lake Victoria (near Jinja, Uganda) during the high flood years of 1961 and 1964 were abridged from Welcomme 1970. Nomenclature for the haplochromine cichlids follows Greenwood (1980). Fishes with accessory air-breathing organs are noted as well as fishes known to use aquatic surface respiration in response to extreme hypoxia.

Family/ *Species*	**Air breather**	**Aquatic surface respiration**	**Lake Nabugabo**		**Lake Manywa**	**Lake Victoria**
			Wetland lagoons	**Juma R. (papyrus)**	**Deep swamp**	**Wetland lagoons**
Protopteridae						
Protopterus ethiopicus	Yes	No	present	present	present	present
Mormyridae						
Gnathonemus victoriae	No	Yes	present			
Petrocephalus catostoma	No	Yes	present			
Cyprinidae						
Barbus magdalenae	No	?	present			
Barbus apleurogramma	No	Yes	present	present	present	present
Barbus kerstenii	No	Yes	present	present		
Barbus neumayeri	No	Yes		present		
Barbus sp.	No	Yes	present	present		
Barbus radiatus	No	?	present			
Characidae						
Brycinus sadleri	No	Yes			present	
Clariidae						
Clarias alluaudi	Yes	No	present	present		present
Clarias liocephalus	Yes	No	present	present	present	present
Clarias werneri	Yes	No		present		
Clarias gariepinus	Yes	No	present		present	present
Clarias sp.	Yes	No			present	
Mochokidae						
Synodontis afrofischeri	No	Yes		present		
Cyprinodontidae						
Aplocheilichthys pumilus	No	Yes	present	present	present	present
Nothobranchius sp.	No	Yes	present			
Cichlidae						
Oreochromis esculentus	No	Yes			present	present
Oreochromis leucostictus	No	Yes	present	present		present
Oreochromis variabilis	No	Yes				present
Tilapia rendalli	No	Yes	present	present		
Oreochromis niloticus	No	Yes	present	present		present
Tilapia zillii	No	Yes				present
Astatoreochromis alluaudi	No	Yes	present	present		present
Astatotilapia cinereus						present
Astatotilapia nubila	No	Yes				present
Astatotilapia velifer	No	Yes	present	present		
Haplochromis obliguidens						present
Harpagochromis guiarti						present
Harpagochromis squamulatus						present
Lipochromis cryptodon						present
Lipochromis obesus						present
Lipochromis parvidens						present

Table 2. (Continued).

Family/ ***Species***	**Air breather**	**Aquatic surface respiration**	**Lake Nabugabo**		**Lake Manywa**	**Lake Victoria**
			Wetland lagoons	**Juma R. (papyrus)**	**Deep swamp**	**Wetland lagoons**
Prognathochromis bartoni						present
Prognathochromis longirostris						present
Prognathochromis venator	No	Yes			present	
Pseudocrenilabrus multicolor	No	Yes	present	present	present	present
Ptyochromis granti						present
unid. Haplochromines	No	?			present	
Anabantidae						
Ctenopoma muriei	Yes	No	present	present	present	present
Mastacembelidae						
Atheomastacembelus frenatus	No	No		present		

example, some fish species including *Ctenopoma muriei, Clarias liocephalus*, and *Nothobranchius* sp. are found principally in papyrus swamps and other wetlands.

