# Incorporating Wetlands and Their Ecotones into the Conservation and Management of Freshwater Ecosystems of Africa

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Wetlands are among the world's most productive environments, providing the water and primary productivity upon which countless species of plants and animals depend. They are often characterized by high concentrations of birds, mammals, reptiles, amphibians, fish, and invertebrate species. In addition, wetlands are critical to the maintenance of adjacent ecosystems through nutrient flushing, effects on microclimates, and water-holding capacity. Wetlands are also an important source of products vital to people living in their vicinity. They use seasonal swamps as grazing lands; harvest swamp plants for a variety of purposes including use as materials for roofing, furniture, and fish traps; and exploit wetlands for fisheries and aquaculture.

Wetlands of Africa can be divided into two 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 seasonal wetlands are restricted to land that is only periodically inundated. Detailed inventories on the extent and type of wetlands are incomplete because of the lack of survey data, but it is estimated that there are 85,000 km² of permanent swamp and 400,000 km² of seasonally inundated swamps on the African continent (Beadle and Lind 1960, Beadle 1981, Thompson and Hamilton 1983). In the central basin of the Congo River alone, over 80,000 km² of forest is permanently or seasonally inundated. Although the database for Africa is the least complete worldwide, conservatively Africa's wetlands accounts for 17% of total wetland area in the subtropics and tropics (Crisman and Streever 1996).

African wetlands span an impressive array of types, from marshes (herbaceous plant dominance) to swamps (woody plant dominance), and include some of the largest systems in the world: the Sudd of the Nile River in Sudan, Kafue Flats in Zambia, and the Okavango Delta of Botswana (Denny 1985, 1993; Murray-Hudson and Crisman, chapter 19). As well as these extensive systems, there are many smaller wetlands in river valleys or fringing the edges of lakes.

The emergent sedge papyrus (Cyperus papyrus) dominates much of the 85,000 km² 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). For example, 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 km² in the contiguous Yala Swamp of lakes Kanyaboli and Saru (Britton 1978). Within Uganda, the most extensive 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). Swamps dominated by papyrus are the most common type of swamp in central and eastern tropical Africa and extend down into the Okavango region of southern Africa.

Papyrus is the largest sedge in the world, normally attaining heights of 3-4 m and typically constituting 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 among emergent wetland vegetation in having C<sub>4</sub> photosynthesis (Jones and Milburn 1978, Jones and Muthuri 1997). Its establishment requires an almost continuously waterlogged substrate. The dense canopy of papyrus limits mixing of the water column by both wind and light penetration, intercepting over 90% of the incoming radiation (Thompson et al. 1979, Jones and Muthuri 1997). In combination with high rates of organic decomposition, these conditions result in extremely low oxygen levels in the water beneath the swamp canopy and create a unique habitat for aquatic organisms (Carter 1955, Beadle and Lind 1960, Chapman and Liem 1995, Chapman et al. 1998). One of the mysteries of plant geography is the scarcity of papyrus west of Lake Chad, despite many swampy areas that appear suitable for papyrus; it is reported only at small isolated localities (Beadle 1981).

The next most common swamp plant in East Africa probably is *Miscanthidium violaceum*. *Miscanthidium* swamps are typical of low-nutrient, rather acidic sites, which seem to be too acidic for other reeds and flood-

plain grasses (Beadle and Lind 1960). These wetlands are usually dry enough to support *Sphagnum* spp. and other fen bryophytes (Thompson and Hamilton 1983), but, in general, sphagnum swamps are much rarer in tropical Africa than in cold temperate areas. Seasonally inundated swamps with a tree or palm overstory are very common in the Congo basin; dominant plants include *Mitragyna* sp., *Ficus congensis*, *Raphia farinifera*, *Phoenix reclinata*, *Uapaca* sp.). These swamp forests support a rich and unique fauna.

# **Ecosystems or Ecotones**

An ecosystem is defined both by its distinctive structural components (biota) and its functional processes (interactions among and between biota and physical and chemical, abiotic, factors). It is convenient to place distinct geographical boundaries to ecosystems variously identified as forests, streams, lakes, and so on. Boundaries between adjacent ecosystems are termed ecotones, areas of rapid transition from one system to the other, both in species composition and system function. Because subdisciplines of ecology have developed with a distinct historical bias, classifying wetlands as ecosystems or ecotones is somewhat arbitrary. Limnology (the study of continental bodies of water) was dominated in its early development by zoologists interested in pelagic and benthic animal communities. The vegetated bottom of a lake from the shoreline to the depth limit of plant growth is called the littoral zone (Wetzel 1983). With a bias for open water, limnologists came to think of wetlands as landward extensions of aquatic plant communities. At the other end of the spectrum, terrestrial botanists viewed wetlands as waterward extensions of terrestrial plant communities. Thought of as transitional between land and lake, most wetlands were considered ecotones, although systems such as the Everglades in Florida or the Okavango of southern Africa, because of their vast extent, are regarded as distinct ecosystems (Holland et al. 1990).

In considerations of the conservation and management issue, wetland size is critical in assessing whether an isolated wetland within the land-scape might be functioning more as an ecotone or an ecosystem. It is entirely possible to find wetlands where the width of the ecotonal boundary from all directions constitutes its entire surface area, and thus the system represents an ecotonal wetland. Wetlands of sufficient size to exceed the innermost extent of the ecotone develop an inner core area where little terrestrially associated biotic and abiotic inputs reach; thus, they function more as ecosystems. Once the ability of the ecotone to process

biotic and abiotic inputs from the land or open water is exceeded, the integrity of the core is compromised, and it is incorporated as part of the ecotone.

