

Papyrus Wetlands

12

Julius Kipkemboi and Anne A. van Dam

Contents

Introduction	184
Occurrence of Papyrus Marshes	184
Main Features of Papyrus Marshes	186
Propagation and Expansion	187
Root Architecture and Associated Features	187
Growth, Productivity, Biomass, and Water Transport	188
Zonation	189
Conservation and Management Status	190
Ecosystem Services	190
Biodiversity in Papyrus Marshes	190
Human Dependence on Papyrus Wetlands	192
Threats and Future Challenges	193
References	195

Abstract

Papyrus *Cyperus papyrus* is tropical wetland sedge that can grow up to a height of 5–6 m under optimal conditions. It is dominant vegetation in many wetlands in central, southern and eastern Africa, the Nile valley and in some parts of the Mediterranean in the Middle East and southern Europe. Papyrus is one of the most productive wetland sedge and is structurally and physiologically adapted to

J. Kipkemboi (🖂)

A. A. van Dam (🖂)

Department of Biological Sciences, Egerton University, Egerton, Njoro, Kenya e-mail: jkipkemboi@egerton.ac.ke

Aquatic Ecosystems Group, Department of Water Science and Engineering, UNESCO-IHE Institute for Water Education, Delft, The Netherlands e-mail: a.vandam@unesco-ihe.org

[©] Springer Science+Business Media B.V., part of Springer Nature 2018 C. M. Finlayson et al. (eds.), *The Wetland Book*, https://doi.org/10.1007/978-94-007-4001-3 218

permanently and seasonally flooded wetlands. It propagates through both sexual and asexual reproduction. Wetlands dominated by papyrus are characterized by variable biotic diversity with 187 documented species in various African wetlands. These ecosystems also provide diverse ecosystem services ranging from provisioning, regulating and cultural that support livelihoods especially in sub-Saharan Africa. Like in many global wetlands, papyrus marshes are threatened by anthropogenic activities such as excessive biomass harvesting and conversion to agriculture and human settlement and climate change.

Keywords

Tropical wetlands \cdot Macrophytes \cdot Biodiversity \cdot Ecosystem services \cdot Threats \cdot Conservation

Introduction

Papyrus *Cyperus papyrus* is a tropical wetland sedge that can grow up to 5–6 m under optimal conditions. Very often the term "swamps" is used for papyrus-dominated wetlands, yet these areas are dominated by herbaceous vegetation rather than trees. For consistency we will use the term "marshes" to refer to wetlands dominated by herbaceous vegetation and "papyrus marshes" for wetlands dominated by *C. papyrus*.

Papyrus marshes are predominantly found in riverine and lacustrine areas of tropical Africa and often exhibit high biomass productivity compared to other aquatic macrophytes and terrestrial herbaceous vegetation (Jones and Muthuri 1997; Boar et al. 1999; Mnaya et al. 2007). Papyrus utilizes the C₄ photosynthetic pathway and is characterized by high assimilation of CO₂ and solar energy into biomass (Jones 1987). Jones (1988) assigns a high quantum yield at low levels of incident light and efficient use of nitrogen by C₄ plants compared to those with C₃ pathways. This high biomass translates into numerous uses of the vegetation by the communities living adjacent to these wetlands. Papyrus wetlands are also important habitats for fish and other forms of aquatic and semiterrestrial wildlife.

Occurrence of Papyrus Marshes

Papyrus is considered native to central and eastern Africa and the Nile valley and is found from southern (Okavango), central (Zaire swamps in the present Democratic Republic of Congo), and eastern Africa to Egypt and Ethiopia and some parts of the Middle East (Israel and Syria) and southern Europe (Sicily). Major extensive papyrus wetlands occur in the lacustrine and floodplain wetlands of the White Nile River basin along the shoreline of Lake Victoria (East Africa), the largest tropical lake and second largest freshwater lake in the world; Uganda's Lake Kyoga wetland



Fig. 1 A riverine papyrus marsh in Eastern Uganda (Photo credit: J. Kipkemboi © Rights remain with the author)

complex; the shores of Lake Albert to the Sudd; Bahr el Ghazal; and the Sudd proper and associated upstream wetlands including the Machar marshes of the Sobat River and inflowing subbasins (Baro-Akobo-Pibor). The riparian ecosystem along the White Nile is also dominated by papyrus. Also significant are a number of western Ethiopia river floodplains, which are characterized by papyrus and other emergent macrophytes such as *Phragmites* and *Typha* along the water courses (Rebelo and McCartney 2012). Papyrus is also widely distributed along the River Nile in Egypt. The Nile Delta was dominated by papyrus until the early eighteenth century, but due to regulated flooding and human activities, it has been reduced to remnant stands along some of the delta lakes and lagoons.