Papyrus swamps may also be important in minimizing faunal mixing by creating barriers to the dispersal of fish species that are intolerant of low oxygen. For air-breathing fishes, papyrus swamps and other large swampy divides are not likely to be barriers to dispersal. However, for hypoxia intolerant water breathers, these swamps may limit movement and serve as an isolating mechanism. For non-air breathers that can survive in the dense interior of African swamps, swamp exploitation is likely to be limited by oxygen availability and the efficiency of oxygen uptake for individual species. This has two implications. First, for indigenous fishes that are intolerant of hypoxic waters, dense swamps may be important in promoting faunal diversification by reducing rates of dispersal between populations. This may result in geographical variation between swamp populations and those from open water sections of the drainage or among populations separated by extensive swampy divides. For example, Chapman et al. (1999) examined the role of papyrus swamps in the diversification of *Barbus neumayeri*. They found a strong relationship between the total gill filament length of *B. neumayeri* and dissolved oxygen availability among swamp and stream sites in the Mpanga River drainage of Uganda. Additional studies revealed differences in the respiratory behavior, physiological traits, and RAPD markers between *B. neumayeri* from papyrus swamps and those from open water populations in the same river system (Olowo and Chapman 1996, Chapman et al. 1999), suggesting that hypoxic swamps may pose an ecological and a genetic barrier for this species. Second, papyrus swamps may also function to limit the range extension and habitat use of introduced fishes. This may be extremely important in the Lake Victoria basin, where the spread of introduced species threatens the integrity of many indigenous faunas in lakes and rivers. This is best exemplified by the recent history of the lakes Victoria, Kyoga, and Nabugabo in Uganda. The species flock of haplochromine cichlid fishes in Lake Victoria is one of the most extensive and recent radiations of vertebrates known (Kaufman 1992, Kaufman et al. 1997). However, over 50% of the endemic fishes and many other indigenous species disappeared from Lake Victoria between 1980 and 1986, and many are presumed extinct. The introduced Nile perch *(Lates niloticus)* population is proposed to have been a major contributor to the mass extinction; the decline in endemic haplochromines is almost reciprocal with the increase in Nile perch (Kaufman 1992, Witte et al. 1992a,b, Kaufman et al. 1997).

The severity of the loss in species richness and diversity led to a series of studies directed at identifying potential faunal refugia. Several lines of evidence now suggest that wetlands in the Lake Victoria basin may protect some fishes from Nile perch predation by providing both structural and low oxygen refugia for prey species and serving as barriers to the dispersal of the Nile perch. First, Fish (1956) found that Nile perch require water with high dissolved oxygen, since their blood has a low affinity for oxygen. Further physiological work has shown that Nile perch have a relatively high critical oxygen tension which supports a low tolerance to extreme hypoxia (Schofield and Chapman 2000), and that they select habitats characterized by high dissolved oxygen levels and low structural complexity (Schofield and Chapman 1999). Thus, the expansion of Nile perch from lakes into river systems may be limited by river mouths and valleys choked with papyrus. Second, Chapman et al. (1995) and Rosenberger (1997) found that some of the cichlids from Lake Victoria and Lake Nabugabo can tolerate extremely low levels of oxygen and that lacustrine cichlids endemic to Lake Victoria are more tolerant of hypoxia than ecologically similar species from Lake Tanganyika. This suggests that environments with low oxygen, such as papyrus swamps, are, or have been historically, an important habitat for fishes in Lake Victoria. Third, survey data in Lake Nabugabo, where native populations have declined or disappeared since the introduction of the Nile perch in 1960, indicate that many of the species thought to be rare or extinct in Nabugabo can still be found in wetland areas (lagoons, peripheral swamps, and papyrus choked rivers), where Nile perch are rare (Chapman et al. 1996a,b, Rosenberger and Chapman 1999). Many species found in the wetland lagoons and papyrus choked tributary areas of Lake Nabugabo are extremely tolerant of hypoxia (Rosenberger 1997, Chapman and Chapman 1998, Rosenberger and Chapman 1999). In a detailed study of the ecotonal areas of Lake Nabugabo, Chapman et al. (1996a) found several lines of evidence to suggest that wetlands protect some fishes from Nile perch predation including: a low abundance of Nile perch in wetland ecotones relative to open nearshore areas; a negative relationship between species richness among ecotones and dissolved oxygen; and a positive relationship between species richness among ecotones and structural complexity. In Lake Victoria, Balirwa (1998) found a much higher diversity and abundance of fish species in wetland ecotones than in the open water where Nile perch are prevalent. It is possible that wetlands in the Lake Victoria basin may serve as refugia from Nile perch predation, and that fishes tolerant of hypoxia may use the denser wetlands without adverse effects from the low oxygen conditions that occur there.