### Terrestrial-Wetland Ecotones

Within ecotonal wetlands, it is important to differentiate between the ecotone that starts on the land and extends into the wetland (terrestrial-wetland ecotone) and the ecotone that starts in the open-water system (e.g., lake) and extends into the wetland (open water-wetland ecotone). Terrestrial-wetland ecotones are often extremely dynamic and productive (Wetzel 1990, Gopal 1994) and process sediments and nutrients exported from the watershed. These interactions, however, are not strictly unidirectional. Nutrients and organic matter deposited on land can be cycled and exported to the wetland during high-water periods (Calzada-Bujak et al. 2001), stimulating aquatic productivity; upon recession of water, decomposition of this primary production can recycle back to stimulate growth of terrestrial vegetation and provide an important food source for grazers.

Whereas the outermost extent of the terrestrial-wetland ecotone can usually be defined on structural elements, including plant community composition and soil development, the innermost extent of the ecotone is defined mostly by system functional properties. The influence of nutrients and sediments delivered to a wetland should diminish progressively with increased distance into the wetland as sediments are deposited and nutrients are used for plant production and ultimately are consumed by grazers or deposited as detritus. The innermost point of the ecotone is defined by complete incorporation of materials imported from the watershed as well as how deep into the wetland terrestrial fauna can penetrate. Although defining the inner boundary of the ecotone functionally may be possible, considering structural elements including plant community structure may be of limited value. The width of the terrestrial-wetland ecotone is clearly a reflection of seasonal and interannual fluctuations in water level, and the landscapes with the least topographic relief and the greatest hydrological fluctuation have the widest ecotonal areas.

# Open Water-Wetland Ecotones

Historical bias in how wetlands are viewed is evident in considerations of the open water-wetland ecotone. Many wetland ecologists, reflecting the historical bias of the field set by terrestrial botanists, use the term fringing wetland to describe this area, whereas limnologists, on the basis of an open-water and zoological bias, refer to it as the littoral zone. Whereas the



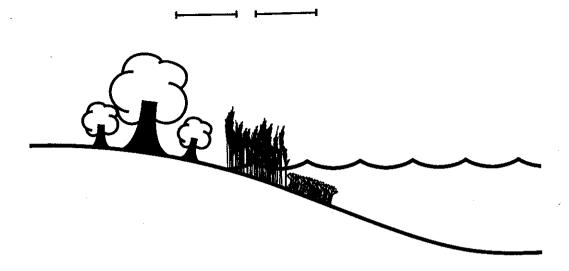


Fig. 10.1. Landscape cross section showing the terrestrial-wetland ecotone, core wetland, and open water-wetland ecotone. Bars represent the length of the ecotone, first the land-to-vegetation ecotone and then the submergent-open water ecotone.

former term primarily reflects plant community structure, the latter stresses both structure and function. Littoral zones are known for their ability to transform watershed-derived inputs of nutrients into organic compounds via high primary productivity, which can be stored over a short term in the zone and eventually exported to open water as dissolved and particulate carbon fractions (Wetzel 1983). Littoral zones of African lakes, as do littoral zones worldwide, exert a strong controlling influence over food webs of open water (Howard-Williams and Lenton 1975), and the community structure and production of pelagic fisheries (Bugenyi 1991), in part, rely on the littoral zone for breeding sites and refugia from predation.

The open water-wetland ecotone is dynamic in its extent and is dictated by the horizontal distance to which waves from open water penetrate into the wetland (this principle assumes that there is an inner core wetland lacking major interactions with the open water; Figure 10.1). The waves bring dissolved oxygen and remove organic fractions derived from primary production and dissolved nutrients. Major storm events in the watershed can momentarily obliterate this structure by passing large volumes of water unidirectionally through the wetland without sufficient residence time to permit a reduction in either nutrients or sediments. The width of the open water-wetland ecotone, then, is usually difficult to define on the basis of plant structure alone because of the dynamics of its functional aspects.

# Conservation and Management of African Wetlands

African wetlands are disappearing at an alarming rate. Although only 20% of African countries have performed an assessment, conservatively, the loss of original wetland area in Africa has been estimated at approximately 52% (Crisman and Streever 1996). Much of this loss reflects a conversion of wetlands to agricultural land, and although drainage of systems at the village level is tantamount to permanent loss of both wetland structure and function, much of the loss of large wetlands results from a conversion to rice production. Although rice production causes the loss of wetland structure, many of the wetland functions can still be realized.

Wetlands are essential throughout the tropics and in Africa in particular (Bacon 1996). Rural populations traditionally have relied on wetlands for potable water, fish, construction material for dwellings and furnishings, and seasonal grazing of cattle (Crisman and Streever 1996). In Uganda, at least 35 species of wetland plants are used in widely practiced traditional medicine, and a collaborative relationship is developing with medical institutions for both research and utilization (Chapman et al. 2001). Recently, however, this seemingly sustainable relationship has been disrupted in direct response to rapidly expanding human populations. Village women have begun encroaching into wetland margins for the development of small garden plots for production of vegetables in response to an expanding cash economy and the development of regional markets. Because of traditional constraints on land tenure, inherited land parcels have become insufficient to support a family. In such societies, young males are faced with two choices: abandon the land and move to the city or search for lands considered marginal for agricultural production. Unfortunately, many such lands are wetlands. Finally, in response to dwindling availability of construction-grade timber and fuelwood due to progressive land clearance, people are mining wetlands for clay to produce bricks.