The Sudd in the floodplains of the Nile River in South Sudan is the single most extensive papyrus marsh. Reports of the size of the papyrus-dominated zone are variable. The Jonglei Investigation Team (Jonglei Investigation Team. The Equatorial Nile project and its effects on the Anglo-Egyptian Sudan. Khartoum: Report to the Sudan Government (unpublished); 1954.) estimated the permanent swamp at 2,800 km², while Mefit-Babtie (1980) gave an estimate on 16,600 km² (Sutcliffe and Parks 1987 and citations therein) as did Chan and Eagleson (1980). An estimate of 7,000 km² provided by Dumont 2009 (cited in Zaroug et al. 2012) differs significantly from the approximately 40,000 km² permanent swamp estimate by Gaudet and Eagleson (1984 – cited in Zaroug et al. 2012).

In eastern Africa, papyrus occurs along the shores of Lake Victoria and in various valley swamps in the five East African countries. Papyrus is the dominant or codominant vegetation in many of the wetlands that cover 11–13% of Uganda's total land surface. Extensive monoculture stands are also found in most riverine marshes (Fig. 1) along rivers in eastern Uganda that drain into the Lake Kyoga system. Extensive systems include the Mpologoma, Nabajuzzi, and Namatala wetlands. Papyrus also dominates many wetlands in western Uganda's Busheyi, Kabala,

Kisoro, Ntungamo, and Rukungiri districts. Occurrence ranges from littoral vegetation of satellite lakes such as Lake Nabugabo and adjacent lakes, to the Rwambeita swamps and valley swamps along the rivers common in western Uganda and extending to Rwanda.

In Kenya, papyrus wetlands are found along Lake Victoria where it forms large stands in the floodplain wetlands of the Nyando, Yala, Sondu Miriu, Nzoia, and Sio rivers, most of which also have isolated upstream riverine marsh stands. Papyrus wetlands are also found in Kahawa swamp in Nairobi, along the riverine marshes in Nyahururu near Thompson falls, Molo river mouth at the shores of Lake Baringo, Tana River, and Loboi swamp near Lake Bogoria. Extensive lacustrine papyrus stands are found along Lake Naivasha's shoreline.

In Rwanda and Burundi papyrus is widespread in many valley swamps. Extensive areas are found in the Kanyaru-Akagera system, the Lake Kivu shoreline, and the Nyabarongo (or Nyawarungu) river at the Rwanda/Burundi border. In Tanzania, extensive areas exist along Lake Victoria and the associated floodplains such as the Mara river wetland and the Kagera river systems, with dense stands fringing either side of the river. Other extensive areas are found in the major river basins such as the Moyowosi/Malagarasi system in which floating mats occasionally detach, causing blockages in the river channels. The permanent swamps of the Pangani river system, including the associated lacustrine environments such as the Nyumba ya Mungu reservoir, are dominated by papyrus (Denny P, Bailey RG. A biological survey of Nyumba ya Mungu Reservoir, Tanzania, July–September 1974. Dar Es Salaam: Report for the Tanzanian Government (unpublished). 1976.). Papyrus also dominates the permanent swamps of the Ruaha/Rufiji system, Rukwa, Burugi/Ikimba, Eyasi/Yaida, and Natron. Along Lake Tanganyika, papyrus occurs in the delta swamps.

Within the Blue Nile, the Lake Tana system and its associated river systems (the Fogera and Dembia floodplains) have papyrus. In the Ethiopian Rift valley lakes, Lake Awassa and Lake Zwai have extensive papyrus stands on their shoreline. Other significant papyrus marshes occur in southern Africa along the Zambezi river system, particularly in the Okavango, Bangweulu, and Kafue flats. In central Africa, major papyrus-dominated areas are found in Lake Upemba and its basin in the Democratic Republic of Congo and in the Lake Chad system. Papyrus distribution is limited by altitude and disappears around 2,300 m above sea level (McClanahan and Young 1996). There is inadequate information on the actual extent of papyrus marshes in Africa. Thompson (1985) provided an estimate of 20,000 km², while Chapman et al. (2001) give an estimate of 85,000 km².

Main Features of Papyrus Marshes

The success and dominance of papyrus over other wetlands plants in permanently saturated and seasonally flooded wetlands can be attributed to its phytosociological and structural adaptations.

Propagation and Expansion

A papyrus marsh starts as a small clump from which rhizomes grow and branch in different directions. New juvenile culms develop behind the tip of the rhizome, while older culms at the aging part of the rhizome senesce gradually. The unique features of papyrus marshes are its propagation and expansion patterns and the ability to form floating mats. Mature culms (stage IV according to the growth stages proposed by Jones and Muthuri 1997) produce seeds from the racemous inflorescence. Propagation can occur sexually and asexually. Propagation by sexual means entails seed dispersal, germination, and seedling establishment. Due to seed distribution potential by different dispersal mechanisms, propagation by seed may lead to faster expansion over a larger area. Sexual propagation also allows exchange of genetic material among individuals and hence promotes genetic diversity. However, seed germination and establishment are highly sensitive stages in plant development, and their success is highly dependent on substrate characteristics, particularly soil moisture and organic content. Vegetative propagation and associated expansion occur through the growth of rhizomes, commonly in one direction but occasionally with branching and the ability to spread in all directions. Since little is known about interspecific competition, successional stages, or the dynamics of the dominant propagation method, these processes merit further long-term investigation.

