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Effects of Land Use Duration on Forage Quality in a Littoral Wetland of Kenya

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MY FAMILY

Summary

Effects of Land Use Duration on Forage Quality in a Littoral Wetland of Kenya

Wetlands are transition areas between terrestrial and aquatic environments that fulfill a wide range of ecosystem services and can be used in diverse direct and indirect ways. Direct uses include livestock grazing, crop production and fishing. In Kenya, 56,000 km^2 of land area is covered by wetland-associated soils. Within this, the riparian land of Lake Naivasha is of particular importance as it surrounds one of the few fresh water lakes in the arid Rift Valley, which is experiencing intensive anthropogenic pressure and is of critical importance as grazing areas for wildlife and livestock. However, the forage nutritional value and attributes have not been studied. Increased land use duration after lake level recession and subsequent continuous grazing of the riparian land is hypothesized to differentially affect soil properties, floral characteristics, biomass production, and forage nutritional quality. Three studies were conducted to (1) determine how species composition and relative abundance of the forages are affected by duration of land use, (2) determine the effect of continuous grazing and soil types on biomass productivity and nutritional quality, and (3) determine the intake and digestibility of pasture grasses by sheep. Land use duration lead to change in species composition from a dominance of Kikuyu grass (*Pennisetum clandestinum*) to that of Naivasha star grass (*Cynodon plectostachyus*) independent of soils type. Increased land use duration reduced biomass production while increasing forage nitrogen (N) concentration. On the other hand, metabolizable energy content was not affected by land use duration but was rather affected by soil type. Land use duration was associated with increased lignin content and reduced N and fibre digestibility, but did not affect intake and digestibility of dry matter. The littoral pastures of Naivasha provides sufficient quantity and quality feed for ruminants during the dry season that can supply most minerals required by grazing ruminant but a high iron content may negatively influence feed intake. Optimum stocking densities and feed supplementation strategies need to consider the toposequence position in the riparian land and be adjusted according to land use duration and plant species composition as these affect quantity and quality of forage. The chronosequence is a suitable model to study processes and trends of changing resource base quality, particularly studies on forage quality and availability in riparian wetlands.

Zusammenfassung

Effekte der Landnutzungsdauer auf die Grobfutterqualität litoraler Feuchtgebiete in Kenia

Feuchtgebiete erfüllen als Übergangsbereich zwischen Land und Gewässern eine Vielzahl von Funktionen als Ökosystem und können auf verschiedene Weise sowohl direkt als auch indirekt genutzt werden. Die direkte Nutzung umfasst dabei Weidewirtschaft, Getreideproduktion und Fischerei. In Kenia sind etwa 56.000 km² der Gesamtfläche von Feuchtgebieten bedeckt, von denen die Ufergebiete des Naivashasees von besonderer Bedeutung sind. Diese umgeben einen der wenigen Süßwasserseen des ariden Rift Valley, unterlagen in der Vergangenheit einer intensiven Nutzung durch verschiedene Seiten und unterliegen auch heute noch starken Interessenkonflikten. Sie sind von immenser Bedeutung als Weidefläche sowohl für Wild- als auch für Nutztiere, der Futterwert der Vegetation wurde bisher jedoch nicht ausreichend charakterisiert. Die Hypothese ist, dass eine gesteigerte Landnutzungsdauer nach Rückgang des Hochwassers und eine nachfolgend dauerhafte Beweidung der Ufergebiete die Bodeneigenschaften, die botanische Zusammensetzung und Biomasseproduktion sowie den Futterwert der Pflanzen verändert. In insgesamt drei Studien wurde untersucht, wie die botanische Zusammensetzung und Artenvielfalt durch die Dauer der Landnutzung beeinflusst wird, wie Dauerbeweidung und verschiedene Bodentypen die Biomasseproduktivität und den Futterwert der Vegetation beeinflussen und wie sich die Futteraufnahme und Verdaulichkeiten von verschiedenen Weidegräsern bei Schafen darstellen. Die Dauer der Landnutzung führte unabhängig vom Bodentyp zu Veränderungen in der botanischen Zusammensetzung, ausgehend vom Kikuyu-Gras (*Pennisetum clandestinum*) als dominante Spezies hin zum Naivasha Star Gras (*Cynodon plectostachyus*). Eine erhöhte Landnutzungsdauer reduzierte die Produktion von Biomasse bei einer Erhöhung der Stickstoff (N)-Konzentration in den Pflanzen. Die Gehalte an umsetzbarer Energie dagegen wurden nicht von der Dauer der Landnutzung, wohl aber vom Bodentyp beeinflusst. Weiterhin führte eine verlängerte Landnutzungsdauer zu erhöhten Lignin-Konzentrationen und verringerten N- und Faserverdaulichkeiten, beeinflusste jedoch nicht die Trockenmasseaufnahme und -verdaulichkeit. Die Uferflächen des Naivashasees stellen in der Trockenzeit Futter in ausreichender Quantität und Qualität für Wiederkäuer zur Verfügung. Es enthält die meisten essentiellen Mineralstoffe; jedoch könnten sehr hohe Eisengehalte negative Auswirkungen auf die Futteraufnahme haben. Zur Planung optimaler Besatzdichten und Zufütterungsstrategien sollte die Toposequenz des Ufergebiets berücksichtigt und entsprechend der Landnutzungsdauer sowie der botanischen Zusammensetzung angepasst werden, da diese sowohl die Futtermenge als auch dessen Qualität beeinflusst. Die Chronosequenz stellt ein geeignetes Modell zur Überprüfung des Prozesses und der Entwicklung einer sich wandelnden Ressource und deren grundlegender Qualität dar, insbesondere hinsichtlich der Untersuchung der Futterqualität sowie deren Verfügbarkeit in Ufergebieten.

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List of Acronyms and Abbreviations

ASAL	Arid and Semi- Arid Land
DAAD	Deutscher Akademischer Austausch Dienst
DFG	Deutsche Forschungsgemeinschaft
FAO	Food and Agriculture Organization
GfE	Gesellschaft für Ernährungsphysiologie
GOK	Government of Kenya
GPS	Global Positioning System
HGT	Hohenheim gas test
ILRI	International Livestock Research Institute
JRC	Joint Research Centre
KARI	Kenya Agricultural Research Institute
KNBS	Kenya National Bureau of Statistics
ME	Metabolizable Energy
MEMR	Ministry of Environment and Mineral Resources
NACOSTI	National Commission for Science, Technology and Innovation
NEMA	National Environment Management Agency
NCST	National Council for Science and Technology
nMDS	Non- Metric Multidimensional Scaling
NRC	National Research Council
UNEP	United Nations Environment Programme
VDLUFA	Verband Deutscher Landwirtschaftlicher Untersuchungs und Forschungsanstalten

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CHAPTER 1: GENERAL INTRODUCTION

1. General Introduction

1.1 Wetlands

Wetlands are transition areas between terrestrial and aquatic environments and can be either dry or wet depending on climatic and hydrological attributes of the specific area or the surrounding catchment. They may be permanently or seasonally flooded, or may only be moist during the wet season or during seasons of extreme weather conditions (Keddy, 2010). Various definitions of the term "wetland" exist, most of them tending to be specific to the particular wetland function in focus at the time of formulating the definition. The Ramsar convention generally defines wetlands as "*areas of marsh, fen, peat land, or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed 6 metres*" (Ramsar Information Bureau, 1998). While Brinson (1993) restricted the definition to "*areas that are permanently flooded with a water layer not exceeding several meters in depth*", Windmeijer and Andriesse (1993) and Finlayson et al. (1999) defined them as "*areas where the water table in the driest month is less than 60 cm below the soil surface*" and "*areas of land in which periods of flooding and emergence of ground alternate*" respectively. There are, however, no agreed methods of defining wetlands resulting in imprecise quantification of the area under wetlands with different authors estimating that between 700 million (Aselmann and Crutzen, 1990) and 1024 million (Scharpenseel, 1993) hectares, translating to between 5 percent to 7 percent of the earth's surface, are covered by wetlands.

Wetlands have been classified by Stewart and Kantrud (1971) using seven zones depending on the vegetation found. These zones are: wetland-low-prairie zone, wet-meadow zone, shallow-marsh zone, deep-marsh zone, permanent-open-water zone, intermittent-alkali zone, and fen (alkaline bog) zone. The presence or absence and the distributional pattern of these zones gave rise to seven classes of wetlands. These classes are ephemeral, temporary wetlands, seasonal ponds and lakes, semi- permanent ponds and lakes, permanent ponds and lakes, alkali ponds and lakes, and fen ponds (Steward and Kantrud, 1971). Other classifications have used different criteria. Adamus (2001) used a hydrogeomorphic system and classified wetlands into riverine, depressional, slope, flats, lacustrine fringes and estuarine fringes. Cowardin et al. (1979) classified wetlands according to a hierarchical structure progressing from systems and sub-systems to classes and identified Marine, Estuarine, Riverine, Lacustrine and Palustrine wetland systems. Each system has a number of subsystems which are divided into several classes depending on the vegetation present (Figure 1).

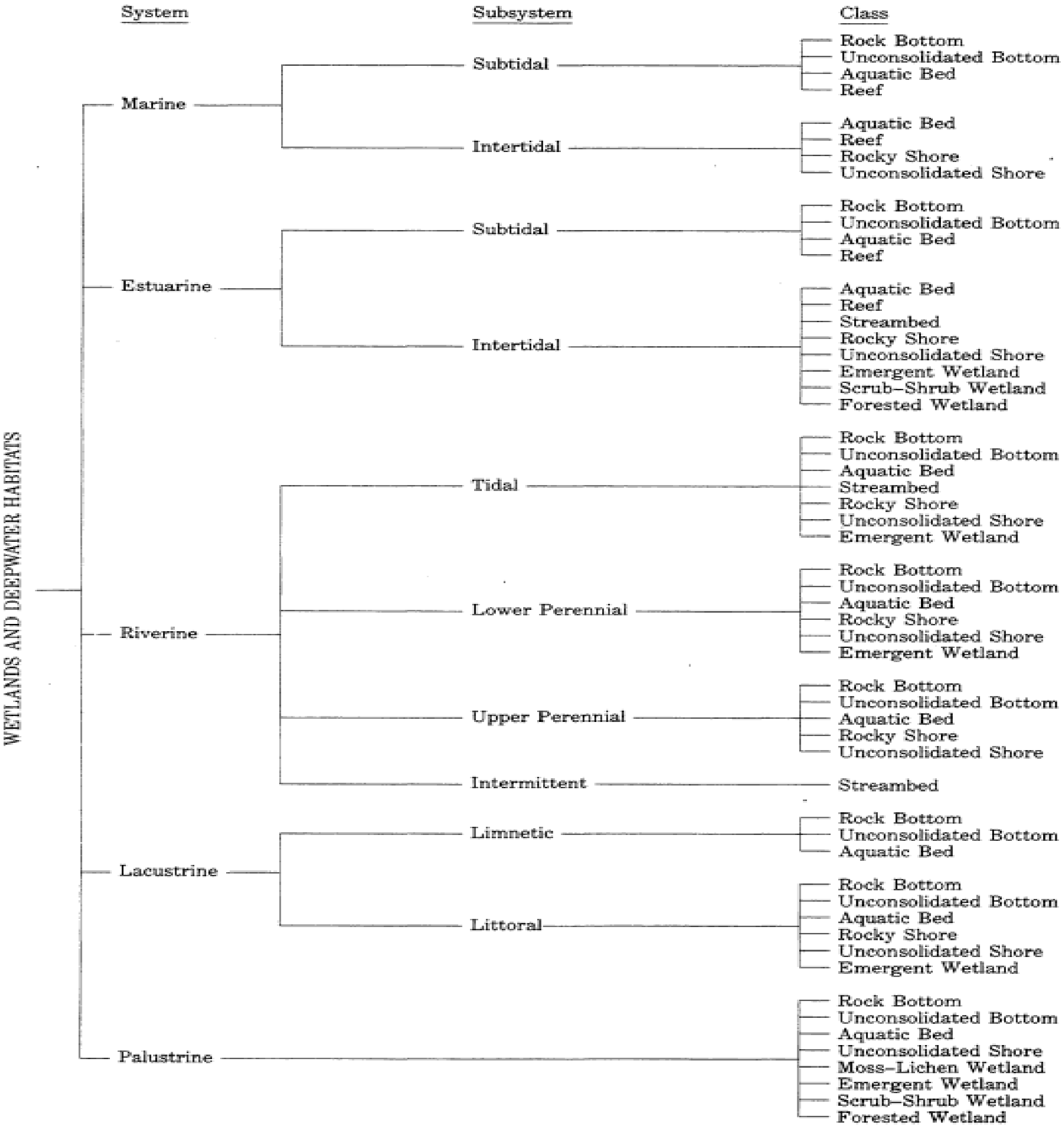

Figure 1: Classification of wetlands including deep water habitats (Cowardin et al., 1979)

The importance of wetlands is derived from their functions and uses. The functions of wetlands are defined as the normal or characteristic activities that take place in wetland ecosystem or simply the things that wetlands do (Babier, 1994). While it is acknowledged that not all wetlands perform all functions to the same degree and magnitude (Babier, 1994), Richardson (1994) and Keddy (2010) identified various attributes which are generally given as functions of wetlands. These are:

Hydrological flux and storage. These are the recharge and discharge of water from the water body as well as climate control through evapotranspiration export which is the large scale atmospheric loss of water.

Biological productivity including net primary and secondary productivity, and carbon storage and fixation.

Biogeochemical cycling and storage. Nutrient source or sink of carbon, nitrogen, sulphur and phosphorus, and their transformations through oxidation/reduction reactions, denitrification, sediment and organic matter reservoir.

Plant community and wildlife habitat including as a sanctuary for endangered and unique species and as a repository for biodiversity.

Decomposition and release of nutrients through microbial action.

Recording history

Wetland uses can be direct or indirect. The direct uses could be both commercial and non commercial activities and are categorized (Babier, 1994; Smardon, 2006) as:

Consumptive uses. These include livestock grazing, fuel wood collection, forestry activities, crop production, water use, hunting and fishing.

Non consumptive uses including recreation, tourism, in situ research and education, and navigation along water courses.

Indirect uses of wetlands are the functional values of wetlands such as flood control, and storm protection. Based on these uses therefore, users of wetlands are varied, each deriving a particular good and service from the wetland. Users will include rural and urban populations, governments, scholars, educational institutions, farmers, industry, pastoralists, environmentalists, wildlife, and practically every living organism that can derive something from the rich and productive wetland ecosystem. These uses and users of wetlands do not always interact in harmony. With proper planning, however, it is possible to optimize all the beneficial uses and conserve the environment (Dixon and Wood, 2003).

1.2 Tropical wetlands

Tropical wetlands, both marine and fresh water, cover in excess of 500 million hectares worldwide (Downing et al., 1993). Fresh water wetlands are known to be the most productive agricultural and natural ecosystem on earth (Downing et al., 1993) and are important agricultural production centres with growing importance (Windmeijer and Andriesse, 1993). Fresh water wetlands have been geomorphologically characterized by Roggeri (1995) as either (1) flood plains or alluvial lowlands, which are fringing floodplains, and inner delta floodplains; (2) Valley bottoms including small valleys, headwater lowlands and small overflow valleys; (3) littoral or lakeshore wetlands; and (4) depressions—wetlands in river and lake systems, formed by springs (blister wetlands) and isolated low lying areas. Flood plain wetlands are subject to inundation by lateral overflow water from rivers or lakes associated with them. Valley bottom wetlands are depressed areas that are surrounded by upland slopes and may or may not run along well developed streams, while lake littorals are wetlands immediately surrounding lakes and are intermediary areas between terrestrial and aquatic ecosystems. Studies on inland valley bottoms include measurements of plant available moisture in the root zones in Kenya (Boehme et al., 2013), soil characteristics and their constraints to crop production in Nigeria (Ogban and Babalola, 2003) and Kenya (Kamiri et al., 2013), response of rice to agronomic management under different hydrological regimes in Ivory Coast (Touré et al., 2009), and soil fertility parameters in West Africa (Issaka et al., 1997). In flood plains, studies focus on ecological and socio- economic attributes of food production in Kenya (Leauthaud et al., 2013), forest floristic composition and net primary production in the Peruvian Amazon (Nebel et al., 2001a; Nebel et al., 2001b). On the other hand, there is only little research on lake littoral zones besides vegetation ecology in Kenya (Gaudet, 1977; Morrison and Harper, 2009)

Fresh water wetlands, including lake littorals, are a critical source of water and nutrients for the communities living near them (Thompson, 1996), particularly in areas where water is progressively becoming scarce and, or the demand increases. It is estimated that at least 25 African countries would be water scarce by the year 2025 (UNEP, 1999). Already, a number of local conflicts have been attributed to competition for water and the control of access to wetlands (El-Kharraz et al., 2012). The introduction and rapid spread of irrigated farming around wetland zones is likely to increase the competition for water and conflict potentials among different users. Fresh water wetlands are also home to an important share of the world's biodiversity. They are breeding sites for several mammal and bird species, regulate the water flow and quality of lakes and rivers, and are sources of food and feed for the millions of species of living organisms dependent on them. These wetlands also receive the heaviest pressure from human activities and are therefore threatened. They have become centres of settlements, crop production, grazing grounds, access points for water extraction for humans and animals, and also sites for agro-industrial activities. To ensure a continued provision of these diverse functions and services, many of these sites have been protected under the Ramsar Convention on Wetlands (Ramsar, 2010). This convention is an intergovernmental treaty that provides the framework for national action and international cooperation for the conservation and wise use of wetlands and their resources. This is in an attempt to slow and manage the exploitation of these natural wetland resources, especially the biodiversity.

In riparian zones used as pasturelands, the incentive to graze livestock is related to the fact that riparian pastures are relatively more productive than those of upland areas during the dry season due to the favourable moisture conditions (Butler et al., 2008) and the wetland vegetation types which are known to influence grazing patterns of wildlife and livestock, especially during the dry season (Muthuri and Kinyamario, 1989). Depending on the plant species present and their quality as a feed, poor grazing management can lead to reduced stand density and forage ground cover (McGinty et al., 1979; Loch, 2000). A characterization of the quality, quantity and the seasonal dynamics of riparian vegetation will be a prerequisite to improve the grazing management, particularly in the littoral wetlands of lakes.

1.3 Wetlands in Kenya

Kenya is one of the countries in Africa which is considered water insufficient. The country is 80% arid and semi arid (ASAL) and the average rainfall is 800mm annually. The rainfall pattern is mostly bimodal in the remaining 20% of the land mass but in the ASAL, it is mostly unimodal. The unimodal rainfall falls for a few days between the months of March and May and within this period, the total precipitation could be as high as 300mm in two days indicating torrential rainfall which increases soil erosion, destroys infrastructure and feed resources as well as increasing water collection within body masses downstream. Coupled with increased dependence on livestock keeping as an economic activity which has over the years led to overgrazing, the unimodality of precipitation has presented a sharp seasonal availability of pastures for only less than half a year in the ASAL and a prolonged period of scarcity.

Annually, there are on average 8 months of dry spell in most parts of the country and for grazing ruminants, this means elongated periods of feed scarcity. Traditionally, the pastoral communities would move with their livestock from higher altitude to lower altitudes where the pastures grew faster and water was available during the rainy season. It was also warmer downstream than in the higher altitudes and the weather favoured better welfare for both the herdsmen and the young stock. They would move progressively upstream to end up at the high altitude zones during the dry season as they could still access stream and spring waters. Due to the cooler temperatures in the hill country, the pastures persisted longer and were thus utilized for dry season feeding. This cyclicity completely collapsed with increased human and livestock population, resultant overgrazing, land adjudication and environmental degradation.

However, the country is endowed with a number of water bodies and rivers which constitute the Kenyan wetlands. It is estimated that 14,000 km^2 of Kenya’s land area is covered by water bodies (Crafter et al., 1992), translating to 2.5% of the country’s total surface area while wetland-associated soils cover 10% of the total surface area (Wamicha, 1997). These wetlands are diverse in nature and distribution (Figure 2) and include the shallow lakes Nakuru, Naivasha, Magadi, Elmentaita, Baringo, Ol'Bolossat, Amboseli and Kamnarok; the edges of Lake Victoria; Lorian, Saiwa, Yala, Shompole swamps; Lotikipi and Kano plains; Tana River Delta; as well as the coastal wetlands including the mangroves swamps. The main flood plain wetland used for both crop cultivation and livestock keeping in the country is the Bura irrigation scheme within the Tana River Delta. Most other river flood plains such as Yala, Ahero and Ewaso Ng’iro are periodically used for food and feed production accentuating their importance. Particularly, the littoral fringes of permanent fresh water lakes in the drier areas of Kenya are traditionally important for both nomadic and sedentary communities as sources of water for domestic uses as well as for watering livestock. They have also become sources of irrigation water for small-scale vegetable and maize farming as well as for agro-industrial enterprises. Lakes Victoria and Naivasha are the most important fresh water lakes of Kenya with the littoral riparian lands being intensively used by surrounding communities. However, because of the importance of these riparian environments as sites for biodiversity and a range of regulatory and cultural services, Lake Naivasha has been partially protected and is among the five Ramsar sites in Kenya.

1.4 Lake Naivasha

Lake Naivasha (0^0 45’S, 36^0 20’E) is Kenya’s second largest fresh water body located in a high altitude trough of the Rift Valley at an altitude of 1890m (2010 level). It covers a surface area of about 140 km^2 and has a maximum depth estimated to be 6 metres. It is the only fresh water body in a system of otherwise alkaline-soda Rift Valley lakes (Harper and Mavuti, 2004) with an estimated electrical conductivity of the water being 250µs/cm (Everard et al., 2002). The lake is bounded by Ndabibi plains to the west and Ilkek plains to the north of Naivasha town. The Mau escarpment to the western fringe rises to 3080 metres above sea level, the topography to the south rises to 2430 m.a.s.l, while the Kinangop plateau to the east rises to a maximum of 2740 m.a.s.l. The geology of the area around the lake is mainly composed of succession of late tertiary and quaternary volcanoes intervening lacustrine beds (Ayenew et al., 2007). The soils on the lacustrine plains around the lake have developed on sediments from volcanic ashes, ranging from well drained to poorly drained soils, fine to sandy silts and clay loams with variable fertility (Clarke et al., 1990) and have been described as lacustrine sediments and alluvial deposits (Girma et al., 2001). An example of a lacustrine system is illustrated in Figure 4.

Lake Naivasha wetland has inflows from river Malewa, which drains the Aberdare plateau range and contributes 90% of the total inflows (Ayenew et al., 2007), river Gilgil, draining the Rift Valley escarpment ridges, and river Karati which is seasonal and contributes minimally. Figure 3 shows rainfall and temperature averages of Lake Naivasha area based on a set of global climate layers (climate grids) with a spatial resolution of about 1 square kilometre, the WorldClim 50-year monthly climate data. The Lake supports a complex vegetation of terrestrial (example: *Acacia xanthophloea*) and littoral plants (examples: *Cyperus papyrus* and *Potamogeton spp*), providing foraging and breeding ground for many resident and migrant bird species (Wetlands International, 2007) including more than 350 species of water birds. Hundreds of hippopotamuses and several species of large mammals including buffalo and waterbuck live in the riparian area. The water from this lake and its inlet rivers is used for drinking, washing, and livestock watering by some 800,000 people (KNBS, 2012) who live within the Lake Naivasha catchment measuring about 2150 km^2 (Morrison et al., 2013).

