Long- and Short-Term Dynamics of the Wetlands in the Amboseli Savanna Ecosystem, Kenya

by

Sunita Sarkar

A thesis
presented to the University of Waterloo
in fulfillment of the
thesis requirement for the degree of
Doctor of Philosophy
in
Biology

Waterloo, Ontario, Canada, 2006

©Sunita Sarkar 2006

AUTHOR'S DECLARATION FOR ELECTRONIC SUBMISSION OF A THESIS

I hereby declare that I am the sole author of this thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

I understand that my thesis may be made electronically available to the public.

Abstract

The wetlands of the semi-arid savanna ecosystem of Amboseli are the critical dry-season range for a diverse wildlife population, as well as for livestock and humans. Changes in the migratory patterns and increases in the population of the elephants in the ecosystem, as well as a shift in the lifestyle of the growing human population from predominantly nomadic pastoralist society to a sedentary agrarian community, has had far-reaching effects on the ecosystem and the wetlands. In this thesis, the current status of the wetlands and the changes in vegetation over the last four decades were examined using satellite imagery and long-term census data. Studies were also conducted to determine the impact of grazing by elephants and other large mammals on wetland vegetation, and the flooding patterns and extents of some of the wetlands were examined.

Long-term aerial count data indicated that the wetlands that are currently protected by the Amboseli National Park have been under increasing use year-round by elephants since 1975. These wetlands showed a rapid increase in extent between 1950 and 1976. This corresponds to the elephant-driven decline in *Acacia xanthophloea* woodlands, which may have changed the hydrology of the area. Since then, only one of the wetlands, Longinye, has shown dynamic changes in extent. This is either the effect of the blockage of water flow by vegetation or the creation of new channels by elephants and hippopotami. The wetlands had a diverse range of wetland habitat from areas of open water with scattered tall *Cyperus papyrus* communities in the centre of one wetland to large expanses of seasonally inundated *C. laevigatus* and *Cynodon dactylon* dominated habitats fringing the wetlands. Most of the wetland habitats were composed of short sedges and grasses, which was shown to be the direct result of elephant grazing. Elephants tended to keep the vegetation of a control wetland short and of low biomass during both wet and dry seasons, whereas the vegetation in a treatment wetland, where elephants were excluded, showed a rapid increase in biomass and height. Other herbivores were shown to maintain conditions of short vegetation of low biomass through grazing pressure in the dry season. The impact of natural and simulated grazing on growth of the vegetation was studied and only under simulated grazing pressure was growth increased in the seasonally inundated *C. dactylon* grasslands, as well as the floating mat communities dominated by *C. laevigatus* that occur in the shallow water wetlands. This indicates that natural grazing may be detrimental either to the plants or the soil.

The wetlands that are under human use had predominantly shallow water and seasonal wetland habitat. Deep water habitat with *C. papyrus* communities was only present in one of these wetlands, Kimana, which is also the only wetland outside the park that is used by livestock and wildlife, as well as to irrigate a large area of land around the wetland. Two other wetlands, Namelok and Lenkir that were predominantly used for irrigated agriculture, were largely composed of seasonally inundated wetland habitat. A fourth wetland, Esoitpus, has been almost completely drained and this has most likely resulted in the development of *A. xanthophloea* and *C. dactylon* dominated riverine and *C. laevigatus* / *C. dactylon* dominated seasonally inundated wetland communities.

Overall, the wetlands in the park provide a measure of habitat diversity that may be useful for various invertebrate and vertebrate communities. However, the present lack of tall sedges may negatively impact the bird community. This state can be reversed by the exclusion of elephants from

some wetlands for short periods of time. On the other hand, the wetlands outside the park appear to be facing rapid draw-down. Hence, there is an urgent need for sound water management practices for these wetlands.

Acknowledgements

There are two people without whom I would not have written this thesis, thus fulfilling one of my ultimate goals of having a PhD, and they are Dr. David Western (Jonah) and Dr. W. D. Taylor (Bill).

Jonah first introduced me to Amboseli as an intern in his Amboseli Monitoring Program. This gave me the opportunity to appreciate the beauty of the landscape, even without the trees, the exquisite elephants, and the life-giving green of the wetlands of this part of my country. I would not have gotten a chance to mesh animals, plants, and water together to create what is now this thesis, if it hadn't been for Jonah's lifelong work on understanding the ecosystem function in Amboseli. Jonah has provided the long-term data sets and the maps that I use in chapter 2, and through his funding the remote sensing data was made available and the enclosure study and all my field expenses were possible. For all this and your input into the preparation of this thesis, thank you Jonah.

Without Bill, however, none of this would have come to fruition. Without ever meeting me, Bill gave me a chance to pursue my goal and has always had more faith in my abilities than I have. He has guided me when I needed it the most. He has given me encouragement and, more importantly, been enthusiastic about the project throughout. For your interest in Africa, and all things African, for your kind and understanding supervision and guidance, and for financial assistance through research assistantships, I thank you Bill.

I would have no data if it were not for David Maitumo, veteran field assistant for the Amboseli Monitoring Program and the African Conservation Centre (ACC), Nairobi. His help was invaluable in the field. Without him I would not know one plant from another and which dung pile was from which animal! He carried out most of my field work for chapters 3 and 4 when I was in Waterloo and always gave his best. He spent an entire week driving and walking across Amboseli to collect data for chapters 2 and 5. *Asante sana* David, for your unassuming ways, your knowledge, and your help, in the most important way, in every chapter of this thesis.

The entire staff of ACC has had some role in getting me to this point. A few, however, have been critical. Daniel Macharia, GIS and Remote Sensing Specialist, is still rather new to ACC but has already become one of the most important people to my work. I have never met Daniel in person, but he has never denied me any help I needed for chapters 2 and 5 of this thesis. He accompanied David Maitumo to the field to collect data and he has emailed me numerous times answering numerous questions that I have had. For your continued assistance to someone you have never met in person, *Asante sana* Dan. Victor Mose, assistant *extraordinaire*, who is with the monitoring program, is very dear to me. He has been my go-to person for data and has always been willing to help and has done so promptly. For all your help, *asante sana*, Vic. Sam Kamau, Teresa Njeri, Zippy Wanakuta, Eluid Wanakuta, and Lucy Waruingi all either with or formerly of ACC have been of support in one way or another and I want to send them all a big THANK YOU! I must include Byron Anangwe of RCMRD for his tireless help with acquiring the satellite images and with all the questions I had.

I want to also thank my committee for volunteering their time on different occasions so that I could fulfill the requirements for my degree. They have always been enthusiastic and full of comments and questions. Dr. Hawthorn, thank you for thinking of me when you read about African issues. Thank you, Dr. Hawthorn, Dr. Murphy, and Dr. Warner. I also want to thank Anne Grant for her assistance with the data analyses for chapters 2 and 5, and the Department of Geography at the University of Waterloo, for access to GEOMATICA software used in the analyses of these data. Jennifer Lehman, the best Graduate coordinator a department can have, thank you for all your help.

I must acknowledge the financial support I received through NSERC PGSB, OGSST, the University of Waterloo Doctoral Thesis Completion Award, and Teaching and Research Assistantships.

My family that has always been my strength and source of inspiration, thank you for always being there for me and for believing in everything I do. My friends, who have always seen the good in me, who have called to ask how I was doing during the painful task of writing a thesis, Ashnoor and Maya thanks for this especially, who have accepted me for who I am and have always believed in me, thank you!

My colleagues at the lab, Sunni for her friendship, companionship and for being my gym buddy, Mo for being a great first office mate and for our discussions, Vicky for just being Vicky, and Scott for his help with thesis-related issues, are just a few of the people I must thank. You have all been very helpful in your own way in getting me to this point in my degree.

My Jason and Chyanne who have kept me sane throughout this process, I think everyone thanks you! Jason, you have shown me so much love and support that I will be indebted to you all my life. Your constant encouragement, humour, and cooking have pulled me through writing this thesis. Thank you and I love you. Chyanne, meow meow meow!

Finally, my mother and father are the reason I exist. So thank you for that. Dad you wanted me to have a Doctoral degree, and here is one big step towards that end. Thank you for supporting me when I needed it and just being there. Mum, you know how important you have always been in my life. Your support and love are appreciated always. Thank you for being there for me Ma. To both of you I dedicate this thesis.

Table of Contents

List of Tables

List of Figures

Chapter 1

General Introduction

The Amboseli ecosystem (Figure 1.1a) is found in eastern Kajiado District, southern Kenya, and is approximately 3000 km^2 (Western, 1975). It is considered either a semi-arid (Moss, 2001) or an arid (Western, 1975; Georgiadis *et al.,* 1989) bushed grassland savanna, based on the rangeland classification developed by Pratt *et al.*(1966). Within the ecosystem, 600 km^2 has traditionally been designated as dry-season range for wildlife, livestock, and humans (Western and Sindiyo, 1972). This area is comprised of aquifer-fed perennial springs and wetlands, the latter being the focus of this work. In order to understand the importance of these wetlands to the ecosystem it is important to introduce the nature of the surrounding ecosystem.

In the following sections, I define and describe savanna ecosystems with particular reference to semi-arid and arid savannas. I review the interactions between the fauna and flora of semi-arid and arid savannas, with particular attention to the role of water, and cover the occurrence and importance of wetlands in dry lands. I then present a brief history of Amboseli and review the roles of elephants and humans in this ecosystem. Finally, I present the rationale and objectives of my research.

1.1 Savanna Ecosystems

About one-third of the world's surface is classified as savanna, with more than 50% of Africa, Australia and South America, and about 10% of tropical Asia, covered by this ecosystem type (Skarpe, 1991). At present, the common definition of a savanna is: an ecosystem that is either tropical or subtropical, characterized by a continuous and often heliophilous C_4-grass-dominated herbaceous layer, with a significant presence of woody species that do not form a closed canopy or a continuous cover (Adams, 1996). Due, however, to the varied form and composition of savanna vegetation and the climatic conditions under which they occur, categorizing savannas is problematic (Adams, 1996). Skarpe (1991) mentions definitions of savannas based on edaphic and climatic characteristics, as well as anthropogenic impacts (secondary or derived savannas), whereas Adams (1996) uses a categorization method based on floristic composition and physiognomy of the savannas. Here, the latter will be used as the remainder of the thesis is focused on vegetation and the impacts of herbivores and humans on vegetation. However, since humans have been part of the savanna ecosystems in Africa for thousands of years, many of the species considered characteristic of certain savannas are in fact the result of human activity (Skarpe, 1991).

There are five broad categories of savanna, going from humid to dry climates: (1) savanna woodland, (2) savanna grassland, (3) savanna parkland, (4) low tree and shrub savanna, and (5) thicket (Adams, 1996). There are, however, savanna mosaics of woodland, tall-grassland, and wetland communities where seasonal inundation and complex patterns of valleys, rivers, lakes, and wetlands occur (Adams, 1996). The Great Rift Valley region of East Africa has the most impressive and extensive mosaics in Africa due to the presence of rich volcanic soils and diverse landscapes (Adams, 1996). One important trait of a savanna ecosystem, regardless of how much rainfall it may receive, is that it is highly dynamic (Skarpe, 1991), and almost all the tree/shrub species are either semi-deciduous or deciduous (Adams, 1996).

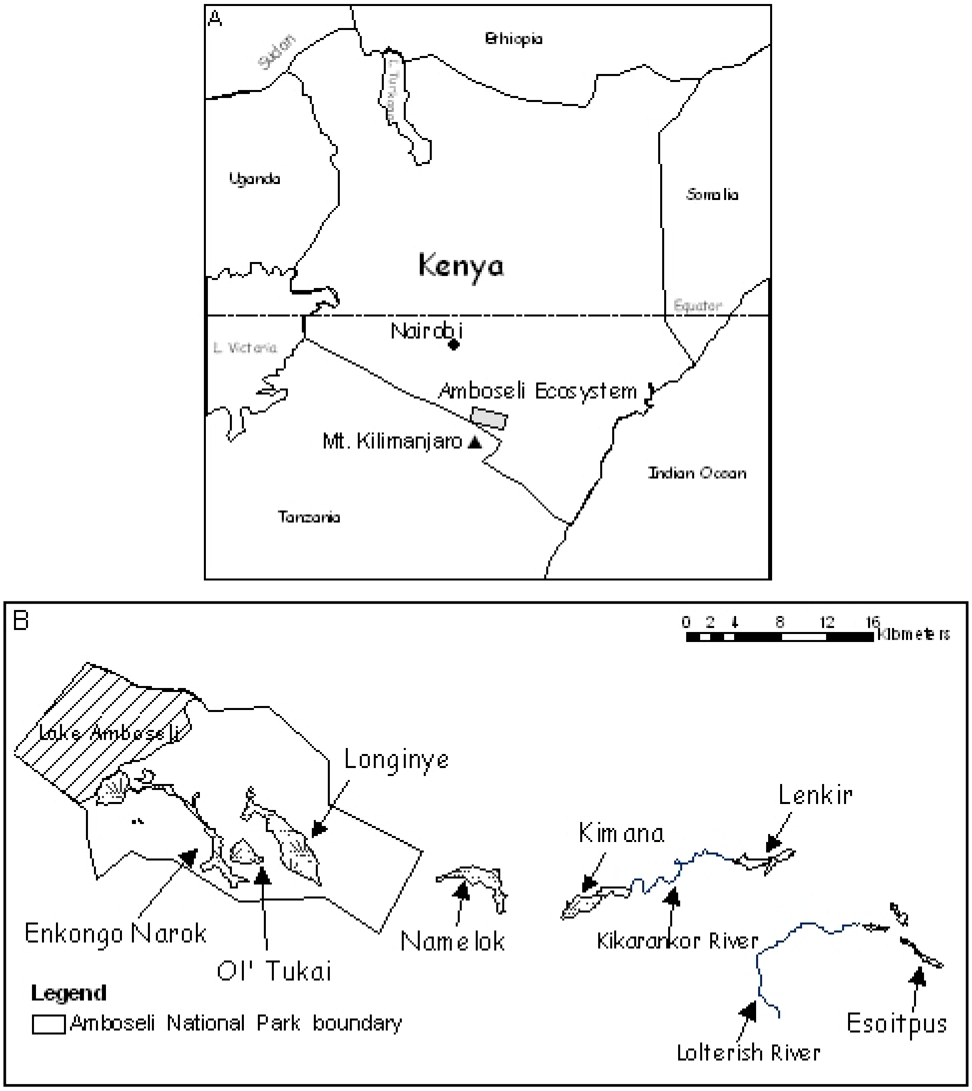

Figure 1.1. The location of Amboseli Ecosystem (shaded box), Kajiado District, southern Kenya (A), and (B) the layout of the wetlands of the Amboseli Ecosystem.

Savanna woodlands occur primarily where there is sufficient rainfall or water run-on from other parts of the landscape (Swift *et al.,* 1996). In this biome, trees are greater than 8 m in height and there is a well defined stratum of tall (>0.8 m) mesophytic, perennial grasses (Adams, 1996). In Africa, savanna woodlands are either predominantly of the genera *Brachystegia*, *Isoberlinia*, and *Julbernardia* or are dominated by *Colophospermum mopane* (J. Kirk ex Benth.) J. Léonard trees

(Adams, 1996). In Africa, humid savanna woodlands are found in areas with annual rainfall above 600 mm y^{-1}, such as around the fringes of the tropical forests of the Zaire Basin and the *miombo* forest of Tanzania.

Savanna grasslands are defined as treeless areas of tall tropical grasslands that, in Africa, are dominated by a mixture of *Hyparrhenia*, *Themeda*, *Setaria*, and *Echinochloa* (Adams, 1996). However, these biomes normally occur with savanna woodlands and are commonly a major component of savanna mosaics as opposed to being a separate biome (Adams, 1996). The savanna grasslands in Africa constitute the floodplains of rivers and basins, for example the Kafue Flats along the Kafue River in Zambia, and the borders of wetlands, such as the Sobat Basin in southern Sudan and the Sudd in the White Nile Basin (Adams, 1996). In areas where rainfall is high, but highly variable, seasonally inundated savanna grasslands are critical for dry-season grazing. The fringing wetlands along the edges of Lake Baringo, located in the Kenyan portion of the Rift Valley, are an example of savanna grasslands dominated by, in this case, the grazing and flood-tolerant rhizomatous perennials *Cynodon dactylon* (L.) Pers., *Cynodon plectostacyhus* (K. Schum.) Pilg., and *Echinochloa haploclada* (Stapf) (Little, 1996; Thompson, 1985). The *Il Chamus* herders have used these areas as grazing grounds for their livestock during the dry-seasons and drought-years since the eighteenth century (Little, 1996).

Most of the savannas in the world, including those in Sudan, Guinea, and East Africa, are humid (Skarpe, 1991). The neotropics contain the world's largest area of humid savannas. Some examples are the Brazilian *cerados*, which include the savanna woodlands (*cerradão*), the progressively less arboreal grasslands (*cerrado*) and the nearly treeless open grasslands (*campos*), and the Venezuelan *Ilanos* (Furley, 1999). The latter two are the closest to the savanna grasslands of Africa (Adams, 1996), but as in Africa, there is a gradation from one form to the next based on the tree cover and type of tree/shrub present.

Savanna parklands, like savanna woodlands, have a layer of mesophytic, perennial grasslands, but the height of these grasses ranges from 0.4 to 0.8 m (Adams, 1996). The woody vegetation is less than 8 m in height and is dominated by tree species in the genus *Acacia*, which are found scattered throughout the grasslands along with other deciduous trees from the genus *Terminalia*, *Piliostigma*, and *Combretum* (Adams, 1996). Savanna parklands occupy an intermediate position between savanna woodlands and low tree and shrub savanna, with rainfall ranging from about 400 to 800 mm y^{-1}. The transition from parkland to low tree and shrub savanna is gradual and occurs where the annual rainfall is between 350 and 400 mm y^{-1} (Adams, 1996; Swift *et al.*, 1996). Together with the low tree and shrub savannas, the parklands cover a large area of the Sudano-Sahelian zone and the Horn of Africa, and are found, to a smaller extent, in Namibia, Botswana, and the northern parts of South Africa (Adams, 1996).

The low tree and shrub savannas are classified as semi-arid when regional rainfall falls below 400 mm y^{-1} and as arid when rainfall is below 150 mm y^{-1} (Swift *et al.*, 1996). In the semi-arid savannas, the dominant low-growing tree/shrub genus is also *Acacia*, though composition does vary from place to place (Adams, 1996). There is, of course, a dominant herbaceous layer present. However, with decreasing annual rainfall there is a general change in dominance from perennial grasses, such as *Sporobolus*, *Cynodon*, and some species of *Eragrostis*, to annuals like *Aristida* and *Eragrostis* *cilianensis* (Swift *et al.*, 1996). Grasses are also less than 0.8 m in height (Adams, 1996). Dwarf shrubs and desert grasslands gradually replace more arid low tree and shrub savannas and the boundary between desert and savanna is not sharp (Adams, 1996).

The final savanna type is thicket, which, unlike a "true" savanna, has no herbaceous layer (Adams, 1996). However, thickets commonly form dense, impenetrable clumps of evergreen or deciduous shrubby vegetation in areas that were once heavily grazed or severely burned. They can be transformed back to savanna grasslands and were therefore included in this classification by Adams (1996).

The only detailed information about vegetation in the Amboseli ecosystem is for the western part of the ecosystem from Lake Amboseli to just east of Longinye (Figure 1.1b). The area to the east of the park boundary, which includes the other smaller wetlands, has not been described in any detail in the literature. Based on personal observations, the area to the east of the park is now dominated by *Acacia drepanolobium* Harms ex Sjostedt and other *Acacia* shrub species, with scattered herbaceous ground cover. This may be the direct result of the creation of the Amboseli National Park in the mid-1970s, due to the exclusion of livestock from the park and the compression of elephants into the park (as will be described in more detail below), which promoted grazing and reduced browsing in this area. This phenomenon is common in many areas bordering parks and reserves in Africa (Western and Gichohi, 1993b).