Gaudet (1977) studied in detail the successional events in a drawdown marsh along the shores of Lake Naivasha. Hydric organic soils are ideal for the development of papyrus seeds transported by animals or water currents. Once the seeds germinate, the young plants thrive and grow quickly within saturated nutrient-rich organic soils and silts (Fig. 2), becoming distinctly different from other *Cyperaceae* as the culm height increases and inflorescence develops. Papyrus has an exceptional ability to respond to nutrients through root recruitment and growth in length as well as biomass accumulation compared to most other emergent vegetation (Kipkemboi et al. 2002). The ability to respond to nutrients in the interstitial water gives papyrus a competitive advantage over other emergent macrophytes. Although it is common to observe monoculture stands of papyrus with few herbs and shrubs, the climax stage may also occur as a mixed stand. Stable climax communities are uncommon in easily accessible areas due to human activities such as burning, livestock grazing, and harvesting of aboveground biomass.

Root Architecture and Associated Features

Papyrus occurs under a wide hydrological gradient from firmly rooted in the substratum to loosely anchored and easily detached floating mats and even islands (Azza et al. 2000). Its tolerance to flooding enables papyrus to dominate in fringing zones and permanently saturated areas while retaining its presence in seasonally saturated areas. Papyrus possess aerenchymatous tissue extending from the stem to the rhizomes and roots which contributes to buoyancy and enables the plant to form



Fig. 2 A young papyrus seedling (Photo credit: J. Kipkemboi © Rights remain with the author)

floating mats in low energy sheltered areas (Azza 2006). Roots occur at the rhizome nodes and play a role in anchoring the plant as well as in nutrient uptake. In floating mats, the roots dangle in the water column.

Papyrus mats are a result of intertwining rhizomes that can be secure in relatively firm soils towards the edge of the swamp substratum or may in muddy zones give rise to floating mats whenever the water level rises. As floating islands, these mats occasionally attain considerable size, covering open water bodies such as lakes. The roots on the rhizome mats play a significant role in determining the plant response to nutrient availability, especially in wetlands receiving wastewater (Kipkemboi et al. 2002). Papyrus roots have been found to be associated with nitrogen fixing bacteria (Mwaura and Widdowson 1992).

Growth, Productivity, Biomass, and Water Transport

Papyrus exhibits high growth rates compared to many other wetland plants, attaining heights up to 3.5–4 m within 4 months (Thenya 2006), and is capable of high

biomass productivity and a higher standing biomass than many emergent macrophytes. Values of 14–21 g/m²/day have been reported for Lake Naivasha (Muthuri et al. 1989). Although highly variable, values of 1.4–8.5 kg/m² are commonly reported for aboveground biomass, while 9–12 kg/m² have been reported when belowground (rhizomes and roots) are included (Muthuri et al. 1989; Boar et al. 1999; Kipkemboi et al. 2002; Mnaya et al. 2007; Terer et al. 2012 and references therein). Annual net productivity is about 5 kg/m²/year (Jones and Muthuri 1997). The nitrogen and phosphorus in the plant biomass is variable in the different plant parts. Mean (dry matter) values for nitrogen and phosphorus range from 0.7 to 1.16% and from 0.13 to 0.16%, respectively (Gaudet and Muthuri 1981; Muthuri and Jones 1997; Boar 2006). A high growth rate and biomass imply greater carbon sequestration and storage.

Papyrus is also known for its high water fluxes. Based on a study in a papyrus marsh at the Lake Victoria shoreline, Saunders et al. (2007) reported a daily vapor flux from the papyrus canopy through evapotranspiration of as high as 4.75 kg/m² of water per day. This estimate is about 25% greater than loss through evaporation from open water. High water loss in papyrus marshes has also been reported for The Sudd in South Sudan. For instance, Sutcliffe and Parks (1989) indicate that an annual evaporation of 2,100 mm is reasonable, while Mohamed (2005) estimated evaporation of 1,460 and 1,935 mm per year in the dry and wet years, respectively. From these studies, it can be concluded that papyrus marshes play an important role in moisture circulation and influence local and regional hydrological cycle and climate.