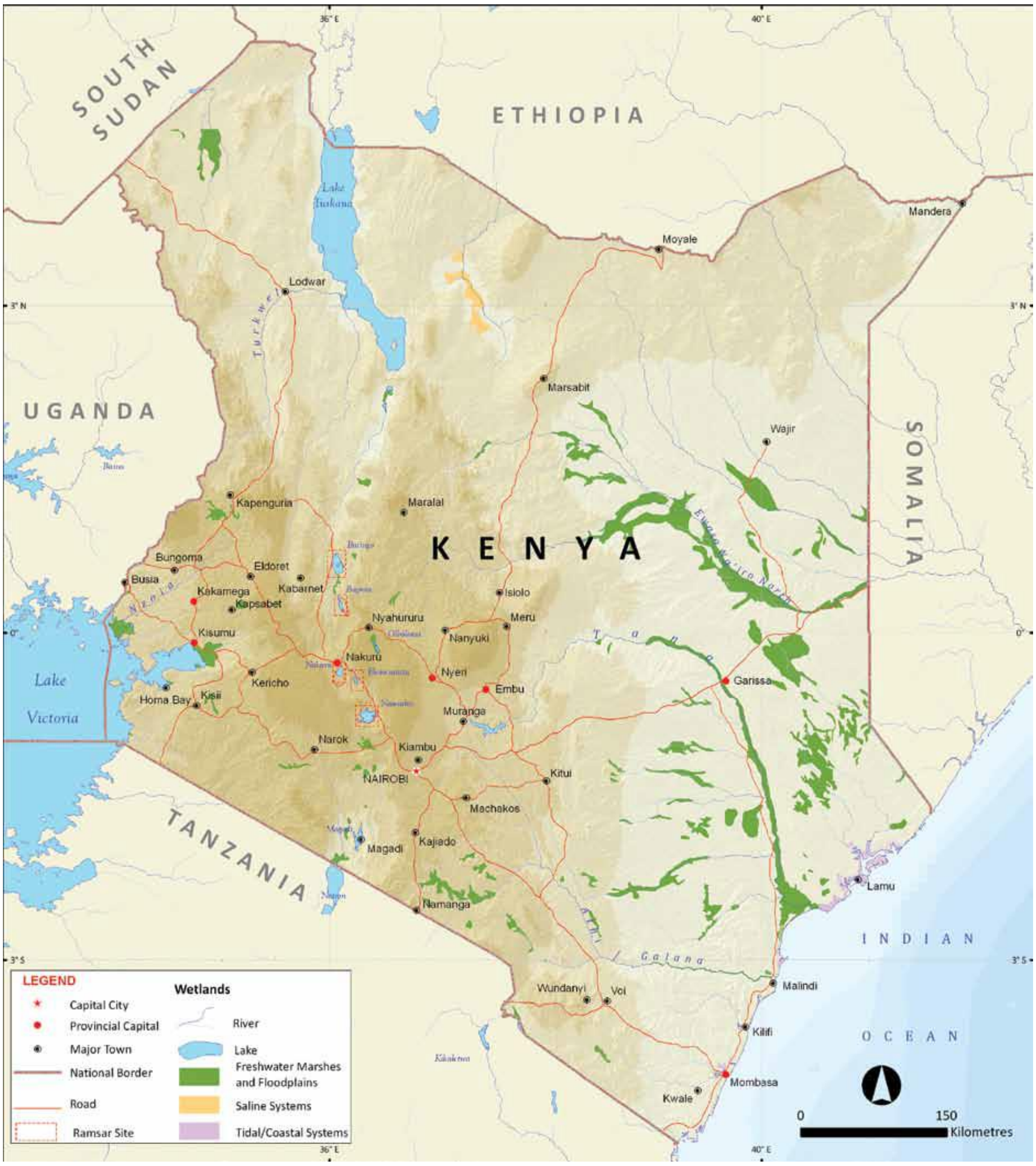

Figure 2: Map of Kenya indicating distribution and types of wetlands (Source: NEMA, 2011)

In recent decades, the riparian zones of this lake have been opened up for cultivation, and the biggest activity is the growing of cut flowers for export. Kenya is the leading exporter of cut flowers and Naivasha supplies about 75% of these. Flower export is a top foreign exchange earner contributing significantly to the Kenyan economy. There are over 40 large scale flower farms around Lake Naivasha employing more than 50,000 people. However, the flower farms abstract water from the lake for irrigation, exerting pressure on the lake water level that is subjected to inverse fluctuations and has been periodically declining (Verschuren et al., 2000). At least 80% of the perimeter of the lake is under diversified forms of land use. The increase in population around Lake Naivasha, mainly driven by the in-migration of labourers to work in flower farms, has increased the pressure on the lake's resources as people partially depend on the lake water for their domestic use and use the riparian land for food crop production and as grazing ground for livestock. Individual households (agrarian and pastoralist), resource-poor smallholder farmers, large-scale commercial entrepreneurs, wildlife, livestock, public institutions and hospitality industry depend on Lake Naivasha for their daily water supply.

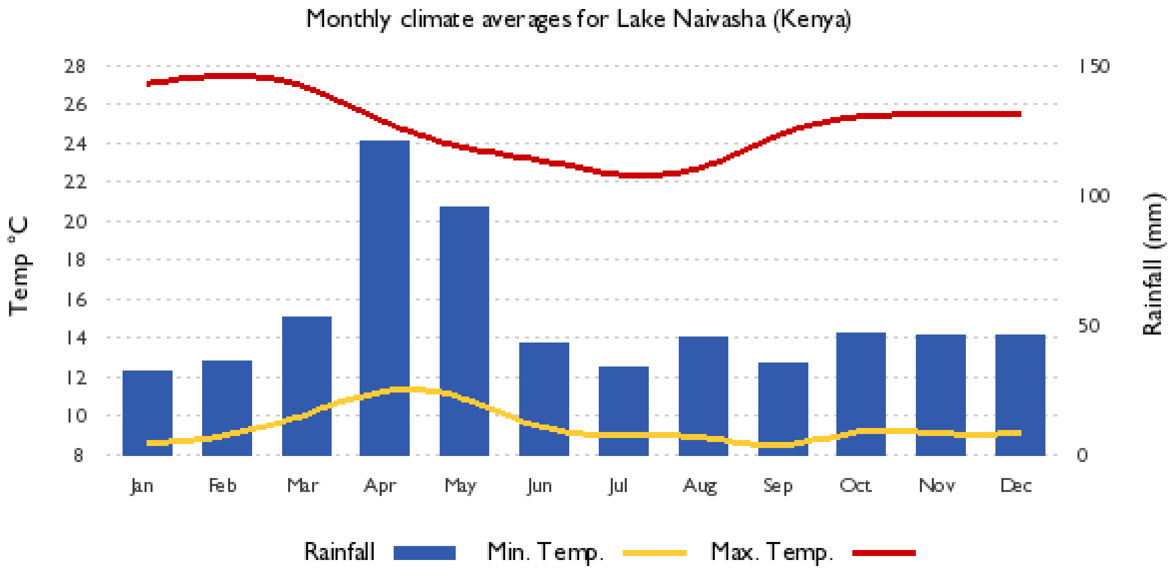

Figure 3: Long-term average temperature and rainfall patterns in Lake Naivasha (JRC, 2010).

Resource uses around Lake Naivasha include wildlife conservancy and livestock ranching, food crop production, tourism, pastoralism, fishing and intensive greenhouse floriculture and horticulture. Former stock rearing, ranching, wildlife reserves, and cultivation of sisal are rapidly giving way to irrigated commercial floriculture. Floricultural technology, including intensive use of pesticides has grown quantitatively over the past two decades and this has seen rapid encroachment of riparian land. Besides destabilizing fragile ecosystems, the encroachment into the riparian land severely constrains access by pastoralist livestock to grazing and this limits livestock productivity (Scoones, 1991). Commercial floriculture has relegated livestock production and wildlife grazers to the much drier peripheries of the riparian areas contributing to increased grazing pressure and social conflicts. Compounded by the receding water levels, the fencing off of cultivated areas has cut off watering points for both livestock and wildlife and exacerbated the disturbance of the livestock-wildlife balance previously existing in the wetlands of Lake Naivasha. In recognition of the importance, and need for protection, of this ecosystem, Lake Naivasha was declared a Ramsar site in April 1995 (Ramsar, 2009)

1.5 Wetland Pastures and Pastoralism

Because of the absence of a uniform way of defining wetlands, many definitions have tended to vary according to the needs of each audience (Tiner, 1999). For the purposes of this thesis, the definition by Finlayson et al. (1999) is adopted with the following modifications:

Inclusion of areas that were part of the lake during the previous 30 years but have been exposed due to progressive lake shrinkage;

Exclusively consisting of littoral areas that are permanently under grass and other annual and perennial plants and are only inundated during seasons of extreme high water and does not include open water areas.

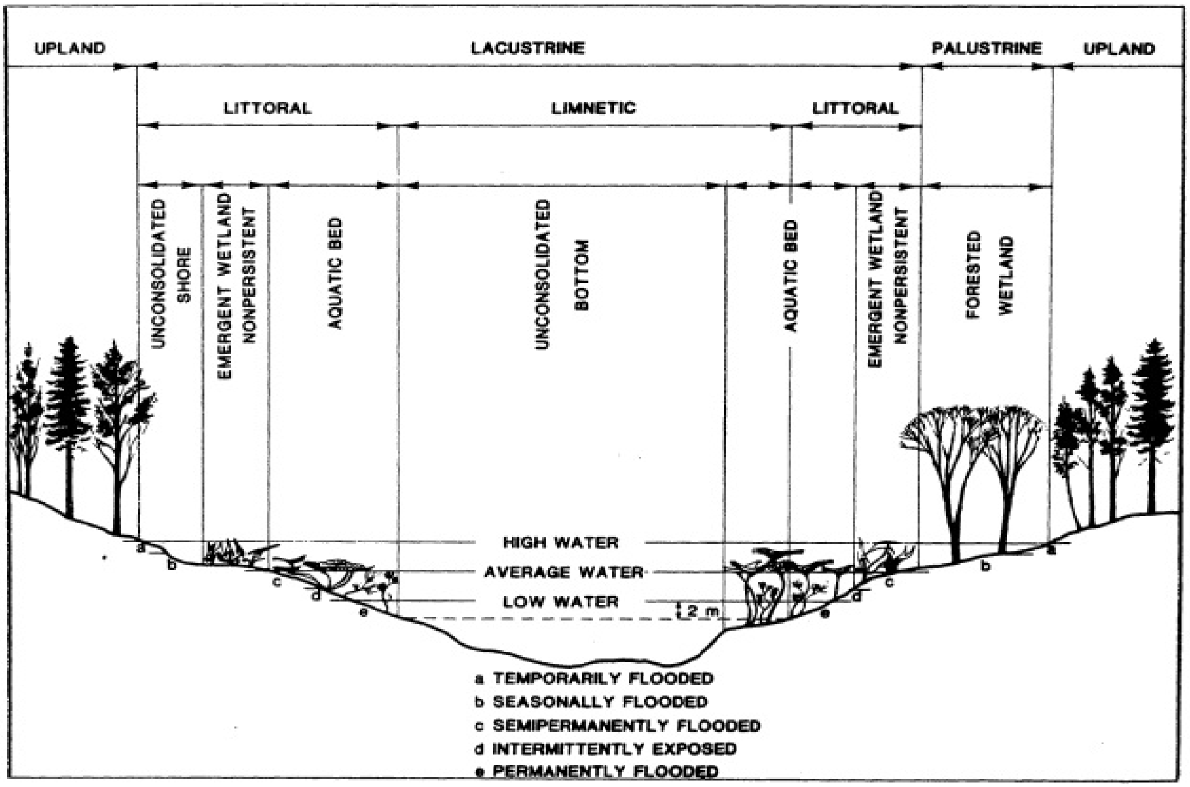

Figure 4: The Lacustrine system and its distinguishing features (Cowardin et al., 1979)

This thesis specifically addresses the northern littoral wetlands of Lake Naivasha where a portion of the lake shore remains largely uncultivated and is currently used as a wildlife sanctuary and can be accessed by Maasai pastoralists for dry season feeding of their livestock. The National Animal Husbandry Research Centre of the Kenya Agricultural Research Institute (KARI) has a farm adjacent to the northern shore of the lake and during the dry season, their livestock also use the natural pastures on this uncultivated portion of the riparian land. The north portion of the riparian borders the largest inlet, River Malewa. Part of the north shore was a flood plain and formed much of the former papyrus swamps.

In addition to the various species of wildlife animal grazers roaming the littoral, various livestock production systems are practiced. There is the seasonal pastoralism by the Maasai during the dry season which is usually between the months of December to March every year. Several herds of cattle and sheep, each numbering more than a hundred heads, are usually present each day of the three months of the dry season. Dairy ranching is practiced by KARI, by grazing their dual-purpose Sahiwal herd and goat flocks on the littoral pastures during the same dry season. Small-holder production systems are also practiced by landless peasants who maintain a few animals, grazing them whole-year round on the riparian pastures. Others would harvest the pastures for use in feeding their animals away from the littoral area. There are no data in literature on the number of pastoralists or small scale farmers who use the lake Naivasha littoral to feed their livestock but Harper et al. (2009, unpublished) reports counting over 30,000 heads of cattle coming to water on the southern part of the lake per day during the dry season.

1.5.1 Dry season feeding and resource conflicts in the Naivasha wetland

Because of scarcities of livestock feeds, the rangeland surrounding Lake Naivasha has been experiencing dry season livestock starvation. In the particularly severe 2008-2009 drought, the Government was forced to provide emergency hay to farmers in some ASAL areas severely affected by drought. These areas included Kajiado where most of the migrant cattle that graze along the lake Naivasha riparian during the dry season originate. This intervention was however late and insufficient to mitigate the feed shortage occasioned. It is estimated that between 18 and 33% of the cattle died of starvation during the period (ILRI, 2010). Apart from the deaths which are absolute economic loses, loss of body condition and loss of production constitute an economic loss for the farming communities and negatively contributes to national economy.

Pastoralist livestock and wildlife are increasingly depending on the Lake Naivasha wetland grazing resources for their dry season feeding and also easy access to water. As anthropogenic activities like agriculture and human settlements as well as climate changes increased, ruminant and pseudo-ruminant wildlife have been ousted from most of their former habitats around the lake and are now dependent on the few riparian open spaces for their survival. Due to this convergence of increasing dependence on increasingly limited resources, human-human as well as human-wildlife conflicts have often arisen. Government and environmentalists have raised awareness on these conflicts. Issues of conservation and balancing of feed resource exploitation within this wetland between wildlife and pastoralist livestock and other riparian users during the dry season are now imperatives.

1.5.2 Riparian plant species around Lake Naivasha

In the Lake Naivasha riparian land, plant collection started as early as 1920's (East African Herbarium, Nairobi). Gaudet (1977) quotes several authors suggesting that the ecology of Lake Naivasha has been a subject of speculation since 1929. Early vegetation surveys include those by Beadle (1932) and Jenkin (1936). Table 1 gives a list of major plant species found around the lake.

Of the grasses recorded by Gaudet (1977) on the eastern shores of the lake, he observed that cattle and hippos preferred to graze on *Pennisetum clandestinum*. There is very little in literature about grasses and forbs found on the other parts of the lake Naivasha riparian considering that although the lake water could be relatively homogenous, the geological formation and soil types are varied. Harper et al. (1995), however, noted that *Cynodon spp* and other grasses replaced papyrus when the lake receded between 1983 and 1987. It is likely that other parts of the riparian could have a number of other different grasses and forbs as well as different relative proportions in the ground cover. Likewise, the climatic changes and changes in land use may also lead to species changes over time. Rich plant diversity has been linked to higher biomass productivity (Tillman, 1999) and that ecosystems experiencing high temporal fluctuations in resource availability often imply higher overall primary productivity as different species can reach peak productivity at varying periods over yearly cycles (Silva et al., 2009). The species dynamic changes have sustainability implications as well as the nutritional quality of the natural forages as utilized by ruminants along the riparian grassland of Lake Naivasha.

Table 1: Major plant species of the Lake Naivasha riparian land.

Species	**Family**	**Source**
Acacia drepanolobium	Fabaceae	Agassiz and Harper (2009)
Acacia seyel	Fabaceae	Agassiz and Harper (2009)
Acacia xanthophloea	Fabaceae	Agassiz and Harper (2009)
Achyrantes aspera	Amaranthaceae	Own survey (2011)
Acocanthera schimperi	Apocynaceae	Own survey (2011)
Amaranthus dubius	Amaranthaceae	Own survey (2011)
Cassia didymobotrya	Fabaceae	Own survey (2011)
Centrosema pubescens sp.	Fabaceae	Own survey (2011)
Conyza bonariensis	Asteraceae	Gaudet (1977)
Cynodon plectostachyus	Poaceae	Own survey (2011)
Cyperus laevigatus	Cyperaceae	Gaudet (1977)
Cyperus papyrus	Cyperaceae	Gaudet (1977)
Cyperus rotundus	Cyperaceae	Own survey (2011)
Datura stramonium	Salanaceae	Own survey (2011)
Euphorbia candelabrum	Euphorbiaceae	Own survey (2011)
Lotus uliginosus	Fabaceae	Own survey (2011)
Pennisetum clandestinum	Poaceae	Own survey (2011)
Poa palustris	Poaceae	Own survey (2011)
Senecio flaccidus	Asteraceae	Own survey (2011)
Sesbania sesban	Fabaceae	Own survey (2011)
Sida adoensis	Malvaceae	Own survey (2011)
Solanum incanum	Solanaceae	Own survey (2011)
Solanum nigrum	Solanaceae	Own survey (2011)
Sonchus oleraceus	Asteraceae	Gaudet (1977)
Tagetes minuta	Asteraceae	Own survey (2011)
Trifolium semipilosum	Fabaceae	Own survey (2011)
Verbena bonariensis	Verbenaceae	Own survey (2011)

Schaich et al. (2010) classifies plant species whose presence exceeded 25% of vegetation cover to be dominant. Some plant species can become successful and dominant as to discourage the growth of other species in the same locality thereby necessitating some form of control to maintain a healthy biodiversity. If the species intended for control is palatable to ruminants, it is a double benefit to use grazing as a control measure.

1.6 Grazers of the Lake Naivasha riparian

The fringe zones of Lake Naivasha is habitat to over 50 large wild mammal species including grevy's zebra (*Equus grevyi*), beisa oryx (*Oryx beisa*), gerenuk (*Litocranius walleri*) (Mavuti and Harper, 2006; Becht et al., 2006). There are also the common Hippopotamus (*Hippopotamus amphibious*), and cattle (*Bos indicus* and *Bos taurus*) from pastoralists (Harper and Mavuti, 2004; Mavuti and Harper, 2006) during the dry season. Morrison and Harper (2009) estimated that there were up to 1,500 buffalos (*Syncerus caffer*) grazing the lake Naivasha riparian. There are also found waterbucks (*Kobus ellipsiprymnus*), and common zebra (*Equus burchelli*). These different species have different feeding habits, preferences for different species and also differ in numbers present and body sizes. The complexity of the grazing population on the riparian area available to grazers round the year is such that it is almost impossible to quantify what each species contributes to the grazing pressure. There is no literature documenting the herbivore grazers' carrying capacity of Lake Naivasha riparian.

1.7 Chronosequences at Lake Naivasha

Chronosequence is a term used to denote a sequence of communities that characterizes a range of time since a disturbance or a set of sites formed from the same parent material or substrate that differs in the time since they were formed (Walker et al., 2010) and for the purposes of this thesis, this term is used to describe the sequence of land use durations since the soils were exposed to primary and secondary plant successions. Land use in the study area is continuous grazing and the disturbance is the soil exposure to aerobic conditions as the lake receded.

The amount of precipitation, evaporation rates, and water abstraction for various uses are the drivers influencing lake levels. The floodplains surrounding water bodies such as lakes are often particularly affected as a slight drop in water level exposes, and increase in level inundates, a large area. Spatial and temporal patterns of floods are known to influence the distribution of wetland vegetation (Hejnỳ and Segal, 1998). Keddy (2010) explains that any change in the hydrological regime of a lake is always expected to cause major changes in the distribution of plants surrounding the lake and also its wetland vegetation zonation. The recession of the lake due to reduction in the water level can be temporary or permanent.

Lake Naivasha has experienced an overall lake recession which has been permanent over a long period of time (Figure 5) but there have also been seasonal, temporary fluctuations. This recession has been accelerated in recent years by water abstractions to the flower farms around the lake. The rainfall pattern in Naivasha indicates reduced rainfall over the last 30 years, further aiding in the accelerated recession of Lake Naivasha (Figure 6). The exposed land has had plant species successions and the land has been used for various anthropogenic activities and a clear chronosequence of land use established.