Dense emergent swamps in East Africa also provide important habitats for a variety of terrestrial animals; and aquatic and terrestrial habitats are closely interdependent in a number of contexts. One example is the creation and/or maintenance of aquatic habitat by large terrestrial animals. In Kibale National Park, Uganda, we have found that the forest elephants play an important role in the maintenance of valley swamp pools. Forest elephants periodically visit the papyrus swamps that choke the forest river valleys. Their wallowing activities create open pool habitat with slightly elevated levels of dissolved oxygen, and these pools are quickly invaded by swamp fishes, increasing local fish productivity (Chapman and Chapman, unpublished data). As the pools fill with dense swamp vegetation, catch per unit effort declines. Hippopotamus also create pools and channels as they move through fringing swamps to and from their terrestrial feedings grounds.

The dense interior of swamps is generally depauperate with respect to large mammals. There are exceptions; however, and one of the best known is the sitatunga *(Limnotragus spekei)*, an ungulate that is particularly well adapted to swamp life. Its hooves are elongated to spread its weight over the insecure swamp vegetation (Beadle 1981) where it spends much of the day (Beadle and Lind 1960). In contrast to the interior of dense emergent swamps, seasonally inundated swamp grasslands are very rich in wildlife, both in species and numbers (Howard-Wiliams and Gaudet 1985).

The same pattern occurs with respect to wetland avifauna, where swamp ecotones and seasonal wetlands are usually very rich in bird species and biomass; and deep central areas of the emergent swamps are more depauperate. Britton (1978) carried out a 16-month survey of a papyrus swamp fringing the shores of Lake Kanyaboli in Kenya. He documented 85 bird species of which eight were locally restricted to papyrus. However, compared to four other habitats in western Kenya (the undergrowth of Kakamega Forest, thicket at Ng-iya, seasonally inundated *Acacia seyal* savanna at Kadenge, and savanna at Ng-yia), the papyrus swamp had the least diverse and least speciose avifauna (Britton 1978). The most characteristic of the emergent swamp birds is the shoe-billed stork *(Balaeniceps rex)* which reaches over a meter in height with a distinctive and massive shoe-shaped bill. It inhabits large tracts of undisturbed papyrus and *Miscanthidium* swamp (1978). Other swamp papyrus swamp dwellers include species such as the black coucal *(Centropus toulou)*, the papyrus gonolek *(Laniarius mufumbiri)*, the greater swamp warbler *(Acrocephalus rufescens)*, the yellow swamp warbler *(Chloropeta gracilirostris)*, the Carruthers' cisticola *(Cistocola carruthersi)*, the papyrus canary *(Serinus koliensis)*, and the slender-billed weaver *(Ploceus pelzelni)*.

It is clear that wetlands harbor unique assemblages of plant and animal taxa, and that community structure and diversity varies among wetlands in East Africa. Ecotonal areas tend to be richer than the dense interior of permanent swamps. However, the permanent swamps may still be very important in the maintenance of faunal structure and diversity; and their degradation may precipitate declines in the diversity and richness of swamp taxa through loss of habitat, faunal mixing, and loss of refugia. In the following sections, we discuss patterns of wetland use and degradation in East Africa as well as current wetland policy perspectives.

Wetlands and Humans – Exploitation and Economic Considerations

In his chapter on "Economics and hydrological management of African floodplains", Adams (1996) summarizes the African plight very well. He states that Africa's rivers and floodplains have often been looked to as places that might provide resources to overcome the diverse and serious challenges of poverty and hunger in the continent. The World Bank Review (1990) identified a series of key economic problems in sub-Saharan Africa including, debt, weak agricultural growth, declining industrial output, poor export performance, declining institutions, and deteriorating socio-economic and developmental conditions. Economic growth in Africa has been overtaken by population growth. Agricultural production has only grown by 1.5-2% per year (Adams 1996), and the volume of agricultural export has declined. Food production per capita fell in the 1970s, and despite recovery in many places it remains depressed. An expanding and accelerating trend in East Africa is the exploitation of wetlands in an effort to meeting these increasing human resource needs.

Wetland Agriculture

Agricultural products like rice, sweet potatoes, yams, green vegetables, maize, cassava, beans, etc. provide the food and very often these days, income. Swamp farming (or residual moisture farming and relatively recently irrigated cropping) has been practiced in East Africa for some time now. Fertilizer uptake or use in the wetlands is poor, although many farmers are eager to obtain and use it. Irrigated cropping in the wetlands/swamps is quite different from the practice of residual soil moisture farming in the swamps; and the former is a long time tradition of dry season cultivation in the region. Grazing, particularly in seasonal wetlands, has been increasingly important over the past few decades with livestock including sheep, goats, and cattle.