Zonation

Plant zonation is a distinct feature in papyrus marshes. Emergent macrophytes can occur as monospecific bands in littoral wetlands. Species forming these bands reflect their ability to tolerate waterlogged conditions and water that sometimes rises above the substrate. There is a clear zonation of papyrus, Typha sp., Phragmites sp. and Miscanthus sp. from the saturated to the less saturated zones. In complex associations in large swamps, a mosaic of monospecific pockets of individual macrophyte stands is formed. Mixed stands occur where monospecific stands meet. In Lake Victoria, both in the littoral zone and at river mouths, it is common to find a fringe of papyrus, Vossia cuspidata and Pennisetum purpureum at the swamp/open water edge. In the mouths of large rivers draining into Lake Victoria, such as the Mara and Nyando rivers, Vossia usually occurs as floating mats and gradually gives way to fringing stands of papyrus which may be partly rooted, while Typha, Phragmites and other Cyperus spp. usually occur on the outer and often less wet parts of the swamp. At the interface zone in Lake Victoria, the papyrus fringes are connected to the floating mats of water hyacinth Eichhornia crassipes or, in some areas, rooted floatingleaved water lily Nymphaea spp.

Conservation and Management Status

Most papyrus wetlands do not have any conservation or protection status. In many East African wetlands, the management is determined by the livelihood activities of communities living around them. In many African countries, land tenure in wetlands is often unclear although the majority of the wetlands are treated as belonging to the state. Because of a lack of wetland policies or weak implementation strategies where policies do exist, most livelihood and development activities in wetlands are unregulated. As a result, many papyrus marshes are threatened by overexploitation.

Even within conservation areas, e.g., Ramsar sites, the policies for ensuring sustainable utilization are inadequate. Many of these wetlands have been converted to agricultural crop production areas. Owino and Ryan (2007) reported a loss of up to 50% of papyrus coverage in selected wetlands in the eastern shores of Lake Victoria adjacent to Winam Gulf from 1969 to 2000; and this was projected to be a loss of nearly 80% by 2020 if the trend continued unchecked. About a 70% loss of papyrus wetland has also been reported for Lake Naivasha over a period of 35 years (Boar et al. 1999). Lack of quantitative inventories is a major hindrance to monitoring losses of wetlands in many African countries.

Ecosystem Services

The high productivity and multiple uses of papyrus biomass correlate with the numerous products, functions, and uses provided by these ecosystems. Virtually every part of the plant, from rhizomes and culms to the umbel, can be used although this varies from community to community. In many instances, the rhizomes are used for fuel wood, while the culms are mainly used for craft making. At the tender stage, the umbel forms good fodder for livestock, while mature umbels are used by some communities for making brooms for sweeping. Besides these provisioning ecosystem services, papyrus marshes deliver important regulating services. They have been used for wastewater treatment (Chale 1985; Kansiime and Nalubega 1999; Mburu et al. 2015), and their carbon storage was estimated at 88 t C/ha in biomass and 640 t C/ha in the peat under permanently flooded papyrus (Saunders et al. 2014). Table 1 summarizes the common ecosystem services of papyrus wetlands.

Biodiversity in Papyrus Marshes

Floral and faunal diversity in papyrus marshes is variable (Chapman et al. 2001). Although these wetlands are characterized by the dominance of papyrus, they host a wide range of true aquatic macrophytes and semiterrestrial plants. One common feature in papyrus marshes is the presence of monoculture stands and discrete zones or pockets of plants of similar life forms. Apart from *Cyperus papyrus*, the other dominant emergent macrophytes in eastern Africa wetlands are *Typha domingensis*, *Phragmites mauritanius*, and *Miscanthus violaceus* (Denny 1985; Kipkemboi et al. 2002).

Category	Examples
Provisioning services	
Biomass production	House construction, thatching, mat making, paper making, crafts and furniture, fuel wood, livestock fodder
Food production	Fish, wild game, seasonal crops
Clay mining	House walls smoothening
Regulating services	
Water quality improvement	Wastewater purification in natural and constructed wetlands
Hydrological regulation	Water storage and loss
Climate regulation	Evaporative cooling, carbon sequestration
Biodiversity and habitat	Wildlife habitat, tourism
Cultural services	
Education Ecotourism	Scientific insights on wetland biogeochemistry, hydrology and ecological studies Bird watching and other wild game observation areas.
	Dird waterning and other with game observation areas.

Table 1 Common ecosystem services of papyrus marshes in sub-Saharan Africa

Very few other plants are found growing within mature papyrus stands, perhaps because of the competitive advantage the sedge has over other emergent vegetation. There is a distinct difference in floral diversity between permanent and seasonally flooded areas. The seasonally flooded areas tend to be richer in species due to human disturbance and because most species occurring in this zone are predominantly opportunistic terrestrial herbs and not necessarily aquatic macrophytes (Rongoei et al. 2014).