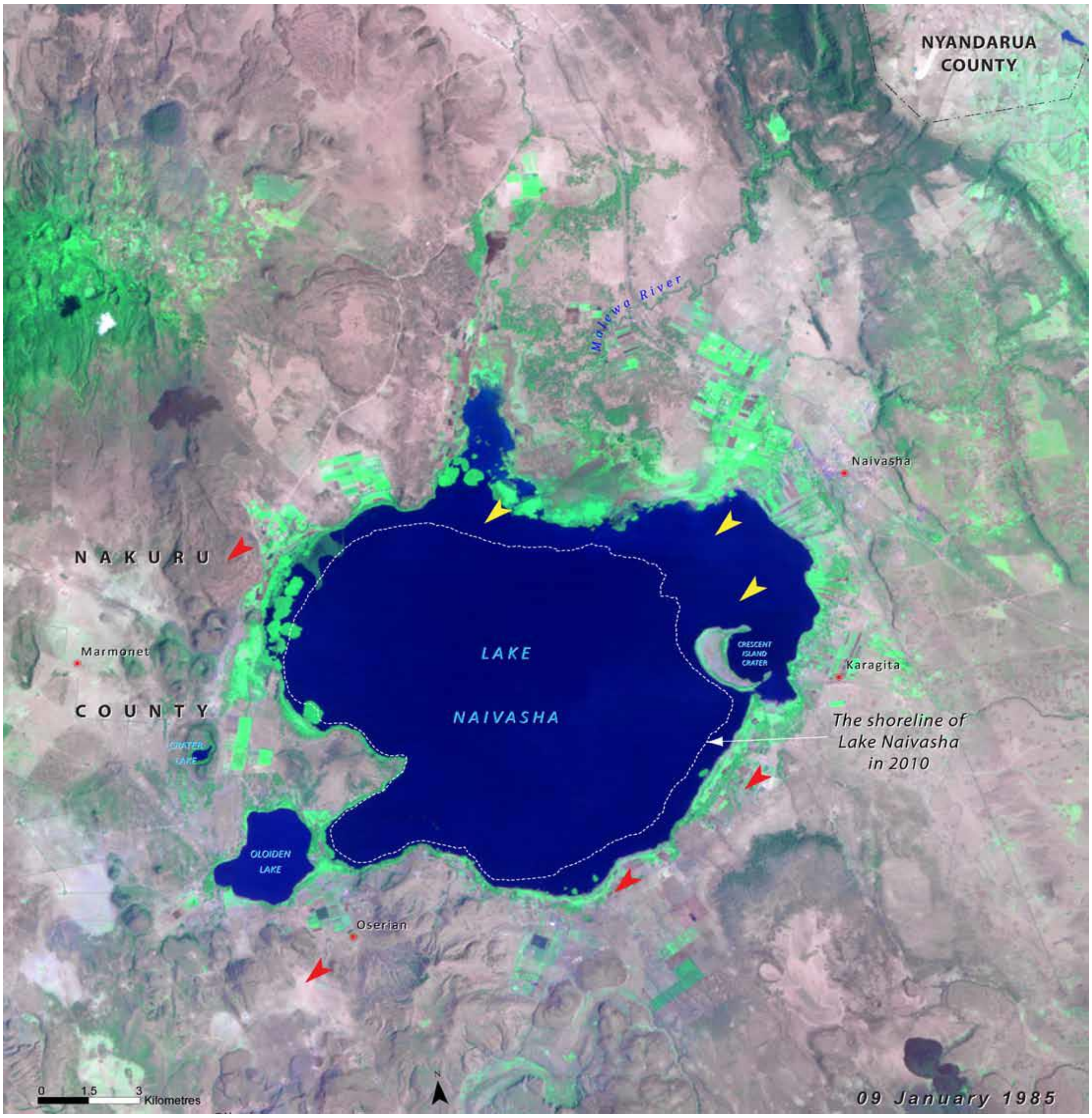

Figure 5: A satellite image of Lake Naivasha in 1985 with superimposed line showing the shorelines in 2010. (Source: MEMR, 2012)

1.7.1 Plant species changes

Secondary plant succession on the land exposed by the receding lake during a permanent reduction of the water levels gives rise to floristic changes (Odland, 2000; Su et al., 2012;). As the distance from the lake edge increases, ground water depth increases too and this leads to increased water stress to the plant species present. Grime (1973) documented that increased water stress results in an initial increase in species. Prolonged or increased stress would finally lead to a decrease in species diversity (Grime, 1973).

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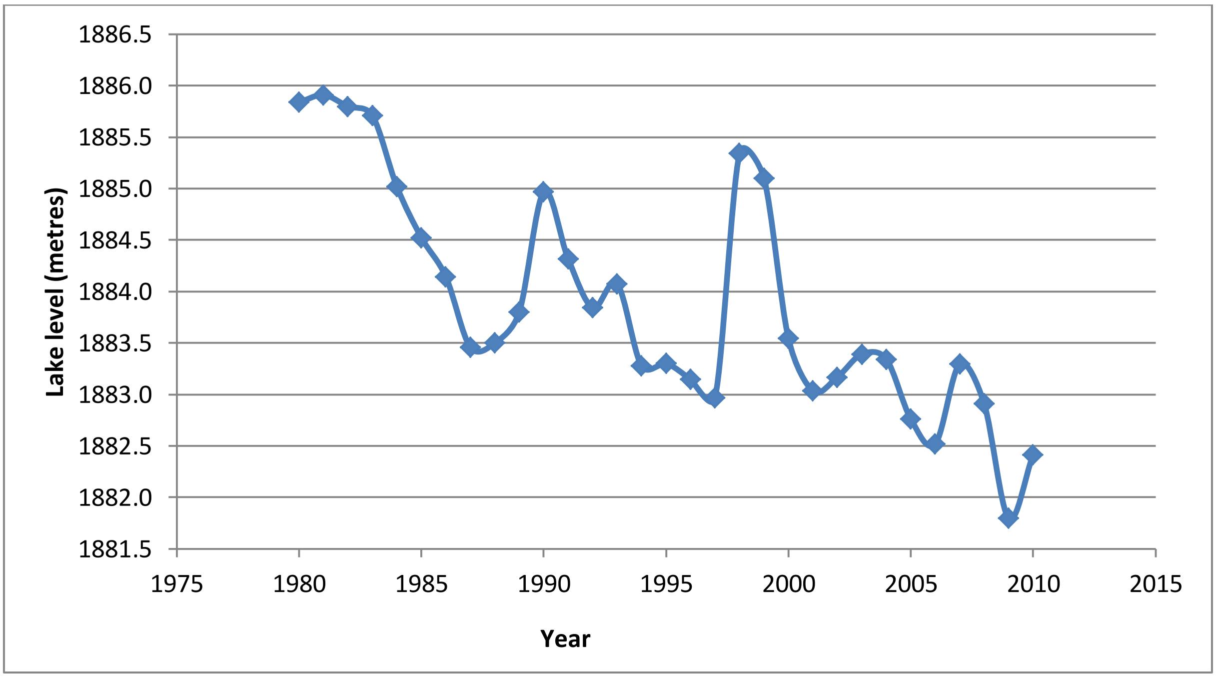

Figure 6: Lake Naivasha levels from 1980 to 2010 (Source Homegrown-Sulmac flower farm)

Vegetation studies around Lake Naivasha have largely been on Papyrus (Gaudet, 1977; Muthuri et al., 1989; Muthuri and Jones, 1997; Boar, 2006; Morrison and Harper, 2009). These centred on the importance of Papyrus in maintaining the swamps and in filtering the inflow into the lake. Other species were mentioned only in so far as they succeed papyrus, the drier the land became after recession. There is therefore very little one can find in literature on grass and forb species changes during natural receding of Lake Naivasha. The change in the characteristics of the grass and forb species covering the exposed land area after the receding of Lake Naivasha over the years is of interest for ruminant nutrition, as we can infer carrying capacities and potential nutritional benefits to ruminants. Environmental protection and management of conflicts between human users as well as human-wildlife conflicts will be consequential benefits from knowledge of the floral patterns on riparian floodplains. This thesis describes changes in natural littoral forage species composition and changes in their nutritional quality with increased duration of land use after receding of Lake Naivasha.

1.8 Approaches to studying wetland pastures

1.8.1 Remote sensing

In studying temporal vegetation dynamics over a wide area of study, several tools have been developed to overcome the difficulties of area of coverage as well as the time span over which data needs to be collected (Petit et al., 2001). Among the tools that have been used in Kenya are aerial photography, Geographic Information System (GIS) maps as well as remote sensing. Remote sensing is the use of aerial sensor technologies to capture natural or projected radiation on an object of interest. It uses the simultaneous multi-spectral platforms which take images in multiple wavelengths of electromagnetic radiation to produce maps of land cover. It is a fast method of data collection and can be used in inaccessible areas. For example, Maluki (2007) mapped land use and land cover changes using remote sensing in Mbeere District, while Olson (2004) used both aerial photographs and satellite images to map vegetation cover in both Embu and Mbeere Districts. Using remote sensing Were et al. (2013) investigated the spatial and temporal land cover changes in the Lake Nakuru catchment, while Kirui et al. (2013) studied the mangrove forests at the Kenyan coast. In Lake Naivasha, remote sensing has been used to map land use/cover changes around the lake (Naliaka, 2011), the intensity of land use within the catchment basin on the quality of the lake water (Onywere et al., 2012), the decline of the lake water storage (Awange et al., 2013), and to evaluate spatio-temporal variation in chlorophyll-*a* (Ndungu et al., 2013). Studies on plant communities within grassland vegetation using the remote sensing technique may not be accurate and require additional field ground survey in order to allow observation and description of processes of land cover (Petit et al., 2001). This is because the minimum community area for grassland vegetation is 1 m x 1 m (Zhang, 2000) which may not be exclusively captured remotely by satellite.

1.8.2 Ground study and vegetation survey

As a validation to the remote sensing approach, ground studies are usually done in areas where the accessibility is relatively easy, and the area of coverage can permit the study within the time constrains. This is especially so if the study is interested in individual grass and forb species present as well as study of plant succession at the micro level. Primary succession after land exposure from receding of a water body has been studies with the use of transects where species were recorded in places of minimal disturbance (Rydin and Borgegärd, 1988). Celaya et al. (2007) explored the vegetation dynamics where the exposed land mass after reduction of water level was also exposed to continuous grazing pressure. There is no literature on any research describing the vegetation dynamics of littoral Lake Naivasha pastures after several years of continuous grazing. This thesis presents results of using ground study and vegetation survey as the best approach in order to capture individual forage species presence and relative abundance within the lake Naivasha riparian.

1.8.3 Land use duration approach

Climate-induced permanent receding of a lake takes a long period of time, in the scale of decades or centuries. It is therefore possible, for purposes of study, to mark spots of the exposed land corresponding to specific number of years of exposure, and designate these as chronosequence positions in the study of pastures. The exposed land experiences primary, then secondary plant successions, as well as periods of stabilization of plant communities. The specific species emergence, growth and stability are determined by edaphic factors, both biotic and abiotic, as well as water availability. Type of land use as well as the degree of use, as disturbance factors, will determine the status and the stability of the plant community present as well as acting as feedbacks to the edaphic environment. Using land use duration (chronosequence) as a basis for studying plant succession is good for successions of decadal to millennial time-scales and where sites of different ages follow the same trajectory (Walker et al., 2010). The lake Naivasha littoral pasture use is by wildlife grazing all-year round and nomadic pastoralism for at least three months of the year. Since no cultivation is practiced and the pastures are wild natural species, the land has a Ruthenberg index (R) of 0 according to the following formula:

R = (Number of years of cultivation / Length of cycle of land utilization) x 100
(Ruthenberg, 1980)

Riparian pastures are good examples of plants in various stages of succession and since chronosequence positions can be identified using the specific points of lake levels during recession, it is possible to use land use (grazing) duration to study the riparian Lake Naivasha pastures.

1.8.4 Grazing as land use and in assessing pastures

Sustained moderate to high grazing pressure on pastures has been known to affect herbage shoot re-growth, eventual reproduction and biomass yield (Clary and Kinney, 2002; Matheson et al., 2002). Following intensive grazing, unpalatable forage species and forbs rapidly assume dominance further suppressing palatable forage species (Hickerman and Hartnett, 2002). Increased grazing intensity is known to reduce biomass yield and has little effect on percent Carbon of above ground plants (Han et al., 2008). Intensive grazing could, therefore, lead to decrease in soil quality and fertility as soil organic carbon and total Nitrogen decrease with increased grazing intensity for soil depths up to 30cm (Han et al., 2008). However, in some situations, intensive grazing can eliminate undesirable species (Anderson and Calov, 1996) and maintain an ecologically healthy species balance.

The effects of grazing livestock on species composition have been shown through work done in different wetlands. Studies on wet and dry meadows have shown that up to three years of deferred grazing does not affect above ground net primary production although seasonal grazing deferral on the wet meadows can yield benefits to livestock productivity (Bottolph and Coppock, 2004). Where dominant species are reduced through grazing, species richness has been increased (Jacobs and Naiman, 2008) but if the dominant species are not palatable or are resistant to grazing, then a decrease in species richness will result (Keddy, 2010). Species richness declines also when trampling or over-consumption of certain species is sufficient to eliminate more species than are recruited (Champion et al., 2001) and this happens under high intensity cattle grazing (Tanner, 1992). Bakker (1985) found that when cattle are grazed at the rate of 1.6 animal units/ha, forage selection depends on the amount of newly produced biomass not on its protein content and digestibility. Therefore, under heavy grazing, species that have recently produced biomass are more likely to be impacted. Species composition is also affected by trampling, with some species being better adapted to compact soils (Wardle,

1991) and others requiring bare batches created by trampling to establish such as annual or stoloniferous species (Grevilliot and Muller, 2002). Various researchers (Buxton et al., 2002; Forsyth et al., 2003; Walker et al., 2003; Ewans, 2004), working to determine optimal grazing necessary for conservation of wetlands have generally concluded that the effects of grazing are so variable that grazing decisions should be based on conservation objectives specific to each site.

In order to study natural pastures through grazing, elaborate structures for paddocks, a large area of natural pastures, and many animals for use in the study as well as large quantities of feed will be required. This is not possible with the Lake Naivasha forages since this would necessitate the exclusion or relocation of all the resident wildlife as well as the prohibitive cost involved. Alternative evaluation methods exist and this thesis reports results of evaluation of the natural forages of littoral Lake Naivasha using *in vitro* and *in vivo* methods.

1.8.5 Feed evaluation using *in vitro, in situ,* and *in vivo* approaches

Whereas biomass productivity in wetlands has been studied variously using remote sensing (Moreau et al., 2003) and ground survey (Jacobs and Naiman, 2008), the true benefits of the biomass in animal nutrition can only be assessed by determining whether these feeds can be consumed voluntarily, degraded, digested and metabolized by the grazers. The quantity consumed can be inferred by relative harvest of the material from the field by the grazers but this presents an uncertainty as to which species of grazers did actually pick the material especially in free ranging grassland with several species of both large and small ruminants and pseudo-ruminants. There are, however, several approaches in the assessment of feeds which can be applied to riparian pastures to obtain accurate values of nutritional quality, intake and digestibility.

In vitro evaluation of feed involves use of laboratory techniques such as chemical analysis and artificial digestion and degradation mimicking the animal situation to assess feed. These methods are at best predictive of feed value as the best arbiter in assessment is the target animal itself (Mould, 2003). *In vitro* methods always use substrate disappearance to assess degradation and rarely provide information regarding the quantity of derived end-products available to the host animal (Mould, 2003). However, in ranking feeds in terms of quality, *in vitro* evaluation is a useful and accurate tool (Sheng et al., 2008). As a rapid evaluation method, *in vitro* method of feed analysis offers a fast, cheap and reliable alternative to evaluations using animals.

An *in situ* evaluation method uses rumen degradability to assess the extent to which a feed sample is fermented by rumen microbes. It is a technique using special bags into which feed samples are weighed and incubated in the rumen. Fermentation substrates as well as soluble materials are diffused out of the bags and the disappearance is calculated to represent what was degraded within the incubation time. Often times, rumen degradation is synonymous to digestibility (Mehrez and Ørskov, 1977). The advantage of this method is its ability to estimate degradability of specific feed constituents like crude protein, organic matter and Neutral Detergent Fibre. It is also used to assess the feed degradation kinetics (Ørskov and McDonald, 1979). This method has been used to assess various feeds (Melaku et al., 2003; Tagliapietra et al., 2011; Krizsan and Huhtanen, 2013) though it has limitations. It only measures disappearance of feed and not the actual fermented substrate and it requires the use of rumen-canulated animals which is expensive and raises ethical issues of animal welfare (Nocek, 1988; Stern et al., 1997).

In vivo methods use the whole animal system to assess feed. The animal is fed with the experiment feed which is then processed through the gastro-intestinal tract, undergoing all the natural mechanical, microbial and enzymatic action. *In vivo* evaluation therefore measures the true nutritional worth of the feed from the animal's perspective. It allows for voluntary feed intake, nitrogen balance (Adesogan et al., 2002) as well as true digestibility to be measured. This method is however expensive as feed required should be sufficient to meet the animal's nutrient requirements. It requires frequent feed and animal handling and the choice of feed by the animal is limited by the researcher's desires. In feed evaluation, this method remains the best method to assess and rank feeds. The results presented in this thesis demonstrate how forage species dynamics and the nutritional quality of natural forages change within the littoral riparian of Lake Naivasha when they are subjected to continuous grazing.

CHAPTER 2: STRUCTURE AND SCOPE OF THESIS

2. Scope and Structure of Thesis

2.1 Scope

This PhD thesis presents work undertaken as part of a Deutsche Forschungsgemeinschaft (DFG)-funded project on “Resilience, Collapse, and Reorganization in African Savannah systems” and co-funded by Deutscher Akademischer Austausch Dienst/National Commission for Science, Technology and Innovation (DAAD/NACOSTI) grant. It presents results on the determination of how the durations of land use, as the lake recedes, have affected the species composition and quality of forage in the wetlands of Lakes Naivasha. The choice of lake Naivasha riparian was informed by the fact that it is a fresh water lake within a series of alkaline lakes of the Rift Valley, Kenya and also because it has experienced intensive use by various stakeholders. This has often led to conflicts therefore necessitating a multi-sectoral study to seek ways of better and beneficially exploiting the resources around the Lake.

2.2 Hypothesis and objectives

Increased land use duration after lake recession and subsequent continuous grazing of the Lake Naivasha riparian grasses is hypothesized to affect soil properties, floral characteristics, biomass production, and forage nutritional quality, consequently differentially affecting livestock productivity.

To test this hypothesis, the main objective of the study is to determine how the species composition and abundance as well as nutritional quality of the naturally occurring forage are affected by the chronosequence position (duration of land use by continuous grazing) including soil type and soil moisture availability and their changes along the toposequence of the riparian wetlands of Lake Naivasha. Knowledge of this will inform strategies to enhance resilience of the wetlands, increase livestock productivity and reduce land use conflicts.

The specific objectives addressed include:

1) To determine how species composition and relative abundance of the forages currently grazed and browsed along a chronosequence of the Lake Naivasha riparian land are affected by duration of land use (Chapter 3).

2) To determine the effect of continuous grazing duration and soil types on biomass Productivity and nutritional quality of natural pastures of Lake Naivasha riparian (Chapter 4).

3) To determine the intake and digestibility of the natural pasture grasses of Lake Naivasha riparian by sheep (Chapter 5).

4) To determine the interaction between soil type and duration of land use in their effect on feed nutrient quality and availability as well as the implication of this interaction on livestock productivity (Chapter 6).

These objectives are addressed and presented in the present thesis using the following format:

a) Chapter 1: General introduction

b) Chapter 2: Scope and structure of thesis

c) Chapter 3: Floristic changes in grasslands along a chronosequence at Lake Naivasha, Kenya (Objective 1).

d) Chapter 4: Biomass and quality changes of forages along land use and soil type gradients in the riparian zone of Lake Naivasha, Kenya (Objective 2).

e) Chapter 5: Feed intake and digestibility of natural vegetation in the riparian land of lake Naivasha, Kenya (Objective 3).

f) Chapter 6: General Discussion and Conclusion (Connecting objectives 1, 2 and 3) (Objective 4)

g) References

CHAPTER 3: FLORISTIC CHANGES IN GRASSLANDS ALONG A CHRONOSEQUENCE AT LAKE NAIVASHA, KENYA

3. Floristic changes in grasslands along a chronosequence at Lake Naivasha, Kenya

3.1 Introduction

A continuous decline in the water table has been observed between the 1980s and 2008 at Lake Naivasha Kenya. This decline has been attributed to water abstraction from the main inlet River Malewa for domestic use in Nakuru town and direct abstraction of the lake water for irrigation in the floricultural farms (Mekonnen et al., 2012). Domestic water demand has also been increasing due to the human immigration to settlements allocated on the lake's fringes (Hickley et al., 2004). Such anthropogenic effects have been exacerbated by a decline in annual rainfall between 1960 and 2008 (Awange et al., 2013). Declining and irregular rainfalls have resulted in strong fluctuations of the water level of Lake Naivasha (Harper et al., 1990) and lead to a significant increase in the area of riparian land.

Lake recession, but also clear-cut of vegetation for access to the water resources or for cultivation, has highly impacted on the aquatic and riparian vegetation, which was formerly mainly dominated by papyrus (*Cyperus papyrus*) (Harper et al., 1990). This impact is highly noticeable at the North Swamp, an area of about 11 km^2 formerly occupied by papyrus (Harper, 1992). One of the main factors restricting the regeneration of papyrus is the increase in grazing pressure by cattle, African buffaloes and other large herbivores (Boar, 2006; Morrison and Harper, 2009). While decline in papyrus reeds in Lake Naivasha has been broadly studied since the late 1970s (e.g. Gaudet, 1977), there is no information available on the succession of plant communities developed under grazing use and progressive water recession. Such knowledge is of high importance as the riparian land is an important feed resource area for both livestock and wildlife, particularly during the dry season.

The riparian land is currently covered by grassland communities and individual fever trees (*Acacia xanthophloea*). Such communities occupy soils that were formerly covered by lake water and are currently exposed to terrestrial conditions. The duration of exposure depends on the location of the land with respect to the lake's fringes, with longer exposure for distant locations and shorter exposure for locations closer to the lake's fringes. Since decadal periods of change can be detected using secondary plant successions (Walker et al., 2010), studies on exposure chronosequence (space-for-time substitution) can provide information on floristic changes in the grasslands as affected by land use duration. Floristic changes are likely to be associated not only with the duration of land use but also with changes in soil properties or moisture availability and will impact on both the quantity and quality of forage in the riparian land.

This work addresses the following questions: 1) to what extent does the duration of land use affect the species composition and diversity in grasslands of Lake Naivasha? 2) Which are the key determinants of these changes? 3) Is there an affinity of single plant species to a chronosequence position?

3.2 Material and Methods

3.2.1 Study site

This study was carried out on the former north swamp of Lake Naivasha, Kenya (0°43'31.11"S, 36°22'12.80"E); on land adjacent to the premises of the Kenya Agriculture Research Institute (KARI). The land area is characterized by natural vegetation which is grazed by both wildlife and pastoralist livestock, particularly during the dry season when pastures are scanty elsewhere. The climate is cool tropical and semi-arid with average temperatures of 16-20°C and annual rainfall of 620 mm (Clarke et al., 1990). The rainfall is concentrated in two short rainy seasons, between Apr-May and Jan-Feb (Gaudet and Melack, 1981).

The soils of the littoral are mainly formed of lacustrine sediments partially mixed or overlaid with alluvial deposits at the fringes and the river mouth of Malewa River (Clarke et al., 1990). According to the differences in soil formation, we henceforth refer to sites of either ‘lacustrine’ or ‘alluvial’ origin.

3.2.2 Experimental set-up, samples and data collection

Based on the general trends of lake water level declines (provided by Homegrown-Sulmac Flower farm) for 30 years, four chronosequence positions were determined, corresponding to 15, 20, 25 and 30 years before start of experiment (± 0.1 m), using a geodetic Leica 500 GPS device (Leica Geosystems AG, Heerbrugg, Switzerland). Chronosequence positions represent duration of exposure to terrestrial conditions and to grazing (land use). Four transects were established across the chronosequence for sample collection. Two transects were located on lacustrine sediments (transect 1L and 2L) and two on alluvial deposits (transect 1A and 2A). In each chronosequence position, plots of 400 m^2 size (total of 16 plots) were demarcated. All vascular plant species present were inventoried and their percentage cover (phytosociological relevés; Dengler et al., 2008) was estimated.