In East Africa, particularly Kenya, wetlands have been used intensively or drained to improve agricultural production (Okeyo 1992). Wetland drainage usually takes place because population pressure and associated food scarcity have forced the development of new agricultural lands. Drainage is normally undertaken to improve agricultural productivity, and the areas targeted for this are marshes and swamps with soils suitable for agricultural production. In the context of agricultural activities, wetlands have a considerable economic importance in sub-Saharan Africa in general (Acreman and Hollis 1996, Adams 1996), and East Africa in particular. Wetlands provide food, other commodities, and incomes in both dry and wet years (in some sub-Saharan countries) and months (in others) for fairly large number of people involved in the agricultural activities.

In Africa, as much as 5% of the population, some 35 million people, depend wholly or partly on the fisheries sector for their livelihood; and wetland fishing is another basic element in the economy of many African wetlands, particularly seasonal floodplains and ecotonal wetlands (Bugenyi 1991, 1993). The life-cycle of many fish species is linked to seasonal flood regimes (Welcomme 1979) as well as to adjacent or ecotone wetlands which may as well act as refugia for many species (Balirwa 1998, Chapman et al. 1994, 1996a,b, Chapman and Chapman 1998, Olowo and Chapman 1996, Rosenberger and Chapman 1999, Schofield and Chapman 1999). Most of these fish species are fished from dug-out canoes with hooks, traps, gill-nets, weirs, and occasionally with beach seines or with spears when fish are in isolated pools (Bwathondi and Mwamsojo 1993). Inland fisheries in Africa produce over 1.5 million Mg of fish annually (Hails 1996). While many fish stocks are already approaching their exploitation limits, there is considerable potential to expand aquaculture or simply fish farming to improve on food security (FAO 1996) for individual families as well as contributing to the market economy. Prospects lie in wetland aquaculture rather than capture fisheries in the long run because the latter is soon reaching its limits. In Uganda, fish farming started in 1953, and peak development was realized in 1968 with 11,000 fish ponds covering 410 ha and yielding 800-900 Mg (=ton) of fish (NEMA 1999). Because of periods of insecurity and economic stagnation from 1970s to the 1980s, and because insufficient research had been done on aquaculture, fish farming declined drastically. However, with the establishment of research in aquaculture by the Fisheries Research Institute in Uganda (this is under the National Agricultural Research Organization, or NARO, which was established in 1992), activity has picked up again, as seen in the increasing aquaculture activities. This fish farming is carried out in floodplains and valley wetland areas. Fish farming in Uganda is expanding, with production figures from 180 Mg in 1994 from 3,000 ponds to 248 Mg in 1996 from 6,000 ponds (NEMA 1999).

What has not caught on yet in East Africa is the concept of "integrated agriculture-fish polyculture management" at fringe swamps which conserves the ecology, structure and environmental integrity of the wetlands, while providing food and cash crops. In Uganda where wetlands/swamps take up 17% of the land area, Denny and Turyatunga (1992) have suggested that fish ponds dug from the landward edge into the swamps, like "fingers" extending into the swamp would mimic the interface zone (which is rich in biota) and provide a sustainable fish production system whilst protecting the ecological dynamics of the swamp. This is still an open ended research question for East Africans, but one with much potential.