# Conservation and Management of Terrestrial-Wetland Ecotones

The terrestrial-wetland ecotone is affected by five broad categories of human disturbance in Africa: mining, wetland resource extraction, deforestation, agriculture, and urbanization.

On average, sub-Saharan countries allocate 58% of their gross national product to their foreign debt (Stuart et al. 1990). This allocation places strong pressures on governments to raise foreign currency, and one means of doing so is through mining of metals. Some current operations have effective environmental safeguards; others do not. For example, leaching from waste piles surrounding a mining operation near Lake George, Uganda, is seriously affecting the lake's wetland (Denny et al. 1995). The impacts of the newly established mining operation at this site are unknown.

Deforestation for timber, fuelwood, and charcoal and to increase agricultural land is rampant throughout the tropics (Chapman and Chapman 1996; Chapman and Chapman, chapter 11). Food and Agriculture Organization (FAO) statistics indicate that forest loss between 1980 and 1995 was 10.5% for Africa, 9.7% for Latin America and the Caribbean, and 6.4% for Asia and Oceania (FAO 1999). Tropical countries are losing 127,300 km² of forest annually: an area greater than Mississippi (122,335 km²) or just smaller than Greece (131,985 km²). Some African countries have the highest losses; for example, the Democratic Republic of Congo converts 7,400 km<sup>2</sup> of forest annually. According to the FAO definition, selective logging is not considered deforestation because it does not decrease forest cover to less than 10% of its original level. Yet, it is clear that selective-logging operations can dramatically affect aquatic systems (see Chapman and Chapman, chapter 11). Currently, it is estimated that between 50,000 and 60,000 km2 of tropical forests are logged each year, approximately a third of the area that is completely deforested (FAO 1990). This represents an area slightly smaller than West Virginia (62,470 km2). The majority of West African forests have already been logged, and with the depletion of the resources in these countries, logging companies are turning to the last remaining large forest blocks in Central Africa.

The importance of wetlands, particularly ecotonal wetlands, to the quality of open water is not well understood for African water, but it is clear that water quality is declining in many lakes associated with large-scale land conversion of the lakeshore. Deforestation and logging increase sediment erosion and reduce watershed storage of water, thereby raising water-level maxima in wetlands and increasing the disparity and decreasing temporal fluctuations between minimum and maximum water levels (see Chapman and Chapman, chapter 11). These effects result in expansion of the terrestrial-wetland ecotone and increase delivery of nutrients and contaminants into the wetland from human activities. Small-scale

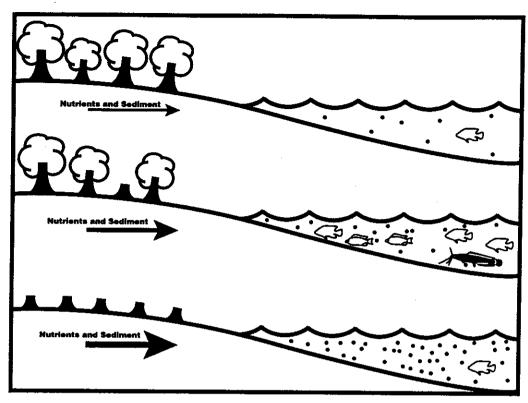


Fig. 10.2. Development of cultural eutrophication in African lakes through progressive watershed deforestation and increased nutrient loading.

clearance of forested watersheds reduces the short-term storage potential of the system, enhancing the nutrient discharge to the adjacent lake and promoting algal productivity, the base of the food web. The end result is that the local fisheries can be progressively stimulated, and it is unlikely that the local population would perceive any negative changes in the water quality of the system until the watershed had undergone radical forest devastation (Figure 10.2). As seen for watersheds throughout Africa, elimination of native forest cover and replacement by dense human occupation results in a noticeable decline in water quality associated with both nutrients from soil release and human wastes and increased delivery of inorganic sediments to the lake. The end result is problem blooms of bluegreen algae and occasional fish kills. Understanding the role played by wetland ecotones and ecosystems in trapping and transforming nutrients and sediments from the watershed is key to the development of long-term management plans for African lakes and streams.

Wetlands are of major importance in sub-Saharan African agriculture (Acreman and Hollis 1996, Adams 1996). Nutrient loading to wetlands,

however, is markedly increased from agricultural operations (Mitsch and Gosselink 1993). Increasingly, pressures from expanding human populations and rigid land-tenure systems are forcing African agriculture beyond the ecotone and into wetland interiors. The impact of such activities on wetlands is a matter of scale—whether the operation is at the village or regional level and whether the altered wetland is small or large. Families and villages have drained small wetlands throughout East Africa for the production of bananas, taro, and yams (Okeyo 1992). Individuals using hand tools can easily drain such systems by constructing ditches through the system's interior. Although wetlands are easily drained, rapid oxidation of the highly organic wetland soil restricts agricultural production within 5 years of drainage, and such areas often fall into disrepair. Such drained wetlands no longer efficiently filter the water flowing through them, and their inability to filter the water can markedly affect water quality downstream. A preliminary assessment of limnological data from Lake Saka in western Uganda suggests that eutrophication was accelerated when local villagers drained a fringing wetland (Crisman et al. 2002).