One of the earlier descriptions of the basin and surrounding areas is given by Western and Sindiyo (1972). They describe the ecosystem outside the basin (roughly, the region outside the park boundary) as having woody vegetation dominated by *Commiphora* and *Balanities* spp., *Acacia nubica* Benth., and *A. mellifera* (Vahl.) Benth., and a herbaceous layer composed of *Aristida keniensis* Henrard, *Chloris gayana* Kunth, and *Sericocomopsis pallida* (Moore) Schinz (Western and Sindiyo, 1972). *Commiphora* and *Balanities* trees tend to occur primarily in well-drained sites near or on the foot-hills of mountains (Swift *et al.*, 1996), and for this reason this type of wooded area is found at the base of Mt Kilimanjaro to the south. *Acacia nubica* and *A. mellifera* are both shrubs; the former is found in the south, between the *Commiphora – Balanities* woodlands and the beginning of the basin (Western and Sindiyo, 1972). *Acacia mellifera*, which forms dense thickets in dry areas (Adams, 1996), is found in the drier open scrub to the northwest. Hence, based on the Adams (1996) classification presented above, the Amboseli ecosystem outside the basin is a mixture of low tree and shrub savanna and thicket.

The basin, however, was described in 1972 as having areas of bare soils that were seasonally inundated, the lakebed dominated by *Psilolemma jaegeri* (Pilger) S.M. Phil. (formerly *Odyssea jaegeri* (Pilg.) Hubb.) forming the western edge of the basin, alkaline grasslands dominated by *Sporobolus* species fringing northern edges of the Enkongo Narok and Longinye wetlands (Figure 1.1b), and *A. tortilis* (Forsk.) Hayne woodland along the southern and northern edges of the basin (Western and Sindiyo, 1972). There were also open *Acacia xanthophloea* Benth. woodlands with a shrub layer of *Azima tetracantha* Lam. and *Salvadora persica* L. fringing the southern boundary of the Enkongo Narok and Longinye wetlands and completely surrounding the Ol' Tukai wetland (Western and Sindiyo, 1972). However, since the 1960's the *A. xanthophloea* trees had been dieing-off and have now been completely replaced by *Suaeda monoica* Forsk. and *S. persica* (Western and

Maitumo, 2004). The only indication that *A. xanthophloea* occurred in the area around Ol' Tukai is the presence of dead and dried tree trunks (*personal observation*). The presence of wetlands, woodlands, and grasslands favours the classification of the Amboseli basin as savanna mosaic even though the surrounding area is dry savanna.

1.2 Semi-arid savanna ecosystems

In semi-arid savannas rainfall is sparse and always highly variable (Altmann *et al.,* 2002; Wolanski and Gereta, 2001). In the dry savannas of the equatorial belt of Africa, within which lies East Africa, the reason for this variability is the *El-Niño*-Southern-Oscillation (ENSO) cycle that causes increased rainfall during the *El-Niño* episode and drought conditions in the *La-Niña* episode (Plisnier *et al.*, 2000). The opposite happens for instance in southern Africa and South America (Holmgren *et al.,* 2006). In addition to being highly variable and scarce, the rainfall that does fall on East African semi-arid savannas is bimodal in distribution (Swift *et al.*, 1996). This distribution is caused by the movement of the Intertropical Convergence Zone (ITCZ), a band of low pressure where the trade winds from the northern and southern hemispheres converge (Hulme, 1996). The peaks in rainfall in a particular region occur when the ITCZ passes overhead. As the ITCZ moves north, the long rains of March to May occur, whereas when the ITCZ moves south, the short rains of October to early December fall (Swift *et al.*, 1996).

The Amboseli ecosystem lies in the rain-shadow of Mt. Kilimanjaro (Figure 1.1a). Rainfall over the Amboseli ecosystem varies from 350 mm y^{-1} to 500 mm y^{-1}, with higher rainfall amounts falling closer to the foothills where altitudes are greater (Githaiga *et al.,* 2003). Around the Basin, however, rainfall is rarely higher than 350 mm y^{-1}, except during an *El-Niño* episode of the ENSO cycle. The short rains occur in November and December, and the long rains in March or April through to May (Georgiadis *et al.*, 1989). A long dry season occurs between June and October, which is often preceded by failure of one or both of the previous rainy seasons (Altmann *et al.,* 2002). Altmann *et al.* (2002) also report that both the maximum and minimum diurnal temperatures in the Amboseli Basin have risen by 0.275°C and 0.071°C, respectively, between 1971 and 1996.

Under the conditions prevalent in semi-arid savannas, including Amboseli, the vegetation has to be able to respond quickly to the changes in climate in order to survive. Grasses are phenologically adapted to rapidly respond to rainfall, resulting in lush green high quality lawns soon after the onset of rains (Swift *et al.*, 1996; Western and Lindsay, 1984). However, these lawns last only over the duration of the rains and partly into the dry season, depending on the type of grass and the grazing pressure (Swift *et al.*, 1996). Most of the woody vegetation, on the other hand, has morphological adaptations that either reduce water loss or increase water storage, or the trees have root systems that enhance water uptake from the aquifers (see Adams (1996) for more detail). The dominant *Acacia* trees and shrubs have micro-phyllous pinnate leaves that reduce water loss (Adams, 1996). They are found around ephemeral stream beds, permanent water courses, and areas that receive water from other parts of the landscape via run-off (Swift *et al.*, 1996). *Acacia tortilis* trees have deep tap roots that easily access the water table and shallow lateral roots that absorb water in the upper layers of soil (Belsky *et al.,* 1993). It has been shown that *A. tortilis* trees undertake the process of hydraulic lift, which is when water moves from relatively wet to dry soil layers through plant roots, in particular during the night when the stomata are closed and water potential differences can drive this movement

(Ludwig *et al.,* 2003). This process is not only beneficial to the tree, by increasing the water content of the upper levels of the soil, it has also been shown to benefit the herbaceous under-story in the semi-arid savanna ecosystem of the Tsavo National Park, Kenya (Belsky *et al.,* 1989; Belsky *et al.*, 1993). *Acacia xanthophloea*, on the other hand, is not common in semi-arid savannas (Swift *et al*., 1996), as this species requires a shallow water table, such as around the southern edges of the wetlands of the Amboseli (as described in the previous section), as well as sufficient rainfall (Western and Sindiyo, 1972).

The invertebrate and small vertebrate (including fish) communities in savannas deal with the climatic conditions by aestivation underground during dry seasons, and/or being r-strategists (Adams, 1996). There have been more studies conducted on the impacts and importance of termites, in particular the fungus-growing termites (Isoptera, Termitidae, subfamily Macrotermidinae), in African savannas than on any other invertebrate (for example Grant and Scholes, 2006; Schuurman, 2006; Ndiaye *et al.,* 2004a; Ndiaye *et al.,* 2004b). This is because of their critical role in plant litter turn over, creation of "fungal gardens" (Swift *et al*., 1996) and fertile mounds that support good quality forage for herbivores (Grant and Scholes, 2006). The migratory (*Locusta migratoria* L.) and red (*Nomadacris septemfasciata* Serv.) locust are also extensively studied due to their damaging effects on grasses and cereal crops (Adams, 1996). Other invertebrates and smaller vertebrates are important to the African dry savanna, and some studies have been done on the their distribution in these biomes (for example Linzey and Washok, 2000; Dangerfield, 1997).

A larger number of species of wild mammals occur in African savannas as compared to the savannas in South America, Australia, and Asia (Skarpe, 1991). A clear empirical relationship between large herbivorous mammal biomass in African savannas and rainfall has been suggested (Coe *et al.,* 1976). However, herbivore biomass in some dry ecosystems far exceeded the biomass predicted by rainfall alone (Coe *et al*., 1976). This was because of factors such as high water tables that manifest as wetlands, such as in Amboseli, or as richer vegetation, such as in Lake Manyara National Park in Tanzania, or because of highly fertile volcanic and alluvial soils that support richer vegetation, such as in the Rwindi plains, Zaire and Rwenzori National Park, Uganda (Coe *et al.*, 1976). Due partly to these factors that enhance the diversity of the habitats within an ecosystem, East African savannas support the greatest variety and density of large mammals in the world (Little, 1996). Amboseli is no exception and, in fact, has a richer variety of large mammals compared to some larger parks in Kenya (Western, 1994).

Most savannas are dominated by a few species, most often by elephant (*Loxodonta africana africana* Blumenbach), cape buffalo (*Syncerus cafer* Sparrman), the endangered Burchell's (plains) zebra (*Equus burchelli burchelli* Gray; syn. *Equus quagga burchelli*) and Grevy's zebra (*E. grevyi* Ousta.), wildebeest (*Connochaetes taurinus* Burchell), and hippopotamus (*Hippopotamus amphibus* L.), although livestock, including cattle, water buffalo, sheep, goats, camels, and donkeys, now dominate the large herbivore fauna in most savannas (Skarpe, 1991; Swift *et al*., 1996). Grazers dominate this biome and as the aridity of the savanna increases so does the relative importance of each grazer species, in terms of its impact on the vegetation (Skarpe, 1991), as well as on other herbivores (Fritz *et al.,* 2002) in the ecosystem. Overall, however, the ability of these dry and variable areas to support a diverse large mammal population is dependent on a seasonal migration system that a large portion of the animals follow in order to utilize the scarce water resources of the land (McNaughton, 1990). This is the subject of the next section.

1.3 Seasonal migration and grazing patterns of large mammals in semi-arid savannas

Some of the most spectacular migrations occur in eastern Africa, including the well known migration of 1.3 million wildebeest and 0.6 million plains zebra and Thomson's gazelle or "tommy" (*Gazella thomsonii* Gunth.) between the Serengeti and Mara ecosystems (Thirgood *et al.,* 2004) and the lesser known migration of a single herd of about one million white-eared kob (*Kobus kob leucotis,* Licht. and Peters) in Equatoria Province, Sudan (Adams, 1996). Impressive herds of wildebeest also migrate between the arid Kalahari of Namibia and the Okavango Delta of Northern Botswana each year (Thirgood *et al.,* 2004).

Seasonal migrations occur according to rainfall patterns, with animals moving into areas of low annual rainfall or away from permanent water sources in the wet season and vice versa in the dry season (Western, 1975; McNaughton, 1990). The Serengeti-Mara migration is characterized by movement between areas of differing annual rainfall. Animals move to the drier southern plains of the Serengeti in order to take advantage of the new, highly productive and nutritious grasses in the wet season, but move back to the wetter Mara ecosystem to the north where water is of better quality and more readily available when the dry season begins (McNaughton, 1985; Wolanski and Gereta, 2001; Thirgood *et al*., 2004). The Amboseli ecosystem and the Okavango Delta-Kalahari savanna ecosystem are characterized by the movement of animals toward or away from permanent wetlands. Animals move away from the permanent wetlands at the onset of rain in order to take advantage of the large grazing area in the surrounding wet season range, but quickly return to the wetlands (dry season range) when rains cease (Western, 1975; Ellery *et al.,* 2000).

Grazing succession describes the sequential movement of animals starting with the larger herbivores and followed by smaller herbivores that is the result of differential tolerance of herbivores to forage quality based on body size and digestive systems (Maddock, 1979). Larger herbivores have greater food requirements and, hence, will concentrate early in the season in habitats that will maximize their rate of energy assimilation, a phenomenon that is consistent with the optimal foraging theory (Western and Lindsay, 1984). However, due to the morphology of their mouths, once the vegetation is too short to eat, the larger herbivores will move on to other habitats leaving the herbaceous layer better suited for smaller herbivores (Maddock, 1979). Furthermore, non-ruminants such as zebra and elephants can tolerate the poorest-quality food and, hence, move into areas with tall grasses or sedges first. They are then followed by similar sized or smaller ruminants, such as the wildebeest, that are less tolerant of poor quality forage (Maddock, 1979; Western and Lindsay, 1984). In this way, herbivores facilitate one another and increase their success rate in dry savannas (Arsenault and Owen-Smith, 2002).

The grazing pattern in the dry season results in herbivores moving towards pastures of decreasing quality but increasing water availability. For example, in the Amboseli Basin, herbivores, led by elephants, will move from relatively higher quality vegetation in the bushed-grasslands and open woodlands towards the poorer quality vegetation in the wetlands as the dry season advances (Western and Lindsay, 1984). As the larger herbivores migrate down the food-quality gradient, they are thought to leave in their wake better quality forage by encouraging new growth when grazing levels are intermediate (McNaughton, 1985). The process by which the plants respond to grazing by increasing their growth rate to compensate for tissue loss is called "overcompensation" (McNaughton, 1985; Dyer *et al*., 1993). Plants store photosynthates as reserves used for root growth, seed and flower production. However, when foliage is lost due to grazing, for example, the reserves are redirected to replace the lost tissue and hence, foliage productivity is increased to levels higher than what would have occurred without loss of leaf tissue (Turner *et al*., 1993). There have been a number of studies on the impacts of grazing on the vegetation of semi-arid savannas in Africa (see for example McNaughton, 1985; Belsky, 1988; Augustine, 2003; Birkett and Stevens-Wood, 2005), but there is still debate as to the level of grazing and the other factors, such as rainfall and nutrient levels, that are required for overcompensation in these ecosystems (Georgiadis *et al*., 1989). Furthermore, degradation by replacement of palatable grasses by unpalatable grasses or the reduction of plant biomass due to low soil water availability resulting from trampling due to heavy grazing is also a concern that has been studied extensively, especially in livestock-dominated areas (Skarpe, 1991).

Competitive exclusion of larger herbivores by smaller herbivores from habitats that are more suitable to the former's nutritional needs has been reported to occur during the dry season in the Serengeti-Mara ecosystem (Dublin, 1995). This happens as a result of the smaller herbivores maintaining short, and hence, inaccessible pastures that then force the larger herbivores into other habitats (Dublin, 1995; Arsenault and Owen-Smith, 2002). This competition between herbivores intensifies as the dry season progresses and vegetation biomass decreases, but does decrease once the rains begin and the animals are able to take advantage of a larger wet season range (Fritz *et al.,* 2002). This phenomenon has not been studied in Amboseli. However, because the two ecosystems are quite similar, except for the occurrence of permanent wetlands, it is possible that competitive exclusion may be taking place in Amboseli during the dry season.

1.4 Wetlands in semi-arid savannas

Wetlands are not easily defined due to their considerable range of hydrologic conditions and their great variation in location, size, and human influence (Mitsch and Gosselink, 2000). The definition of a wetland, as coined by the Ramsar Convention (sponsored by UNESCO in Ramsar, Iran, in February 1971), is an area "of marsh, fen, peatland 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 six meters" (Denny, 1985). This is a broad definition for both management and scientific purposes, and most authors or sectors will adjust the definition to a more suitable one for their own use. For instance, Kenya has, through the National Wetlands Standing Committee (NWSC), defined Kenyan wetlands as, "areas of land that are permanently, seasonally, or occasionally waterlogged with fresh, saline, brackish, or marine waters at a depth not exceeding six meters, including both natural and man-made areas that support characteristic biota" (Kiai and Mailu, 1998). This definition, according to the authors (Kiai and Mailu, 1998), is more suited to the exploitation of wetlands under the 'wise-use principle" since the Ramsar definition was created with the intention of protecting migratory waterfowl habitat. Either definition includes all the wetlands and Lake Amboseli within the Amboseli ecosystem.

Classification of wetlands is usually done in terms of their geomorphology and physical attributes, hydrology, geochemistry (salinity), sediment characteristics and stratigraphy, vegetation structure, or floristics (Mitsch and Gosselink, 2000). However, classifications can also include the socio-economical value of the wetlands depending on the mandates and interests of the sectors that create the classification scheme (Mitsch and Gosselink, 2000). A number of classifications have been used in the literature for African wetlands, most of which are simple and can easily be used without detailed taxonomic and hydrological information on the wetlands (Hughes, 1996; Harper and Mavuti, 1996). In 1996, various government institutions and non-profit groups in East Africa adopted a classification based on their origin (subtidal or intertidal marine or estuarine wetlands; lacustrine or palustrine sodic/saline wetlands; lacustrine, palustrine, or riverine freshwater wetlands; aquaculture/mariculture or agriculture man-made wetlands) and character (temporary or permanent, herbaceous or woody) (Kiai and Mailu, 1998).

The southern part of the Amboseli ecosystem that includes the Amboseli Basin and the wetlands to the east are the discharge zone for much of the groundwater originating in the forests on the northern slopes of Mt. Kilimanjaro that lies to the south (Western, 1975). Most of the water entering the wetlands is from aquifers, except for the eastern most wetland, Esoitpus, which is fed by the Lolterish River (Figure 1.1) that is the culmination of springs originating from Mt. Kilimanjaro (Githaiga *et al.*, 2003). Lake Amboseli is part of a Pleistocene lake bed that dried up and now only floods seasonally (Western, 1994; Western and Sindiyo, 1972). Based on the one study conducted on the hydrology of the lake and wetlands, only Lake Amboseli and Ol' Tukai wetland (Figure 1.1) are found on Pleistocene lacustrine and fluviatile deposits, whereas the Enkongo Narok, Longinye, Kimana, Namelok, Lenkir and Esoitpus wetlands are all found on volcanic rock, mainly basalts (Irungu, 1992). These aquifers have fresh water. However, when the lake floods after heavy rains the resultant flood waters are saline due to the accumulation of salts on the surface of the lake bed during preceding dry years (Irungu, 1992). The expansion and shrinkage of the wetlands is driven primarily by local rainfall and seasonal runoff, whereas the perennial extent is determined by the groundwater inflow component (Irungu, 1992). In the Okavango Delta, *Cyperus papyrus* L. and hippos have been shown to regulate hydrology and, hence, water distribution over the entire surface of the Delta (Ellery *et al.*, 2000). Irungu (1992) proposes that shifts in the wetlands of Amboseli are a result of channel-blockage by vegetation and the small sediment load collected during the shrinking and expansion of the wetlands. The impacts of animals on the hydrology of the Amboseli wetlands have not been studied.

The vegetation within the wetlands of Amboseli has not been described in detail. However, they were classified in 1972 as sedge-dominated wetlands, in particular *C. papyrus* and *Cyperus immensus* C. B. CI., with fringing zones of *Solanum incanum* L., *Triplocephalum holstii* O. Hoffm., *Pluchea dioscordis* D. C., and *Sesbania goetzi* Harno shrub (Western and Sindiyo, 1972). Based on the classification adopted for East Africa (Kiai and Mailu, 1998), the Amboseli wetlands are therefore freshwater, palustrine, herbaceous, permanent swamps or marshes. The term “swamp” is commonly used in the African literature to refer to freshwater, herbaceous marshes (Hughes, 1996), unlike in the Canadian wetland classification system where marshes are herbaceous and swamps are tree-dominated (Mitsch and Gosselink, 2000). Lake Amboseli, which is dominated by *P. jaegeri* and is only seasonally inundated, is a palustrine, temporary, seasonally or occasionally inundated depression.

Just as wetlands are important dry-season ranges for wildlife in dry savannas, they are of great importance to the people of the African continent because they provide seasonal or year-round water, fodder for livestock, and food (Hughes, 1996). This makes wetland habitats especially significant and yet they are one of the most threatened habitats in Africa partly due to a lack of knowledge about their ecology and partly due to drastic changes in land-use, such as irrigation schemes, that have disrupted their natural states (Haack, 1996; Hughes, 1996). However, the amount of scientific knowledge on the wetlands of Africa is dependent on the region in question. The Okavango Delta for example, has been studied quite extensively since the 1970's (McCarthy *et al.,* 2003) and there have been some studies dating back to 1960 that deal with nutrient loads and hydrology of wetlands in Africa (Howard-Williams and Thompson, 1985). Some wetlands in Kenya have also received a lot of attention since the 1970's due to their economic importance or some other particular property. For example, the *C. papyrus*-dominated wetlands around Lake Naivasha are not only of significant economic importance as sources of water for industry. but have also been the site for various studies on the physiology and ecology of *C. papyrus* mats (see Gaudet, 1979; Boar *et al.,* 1999; Becht and Harper, 2002; Jones and Humphries, 2002). Also, the wetlands of Lake Victoria are an important habitat for fish that are in turn extremely important for the inhabitants living around the lake (Chapman *et al.,* 2001). In Kenya, however, many smaller wetlands that are less important to the national economy, but immensely important to local wildlife and the livelihoods of the indigenous human communities, have yet to be studied. Furthermore, the literature is skewed towards human use (for example Scoones, 1991; Mungai, 1992; Gichuki, 2000; Terer *et al.,* 2004) rather than the broader importance of wetlands to the surrounding ecosystem.

Studying the impacts of grazing on wetland vegetation by both wildlife and livestock is becoming increasingly important as a result of changing land use that directly or indirectly impacts the hydrology of the wetlands, altered wildlife and livestock populations, and changing global climate (Scoones, 1991; Hughes, 1996; Hughes, 2003). Studies have been conducted on the impacts of grazing on many African wetlands, for example the *Dambos* of Zimbabwe (Scoones, 1991) and the fringing wetlands of Lake Victoria in the Magu District of Tanzania (Hongo and Masikini, 2003). However, most of these studies focus on the impacts of grazing by livestock, whose movements are directly controlled by humans and, hence, do not provide a comparative example for wildlife grazing impacts.

