Vascular Plants in Eastern Africa Rift Valley Saline Wetlands

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Abstract

Plants form a major component of aquatic biota by virtue of their trophic position. Most inland saline ecosystems, particularly lakes in the East African Rift System, are known as spectacular avian habitats. The population density of Lesser Flamingos is especially high due to the frequently high algal biomass productivity, which forms the main food. These environments also provide habitats to a unique vegetation of vascular plants adapted to saline environments. Vascular plants in the littoral zone and the associated floodplains of EARS lakes are dominated by two families—Poaceae and Cyperaceae—but about ten other families are commonly observed in shoreline areas with mild salinity. The two halophytes *Cyperus laevigatus* and *Sporobolus spicatus* are common along the shores of most East African saline lakes. Although the contribution of these plants to allochthonous input into the open water may not be significant, they play a significant role in providing nutrition to terrestrial herbivores associated with these ecosystems. The open-water and littoral zones of highly saline lakes are devoid of aquatic macrophytes with a few exceptions where freshwater percolates into the system. In most East African saline wetlands, salinity to some extent limits higher plant diversity. This prevents these ecosystems from being choked by noxious vascular aquatic weeds, particularly floating macrophytes that prefer low salinity conditions. Nonetheless, in some saline wetlands in Australia and parts of Europe, higher plant diversity and biomass occur.

11.1 Introduction

Inland saline aquatic habitats comprise the open-water areas of shallow athalassic lakes, their adjacent floodplains and pockets of saline areas in palustrine systems. They also include lake

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margins of some freshwater lakes, especially in regions with excessive evapotranspiration occasioned by aridity. Lakes of the East African Rift System are some of the most spectacular wetlands and are well known for their avian densities, particularly the flamingos. Accordingly, most of them can easily meet the criteria for Ramsar sites. The avian population and diversity are supported by the microflora and macrofauna—mainly phytoplankton and macroinvertebrate communities in the lake. In the case of piscivorous fish, this support is often indirect via secondary production. Vascular plants are restricted by salinity and poorly documented in these ecosystems (Brock and Shiel 1983; Brock et al. 2005; Wetzel 1983). Vascular aquatic plants comprise life forms adapted to hydrophytic conditions characterized by two major stressors: low oxygen availability and salinity. Aquatic macrophytes adapted to saline environments are referred to as halophytes. Using the conventional aquatic macrophyte life form classification, these plants are categorized into emergent, submerged, rooted floating leaved and floating plants (Denny 1985). Vascular plant composition and consequently the contribution to aquatic primary productivity are largely determined by the prevailing environmental conditions such as the nutrient supply, turbidity or salinity. Unlike in marine ecosystems, inland saline ecosystems lack constancy in the environmental conditions due to unpredictable seasonality-driven changes in hydrology. Aquatic plants here have evolved physiological, structural and biochemical means of dealing with saline environments and hence exhibit different levels of adaptation to salinity (Haller 1974).

11.2 Stress Gradients in Saline Wetlands

The aquatic environment is characterized by factors that limit the dispersal and growth of terrestrial organisms. In wetlands, the main stressors are anoxia, wide variability in salinity and water level fluctuations. This chapter focuses on salinity as a forcing factor in the occurrence of vascular plants in inland saline wetlands. High salinities are naturally associated with coastal environments and are uncommon in inland waters. However, due to continued accumulation of salts washed out from the catchments, some lakes and adjacent wetlands tend to develop elevated salinity over time. This is particularly true in situations where water loss due to evapotranspiration is exceedingly high. Vascular plants are limited in saline inland waters due to the inability of most macrophytes to overcome salt stress. Salinity stress restricts the growth of typical inland wetland macrophytes (Brock 1981, 1982; Sim et al. 2006). Where salinity exceeds 1000 mg L^{-1}, this factor becomes the main regulator of species occurrence (Denny 1985). Some aquatic macrophytes, however, grow in salinities of up to over 100,000 mg L^{-1} (Brock and Lane 1983; Brock et al. 2005) This is one reason why most littoral zones of saline lakes are often devoid of aquatic plants suitable for microphytes adapted to saline conditions. In such cases, there is a reduced autochthonous biomass production contribution from littoral zones to the adjacent open-water ecosystems (McKee and Mendelsohn 1989).