Although still in their infancy, some large-scale agricultural operations, especially rice production, have been developed in the terrestrial-wetland ecotonal area. Although wetland structure, especially that of the plant community, has been radically altered in such operations, many wetland functions (sediment trapping, nutrient uptake, soil formation, water storage) are still operative. Such agricultural systems have the potential to serve as environmental buffers for both watershed discharges and further encroachment into wetland core areas. Whether retention of wetland function at the expense of wetland structure is viewed positively depends on the purpose for which the wetland is being managed. Arinaitwe (1993) reported lower species richness of Afrotropical birds in the rice scheme of eastern Uganda than in the adjacent papyrus swamp. The loss of habitat structure in the rice fields benefited large wading birds and ducks but was considered detrimental to other wetland bird species. The impact of ecotonal agriculture is poorly studied and presently must be viewed on a case-by-case basis, balancing alteration in system structure against the functional needs of the wetland.

Since the end of the nineteenth century, when approximately 95% of the African population was rural, the continent has witnessed progressive urbanization (Grove 1989). The rapid expansion of urban populations is partially in response to a lack of availability of arable land, environmental degradation, security issues, and the desire for improvement in economic status. Many African cities lack the infrastructure and the funds to effec-

tively treat solid wastes and sewage generated by the population influx. Wetlands often become the repositories of both.

Massive point-source loading of raw sewage from urban areas can quickly disrupt the ability of a wetland to assimilate nutrients; this disruption leads to increased loading on adjacent lakes and promotion of eutrophication. If loading does not exceed the ability of a wetland to accommodate it, such systems can serve as natural treatment options for domestic wastewaters (Mitsch and Gosselink 1993). Many cities in the Lake Victoria basin, especially in Uganda, are built adjacent to fringing or valley swamps of papyrus adjacent to the lake. A slowly emerging literature suggests that such swamps are a viable option for effective treatment of both raw sewage (Gaudet 1978, Bugenyi 1993, Otto 1998) and primary-treated sewage (Chale 1985). Use of natural wetlands in the tropics for multiple purposes, including the treatment of domestic wastewaters and associated product development based on the plants treating the wastes, can be a valuable tool for the conservation of wetlands (Crisman et al. 1996). If economic benefit is infused as part of the treatment process, the local community has a vested interest in ensuring proper operation of the wetland as a waste-processing system.

Constructed wetlands, widely used throughout the developed world (Kadlec and Knight 1996), provide a controlled environment to maximize waste treatment and serve important hydrological and conservation functions (Denny 1997). Constructed wetlands have been used for water treatment in South Africa (Wood 1990) and Kenya (Nyakango 1997). As does large-scale rice agriculture, such systems can serve as effective buffers against further degradation of core wetlands by fixing the boundary of the terrestrial-wetland ecotone and potentially enhancing wetland functions through intensive management.

Although rice agriculture and constructed wetlands might serve as important buffers for core wetlands, other human activities can extend the ectonal area deep into the wetland. Building roads through wetlands expands the terrestrial-wetland ecotone, and, although the interaction zone is linear and narrow, it encourages colonization by invasive species and nonsustainable extractive activities by humans (Crisman 2000). Increasingly, canals are being dug through papyrus swamps in Africa to facilitate watershed drainage and human transportation. Such canals disrupt the ability of the wetland to treat nutrients and remove sediments, and they alter the water flow. Construction on the largest scale of this type in Africa, the Jonglei Canal, was started in the 1980s to enhance boat traffic to the upper Nile and to enhance water delivery to northern Sudan through

reduction in losses in the wetland via evapotranspiration. Now that the potential environmental and conservation damage associated with completion of this project have been recognized, its status is uncertain.

To meet local and export demands for fish, fish aquaculture is being developed in floodplains and wetlands throughout Africa (Chapman et al. 2001). For example, production in Uganda expanded from 180 tonnes from 3,000 ponds in 1994 to 248 tonnes from 6,000 ponds in 1996 (NEMA 1999). Denny and Turyatunga (1992) suggested that constructing fish ponds from the land and extending them like fingers into a swamp would provide many of the functional aspects of the ecotone and protect the core swamp area, while providing a valuable economic return to local economies. The assessment of such systems is scant, and it is critical to determine if such constructed ponds will adversely affect the integrity of the core wetland.

From a management perspective, the most difficult question is how to define the outermost extent of the terrestrial-wetland ecotone. In the face of expanding human populations and increased pressure for maximizing agricultural production, it is unlikely that any portion of the landscape comprising more than the 10-year floodplain will be afforded special status as an ecotonal protection area. To date, perhaps the most complicated situation for developing sound management plans for terrestrial ecotonal areas in Africa is the one in Lake Chad (Kindler et al. 1990). Chad has arguably the widest ecotonal area of any African freshwater ecosystem. In addition to the conflicting interests from expanding human populations, irrigation schemes, fisheries, and conservation is the fact that implementation of any plan requires agreement among the nations that share the wetland.