There have been studies on the impacts of grazing on wetland vegetation by wildlife in other parts of the world. For example, the impact of the exotic rodent, nutria (*Myocastor coypus* Molina), on the Louisiana coastal wetlands (Johnson Randall and Foote, 2005) and the impacts of the lesser snow geese (*Chen caerulescens caerulescens* L.) on Arctic salt marshes (for example Srivastava and Jefferies, 1995; Srivastava and Jefferies, 1996; Jefferies and Rockwell, 2002) and the wetlands of Bylot Island (Gauthier *et al.,* 1996). There have also been numerous studies on the impact of large-scale livestock grazing in wetlands (for examples from California see Marty, 2005; Jackson and Allen-Diaz, 2006).

The studies conducted on livestock grazing in African systems (Scoones, 1991; Hongo and Masikini, 2003) generally agree that under traditional grazing regimes wetland vegetation was maintained in a highly productive state. However, with increasing grazing pressure there was a resultant decrease in productivity and a change in species composition. This was similar to the results from the studies done on the impacts of the lesser snow geese on both Arctic salt marshes and the Bylot Island wetlands, where a decrease in vegetation and increase in soil erosion resulted from an increasing goose population (Jefferies and Rockwell, 2002; Gauthier *et al*., 1996). The impact of grazing by nutria also increased marsh erosion as a result of a change in stand structure (Johnson Randall and Foote, 2005). On the other hand, Marty (2005) reports an increased diversity as a result of the removal of exotic species by cattle grazing on vernal pools in the Central Valley of California. These results imply that the history of the wetland and of grazing, and the type of grazer, are important in determining the impacts of grazing on wetland vegetation.

There has been renewed interest in conservation of African wetlands since the late 1980's, with their importance based on both wildlife and human use (Hughes, 1996). In Kenya, there have been calls for more ecological studies on wetlands in order to properly conserve these ecosystems. These, however, are also the areas around which the human population is increasing rapidly (Mavuti, 1992; Ole Nkako, 1992). Wetlands cover about 14,000 km^2 of Kenya, but many of these are coming under private ownership due to the lack of a national wetland policy (Kareri, 1992; Ole Nkako, 1992). In fact, in the 1994-1996 development plans for Laikipia District in Kenya, the draining of parts of Ewaso Narok wetland for cultivation was still being recommended (Thenya, 2001).

In 1990, Kenya ratified the Ramsar Convention and Lake Nakuru National Park was the first to be included in the list of wetlands of international importance. Although many other wetlands, including Amboseli, were already under the protection of the Kenya Wildlife Service by 1991, as part of the national parks and reserves system, laws to protect them were not being enforced (Ole Nkako, 1992). In 1999, the parliament of Kenya enacted its first comprehensive piece of environmental legislation, the Environmental Management and Coordination Act, that gives each citizen the right to bring an action to stop environmental damage without the need to show personal loss or injury resulting from the environmental damage (Wamukoya and Situma, 2000). Currently, a new constitution is under review in which tighter and clearer legislation on the environment are being sought (`http://www.nema.go.ke/ENVILEGILATION.ASP`; Last updated in 2006).

1.5 A brief history of the Amboseli ecosystem

The history of the Amboseli ecosystem is described in depth in Western (1994). The ecosystem has been home to the Maasai people for centuries. During the colonial occupation of Kenya, the Amboseli ecosystem was recognized for its large herds of wildlife and was incorporated into the Southern Reserve, the remnant of Maasailand after expropriations for British settlers. In 1911, the Southern Reserve, along with the Amboseli ecosystem, was incorporated into the Maasai Treaty that allowed the Maasai people to continue using the land as they were and, inadvertently, protecting the wildlife from hunting and permanent settlement by non-Maasai (Western, 1994). By 1945, the colonial government decided to turn Amboseli, along with other parts of Maasai territory, into a national park, but was unsuccessful due to the standing Maasai Treaty. As a result, a temporary solution was sought and a 3,260-km^2 area was established as the Amboseli National Reserve that was kept open to the Maasai pastoralists, but administered by the colonial board of the Kenya National Parks.

In the early 1960's (pre-independence), the Amboseli National Reserve became the Amboseli Game Reserve under the administration of the Olkejuado Maasai County Council and, except for a 78-km^2 area around Ol' Tukai, was open to livestock (Western, 1994). By 1974 (post-independence), an area of 388 km^2 within the basin was set aside as the Amboseli National Park (Figure 1.1b) under the management of the Kenya Wildlife Services partly due to a vested interest in the income the reserve was generating and partly because of international pressure to remove the Maasai pastoralists who were thought to be destroying the woodlands (Western, 1994). The wetlands to the east of the park, including Namelok, Kimana, Lenkir and Esoitpus (Figure 1.1b), became part of group ranches that were meant for the Maasai to use as joint grazing land (Southgate and Hulme, 2001). The Maasai were discouraged from grazing livestock within the boundaries of the park. However, soon after 1977, the Maasai began using the wetlands on the periphery of the park as a result of droughts and failed promises by the Kenya Wildlife Services to provide boreholes for livestock watering outside the park boundary (Lindsay, 1987).

The link between the Maasai and the animals and ecosystem within the park was broken, even though the park was never fenced off from the surrounding ecosystem. This resulted in a number of changes. Firstly, the removal of livestock from the park meant that zebra and wildebeest populations faced decreased competition for resources and their numbers increased (Lindsay, 1987), as did the population of the elephants (Moss, 2001). Secondly, the Maasai no longer had access to wildlife, which they considered "second cattle" in times of extreme drought and to which they afforded protection (Western, 1994; Western and Gichohi, 1993b). This had severe consequences on the populations of elephants in later years when poaching became rampant. Thirdly, the Maasai came under increasing pressure due to drought and reduced access to the large wetlands in the park, which prompted a shift in their lifestyle to a more agrarian-based one (Lindsay, 1987). Fourthly, the availability of wetlands to wildlife outside the park became increasingly restricted as the lifestyles of the Maasai changed and the human population around the wetlands grew through immigration (Lindsay, 1987; Worden *et al.,* 2003). This meant that the park wetlands were used by more animals. Furthermore, between 1983 and 1984, the population of black rhinos (*Diceros bicornis* Gray) that had already been declining since the 1950's (Western and Sindiyo, 1972) was wiped out as a result of the initiation practices of Maasai "junior" warriors, who actively hunt wildlife during the initiation process (Lindsay, 1987). Presently, the Maasai have resumed their protective role towards wildlife in areas outside the park mainly for ecotourism purposes. They do, however, face the problem of wildlife, especially elephants, raiding the irrigated fields around the wetlands and springs. Many Maasai have been fatally wounded in their attempts to distract the animals (D. Western, *pers. comm.*).

Western and Gichohi (1993b) have shown that the creation of protected areas causes segregation effects, which are a suite of threats that include the social and economic repercussions of displaced societies and ecological changes throughout the ecosystem, both inside and outside the protected area. The history of the Amboseli ecosystem shows many of these effects. Currently, both the elephant (Moss, 2001) and human (Southgate and Hulme, 2001) populations are increasing in the ecosystem. Both can be considered keystone species and, hence, the challenges facing the Amboseli Ecosystem, including the wetlands, are increasing. For this reason, elephants and humans are the focus of the next two sub-sections.

1.5.1 Elephants in Amboseli

Elephants greatly affect the structure of vegetation and, indirectly, animal communities wherever they occur (Laws, 1970). In 1976, the first continent-wide census of elephants estimated the population to be 1.34 million ranging over 7.3 million km^2, but by 1987 this number had decreased to 760,000, and in 1989 to 608,000 (Stiles, 2004). East and Central Africa had the highest number of elephants compared to the south and west in 1979, but from this period to 1998 elephant numbers decreased by 20% in East Africa and 50% in Central Africa (Stiles, 2004).

Estimates of the elephant population in Amboseli during the 1960's vary between 700 and 1200. Under pressure from poachers and drought, the population was reduced to 480 by the end of 1978, but it increased to 1087 by 1999 (Moss, 2001). Beginning in 1977 until 1991, elephant movement was severely restricted to within the boundaries of the park (Koch *et al.,* 1995). Elephants had stopped moving out of the park in the wet season, apparently in response to the poaching threat outside the park boundaries, and instead used the park ecosystem year-round. Post-1991, elephants began moving out of the park again (Koch *et al.,*1995), but due to their dependence on water sources they remained within 50 km of the Amboseli Basin (Western, 1975). Furthermore, elephants no longer had free access to all the wetlands outside the park, except, to a limited degree, the Kimana wetland since 1998 (Worden *et al*., 2003).

Through the combination of an increasing elephant population and curtailed wet-season migration, the already declining *A. xanthophloea* woodland that dominated the Amboseli landscape was lost due to increased browsing pressure (Western and Maitumo, 2004). The *A. xanthophloea* woodlands were eventually replaced by xeric shrub and grassland habitat (as mentioned in section 1.1), and an overall decrease in habitat heterogeneity ensued (Western and Maitumo, 2004). This phenomenon is not unique to Amboseli. Many other parks and protected areas have had similar declines in woody species as a result of increasing elephant populations (for example Pellew, 1983; Prins and van der Jeugd, 1993; Cumming *et al.,* 1997; Mosugelo *et al.,* 2002). In each case, it is thought that elephants began the decline in woody species through their browsing habit but other ungulates, such as the impala (*Aepyceros melampus* Licht.), granivorous birds, rodents, and primates that feed on the seeds of the trees, invertebrates that feed on or infect seedlings, seeds, and mature trees, as well as fire, help maintain the grassland habitat by reducing seedling recruitment (Prins and van der Jeugd, 1993; Sinclair, 1995; van de Koppel and Prins, 1998; Mosugelo *et al.,* 2002; Western and Maitumo, 2004). However, in Amboseli National Park, elephants are thought to be the primary driving factor for loss of woodland within park boundaries, whereas fire is not a dominant factor because of the patchy vegetation unlike in other savanna (Western and Maitumo, 2004). The decrease in woodland has driven the extinction of the woodland and bushland dwelling bushbuck (*Tragelaphus scriptus* Pallas) and lesser kudu (*Tragelaphus imberbis* Blyth) from the park (Western and Gichohi, 1993b). On the other hand, areas to the east of the park are seeing an increase in woody vegetation and a resultant increase in the browsing community (Western and Maitumo, 2004).

The impact of elephants on wetland vegetation in the park is as yet unknown. A decrease in the tall *C. papyrus* and *C. immensus* sedges in the wetlands, and a loss of the fringing zones of *S. incanum*, *T. holstii*, *P. dioscordis*, and *Sesbania goetzi* around the wetlands, have been observed (Western, 1997). No formal studies have been conducted to confirm and explain these changes and to assess the impacts these observed changes may have had on the ecosystem.

1.5.2 Humans in Amboseli

Pastoralism has been a significant part of the East African savannas for three thousand years, though the Maasai pastoralists only arrived 500 years ago (Western, 1994). In order to survive the droughts and dry-seasons in the Amboseli ecosystem, the Maasai shadowed the movements of wildlife into the wetlands and, in addition, used the forest-edge pastures at the foothills of Mt. Kilimanjaro (Western, 1994).

The group-ranches created in the mid-1970's were joint ownerships that were established in order to maintain traditional herding practices that made use of the wetlands to the east of the park, as well as government-maintained boreholes, during the dry seasons (Lindsay, 1987; Southgate and Hulme, 2001). Some Maasai began to use agriculture to augment or completely replace their traditional nomadic, pastoralist lifestyle in the early 1970's (Campbell, 1986) because of losses to livestock that resulted from a combination of reduced dry-season access to wetlands and recent droughts (Lindsay, 1987). There was also an increased fear among the Maasai of a further loss of land to the government (Southgate and Hulme, 2001). This prompted the subdivision and sale of parts of the group ranches (Southgate and Hulme, 2001). Land that lay adjacent to the wetlands and that happened to become the property of one person was no longer available to the community free of charge for livestock grazing. This resulted in the further loss of the traditional seasonal movements of livestock herds, especially for the poorer herders who were unable to pay for access to the wetlands (Western, 1994).

Semi-arid lands, such as Amboseli, are mesic enough to support vegetation growth and, hence, high populations of animals, but they are still too dry to support agriculture (Swift *et al*., 1996). In Amboseli, agriculture was possible only through the use of irrigation with water from the wetlands (Githaiga *et al*., 2003). This change in land use was exacerbated by agrarian non-Maasai communities immigrating into the area following independence (Southgate and Hulme, 2001). The population in this area rose dramatically and, as indicated by the increase in density from 7.5 people km^{-2} in 1986 to 18.1 km^{-2} in 1996, is still rising (Southgate and Hulme, 2001). At the present time, Namelok and parts of Kimana wetlands are fenced in order to protect farms from wildlife and to reduce human-wildlife conflict (Worden *et al*., 2003). Water is also being extracted from the wetlands for consumption by an increased local population in, and rapidly developing cities and industrial areas north of the Amboseli ecosystem (Githaiga *et al.,* 2003).

Some local communities who have lived around wetlands for centuries have managed to maintain the integrity of their wetlands to a certain degree using traditional knowledge. For example, the Pokomo and Wardei people of the Tana River District in Kenya, who use wetlands for dry-season cultivation, still allow wetland vegetation to regenerate in the wet season (Terer *et al*., 2004). The traditional knowledge of the people dwelling around wetlands is being used in some parts of Kenya to conserve wetlands (Gichuki, 2000; Terer *et al.*, 2004) and there has been a concerted effort in other parts of Africa to incorporate traditional knowledge and values to the development of wetlands (Hughes, 1996). Unfortunately, in Amboseli, traditional land-use has been altered and it is highly unlikely that the people will return to a predominantly pastoral lifestyle (Southgate and Hulme, 2001).

The changes in the Amboseli wetlands due to changing human use, however, have not been quantified. A recent report does raise concerns about increased pollution of the water from the expanding farms in the area, and the resultant invasion of toxic algae (Githaiga *et al.*, 2003), but there has been little in-depth work conducted on the effects of altered hydrology as a result of water extraction. Drawdown has been shown to increase plant diversity in wetlands (Catarino *et al.,* 2002; Mulhouse *et al.,* 2005). However, if drawdown is permanent, there is a subsequent loss of aquatic and sedge vegetation that functions as a sediment trap, valuable habitat for both vertebrates and invertebrates, natural flood-control structures, and food and building material for humans (Howard-Williams and Thompson, 1985).

Though long-term monitoring of wetlands is essential for sustainable use, there are few monitoring schemes that have been successful (Bennun, 2001). One example of a successful monitoring program centered on wetlands has been Lake Naivasha, which has so far been funded via research grants from universities outside of Kenya rather than by local funds (Bennun, 2001). Scientists have called for increased international co-operation and assistance in research and capacity building for sustainable use of wetlands in Africa (Denny, 2001; Junk, 2002). In the meantime, in Kenya, grass-roots work and the hope that the new constitution will give wetlands the protection they deserve are the two important forces that continue to drive wetland conservation efforts.

1.6 Rationale and layout of thesis

The Amboseli wetlands are critical for the survival of the people and animals in this ecosystem. However, the impact on the wetlands of the reduction in wet season migration of elephants out of the park and, hence, the compression of a growing elephant population within the park's confines, have not been quantified. Neither have the impacts of grazing and human land use on wetland vegetation. Furthermore, the history of the wetlands offers a unique opportunity to study the dynamics of, and alterations to, wetlands in semi-arid savannas. Hence, the hope is that this thesis will not only add to the knowledge on this ecosystem that will be valuable to its sustainable management, but that the insights gained will assist in the management of other wetlands in semi-arid savanna.

In Chapter 2, remotely sensed images, hand-drawn maps, and elephant and vegetation monitoring data from Dr. D. Western, were used to document the vegetation and long-term dynamics of the Amboseli National Park wetlands. The goals were to classify the vegetation communities currently constituting these wetlands, and to determine the extent of use of the wetland habitats by elephants and the role elephants have played on wetland flooding and vegetation. This chapter provides more detail to previous vegetation maps of the park, it shows how dynamic the flood patterns of the wetlands have been, and it also shows the level of dependence elephants have had on the wetland habitats over time.

In Chapter 3, two main objectives were accomplished. The first was to document the seasonal dynamics of the grass-dominated, seasonally inundated edge and the sedge-dominated, permanently inundated centre of a small, reference wetland to the south of Enkongo Narok (Figure 1.1b). Changes in plant biomass and species composition, animal use estimated using dung counts, and water quality were monitored over a period of two and half years. The second objective was to study the impacts of elephants on wetland vegetation and the subsequent use of these wetlands by other mammals over time. The latter objective was accomplished by monitoring the vegetation and animal use of a wetland that had been enclosed within an electric fence that allowed all species other than elephants and giraffe from accessing the wetland. These data were compared to that of the reference wetland that was adjacent to the enclosed wetland, but open to use by elephants. The edge and centre were, again, treated separately. The impact of season and elephants are key factors in these wetlands and in this chapter both these factors are studied. The results of this chapter give a small-scale view of the effects of elephants that were studied on a large-scale in chapter 2. This is the first study that looks at the seasonal changes in wetland vegetation in Amboseli, and, except for wetlands fringing Lake Naivasha and Lake Victoria, is the first to study these dynamics in wetlands in Kenya.

Chapter 4 is a study on the impacts of natural and simulated grazing on wetland vegetation, in terms of biomass and species composition. Vegetation from the grass-dominated, seasonally inundated edge and the sedge-dominated, permanently inundated centre were studied separately. This study was not restricted to the effects of elephant grazing and was done on a smaller scale using 1-m^2 grazing cages. The aim was to compare grazed and un-grazed plots in the two parts of a wetland in order to determine the impact on plant growth and species composition. The goal of this study was to determine whether sustained grazing, as is expected when seasonal migration is curtailed, can be carried out on the wetland vegetation with minimal damage. The study was set up to the north of the Ol' Tukai wetland.

In Chapter 5, the current vegetation in the wetlands outside the park is described using remotely sensed images and the impacts of long-term land-use changes on vegetation are interpreted using change detection methods and available literature. This work contributes to the knowledge base by showing the level of agricultural activity around the wetlands, the impacts of water extraction, and the effects of the decreased elephant population on the savanna vegetation.

The final chapter, chapter 6, is a synthesis of the results from each of the data chapters. The outcomes of chapters 2 to 5 are restated and drawn together in order to provide a complete picture of the fate of the Amboseli wetlands under the pressure of elephant use and changing human activities. Suggestions for future work are also included.

Chapter 2

Current and Long Term Condition of the Wetlands of Amboseli National Park

2.1 Introduction

The wetlands of the Amboseli National Park (Figure 2.1) are maintained by perennial groundwater inflows from the south that are fed by precipitation on the northern slopes of Mt. Kilimanjaro. However, local precipitation drives the seasonal changes in their areal extents (Irungu, 1992). The wetlands make up the critical dry-season range for wildlife and, historically, for the nomadic pastoralist Maasai community in the area (Western, 1994). Yet they cover less than 4% of the 360 km^2 park ecosystem (Western and Sindiyo, 1972). The wetlands are a key resource area for the Amboseli ecosystem and are important to the maintenance of the rich diversity of animals found there, that rivals the diversity in other parks fifty times the size of Amboseli (Western, 1994). Key resource areas are fundamental components of spatially and temporally variable arid and semi-arid ecosystems and important determinants of ecological patterns and processes (Worden *et al*., 2003). Hence, any changes to them can have important implications for the structure and function of the ecosystem at a variety of scales (Worden *et al*., 2003).

Two major perturbations that occurred in the Amboseli ecosystem during the early 1970's may have had large impacts on the wetland habitats of the Amboseli National Park. These perturbations include the modification of wet season migration of the Amboseli elephant population due to the threat of poaching (Koch *et al.,* 1995), and the change in land use around the wetlands outside of the park from predominantly livestock and wildlife watering and grazing pastures to irrigated agriculture (Worden *et al*., 2003).