Irrigation has been generally slow to develop in East Africa despite the fact that irrigated land is more than twice as productive as rainfed cropland (FAO 1996). By 1996, only 16% of the world's croplands were irrigated, but those lands yield some 36% of the global harvest. In developing countries, irrigation increases yields for most crops by 100 to 400%. Irrigation also allows farmers to reap the economic benefits of growing higher-value cash crops. In the developing world, where about 20% of arable land is irrigated, the prevalence of irrigation varies widely within and among countries and crops. In Africa, where only about 10% of food production comes from irrigated lands, irrigation has been developed on 30% of 42.5 million ha with irrigation potential (FAO 1996). By 1990, Africa had only 14 million ha irrigated compared to 112 million ha in Asia and 98 million ha in the developed countries (FAO 1996), and a very small proportions of the area deemed to be suitable for irrigation is actually developed. There has been low rate of growth in irrigated areas rising by 148,000 ha a year between 1965 and 1974, and by 157,000 ha between 1974 and 1982 (FAO 1985). World Bank estimates that to achieve food security in Africa, food production must grow by 4% per year (World Bank 1990), and a similar rate of growth in export crops will be necessary to provide foreign exchange. Increased agricultural output can be achieved in two ways, by extending cultivation on to new lands or by intensifying productivity on existing land through technological change, particularly irrigation.

Other Economic Values of Wetlands

Wetland plants are a major source of materials on which a large number of people depend, particularly in the subsistence economies of tropical countries (Bacon 1996); and in addition to the variety of goods produced and services (Table 3), the quantities exploited are impressive. For example, in Uganda there are 22 species of edible wetland plants (Table 4) and 35 species of medicinal plants frequently used by people to cure ailments (Table 4) ranging from simple coughs and headaches, stomach troubles, and heart palpitations, to gonorrhea and impotence. There is, in Uganda, collaboration between local medicine practitioners and "modern" and "alternative" medicine institutions where research on local herbs is yielding good results that benefit all concerned parties.

Throughout the world, and in East Africa in particular, wetlands produce a variety of animals of commercial importance. On shores of Lake Victoria in Uganda and in naturalized aquaria and ponds in Mombasa, Kenya, crocodiles are reared for food, skins, sport, and tourism. There is a thriving ecotourism business based on Lakes Nakuru, Baringo and more recently Naivasha (Visser 1993). Other wetland-based tourist sites include the Kazinga Channel, which connects Lakes George and Edward; and small locally-run tourist sites, like the Bigodi wetland site in Kibale National Park and the Lwamunda Swamp of Lake Nabugabo. This expanding ecotourism industry has a multiplier effect on the economy through expenditure on transport, food, camping gear, hunting, and fishing gear, license fees, photographic supplies, visitor facilities, and related goods and services.

One other "goods and services" value of wetlands relates to their "consumption capacity" to act as a buffer and sponge off contaminants (e.g., wastewaters and rainwater runoff, Chale 1985, Bugenyi 1993). The technology of "wetland wastewater treatment" (Brix and Schierup 1989, Crisman et al. 1996) can and has been applied in developing countries in the treatment of the domestic and industrial wastewaters (Denny 1997) and is low cost in terms of investment and operation. The use of constructed wetlands is also useful in this context because of the competing functional values of natural wetlands such as biodiversity conservation, habitat and breeding sites for wildlife, hydrological, and hydraulic functions (Denny 1995). Natural wetlands can be compromised by the direct loading of wastewater. Therefore, the use of constructed wetlands specifically designed for the purpose of water quality improvement, is a viable alternative that is not subject to the competing demands of natural wetlands. In East Africa, research on constructed wetlands is still in its infancy, but it has been applied to water treatment problems in South Africa (Wood 1990) and Kenya (Nyakango 1997).

Table 3. Wetland plants and products and their socio-economic and functional importance (adapted from Bacon 1996 and Balirwa 1998).

Wetland plants, products, and functions	**Socio-economic and cultural importance**
Source of materials	
1. Construction materials including bricks, papyrus, timber	House building, thatching, matting, pottery, baskets, furniture, fencing, boats, floats, paper
2. Fuel	Firewood, charcoal, briquettes
3. Fishing materials; floats, fish poisons, fish traps and baskets	Needed for fishing and as a source of income
Food and beverages	Vegetables, fruits, roots, leaves
Medicines	Treatment of various ailments including: arthritis, rheumatism, skin rashes, hemorrhoids, snake bites tuberculosis
Agricultural, horticultural, and aquacultural products	Fodder, fish feeds, green manure, food crops insect repellants, ornamental pond plants, and fish for food and as a source of income
Water sources	Domestic, industrial and livestock consumption
Biodiversity conservation	Recreation, tourism, wildlife protection
Habitat for spawning, feeding and refuge for young fish	Fish as food and as a source of income
Nutrient and pollutant retention	Biofilters (nutrient strippers) and waste water treatment systems

Table 4. Some edible and medicinal plants from the wetlands of Uganda (data abridged from NEMA 1999).