# Conservation and Management of Open Water-Wetland Ecotones

Open water-wetland ecotones serve as extremely important nurseries and refugia for small fishes from larger predators and thus can contribute significantly to both biodiversity and fisheries production. Nowhere is this benefit better exemplified than in the Lake Victoria basin. The species flock of endemic haplochromine cichlids (more than 600 species) in the Lake Victoria basin of East Africa is one of the most recent, diverse, and extensive radiations of vertebrate taxa anywhere in the world (Greenwood 1980, Kaufman et al. 1997). The predatory Nile perch (*Lates niloticus*) was introduced into Lake Victoria from lakes Albert and Turkana during the late 1950s and 1960s to convert low-value haplochromines into higher value and more easily captured and preserved fish flesh (Fryer

1960, Hamblyn 1961, Ligtvoet et al. 1995). The dramatic increase in Nile perch in the 1980s in Lake Victoria was followed by a drastic decline in populations of several indigenous species (Ogutu-Ohwayo 1990; Kaufman 1992; Witte et al. 1992a, 1992b; Kaufman et al. 1997). Most notable was the disappearance of over 50% of the endemic haplochromine cichlids from Lake Victoria (Kaufman 1992, Witte et al. 1992a, Kaufman and Ochumba 1993). The introduced Nile perch population is proposed to have been a major contributor to the mass extinction; the decline in endemic haplochromines was almost reciprocal with the increase in Nile perch (Ogutu-Ohwayo 1990; Kaufman 1992; Witte et al. 1992a, 1992b).

The tremendous loss of biodiversity led scientists and managers to try to identify faunal refugia, habitats where indigenous fishes might hide from the introduced predator. It is now known that wetlands protect some prey from Nile perch predation; they serve as both structural and low-oxygen refugia for prey that can tolerate wetland conditions, and they serve as barriers to the dispersal of Nile perch (Chapman et al. 1996a, 1996b; Kaufman et al. 1997; Balirwa 1998; Chapman and Chapman 1998; Rosenberger and Chapman 1999; Schofield and Chapman 1999). Some haplochromine cichlids and indigenous noncichlids have a relatively high tolerance to low oxygen (Chapman et al. 1995, Chapman and Chapman 1998, Rosenberger and Chapman 2000), whereas Nile perch have a relatively low tolerance of this condition (Schofield and Chapman 2000). This difference helps to explain why some indigenous species persist in wetland refugia and why Nile perch are unable to exploit these habitats.

The ecotonal wetlands are particularly important refugia because interaction with the main lake waters increases dissolved oxygen content and reduces carbon dioxide levels (Balirwa 1998, Rosenberger and Chapman 1999). These marginal wetlands still contain most functional elements required by the indigenous fauna and a much higher diversity than in other areas currently lumped into the inshore zone. Areas deep in the fringing swamp are less rich because the dense fringing swamps act much as a biological filter, limiting colonization and survival to species that can tolerate the extreme conditions therein. However, even areas within the fringing swamp are important in the maintenance of a subset of the basin fauna (Figure 10.3) (Chapman et al. 1996b, Balirwa 1998, Chapman and Chapman 1998). These findings have led to increased concern for maintaining the integrity of wetlands, particularly of open water-wetland ecotones in key areas within the basin.

One threat to open water-wetland ecotones in Africa is the introduc-

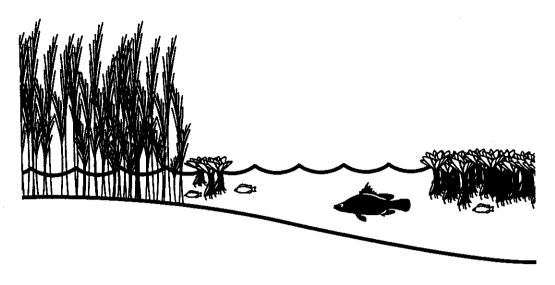


Fig. 10.3. Cross section of the current Lake Victoria open water-wetland ecotone, including the invasive species water hyacinth and Nile perch.

tion of nonindigenous plant species that have the potential to change both the structure and function of the ecotone. In East Africa, the free-floating macrophyte water hyacinth (Eichhornia crassipes), native to central Brazil, appeared in Lake Naivasha in Kenya in 1982 and in Lake Kyoga in Uganda in 1988. It was first reported in the Ugandan waters of Lake Victoria in 1989 and in Tanzanian waters in 1990 (Twongo et al. 1995). The weed became firmly established in lakes Victoria, Naivasha, Kyoga, and Albert and along the River Nile. Water hyacinth has two distinct forms, stationary fringes along shorelines and mobile mats. In Lake Victoria, the weed had established at an average fringe width of 10–15 m by 1995, but more recently it has disappeared almost completely over most of its previous range (Twongo 2001). Incorporation of water hyacinth as a component of the plant community likely changed not only the structure but also the function of the open water-wetland ecotone.

Water hyacinth invasion into Lake Victoria had significant socioeconomic and environmental impacts, including disruption of transport, reduction of water supply, reduction of water quality for humans and livestock, and spread of water-borne diseases (Twongo 1996, 2001). The impact of the introduction of water hyacinth on biodiversity is controversial, but the plant's introduction may have been beneficial for some species, especially for hypoxia-tolerant fishes such as the lungfish (*Protopterus aethiopicus* and *Clarias gariepinis*). In general, however, water

hyacinth seems to reduce the diversity of plankton, floating and submerged macrophytes, macroinvertebrates, and fish (Twongo et al. 1995). The current state of dramatic remission of the water hyacinth infestation may be permanent; however, the nutrient enrichment of Lake Victoria and related water bodies provides potential for the proliferation of water hyacinth if regionally coordinated control measures are not in place (Twongo 2001).

### Conservation and Management of Wetland Ecosystems

By the nature of their size, wetlands that are considered ecosystems require major disruptions before their structure or function will change. However, a number of wetland ecosystems are threatened by major water-diversion projects that are designed either to meet the growing need for scarce water or to provide hydroelectric power.