Elephants are water-dependent animals and in Amboseli are not seen further than 50 km away from the wetlands at any time during the year (Western, 1975). However, they did maintain a seasonal migration in which they used the wetlands less during the wet season and more during the dry season (Western and Lindsay, 1984). This migration was maintained till about 1977 after which the threat of poaching increased, as did the number of drought years (Koch *et al.,* 1995; Western, 1975). Elephants remained inside the park, where the threat from poachers was less and there was access to the wetlands during the droughts. The population of the elephants stood at over 1000 in 1999, which is almost double the number of elephants in the 1970's (Moss, 2001). The increase in elephant numbers and subsequent restriction to within the park boundaries has been shown to have accelerated the destruction of *Acacia xanthophloea* woodlands that occurred to the south of the wetlands (Western and Maitumo, 2004). This area had dense *A. xanthophloea* woodlands due to the presence of the same shallow water table that feeds the wetlands of the park (Swift *et al*., 1996; Irungu, 1992). The woodlands had been receding since the 1960s and were being replaced by xeric scrub habitat dominated by *Sueda monoica* and *Salvadora* (Western, 1994; Western and Maitumo, 2004).

However, the collapse of the woodlands was exacerbated by the concentration of elephants inside the park in the late 1970s to early 1990s (Western and Maitumo, 2004).

The compression of elephants inside the park may have affected the wetlands in two ways. Firstly, trees can have large impacts on groundwater levels and since *A. xanthophloea* were accessing water from the aquifers that fed the wetlands, removal of this band of trees could have caused changes in the extents of the wetlands. Secondly, the year-round use of the wetland habitat by elephants likely put considerable pressure on wetland vegetation structure and species composition, which has been observed but not formally documented (Western, 1997).

The human population to the east of the park is rapidly increasing (Southgate and Hulme, 2001) and is concentrated around the wetlands that occur in this particular area (see Chapter 5). Traditionally, the pastoralist Maasai community used the wetlands in harmony with wildlife (Western, 1994). Since the early 1970's, almost at the same time as elephant migratory pattern changed, the Maasai moved to irrigated agriculture around the wetlands outside the park as a means to supplement their pastoralist lifestyles (Lindsay, 1987). This move to agriculture has resulted in the complete exclusion of wildlife from the Namelok wetland (Figure 2.1a) for example (Worden *et al.*, 2003). Hence, for wildlife in this area, the only guaranteed access to water is inside the park, which translates to even greater importance for the Amboseli National Park wetlands.

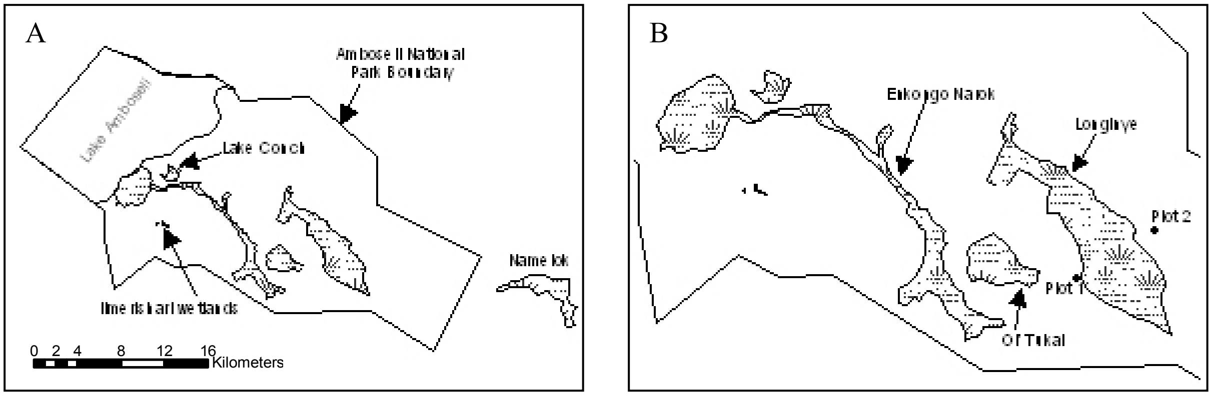

Figure 2.1. The wetlands of Amboseli National Park (A), in particular the Enkongo Narok, Longinye, and Ol' Tukai wetlands shown in (B) that are the focus of this study. The position of Lake Amboseli, Lake Conch, Ilmerishari wetlands (see Chapter 4), and Namelok (see Chapter 5), which lies outside of the park boundary, are indicated to provide context. Plot 1 and 2 indicated in (B) are the locations for the NYASI study. The geographic location of the park is 02°33'S, 37°06'E.

The loss of wetland habitat can have far reaching impacts on the wildlife in this area and subsequently can lead to the loss of tourism. Currently, not much is known about the long-term dynamics of these wetlands or the current vegetation in the wetlands. Unfortunately, wetland conservation and ecological study are only a recent development in sub-Saharan Africa (Haack, 1996) and, hence, lack of information for wetlands that are as small as the Amboseli wetlands is not uncommon.

One way of studying long-term changes in wetland vegetation is using remotely sensed images from the period of interest to examine how vegetation classes have changed in extent. The first step is to classify the image by spectral composition. Unsupervised classification is one option for executing this first step, whereby a computer-generated spectral classification is produced based on user specifications. The spectral classes developed by these procedures, however, are not linked to real information and the user has to then relate the spectral classes to vegetation classes based on ground information (Campbell, 2002). This process requires sufficient ground information from that period to accurately classify the images. The second option is to use supervised classification, which requires *a priori* information about the vegetation or landscape classes in which the user is interested (Richards and Xiuping, 1999). This information must come from the period of interest and is used to assign a particular information class to an area whose spectral class is then used to identify other areas of the same type (Richards and Xiuping, 1999). Hence, supervised classification is useful in describing vegetation classes in an image for which the user has sufficient ground information.

Vegetation indices that measure vegetation vigor based on brightness values recorded on certain bands of the satellite sensor (Campbell, 2002) are a better option for studying temporal change in vegetation. The basis for vegetation indices is the differential absorption and reflectance of energy by green vegetation in the red and near-infra red portions, respectively, of the electromagnetic spectrum (Lyon, 2001). In general, green vegetation absorbs energy in the red region and is highly reflective in the near-infrared region (Lyon, 2001). The Normalized Difference Vegetation Index (NDVI) has been used to detect changes in terrestrial (Lyon, 2001) as well as wetland vegetation (Lee and Marsh, 1995). It is a ratio of near-infrared (NIR) minus red (R) over NIR plus R, which produces an index that ranges between -1 for no vegetation to +1 for completely healthy green vegetation cover (Gibson and Power, 2000; Campbell, 2002).

Change detection using NDVI is simply a matter of subtracting the NDVI of one pixel in an image of an earlier year from the NDVI of the same pixel in an image from a later year. Even though the result of this arithmetic operation indicates a change in radiance properties of that pixel, it does not directly indicate changes in the amount of vegetation present (Jano *et al.*, 1998) or the type of vegetation present. Interpretation of these images must therefore be done with caution. However, if the images are from periods that are relatively similar and the differences in conditions between the image dates are known and accounted for, then change detection images can be useful in identifying trends in vegetation change.

Images obtained from the LANDSAT satellites have been successfully used in a number of wetland studies to classify vegetation types even though the spatial resolution of the sensors are not considered sensitive enough, in most cases, to clearly delineate the steep ecological gradients that occur in wetlands (Harvey and Hill, 2001). They have however, been credited with having sufficient spectral resolution, especially in the longer infra-red wavelengths, to distinguish between general vegetation types during classification (Dottavio and Dottavio, 1984; Harvey and Hill, 2001).

The main aim of this study was to document the vegetation and dynamics of the Amboseli National Park wetlands. This was done using satellite imagery as well as long term data on elephant numbers and herbivore grazing collected by Dr. D. Western. These data were also used to determine whether elephants have changed their seasonal use of the wetland habitats and if there was a corresponding increase in herbivore grazing in both the wet and dry seasons in two permanent plots located in wetland habitats (Figure 2.1b). Hand-drawn illustrations of wetland extent and flooding patterns were used to document the dynamics of the wetlands, to determine whether *A. xanthophloea* woodland loss and changes in use of the wetlands by elephants have had an impact on the flooding regime of the wetlands. Satellite imagery was used to describe the current vegetation types that occur in the wetland habitats and the vegetation changes that have occurred between 1976 and 2002.

2.2 Materials and Methods

2.2.1 Long-term elephant use patterns and herbivore grazing studies

The use of the wetland habitat within the park by elephants was determined from 27 years of aerial counts of elephants in the wetlands conducted by Dr. D. Western, as part of his BASIN study. Counts were conducted in both dry and wet seasons since 1975 (Western and Lindsay, 1984). Details of how the counts were conducted are described in Western (1973). The data presented in this study are meant to describe any changes in patterns of use. The data are not meant to estimate the population of elephants in the park and hence, a data smoothing option that was easily done using the available software was used. The locally weighted regression (LOWESS) method was used was it is model free and allows for the determination of the unbiased form of the relationship between two variables (Prince and Silva, 2002). The LOWESS option in SYSTAT 11 (Systat Software Inc., 2004) was applied to the temporal count data using a 0.5 tension setting.

Changes in the seasonal grazing patterns of herbivores in the grass-dominated, seasonally inundated wetland habitat of the park was determined using permanent plots shown in Figure 2.1b. These plots are part of a more than 24-year, park-wide study by Dr. D. Western. A plot is a circle of 10-m radius around a permanent central point and sampling is done along 12 transects radiating from this central point (D. Western, *pers. comm.*; *personal observation*). In each approximately 150 m^2 plot, the percentage of vegetation showing grazing damage is recorded along with other variables. The plots are monitored on a 3 to 6 week basis. The grazing data for the Swamp1 plot (plot 1 in this study) and Swamp Edge plot (plot 2 in this study) from 1976 to 2002 are used here. Plot 1 has a *Cynodon dactylon* (L.) Pers. and *Digitaria scalarum* (Schweinf.) Chiov. grass community, and plot 2 is dominated by *Sporobolus spicatus* Kunth and *Cyperus laevigatus* L. These species are characteristic of saline wetland edges and they have either strong or partial clonal propagation (Thompson, 1985)

Both data sets were separated into wet and dry season counts using greenness and biomass data from 3 permanent bushland plots located along the northern boundary of the park. At the onset of the rainy season, elephants used to move to the bushlands to feed, indicating the start of the seasonal migration for all the herbivores in the park (Western and Lindsay, 1984). Wet seasons were, therefore, identified as periods when the percent greenness of the bushland plots was above 25% (D. Western, *pers. comm.*). Migration back towards the basin at the onset of the dry season is a slow process and need not reflect rainfall over previous days (Western, 1975). Elephants moved back to the basin faster and in response to a reduction in biomass in the bushland plots (Western and Lindsay, 1984). Hence, percent biomass deviation from the mean long-term biomass of the bushland plots is a better way of identifying dry seasons. When the deviation is between -50 and 0% for a month it is considered a dry month and a deviation below -50% is a drought month. Since this study deals with the impacts of elephants and other herbivores on wetland vegetation, it is better to use this definition of season rather than calendar months or rainfall.

2.2.2 Wetland extents

Extents of the Amboseli National Park wetlands have been monitored by Dr. D. Western since 1979. He has drawn the mean extents, or in the cases of extreme changes in a year, the monthly extents of the wetlands using a 1 km x 1 km grid map of the park. He flies over this area during wet and dry season months and draws out the extents of the wetlands. For earlier years he used information from other sources such as the Royal Air Force for the 1950 map, and Survey of Kenya maps for 1961, 1967, and 1976 wetland extents. Using this information he has compiled illustrations of the extents on paper maps. The extents are taken to be the edges of "wet" ground with sedge-grass communities and surface water.

I registered the paper maps to the Universal Transverse Mercator (UTM) grid using a 2002 satellite image as the reference image in the ORTHOENGINE tool in GEOMATICA v. 10.0 (PCI GEOMATICS, Richmond Hill, ON, Canada). A first-order polynomial equation was adopted to achieve a higher accuracy of geo-correction since it was difficult to identify large numbers of highly accurate ground control points, or GCPs (Harvey and Hill, 2001). Between 12 and 16 GCPS were needed to register the maps to the 2002 image with minimal distortions. I then translated the files into geoTIFF format in GEOMATICA FOCUS and exported them to the ArcMap tool in ArcGIS v.8.2 (ESRI, Redlands California). In ArcMap I digitized the extents of the wetlands and converted them into maps. The accuracy of the maps in terms of area has not been quantified but the aim of this study was to look at the trends and patterns of flooding of the wetlands.

2.2.3 Satellite imagery

All images for this study were acquired from LANDSAT satellites. The first LANDSAT satellite was placed in orbit in 1972 to provide frequent, low-resolution, multi-spectral digital imagery of the Earth's surface (Richards and Xiuping, 1999; Jano *et al*., 1998). To date, six satellites have been successfully launched, carrying different payloads that result in varying spectral resolution (Richards and Xiuping, 1999). They are all sun-synchronous, near-polar orbits that acquire image data nominally at 9.30 a.m. local time on a descending (north to south) path (Richards and Xiuping, 1999). The first three satellites (LANDSAT 1 to 3) carried the Multi-Spectral Scanner (MSS) as the principal sensor (Richards and Xiuping, 1999). This sensor registered data in four spectral bands and each image covered a swath of 185 km wide (Campbell, 2002). The next two satellites (LANDSAT 4 and 5) had the Thematic Mapper (TM) as the principal sensor that detected reflectance in seven spectral bands and had a nominal ground resolution of 30 m (Richards and Xiuping, 1999). The latest satellite to successfully enter orbit was LANDSAT 7, which carries the Enhanced Thematic Mapper + (ETM+) as the principal sensor (Campbell, 2002). The new sensor is different from TM sensors in spectral resolution, with the inclusion of thermal and panchromatic bands (Richards and Xiuping, 1999). However neither of these bands was utilized in this study.

2.2.3.1 Image acquisition

LANDSAT images from 1976, 1987, 1993, and 2002 were acquired from the Regional Centre for Mapping and Resource Development (RCMRD) based in Nairobi, Kenya. Images were selected based on availability, cloud cover, and cost. The aim was to cover each decade with at least one image that was taken from the same month as the other images, and as far as possible that that month should be in a dry period. Due to a lack of good quality images and cost, it was not possible to select more than one image per decade. Fortunately, there were images of relatively good quality from February of each of the years except 1976, which unfortunately had about 50% cloud cover in the area of interest. However, because there was still some information that could be derived for the wetlands and it was the only image available from the 1970's, the image was retained. February is generally considered part of the short dry season that occurs between the short rains of November and December and the long rains of April and May. Dry season images were used to help delineate the wetland habitats from the surrounding dry vegetation.

The image from 1976 was from path 180 and row 62 of LANDSAT MSS 2, which had poor spatial resolution and a nominal ground resolution of 57 m x 57 m. Images for the remaining years were obtained from path 168 and row 62 of LANDSAT TM 4 (1993 image), TM 5 (1987 image), and ETM+ 7 (2002 image). These images were of greater spectral and spatial resolution with a nominal ground resolution of 28.5 m x 28.5 m.

2.2.3.2 Image pre-processing

All the images were already registered to the UTM grid. However, the 1993 image needed geo-correction, which was conducted using the 2002 image as the reference image. The geo-correction procedure was conducted as described above using a total of 12 GCPs to correct the 1993 image to within 0.11 pixels (3.08m) of the 2002 image.

Since the area covered by the wetlands of interest was less than 20% of the entire image scene, sub-sets of the images were excised using the FOCUS tool in GEOMATICA. As far as possible the dimensions of the images from the different years were maintained. However, due to differences in the sensors and the coverage of each scene, this was not always possible. Masking of the areas covering the wetlands was also required at the classification step for the 2002 image in order to reduce class confusion and concentrate the classification process to the wetlands (Harvey and Hill, 2001).

The NDVI is highly sensitive to atmospheric variation, which requires that images are as close in date as possible to ensure that the angle of the sun and the conditions are as closely matched between dates. Also, rigorous pre-processing is required to ensure spectral differences are not a result of differences in sensor calibration or atmospheric differences between dates (Campbell, 2002). The dates of most of the images were within days of each other however, there may still have been differences in the spectral signatures of the images due to atmospheric differences between the dates.

In order to minimize these differences caused by the atmosphere, the images were corrected using the MATCH and LUT algorithms in FOCUS. MATCH allows the user to match the histograms of a spectral band in one image to the histogram of the same band in a second image. This procedure generates a look up table (LUT) that is then used to create a corrected histogram for the band in the second image, using the LUT algorithm. I used additional masks to focus on the areas of interest so that the matching procedure used these portions and thereby, enhanced the NDVI change detection results. I also masked out clouds and cloud shadow from the 1976 image to exclude them from the NDVI calculation. Prior to matching histograms for the 1976 to 1987 comparisons, the 1987 images were re-projected from 28.5m x 28.5m pixels to 57m x 57m pixels to match the 1976 image.

2.2.3.3 Image classification

In order to conduct a successful supervised classification one needs a lot of auxiliary and ground data, which can be difficult to come by in certain areas (Harvey and Hill, 2001; Haack, 1996). Hence, the first classification I conducted on the 2002 image was an unsupervised classification using spectral bands 2, 3, 4, and 5, which cover the green to middle infrared portions of the electromagnetic spectrum. These bands had proven useful in a study on the tropical freshwater swamps in Northern Territory, Australia (Harvey and Hill, 2001). The process was undertaken to simplify the raw image into 20 classes using 100 iterations of the K-means clustering algorithm in FOCUS. The result was an image with a good amount of separation within the boundaries of the wetlands, which was the requirement. These classes were then used to identify ground truth sites that would be used in a supervised classification.

The groundtruthing exercise was conducted by two assistants based at the African Conservation Centre in Nairobi, Kenya. One was an expert in the vegetation and land-use practices of the area and the other is a GIS and remote sensing expert. They located the sites I had identified using hand-held GPS and visited as many of these sites as they were able to over the week of April 24, 2006. They identified the dominant plant species, the understory species and any other obvious species present. They also noted any human land use and took photographs in the north, east, south and west directions for my use during the classification procedure. A sample of photographs of the wetlands in the park is presented in Figure 2.2 in order to provide a visual picture of the types of vegetation classes that were encountered during the ground truthing exercise.

Normally, groundtruth information should be collected close to the date of image capture so that incorrect identifications of rapidly changing vegetation classes are not made (Campbell, 2002). In this case, unfortunately, financial constraints meant that a 2002 image had to be used over a more recent and, hence, more expensive image. Furthermore, the fact that ground truthing was conducted in April, which is normally wetter than February when the 2002 image was captured, also meant that some decisions had to be made on what vegetation would have occurred in certain areas in February of 2002 when conditions were drier. I assumed that there were no large changes in the vegetation between the year of image capture and the year the groundtruthing exercise was conducted, but that the accuracy of the image was therefore not going to be as high as I would have liked.

The information I received from the ground-truthing team was used to create training classes for the supervised classification procedure. At least 100 pixels were used to identify any one training class and the distribution of these was as widely spread as possible, which is recommended by Campbell (2002). The signature and separability statistics of the training classes were examined. Class histograms were examined for normal distributions (Campbell, 2002) and the Bhattacharrya distance statistic was used to identify those classes that were not clearly separate from another class. The Bhattacharrya distance statistic ranges from 0 to 2, with 2 being the best separation between a pair of training classes and 0 indicating that these classes are identical (Gibson and Power, 2000). Values between 1 and 1.9 indicate poor separability, and values greater than 1.9 indicate good separability (Gibson and Power, 2000). Classes with distance of less than 1.9 were usually either aggregated or the training areas on the images were corrected to reduce overlap between the two classes. In some cases the classes were not similar on the ground even though the Bhattacharrya distance was less than 1.9. These classes were retained in order to reduce the percentage of the null class, which is where they ended up if the training class was removed.

Once the classes were finalized, the Maximum Likelihood algorithm with the null class option in FOCUS was used to conduct the supervised classification. This algorithm uses the means and variances of the classes derived from the training dataset to estimate the probability of a correct classification for a pixel (Campbell, 2002). It considers several classes and spectral signatures simultaneously, which makes it a powerful but highly computer-intensive algorithm (Campbell, 2002). It is more sensitive to the quality of the classes, which necessitates the examination of the class histograms as stated above.

Following classification, the images were examined and compared to a generalized vegetation map I had of the park to identify any areas that appeared to stand out. I then conducted an accuracy assessment using 60 random sites and all the auxiliary information and ground data I had access to in order to determine how accurately the images were classified based on the training information I had provided. The classified images were then exported as geoTIFF files to the ArcMap tool in ArcGIS in order to generate cartographic maps.

Image classification was not attempted for the images from 1976, 1987, and 1993 because of a lack of good ground data from these periods. Hence, these images were only subjected to NDVI change detection analyses.