In each plot, three bulk soil samples (composites five sub-samples) were taken at a depth of 0-15 cm. The samples were air-dried, sieved (<2 mm) and dry stored for laboratory analysis. Laser diffraction technique (Retsch LA-950 V2 Horiba) was used to determine soil texture. Soil pH (H_2O) and electrical conductivity (EC_{25}) were measured in a suspension with soil to water ratio of 1:2.5. The inorganic carbon content was measured by Scheibler method (Tatzber et al., 2007). Ground sub-samples were analyzed for total C and N using a CNS Elemental Analyzer (EuroEA 3000, Euro Vector SpA, Milan Italy). Available P was measured according to Olsen and Sommers (1982), 1.5 g of air-dried soil (<2 mm) being extracted with 30 ml of 0.5 M $NaHCO_3$ (pH 8.5), shaken for 30 minutes and analyzed colorimetrically at 880 nm wavelength (Genesys 10 UV, Thermo Fisher Scientific Inc., Waltham, MA, U.S.A). Soil moisture content was determined in pits up to 100 cm depth in each plot. Soil horizons were identified according to FAO (2006) and three 100 cm^3 core samples were taken from each soil horizon. The core samples were weighed fresh, then oven-dried at 105°C for at least 24 h, and weighed again. The volumetric soil water content (*SWC*) was calculated for each horizon as $SWC = (FW - DW) / DW * BD$, where *SWC* being the volumetric soil water content, *FW* the mean soil fresh weight (g), *DW* the mean soil dry weight (g), and *BD* being the mean bulk density (g/cm^3). For each plot, a curve of volumetric water content depending on soil depth was calculated using a non-parametric local regression (LOESS) with a span of 100 mm (Dormann and Kühn, 2008). The total water content for the first 1000 mm of soil was estimated as the area below the curve, using partial integration (water content simulated at steps of 10 mm depth). Samples were taken between Dec 2010 and Jan 2011. For the nomenclature of vascular plant species, the African Plant Database (URL: http://www.ville-ge.ch/musinfo/bd/cjb/africa/recherche.php) was used as reference.

3.2.3 Statistical analyses

Statistical analyses as well as plotting were carried out using “R” (version 2.11.1; http://CRAN.R-project.org). The floristic relationships between plots were assessed by ordination analysis and non-metric multidimensional scaling (nMDS) (using *metaMDS* in the R-package *vegan* (version 2.0-5; http://CRAN.R-project.org/package=vegan). The number of dimensions was fixed at two, to allow for visual interpretation of the ordination, and using the Bray-Curtis index as dissimilarity measurement (Lepš and Šmilauer, 2003). In the ordination diagrams, we overlaid surfaces showing the trends of chronosequence positions as isolines (function *ordisurf* in *vegan*) and vectors showing the general trends of soil physical-chemical properties (function *envfit* in *vegan*). Floristic dissimilarities and plot-related variables (transect identity, chronosequence position, soil physical-chemical properties and soil water content) were correlated using a series of Mantel tests by calculating the Pearson’s coefficient of correlation after 1,000 permutations (function *mantel* in *vegan*).

The diversity values within chronosequence positions were compared by calculating the species richness in each plot and estimating their evenness according to Pielou (1966). Each matrix was tested as a correspondent to chronosequence position using the Kruskal-Wallis test (function *kruskal.test* in R). The affinity of single recorded species to chronosequence positions was determined by species indicator analysis (Dufrêne and Legendre, 1997), considering both frequency and abundance of species in each chronosequence position. Indicator values were calculated using the function *indval* in the R-package *labdsv* (version 1.5-0), setting the number of iterations to 100. Changes of abundance of species along the chronosequence were quantified as average cover, excluding zero values from the calculation.

3.3 Results

3.3.1 Floristic composition and soil properties

In total, 12 vascular plant species were recorded in the studied grasslands. From them, only Kikuyu grass (*Pennisetum clandestinum*) and Naivasha star grass (*Cynodon plectostachyus*) had cover values >50%, *Senecio mesogrammoides* (Compositae) reached a cover value of 12.5%, which was much higher than that of any of the other recorded species (Table 2). In general, soil conditions were relatively favourable for plant growth, as indicated by high total

N (4.3 g kg^{-1}), plant available P (20.7 mg kg^{-1}), organic C (49 g kg^{-1}) contents, and a near neutral pH (7) (Table 3). The average electric conductivity of 0.5 dS m^{-1} indicates slight salinity. Soil tended to be silt loam (FAO, 2006) with average moisture of 340 mm for the first 100 cm. Figure 7 shows the average volumetric water content, across all chronosequence positions, of the soils within the experiment plots during the experiment period.

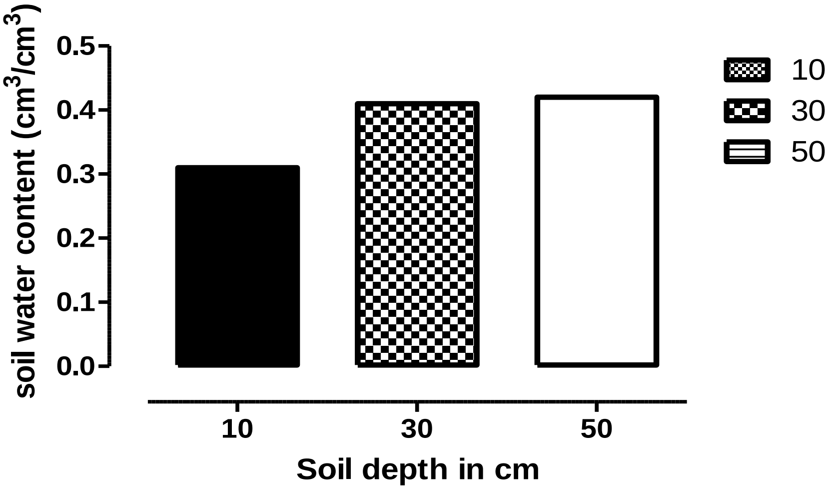

Figure 7: Average soil water content of the study area during the data collection period

Table 2: Mean percent land cover of vascular plant species per chronosequence position at Lake Naivasha, Kenya.

Species	% Land cover per chronosequence position (years)				
	15	20	25	30	overall
Pennisetum clandestinum	96.8	66.3	51.3	26.3	60.1
Cynodon plectostachyus	16.0	46.0	58.8	86.3	51.8
Senecio mesogrammoides	8.4	17.8	20.0	3.8	12.5
Achyranthes aspera	0.4	1.9	2.0	3.8	2.1
Cycnium tubulosum ssp. *montanum*	0.3	1.3	0.1	4.5	2.1
Datura stramonium	-	-	2.0	-	2.0
Verbena brasiliensis	0.3	0.5	1.9	3.3	1.5
Conyza bonariensis	-	0.5	1.3	-	0.9
Lotus pedunculatus	0.5	0.1	0.5	0.7	0.6
Solanum incanum	0.5	-	-	0.2	0.3
Sesbania sesban	0.3	-	0.1	-	0.2
Cassia didymobotrya	0.1	0.1	0.1	-	0.1

3.3.2 Dissimilarity patterns and relations to soil variables

The stress value of the nMDS ordination of 0.19 indicates a relatively good correspondence between observed dissimilarity patterns and ordination coordinates according to Backhaus et al. (2006). Figure 8 shows a clear trend in the plot distributions according to chronosequence position, from the lower left corner (15 years) to the upper right corner (30 years). Nevertheless, plots located at higher chronosequence position (30) seem to be floristically more similar than plots located at the lowest position (15). Looking at the centroids of transects (Figure 8), there are two clear groups namely A-B and C-D. Those groups correspond to the soil types where transects are located, A-B corresponding to lacustrine sediment soils (transects 1L and 2L) and C-D to alluvial deposit soils (transects 1A and 2A). According to the direction of vectors, the chronosequence position appears to be positively correlated with the sand and negatively with the silt, organic carbon, total nitrogen and moisture of the soil. Available P and electric conductivity tend to have higher values in alluvial deposit soils, while pH and clay content appear to be higher in lacustrine sediment soils. According to permutation methods, variables with a significant effect on similarity patterns are the chronosequence position, the total N and organic carbon contents and the pH (Table 3). On the other hand, transect identity, soil texture (proportions of sand, silt and clay) and soil moisture did not significantly affect similarity patterns as measured by the Bray-Curtis index. According to the Kruskal-Wallis test, neither the species richness nor the evenness is significantly different ($P > 0.05$) between chronosequence positions (Table 4).

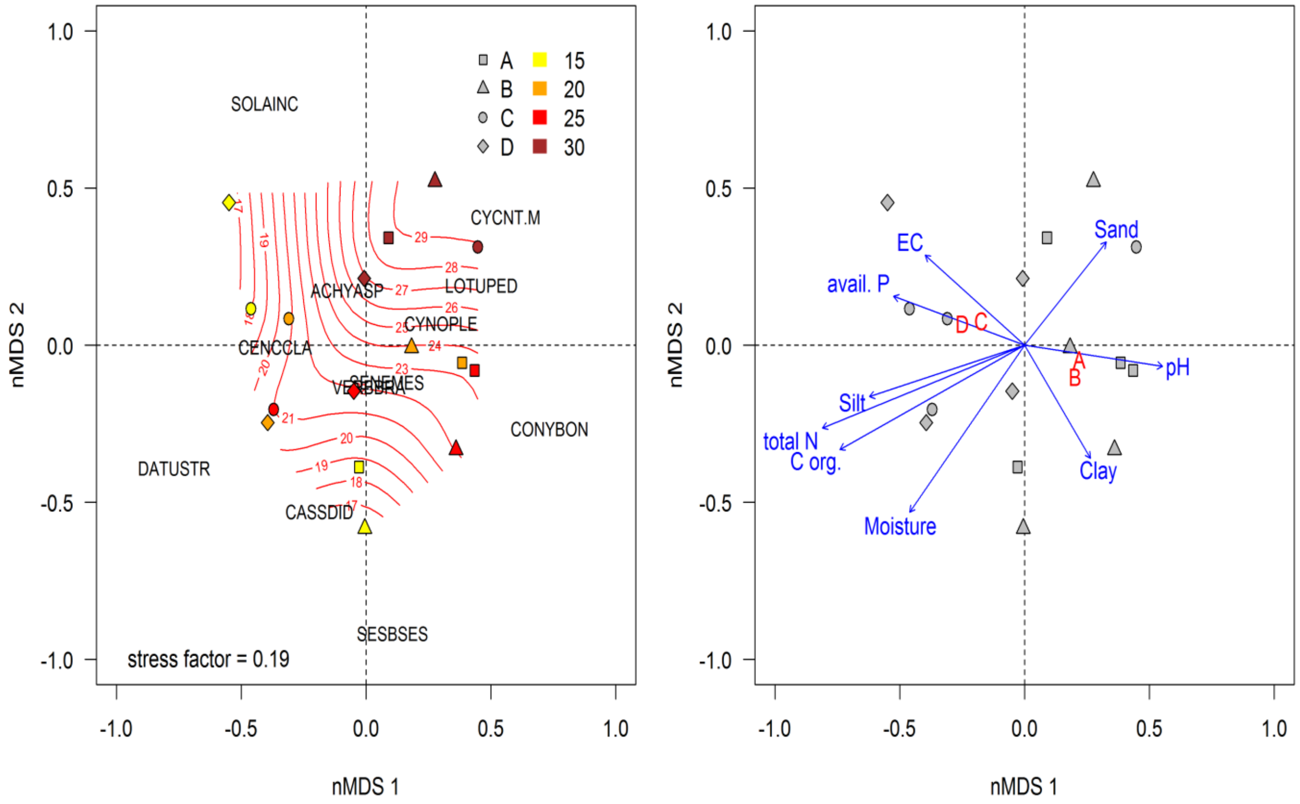

Figure 8: Ordination diagram of species and soil parameters

nMDS: non metric multidimensional scaling; A, B, C, D: transect lines 1L, 2L, 1A and 2A respectively; 15, 20, 25, and 30: chronosequence positions(years of land use); EC: electrical conductivity; P: Phosphorus; N: Nitrogen; Corg: organic Carbon.

Species codes are SESBSES (*Sesbania seban*), CENCCLA (*Cenchrus clandestinus*, synonym of *P. clandestinum*), CASSDID (*Cassia didymobotrya*), VERBBRA (*Verbena brasiliensis*), SENEMES (*Senecio mesogrammoides*), CONYBON (*Conyza bonariensis*), DATUSTR (*Datura stramonium*), CYCNT.M (*Cycnium tubulosum ssp*. montanum), LOTUPED (*Lotus pedunculatus*), ACHYASP (*Achyranthes aspera*), SOLAINC (*Solanum incanum*), and CYNOPLE (*Cynodon plectostachyus*).

Table 3: Permutation tests (mantel test) comparing dissimilarities with transects (soil types) and chronosequence positions (land use duration) at Lake Naivasha, Kenya.

Variable	units	Average ± SE	Mantel R	P value	
Transect	-	-	0.113	0.204	ns
Chronosequence	-	-	0.331	0.010	**
Total N	g kg^{-1}	4.3 ± 0.31	0.467	0.001	**
Available P	mg kg^{-1}	20.7 ± 2.17	0.108	0.143	ns
Organic C	g kg^{-1}	49.0 ± 3.81	0.427	0.002	**
pH	-	7.0 ± 0.17	0.224	0.041	*
Electric conductivity	dS m^{-1}	0.5 ± 0.11	0.034	0.615	ns
Sand	%	8.4 ± 1.35	-0.002	0.983	ns
Silt	%	81.3 ± 1.07	0.145	0.073	ns
Clay	%	10.4 ± 0.78	0.120	0.099	ns
Moisture	mm	340.4 ± 26.3	0.147	0.059	ns

Mantel R is equivalent to a Pearson’s correlation coefficient. P value is the degree of significance, which is either non-significant (ns, $P > 0.05$), significant (*, $P < 0.05$) or highly significant (**, $P < 0.01$).

Table 4: Diversity parameters of floral inventories compared between chronosequence positions (land use durations) in the riparian land of Lake Naivasha, Kenya by Kruskal-Wallis test.

Variable	Average ± SE	χ^2	d.f.	P value
Species richness	6.6 ± 0.32	0.86	3	0.835
Evenness	0.4 ± 0.04	1.68	3	0.642

Table shows values of chi squared (χ^2), degree of freedom (d.f.) and significance (P value).

3.3.3 Species responses to chronosequence position

The species analysis showed that few species are good indicators for the low chronosequence positions while most species were related to the chronosequence position 30 years (Figure 9). Changes on the species indicator values along the chronosequence reflect the species turnover during the succession as the lake water level declines. The most obvious trend is shown by the reduction of abundance of Kikuyu grass (*Pennisetum clandestinum*) and the increase of Naivasha star grass (*Cynodon plectostachyus)*; (Table 2) as the grazing duration increases. This indicates that Naivasha star grass tolerates low soil moisture and poor soil fertility much better than Kikuyu grass. An increasing soil pH along the 1L and 2L transects with increasing distance from the Lake margin tended to favour *C. plectostachyus* which is known to tolerate alkaline soils.

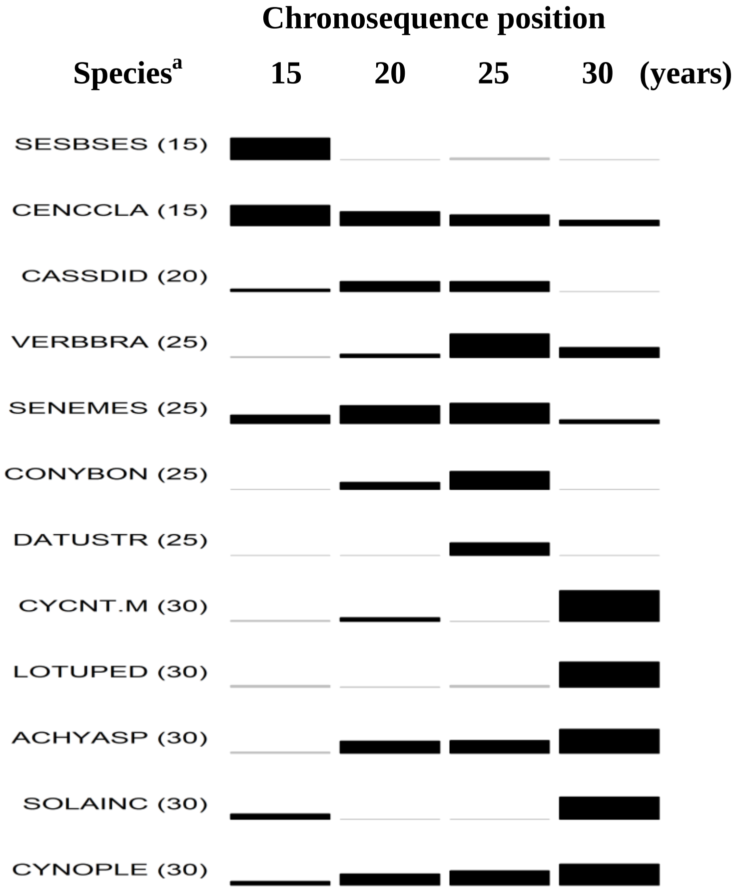

Figure 9: Relative indicator values of species per chronosequence position

In parenthesis is the chronosequence position with the maximum indicator value for each species. Grey bars are non-significant indicator values (P > 0.05). Values of the bars vary from 0 to 0.7 (see Table 3).

[a]Species codes are SESBSES (*Sesbania seban*), CENCCLA (*Cenchrus clandestinus,* a synonym of *P. clandestinum*), CASSDID (*Cassia didymobotrya*), VERBBRA (*Verbena brasiliensis*), SENEMES (*Senecio mesogrammoides*), CONYBON (*Conyza bonariensis*), DATUSTR (*Datura stramonium*), CYCNT.M (*Cycnium tubulosum* ssp. *montanum*), LOTUPED (*Lotus pedunculatus*), ACHYASP (*Achyranthes aspera*), SOLAINC (*Solanum incanum*), and CYNOPLE (*Cynodon plectostachyus*)

3.4 Discussion

3.4.1 Floristic succession and its relations to soil parameters

Clear relationships between similarity patterns and chronosequence positions support the hypothesis of determination of species composition under grazing by the duration of land exposure to aerobic soil conditions in the riparian land. Such changes show a “convergent succession” according to the schemes proposed by Walker et al. (2010). Soil type (alluvial deposits or lacustrine sediments) is likely to be a stronger determinant of species composition during early succession stages and under high soil moisture contents, while in older succession stages and on drier soils, the grasslands species composition appear to be indifferent to soil types. Soil types do not have a significant effect on the overall species composition according to the Mantel test. Changes in species composition along the chronosequence are associated only with the soils’ contents in total N, organic C as well as the pH. While C and N declined with receding lake water level, the pH tended to increase. Against our expectations, soil moisture content did not significantly affect species composition, reinforcing the importance of use duration (determined by the exposure of soils to aerial conditions) on species composition. Floral successions related to lake recession indicate a convergence of species composition and no chronosequence effects on species diversity. Consequently, land exposure or land use duration can entail a compensatory replacement of species as well as a shift in species dominance.

3.4.2 Shifts in species dominance

The analysis of indicator species highlights a gradual shift in the dominance from *P. clandestinum* to *C. plectostachyus*. While the semi-aquatic *Sesbania sesban* is strongly associated with young chronosequence stage (15 years), the typical dryland species *Cycnium tubulosus* ssp. *montanum*, *Lotus pedunculatus*, *Achyranthes aspera* and *Solanum incanum* are associated with older chronosequence positions. All other plants reached their maximum indicator values at the mean position of land use duration and are therefore not suited to serve as indicators for land use duration. Similar changes in cover have been reported for fen grasslands dominated by *Paspalum distichum* in India (Middleton et al., 1991). In this study, however, the decline in cover of *P. distichum* occurred just after three years and was associated with a reduction in overall cover, without a compensatory increase in dominance of a competitor species.

Both, *C. plectostachyus* and *P. clandestinum* are adapted to conditions of the humid tropics and had been introduced from tropical Africa to other mountainous regions near the equator (Mears, 1970; López-González et al., 2010). While *P. clandestinum* characterizes the early succession stages and is adapted to high soil fertility (Mears, 1970), *C. plectostachyus* reportedly tolerates soil alkalinity (Singh et al., 2013). These adaptive features are clearly reflected in the observed species dominance at Lake Naivasha. These findings support the progressive floristic transition scenario suggested by Froend and Sommer (2010).

In conclusion, land use duration following a chronosequence of lake recession strongly affects species composition in the riparian land of Lake Naivasha, independent of the soil type. The succession can be summarized as the shift in dominance from kikuyu grass at early succession stages to Naivasha star grass in the later stages. This shift is also associated with changes in certain soil attributes.

CHAPTER 4: FORAGE BIOMASS AND QUALITY CHANGES ALONG LAND USE AND SOIL TYPE GRADIENTS IN THE RIPARIAN ZONE OF LAKE NAIVASHA, KENYA

4. Forage biomass and quality changes along land use and soil type gradients in the riparian zone of Lake Naivasha, Kenya

4.1 Introduction

Kenyan wetlands cover an area of approximately 14,000 km^2 (GOK, 2013). They fulfil important ecological, economic, and social functions. Though the characterization of wetlands has traditionally been sectoral, the use policy of Kenyan wetlands includes aspects of biodiversity conservation to allow an agricultural exploitation under the “wise use” policy (Kiai and Mailu, 1998). Among the recognized options under the “wise use” policy is the grazing by wildlife and domestic ruminants during the dry season, particularly during periods of drought and in arid and semi-arid areas (Kiai and Mailu, 1998; GOK, 2013). There, pastoralism is recognized as the most important livelihood strategy (Sanford, 1983). In Kenya, more than 80% of the land is classified as arid or semi-arid, and pastoralism is the dominant livelihood system (Bourn and Blench, 1999). Demographic growth and increasing pressure on the available land and water resources as well as increasingly variable and unpredictable precipitation patterns have recently enhanced the pressure by pastoralists on wetlands as sources of water and pasture. In the fringes of Lake Victoria, massively increased numbers of pastoralist livestock during the dry season have led to the degradation of the environment due to over grazing (Hongo and Masikini, 2003). In the Ewaso Narok swamp, a combined use by pastoralists and small scale farmers has led to the destruction of both the wetland and the rangeland and increased human-wildlife conflict (Thenya, 2001).

Dry season foraging zones in Kenya’s rangelands have been studied as key resource areas (Ngugi and Conant, 2008) with aims being the understanding of their dynamics and to identify, protect and restore critical forage areas. Some of these resource areas are utilized sparingly as grazing reserves (Ruttan and Mulder, 1999), while others are in constant use, both by pastoral ruminant and by wildlife grazers. The land of Lake Naivasha riparian is one such key resource area, where a portion of the lake fringe is accessible to both all-year wildlife and dry season pastoralist livestock grazing. Since 1910, the lake levels have varied by at least 9 m (Becht and Harper, 2002) and in the last 30 years, the rate of decline has been accelerated by reduced rainfall and increased water abstraction mainly for domestic uses and the growing of cut flowers or vegetables on farms adjacent to the lake. The reduction in the lake level has incrementally exposed land surfaces where grasses have established creating a chronosequential transect of continuous grazing for durations of 1-30 years. It is estimated that there are over 50 species of wild grazers roaming the northern shores of lake Naivasha (Mavuti and Harper, 2006), most of them permanently resident and utilizing the open grassland and water resources.