African examples of large-scale water-diversion projects are not difficult to find. In Namibia, an ambitious and controversial scheme is under way for transferring water in an open canal over a distance of about 800 km from the Okavango River on the northern border to the capital city of Windhoek (see Day, chapter 3, and Brown and Buenfil, chapter 18). The ecological impacts of this transfer on the Okavongo wetland system are largely unknown (chapter 18). Similarly, the construction of hydroelectric dams often dramatically changes water flow regimes, either drowning wetlands or withholding sediments that would have ended up in the wetlands. The construction of hydroelectric dams on the White Nile in Uganda (see Kaufman, chapter 12) and on the Blue Nile (see Zinabu, chapter 6) will affect wetlands in both areas.

#### Conclusions

In Africa, wetlands function as both ecotones and ecosystems. Each has distinct functions that are often difficult to recognize from the structure of the plant community and basin size alone. Far too often it is felt that small wetlands have little value and that encroachment into large wetlands will have little lasting impact because of the size of the systems.

The role to be played by wetlands in sustainable management schemes for Africa is not always clear-cut. Wetlands must be considered within both the human and environmental contexts in terms of multiple interests that control and are controlled by the wetlands. By far, the most daunting tasks in the twenty-first century for aquatic managers and conservation biologists will be to identify the importance of African wetlands, to iden-

tify how best to conserve and manage them, and to convince policy makers that appropriate action is required. As human populations continue to grow in Africa, understanding the multifaceted role of wetlands in regional ecology, conservation, water quantity and quality, and the local economy is critical for sound environmental management.

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# **Bibliography**

- Acreman, M.C., and G.E. Hollis, eds. 1996. Water management and wetlands in sub-Saharan Africa. Gland, Switzerland: IUCN.
- Adams, W.M. 1996. Economics and hydrological management of African flood-plains. Pages 21–33 in Water management and wetlands in sub-Saharan Africa, ed. M.C. Acreman and G.E. Hollis. Gland, Switzerland: IUCN.
- Arinaitwe, J. 1993. The importance of rice schemes for water birds in Uganda. Pages 515-522 in *Proceedings of the VIII Pan-African Ornithological Congress*. Accra, Ghana: Ostrich.
- Bacon, P. 1996. Wetlands and biodiversity. Pages 1-17 in Wetlands, biodiversity and the Ramsar convention: The role of the convention on wetlands in the conservation and wise use of biodiversity, ed. A.J. Hails. New Delhi, India: Ramsar Convention Bureau, Ministry of Environment and Forests.
- Balirwa, J.S. 1998. Lake Victoria wetlands and the ecology of the Nile tilapia, Oreochromis niloticus Linne. Ph.D. diss., Wageningen Agricultural University, Wageningen, The Netherlands.
- Beadle, L.C. 1981. The inland waters of tropical Africa: An introduction to tropical limnology. London: Longman.
- Beadle, L.C., and E.M. Lind. 1960. Research on the swamps of Uganda. *Uganda Journal* 24: 84-97.
- Britton, P.L. 1978. Seasonality, density and diversity of birds of a papyrus swamp in Western Kenya. *Ibis* 120: 450–466.
- Bugenyi, F.W.B. 1991. Ecotones in a changing environment: Management of adjacent wetlands for fisheries production in the tropics. Verhandlungen Internationale Vereinigung Limnologie 24: 2547–2551.
- Bugenyi, F.W.B. 1993. Some considerations on the functioning of tropical riparian ecotones. *Hydrobiologia* 251: 100–107.

Paragraph und

- Calzada-Bujak, I., L. Serrano, J. Toja, and T.L. Crisman. 2001. Phosphorus dynamics in a Mediterranean temporary pond, Donana National Park, Spain. Verhandlungen Internationale Vereinigung Limnologie, 27: 3986-3991.
- Carter, G.S. 1955. The papyrus swamps of Uganda. Cambridge: Heffer.
- Chale, F.M.M. 1985. Effects of a Cyperus papyrus L. swamp on domestic waste water. Aquatic Botany 23: 185-189.
- Chapman, C.A., and L.J. Chapman. 1996. Mid-elevation forests: History of disturbance and regeneration. Pages 385-400 in East African ecosystems and their conservation, ed. T.R. McClanahan and T.P. Young. Oxford: Oxford University Press.
- Chapman, L.J., and C.A. Chapman. 1998. Hypoxia tolerance of the mormyrid *Petrocephalus catostoma:* Implications for persistence in swamp refugia. *Copeia* 1998: 762–768.
- Chapman, L.J., and K.F. Liem. 1995. Papyrus swamps and the respiratory ecology of Barbus neumayeri. Environmental Biology of Fishes 44: 183-197.
- Chapman, L.J., L.S. Kaufman, C.A. Chapman, and F.E. McKenzie. 1995. Hypoxia tolerance in twelve species of East African cichlids: Potential for low oxygen refugia in Lake Victoria. Conservation Biology 9: 1274–1288.
- Chapman, L.J., C.A. Chapman, R. Ogutu-Ohwayo, M. Chandler, L. Kaufman, and A. Keiter. 1996a. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conservation Biology 10: 554-561.
- Chapman, L.J., C.A. Chapman, and M. Chandler. 1996b. Wetland ecotones as refugia for endangered fishes. *Biological Conservation* 78: 263-270.
- Chapman, L.J., C.A. Chapman, and T.L. Crisman. 1998. Limnological observations of a papyrus swamp in Uganda: Implications for fish faunal structure and diversity. Verhandlungen Internationale Vereinigung Limnologie 26: 1821–1826.
- Chapman, L.J., J. Balirwa, F.W.B. Bugenyi, C.A. Chapman, and T.L. Crisman. 2001. Wetlands of East Africa: Biodiversity, exploitation, and policy perspectives. Pages 101–132 in Wetlands biodiversity, ed. B. Gopal. Leiden: Backhuys.
- Crisman, T.L. 2000. Wetland ecotones and the role of the private sector in conservation and management of the Pantanal. Pages 203-210 in *The Pantanal of Brazil*, *Bolivia and Paraguay*, ed. F.A. Swarts. Gouldsboro, PA: Hudson MacArthur.
- Crisman, T.L., and W.J. Streever. 1996. The legacy and future of tropical limnology. Pages 27–42 in *Perspectives in tropical limnology*, ed. F. Schiemer and K.T. Boland. Amsterdam: SPB Academic Publishing.
- Crisman, T.L., L.J. Chapman, and C.A. Chapman. 1996. Conserving tropical wetlands through sustainable use. *Geotimes* (July): 23-25.
- Crisman, T.L., L.J. Chapman, C.A. Chapman, and J. Prenger. 2002, Cultural eutrophication of a Ugandan highland crater lake: A twenty-five-year comparison of limnological parameters. Verhandlungen Internationale Vereinigung Limnologie 27: 3574–3578.