Edible Plants		**Medicinal Plants**		
Plant Species	**Part Uses**	**Plant Species**	**Disease**	**Part Used**
Afromomum angustifolium	Fruits	*Aframomum sanguienum*	Intestinal Worms	Fruit and seeds
Afromomum sanguineum	Fruits	*Aspilia pluriseta*	Malaria	Root
Azima tetracantha	Fruits	*Cassia didymobotrya*	Tape Worms	Leaves
Balanites aegyptiaca	Fruits and leaves	*Costus afer*	Helminthiasis	Root
Commelina berghalensis	Leaves	*Cyperus digitatus*	Cough	Leaves
Cyperus esculentus	Tubers	*Cyperus distaus*	Restrosternal	Leaves
Diospyros mespiliformus	Fruits and seeds	*Cyperus papyrus*	Oedema	Leaves
Elaeis guineenis	Fruits and stems	*Ficus thonningii*	Influenza	Bark
Ficus natalensis	Fruits	*Flagellaria guineensis*	Chest Pain	Leaves
Ficus sycomorus	Fruits	*Hygrophia auriculata*	Palpitations	Leaves
Ficus thonningii	Fruits	*Justicia angleriana*	Abdominal	Leaves
Fucus sur	Fruits	*Malanthera scandens*	Malaria	Leaves
Ipomea aquatica	Leaves	*Mariscus squarrosus*	Male impotence	Whole plant
Nymphaea caerulea	Rhizomes	*Maytenus bushananii*	Headaches	Leaves
Nymphaea lotus	Rhizomes	*Momordica foetida*	Measles	Leaves
Phoenic reclinata	Fruits	*Mukia maderaspatensis*	Infertility	Root
Physallis micrantha	Fruits	*Phoenix reclinata*	Impotence	Leaves
Portulaca oleraceae	Leaves, stems, and seeds	*Pistia stratoites*	Cough	Whole plant
Raphia farinifera	Fruits	*Rhus vulgaris*	Rabies	Root
Syzygium guineense	Fruits	*Scandoxus multiflorus*	Leishmaniasis	Root
Tamarindus indica	Fruits	*Sesbania sesban*	Gonorrhoea	Roots
Typha domingensis	Roots	*Symphonia globulifera*	Cough	Root/stem

Wetland Degradation in East Africa

Many human exploitation activities in East African wetlands are sustainable; however, an expanding and accelerating trend is large-scale drainage and conversion to large tracts of agricultural land. Wetlands are also threatened by irrigation schemes, improved transport along waterways, industrial pollution, and mining extracts. On a more local scale, overexploitation occurs in the context of harvesting resources like clay for bricks, building, and pottery, and papyrus for thatching houses and making carpets/mats. Small wetlands are also degraded by repeated gardening or cultivation or clearing fresh land for more areas to grow produce, over grazing of cattle in the wetlands, and small-scale burning by individual farmers.

Papyrus is the fastest growing herb in the world, and there is clearly the potential for sustainable harvest on a local scale. However, continuous cropping of papyrus could have very serious ecological effects, among which is the loss of large quantities of nutrients removed with the harvested papyrus biomass that would otherwise be recycled (Muthuri et al. 1989). The interface of papyrus swamps and the open water is often a chemically rich habitat that harbors a high diversity and biomass of aquatic organisms. One reason for productive ecotones is that what goes into papyrus swamps must eventually come out again, and it does so at the ecotone. During the dry season, papyrus stores nutrients that are released in the sludge fan during periodic flushing in wetter periods (Thompson 1976). Large-scale conversion of papyrus may impact adjacent systems through loss of nutrients and loss of nutrient flow into lower gradient habitats.