2.2.3.4 NDVI change detection

The bands used for NDVI calculation for the 1976 MSS image were spectral bands 2 and 4 (Lee and Marsh, 1995), whereas for the remaining years spectral bands 3 and 4 were used (Campbell, 2002). These bands correspond closely to one another, in that MSS band 2 and TM band 3 both cover the 0.6 to 0.7 mm range, while band 4 on MSS covers the 0.8 to 1.1 mm range and band 4 on the TM and ETM+ sensors cover the 0.76 to 0.9 range (Richards and Xiuping, 1999). Hence, these were the bands that were corrected using the MATCH and LUT algorithms mentioned above for the images of the later decade using the images from the earlier decade. This was done for each set of comparisons (1976 to 1987, 1987 to 1993, and 1993 to 2002). A 32-bit real image of NDVI values for each year was then produced using the raster calculator in FOCUS. The original bands (2 and 4 for 1976, or 3 and 4 for the other years) for the earlier decade were used to calculate the NDVI for this decade, whereas the correct bands for the later decade were used to calculate its NDVI. The two NDVI images were then subtracted, earlier decade from later decade, using the ARI algorithm in FOCUS that allows a user to conduct simple arithmetic operations on image data. The resultant change detection image was then exported to a geoTIFF file to ArcMap where it was displayed using the mean ± 2 standard deviations in order to highlight the positive and negative changes in NDVI from one decade to the next.

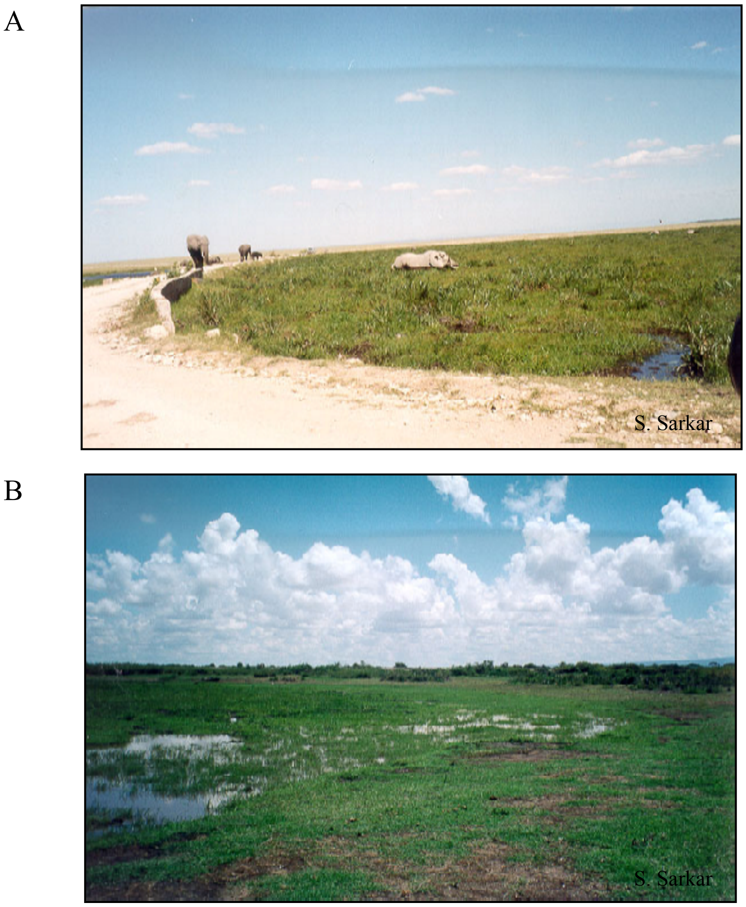

Figure 2.2. Typical scenes showing (A) *Cyperus* dominated deep water wetland class, and (B) *Cyperus laevigatus* dominated seasonal wetland class.

2.3 Results

2.3.1 Long term elephant use patterns and herbivore grazing studies

Long term aerial count data indicate that the number of elephants seen on the edges of the wetlands in the wet season rose steadily from 1975 to 1985, peaking in 1991 and then falling off by 2004 to a number higher than that in 1975 (Figure 2.3a). In the permanent wetland habitat, however, elephant numbers increased during the wet seasons of 1975 onwards (Figure 2.3b). Dry season elephant numbers have steadily increased, except between 1987 and 1996, in the wetland-edge habitats (Figure 2.3a). A similar trend is also seen in the permanent wetland habitats (Figure 2.3b).

Herbivore grazing damage measured in the permanent plots 1 and 2, which are located in the wetland-edge habitat of the park, was almost 100% in plot 1 and above 75% in plot 2 in the dry seasons of 1976 to 1980 (Figure 2.4). Following this, dry-season grazing damage dropped rapidly to less than 10% in plot 1 until 1995 after which it increased steadily (Figure 2.4a).

In plot 2, however, dry-season grazing declined to about 40% in 1985, leveled off for about 5 years, and then increased to 60% in 1997 (Figure 2.4b). Following this, grazing damage in the dry season appears to be declining (Figure 2.4b) and in January 2003, which is the last data point in this set, 19% of the vegetation showed grazing damage.

Wet-season grazing was similar in both plots and showed a steady increase from 1975 to 1985 (Figure 2.4). Following this, the two plots did not give similar trends in grazing damage, with plot 1 showing first a leveling off until 1997, and then an increase in grazing damage after 1997 (Figure 2.4a). Plot 2 grazing damage, on the other hand, leveled off until 1990, then increased until 1997, and has since leveled off again (Figure 2.4b)

2.3.2 Wetland extents

The Enkongo Narok wetland in Amboseli National Park steadily lengthened from 1950 to 1976, whereas Ol' Tukai appeared to split from a single wetland in 1950 into two distinct wetlands in 1976 (Figure 2.5). Longinye's flooding pattern changed, showing a lengthening in the northwestern portion in 1967, which returned to almost 1950 dimensions by 1976 (Figure 2.5c and d). The Ilmerishari wetlands were first noticed along with another small wetland to its southwest in 1967, and Lake Conch was created (Figure 2.5c). The absence of these wetlands in the 1950 and 1961 maps may either have been an omission, either deliberate or not, by the cartographer or these wetlands may not have existed until 1967. Total annual rainfall was not available for the period before 1968. Precipitation between 1968 and 1976, however, indicates a dry period (Figure 2.6a) which might explain the shrinking of Lake Conch, the splitting of Ol' Tukai and the recession of Longinye (Figure 2.5d). These data, however, do not help to determine why the Ilmerishari wetlands were not included in the earlier maps.

By 1979, Longolong (Figure 2.7a) had been created at the northwestern end of Enkongo Narok, which had now extended to its current length, and Lake Conch had been re-flooded. This corresponds to the increasing amounts of precipitation that fell between 1976 and 1979 (Figure 2.6a). From 1979 to 1989, Enkongo Narok, Ilmerishari, and Ol' Tukai wetlands did not change much, except that Lake Kioko had clearly formed off the eastern edge of Enkongo Narok by 1979 (Figure 2.7a).

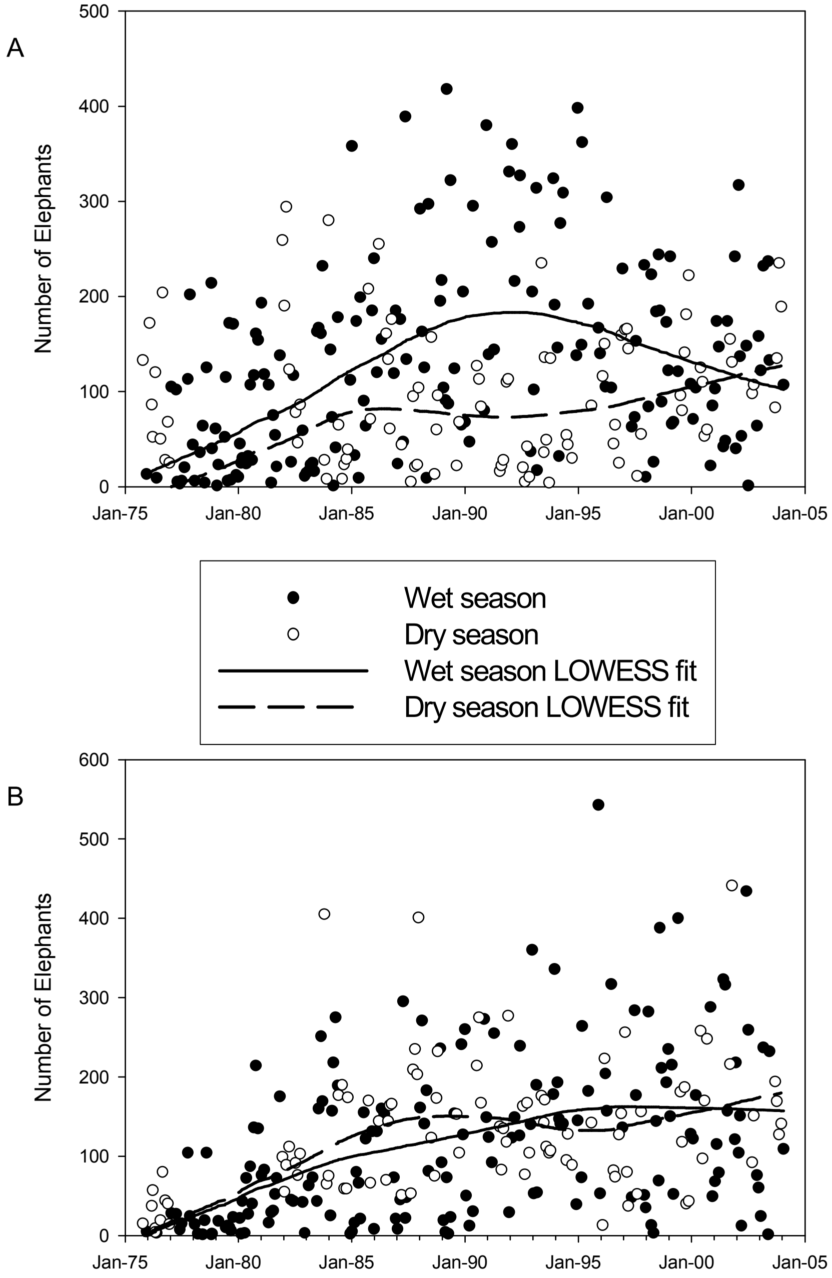

Figure 2.3. Elephant count data for (A) the edges of the wetland and (B) the permanent wetland habitats in the Amboseli National Park in the dry and wet seasons. The pattern of use over time is indicated by the LOWESS line of fit for each season over time.

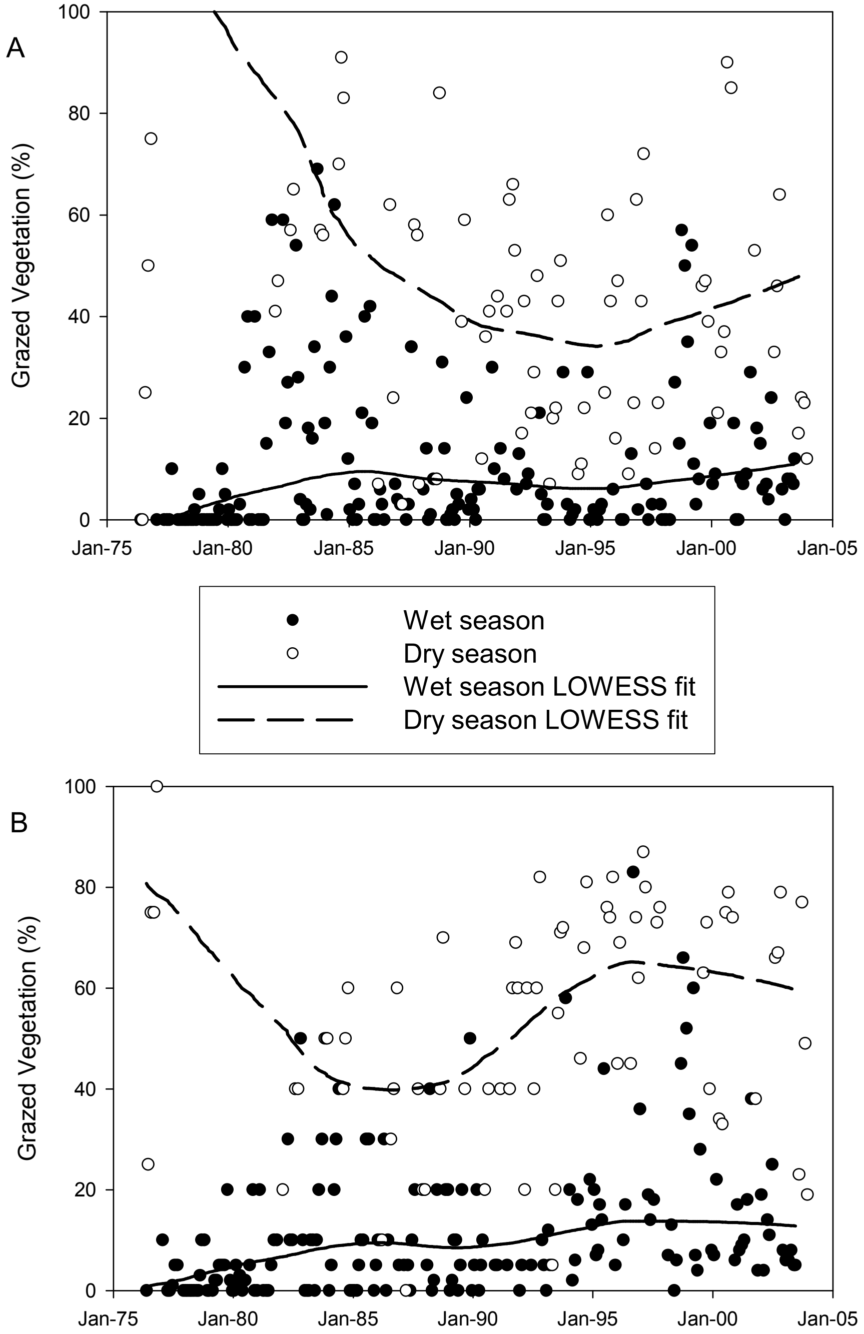

Figure 2.4. Percentage of grazed vegetation in the wetland-edge habitats of (A) plot 1 and (B) plot 2, which are indicated in figure 1.1b, during the dry and wet seasons over 24 years. Low order LOWESS smoothing was applied to extract the pattern of grazing in each season (shown by the solid and hatched lines) over time.

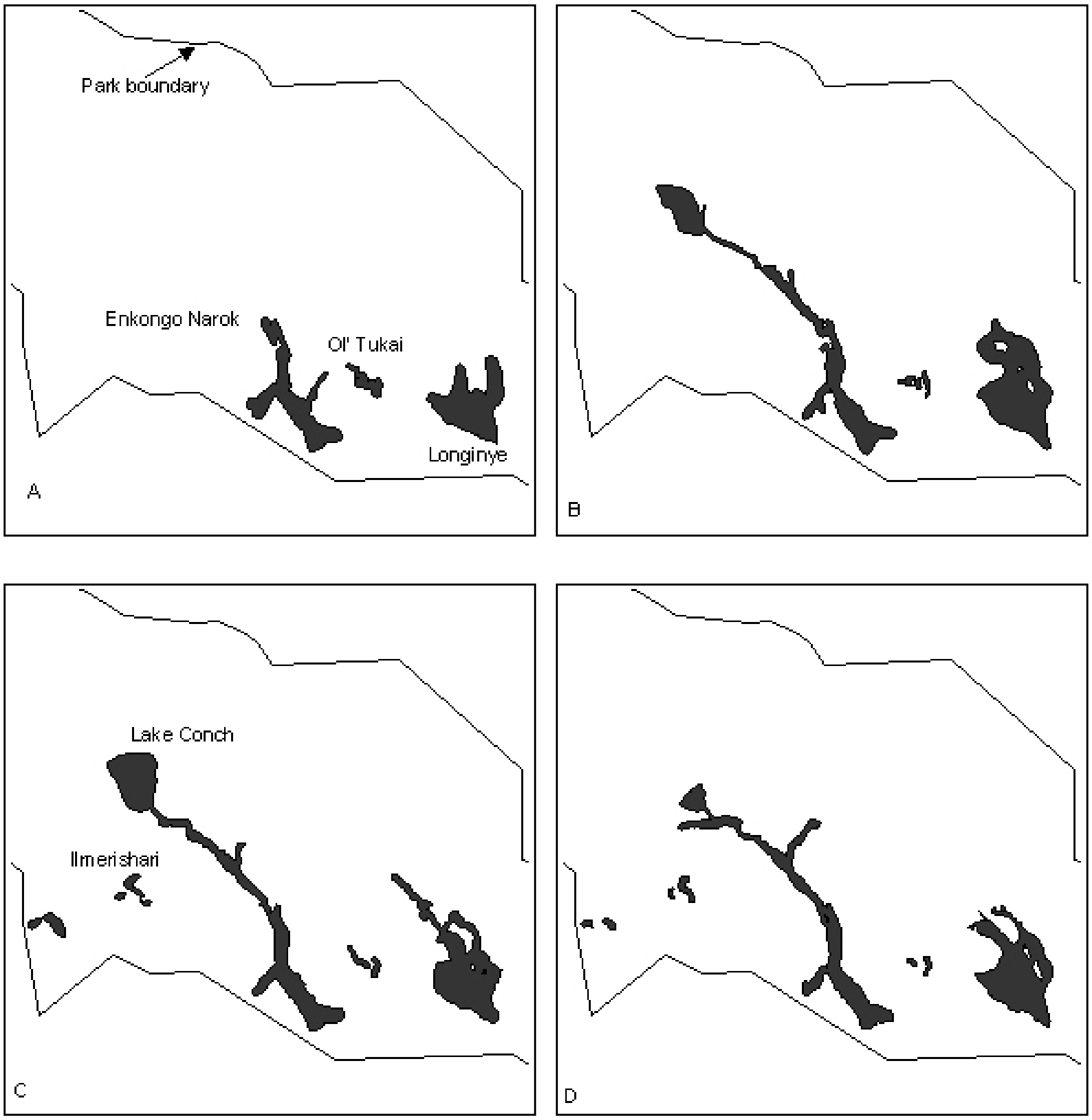

Figure 2.5. Change in extent of the Enkongo Narok, Longinye and Ol' Tukai wetlands in the Amboseli National Park for the period during which elephants migrated out of the park boundary during the wet season, (A) 1950, (B) 1961, (C) 1967, and (D) 1976. Note that the Ilmerishari wetlands were captured only after 1961. Images were derived from hand-drawn illustrations by Dr. D. Western and were based on various sources in order to represent the mean extent of the wetlands for a particular year.

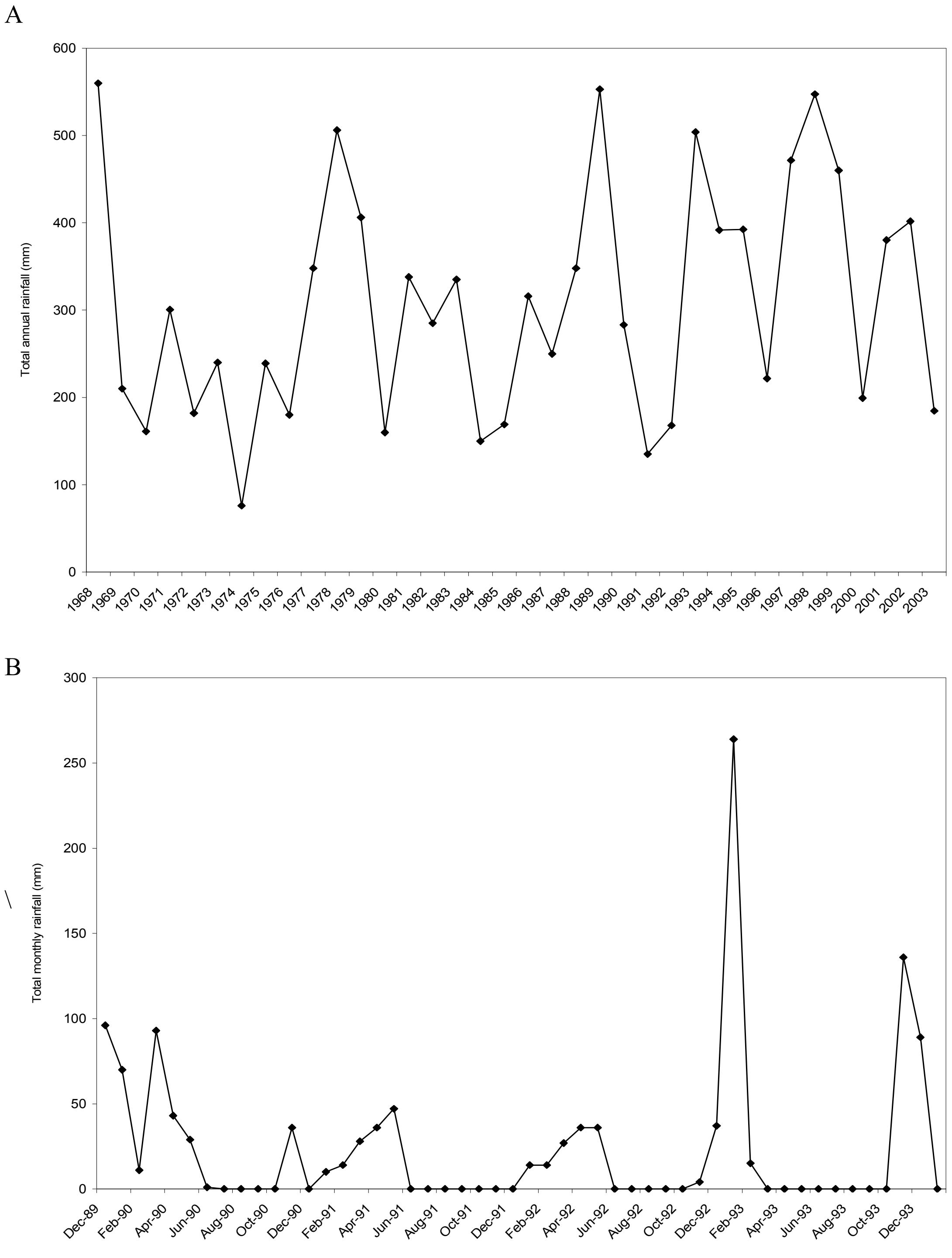

Figure 2.6. (A) Total annual precipitation from 1968 to 2003 and (B) total monthly precipitation for December 1989 to January 1994 in Amboseli National Park, southern Kenya. Data were collected at the Ol' Tukai weather station inside the park.