- Denny, P., ed. 1985. The ecology and management of African wetland vegetation. Dordrecht, The Netherlands: Dr. W. Junk.
- Denny, P. 1993. Wetlands of Africa: An introduction. Pages 1-31 in Wetlands of the world: Inventory, ecology, and management, ed. D.F. Whigham, D. Dykjova, and S. Hejny. Dordrecht, The Netherlands: Kluwer Academic.
- Denny, P. 1997. Implementation of constructed wetlands in developing countries. Water Science Technology 35: 27-34.
- Denny, P., and F. Turyatunga. 1992. Uganda wetlands and their management. Pages 77-84 in Proceedings of the Third International Wetlands Conference, Rennes, France (1988). Aulla, Italy: Intecol.
- Denny, P., R. Bailey, E. Tukahirwa, and P. Mafabi. 1995. Heavy metal contamination of Lake George (Uganda) and its wetlands. Hydrobiologia 297: 229-239.
- Ellery, W.N., K. Ellery, K.H. Rogers, and T.S. McCarthy. 1995. The role of Cyperus papyrus L. in channel blockage and abandonment in the northeastern Okavango Delta, Botswana. African Journal of Ecology 33: 25-49.
- FAO 1990. Forest resources assessment 1990—Tropical countries. FAO Forestry Paper 112. Rome: FAO.
- FAO. 1999. State of the world's forests. Rome: FAO.
- Fryer, G. 1960. Concerning the proposed introduction of Nile perch into Lake Victoria. East African Agricultural Journal 25: 267-270.
- Gaudet, J.J. 1978. Effects of a tropical swamp on water quality. Verhandlungen Internationale Vereinigung Limnologie 20: 2202-2206.
- Gopal, B. 1994. The role of ecotones (transition zones) in the conservation and management of tropical inland waters. Mitteilungen Internationale Vereinigung Limnologie 24: 17–25.
- Greenwood, P.H. 1980. Towards a phyletic classification of the "genus" Haplochromis (Pisces, Cichlidae) and related taxa. Pt II: The species from lakes Victoria, Nabugabo, Edward, George, and Kivu. Bulletin of the British Museum (Natural History) Zoology 39.
- Grove, A.T. 1989. The changing geography of Africa. Oxford: Oxford University Press.
- Hamblyn, E.L. 1961. The Nile perch project. Pages 26-32 in EAFFRO Annual Report (1960). Jinja: EAFFRO.
- Harper, D.M., and K.M. Mavuti. 1996. Freshwater wetlands and marshes. Pages 217-240 in East African ecosystems and their conservation, ed. T.R. McClanahan and T.P. Young. Oxford: Oxford University Press.
- Holland, M.M., D.F. Whigham, and B. Gopal. 1990. The characteristics of wetland ecotones. Pages 171-198 in Ecology and management of aquatic-terrestrial ecotones, ed. R.J. Naiman and H. Decamps. MAB Book Ser. 4, UNESCO, Paris. Carnforth, England: Parthenon Publishing.
- Howard-Williams, G.H., and G.M. Lenton. 1975. The role of the littoral zone in the functioning of a shallow tropical lake ecosystem. Freshwater Biology 5: 445-459.