Continuous grazing of permanent pastures constitutes a disturbance which, together with other biotic and abiotic factors, helps determine the balance of species present in a particular environment (Chaneton and Facelli, 1991; Matějková et al., 2003). Highly palatable plant species tend to be grazed more and depending on the grazing pressure, can be decimated and eliminated from the environment, while the less palatable ones dominate. However, in a mixture of species with related palatability, the selection is not so intense as to negatively impact on one species over another. In such a case, grazing will help maintain species balance as it will reduce competition for light and other resources thus providing slow-growing plants a chance to compete and survive (Kotowski and van Diggelen, 2004). The natural grassland of Lake Naivasha are dominated by Kikuyu grass (*Pennisetum clandestinum*) and Naivasha star grass (*Cynodon plectostachyus*) that are both classified as very palatable to ruminants (Fulkerson et al., 2007; Georgiadis and McNaughton, 1988). Naivasha star grass is known to be more resistant to drought stress and to better tolerate alkaline and sodic soils (Uddin et al., 2009) than Kikuyu grass. Both species are also known to be highly adaptable to high grazing pressure and have the ability to rapidly regenerate after intensive grazing and trampling (Georgiadis and McNaughton, 1988; Herrero et al., 2000).

Biomass productivity is one of the most critical parameters in the economic viability of a ruminant feed. High biomass production lowers the costs of production in a ruminant-based livestock production system. Moreira et al (2004), studying *C. plectostachyus* response to drought stress, observed a linear reduction in forage dry matter availability during the dry season and a quadratic increase during the wet season. This seasonality of feed availability leads to a dry season reduction or loss of production, loss of body condition, starvation and even death of the pastoralist livestock and wildlife. Above-ground biomass productivity depends on the ratio of nitrogen to phosphorus as well as overall nutrient supply (Güsewell and Bollens, 2003). Pasture quality assessments are critical in estimating the nutritional level of the grazers and in establishing mitigating measures to avoid economic losses. Other than biomass production, the nitrogen/crude protein (CP) and metabolizable energy (ME) content are commonly used to assess pasture quality.

The chronosequence formed by the receding lake water levels of Lake Naivasha provide a unique model to study the effects of land use duration, here of continuous grazing for 1-30 years, on feed resource availability and forage quality. The aim of this work was to determine the effect of seasonality and of continuous grazing on feed availability and quality in the riparian grassland of Lake Naivasha.

4.2 Materials and Methods

4.2.1 Study site at Lake Naivasha

The experiment was conducted between December 2010 and August 2011 using the natural permanent pastures of the Lake Naivasha riparian land, adjacent to the Kenya Agricultural Research Institute research farm (0°43'31.11"S, 36°22'12.80"E, altitude 1890 – 1891 m.). The area is continuously grazed by wild herbivores and additionally used by pastoralist livestock during the dry season. The mean annual rainfall in Naivasha is 620 mm in a unimodal distribution pattern, mean temperatures of 16-20° C, and the highest evaporation recorded in January and February (Gaudet and Melack, 1981). The soils in the study area are formed on lacustrine sediments as parent material with a mixture of volcanic ash or pyroclastic material (Siderius and Muchena, 1977). In parts of the study area, the lacustrine sediments are overlaid by recent alluvial deposits.

4.2.2 Sampling units – plots and sub-plots

Corresponding to the number of years the land had been exposed by the receding lake, four positions were identified based on lake level records since 1980 using a geodetic GPS 500 (Leica Geosystems AG, Heerbrugg, Switzerland) coupled with Nikon AP-7 Automatic survey level. These positions corresponded to 15, 20, 25 and 30 years of exposure from the lake and equivalent durations of continuous grazing. They were designated as chronosequence positions 15 to 30 (Chr15, Chr20, Chr25 and Chr30). Additionally, along a gradient from pure alluvial deposit to pure lacustrine sediment, four soil types were selected perpendicular to the chronosequence positions. These were designated as 1A (shallow alluvial on lacustrine sediment), 2A (pure alluvial), 2L (lacustrine sediment with some alluvia) and 1L (pure lacustrine sediments). Sixteen exclusion plots, measuring 20 m x 20 m each, were fenced off;

four for each of the four land use duration chronosequence positions and the four soil types. The exclusion plots were located approximately 150 m away from each other along each chronosequence transect and on open grassland away from large trees. Each plot was sub-divided into sixteen 5 m x 5 m sampling units. The plots were initially mowed to approximately 5 cm above the soil surface and allowed to grow until sampling time.

4.2.3 Sampling procedure

The plant species present in each plot as well as their relative proportions within the plant mix were recorded in December 2010, in April 2011, and in August 2011. The average monthly precipitation during the data collection period was 43.9 mm and the distribution did not present a clear distinction of a wet and dry season (Figure 10). Four replicate biomass samples per exclusion were harvested monthly by randomly placing a 1 m^2 frame, once in each of four of the 16 sub-plots in a random arrangement. Four different sub-plots were sampled each month (February, March and April) during the dry season. Thereafter, the plots were all mowed again to approximately 5 cm above the soil surface and monthly samples (May, June, July and August) were taken during the rainy season. In each plot, three bulk soil samples (composites five sub-samples) were taken at a depth of 0-15 cm. The samples were air-dried, sieved (<2 mm) and dry stored for laboratory analysis. Frequency domain reflectometry (FDR) soil moisture sensors were placed at each of the 1L and 2A plots with permanently installed sensors at soil depth of 10 cm (0–20 cm), 30 cm (20–40 cm) and 50 cm depth (40–60 cm) (Decagon Inc.; EC-5 sensor; EM-5b data logger). Precipitation was recorded daily using two rain gauges placed, one at chronosequence position 30 in the pure lacustrine soil line and the other at chronosequence position 25 of the pure alluvial soil line.

4.2.4 Sample processing

The harvested biomass material were weighed, dried at 60 ^{0}C for 24 h and a portion milled to pass a 1 mm sieve and stored in air tight plastic containers for laboratory analysis. Another portion was weighed and again oven-dried at 105 ^{0}C for 24 h to determine dry matter content. The soil samples were air-dried and sieved (<2 mm) and stored air-tight until laboratory analysis.

4.2.5 Analyses

After the vegetation samples were dried at 105 ^{0}C for 24 h to determine dry matter (DM) content, the DM productivity was calculated from the percent DM content and the initial weight of the fresh biomass. Soil pH and electrical conductivity (EC) were measured in a soil to water suspension ratio of 1: 2.5. The volumetric soil water content (SWC) was assessed with the loggers recording moisture measurements at hourly intervals during the period from November 2010 to August 2011.The sensor outputs were calibrated to field conditions and SWC calculated. Ground soil sub-samples were analyzed for total C and N using a CNS Elemental Analyzer (EuroEA 3000 Euro Vector SpA, Milan, Italy). Total plant nitrogen was analysed using the Dumas combustion according to VDLUFA (2012) method 4.1.2. The N content was multiplied by 6.25 to get the crude protein content of the pastures. Gas production from the *in vitro* degradation of the pasture was done using the Hohenheim gas test (HGT) (Menke and Steingass, 1988) method 25.1 (VDLUFA, 2012) and the 24 h gas values were used to calculate the metabolizable energy (ME) values of the feed. The ME was calculated using the following formula (GfE, 2008):

$$\text{ME (MJ/kg DM)} = 7.81 + 0.07559(\text{GP24}) - 0.00384\text{ash} + 0.00565\text{CP} + 0.01898\text{EE} - 0.00831\text{ADF}_{om}$$

Where GP24 = Gas produced after 24 h incubation of 200 mg of sample, CP = crude protein, EE is ether extract and ADF_{om} = Acid detergent fibre expressed exclusive of residual ash. CP, ash, ADFom and EE are in g/kg DM; GP24 is in ml.

4.2.6 Data analysis

The data were recorded in EXCEL spreadsheets and included plant species diversity and relative abundance, biomass production for each plot, soil parameters (EC, pH, soil water content, total N and organic C), plant N and calculated metabolizable energy per plot.

Analysis of variance was performed using GenStat (GenStat Release 10.3 DE of 2011). Comparison of means was done using contrasts (Buysse et al., 2004) for orthogonal designs in GenStat and the least significant difference (LSD) was set at 95% confidence level.

4.3 Results

4.3.1 Rainfall and soil parameters during the experiment period

Average monthly rainfall during the experiment period was below the area's monthly average (43.9 mm vs 51.6 mm). Figure 10 shows the amount and distribution of precipitation during the experiment period and Figure 11 shows the soil moisture content recorded using moisture sensors at different depths below the ground surface. Table 5 provides selected soil chemical attributes of the experimental plots.

4.3.2 Species diversity and relative abundance during the experiment period

Table 6 shows the species of grasses and forbs and their relative percentage cover within each of the plots. The plots were dominated by the grass species *Pennisetum clandestinum* and *Cynodon plectostachyus*. Of the forbs, *Senecio flaccidus* had a significant presence in a number of plots, the rest of the species being just present as few individual plants.

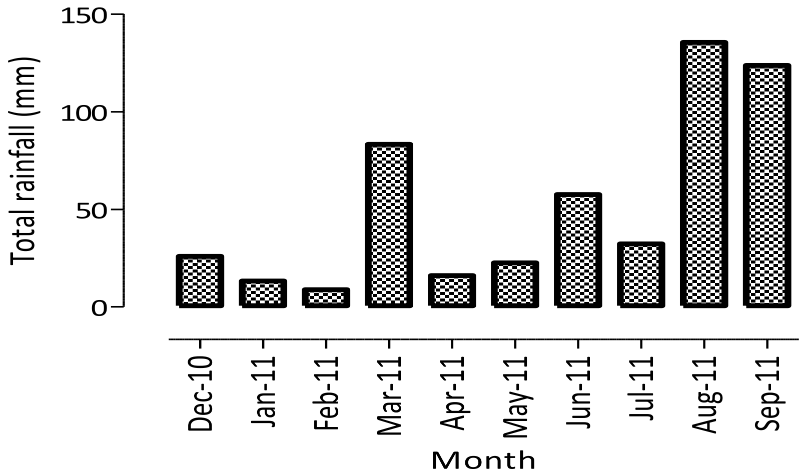

Figure 10: Rainfall distribution between December 2010 and September 2011 recorded at the riparian land of Lake Naivasha, Kenya.

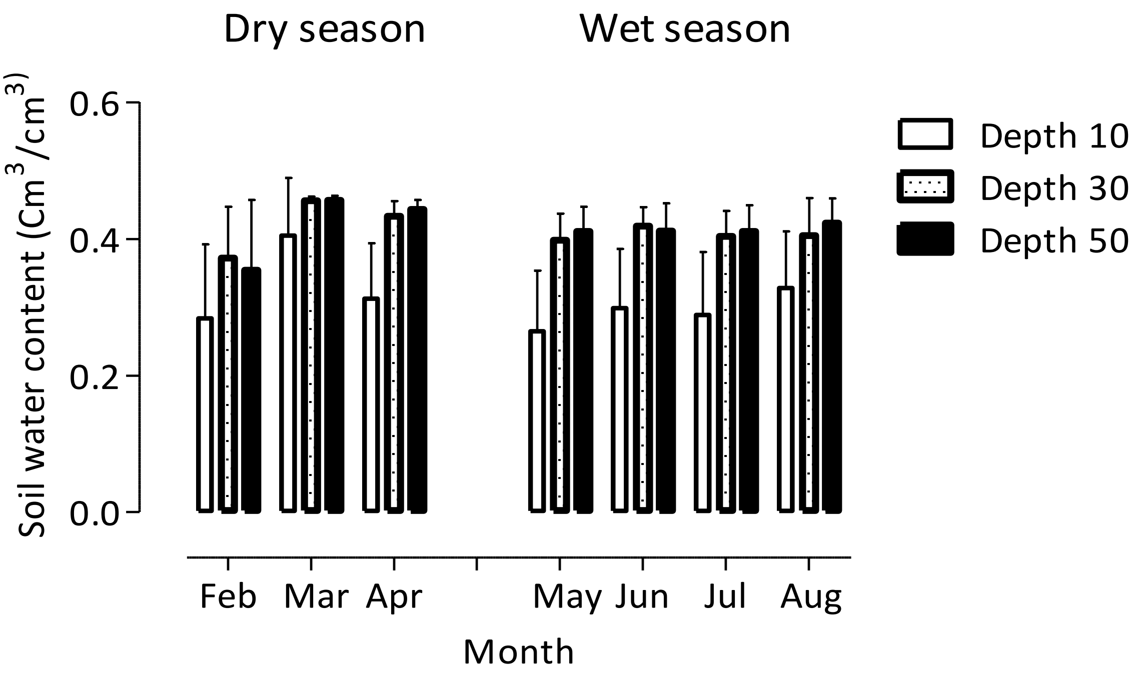

Figure 11 : Volumetric soil water content at 10 cm, 30 cm and 50 cm depth from February to August 2011

4.3.3 Dry matter production

There was a significant reduction in the dry matter productivity with increased land use duration. This was recorded both during the dry season (Figure 12) and the wet season (Figure 12).The quantity produced in chronosequence position 15 was highest ($P < 0.05$) while chronosequence positions 25 and 30 were lowest, and did not differ among themselves ($P > 0.05$) both during the dry and wet seasons.

Mean monthly biomass production indicate that on the alluvial soils nearest the River Malewa (2A) the highest ($P < 0.05$) biomass production occurred during the dry season, while biomass accumulation was lowest ($P < 0.05$) (Figure 13a) on the lacustrine sediment soils (2L). In the wet season, more biomass ($P < 0.05$) was produced on the alluvial soils (2A) than on the lacustrine one (1L), which in turn was more productive than soils formed on mixed alluvial/lacustrine sediments (2L and 1A) (Figure 13b). Total biomass production over time with monthly harvesting is presented in Figure 14. After the harvest in April, the plots were all mowed and allowed re-grow.

There was a significant positive correlation (r = 0.61) between the soil moisture content and monthly DM productivity during the wet season, DM production increasing with an increase in soil moisture content. In the dry season, there was no correlation (r = 0.18). Soil pH and electrical conductivity and available P did not influence DM productivity. Soil N had a positive effect on DM production, with a correlation coefficient of 0.61 while organic Carbon content of the soil was weakly correlated to biomass productivity (r = 0.52)

4.3.4 Nitrogen changes

The N content was highest ($P < 0.05$) in forages from 1A soil type followed by 2A, while the lacustrine soil pastures had lower N content ($P < 0.05$) and did not differ from each other (Table 7). There was an increase in the N content of the pastures with increased duration of land use with the younger chronosequence positions (15 and 20) having lower ($P < 0.05$) N than the older ones (25 and 30) (Table 7). There was a significant reduction in the N content of the pastures with age of growth, with August pastures having the lowest ($P < 0.05$) content (Table 7). February and April harvests had highest values though February and June values did not differ. There was no correlation ($P = 0.739$) between soil total N and pasture N content. An increase in the soil pH was associated with reduced pasture N ($P < 0.05$) while EC did not have a significant effect.

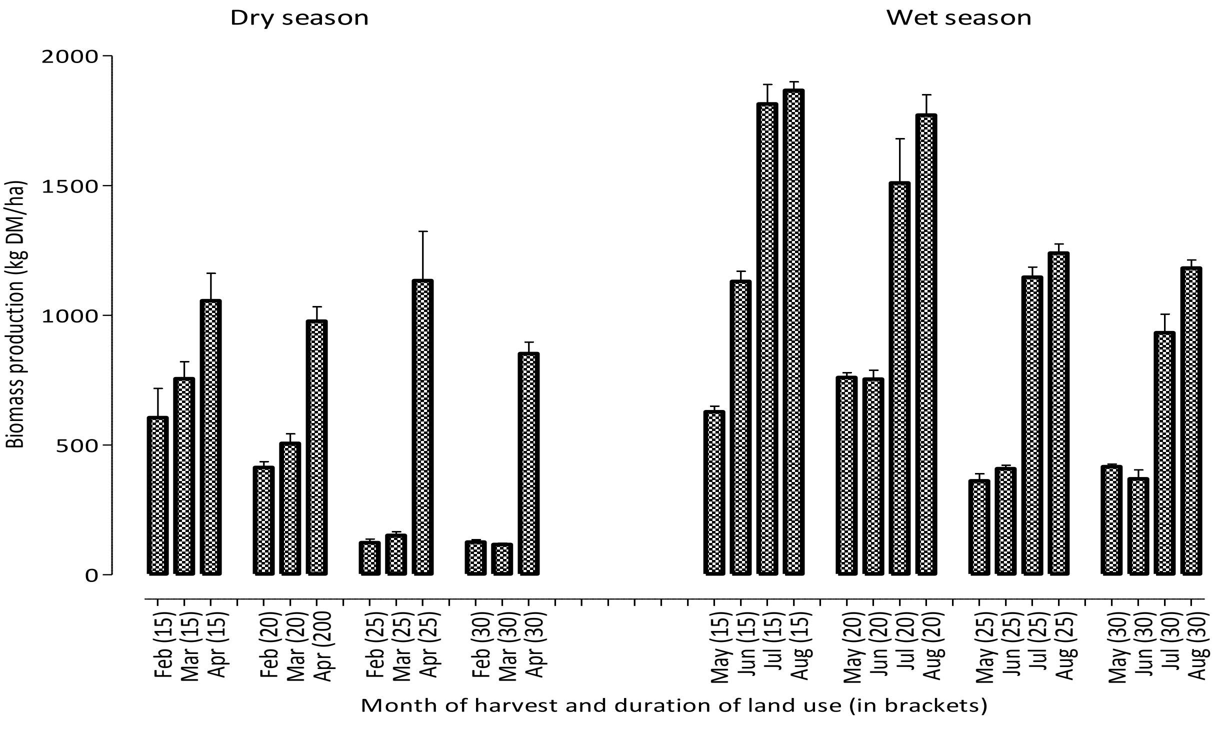

Figure 12 : Monthly biomass production per duration of land use during the dry and wet seasons

Table 5: Selected soil chemical properties of the observation plots on different soil types and under different durations of land use in the riparian land of Lake Naivasha.

Soil type	Plot	Total N (g/kg)	Corg (g/kg)	pH	EC (ds/m)	P (mg/kg)
Lacustrine 1	1L15	5.3	65.0	7.0	0.3	19.4
Lacustrine 1	1L20	3.8	40.5	7.7	0.5	19.0
Lacustrine 1	1L25	3.3	37.4	7.5	0.4	10.8
Lacustrine 1	1L30	2.7	28.6	7.8	0.2	16.9
Lacustrine 2	2L15	3.6	43.3	7.8	0.5	7.6
Lacustrine 2	2L20	4.6	56.1	7.2	0.5	13.1
Lacustrine 2	2L25	3.2	36.1	7.7	0.6	12.6
Lacustrine 2	2L30	2.6	28.3	7.8	0.3	16.9
Alluvial 1	1A15	6.5	71.5	6.4	0.4	41.5
Alluvial 1	1A20	5.7	71.4	6.2	0.3	28.4
Alluvial 1	1A25	4.2	48.0	6.5	0.3	18.4
Alluvial 1	1A30	3.4	41.1	6.2	0.2	20.9
Alluvial 2	2A15	4.5	47.6	7.1	2.1	12.8
Alluvial 2	2A20	6.6	77.7	6.3	0.3	29.2
Alluvial 2	2A25	3.9	43.2	6.0	0.2	29.7
Alluvial 2	2A30	4.2	47.6	6.2	0.2	21.1
SD		*1.2*	*14.8*	*0.7*	*0.4*	*8.4*

N =Nitrogen, Corg = organic carbon, EC= electrical conductivity in deci-siemens (ds)/ metre, P= phosphorus; 1L, 2L, 1A and 2A: soil types; 15, 20, 25 and 30: chronosequence positions. SD: standard deviation.

4.3.5 Metabolizable energy changes

The ME content was similar for the pastures from all the chronosequence positions, the average ranging between 9.6 and 9.9 MJ/Kg DM. Between the soil types, there was a significant increase ($P < 0.05$) in ME content of pastures from the lacustrine to alluvial soils (Table 7), with the 1A pastures having the highest values ($P < 0.05$). The ME of the pastures increased significantly after the onset of the rains in late March, recording the highest values in April and then declining steadily as the growing season progressed. The values were lowest ($P < 0.05$) in February and highest in April (Table 7). Of the soil parameters, only pH was associated with ME. Pasture ME was negatively ($r = 0.59$) associated with soil pH in the same way pasture N was ($r = 0.53$), as pasture N and ME are correlated.

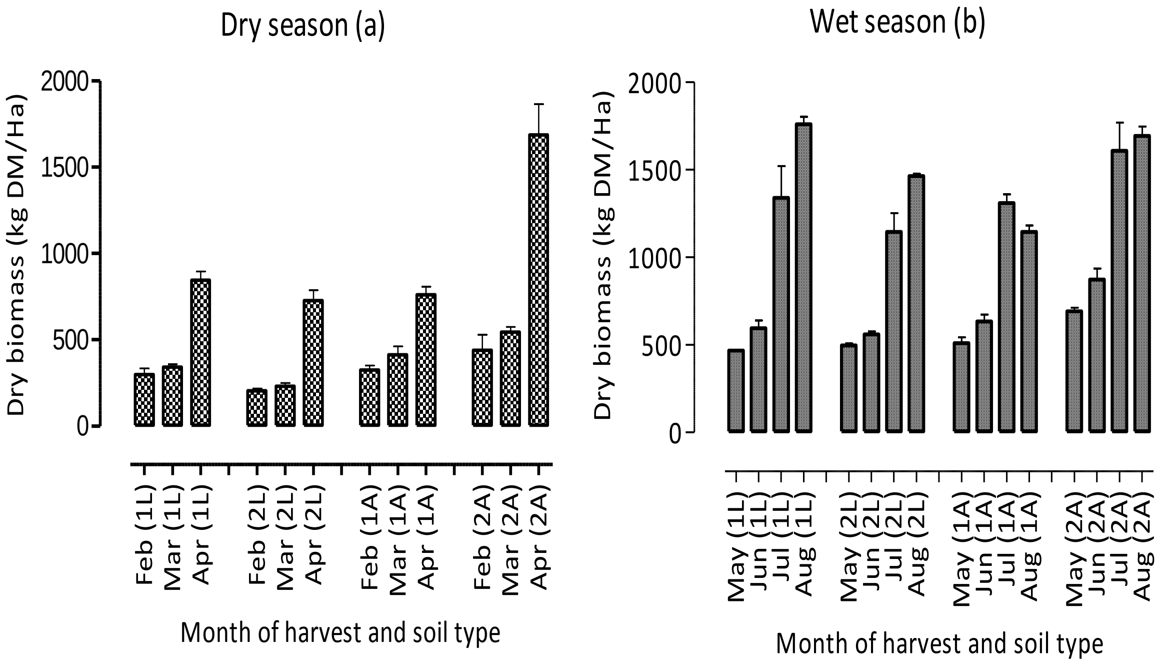

Figure 13: Monthly biomass changes per soil type: (a) Dry season (b) Wet season in 2011 in the Lake Naivasha riparian land.