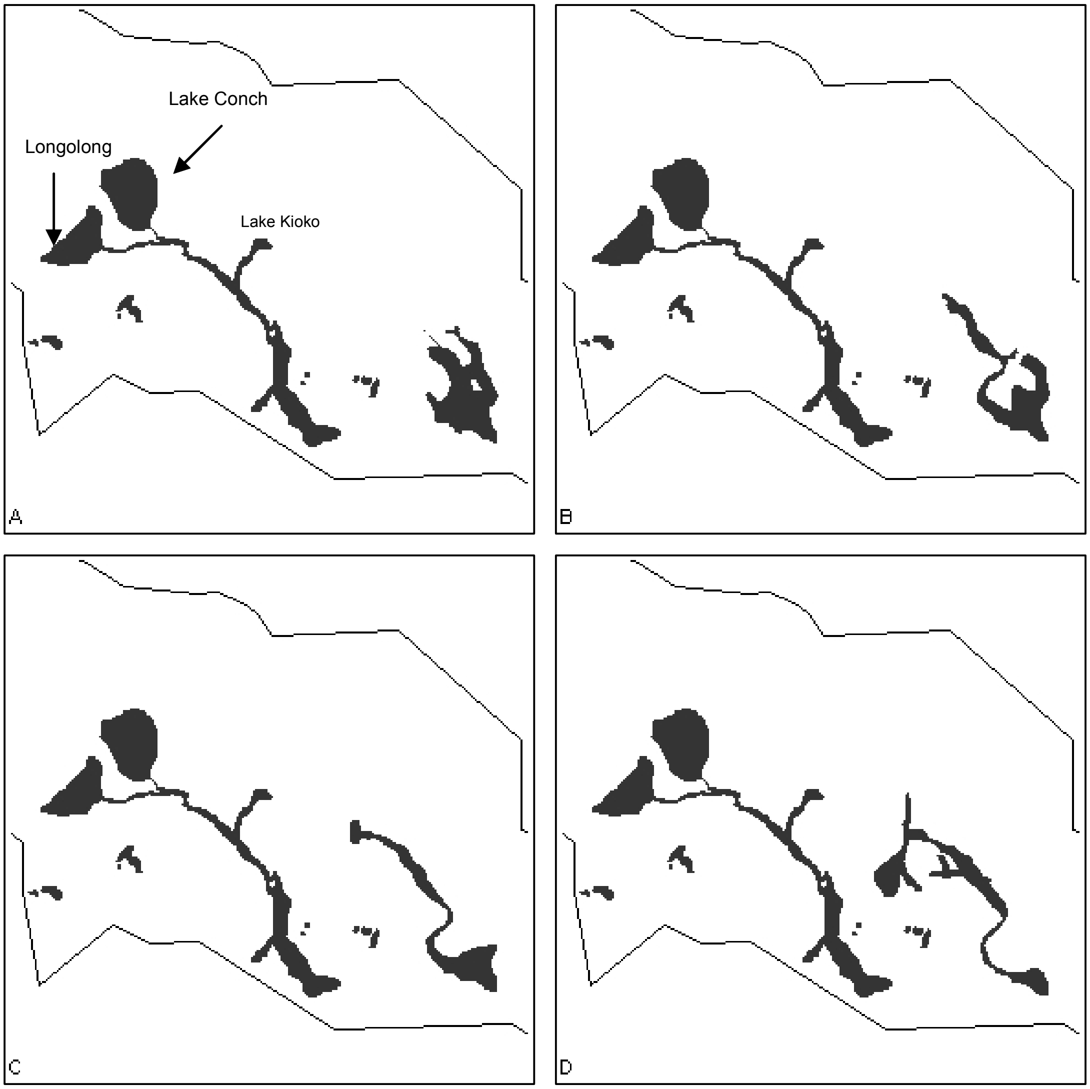

Figure 2.7. Change in extent of the Amboseli National Park wetlands in (A) 1979, (B) 1983, (C) 1985, and (D) 1989, a period during which the elephant population remained within the park boundary throughout the year. Figures were derived from hand-drawn illustrations by Dr. D. Western from his personal aerial surveys and were based on the mean extent of the wetlands for a particular year.

Longinye, on the other hand, changed the most during this period (Figure 2.7). In 1983, Longinye began to dry up in the centre (Figure 2.7b). By 1985, water was no longer moving into the centre, but rather the wetland had become more elongated in a southeast to northwest direction with a pool in the southeast where the springs of this wetland most likely occur (Figure 2.7c). In 1989, there was no longer a pool to the southeast, but instead the water was pooling in the northwest end of the wetland, which had now developed a distinct shape (Figure 2.7d).

Annual precipitation between 1979 and 1989 varied, with 1980, 1984 and 1985 having the lowest rainfall and 1979 and 1989 having the highest rainfall during this period (Figure 2.6a). It appears that the changes in Longinye are related to change in course rather than a direct effect of rainfall since no changes were seen in the other wetlands during this period.

From 1989 to 1990, Longolong, which lies on the northwestern end of Enkongo Narok, had begun to dry up and Longinye no longer had the pool in the northwest end (Figure 2.7d; Figure 2.8a). This might be related to the decrease in rainfall from 1989 to 1990 (Figure 2.6a). Ol' Tukai, however, had re-flooded (Figure 2.7d; Figure 2.8a). Hence rainfall was not affecting this wetland as might be the case in Longinye and Longolong.

In April 1991, Longinye had flooded into the Ol' Tukai wetland and some of the previous areas of flooding seen in 1979, 1983, and 1989 (Figure 2.7a, b and d; Figure 2.8b) were also inundated. This occurred after four months of below 50 mm of rainfall (Figure 2.6b). Three months later, in July 1991, Longinye had re-flooded the channels that were last inundated in 1983 (Figure 2.7b; Figure 2.8c). Local rainfall had, however, fallen to zero (Figure 2.6b). During this period, both Longolong and Lake Conch located on the northwestern end of Enkongo Narok had also increased (Figure 2.8c). This latter increase in extent did not change in 1992, although Longinye had begun to shrink once more and Ol' Tukai was represented only by a small wetland on the eastern side of Enkongo Narok (Figure 2.8d). Rainfall patterns in 1992 were similar to that of 1991 (Figure 2.6b).

Longinye changed the most drastically between January and October 1993, whereas the other wetlands to its west did not change much (Figure 2.9a - d). From 1992 (Figure 2.8d) to January 1993 (Figure 2.9a) Longinye had shortened and re-flooded the pool on the northwestern end seen in 1989 (Figure 2.7d). However, within a month this pool had increased in size, re-flooding what used to be Ol' Tukai (Figure 2.8a). The channel to the southeast had lengthened and Longinye had expanded into Enkongo Narok at Lake Kioko (Figure 2.9b). These expansions occurred in tandem with a huge increase in monthly rainfall that occurred in January 1993 (Figure 2.6b). The expansion of Longinye into Enkongo Narok and the large pool was drastically reversed by July 1993, with the largest decrease in extent occurring at the points where Longinye met Lake Kioko, and where the pool occurred. Further reduction in extent of these areas had occurred by October 1993 (Figure 2.9c and d). These followed a reduction of monthly rainfall from about 250 mm in January to zero between March and October 1993 (Figure 2.6b).

There was some expansion of the centre of Longinye in 1994, followed by re-flooding of the southeastern channels in 1999 (Figure 2.9e and f). On the other hand, Longolong, on the northwestern end of Enkongo Narok, increased in size between 1994 and 1999 and a channel that lay to the southwest of Longolong was flooded (Figure 2.9e and f). These increases do correspond to years when annual rainfall was above 300 mm (Figure 2.6a).

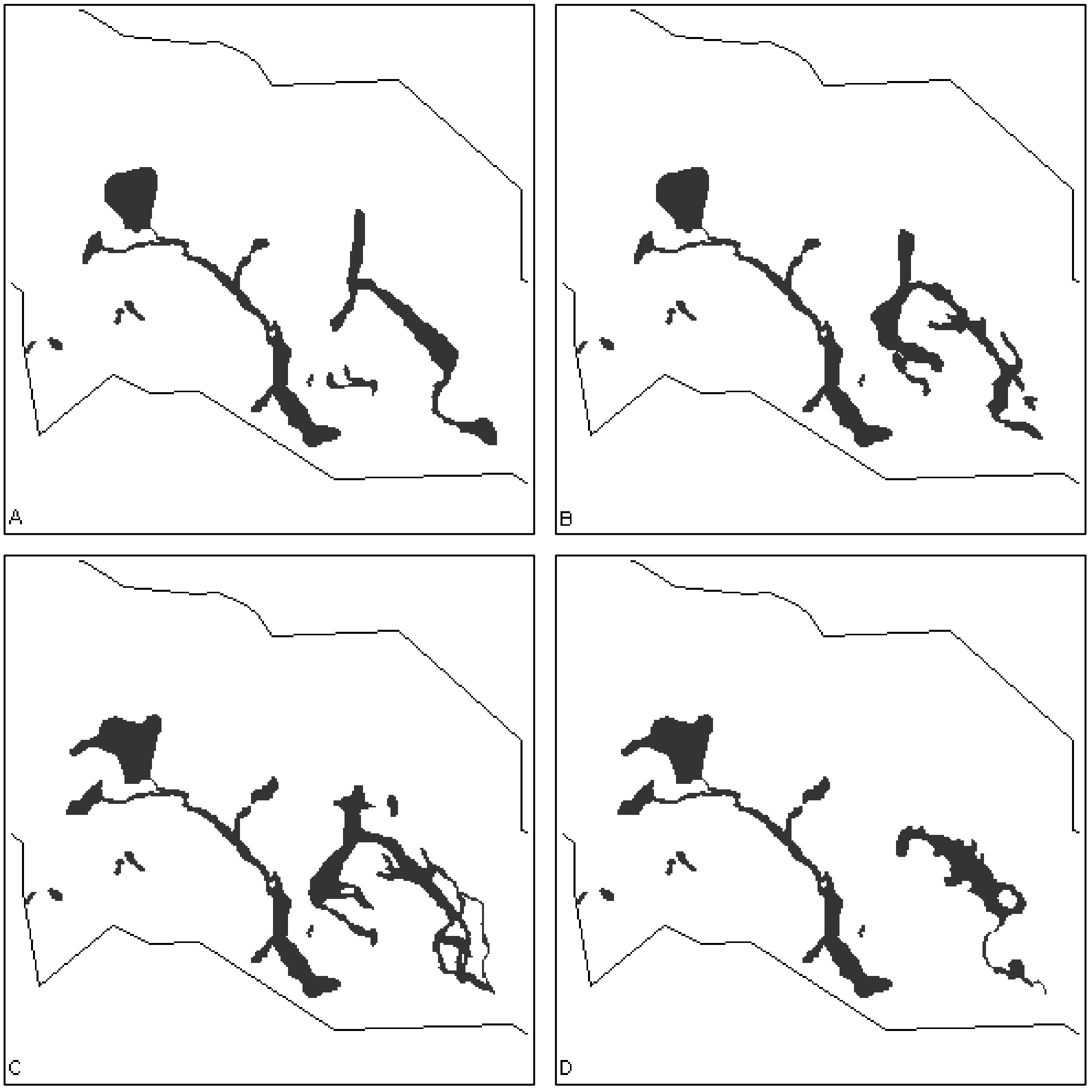

Figure 2.8. Change in extent of the Amboseli National Park wetlands for the period during which the elephant population was beginning to renew migrations outside the park boundary during the wet season, (A) 1990, (B) April 1991, (C) July 1991, (D) 1992. Figures were derived from hand-drawn illustrations by Dr. D. Western from his personal aerial surveys and were based on the mean extent of the wetlands for a particular year or in the case of 1991 when the wetlands changed a lot these are illustrated separately.

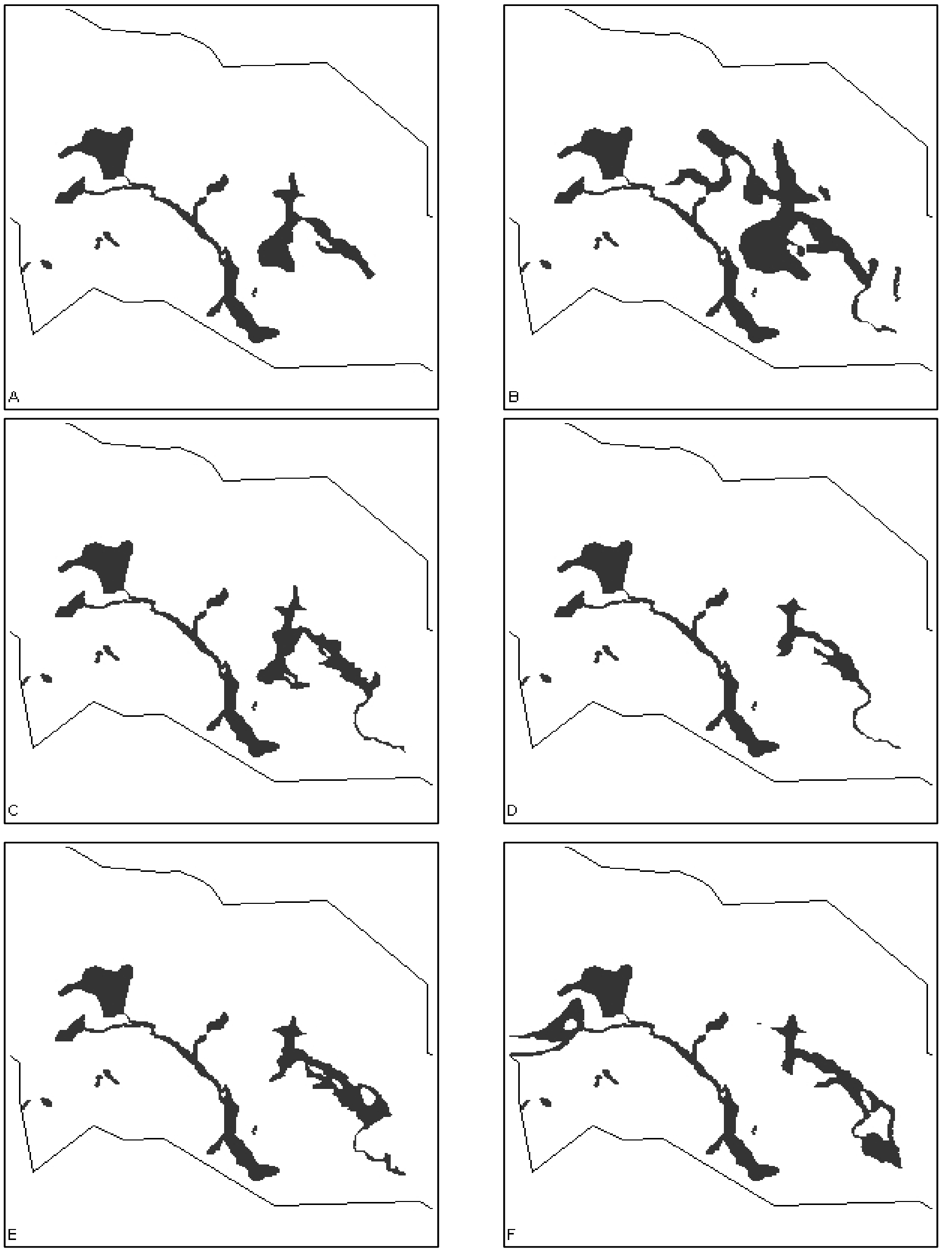

Figure 2.9. Change in extent of the Amboseli National Park wetlands for 1993 during which the wetlands changed extensively as a result of El niño events, (A) January 1993, (B) February 1993, (C) July 1993, (D) October 1993, and the extents of the wetlands in following years (E) 1994, and (F) 1999. Figures were derived from hand-drawn illustrations by Dr. D. Western from his personal aerial surveys and were based on the mean extent of the wetlands for a particular year or in the case of 1993 when the wetlands changed a lot these are illustrated separately.

2.3.3 Current status of vegetation: 2002 image classification

A total of 15 classes were identified in the 2002 image. However, to reduce the number of categories presented in Figure 2.10, the more similar classes not related to wetland habitats, such as grassland and scrubland, were aggregated to obtain a total of 9 classes. Accuracy assessments were conducted on the original 15 classes and this meant an overall Kappa index of 0.525 ± 0.004 and an overall accuracy of 60% for this map. The percent of the area that was not classified into an information class (null) was about 0.3% (Table 2.1). The riverine vegetation class and the open scrubland class had a Bhattacharrya distance of 1.4 between them, which was also the lowest separability distance for this classification. These classes were not aggregated because it was decided that the lack of good separation was a result of mixed pixels, since these two vegetation classes appear close to one another (Figure 2.10).

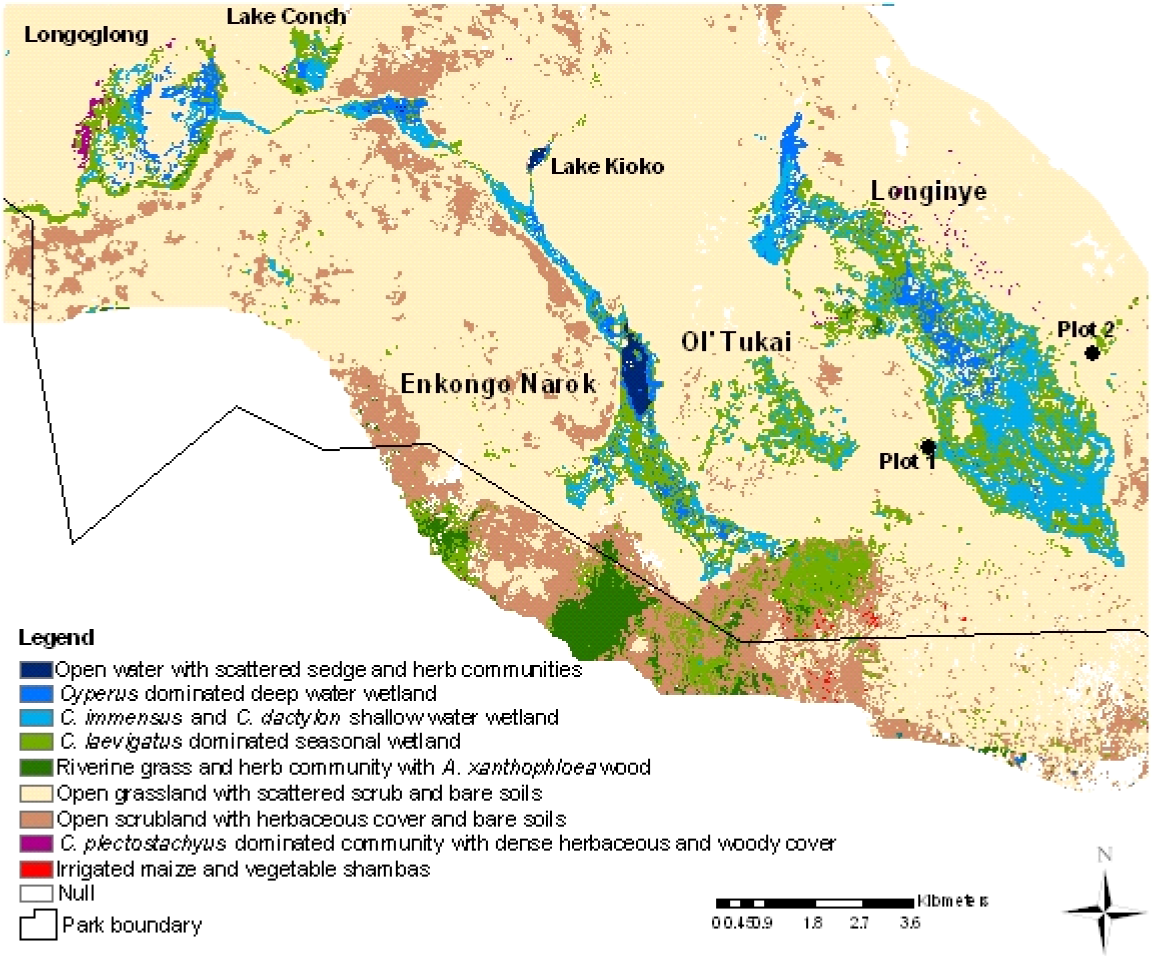

Figure 2.10. The main vegetation classes found in and around the Amboseli National Park wetlands that were derived from a supervised classification using bands 2 to 5 of a February 2002 LANDSAT ETM+ image.