11.3 Causes of Salinity in Inland Wetlands

Salinity in inland water originates from the ionic contribution from the rocks and soils of the drainage basin. Salinity as indicated by total ionic concentration is closely correlated with conductivity. The dominant ions in most East African soda lakes (EASL) are sodium and hydrogen carbonate, but in some systems HCO_3^- is replaced by chloride (Talling and Talling 1965 in Denny 1985). Conductivity strongly correlates with total alkalinity (HCO_3^- + CO_3^{2-} + OH^-). pH increases as alkalinity increases.

Elevated salinity is induced by the prevailing climatic conditions, particularly by a negative water balance. This phenomenon is common in shallow tropical lakes with no outlets. Here, salts tend to accumulate as a result of evaporation of rain or fresh groundwater and/or evapotranspiration by aquatic plants. Ions are then concentrated in the substrate, leading to sharp salinity gradients. The lithology in the catchment area coupled with climatic conditions largely influences the degree of salinization.

Salinity can also be caused by anthropogenic activities such as discharge of wastewater containing high levels of salts to wetlands (Kitzhner et al. 2011). Examples of such wastewater sources are aquaculture mines and floriculture. Irrigation in arid areas has also been known to create suitable conditions for salinization of soils (McEwan et al. 2009). With increasing demand for agricultural produce and unreliable rainfall, irrigated agriculture, which depends largely on groundwater, is taking preference over rain-fed production in many low rainfall areas of the East African Rift Valley.

11.4 Occurrence of Inland Saline Environments

Inland saline wetlands are mostly associated with shallow EASL, which experience major hydrological changes. These changes occur over varied time scales, potentially even centuries or longer. A persistent negative water balance is thought to have resulted in separation of previously large freshwater lakes into smaller ones. For instance, Lake Elementaita and Lake Nakuru were once joined, forming a single large freshwater lake (Nilsson 1932 cited in Harper et al. 2003), but are currently separate, shallow and saline ecosystems. The salinity can vary within an order of magnitude, and occasionally these lakes have dried. Inundation of the shoreline by saline and alkaline water creates saline soils, thus offering an environment conducive to salt-

Fig. 11.1 *Cyperus laevigatus* on the shore of Lake Nakuru, Kenya, (**a**) and growing in a pocket of sodic soil at the shore of Lake Victoria, Kenya (**b**) (Photos: J. Kipkemboi)

tolerant macrophytes (Fig. 11.1a). In some freshwater lakes, pockets of sodic saline soils are common in floodplain wetlands, especially in locations characterized by aridity. For instance, on the northeastern shores of Lake Victoria in Kenya off Winam Gulf, there are pockets of sodic areas where *Cyperus laevigatus* is the only macrophyte (Fig. 11.1b) (J. Kipkemboi, personal observation).

11.5 Vascular Plant Adaptations to Salinity

Salinity is one of the forcing factors that determine species composition in wetlands. Other determinants that affect plant growth are rainfall, soil characteristics, nutrient supply, flooding depth and flooding duration. All these variables interact individually or through interactions among factors and between plants themselves. In freshwater environments, the osmotic concentration of the cytoplasm in living cells is usually higher than that of the surrounding medium. This enables the cells to develop turgor, i.e. absorb water until the turgor pressure of the cytoplasm is balanced by the resistance of their cell membrane (Mitsch and Gosselink 2000). At the cell level, plants overcome salinity stress in the same way as Bacteria. In addition, however, vascular plants have evolved adaptations that take advantage of their structural complexity. The principal mechanism of adaptation to salinity by aquatic macrophytes is exclusion, excretion and induced compatible solute biosynthesis (Bohnert et al. 1995). Some plants do not exclude salts at the roots but have secretory organs at the leaves. The leaves of many marsh grasses are covered by crystalline salt particles excreted by specialized, embedded salt glands (Khan and Weber 2006; Ramadan 2000 and references therein). Rout and Shaw (2001) proposed a possible role of antioxidative enzymes in salt tolerance of submerged macrophytes. At pH > 8.3, inorganic carbon is available as hydrogen carbonate and carbonate; free carbon dioxide is no longer present. Submerged plants can therefore be categorized as bicarbonate and non-bicarbonate users (Denny 1985).

Eastern African saline lakes exhibit a great diversity in salinity characteristics. The littoral wetlands of African athalassic lakes have elevated salinities sometimes in excess of 160 mS cm^{-1} (Talling and Talling 1965 in Denny 1985). Salinity exerts selection pressure and restricts plant community development. Information on morphological, anatomical and physiological adaptations is scanty. According to Flowers et al. (1986), the most tolerant families are Chenopodiaceae and Poaceae. Even within the same genus, single species exhibit different tolerance levels. For instance, *Sporobolus spicatus* can tolerate much higher salinities than *S. robustus* (Finlayson and Moser 1991). The slightly less alkaline floodplain surrounding the most EASL is dominated by freshwater emergent macrophytes and by *Sesbania sesban*, with scattered *Acacia xanthophloea* trees (White 1983).