Papyrus develop long culms supporting a 50 cm diameter umbel characterized by hundreds of cylindrical rays radiating from the tip of the culm. This canopy effectively shades the vegetation underneath. Occasionally, *Cynodon* sp. and *Leersia hexandra* occur entangled on the rhizomes of the fringe vegetation and may be moved to the open water with detached floating mats. Within the papyrus-dominated zones, many other species occur. Common species include climbers such as *Mikania* sp., *Ipomoea cairica*, and several other *Ipomoea* species, herbs such as *Commelina* sp., ferns (e.g., *Thelypteris striata*) and mosses underneath (Denny 1985). The pools between rhizomatous rafts may have floating plants such as *Lemna gibba* and *Azolla* spp. (Gaudet 1977). Other species that have been recorded in papyrus marshes are *Pyncbostacbys defixxifolia*, *Polygonum salicifolium*, *Cyperus dives*, and *Egna* sp. (Boar et al. 1999; Rongoei et al. 2014).

One of the key ecological values of papyrus marshes is habitat for a number of wetland endemic and some terrestrial fauna. Among the common residents in papyrus wetlands are representatives of a number of vertebrate groups (amphibians, reptiles, fish, birds, and mammals), insects, and a wide diversity of aquatic invertebrates. The lower water-saturated region is suitable for fish, worms, and larval stages of insects, while the canopy is ideal for perching birds. Papyrus marshes provide habitats for several avian species. Some common avian species are given in Table 2.

Table 2 Common bird species in papyrus and papyrus edge swamps (List compiled from species reported in Maclean et al. 2006) 2006)	Common name	Scientific name
	Papyrus gonolek	Liniarius mufumbiri
	Greater swamp warbler	Acrocephalus rufescens
	Carruther's cisticola	Cisticola carunthesi
	Papyrus yellow warbler	Chloropeta gracilostris
	Papyrus canary	Serinus koliensis
	Swamp flycatcher	Muscicapa aquatica
	Crowned crane	Balearica regulorum
	Grey heron	Ardea cineria
	Shoebill	Balaeniceps rex
	Hamerkop	Scopus umbreta
	Black headed weaver	Ploceus cucullatus
	African pied kingfisher	Cervle rudis

In eastern Africa, several fish families can be found in papyrus marshes and lake fringes, such as Protopteridae, Clariidae, Anabantidae, Mormyridae, Bagridae, Shilbeidae, Cichlidae, Mochokidae, and Mastacembelidae. Fish species diversity in papyrus marshes includes both non-air- and air-breathing fish. High organic production in papyrus marshes, especially in areas where the water is above the substrate, creates a requirement for adaptation to hypoxia (Chapman et al. 1999). The air-breathers can tolerate the low oxygen conditions and include lungfish *Protopterus aethiopicus*, catfish *Clarias* spp., *Ctenopoma muriei*, and some waterbreathing fish such as *Barbus neumayeri*, *Oreochromis* spp., and *Labeo* spp. Fish diversity is not necessarily related to the high biomass productivity of the sedge but rather to the different microenvironments in the papyrus wetland suitable for spawning, foraging, and refuge.

Although fish and birds are some of the widely studied animals in papyrus marshes, there is a plethora of other animal species that add to the faunal diversity (Table 3). Among these are mammals such as the swamp antelopes: sitatunga *Tragelaphus spekei* and the kobs *Kobus leche*. In some areas, hippos *Hippopotamus amphibius* associate with papyrus marshes. Otters (*Aonyx* spp.) occur especially where the water level is usually above the soil surface and there are fish. In the majority of tropical swamps and marshes, reptiles and amphibians are common among the vegetation. Among the commonest reptiles are the African python *Python sebae* and the monitor lizard *Varanus* sp., while amphibians are represented by frogs and toads. There is also a wide diversity of insects in their larval and adult stages.

Human Dependence on Papyrus Wetlands

Due to the diversity of functions and use values, papyrus wetlands support millions of people both directly and indirectly. The nature of dependence on wetlands for livelihoods and ecosystem benefits varies from place to place. The goods and services derived from papyrus marshes are intricately intertwined with culture,

		No. of	
Category	Study area	species	Source
Herbaceous	Lake Victoria	34	Chapman
vegetation			et al. 2001
	Kibale forest	36	Chapman
			et al. 2001
Trees	General east Africa	8	Chapman
			et al. 2001
Amphibians	Lake Nabugabo	6	Behangana and
			Arusi 2004
Fish	Sondu Miriu	28	Gichuki et al. 2001
	Lake Victoria	30	Balirwa 1998
	Lake Nabugabo	18	Chapman
			et al. 2001
Avian	Select Ugandan wetlands	6	MacLean et al. 2006
Mammals		No data	
Reptiles		No data	
Invertebrates	Nyando	14	Mwagona 2013
Microbial diversity	Floating papyrus mat along the	7	Rifaat et al. 2002
(bacteria)	Nile in Egypt		

Table 3 Species richness in papyrus wetlands

prevailing economic conditions and livelihood options, and cultural interest. Papyrus wetlands attract various interest groups such as crop farmers, livestock herders, fishermen, craft makers and cottage industries, knowledge institutions, and conservationists. Compared to other emergent macrophytes, papyrus has by far the highest number of uses (described above). In some papyrus wetlands, cottage industries are the most reliable source of income. Farmers and fishermen are by far the largest direct beneficiaries of papyrus wetlands in many sub-Saharan African countries.