The *C. laevigatus*-dominated seasonal wetland class, on the other hand, had a distance value of 1.6 between it and the *Cyperus* dominated deep wetland and *Cyperus immensus*/*Cynodon dactylon* shallow wetland classes. These vegetation classes are very similar due to the sedge and water components. However, when I did aggregate these classes the separability did not change much. Therefore, I assumed that since these vegetation types are linked, they might be present close to one another making them harder to separate and hence, they were not aggregated. It is important, therefore, to keep in mind that the percent coverage of these classes may have been either under- or over-estimated on the classification map.

The classified map (Figure 2.10) and the wetland extent image from 1999 (Figure 2.9f) are quite similar, except for Lake Conch and Longolong, suggesting that the accuracy of the classified map, with respect to the wetland habitats, is high. There were five wetland habitats that were distinguishable, albeit with some inaccuracy as mentioned above. The habitats include an open water habitat, a *Cyperus*-dominated deep water habitat, a shallow water habitat covered with *C. immensus* and mats of *C. dactylon*, a *C. laevigatus*-dominated seasonal wetland and a riverine community (Figure 2.10; Table 2.1). However, altogether these habitats did not make up more than 9% of the area classified (Figure 2.10; Table 2.1). Enkongo Narok had more sedge dominated deep and shallow water habitat than Longinye, which was predominantly *C. laevigatus* seasonal wetland (Figure 2.10).

Grassland communities were dominant in the classified area, which is in fact the current status of the park (Figure 2.10; Table 2.1). Of the area covered by wetland habitats, the open water habitat was the smallest at less than 1%, followed by the riverine habitat at 1% (Figure 2.10; Table 2.1). Seasonal wetland habitat was the largest of the wetland habitats, at almost twice that of the shallow water habitat and four times the deep water habitat (Figure 2.10; Table 2.1). The *Cynodon plectostachyus* (K. Schum.) Pilg. - dominated community was more prevalent in the area to the east of the park as was the irrigated shambas class (see chapter 5 under Namelok), which within the park boundaries is a misclassification (Figure 2.10).

2.3.4 Temporal change in vegetation: 1976 to 2002 NDVI change detection

There was a 1% decrease in NDVI between 1976 and 1987 (Figure 2.11a). Most of the decrease seen between 1976 and 1987 was in the Enkongo Narok wetland that lies at the western most end of Figure 2.11a. There was a decrease in NDVI around the top of Lake Conch, as well as along the length of Enkongo Narok (Figure 2.11a). The latter correspond to areas that were classified as open water and deep water habitats in the 2002 satellite image (Figure 2.10) and to areas that did not show a change in extent between 1976 and 1989 (Figure 2.5d; Figure 2.7). Water has an NDVI close to zero hence, if precipitation was higher in 1987 and caused an increase in open water in these areas compared to 1976, then NDVI would decrease. It is important, therefore, to consider the amount of rainfall that has fallen in the area preceding the date on which an image was captured in order to account for such situations. The monthly rainfall amounts for four months preceding the capture of each image used in these analyses are presented in Table 2.2. Rainfall from October to February 1976 was lower than the same period for 1987 primarily because of the differences in the October and November rains (Table 2.2). The location of the decrease in NDVI within Enkongo Narok more likely implies that open water areas occurred in these locations.

Table 2.1. Species included in the vegetation classes from the supervised classification of the Amboseli national park wetlands area in southern Kenya along with the area covered by each class as a percentage of the total classified area.

	Vegetation Class	**Area (%)**	**Dominant Species**	**Other Species**
1.	Open water with scattered sedge communities	0.15	*Cyperus papyrus*	
2.	*Cyperus* dominated deep water wetland (permanently inundated)	1.05	*Cyperus immensus, Cyperus laevigatus*	*Azolla spp., C. dactylon, Senna didymobotrya*
3.	*C. immensus* and *C. dactylon* dominated shallow water wetland (mostly inundated)	2.70	*C. immensus, Cynodon dactylon*	*Solanum incanum, Withania somnifera, Phoenix reclinata*
4	*C. laevigatus* dominated seasonal wetland (inundated during periods of high rainfall)	4.36	*C. laevigatus*	*Digitaria scalarum, Sporobolus spicatus,* *C. dactylon*
5.	Riverine grass and herbaceous community with *A. xanthophloea*	0.92	*Cyathula erinacea, Dactyloctenium aegytium, Cyperus merkeri, Sporobolus fimbriatus*	*Acacia xanthophloea, Azima tetracantha, Eriochloa nubica*
6.	Open grassland with scattered scrub and bare soils	54.68	*Psilolema jaegeri, C. dactylon, S. spicatus*	*Sporobolus kentrophyllus, S. sanguineus, S. consimilis, Cynodon plectostachyus, S. persica, S. monoica*
7.	Open scrubland with herbaceous cover and bare soils	6.16	*Tribulus terristris, Suaeda monoica, Salvadora persica*	*Balanites aegyptiaca, Acacia tortilis, Justicia uncinulata,*
8.	*C. plectostachyus* dominated communities with dense herbaceous and woody cover	0.08	*C. plectostachyus*	*Setaria verticillata, Amaranthus graecizans, Leonotis nepetifolia, A. xanthophloea, A. tetracantha*
9.	Irrigated maize and vegetable shambas (fields)	<0.05	*Maize*	*Bananas, Tomatoes, Onions*
10.	Null – areas not assigned to a class	0.27		

The decrease in NDVI at the top of Lake Conch is less likely to be the effect of a pool of water (Figure 2.11a). The lake increased in extent from 1976 to 1979 but did not change until July 1991 (Figure 2.5d; Figure 2.7; Figure 2.8). Hence, assuming the maps of the wetland extent are accurate, the decrease in NDVI was not the effect of flooding over the vegetation, but rather a decrease in vegetation.

The increase in NDVI was over 3% of the image, which was expected as a result of the wetter conditions in 1987 as compared to 1976. However, almost all of the increases occurred within the wetland boundaries (Figure 2.11a). This indicates that the rainfall was not sufficient to cause increases in greenness in the surrounding habitats. In Longinye (the easternmost wetland) the increases correspond to the extent of the wetland shown in Figure 2.7c and Figure 2.7d. In Ol' Tukai, the increase in NDVI was around the areas classified in the 2002 image as seasonal wetland (Figure 2.10; Figure 2.11a).

From 1987 to 1993, there was a 3% increase and a 3% decrease in NDVI even though the period between October 1986 and February 1987 was drier than the same period between 1992 and 1993 (Table 2.2). Most of the increase occurred in the drier habitats surrounding the wetlands, most likely as a result of the major rain event of January 1993 (Figure 2.11b; Table 2.2). The decreases, on the other hand, occurred along the edges of Enkongo Narok, in Longolong and Lake Conch, around Ol' Tukai, as well as on the northwestern tip of Longinye (Figure 2.11b). Most of these changes are the result of flooding due to the above average rainfall (Table 2.2) that may have also caused the large changes in extent in the Longinye wetland seen in Figure 2.9b. The decreases in NDVI along the edges of Enkongo Narok, however, might be the result of the failed short rains of November and December 1992 that followed a long dry season of no rainfall from July to October 1992 (Figure 2.6b; Table 2.2). Such failures in rainfall prompt herbivores to rely heavily on the wetlands for food and water (Western, 1975; Western and Lindsay, 1984).

Rainfall for 2002 was lower than that in 1993 primarily because of the January 1993 rain event (Table 2.2). However, the decrease in NDVI was only about 1% and the increase was 3% (Figure 2.11c). Some of these increases occurred in areas that showed decreased NDVI for 1987 to 1993 (Figure 2.11b and c). This indicates a change from open water to vegetated habitats, which corresponds to the classified image from 2002 (Figure 2.10). The increase in vegetation may have been prompted by the heavy rains that fell in December 2001 (Table 2.2). The decrease within Enkongo Narok occurred where the open water habitat now exists, and this might suggest a return to an open water habitat in this part of the wetland (Figure 2.10; Figure 2.11c). Interestingly, there was no change in NDVI within Ol' Tukai (Figure 2.11c).

2.4 Discussion

The results from long-term aerial counts for elephants reflect an overall increase in year-round use of the permanent and seasonal wetland habitats of the Amboseli National Park from the mid 1970's to the 1990's. This period corresponds to the time during which elephant migration out of the park in the wet season is reported to have stopped due to the threat of poachers (Koch *et al.,* 1995). It also corresponds to the period when elephant populations were steadily increasing as reported by Moss (2001) as is clearly seen with the increasing dry-season numbers.

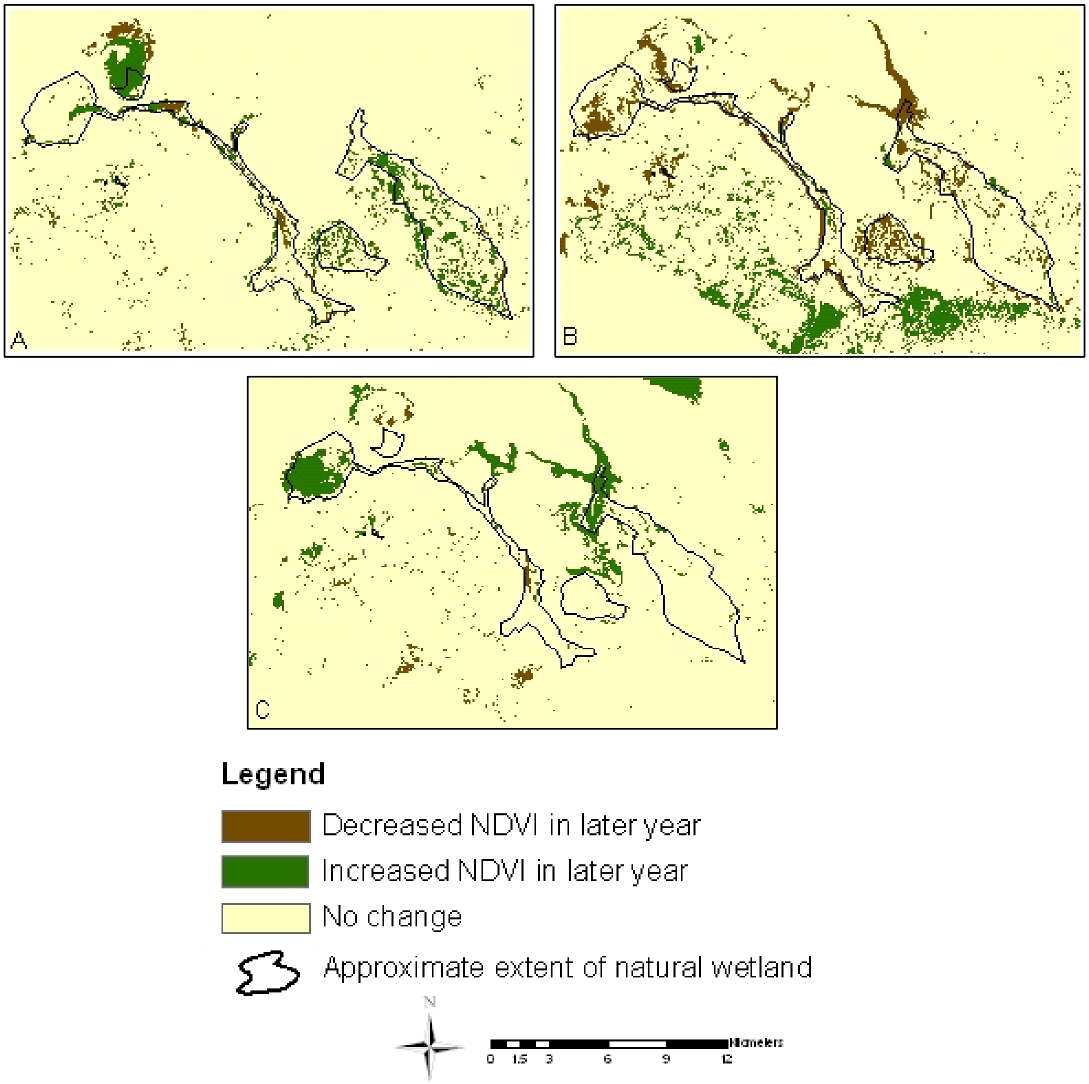

Figure 2.11. Detection of change over four decades in the Normalized Differential Vegetation Index (NDVI) for the Amboseli National Park wetlands where (A) is the difference image for 1976 to 1987, (B) is the difference image for 1987 to 1993, (C) is the difference image for 1993 to 2002. The difference images were derived by subtracting the NDVI values of the earlier year from those of the later year so that an increase in NDVI indicates more vegetation vigor in the later decade as compared to the earlier decade. The wetlands, as indicated by the approximate extents are, from left to right, Enkongo Narok, Ol' Tukai (smallest one), and Longinye.

Table 2.2. Monthly rainfall (mm) values for the 4 months preceding the month in which an image was captured for the years used in an NDVI change-detection analyses for the Amboseli wetlands, Kajiado District, southern Kenya.

Month	**1976**	**1987**	**1993**	**2002**
October	7	59	0	24.0
November	46	93	4	50.5
December	44	43	37	130.9
January	0	28	264	61.0
February	28	4	15	0.0
Total	125	227	320	266.4

From 1990 to 1995, dry-season elephant numbers in the permanent wetland habitat leveled off, but wet season numbers began to level off after 1995. The increase in numbers in the wet season during this period occurred when elephant migration out of the park in the wet season is thought to have resumed (Koch *et al.*,, 1995). A combination of factors is more than likely playing a role in this change in preference. Elephant numbers have almost doubled since 1960 (Moss 2001), while wetland habitat outside of the park available to elephants has decreased since the 1980's as a result of human land-use changes (Western and Lindsay, 1984; Worden *et al*., 2003; also see chapter 5). However, elephants are water-dependent species that have been reported to remain within 50 km of the Amboseli National Park (Western, 1975).

In a study of elephant herd dynamics, it was estimated that 42% of the population was located more than 10 km from the wetlands during the wet seasons and only 17%, during the dry season (Western and Lindsay, 1984). Hence, the loss of wetland habitat outside the park may have resulted in the elephants remaining within the park due to their water-dependence. In addition to these factors, the incidences of poaching that occurred in Kenya from 1989 onwards (Stiles, 2004) may also have played a role in keeping elephants inside the park. Taken together, the results lend support to the hypothesis that elephants have increased their reliance on the permanent wetlands of Amboseli National Park throughout the year since the mid-1970s. However, with the lack of grazing data for the permanent-wetland habitat, it is not possible to conclude that grazing by other herbivores has also changed over time.

The increase in elephant numbers and change in elephant migratory patterns are not as obvious, however, in the wetland-edge habitat. Here, elephants were only seen in higher numbers in the wet seasons of 1985 to 1990, whereas from 1990 onwards there has been a decreasing trend in the average number of elephants seen in this habitat. However, the total number of elephants using the habitat is still higher than it was in 1975. The long-term permanent plot data for herbivore grazing damage shows only a slightly increasing trend in grazing damage in both plots. Since grazing damage was identified by teeth marks, this implies that other herbivores have also not been relying heavily on this habitat for wet season grazing, but that there has been some increase in use over time. Whether this is related to reduced access to wetlands outside the park as reported by Worden *et al*. (2003), or another factor, is not clear.

In the dry seasons of 1976 to 1980 herbivores, other than elephants, relied heavily on the wetland-edge permanent plots, albeit the *C. dactylon* / *D. scalarum* dominated plot 1 was more heavily used than the *S. spicatus* / *C. laevigatus* dominated plot 2. This reliance on the plots was reversed by the 1990's, though the plots did not show the same trends. The increased grazing damage in the 1970's is most likely the result of droughts during that decade (Western, 1994). The decrease in grazing damage in the 1990's corresponds to the large increase in local rainfall that also clearly affected the extent of the wetlands in the park.

The differences in grazing damage in the dry season between the plots after the mid-1990's may be the result of changes in herbivore habitat selection since the species present in both plots are acceptable dry-season forage (Little, 1996; McNaughton, 1985). Herbivores select forage based on nutrient, protein, and energy content (Owen-Smith and Novellie, 1982; McNaughton, 1985; McNaughton, 1990). These qualities in forage deteriorate from the wet to the dry season, forcing herbivores to select other habitats that suit their metabolic needs (Western and Lindsay, 1984). Hence, plot 1 may have better quality forage in the dry season than plot 2, and this could be caused by a difference in soil moisture and nutrient levels, for example. Another possible factor is the relative salinities of the two plots. If plot 2 is more saline than plot 1, as indicated by the relatively more saline tolerant plants in the former (Thompson, 1985), herbivores may avoid this area.

The extent and flooding patterns of the wetlands, especially Longinye, are highly dynamic. Between 1950 and 1976 there was a large increase in the extents of all the wetlands. This may be related to the loss of woodland to the south of these wetlands, as hypothesized. Trees have a large impact on groundwater in both positive and negative ways. They lose more water through evapotranspiration than do other vegetation and they can extract water from deep aquifers (Le Maitre *et al.*, 1999). However, they also increase infiltration into soils and help recharge aquifers that underlie low-permeability soils (Le Maitre *et al.*, 1999). The decrease in *A. xanthophloea* woodlands in the park by the mid-1960's (Western and Maitumo, 2004), could have caused an increase in the amount of water reaching the wetlands during periods of high rainfall on Mt. Kilimanjaro. Large-scale losses of the woodlands do correspond to the increase in wetland extent from 1950 to 1976.

It is not possible, however, to determine whether the changes in extent of the wetlands are more rapid from rain event to rain event now than pre-1980 because of a lack of fine-scale data. In the years in which monthly extents were digitized, that is, 1991 and 1993, the wetlands did appear to increase and decrease in response to local rainfall.

In the Amboseli National Park wetlands, the inflow of water into the wetlands is via aquifers fed by Mt. Kilimanjaro to the south. Based on the direction of changes in extent of Enkongo Narok and

Longinye, the general direction of flow of water along the wetland channels appears to occur in a northwest direction. However, I have personally observed the presence of channels created by hippos within the shallow water wetland habitats and elephants commonly wallow in the wetlands for long periods of time during the day (Figure 2.2a). These activities may increase the connectivity between the shallow wetland habitats. In the Okavango Delta, channels created by hippos have been shown to alter the hydrological condition of the wetlands (Ellery *et al.*, 2000). It is therefore likely that some of the alterations in the course of Longinye from the 1960's to 1999 are the result of re-flooding of channels maintained by hippo, and maybe elephant, activity. Channel flow in Longinye may also have been altered by vegetation as suggested by Irungu (1992). Vegetation is commonly an engineer in the hydrological conditions of wetlands (Mitsch and Gosselink, 2000). Ellery *et al*. (2000) report that, in the Okavango Delta, *C. papyrus* mats cause large changes in inflow channel morphology, ultimately leading to the collapse of a channel. The Amboseli wetlands are currently covered by floating vegetation mats and in the 1970's the dominant species in the wetland was reported to be *C. papyrus* and *C. immensus* (Western and Sindiyo, 1972). Hence, it is likely that vegetation has played a role in long-term alterations in channel flow and inter-connectivity of the wetland habitat. Why Enkongo Narok does not showing similar changes in extent is unclear, but it may be because of the differences in the wetland habitats that make up the two wetlands.