Wetland conversion may also contribute to a decline of faunal diversity through loss of habitat, destruction of refugia, and faunal mixing. For example, permanent and seasonal swamps are important year round habitats for some indigenous fishes and birds and seasonal feeding and breeding grounds for many species. Loss of wetlands means loss of habitat for these species, many of which are important to local fisheries and ecotourism. Of particular importance for fishes are the marginal wetlands or ecotones where the emergent wetland meets the open waters of lakes and rivers. Here oxygen levels are higher because of interaction with the open waters of the river or lake, and fish do not encounter the respiratory challenges imposed by the dense swamp interior. Loss of wetland may contribute to loss of refugia for prey species from swamp intolerant predators (Chapman et al. 1996a,b, Rosenberger and Chapman 1999, Schofield and Chapman 1999). As noted above, this is particularly critical in the Lake Victoria basin where wetlands serve as refugia for some indigenous fishes from the introduced Nile perch.

Swamp channelization has been adopted as a means of creating agricultural land and improving transport through swamps. In the steeper valleys, the straight, cleared channels reduce hydraulic resistance and decrease the water-holding capacity of the wetland, which encourages fast removal and more dramatic seasonal flooding (Denny and Turyatunga 1992). In addition, there is the question as to whether channelization will remove barriers among populations whose genetic integrity was maintained by swampy divides or facilitate the expansion of introduced species whose dispersal was limited by dense swamps.

Almost every major river in Africa has experienced construction of man-made lakes. In Uganda, the Owen Falls Dam was completed in 1954-55. It has now been extended by building another one on the side of the downstream River Nile, and it is near completion. There are plans to build two more dams downstream, one at or near the Bujagali Falls and another at Karuma Falls further downstream. These dams have many socio-economic and other ecological impacts. With respect to wetlands, one major impact downstream is regulation of flow preventing or decreasing inundation of downstream floodplains. For example, the construction of the Bakolori Dam on the River Sokoto reduced the magnitude of the wet season floods which supported an extensive wetland floodplain agricultural system and a fishery on which an estimated 50,000 people depended (Adams 1985). There was a substantial decline in both wet and dry season fishing; fishing virtually ceased in a number of villages or became confined to the wet season riverbed (Adams 1985).

The invasion of water hyacinth has also been a major perturbation to the wetland ecotonal areas of infested lakes. Hyacinth has a number of potential negative effects on lakes by reducing light penetration, limiting water-column mixing, and increasing detrital inputs. By shading out the sun, it is likely to provide concealment of ambush predators that feed on indigenous species. Futher, it seems to shade out other forms of bottom-dwelling vegetation that often is located just outside of the papyrus beds (such as *Ceratophyllum*). Large floating mats has posed navigational hazards, and blocked fish landings.

Management and control of water hyacinth and other weeds have been a problem in East Africa. One needs control methods that are environmentally friendly. Uganda has relied, successfully, on three methods: physical removal, mechanical removal, and biological control. The third method at present appears to be the most environmentally friendly, although it took sometime before it was effective. Biological control involves the use of beetles that specifically feed on water hyacinth. At this point, a control program that uses all three of these methods is recommended. However, one of the best ways to fight the weed is to control the courses of the nutrients into the lake (Twongo et al. 1995, Twongo and Balirwa 1996) which will decrease its proliferation. Recently, there has been a dramatic decline in the abundance of water hyacinth in Lake Victoria; however the nutrient enrichment of the system and related water bodies provides potential for the proliferation of water hyacinth if regionally coordinated control measures are not in place (T. Twongo, pers. comm.).

Policies for the Wise Use and Conservation of Wetlands

Humans have been linked with wetlands for millions of years, but their importance has changed with time. Back in the swampy environments of the Carboniferous Period, some 350 million years ago, wetlands produced and preserved many of the fossil fuels (coal and oil) upon which we depend today (Barbier et al. 1997). More recently, wetlands along some of the major rivers of the world including the Tigris, Euphrates, Niger, Nile, Indus, and Mekong, nurtured the great civilizations of history. These wetlands provided fish, drinking water, pasture land and transport, and were part of the cultural history of early people, being a central element of mythology, art, and religion.