- Hughes, R.H., and J.S. Hughes 1992. A directory of African wetlands. Gland, Switzerland: IUCN.
- Jones, M.B., and T.R. Milburn. 1978. Photosynthesis in papyrus (Cyperus papyrus L.). Photosynthetica 12: 197-199.
- Jones, M.B., and F.M. Muthuri. 1997. Standing biomass and carbon distribution in a papyrus (*Cyperus papyrus* L.) swamp on Lake Naivasha, Kenya. *Journal of Tropical Ecology* 13: 347–356.
- Kadlec, R.H., and R.L. Knight. 1996. *Treatment wetlands*. Boca Raton, FL: Lewis. Kaufman, L.S. 1992. Catastrophic change in species-rich freshwater ecosystems: The lessons of Lake Victoria. *Bioscience* 42: 846–858.
- Kaufman, L., and P. Ochumba. 1993. Evolutionary and conservation biology of cichlid fishes as revealed by faunal remnants in northern Lake Victoria. Conservation Biology 7: 719–730.
- Kaufman, L.S., L.J. Chapman, and C.A. Chapman. 1997. Evolution in fast forward: Haplochromine fishes of the Lake Victoria region. *Endeavour* 21:23–30.
- Kindler, J., P. Warshall, E.J. Arnould, C.F. Hutchinson, and R. Varady. 1990. The Lake Chad conventional basin: A diagnostic study of environmental degradation. N'djamena, Chad: Lake Chad Basin Commission (LCBC).
- Ligtvoet, W., P.J. Mous, O.C. Mkumbo, Y.L. Budeba, P.C. Goudswaard, E.F.B. Katunzi, M.M. Temu, J.H. Wanink, and F. Witte. 1995. The Lake Victoria fish stocks and fisheries. Pages 12–53 in Fish stocks and fisheries of Lake Victoria: A handbook for field observations, ed. F. Witte and W.L.T. van Densen. Ridderkerk, The Netherlands: Minister of Development Cooperation.
- Mitsch, W.J., and J.G. Gosselink. 1993. Wetlands. New York: Wiley Press.
- NEMA. 1999. State of environment report for Uganda. Kampala, Uganda: National Environment Management Authority.
- Nyakango, J.B. 1997. Performance evaluation of a constructed wetland and removal optimization in maturation ponds. M.S. thesis, DEW008, Wageningen Agricultural University, Delft.
- Ogutu-Ohwayo, R. 1990. The decline of native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and Nile tilapia, Oreochromis niloticus. Environmental Biology of Fishes 27: 81-96.
- Okeyo, D.O. 1992. Wetland fish of Kenya. Pages 47-53 in Wetlands of Kenya, ed. S.A. Crafter, S.G. Njuguna, and G.W. Howard. Proceedings of a seminar on wetlands of Kenya. Gland, Switzerland: IUCN.
- Otto, G.M. 1998. Evaluation of *Cyperus papyrus* L. for the treatment of wastewater in eastern equatorial Africa. M.S. thesis, University of Florida, Gainesville.
- Rosenberger, A.E., and L.J. Chapman. 1999. Hypoxic wetland tributaries as faunal refugia from an introduced predator. *Ecology of Freshwater Fish* 8: 22–34.
- Rosenberger, A.E., and L.J. Chapman. 2000. Respiratory characters of three haplochromine cichlids: Implications for persistence in wetland refugia. *Journal of Fish Biology* 57: 483-501.

- Schofield, P.J., and L.J. Chapman. 1999. Interactions between Nile perch, *Lates niloticus*, and other fishes in Lake Nabugabo, Uganda. *Environmental Biology of Fishes* 55: 343–358.
- Schofield, P.J., and L.J. Chapman. 2000. Hypoxia tolerance of introduced Nile perch: Implications for survival of indigenous fishes in the Lake Victoria basin. *African Zoology* 35: 35-42.
- Stuart, S.N., R.J. Adams, and M.D. Jenkins 1990. Biodiversity in sub-Saharan Africa and its island: Conservation, management, and sustainable use. Gland Switzerland: IUCN.
- Thompson, K. 1976. Swamp development in the headwaters of the White Nile. Pages 177-196 in *The Nile*, biology of an ancient river, ed. J. Rzoska. The Hague: Dr. W. Junk.
- Thompson, K., and A.C. Hamilton. 1983. Peatlands and swamps of the African continent. Pages 331-373 in *Ecosystems of the world*, ed. A.J.P. Gore. Amsterdam, The Netherlands: Elsevier.
- Thompson, K., P.R. Shewry, and H.W. Woolhouse. 1979. Papyrus swamp development in the Upemba Basin, Zaire: Studies of population structure in Cyperus papyrus stands. Botanical Journal of the Linnaean Society 78: 299-316.
- Twongo, T. 1996. Growing impact of water hyacinth on nearshore environments of lakes Victoria and Kyoga (East Africa). Pages 633-642 in *The limnology, climatology and paleoclimatology of the East African Great Lakes*, ed. T.C. Johnson and E.O. Odada. Amsterdam, Netherlands: Gordon and Breach.
- Twongo, T. 2001. Water hyacinth proliferation, impacts and control in lakes Victoria and Kyoga, East Africa. Report to National Agricultural Research Organization, Uganda.
- Twongo, T.K., F.W.B. Bugenyi, and F. Wanda. 1995. The potential for further proliferation of water hyacinth in Lakes Victoria, Kyoga, and Kwonia, and some urgent aspects for research. *African Journal of Tropical Hydrobiology and Fisheries* 6: 1–10.
- Wetzel, R.G. 1983. Limnology. 2nd ed. Philadelphia: Saunders College Publishing.
- Wetzel, R.G. 1990. Land-water interfaces: Metabolic and limnological regulators. Verhandlungen Internationale Vereinigung Limnologie 24: 6-24.
- Witte, F., T. Goldschmidt, J. Wanink, M. van Oijen, K. Goudswaard, E. Witte-Mass, and N. Bouton. 1992a. The destruction of an endemic species flock: Quantitative data on the decline of the haplochromine cichlids of Lake Victoria. *Environmental Biology of Fishes* 34: 1–28.
- Witte, F. T. Goldschmidt, P.C. Goudswaard, W. Ligtvoet, M.J.P. van Oijen, and J.H. Wanink. 1992b. Species extinction and concomitant ecological changes in Lake Victoria. *Netherlands Journal of Zoology* 42: 214–232.
- Wood, A. 1990. The application of artificial wetlands in South Africa. Pages 235–240 in Constructed wetlands for water pollution control, ed. P.F. Cooper and B.D. Findlater. Oxford: Pergamon Press.

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