In the Lake Victoria and the Lake Kyoga ecosystems, papyrus wetlands are important fish nursery areas. These wetlands support the livelihoods of millions of rural populations; however, many of them are threatened by conversion to rice production. In Nyando wetland in Kenya, some local communities have initiated restoration of the papyrus vegetation for producing biomass for craft making (Fig. 3).

Threats and Future Challenges

Wetland loss globally is alarming (Davidson 2014), and papyrus wetlands are no exception. Like many other wetlands, they are primarily threatened by human population growth and associated anthropogenic activities such as unchecked urban development, human settlement, conversion to agriculture, water abstraction and diversion, pollution, introduction of alien species, and overexploitation. These threats are now aggravated by climate change. In many parts of sub-Saharan Africa, land use change and pressure from agriculture is the major threat. The increasing



Fig. 3 A regenerating papyrus wetland replanted by a local community in Nyando floodplain (Photo credit: J. Kipkemboi © Rights remain with the author)

demand for food by the fast growing population coupled with uncertainly of terrestrial rainfed agriculture due to climate change vagaries has led to more papyrus marshes being drained for agriculture. Papyrus wetlands are also affected by excessive biomass harvesting (Terer et al. 2012). Harvesting compromises aboveground plant attributes such as biomass production, culm density and height, as well as shoot regeneration. There are differences in opinion on recommended harvesting frequency (ranging between 6 and 12 months; Osumba et al. 2010; Terer et al. 2012). Burning of wetlands is also common in many areas to reduce the amount of senesced biomass and to allow fresh biomass to regenerate as pasture for livestock grazing. In other places, burning may be associated with clearing wetland margins for seasonal agriculture or for game hunting. Whatever the reason, burning disrupts the climax community and re-sets community succession. Frequent burning may also reduce the resilience of the wetland vegetation. In some wetlands, invasive species have been reported. In the case of papyrus marshes, some of these species include climbers, such as Ipomoea spp., and trees, such as the ambatch tree Aeschynomene sp. Hydrological modification is by far the most serious threat to any wetland as this affects the key ecosystem properties. In many parts of sub-Saharan Africa, hydrologic modification at the landscape and within the wetlands is seen as a threat to wetland habitat integrity (Maclean et al. 2014). Damming of the upstream rivers may compromise floodplain wetlands, whereas localized drainage in wetlands can completely alter the key properties of the ecosystem.

The challenges facing papyrus wetlands in Africa cannot be separated from other general environmental resources in the region. The trade-off between livelihood demands from the human population living adjacent to papyrus marshes and sustainable use of wetlands is poorly understood in many wetlands and will remain a challenge for many African countries for decades to come (van Dam et al. 2013; Zsuffa et al. 2014). Lack of appropriate legislative framework to guide sustainable use of wetlands is an impediment in countries in Africa. Whereas some countries have developed or are in the processes of developing appropriate policies, implementation remains a challenge in an environment where poverty and direct dependence on wetland use values by the local communities is high (Nasongo et al. 2015). Policies are often not accompanied with matching allocation of financial and human resources. More often than not, there is also inconsistency in policies and differences in institutional priorities in many countries. More research in ecology, governance, institutional, and socio-economic aspects of papyrus wetlands is required for sustainable utilization and successful conservation of these ecosystems (van Dam et al. 2014).