In recent years there has been increasing awareness of the fact that natural wetlands provide free of charge many valuable functions (e.g., flood alleviation, ground water recharge, retention and regulation of pollutants and water plant nutrients); products (e.g., fish, fuelwood, timber, crafts, herbal medicines, rich sediments used for agriculture in the flood plains); refugia for fish and other fauna; and other attributes (biodiversity, aesthetic beauty for tourists, cultural heritage, and archeology). The world's wetlands are now recognized as some of the most important and productive ecosystems on Earth (Mitsch and Gosselink 1993), and it is recognized that wetland conservation and management are shared responsibility for all concerned. However, the development of aquatic conservation as a discipline has clearly lagged behind terrestrial conservation, both temporally and intellectually. It was not until the 1970s that wetland protection received any appreciable attention globally. Clearly, the most important international combined action for wetland protection is the "Convention on Wetlands of International Importance", commonly referred to as the "Ramsar Convention" that it resulted from an International Conference in Ramsar, Iran, in 1971. To protect wetlands critical for internationally migratory fauna, this treaty requires that signatory nations promote the wise use of all wetlands and identify candidates for inclusion in the "List of Wetlands of International Importance" based on their international significance in terms of ecology, botany, zoology, limnology, or hydrology (Navid 1989). Thus, the Convention serves as an intergovernmental treaty that provides a framework for international cooperation for the conservation of wetland habitats. The "wise use of wetlands" as defined by the Ramsar Convention Bureau (1996), is "their sustainable use/utilization for the benefit of mankind in a way compatible with the maintenance of the natural properties of the ecosystem" (Smart 1996). In the African Region, which includes the mainland continent and the island states of Cape Verde, Comoros, Madagascar, Mauritius, Sao Tome and Principe, and Seychelles, making up a total of 53 States, 23 are contracting States to the Ramsar Convention (Kabii 1996).

The overall goal of setting policies, by the East African governments, is to promote the wise use and conservation of the East African wetlands so that their ecological and socio-economic functions are sustained for the present and future well being of the people. The Uganda Government (1994) has already gone through all the steps and formed a policy that governs the way wetlands should be looked after by the public.

The policies on wetlands in East Africa should aim at establishment of principles by which wetland resources can be sustainably used while maintaining their biological diversity. The policy proposals are centered on the fact that:

1. There will be no drainage of wetlands unless more important environmental management requirements supercede,
2. Wetlands may be used in such a way that they do not lose their traditional benefits presently obtained from them,
3. Any decision to use wetlands must consider the requirements of all other users.

As for wetland legislation and institutional arrangements, there is always a need for governments to retain control over wetlands, either directly or through the issuing of permits, if resource-use is to be optimized for the benefit of the stakeholder. A strong government institutional arrangement and a sectoral national legislation is needed to reverse the high rate of degradation and ensure sustainable management of the wetland resources. Although there are sectoral laws that govern some aspects of wetlands such as water or land or prevention of pollution, there are no comprehensive laws for management of wetlands as an ecological entity in East Africa (and in Uganda until 1994).

It is recognized and appreciated by the Government that wetland goods and services are trans-boundary resources and by no means the exclusive preserve of the landowner, local community, district, or nation. Uganda's wetlands are a key factor in the wetland/water resources of the neighboring countries in general and Egypt and Sudan in particular. They also support significant numbers of migratory birds from Eurasia and southern Africa. As a result of the importance that is accredited to these wetlands, some of them have been designated "Ramsar Sites", for example Lake George (Department of Environmental Protection, 1995). There are others in progress including: the Sango Bay Wetland area, and the Lake Nabugabo Wetland, both in the Lake Victoria basin in Uganda. Kenya ratified the Ramsar convention in June 1990 and thereafter designated Lake Nakuru National Park as a Ramsar site (Ole Nkako 1993).

Although the goal for protected wetlands should continue to be conservation of endangered and fragile sites, greater efforts should be focused on wetlands outside the protected areas, and new management strategies formulated which incorporate the stakeholders (Kabii 1996). The Government of Uganda, as we have seen above, recently launched such a policy for the conservation of its wetland resources. This was the first of its kind in Africa to have been formulated in accordance with the recommendation from the Ramsar Convention. It encompasses wetlands in protected and non-protected areas and offers the best example in Africa of a strong political will to conserve wetlands and their biodiversity (Kabii 1996).

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