(1L and 2L are lacustrine soils 1 and 2; 1A and 2A are alluvial soils 1 and 2)

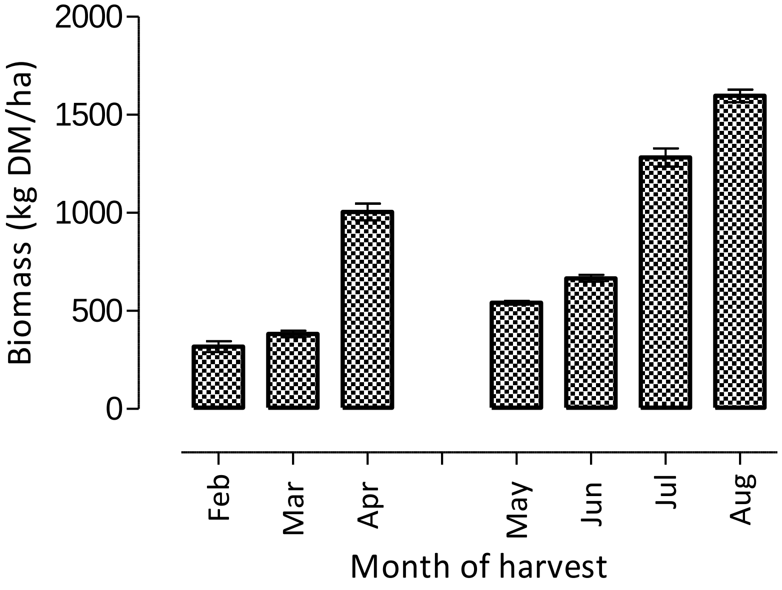

Figure 14: Average monthly biomass production for the dry season (Feb, Mar, Apr) and wet season (May, Jun, Jul, Aug) of 2011within the riparian land of Lake Naivasha

Table 6: Plant species cover (mean of 3) percentage per plot at the riparian of Lake Naivasha, December 2010 to August 2011

Percent cover within plots by plant species (mean of 3 counts) at the riparian of Lake Naivasha, December 2010 to August 2011

Plant Species	1L15	1L20	1L25	1L30	2L15	2L20	2L25	2L30	1A15	1A20	1A25	1A30	2A15	2A20	2A25	2A30	*SD*
Acacia xanthofloea	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	*0.6*
Achyrantes aspera	0	2	1	2	0	3	2	5	0	1	2	1	0	2	0	4	*1.4*
Amaranthus dubius	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	*0.3*
Cassia didymobotria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*0*
Centrocema pubescens sp.	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	*0.8*
Cynodon plectostachyus	28	91	82	78	42	96	88	73	4	4	28	80	16	7	45	67	*32.7*
Cyperus rotundus	0	7	2	2	1	0	4	2	1	0	0	0	0	0	0	0	*1.8*
Datura stramonium	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	*0.4*
Erigeron bonariensis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	*0.2*
Lotus uliginosus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	*0.2*
Pennisetum clandestinum	93	30	5	11	85	11	5	4	98	99	53	7	99	98	63	52	*38.9*
Poa palustris	0	0	0	1	0	0	0	0	0	0	0	1	2	0	0	0	*0.5*
Senecio mesogrammoides	22	22	8	2	5	10	4	1	14	3	4	1	0	2	17	3	*7.1*
Sesbania sesban	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*0*
Sida adoensis	0	2	0	0	0	2	0	1	0	0	0	6	0	0	0	0	*1.4*
Solanum incanum	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	*0.4*
Solanum nigrum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	*0.2*
Tagetes minuta	0	0	0	0	0	0	0	0	0	0	1		0	0	0	0	*0.2*
Trifolium semipilosum	0	0	0	0	0	0	0	0	37	0	0	0	27	0	0	0	*10.6*
Verbena bonariensis	0	0	0	1	0	0	1	0	0	1	0	0	0	0	3	4	*1*
SD	*21.1*	*20.6*	*17.7*	*17*	*20.1*	*20.9*	*19.1*	*15.9*	*22.3*	*21.5*	*12.7*	*17.8*	*22.1*	*21.3*	*16.6*	*17.8*	

1L, 2L, 1A and 2A are soil types; 15, 20, 25 and 30: chronosequence positions; SD: standard deviation.

Table 7: Forage nitrogen and metabolizable energy (ME) changes with soil type, land use (chronosequence positions) and month of harvest.

Parameter	N (g/kg DM)	ME (MJ/kg DM)
Soil type		
1L	16.0^{b}	9.3^{b}
2L	16.7^{b}	9.4^{b}
1A	22.4^{a}	10.4^{a}
2A	20.0^{a}	10.0^{a}
SD	*3.0*	*0.5*
Chronosequence		
Chr15	16.2^{b}	9.9^{a}
Chr20	16.7^{b}	9.6^{c}
Chr25	21.2^{a}	9.7^{bc}
Chr30	21.0^{a}	9.8^{ab}
SD	*2.7*	*0.1*
Month of harvest		
Feb	20.0^{ab}	8.2^{c}
Apr	21.8^{a}	11.2^{a}
Jun	18.5^{b}	10.0^{ab}
Aug	14.7^{c}	9.6^{b}
SD	*3.0*	*1.2*

1L and 2L: lacustrine soils 1 and 2; 1A and 2A: alluvial soils 1 and 2; Chr: chronosequence position; SD: standard deviation; DM: dry matter; ME: metabolizable energy.

4.4 Discussion

The range of soil pH of 6.0 to 7.8, and electrical conductivity (ds/m) of 0.2 to 2.1, were within the range of 4.7 to 8.7 and 0.11 to 2.99 respectively, found by Godson (1999) while studying the soils of the Lake Naivasha wetlands and are classified as moderately acidic to alkaline and also as not salty to moderately salty (FAO, 2006).

The dominant plant form in the littoral grassland of Lake Naivasha is grass and of the grasses, *P. clandestinum* and *C. plectostachyus* are the most abundant species. The altitude, soil, moisture and temperature conditions at the experimental site were within those found by several authors to favour Kikuyu and star grasses. Introduced into the temperate and sub-humid areas of Mexico, Kikuyu grass thrived at altitudes up to 2400 metres above sea level (m.a.s.l) attaining a crude protein contents of 9.6% of DM (Nahed et al., 2003). It is known to persist under annual rainfall of at least 600-700 mm and develop well from sea level to 3500 m (Skerman and Riveros, 1990). It thrives at temperatures between 2 and 30^0 C (Russel and Webb, 1976; Mears, 1970) and can resist drought (Whiteman, 1980), a pH between 5.5 and 8.0 (Russel and Webb, 1976) and high salinity (Skerman and Riveros, 1990; Russel, 1976). However, Muscolo et al. (2013) tested the salt tolerance of Kikuyu grass and found that germination was affected less by salinity than the vegetative growth, concluding that this grass species is moderately tolerant to sodium in soils. Star grass grows in areas up to 2000 m.a.s.l, is adapted to semi-arid conditions of 500-875 mm rainfall (Harlan et al., 1970), tolerates a wide range of soils, stands heavy grazing and is highly palatable to ruminants (Clayton and Harlan, 1970). These conditions documented elsewhere as favouring the establishment, persistence and growth of Kikuyu grass and Naivasha star grass are largely present around Lake Naivasha. The abundance of these two species confirms their persistence under the environmental conditions and grazing pressure of the lake Naivasha riparian.

The biomass productivity of the grass mixture followed the moisture gradient both spatially and temporally. Chronosequence positions with higher soil moisture had higher DM production, and faster growth was recorded during the wet season. This agrees with Liu et al. (2010) who reported a positive correlation between plant biomass and soil water content, but is in contrast to the findings of Tzialla et al. (2006) who noted that distance from the lake shore did not affect total above ground biomass in the Mediterranean climate in Greece. In the wet season, the soils are wet enough to sustain the net C uptake by plants (Ma et al., 2007) hence growth. The photosynthetic processes in the semi-arid tropics are usually limited by water (Bai et al., 2008) and therefore, in the presence of sufficient plant available water growth is improved when the soil conditions are favourable. Even when soils are poor, water availability would still lead to an improved DM production, especially of grasses known to be tolerant to such adverse conditions as reported by Shukla et al. (2011) after growing *Cynodon dactylon* in sodic soils. Apart from the moisture availability, the reduction of DM production with land use is likely to be due to reduction in soil N content and species shift with prolonged land use. Kikuyu grass reduced with increasing land use while Naivasha star grass increased. This difference in species type and the resultant heterogeneity may have mediated the effect of land use on biomass production (Gross et al., 2009). The increase in biomass from the lacustrine sediment to alluvial deposit soils was expected due to the increase in the soil N content along the same gradient. The positive correlation between soil N and DM productivity was contrary to that found by Li et al. (2010) who reported a negative correlation between total above ground biomass and soil total N.

The concentration of nitrogen in the harvested portions of the biomass in our study showed increase in N with increasing years of grazing and reduced biomass. The soils further away from the lake, in areas which had been grazed continuously for a longer period, were drier and the grasses possibly witnessed reduced growth due to limited soil moisture. Higher N fluxes in the soils have been reported during dry periods compared to wet periods of the year in grasslands (Parker and Schimel, 2011; Sullivan et al., 2012) and it is possible that in the drier soils, the grasses had a higher uptake of mineralized N compared to those in the wetter soils hence the higher concentration of N in chronosequence positions 25 and 30 compared to 15 and 20. This concentration/ dilution effect agrees with Abd El Rahman (1973) and Ritchie et al. (2006) who both reported increased plant N concentration with reduced moisture availability. In the lacustrine sediment to alluvial deposit soils gradient, there was a positive correlation between total soil N and N content of the pastures. This suggests that there was an improved N availability when the soil N content was higher, agreeing with the findings of Walley et al. (2002) who noted a positive correlation between soil nitrogen availability and total organic N levels in the 0-15 cm depth. The N concentration reduced with age of growth of the pastures during the growing season of April to August. This is true for tropical grasses as well as legumes. Working with *Stylosanthes guianensis, S. scarab* and *Centrosema pubescens* in Queensland, tropical Australia, McIvor (1979) demonstrated that the concentration of N increased in the growing season and then declined at the end of the growing season. It is also possible that the process of N resorption from the senescing leaves (Carrera et al., 2003) of the perennial grasses after maturity stage had set in thereby reducing the N concentration as the grasses aged.

The metabolizable energy content of the grasses in this experiment was between 8.2 and 11.2 MJ/kg DM. These values are much better than the range between 3.5 and 8.1 MJ/kg DM recorded by Safari et al. (2011) working with the native forages of semi-arid Tanzania. Riparian pastures have better moisture availability and more fertile soils compared to the rest of the rangeland and therefore riparian pastures are expected to be nutritionally better. This reinforces the importance of the wetlands as a key resource area for ruminant nutrition.

Suyama et al. (2007) did suggest that forages having an ME content of 6.7- 9.9 MJ/kg DM would be acceptable as feed for beef cattle, sheep and some classes of dairy cattle. The grasses from the plots in our experiment were above this range and can thus be classed as good forage for meeting the energy requirements of the animals grazing them. The duration of land use up to 30 years did not significantly influence the ME content of the pastures. Several researchers have reported a positive correlation between the herbage ME and true DM digestibility (Tagliapietra et al., 2011), ME and digestible NDF (NRC, 2001) as well as between ME and CP (Mountousis et al., 2011; Islam et al., 2012). In this experiment, we only measured ME and CP of the pastures and considering that on regression, a significant ($P < 0.05$) correlation existed between them, it would have been expected that a longer time of land use would have led to an increase in the ME. It is possible that an increase in the ME values occasioned by an increased N content of the forages was counterbalanced by an ME decrease occasioned by increased fibre fractions, especially ADF and ADL as the years of land use increased. The increased pasture ME from lacustrine sediment to alluvial deposit soils reflects the increase in N content. This is in agreement with the work of (Peyraud and Astigarraga, 1998) who reported a reduction in net energy of forages when reduced rates of N fertilizer application were used with the resultant reduction in forage CP. The seasonal variation in ME was expected as the pastures grew and matured. The expected increase in cell wall content and reduction in cell content, including of water soluble carbohydrates, as forage growth progresses inevitably leads to reduction in ME. Similar results have been reported by Yayneshet et al. (2009) working with mixed grasses in Ethiopia, and Safari et al. (2011) in Tanzania.

The chronosequence is a useful study tool in exploring the pasture production capacity of wetlands as well as in studying the quality attributes of these pastures. Combined with gradients of soil attributes and soil moisture content, it can be used to study pasture changes at various spatial and temporal scales. Continuous grazing and reduced soil moisture content, both during the dry season and with increasing distance from the lake shore affected the composition of pasture grasses as well as forage yield and quality and may thus differentially affect the suitability of the riparian land as pasture ground and feed resource area for ruminants.

CHAPTER 5: FEED INTAKE AND DIGESTIBILITY OF NATURAL VEGETATION IN THE RIPARIAN LAND OF LAKE NAIVASHA, KENYA

5. Feed intake and digestibility of natural vegetation in the riparian land of lake Naivasha, Kenya

5.1 Introduction

In Kenya, arid and semi-arid lands constitute four fifths of the total land mass usually with unimodal rainfall under 600 mm annually. Because of this, pasture availability is seasonal forcing pastoralist livestock keepers to seek alternative coping strategies (Behnke et al., 1993; Scoones, 1994). Such coping strategies include transhumance in search of pasture and water resources. Swamps and areas around water bodies form key resource areas for dry season grazing owing to wetter conditions (Ngugi and Conant, 2008) favouring primary productivity. The land immediately adjacent to the water bodies maintain high soil moisture and will support growth of good quality grasses for most of the year (Tzialla et al., 2006). Particularly in dry environments, these riparian lands are important feed refuge areas for both livestock and wildlife during the dry season when feed resources have been depleted in the uplands, thus mitigating the seasonal scarcity of animal feeds. Thus, the northern riparian shores of Lake Naivasha represent an important all-year feed resource for more than 50 different species of about 3000 wild grazers (Mavuti and Harper, 2006), and a dry season feed refuge for pastoralist livestock (Becht et al., 2006; Morrison and Harper, 2009).

Receding water lines due to temporal recession of water bodies expose “new” land, which supports primary and secondary plant successions usually dominated by grasses. The exposed land presents strong moisture gradients with the earlier exposed areas being drier than the recently exposed ones. The northern shore of Lake Naivasha has very shallow slopes and even minute changes in the lake water level can drastically alter the size of the riparian land area. With a near-continuous decline in the lake water level of Naivasha between 1980 and 2010, there was a substantial expansion of the riparian land area. The gradually uncovered lake floor was rapidly colonized by grasses and has been continuously grazed by wildlife and livestock. The resulting chronosequence of land use (grazing) provide an ideal study framework for assessing the effects of land use duration on soil parameter changes and on the availability and quality of feedstuff.

Digestibility measurements using sheep has become the reference method for the determination of nutritive value in ruminant nutrition (Van Soest, 1994; Dermarquilly et al., 1995) and voluntary intake level is the most important of the nutritional factors (Mertens, 1994). Consequently, this study aimed at assessing the voluntary intake and digestibility by sheep of riparian grassland hay collected from different soil environments and at different durations of continuous land use.

5.2 Materials and Methods

5.2.1 Experimental site

The experiment was conducted from January to March 2012 at the Kenya Agricultural Research Institute (KARI), Naivasha. Pastures were harvested in August 2011 from the northern riparian of Lake Naivasha, (0°43'31.11"S, 36°22'12.80"E, altitude 1890 metres above sea level) adjacent to the KARI land. The climate is cool tropical and semi-arid with average temperatures of 16-20°C and annual rainfall of 620 mm (Clarke et al., 1990). The rainfall is usually unimodal (JRC, 2010) but can also be concentrated in two short rainy seasons, between April-May and January-February (Gaudet and Melack, 1981). Four chronosequence positions were selected to represent 30, 25, 20, and 15 years of exposure from the receding lake water level with subsequent continuous grazing use. Across the chronosequence gradient, four sites were selected representing an edaphic gradient ranging from clay soils formed on alluvial deposits (A) to loamy lacustrine sediment soils (L). The forage species found in the study site indicate a shift in predominance from *Pennisetum clandestinum* to *Cynodon plectostachyus* as the years of land use and distance from the lake shore increases (Table 2).

5.2.2 Experimental animals

Four Red Maasai whether sheep sourced from Naivasha sheep and goats production government farm were used in the feeding experiment. The age range of the sheep was 12-15 months and average body weight (BW) was 16 kg (SD= 0.31) at the beginning of the experiment. They were housed individually in metabolic cages (raised 1 m above the ground, fabricated from wood and metal racks) to allow for separate collection of total faeces and urine. The cages were fitted with feeding troughs and watering buckets and were placed in an open building with soft board half walls. The sheep were drenched with recommended doses of albendazole, an anti-helminthic drug against internal parasites ten days before the start of the experiment.

5.2.3 Forage sampling

We collected herbage from sixteen sampling plots, forming 16 diets. The plots were located along gradients with four chronosequence positions perpendicular to the lake shore (referred to as 15, 20, 25, and 30, representing the number of years of continuous grazing use), and four soil type environments located parallel to the lake shore (referred to as 1A, 2A, 1L and 2L representing the shift from alluvial deposit to lacustrine sediment soils). Each plot measuring 20 x 20 m was fenced off and initially uniformly cut to a grass height of approximately 5 cm in December 2010. After every four months of regrowth (in April and August), the plots were mowed and the herbage was left to wilt for four days before being chopped (approximately 3cm size) and stored as hay for use in the feeding experiment.

5.2.4 Experimental design and feeding

The sheep were offered the 16 forages for intake in a 4 x 4 Graeco-Latin square design (Montgomery, 2009) The factors considered comprised land use duration, soil type, and animal. This design can reportedly accommodate three factors, thus lowering research costs and providing more rapid results (Rad et al., 2011) than a full factorial design (Mertens et al., 2012; Van Derlinden et al., 2013).

Each test feed was initially offered for a ten-day adaptation period, followed by a four-day data collection period for each feeding cycle. The feed allowance was at 110% of the previous day’s intake. The starting quantity at the beginning of the experiment was 1 kg (as fed basis) per sheep. Immediately after data collection, the diet was changed and a new cycle of 10 + 4 days was repeated until all diets had been covered. Water was available *ad libitum*. The test feed was supplemented, at a rate of 30 g/(sheep x day), with a mineral premix containing (g/kg) 30 Ca, 15 P, 800 NaCl, and 1 Mg, as well as (mg/kg) 500 Cu, 775 Mn, 3 Se, 85 I and 1000 Fe. The premix was hand-mixed with the feed before feeding.

5.2.5 Data collection and processing

Feed intake and faecal output were recorded. A sample of feed was taken for each of the four data collection days and the samples bulked and sub-sampled for each diet. Faeces were individually collected, weighed, dried at 60 ^{0}C for 24 hours, bulked and sub-sampled for each sheep and period.

5.2.6 Chemical analysis

Feed and faecal samples were analysed using the methods recommended by the Verband Deutscher Landwirtschaftlicher Untersuchungs- und Forschungsanstalten (VDLUFA, 2012) with method numbers given. Nitrogen (N) was determined by Dumas combustion (LECO Instrumente, Mönchengladbach, Germany, 4.1.2) and crude protein (CP) was calculated as N x 6.25. Dry matter (DM) and ash content were also analysed (3.1 and 8.1 respectively). Neutral detergent fibre (NDF, assayed with heat stable amylase), acid detergent fibre (ADF, expressed exclusive of residual ash, ADFom), and acid detergent lignin (ADL) were analysed using Ankom 2000 Fibre Analyser (ANKOM Technology, Macedon, NY, USA; 6.5.1, 6.5.2, and 6.5.3 respectively). Crude fat (ether extract, EE; 5.1.1) was analysed using a hydrolysis and extraction system (ANKOM Technology, Macedon, NY, USA). *In vitro* gas production using the Hohenheim gas test technique (Menke and Steingass, 1988; 25.1) was performed on the feed samples to estimate the metabolizable energy (ME) content. The ME was calculated using the formula (GfE, 2008):

$$\text{ME (MJ/kg DM)} = 7.81 + 0.07559(\text{GP24}) - 0.00384\text{Ash} + 0.00565\text{CP} + 0.01898\text{EE} - 0.00831\text{ADFom}$$

whereGP24 = Gas produced after 24 h incubation of 200 mg of feed, CP = crude protein, EE is ether extract and ADFom = Acid detergent fibre expressed exclusive of residual ash.

Feed and faecal P content was determined spectrophotometrically (Photometer DU62, UV/VIS, Beckman, CA, USA)according to method 10.6 of VDLUFA (2012) while Ca, Mg, Na, K, Cu, Fe, Zn and Mn, were analysed by atomic absorption using Atomabsorption AAnalyst 200 with Autosampler S10 (PerkinElmer, Waltham, MA, USA).

5.2.7 Calculations and statistical analysis

All data were analysed using analysis of variance (ANOVA) of GenStat for Windows (GenStat Release 10.3 DE of 2011). Comparison of means was done using contrasts (Buysse et al., 2004) for orthogonal designs in GenStat and the least significant difference (LSD) was set at 95% confidence level. The effects of land use duration and soil type on intake and digestibility were estimated using the following model:

$$Y_{ijkl} = \mu + D_i + S_j + A_k + T_l + DS_{ij} + \varepsilon_{ijk},$$

where Y_{ijkl} is the observation for which i and j represents levels of the primary factors and k, and l represent those of the blocking factors; μ = General location parameter or average; D_i = Effect of land use duration l; S_j = Effect of soil type j; A_k=Effect of sheep k; T_l = Effect of period l; DS_{ij} = Interaction effects between duration of land use and soil type; and ε_{ijkl} = Random error.

5.3 Results

5.3.1 Feed characteristics

The quality attributes of the hay samples differed substantially as a function of sampling site. The general quality characteristics are provided in Table 8 while the mineral profile is shown in Table 9.There was, generally, an increase ($P < 0.05$) in ash content of the feed with increased duration of land use with samples from 30 years of land use containing most ash. Hays from grass growing on alluvial (2A) soils (54.5 g/kg DM) or on soils with intermediate features (1A and 2L) between the alluvial and lacustrine sediments (52.6 and 54.5 g/kg DM) contained significantly more ash than hay produced on pure lacustrine (1L) soils (33.2 g/kg DM). In general, ash contents tended to increase with land use duration whereby samples from 30 years of land use on 1L and 2L soil contained more ash (Table 8). There was an increase in the crude protein content of the hay with increased land use, the highest ($P < 0.05$) crude protein content recorded in pastures in plots of 30 years of land use.