11.6 Effects of Salinity on Vascular Plant Physiological Functioning and Diversity

Vascular plant species richness is low in inland saline wetlands compared to their freshwater and marine counterparts (Keddy 2010; Nielsen et al. 2003; Wetzel 1983). The effect of climate-induced salinity can be traced not only in the open-water environment but also in wetland soils. Inland saline wetlands may contain excess soluble salts (saline soils), excess exchangeable sodium (sodic soils) or both (saline-sodic soils). Salinity in inland wetlands is attributed to a mixture of cations of sodium, calcium, magnesium and potassium along with anions of chloride, sulfate, bicarbonate and carbonate. The amount of total salt, individual salt or combination of salts in saline wetlands is usually high enough to retard plant growth, injure plant tissue and/or decrease productivity (Ogle 2010). The intricate relationship between salinity, alkalinity and pH in determining the biogeographical distribution of euhydrophytes has been discussed in detail by

Denny (1985). What is often unclear is whether it is the chloride ion concentration, alkalinity or pH that is the overriding factor in determining vascular aquatic plant distribution. In his description, Denny (1985) demonstrated that even lakes with similar chloride ion concentration have different floristic compositions. He further indicated that alkalinity values >10 meq L^{-1} limit athalassic euhydrophyte tolerance.

Soil salinity can affect plant growth both physically (osmotic effect) and chemically (nutrient and/or toxicity effect). As salinity increases, it becomes more difficult for plants to take up water. Salt-intolerant plants appear drought stricken even at fairly low salt concentrations. Growth and productivity usually progressively decline as salinity levels increase. High concentrations of specific ions, which characterize salinity conditions in many cases, can cause disorders in mineral nutrition. For example, high sodium concentrations may cause deficiencies of other elements such as potassium and calcium, and high levels of sulfate and chloride diminish the rate of nitrate absorption. Specific ions such as sodium and chloride may have toxic effects on plants, reducing growth or causing damage to cells and cell membranes (USDA 2010). Very high pH values and accompanying alkalinity damage plant tissues (Denny 1985). If alkalinity is considered as the major component of salinity, we can conclude that it largely affects vascular plant distribution in saline wetlands.

How does salinity relate to vascular plant diversity? Salinity causes stress to physiological functions and is a limiting factor to the diversity of plants in such areas. Salinity is therefore an overriding factor in species occurrence in littoral zones of athalassic lakes and temporarily flooded depressions in arid areas. Highly saline lakes restrict the establishment of vascular emergent and euhydrophyte plants in the littoral zone. The floodplain may have salt-tolerant genera comprising *Sporobolus*, *Cyperus*, *Diplacne* and *Odyssea*, whilst the periphery with mild salinity hosts less tolerant taxa such as *Scirpus*, *Typha* and *Aeschynomene* (Denny 1985). Table 11.1 presents a list of vascular plants commonly

Table 11.1 Some common vascular plant life forms in East African Rift Valley lakes and other African saline ecosystems categorized by salinity tolerance (Denny 1985; Hughes and Hughes 1992)

	Salinity level tolerance		
Life form	High	Moderate	Low
Emergent macrophytes	*Sporobolus spicatus* Kunth	*Sporobolus marginatus* A. Rich.	*Phragmites mauritanus* Kunth
	Cyperus laevigatus L.	*Sporobolus pyramidalis* (L.) Pers.	*Ipomoea* sp.
	Diplachne fusca L.	*Cynodon dactylon* L.	*Leersia hexandra* Sw.
	Odyssea jaegeri (Pilg.)	*Hydrocotyle* sp.	*Oenanthe* sp.
	Scirpus maritimus Rottb.	*Juncus* sp.	*Paspalidium geminatum* (Forssk.) Stapf
	Scirpus littoralis L.	*Typha* spp.	*Hyparrhenia rufa* (Nees) Stapf
	Scirpus holoschoenus L.	*Commelina* sp.	
Submerged macrophytes		*Ceratophyllum demersum* L.	
Rooted floating leaved macrophytes		*Potamogeton pectinatus* L. *Najas marina*	*Nymphaea* sp.
Floating macrophytes		*Azolla nilotica* L.	*Pistia stratiotes* L.
		Lemna gibba L.	*Ottelia ulvifolia* (R.Br.) Rich
Trees and shrubs		*Aeschynomene elaphroxylon* L.	*Acacia xanthophloea* Benth.
		Pluchea sp.	*Sesbania sesban* (Jacq.) W. Wight