References

- Azza NGT. The dynamics of shoreline wetlands and sediments of Northern Lake Victoria. [dissertation]. Wageningen: Wageningen University and UNESCO-IHE Institute for Water Education; 2006. 170 p.
- Azza NGT, Kansiime F, Nalubega M. Differential permeability of papyrus and *Miscanthidium* root mats in Nakivubo swamp. Uganda Aquat Bot. 2000;67:169–78.
- Balirwa JS. Lake Victoria wetlands and the ecology of the Nile Tilapia *Oreochromis niloticus* Linné. [dissertation]. Rotterdam: A.A. Balkema Publishers; 1998. 247 p.
- Behangana M, Arusi J. The distribution and diversity of amphibian fauna of Lake Nabugabo. Afr J Ecol. 2004;42 Suppl 1:6–13.
- Boar RR. Responses of a fringing *Cyperus papyrus* L. swamp to changes in water level. Aquat Bot. 2006;84(2):85–92.
- Boar RR, Harper DM, Adams CS. Biomass allocation in *Cyperus papyrus* in a tropical wetland, Lake Naivasha, Kenya. Biotropica. 1999;31(3):411–21.
- Chale FMM. Effects of *Cyperus papyrus* L. swamp on domestic wastewater. Aquat Bot. 1985;23:185–9.
- Chan SO, Eagleson PS. Water balance studies of the Bahr El Ghazal Swamp. Cambridge, MA: Department of Civil Engineering, Massachusetts Institute of Technology; 1980.
- Chapman LJ, Chapman CA, Branzeu DA, Mclaughlin B, Jordan M. Papyrus swamps, hypoxia, diversification: variation among populations of *Barbus neumayeri*. J Fish Biol. 1999;54:310–27.
- Chapman LJ, Balirwa J, Bugenyi FWB, Chapman C, Chrisman TL. Wetlands of East Africa: biodiversity, exploitation and policy perspectives. In: Gopal B, Junk WJ, Davis JA, editors. Biodiversity in wetlands: assessment, function and conservation, vol. 2. Leiden: Backhuys Publishers; 2001. p. 101–31.
- Davidson NC. How much wetland has the world lost? Long-term and recent trends in global wetland area. Mar Freshw Res. 2014;65(10):934–41.
- Denny P. Wetland vegetation and associated plant lifeforms. In: Denny P, editor. The ecology and management of African wetland vegetation. Dordrecht: Dr. W. Junk Publishers; 1985. p. 1–18.
- Dumont HJ. The Nile: origin, environments, limnology and human use. Dordrecht: Springer; 2009.
- Gaudet JJ. Natural drawdown on Lake Naivasha, Kenya, and the formation of papyrus swamps. Aquat Bot. 1977;3:1–47.
- Gaudet SC, Eagleson PS. Surface area variability of the Bahr el Ghazal swamp in the presence of perimeter canals. Cambridge, MA: Massachusetts Institute of Technology; 1984.

- Gaudet JJ, Muthuri FM. Nutrient relationships in shallow water in an African lake, Lake Naivasha, Kenya. Oecologia. 1981;49:109–18.
- Gichuki J, Guebas FD, Mugo J, Rabuor CO, Triest L, Dehairs F. Species inventory and the local uses of the plants and fishes of the Lower Sondu Miriu wetland of Lake Victoria, Kenya. Hydrobiologia. 2001;458:99–106.
- Jones MB. The photosynthetic characteristics of papyrus in a tropical swamp. Oecologia. 1987;71:355–9.
- Jones MB. Photosynthetic responses of C3 and C4 wetland species in a tropical swamp. J Ecol. 1988;76:253–62.
- Jones MB, Muthuri FM. Standing biomass and carbon distribution in a papyrus (*Cyperus papyrus*) swamp on Lake Naivasha, Kenya. J Trop Ecol. 1997;13(3):347–58.
- Kansiime F, Nalubega M. Wastewater treatment by a natural wetland: the Nakivubo Swamp Uganda: processes and implications. [dissertation]. Delft: IHE-Delft and Delft University of Technology; 1999. 300 p.
- Kipkemboi J, Kansiime F, Denny P. The response of *Cyperus papyrus* (L.) and *Miscanthidium violaceum* (K. Schum.) Robyns to eutrophication in natural wetlands of Lake Victoria, Uganda. Afri J Aquat Sci. 2002;27:11–20.
- Maclean IMD, Hassal M, Boar RR, Lake IR. Effects of disturbance and habitat loss on papyrusdwelling passerines. Biol Conserv. 2006;131:349–58.
- Maclean IMD, Bird JP, Hassal M. Papyrus swamp drainage and the conservation status of their avifauna. Wetl Ecol Manag. 2014. doi:10.1007/s11273-013-9335-1.
- Mburu N, Rousseau DPL, van Bruggen JJA. Use of macrophyte *Cyperus papyrus* in wastewater treatment. In: Vymazal J, editor. The role of natural and constructed wetlands in nutrient cycling and retention on the landscape. Dordrecht: Springer; 2015. p. 293–314.
- McClanahan TR, Young TP, editors. East African ecosystems and their conservation. New York: Oxford University Press; 1996.
- Mefit-Babtie Sr. Range ecology study, livestock investigation and water supply. First interim report. Khartoum: National Council for the Development of the Jonglei Canal Area (Sudan); 1980.
- Mnaya B, Asaeda T, Kiwango Y, Ayubu E. Primary production in papyrus (*Cyperus papyrus* L.) of Rubondo Island, Lake Victoria, Tanzania. Wetl Ecol Manag. 2007;15:269–75. doi:10.1007/ s11273-006-9027-1.
- Mohamed YA. The Nile hydroclimatology: impact of the Sudd wetland. [PhD dissertation]. Delft: UNESCO-IHE Institute for water Education/Delft University of Technology; 2005. 129 p.
- Muthuri FM, Jones MB. Nutrient distribution in a papyrus swamp. Lake Naivasha, Kenya. Aquat Bot. 1997;56:35–50.
- Muthuri FM, Jones MB, Imbamba SK. Primary productivity of papyrus (*Cyperus papyrus*) in a tropical swamp; Lake Naivasha, Kenya. Biomass. 1989;18:1–14.
- Mwagona PC. Determination of macroinvertebrate community structure along different habitat types in Nyando wetland. [dissertation]. Njoro: Egerton University; 2013. 59 p.
- Mwaura FB, Widdowson D. Nitrogenase activity in the papyrus swamps of Lake Naivasha, Kenya. Hydrobiologia. 1992;232:23–30.
- Nasongo SA, Zaal F, Dietz T, Okeyo-Owuor JB. Institutional pluralism, access and use of wetland resources in the Nyando Papyrus Wetland, Kenya. J Ecol Nat Environ. 2015;7(3):56–71.
- Osumba JJL, Okeyo-Owuor JB, Raburu PO. Effect of harvesting on temporal papyrus (*Cyperus papyrus*) biomass regeneration potential among swamps in Winam Gulf wetlands of Lake Victoria Basin, Kenya. Wetl Ecol Manag. 2010;18(3):333–41.
- Owino AO, Ryan PG. Recent papyrus swamp habitat loss and conservation implications in western Kenya. Wetl Ecol Manag. 2007;15:1–12.
- Rebelo L-M, McCartney M. Wetlands of the Nile Basin: distribution, functions and contribution to livelihoods. In: Awulachew SB, Smakhtin V, Molden D, Peden D, editors. The Nile River Basin: water, agriculture, governance and livelihoods. Abingdon: Routledge – Earthscan; 2012. p. 212–28.