Table 8: Chemical composition of hays (g/kg dry matter unless stated otherwise)

Forage	DM	Ash	CP	NDFom	ADFom	ADL	EE	ME (MJ/kgDM)	ADL/NDF (%)	ADL/ADF (%)
1L15	931.9	32.7	67.4	745	379	88	10.1	9.4	11.8	23.2
1L20	934.1	17.5	65.4	754	387	98	16.2	9.5	13	25.3
1L25	937.2	19.1	56.3	805	411	111	8.4	9	13.8	27
1L30	935	63.5	81.5	688	354	103	6.2	9.2	15	29.1
2L15	928.6	25.4	61.3	817	410	111	14.4	9.3	13.6	27.1
2L20	931	18.2	62.5	769	413	92	9.5	9.3	12	22.3
2L25	929	80.2	64.9	622	391	153	13.6	8.5	24.6	39.1
2L30	939	86.5	112.5	589	319	135	9.7	9.5	22.9	42.3
1A15	937.2	49.4	102.7	623	298	67	16.7	10.5	10.8	22.5
1A20	929.9	61.4	94.9	645	313	82	17.9	9.8	12.7	26.2
1A25	933.5	52.8	100.9	655	304	77	16.2	9.9	11.8	25.3
1A30	929.9	54.3	114.4	657	323	102	10.8	10.1	15.5	31.6
2A15	932.9	59.9	82.9	689	354	75	16.8	9.5	10.9	21.2
2A20	933.5	42.7	98.2	705	319	73	14.6	9.7	10.4	22.9
2A25	934.5	24.4	127.9	760	372	114	16.2	10.2	15	30.6
2A30	934.5	34.1	98.5	710	354	86	14	9.9	12.1	24.3
SD	*3.0*	*21.2*	*21.5*	*65.9*	*38.7*	*22.5*	*3.5*	*0.5*	*3.9*	*5.8*

DM: Dry matter; CP: crude protein; NDFom: neutral detergent fibre exclusive residual ash; ADFom: acid detergent fibre exclusive residual ash; ADL: acid detergent lignin; EE: ether extract; ME: metabolizable energy; 1L: lacustrine soil 1; 2L: lacustrine soil 2; 1A: alluvial soil 1; 2A: alluvial soil 2; 15,20,25,30: number of years of continuous land use; SD: standard deviation; ADL/NDF and ADL/ADF are lignification indices of fibre and lignocelluloses respectively.

Grass hay from lacustrine soil 1 contained more crude protein than that produced on all the other soil types. Lacustrine soil 2 feeds had lower crude protein than alluvial soil 2 but hays from both alluvial deposit soils did not differ in their crude protein content. Forage1L25 had the lowest ($P < 0.05$) crude protein content while 2A25 was highest (Table 8). Hay from plots of 30 years land use had lower ($P < 0.05$) NDFom than the rest of the chronosequence positions, the three of which did not show significant differences ($P > 0.05$). Of the soil types, hay from lacustrine soil 1 had higher ($P < 0.05$) NDFom while those from alluvial soil 1 had lower NDFom than the other soil types. The ADFom trends across the chronosequence positions as well as the soil types follow those of NDFom except that values from lacustrine soil 2 were higher ($P < 0.05$) than from alluvial soil 2. The ADL tended to increase with the years of land use, 15 and 20 years having lower values than 25 and 30 years of land use. Hay produced on alluvial soils also contained lower ADL than the lacustrine soils hay with lacustrine soil 2 hay having the highest ($P < 0.05$) ADL values. Forages 2L25 and 2L30 had highest values while 1A15 had lowest (Table 8). The ME content of the hays were between 8.5 and 10.5 MJ/kg DM with hay 2L25 being lower ($P < 0.05$) than the alluvial soil hays and 1A15 having higher ($P < 0.05$) values than lacustrine soils hay.

Table 9: Mineral content of hays

Forage	P	Ca	Mg	Na	K	Fe	Mn	Cu	Zn
	g/kg dry matter					mg/kg dry matter			
1L15	1.6	3.7	1.6	7.6	9.3	679	67	6	30
1L20	1.8	2.2	0.8	6.4	10.4	349	41	6	32
1L25	1.6	2.4	0.7	5.7	7.5	493	47	7	29
1L30	2.1	3.6	1.1	9.6	11.2	2342	132	12	59
2L15	1.6	3.4	1.4	9.7	11.0	730	91	10	47
2L20	1.6	2.3	0.7	15.3	10.1	323	50	6	29
2L25	1.8	4.8	1.1	23.6	6.3	4196	256	27	129
2L30	2.3	4.3	1.4	14.7	11.7	4281	196	17	75
1A15	3.7	5.9	2.4	14.5	16.5	1755	243	28	85
1A20	2.5	6.1	1.9	21.0	10.8	2701	224	26	98
1A25	2.3	5.3	1.8	12.6	10.3	3951	219	22	84
1A30	2.0	3.6	1.3	5.7	8.0	1553	130	8	47
2A15	2.4	5.3	2.2	10.4	12.2	3854	202	15	76
2A20	2.6	5.1	1.9	7.9	13.4	1787	211	14	57
2A25	2.0	4.0	1.5	8.7	16.2	492	145	9	50
2A30	2.0	3.7	1.3	7.74	12.3	1088	144	9	41
SD	0.5	1.2	0.5	5.1	2.7	1421.5	71.7	7.6	27.7

For forage identification, 1L and 2L: lacustrine soils1and 2; 1A and 2A: alluvial soils1and 2; 15, 20, 25, 30: number of years of continuous land use; SD: standard deviation

There were no clear trends in feed Na content but there was a significant correlation ($r = 0.58$; $P < 0.05$) between ash and Na contents of the feeds. Among the soil types, the order of increase in Na content was alluvial soil 2 < lacustrine soil 1 < alluvial soil 1 < lacustrine soil 2. Calcium and P in hay tended to reduce ($P < 0.05$) with land use duration, highest for chronosequence position 15 for both and lowest in positions 25 for P and 30 for Ca respectively. Along the soil type gradient, the changes in Ca and P values were also similar with lacustrine soil 1 being lowest and alluvial soil 1 highest in the order alluvial soil 1 > alluvial soil 2 > lacustrine soil 2 > lacustrine soil 1. Forage variations existed with 1A20 and 1A15 highest for Ca and P respectively while 1L25 and 2L20 lowest for Ca and P respectively (Table 9). Potassium content tended to reduce with duration of land use, highest at chronosequence position 15 and lowest at 25 ($P < 0.05$). The lacustrine soil pastures had lower K compared to alluvial soil pastures in the order lacustrine soil 1 < lacustrine soil 2 < alluvial soil 1 < alluvial soil 2. Forage 2L25 had the lowest K content while 1A15 and 2A25 had the highest (Table 9).

5.3.2 Dry matter and organic matter intake and digestibility

Figure 15 shows the intakes of dry matter (DMI) and organic matter (OMI), and the DM digestibility (DMD) as well as the OMD of the natural pasture hay from the plots. The DMI and OMI of hay from lacustrine soil 1 were significantly higher ($P < 0.05$) than those from the rest of the soil types, the other three not significantly differing. Comparing geographically neighbouring plots did not show a pattern. There was no significant difference ($P > 0.05$) in DMI and OMI between the hay from the four chronosequence positions although 20 and 25 tended to be lower than 15 and 30. There were also no significant differences ($P > 0.05$) in DMD and OMD among land use chronosequence positions. The DMD and OMD of feed from lacustrine soil 1 hays were higher ($P < 0.05$) than the other three soil type hays, which did not differ from each other. The lacustrine soil 2 hay 2L25 had a lower ($P < 0.05$) DMD and OMD than the rest of the hays.

There was only a weak association between feed NDF content and DM digestibility variables ($P > 0.05$). The NDF content of the feed was negatively correlated ($P < 0.05$) to the DMI but was not correlated with DMD of the hays used in the experiment. The ADF and ADL levels did not correlate with intake and digestibility of DM of the hay by sheep.

5.3.3 Fibre and crude protein digestibility

Feeds from the youngest position in the chronosequence (15 years) had 56.5% NDF digestibility which was significantly higher than those from 25- and 30-year positions, showing a decrease with duration of land use. Forage hay 2L25 had the lowest and 1L15 the highest ($P < 0.05$) NDF digestibility of the forages (Table 10).

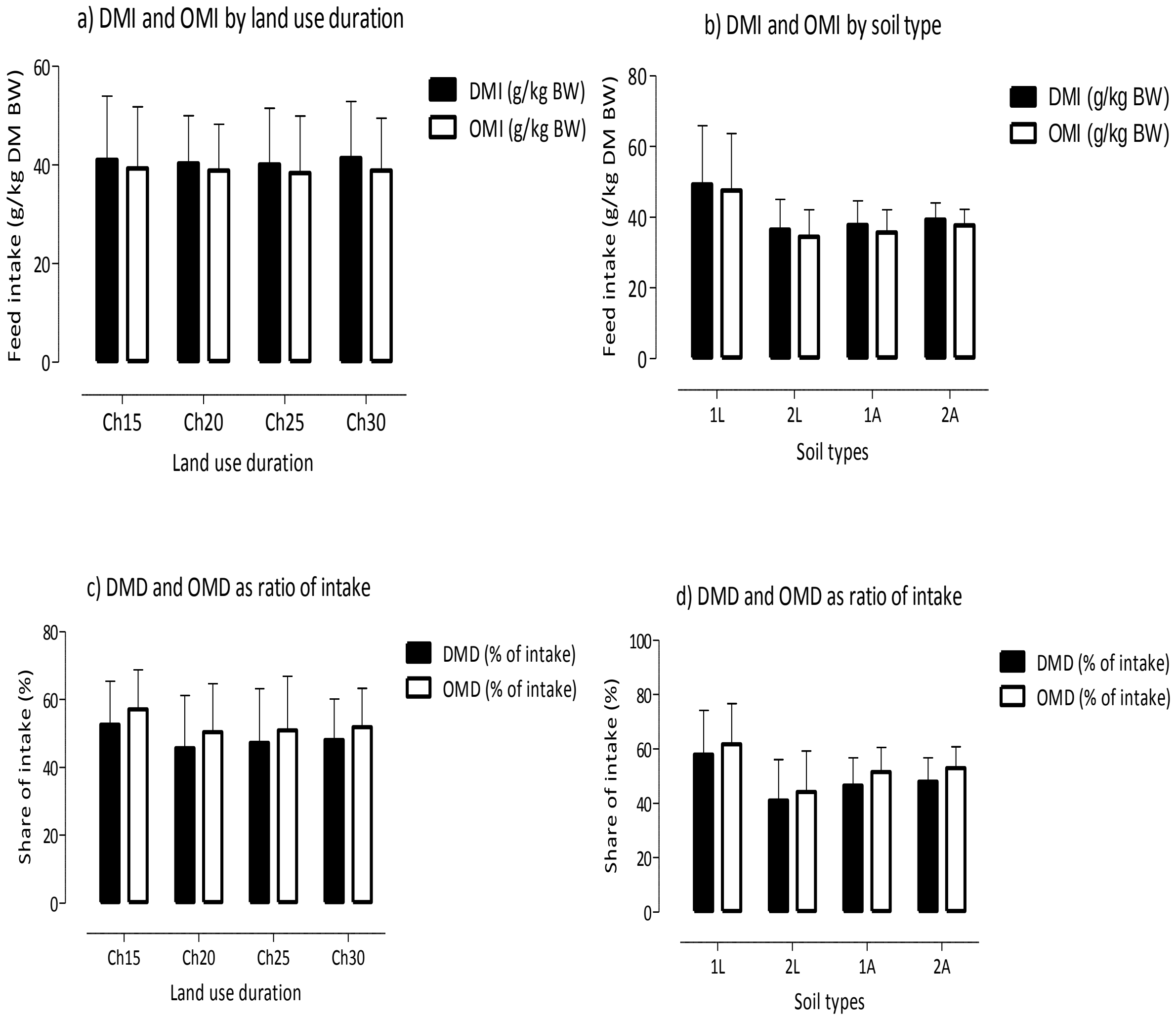

Figure 15: Hay dry matter intake (DMI) and organic matter intake (OMI) in g/kg body weight (BW) for a) land use duration across soil types and b) soil types across all land use durations; DM digestibility (DMD) and OM digestibility (OMD) as percentage of intake for c) land use duration and d) soil types
Land use duration: chronosequence positions 15, 20, 25, and 30; soil types: lacustrine soils 1L and 2L, alluvial soils 1A and 2A.

Feed from the youngest chronosequence position (15) had a higher ($P < 0.05$) digestibility of ADF than the older positions while lacustrine soil 1 hays had significantly higher ADF digestibility than hay from the rest of the soil types. The ADF digestibility of hays from alluvial soil 2 was higher than of those from lacustrine soil 2 and alluvial soil 1.The crude protein digestibility was lower ($P < 0.05$) in hay from chronosequence position 20 compared to 15 and 30 but was not significantly lower than 25. Hay from lacustrine soil 2 had significantly lower crude protein digestibility than hay from the other soil type pastures. There were forage differences with 2L25 having the lowest ($P < 0.05$) crude protein digestibility.

5.3.4 Mineral digestibility

The minerals available to the sheep during the experiment were from the test hay and supplemental mineral mix. Since the premix was availed to each sheep in similar quantities and mixed with the test feed, it was assumed that its intake and effect was evenly distributed and therefore these assumptions are implicit in all calculations. Table 11 shows digestibility of each mineral as a percentage of the quantity consumed by the sheep from the test diets. There was more faecal loss of P by the sheep than was consumed when diets 2A30, 2L25, 2L20 and 1A25 were fed, resulting in negative digestibility values. Negative digestibilities of Ca (2L20 and 2A30), Mg (2A30), K (2L25 and 1A25) and Fe (1L20) were also recorded (Table 11). The digestibility by sheep of all the minerals analysed in diet 2A30 was less than 50% and was negative for macro elements except Na and K.

The two most abundant minerals in the animal's body, Ca and P were present in the feeds at differing ratios. There was a significant ($P < 0.05$) correlation between the Ca:P ratio and both DMI and DMD of the forages offered to sheep in this experiment, where an increase in the Ca:P ratio of a feed was associated with a decreased intake and digestibility.

Table 10: Digestibility (%) of dry matter (DM), organic matter (OM), neutral detergent fibre (NDF), acid detergent fibre (ADF) and crude protein (CP).

Forage	DM	OM	NDF	ADF	CP
1L15	62.0	65.8	67.1	65.2	47.9
1L20	62.3	65.9	66.6	64.6	47.7
1L25	58.3	61.9	63.1	60.4	36.1
1L30	49.4	53.4	51.7	43.4	40.4
2L15	57.5	61.5	65.2	64.2	38.6
2L20	36.2	41.4	42.7	43.2	17.6
2L25	31.0	32.5	23.2	30.8	12.7
2L30	39.7	41.4	28.5	18.5	55.1
1A15	46.8	52.9	48	40.9	49.6
1A20	40.4	45.7	42.8	35.8	30.1
1A25	39.4	45.4	40	27.9	38.4
1A30	59.4	62.2	58.4	49.6	67
2A15	44.1	48.3	45.7	42.5	39.2
2A20	44.0	48.8	49.3	34.7	35.2
2A25	60.1	63.7	65	60.6	67.6
2A30	43.8	50.7	52.8	50	28.5
SD	9.8	9.8	12.9	13.9	14.7

(Note: DM digestibility includes a small portion of digestible mineral premix as this was mixed with the hay feed). 1L and 2L: lacustrine soils 1 and 2; 1A and 2A: alluvial soils 1 and 2; 15, 20, 25, 30: years of continuous land use; SD: standard deviation.

Table 11: Mineral digestibility (%) of forage diets supplemented with commercial mineral mix.

Diet	P	Ca	Mg	Na	K	Fe	Mn	Cu	Zn
1L15	25.4	36.2	60.3	57.6	52.6	39.3	60.8	36.6	64.5
1L20	22.4	-3.6	28.8	65.0	54.6	-34.2	35.6	37.1	39.9
1L25	35.0	29.6	45.1	5.5	49.3	17.0	42.3	58.3	41.0
1L30	15.2	24.5	37.9	81.9	36.3	68.8	68.2	62.1	77.7
2L15	26.2	23.5	42.7	76.7	61.0	55.3	57.1	57.5	67.5
2L20	-21.2	-23.4	7.1	70.7	18.5	0.5	34.9	46.9	40.6
2L25	-16.6	33.1	44.1	68.1	-5.4	81.5	82.2	77.0	83.4
2L30	6.9	29.6	49.1	70.9	36.6	80.8	78.4	68.1	77.5
1A15	18.0	23.2	50.7	81.8	34.5	70.9	55.1	82.9	66.2
1A20	9.4	27.7	23.1	80.4	20.5	79.0	67.5	79.4	73.2
1A25	-3.5	19.9	23.9	59.8	-7.6	71.7	66.8	78.0	63.9
1A30	15.6	28.2	39.7	59.0	31.5	62.9	56.3	44.2	62.0
2A15	16.8	21.8	31.1	77.2	51.9	87.0	67.6	70.2	64.0
2A20	16.0	23.1	34.5	-4.2	46.1	54.5	47.4	64.0	96.1
2A25	30.2	31.2	49.2	72.6	71.5	37.0	55.2	42.4	68.1
2A30	-29.6	-17.0	-7.2	23.4	12.3	49.4	31.7	43.8	24.6
SD	18.3	17.2	16.7	26.0	22.0	32.1	14.7	15.4	17.8

1L: lacustrine soil 1; 2L: lacustrine soil 2; 1A: alluvial soil 1; 2A: alluvial soil 2; 15, 20, 25, 30: number of years of continuous land use; SD: standard deviation

5.4 Discussion

A concurrent study (Chapter 3) showed a succession from *Pennisetum clandestinum* (Kikuyu grass) to *Cynodon plectostachyus* (K. Schum.) Pilger (Naivasha star grass) with increased land use duration and/or increasingly dry soil. These species differ in feed quality attributes. Thus, depending on growing conditions, stage of growth and method of harvest, Kikuyu has reportedly NDF values ranging from 581 g/kg DM (Jackson et al., 1996) to 709 g/kg DM (Nahed et al., 2003), and a N content range from 15.2 g/kg DM (Marais et al., 1987) to 33.3 g/kg DM (Reeves et al., 1996). In sole diet trials with Kikuyu grass, DMI of up to 46 g/kg BW per day by sheep have been recorded (Nahed et al., 2003). On the other hand, Naivasha star grass tends to have higher NDF ranging from 694 g/kg DM (López-Gonzalez et al., 2010) to 843 g/kg DM (Nogueira Filho et al., 2000), but lower N content than Kikuyu grass ranging from 8.7 g/kg DM (Nogueira Filho et al., 2000) to 13.2 g/kg DM (López-Gonzalez et al., 2010). This implies a lower intake and digestibility of star grass compared to Kikuyu grass.

The pasture species mix and their relative proportions have an impact on the quality characteristics and may thus affect the intake and digestibility by different grazers.

The ash content of the forages was within the ranges found in pure stand Kikuyu grass (Nagadi et al., 2000), pure Naivasha star grass (Cabrera et al., 2000) and vetch (Abbedou et al., 2011). The natural permanent pastures of the Lake Naivasha riparian were composed mainly of Kikuyu and Naivasha star grass. The CP content of half the forages were above, and half were below, the 96 g/kg DM recommended for the maintenance of a 50 kg sheep (NRC, 2007). The upper half had values similar to those found in fresh *Digitaria decumbens* by Fanchone et al. (2010), and in *Chloris gayana* pasture by Abate et al. (1981). The average Naivasha riparian grass hay CP content of 87 g/kg DM was below the maintenance requirements for sheep (NRC, 2007). This suggests that the grasses in the different diets were of different species mix and possibly at different stages of maturity though they had all been allowed four months of re-growth. This is consistent with the findings (Chapter 3) on the shift in species dominance from Kikuyu to Naivasha star grass and agrees with the findings of Bruinenberg et al. (2002) on the heterogeneity of temperate pastures from natural and semi-natural grasslands. Increase in N content of the grasses as the duration of land use increased may be due to the fact that with increasing water stress reducing plant growth rate, the grasses took up most of the available N and concentrated it in their tissues compared to grasses with less water stress which had higher biomass growth rate and consequently lower N concentration. A steady increase in rate of N mineralization and availability due to lower soil moisture (Parker and Schimel, 2011) could also have availed ionic N in higher quantities for uptake leading to more plant N at the older chronosequence positions. Plant Ca, P and K reduced with land use duration suggesting that grazing off-takes more of these minerals than can be replaced through animal- and plant-sourced organic matter mineralization and deposition.

Most of the forages had NDF values higher than 600 g/kg DM, beyond which DM intake is known to be limited due to rumen fill (Mertens, 1994). However, the NDF values for the test diets ranged between 58.9 to 81.7% (average 70.2), the average being slightly higher than the 67.6% recorded for *C. gayana* at 8 weeks growth reported by Mbwile and Udén (1997). The ME values for all the diets were above the range of 6.7 - 9.9 MJ/kg DM proposed by Suyama et al. (2007) as being adequate for feeding beef cattle, sheep and low production dairy cattle. Sufficient energy can therefore be derived by ruminants grazing the riparian pastures of Lake

Naivasha. The differences in the overall chemical composition of the feeds as the land use duration increased were not sufficient to significantly change the DMI and DMD between the diets by sheep. However, changes across soil types did have an influence on the DMI and DMD, with forage from 1L soil type having a higher DMI compared to the rest. Considering that NDF tended to reduce from lacustrine to alluvial soils, the higher DMI and DMD at 1L soil were unexpected. Other factors leading to this need to be further investigated. A significant ($P < 0.05$) negative correlation existed between DMI and feed NDF. This agrees with Mertens (1994) especially since the overall NDF of the feeds was 702 g/kg DM which is higher than the DMI-limiting threshold of 600 g/kg DM. Though DMI was likely depressed by the level of NDF, the DMD was not significantly so and since the optimum NDF level for fattening mature beef cows was reported by Buxton (1996) as 700-750 g NDF/kg DM, the feeds in this experiment were within this range, and can, with supplemental N, be candidates for beef fattening. The NDF and ADF digestibility reduced with land use duration confirming the result of the lignification indices (ratio of ADL/NDF and ADL/ADF, Table 8) that indeed a progressively higher proportion of the grass NDF and ADF is made up of indigestible components (ADL) as the duration of land use increased. The digestibility of crude protein in the hay diets reduced with land use duration suggesting that although plant N increased with land use, significantly higher portions of this N are either bound, through complexation, into forms not readily available for microbial action in the rumen (Van Soest, 1994) as the lignin content of the forages increase. At the oldest chronosequence position of 30 years land use, however, the crude protein digestibility was again high implying that the forage species present here had N in forms more available to the rumen microbes (Van Soest, 1994). Precise pathways of this apparent binding and release of N within the pastures growing at different chronosequence positions need to be investigated.