Highly tolerant plants include certain genera of Poaceae, Cyperaceae and Juncaceae. Other families that show appreciable tolerance are Araliaceae, Asteraceae, Ceratophyllaceae, Salviniaceae, Araceae, Fabaceae, Apiaceae and Nymphaeaceae

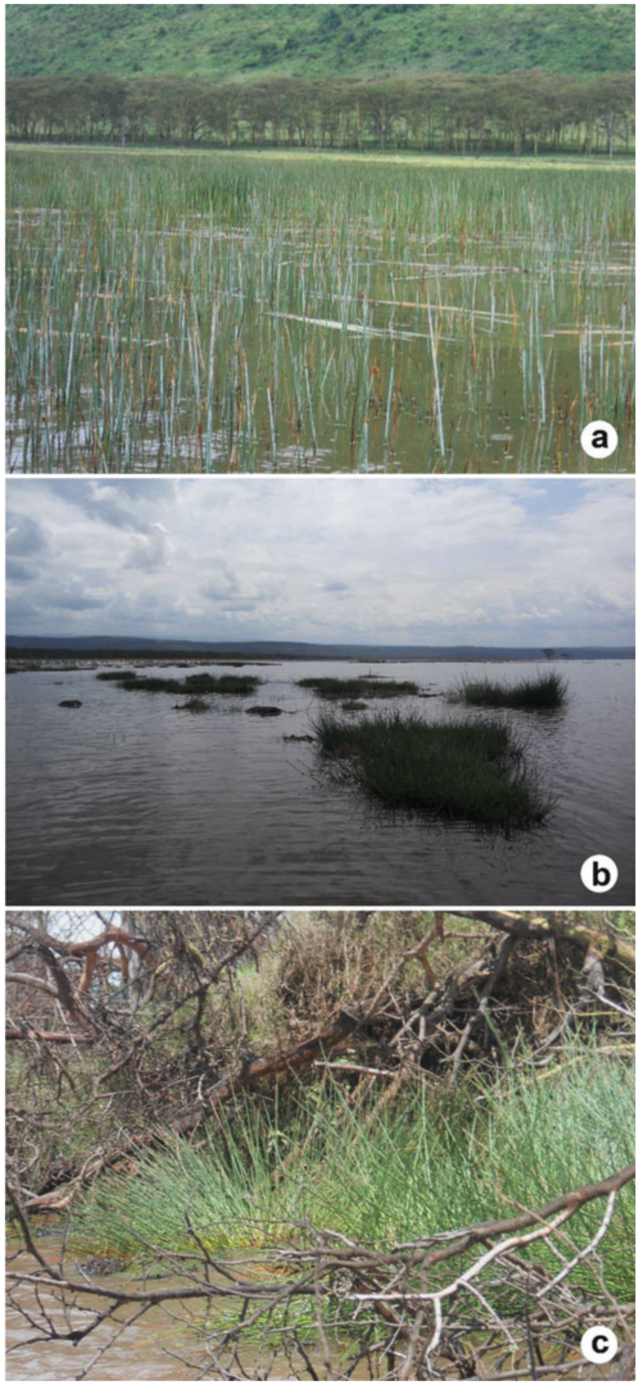

Fig. 11.2 Inundated macrophyte zone (**a**) and floating mats of *C. laevigatus* in Lake Nakuru, Kenya (**b**, **c**) (Photos: J. Kipkemboi)

found in saline wetlands in Africa. In highly saline ecosystems such as lakes Bogoria, Nakuru and Elementaita, euhydrophytes are completely absent. In lakes with mild salinity such as Lake Turkana and Lake Chad, studies have revealed a correlation between salinity and the presence of euhydrophytes (Denny 1985 and references therein).