- Rifaat HM, Márialigeti K, Kovács G. Investigations on rhizoplane Actinobacteria communities of papyrus (*Cyperus papyrus*) from an Egyptian wetland. Acta Microbiol Immunol Hung. 2002;49 (4):423–32.
- Rongoei PJ, Kipkemboi J, Kariuki ST, van Dam AA. Effects of water depth and livelihood activities on plant species composition and diversity in Nyando floodplain wetland, Kenya. Wetl Ecol Manag. 2014;22(2):177–89.
- Saunders MJ, Jones MB, Kansiime F. Carbon and water cycles in tropical papyrus wetlands. Wetl Ecol Manag. 2007;15:489–98. doi:10.1007/s11273-007-9051-9.
- Saunders MJ, Kansiime F, Jones MB. Reviewing the carbon cycle dynamics and carbon sequestration potential of Cyperus papyrus L. wetlands in tropical Africa. Wetl Ecol Manag. 2014;22 (2):143–55.
- Sutcliffe JV, Parks YP. Hydrological modelling of the Sudd and Jonglei Canal. Hydrol Sci. 1987;32 (2):143–59.
- Sutcliffe JV, Parks YP. Comparative water balances of selected African Wetlands. J Hydrol Sci. 1989;34(1,2):49–62.
- Terer T, Triest L, Muthama MA. Effects of harvesting *Cyperus papyrus* in undisturbed wetland, Lake Naivasha, Kenya. Hydrobiol. 2012;680(1):135–48.
- Thenya T. Analysis of macrophyte biomass productivity, utilization and its impacts on various ecotypes of Yala swamp, Lake Victoria basin, Kenya. In: Vlek PLG, Denich M, Martius C, Rodgers C, editors. Ecology and development series no. 48. Gottingen: Cuvillier Verlag; 2006. 207 p.
- Thompson K. Emergent plant of permanent and seasonally flooded wetlands. In: Denny P, editor. The ecology and management of African wetland vegetation. Dordrecht: Dr. W. Junk Publishers; 1985. p. 43–107.
- van Dam AA, Kipkemboi J, Rahman MM, Gettel GM. Linking hydrology, ecosystem function, and livelihood outcomes in African papyrus wetlands using a Bayesian Network model. Wetlands. 2013;33(3):381–97.
- van Dam AA, Kipkemboi J, Mazvimavi D, Irvine K. A synthesis of past, current and future research for protection and management of papyrus (*Cyperus papyrus* L.) wetlands in Africa. Wetl Ecol Manag. 2014. doi:10.1007/s11273-013-9335-1.
- Zaroug MAH, Sylla MB, Giorgi F, Eltahir EAB, Aggarwal PK. A sensitivity study on the role of the swamps of southern Sudan in the summer climate of North Africa using a regional climate model. Theor Appl Climatol. 2012. doi:10.1007/s00704-012-0751-6.
- Zsuffa I, van Dam AA, Kaggwa RC, Namaalwa S, Mahieu M, Cools J, Johnston R. Towards decision support-based integrated management planning of papyrus wetlands: a case study from Uganda. Wetl Ecol Manag. 2014;22(2):199–213.