The forage feeds had equal amounts of commercial mineral mix added and hand-mixed before feeding. While both the individual intake and digestibility of these supplemental minerals within the diet mix were not quantified, they were assumed to be evenly distributed for all the feed and sheep. The diets had sufficient Ca and P to meet the maintenance requirements for both a 50 kg sheep (NRC, 2007) and a 200 kg growing beef bovine (NRC, 1996). Since traditionally, the grasses of the study area are used as dry season feeds for pastoralist livestock and as feed for wildlife grazers, it is likely that the maintenance and even growth of most of these animals are met especially during the season of abundant biomass. The Ca:P ratio of the feeds correlated with the intake and digestibility of the feed. An increase in the Ca:P ratio was associated with reduced feed intake and digestibility. A Ca:P ratio of between 1:1 and 2:1 is desirable for proper feed utilization (NRC, 2007; Underwood and Suttle, 1999) and the majority of the feeds in this experiment were within this range. However, there are spots within the riparian where unique conditions led to the emergence of low quality pastures. The negative mineral digestibilities for P, Ca, K, Mg and Fe in some diets may be due to the presence, in the feeds, of these minerals in complexed forms, unavailable for digestion and absorption. Forage 2L25 within the lacustrine soil 2 and after 25 years of land use, had the lowest N values, was low in digestible N, had lowest dry matter digestibility, and had the highest ash content. There may be unique soil environmental conditions or mineral interactions which have led to the growth, within a small radius of the vicinity of 2L25, of very unpalatable grasses, mainly *C. plectostachyus*.

The permanent natural grass vegetation in the riparian zone of Lake Naivasha has low N contents while the fibre levels are within the range for fattening beef. Increase in duration of land use by continuous grazing after lake water recession leads to an increase in forage fibre content, while reducing the crude protein and fibre digestibility, as well as the contents of Ca, P, and K. These relatively poor feed quality attributes did however not negatively affect the feed intake and its digestibility by Red Maasai sheep. It is concluded that the riparian pastures at Lake Naivasha can provide sufficient energy and may become a good feed resource for ruminants, provided that N can be supplemented. There is a need to further investigate the conditions leading to poor feed quality at specific locations within the riparian pastureland of Lake Naivasha. The chronosequence concept provides an interesting and promising framework for studying effects of land use duration on soil parameter changes and associated effects on feed availability and quality.

6. GENERAL DISCUSSION AND CONCLUSION

6. General Discussion and Conclusion

The following chapter discusses the findings on floristic composition, pasture quality and mineral composition, and forage digestibility in relation to published data and draws some general conclusions and recommendations.

6.1 Floristic composition and diet quality relationship

Two forage grasses, *Pennisetum clandestinum* (Kikuyu grass) and *Cynodon plectostachyus* (Naivasha star grass), together constituted between 75 and 99% of the total vegetative cover of experimental plots analyzed in the frame of this thesis. With increasing distance from the lake shore, and consequently with increasing duration of continuous grazing, we observed a gradual shift in the dominance from Kikuyu grass to Naivasha star grass. This shift was also associated with a reduction in the biomass accumulation. The biomass accumulation by Kikuyu grass is known to show a strong seasonality (Marais, 2001; Botha et al., 2008). In addition, it is known to strongly respond to N supply (Mears, 1970). Consequently, the reduction in soil N content with increasing duration of land use did reduce both the dominance and the productivity of Kikuyu grass. Though both Kikuyu and star grasses are species for the sub-humid tropics, the biomass accumulation by star grass is usually much lower (Boonman, 1993). Thus, while no direct comparative studies are currently available, Kikuyu grass can reportedly produce some 30 tons of dry matter (DM)/ha in Kenya (Mears, 1970) and even up to 50 tons in Australia (Minson et al., 1993). The biomass yield of Naivasha star grass, on the other hand, is only 5-8 tons of DM/ha (Onifade and Agishi, 1990). A shift in the dominance in favour of star grass will therefore result in a reduction in forage yield. It can thus be assumed, that under comparable conditions, star grass will yield less than Kikuyu grass, but also that this reduction in yield is also likely to be determined by reduced soil moisture content. Own observations along the study chronosequence in Naivasha support the assumption that Naivasha star grass performs better than Kikuyu grass under conditions of low soil N and moisture contents, and that the forage production will decline with increasing duration of land use and/or distance from the lake shore.

Kikuyu grass produces herbage that is low in fibre but high in crude protein compared to other tropical pasture grasses (Mears, 1970). The increase in fibre content and a decline in fibre quality attributes with increasing durations of land use, may thus reflect not only a change in resource base quality (soil N and moisture content) but also be the result of a shift in species dominance. The reported fibre content of Kikuyu grass is much lower than that of Naivasha star grass as also observed by Nahed et al. (2003) and Nogueira Filho et al. (2000). A reduction in soil moisture content and consequently in plant available water negatively affects plant growth, especially when coupled with high evaporative rates as occurring in Naivasha (Marais, 2001). Such a deficit in soil moisture may well also be a contributing factor in the observed increase in the fibre content of the forages as suggested by Ritchie et al. (2006) who recorded an increase in fibre, and a reduced digestibility and increased crude protein content in gamagrass forage under conditions of rainfall deficit. The increase in fibre content of the pasture grasses of Lake Naivasha riparian is therefore likely to be a consequence of the competitive tolerance of the species associated with increasingly unfavourable conditions with distance from the lake.

Although the concentration of N in plant tissues increased with land use duration, the total amount of plant N per unit area was reduced due to reduced biomass accumulation. The higher plant N is likely to reflect a concentration with growth inhibition and in the absence of N dilution in growing tissues. Under drought stress, increased plant N was reported also from eight Egyptian forage species (Abd El Rahman, 1973) and gamagrass (Ritchie et al., 2006).

The shift in species dominance with changing duration of land use did not affect the metabolizable energy (ME) content of the forages, suggesting a possibility that both Kikuyu grass and Naivasha star grass do not differ in their individual ME content when grown in similar conditions. Similarly, the ME content of *C. plectostachyus* in Indonesia of 9.3 MJ/kg DM (Evitayani et al., 2004), was comparable to that of *P. clandestinum* of 9.5 MJ/kg DM (Fulkerson et al., 1998). The range of 8.2 to 11.2 MJ/kg DM recorded in the forages of lake Naivasha riparian, is comparable to the 8.5 to 9.5 MJ/kg DM reported for pure Kikuyu grass by Fulkerson et al. (1998) in a sub- tropical environment. Changes in ME across soil type gradient followed the trend observed for the N content of the pastures, suggesting a strong link between crude protein and metabolic energy as reported before (Peyraud and Astigarraga, 1998; Yayneshet et al., 2009; Islam et al., 2012).

6.2 Intake relationship with floristic composition

Despite the observed shift in the species dominance of forage grasses along the study chronosequence, the DM intake and digestibility, and the organic matter (OM) intake and digestibility were largely unaffected. Taken individually in pure stands, Kikuyu and Naivasha star grasses are reportedly similar in attributes influencing feed intake by ruminants. Values for ME range between 8.5 and 9.5 MJ/kg DM for Kikuyu grass in sub-tropical Australia (Fulkerson et al., 1998) and around 9.3 MJ/kg DM for star grass in tropical Indonesia (Evitayani et al. (2004). The crude protein content of 16.2% in star grass can be largely exceeded in Kikuyu grass with up to 29.3% recorded, provided that mineral N fertilizer is applied (Fulkerson et al., 2007). In the present study, the NDFom values were lower after 30 compared to 15-25 years of land use, partially reflecting the observed shift in species composition. As the dry matter intake of the hay was largely unaffected by the duration of land use, we can infer that grown under similar conditions, the resulting difference in critical nutrients, of the dominant species, were not sufficient to influence the dry matter and organic matter intakes of pastures in the littoral zone of the Lake Naivasha.

The floristic composition was not affected by soil types (lacustrine vs. alluvial). Along the soil gradient we did observe a change in the NDF content, which was however not reflected in the feed intake. It may thus be postulated that the NDF changes between lacustrine and alluvial soils were not sufficient to affect forage intake. A shift in the floristic composition will change NDF/ADL contents, depending on the maturity stages of the grasses and their response to environmental conditions. Thus, a drastic shift towards increased fibre content beyond a critical threshold is expected to reduce feed intake (Mertens, 1994). It is therefore possible that the intake of feed from littoral pastures will not be affected by land use duration because of contradictory response patterns. Thus, effects of an increasing N concentration in the forage may be counterbalanced by effects of increasing lignification. As the two main grass species in the riparian land of Lake Naivasha show identical trends, the shift in floristic composition will most likely not affect feed intake by ruminants.

6.3 Pasture quality characteristics and intake and digestibility

Biomass production was related to DM and OM digestibility but showed no relation to feed intake. The biomass accumulation was highest in the youngest chronosequence position and declined with increasing duration of land use. This may well be the result of sufficient availability of soil moisture which is usually the most limiting factor to biomass growth. Sufficient moisture and high soil N favour pasture growth and increase biomass accumulation. With extended growth periods of such pastures, the formation of structural carbohydrates may be delayed. With lower fibre content, the digestibility of pastures from the younger chronosequence positions was higher. Biomass production was also related to digestibility of NDF and ADF as we observed that the pastures with the highest biomass production, which also benefit from higher soil moisture, had higher digestibility. This was possibly due to lower ADL content of the pastures closer to the lake shore and which have shorter duration of land use.

The absence of correlations between pasture N, and ME content on the one part and intake of DM and OM as well as their digestibility on the other, may be a consequence of the contradictory response by the sheep to increasing N and ADL contents of the pastures with increased land use duration. Higher pasture N content is expected to increase intake by ruminants as a result of increased rumen microbial activity (Mathis, 2000). Our observation of an increase in pasture N concentration with increasing duration of land use was not accompanied by an increase in dry matter intake and digestibility as would have been expected. While the crude protein content of forage is known to influence level of intake (Mathis, 2000; Sekine et al., 2003) and digestibility (Spurgin, 2010), we did not record an increase in intake associated with increase in hay N content, possibly due to the increase in lignification of the pastures the further away from the lake shore they were.

On regression, our results showed that there was a negative correlation between CP content of feed and its NDF and ADF, while metabolizable energy negatively correlated with ADF and ADL but not with NDF. As cell contents of the grasses decrease with age and reduced moisture, the proportion of cell wall contents increase and this is reflected in the negative correlation between CP and ME on the one hand, and fibre fractions, mainly cellulose and lignin on the other. The increase in the level of 24 h gas production with increased CP, reflected in the positive correlation in our calculation, is consistent with improved digestibility with increased N content (Spurgin, 2010). An increase in the proportion of fibre with age and moisture stress would therefore lead to an increase in indigestible fibre fractions, particularly ADL, leading to reduced digestibility of the forage. The hay used in the feeding experiment was harvested after four months of growth and by this time, the growth stage of most grasses would indicate reduced N and ME content. It would be similar to the samples harvested in August in our biomass and quality experiment. Therefore, increased N content and increased indigestible fibre content of the forages are likely to have affected intake and digestibility by sheep differentially, leading to contradictory responses and so no response was observable.

6.4 Mineral composition and forage feed quality

Concentrations of mineral elements in forages generally depend on interactions of edaphic, biotic and climatic factors (McDowell, 1976). Soil pH and fertility, forage species and maturity stage as well as season and climate are the factors that determine mineral concentrations in forages. An acid pH is believed to increase absorption of iron (Fe), manganese (Mn), copper (Cu) and zinc (Zn) and to limit the absorption of phosphorus (P), potassium (K), sulphur (S), calcium (Ca), magnesium (Mg) and selenium (Se) by plants (NRC, 2007). Maturity of forages and the reduction of leave to stem ratio would reduce the mineral content as leaves are richer than stems in all minerals (Minson, 1990).

The mineral profile of the hay diets from our experiments indicate that all the macro elements (Ca, P, Mg, Na and K) were present in quantities within the range sufficient to meet the requirements of grazing livestock and below the excess limits (Georgievskii et al., 1982). Although forages in general are known to be low in Na (NRC, 2007), the hay feed had been fortified with a sodium chloride-based mineral premix which elevated the levels of sodium in the diets. Of the micro elements determined in the diets, Cu and Zn were within the optimum range for sheep feeding (Georgievskii et al., 1982; NRC, 2005). Manganese levels above 70 mg/kg DM were suggested by Georgievskii et al. (1982) to be in excess of the requirements by ruminants but NRC (2005) puts the maximum tolerable levels at 2000 mg/kg DM. Wong-Valle et al. (1989) concluded that the minimum level of Mn that can reduce appetite and growth rate in lambs is between 3000– 4500 mg/kg DM. The hay diets in our experiment, with Mn values ranging from 41 to 256 mg/kg DM, were therefore below the levels that would affect intake by sheep.

Only four of the forages we used had Fe values below the maximum tolerable level of dietary iron. The NRC (2005) states that sheep can tolerate up to 500 mg/kg DM of iron in their diet but majority of the forages we used were way above this value. There is a possibility that the high levels of Fe are partly responsible for reduction in intake and digestibility of the forages of the lake Naivasha riparian. Although it was not directly determined as an objective for the purpose of this thesis, we observed that although most of the hay diets had higher than normal Fe content, one of the forages in particular had the highest. This is also the diet with the lowest values of K and highest of Zn and Na. Three of the forages from one of the lacustrine (1L) soils had Fe contents below 700 mg/kg DM while the averages for the forage from the other soil types were more than double the average of the 1L forages. The forages with the lowest values of Fe did record higher intake and digestibility compared to those with higher Fe content. Since all the forages were within acceptable range for all the nutritional attributes except Fe content, it is possible that the reduction in intake and digestibility of 2L, 1A and 2A forages is connected with their high Fe content. An increase in dietary iron to almost 1000 mg/kg DM has been found to reduce liver plasma copper to concentrations indicative of deficiency (Humphries et al., 1983; Ivan et al., 1990).

The levels of iron found in the riparian pastures of Lake Naivasha would presuppose a high availability of Fe in the soils around the lake. Gaudet (1979) recorded high P and Fe content in river Malewa water during periods of high discharge into the lake. Tarras-Wahlberg et al. (2002) found high levels of Cadmium (Cd), Fe, Ni and Zn in both river and lake sediments in Naivasha which are thought to derive from volcanic rocks and/or lateritic soils found in the lake catchment. These sediments are often deposited in the lake fringes and so the high Fe content of the littoral forages could be derived from the iron rich lateritic soils eroded from the catchment (Tarras-Wahlberg et al., 2002) and deposited on the fringes of the lake.

It would be of significant interest to find a direct link between co-association of very high Fe content and depressed hay intake and digestibility especially in one of the forages (2L25). Likewise, since minerals are known to interact with each other and with other non-nutritive factors in either synergistic or antagonistic ways, a deeper study on this may reveal how these interactions play out in the lake Naivasha riparian pastures and the effects of such interactions on the intake and digestibility by ruminants.

6.5 Conclusions and recommendations

The present thesis aimed at studying the effects of soil type and land use duration on pasture and forage quality attributes in an East African Wetland, Lake Naivasha, providing a model study area.

Wetlands are sites characterized by year-round availability of water and by soils that are usually more fertile than those of adjacent upland environments. They provide a wide range of ecosystem services and particularly in water-scarce savannah environments, wetlands exert a strong attraction for humans who use them increasingly for agricultural production. Thus, resource users either settle around wetlands or migrate there seasonally, changing land use, environmental responses and social-ecological interactions within the wetland. The pressure on the resource base increases and intensive grazing can lead to a rapid decline of soil productivity, particularly in arid environments. Most previous studies on forage availability and quality centered on floodplain systems and little is known to date about the riparian wetlands around fresh water lakes.

The choice of the riparian land around Lake Naivasha was guided by the fact that it is one of the few fresh water lakes within a series of alkaline lakes of the Rift Valley of Kenya. The riparian land is heavily contested by both wildlife and (nomadic) pastoralists for access to water and the provision of feed, and also by various other stakeholders frequently leading to conflicts. Wildlife conservationists and pastoralists who both require pasture and water for their animals are key players in shaping the resource uses and the political discourse around the ecology of the riparian land surrounding Lake Naivasha.

An additional dimension for the analysis of the riparian land and its ability to provide quality feed for wild and domesticated animals is the presence of so-called chronosequences. Between 1980 and 1995, the level of Lake Naivasha reduced by 2.5 metres. Since 1980 the deviation of water from the main tributaries of the lake for supplying domestic drinking water to the city of Nakuru, coupled with direct abstraction of lake water for irrigating agro-industrial crops (cut flowers and vegetables for export to the international market) was the main culprit for this trend. This decline was further accelerated during the drought years of 1998 and 2000 and 2004-2009. The resulting exposure of new land and its continuous use as grazing ground resulted in the formation of a chronosequence of land use, making Lake

Naivasha a good model to study land use effects. The chronosequence concept has so far been used in the study of soil nitrogen changes (Roth et al., 2011) and ecological changes (Walker et al., 2010). We hypothesized in this thesis that the chronosequence concept provides an ideal framework for assessing the effects of land use duration and soil type on forage availability and quality.

The main objective of this thesis was to determine how the species composition and abundance as well as nutritional quality of the naturally occurring forage are affected by the chronosequence position (duration of land use by continuous grazing), including soil type and soil moisture availability in a riparian wetland. The results presented in this thesis demonstrate how species dynamics and the nutritional quality of natural forages change within the littoral land of Lake Naivasha. This will help in developing strategies and guiding decisions on how to enhance the resilience of the wetlands and reduce land use conflicts.

The specific objectives of this thesis were as follows:

1. To determine how species composition and relative abundance of the forages currently grazed and browsed along a chronosequence of Lake Naivasha riparian are affected by duration of land use. Chapter 3 of the thesis details this objective. This objective was met and conclusions 1 and 2 below highlight the findings.

2. To determine the effect of continuous grazing duration and soil types on biomass productivity and nutritional quality of natural pastures of Lake Naivasha riparian. This is detailed in chapter 4. The objective was met and conclusions 3 and 4 below summarize the findings.

3. To determine the intake and digestibility of the natural pasture grasses of Lake Naivasha riparian by sheep. This is presented in chapter 5 of the thesis. This was met and conclusions 5 and 6 summarize it.

4. To determine the interaction between soil type and duration of land use in their effect on feed quality as well as the implication of this interaction on livestock productivity. This chapter gives a detailed synopsis of how this objective was met and conclusion 7 gives an overall summary.

The specific objectives formed the three experiments of our study. These objectives were met and the main conclusions of the three experiments conducted between 2010 and 2013 are summarized as follows:

1. Continuous land use by grazing and reduced soil moisture changes forage species composition from a dominance of Kikuyu grass (*Pennisetum clandestinum*) to that of Naivasha star grass (*Cynodon plectostachyus*).
2. The shift in species dominance is largely unaffected by the soil type. However, increased soil N availability favors forage productivity.
3. Continuous grazing and reduced soil moisture content, both during the dry season and with increasing distance from the lake shore affects the composition of pasture grasses as well as forage yield and quality.
4. Continuous grazing and reduced soil moisture content differentially affect the suitability of the riparian land as pasture ground and feed resource area for ruminants.
5. Duration of continuous grazing is associated with increase in lignin content of the forages and while dry matter intake and digestibility are unaffected, protein and fibre digestibility reduces with increased land use.
6. The riparian pastures at Lake Naivasha can provide sufficient energy and may become a good feed resource for ruminants, provided that N can be supplemented.
7. The chronosequence approach provides a novel and suitable framework to study change processes and trends of forage availability and quality.

It is possible, therefore, that reduction in soil moisture and soil N content lead to the shift in dominance from Kikuyu grass to Naivasha star grass, which resulted in reduced biomass production, since star grass produces less biomass than Kikuyu grass. A comparative study on the productivity of these two dominant Naivasha grasses under various soil and environmental conditions would give more insight into this dynamic. That the dry matter and organic matter intake and digestibility were not affected by the shift in species dominance implies that the actions and interactions of nutrient characteristics like CP, ME and lignin of the pastures were not sufficient to cause a change in intake and digestibility as the grazing duration increased. The factors that influenced intake did not depend on the species dominating the pasture mix. Lower lignin content of the forages closer to the lake favored improved digestibility. An increase in plant N did not lead to increased intake as the duration of land use increased and this may be due to the increase in lignin in pastures the further away from the lake shore line.

The littoral pastures of Naivasha can supply most of the minerals required by grazing ruminants. With provision of sodium chloride, animals grazing the littoral pastures are likely to have their mineral requirements satisfied. However, the level of iron in the pastures is very high. The hay having the lowest iron content had the highest intake and digestibility of dry matter and organic matter. The high level of iron may be negatively influencing the intake of the hay of the Lake Naivasha riparian. The high iron content in the pastures could be because of high soil Fe derived from the iron-rich lateritic soils of the catchment area which get deposited at the fringes of the lake. There is need to study the mineral interactions and the link between high iron content and depressed intake and digestibility.

This work demonstrated that the pastures of the littoral Lake Naivasha are of sufficient quantity and quality for use as fattening diet for beef, sheep and as dry season feed for livestock. Pastoralists often use these pastures during the dry season from December to March when the quantity and quality of the littoral pastures is low. Maintenance energy requirements are possibly met during this time and death from starvation is avoided till the next rainy season when better quality pastures become available and they move their livestock away from the riparian area. The littoral pastures therefore serve as insurance against livestock death during periods of pasture unavailability in the pastoral areas surrounding the lake. As the pastoral livestock utilize the low quality riparian pastures for their survival, they prepare the pastureland for the regrowth of better quality pastures during the subsequent rainy and growth season. This benefits the wildlife resident in the riparian area whole year round.

No studies have been done on the carrying capacity and the suitability of the littoral forages as wildlife feed. However, the fact that the wildlife species present usually have their nutrient requirements met by savannah forages, and the results here showing that riparian pastures are better than pastures of dry savannah, then we conclude that the wildlife grazers are nutritionally adequately supplied. Care should however be taken to regulate the number of animals grazing this riparian so as not to overgraze. This is to avoid increased soil erosion and sedimentation of the lake and also to maintain sufficient cover for the filtration of the run off water as they enter the lake after rains. The sustainability of the interaction between livestock, wildlife and the riparian environment will depend on determination of the correct stocking density for both wildlife and seasonally immigrating pastoralist livestock, controlled pastoralist access to the riparian for specific periods of the year, and a grazing use policy negotiated between all stakeholders including wildlife conservationists, pastoralists and small scale livestock keepers around Lake Naivasha.

The chronosequence is a useful study tool in exploring the plant species changes, pasture production capacity of wetlands as well as in studying the quality attributes of these pastures. Combined with gradients of soil attributes and soil moisture content, it can be used to study pasture changes at various spatial and temporal scales. The chronosequence concept also provides an interesting and promising framework for studying effects of land use duration on soil parameter changes and associated effects on feed availability and quality.

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