Although appreciable plant diversity has been recorded in some saline lakes, much fewer typical vascular plants are usually adapted to such an environment. This is often circumstantial: opportunistic plant species exploit environments conducive for succession, particularly when salinity declines as a result of positive water balance during the wet seasons. For example, in Lake Bogoria in Kenya, less than 10 % of the total plant species encountered were true halophytes (Harper et al. 2003). Out of the 27 species of grasses recorded at the lake floodplain, the true halophytes comprised one grass (*Sporobolus spicatus*) and one sedge (*Cyperus laevigatus*). Some emergent macrophytes occur predominantly in coastal wetlands, but sometimes expand to inland saline systems. In the salt pans of southern Africa (the Makgadikgadi), *Scirpus maritimus* and *S. littoralis* occur along southern shores of Lake Chilwa. *S. holoschoenus* is common in northern Africa saline depressions. Information on the microbial flora in the littoral zone of saline environments is scanty, and this is an area worthy of further research.

11.7 Unusual Floating Mats in a Saline Lake?

Floating vegetation is uncommon in the open water of saline lakes. Nonetheless, in exceptional circumstances, floating mats can be observed particularly when the water volume in the lake has increased drastically within a short time, inundating the littoral areas dominated by emergent plants. This phenomenon has been observed in Lake Nakuru in 2011–2014 when the lake volume increased, causing detachment of some *C. laevigatus* mats to float over the lake surface. These mats are distributed by wind to various parts of the lake which previously did not have the macrophytes (Fig. 11.2a–c).

11.8 Ecological Importance of Interactions Between Vascular Plants and Saline Environments

Emergent macrophytes in saline wetlands contribute to primary production and nutrient dynamics and provide habitats for fauna. The diversity and contribution of vascular plants in inland saline wetlands to aquatic productivity is generally lower compared to marine salt marshes. This is partly explained by the exclusion of non-salt-tolerant plants by environmental conditions created by salinity. Salt uptake "spices" the plant biomass and encourages grazing by herbivores. Some salt-tolerant grasses such as *S. spicatus* and *C. dactylon* are highly palatable for herbivores. Palatability affects herbivore preference and consequently determines above-ground biomass of salt-tolerant macrophytes at any given time (Fig. 11.3). These plants are also resilient and can tolerate flooding regime variability and are robust to grazing pressure.

The effect of salinity stress on macrophytes restricts proliferation of noxious macrophytes, particularly floating vegetation, which comprises the most problematic weeds in freshwater wetlands. Thus, it is notable that whereas freshwater environments such as Lakes Victoria and Naivasha have been chocked by floating aquatic weeds, saline systems such as Lakes Turkana, Nakuru, Natron and Bogoria, among others, are devoid of vegetation or have sparse submerged vegetation. Salinity restrictions on vascular plants in saline lakes have both negative and positive ecological significance.

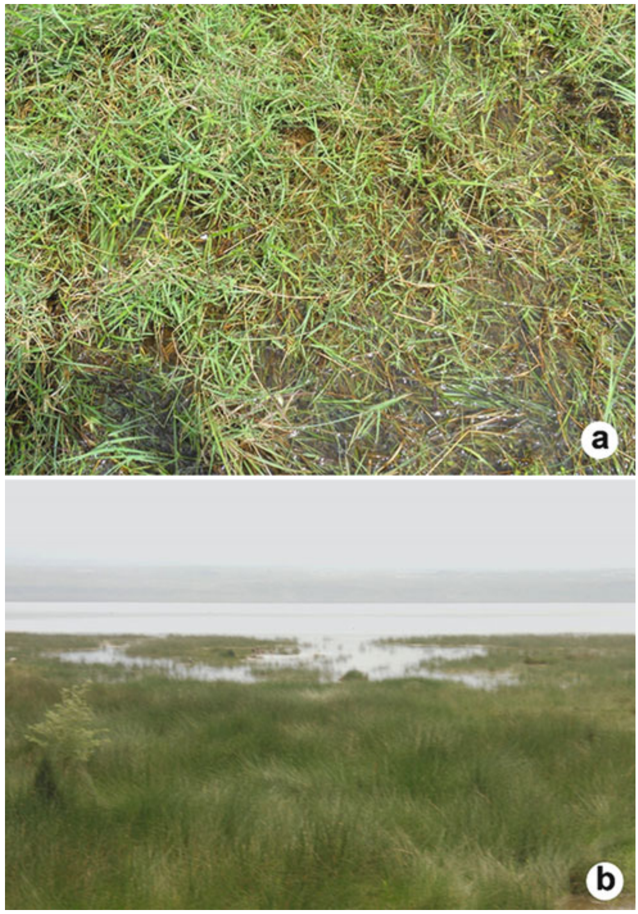

Fig. 11.3 Above-ground biomass in heavily grazed *S. spicatus* (**a**) and less preferred *C. laevigatus* along the shore of Lake Nakuru (**b**) (Photos: J. Kipkemboi)

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