The classification and NDVI results for the Amboseli National Park indicate that the *C. laevigatus* dominated seasonal wetland habitat is the most common of the wetland habitats, followed by the *C. immensus* and *C. dactylon* dominated shallow water wetlands and *Cyperus* dominated deep water wetland. The obvious difference in these habitats is the hydrological condition of each. The species present in these wetland habitats, however, are all tolerant of draw-downs and to certain levels of re-flooding (van der Valk, 1981; Thompson, 1985). Most of the vegetation in the two "wetter" habitats grows as mats that can rise and float when flooding occurs, but that can also become rooted to the sediment during draw downs (van der Valk, 1981; Thompson, 1985). Prolonged flooding or draw-down in any of the wetland habitats would likely shift the balance from one species to another, depending on their tolerance of the prevailing conditions and their ability to compete with other species with similar tolerances (Harper and Mavuti, 1996).

An important characteristic of the seasonal wetland habitat is the ability of the grasses to respond quickly to rainfall (Swift *et al*., 1996). From the NDVI analyses, these habitats tended to increase in greenness even when local rainfall was low and the surrounding vegetation did not respond. Seasonally flooded grasslands in semi-arid and arid savannas are the main source of fodder for livestock around Lake Baringo, Kenya (Little, 1996), and for both livestock and wildlife in Ewaso Narok wetland, Kenya (Thenya, 2001). These habitats, like the Amboseli wetlands, largely support the large mammal populations, especially species such as Thomson's gazelles, sheep and goats that are not capable of entering deeper waters (Howard-Williams and Thompson, 1985), providing much needed dry-season fodder. Over-grazing of these grasslands does, however, tend to favour the establishment of unpalatable, grazing-resistant grasses (Hughes, 1996). The large area of seasonal wetland in Amboseli is critical for dry-season grazing as was also shown by the sustained grazing damage seen in the permanent plots.

In the 1970's, the wetlands of Amboseli were reported as having *C. papyrus* and *C. immensus* as the dominant macrophytes (Western and Sindiyo, 1972). However, in the 2002 image the former species was present only in the open water habitat that covered 47 times less area than the seasonal and shallow wetland habitat and was only seen in Enkongo Narok. *Cyperus immensus* dominated deep water habitat covered 6 times less area than the seasonal and shallow wetlands, although *C. immensus* was also dominant in the shallow water wetlands. The open water habitat in the park appears to have developed between 1976 and 1987, which corresponds to the period when elephants were counted in the permanent wetland habitats in both the wet and dry seasons. Whether or not the altered use of these habitats by elephants has caused the formation of the open water habitat is not definite from the data presented here, but there seems to be a strong coincidence between the two events.

Historically, elephants have removed coarser forage that they are more capable of feeding on than other herbivores, as the dry season progressed. This opened up habitats for medium-sized, followed by small herbivores (Western and Lindsay, 1984; Andere, 1981). Wetland plants, in particular the sedges, are generally very fibrous (Howard-Williams and Gaudet, 1985) and in Amboseli the protein content of wetland vegetation was lower than vegetation in all the other habitat types in both the wet and dry seasons (Western and Lindsay, 1984). Hence, elephants would remove this vegetation in the dry season, allowing other herbivores to take advantage of the more nutritious, new growth in the wetlands. In the wet season, the vegetation would have a chance to re-establish itself either through the seed bank in periods of draw-down or vegetative propagation in periods of flooding (van der Valk, 1981). With increased reliance by elephants on these wetland habitats year-round, however, the vegetation may not have time to recover. This may be responsible for the loss of *C. papyrus* dominated stands from the 1970's and the dominance of floating mats of short grasses and sedges, including *C. immensus*, observed now.

There has been a reduction in bird diversity in the park and a study is in preparation that compares the diversity between 1974 and 2002 (Dr. D. Western, *pers. comm.*). The loss of woodlands resulting from elephant compression in the park is important for the loss of bird diversity (Western and Maitumo, 2004). However, large sedge communities provide nesting habitat for various terrestrial bird species, and open water areas provide refuge and feeding areas for waterfowl (Howard-Williams and Thompson, 1985). These two habitats are poorly represented in the classification map in this study. If elephants are partly responsible for the alteration in this habitat, they are also responsible for the reduction in nesting habitat and resulting bird diversity within the wetlands. Continued use of the permanent wetland habitats by elephants may also have an impact on the seed banks in these habitats. Evidence from a coastal wetland on Lake Erie suggests that species richness can be decreased in otherwise species-rich communities as a result of sediment disturbance (Barry *et al.*, 1998). Whether the current wetland habitats that are dominated by a few species are the result of this type of mechanism is not clear. However, it is not unlikely that sediment disturbance might have an impact on species richness and should be studied.

In Chapter 3 of this thesis, the results of a 3-year study on the impacts of elephants on the vegetation biomass and height, and species composition of two reference wetlands in the park are presented. In Chapter 4, I present the results of a short-term study on grazing impacts on wetland vegetation at a small scale. These should provide more information upon which the impacts of elephants and grazing on wetland vegetation in Amboseli National Park can be determined.

The current heterogeneity of wetland habitats based on their species compositions and water levels that appears in the classification of the wetlands of Amboseli National Park, however, still has the capacity to provide valuable habitat for invertebrates and vertebrates. The ecotonal regions between the shallow and deep water habitats provide unique conditions for growth of various fauna that would otherwise not occur in homogenous wetland habitats (Chapman *et al.,* 2001). These fauna in turn are used as food by birds and fish. It is, therefore, beneficial to the park that these habitats occur over extensive areas.

With the threat of global warming and the reported decline in rainfall by 36% since 1922 in the forests of Mt. Kilimanjaro (Hemp, 2005) that feed the springs of the Amboseli National Park wetlands, there is concern that the wetlands will dry up eventually. The current status of these wetlands does not indicate that this is a happening, most likely due to offsetting effects of the loss of woodlands to the south of the wetlands. However, the current vegetation structure, although diverse enough to provide good habitat for various aquatic invertebrates and vertebrates, is no longer good habitat for birds. There is, therefore, both good and bad news for the wetlands and animal species of the Amboseli National Park. In ecosystems there are both top-down and bottom-up forces that affect populations and community structure (Hunter and Price, 1992). Hence, the conservation of these wetlands for the benefit of most if not all the animal species might require some control of elephant use of the wetlands. At the same time, however, the effects of hydrology on the vegetation, and *vice versa*, needs to be studied and the impacts of changes in vegetation composition and stand structure on the wildlife of the park needs to be better understood before well-informed conservation strategies are developed.

Chapter 3

Seasons and Elephants: Impacts on the Wetlands of the Amboseli National Park, Southern Kenya

3.1 Introduction

The ecosystem and mammalian populations, in particular the elephants, of Amboseli National Park have been studied for many years (Western, 1973; Thresher, 1981; Behrensmeyer, 1993; Moss, 2001; Western and Maitumo, 2004). However, little is known about the seasonal dynamics of the wetlands of the park, in spite of their importance to the wildlife and in turn to Kenya's primary foreign-income generator, tourism (Western, 1994). To date, there has been one hydrological study of the wetlands conducted in the late 1980's (Irungu, 1992), and a more recent survey of land-use around the wetlands and its impacts on water availability for wildlife and livestock both inside and outside the park by Worden *et al*. (2003).

The ecosystem around the wetlands has been changing since the 1960's. As already mentioned in the previous chapter, a large tract of *Acacia xanthophloea* woodland that bordered the southern edges of the wetlands has been completely replaced by xeric shrub habitat (Western and Maitumo, 2004). This may have had an impact on the extents of the wetlands as shown in the results of the previous chapter. The decline in these woodlands has been related to the change in wet-season migration of the elephants from 1977 onwards, as well as the almost doubling of their population since the 1960's (Moss, 2001; Western and Maitumo, 2004).

Elephants are a keystone species in many savanna ecosystems of Africa and, as such, have the capacity to cause large alterations in the ecosystem if their populations change dramatically or if their movements are restricted (Laws, 1970). The change in the migratory patterns of the Amboseli elephant population has meant that more elephants have been using the permanent wetland habitat during both wet and dry seasons since 1975 (see Figure 2.3 in Chapter 2). This change in use of the wetland habitat from dry-season to year-round has likely put considerable pressure on wetland structure and species composition, which has been observed but not formally documented (Western, 1997). This lack of data on the impacts of elephants on wetland vegetation is not unique to the Amboseli wetlands. In the Chobe National Park, elephants were linked to the reduction in riverine woodlands along the Chobe River (Mosugelo *et al.,* 2002). However, there was no mention of the impacts of elephants on fringing wetland vegetation.

The primary objectives of this study, therefore, were to examine the seasonal dynamics of wetlands in the Amboseli National Park and to determine what impacts elephants have on wetland vegetation in terms of species composition, biomass and height, as well as on use by other animals. In order to do this, a reference (treatment) wetland was enclosed in an elephant-proof electric fence that did not exclude smaller herbivores and a second reference wetland, located 325 m away from the first, was used as the control and left untouched. Vegetation and water parameter measurements were taken for the control wetland in order to determine the seasonal changes in production and species composition of the vegetation, as well as the water levels in the edge and permanent wetland (centre) habitats. Conductivity of the water was also measured in order to determine the changes in water quality from season to season. Dung counts were used to quantify seasonal use of the wetland by herbivores. Vegetation production and species composition, as well as frequency of use by herbivores in the control wetland were then compared to the treatment wetland to study the impacts of elephants. This study is not replicated because of its scale. However, it is expected that vegetation will change with season, increasing in biomass and height during the wet season and decreasing in the dry season, and that the removal of elephants will have a positive effect on both biomass and height of the vegetation. Hence, results that support these expectations can be assumed to not be the result of chance.

3.2 Study Site

The wetlands that are of particular interest in this study are located in the southwestern corner of the park (Figure 3.1a). They lie just north of the Ilmerishari hills, hence are commonly known as the Ilmerishari wetlands. The Ilmerishari wetlands appear to receive water along their southeastern boundaries. From the results presented in Chapter 2, it appears that the water flow in the larger wetlands is in a southeast to northwest direction.

Surrounding the control wetland to the north and east is a tall, dense, *Sporobolus consimilis* Fresen. grass community, whereas to the west there is a community of short grasses, tall *S. consimilis* and scrub. To the south of the control there is a mixed scrubland community of *Suaeda monoica*, *Azima tetracantha*, and *Salvadora persica*. The treatment wetland has a dense scrub community around it that forms almost a continuous boundary between it and the control wetland to the west. On the eastern edge of the enclosure, there is a discontinuous layer of grass and herbaceous cover with scattered scrub, mainly a mixture of *S. monoica* and *S. persica*. The area around the two Ilmerishari wetlands used to be dense *A. xanthophloea* woodland habitat in the early 1970s (Western and Sindiyo, 1972).

3.3 Materials and Methods

3.3.1 Enclosure set-up and Sampling

The 3 transects in the control wetland were established as shown in Figure 3.1b. Each transect was sampled at three points (zones). Zone 1 was located on the southeastern end of each transect, zone 2 was in the middle of each transect, and zone 3 was at the northwest end (Figure 3.1b). Transect 3 was also sampled at a fourth zone that was located in the centre of the protrusion (Figure 3.1b).

The electric fence that enclosed the treatment wetland was erected in August of 2001. The fence consisted of 3-m tall treated-wood posts sunk into the ground 1 m and linked to one another by electric wire (Figure 3.2a). At each post a metal rod (outrigger) that was connected to the electric fence wires protruded 0.5 m outward of the fence in order to deter elephants from kicking down the posts (Figure 3.2a). At the entrances to the enclosure, wire droppers that were also connected to the main electric wires were used to prevent elephants from walking into the wetlands through these openings (Figure 3.2b). The fence was designed by Dr. D. Western and similar enclosures have been built around the Namelok wetland to the east of the park (see Chapter 5).

The initial plan for the enclosure was to study effects on vegetation on the edges of the wetland, but sampling was soon extended to include the centre of the wetland when I began my study. Hence, formal and complete observations of the entire wetland were not started until October 2002. The wetland was traversed by 5 transects placed approximately 50 m apart, as shown in Figure 3.1b. Each transect was sampled at three zones similar to what was done for the control wetland. One zone was on the eastern edge (zone 1), one in the middle (zone 2), and one on the western edge (zone 3). For the comparisons between the control and treatment wetland vegetation, transect 1 of the treatment wetland, which was outside the fence, was added to the control wetland transects to balance the data matrix.

Measurements of water depth and conductivity, as well as dung counts, were conducted between October 2002 and December 2003. Vegetation parameters were sampled from October 2002 until July 2005. Conductivity measurements were stopped because the probe was no longer available, and, hence, water depth measurements were also, inadvertently, stopped. Dung counts were stopped when the vegetation around the wetland had increased in density to the point where chance intimate encounters with buffalo became a significant threat.

Wet and dry seasons were determined using the same criteria outlined in Chapter 2, using greenness and biomass data from 3 permanent bushland plots located along the northern boundary of the park. Wet seasons were identified as periods when the percent greenness of the bushland plots was above 25%. Dry seasons and droughts were identified as periods when the percent biomass deviation from the long-term mean biomass was between -50 and 0% and below -50%, respectively.

3.3.2 Vegetation and Water Assessment

Above-ground biomass (referred to as biomass from here on) was estimated using the canopy-intercept method as described in McNaughton (1979a) and Western and Gichohi (1993a). This method is non-invasive and easily repeatable (McNaughton, 1979a). A one-meter long bar with ten evenly spaced holes drilled into it was placed on an upright frame (Figure 3.2c). Five pins were randomly placed into the ten holes so that they contacted the vegetation at a 54° angle, which was found to minimize error and maximize information (Western and Gichohi, 1993a). At each zone on each transect, hits per species on 4 placements of the slanted pin-frame were recorded. The mean hits per pin for each species was then used to calculate biomass using calibration equations previously developed for the frame (see Appendix A for details on the calibration). Five height measurements, from sediment to tip of the top leaf, of each species were taken per frame.

At each zone on each transect, three samples of water were also collected in three 50-ml plastic bottles for analyses using a combination pH and conductivity meter. Though the meter was capable of in situ measurements, it was not feasible to carry it along with the other instruments during sampling as the terrain was very unstable as one moved into the wetland. Hence, the measurements were made at the edge of the wetland on water samples collected from each zone.

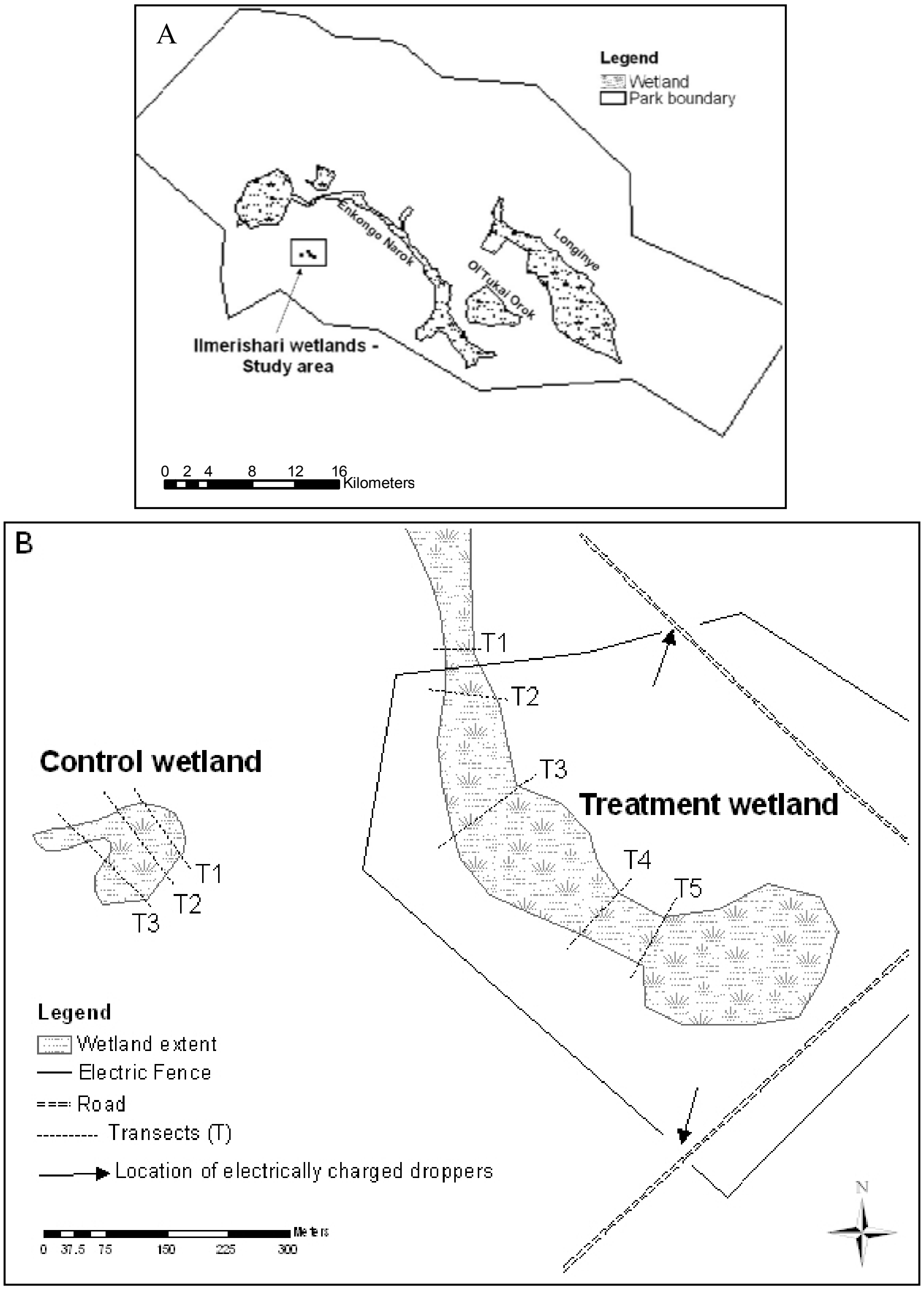

Figure 3.1. The wetlands of Amboseli National Park, southern Kenya (A), and (B) a close up view of the Ilmerishari wetlands (02°39'S, 37°13'E) showing the location of transects and enclosure.

I attempted to measure the depth to the top of the water table using either copper rods or wooden stakes. In the case of the former, the rods were stolen and in the latter case the stakes were not easily removed from the ground and ended up breaking. Depth of the water at each zone was, therefore, measured using a meter rule in order to determine the "wetness" of the zone at time of sampling.

3.3.3 Dung Counts

Dung counts were conducted along a total of twelve transects placed in four locations. The first set of 3 transects crossed the control wetland (control) from south to north, the second crossed the treatment wetland (Inside Enclosure) from east to west, the third ran from the western fence of the enclosure outward and the fourth ran from the eastern fence outward. Each transect was 100-m long and sampling was conducted within a 10-m strip (5m on each side of the transect). Dung piles were counted along each transect and assigned to their respective species. They were then destroyed by crushing them in order to prevent re-counting during the next sampling.

The data for each species counted along transects in one location were summed to give the total number of dung piles per species per location per date. The dates that fell within a dry or drought month were then summed, as were the dates that fell within wet months. The separation of the counts allowed the wet and dry season use-patterns for each species to be compared between the wetlands and the surrounding savanna. In order to express use-patterns in terms of the representation of each species per location, the relative abundance of dung of each species was calculated for each location. The dung counts were not intended to estimate the population of the animals.

Chi-square analyses were used to compare the wet and dry season dung counts for each species in the control versus the treatment wetland. This was used to determine if any of the animals preferred one wetland over the other during the period of study. The analyses were conducted manually, using 1 degree of freedom (df) and a chi-square table to determine significance at a Type 1 error rate (*P*) of 0.05.

3.3.4 Statistical Analyses

All the data, except dung counts, were analysed using Repeated Measures ANOVA (RM-ANOVA) in order to test the effects of time on the various parameters separately. In all the analyses for the control wetland, zone and transect were used as between-subjects factors (main effects) and frames or water samples were used as the replications. For the comparison of the wetlands, the location, that is, control or treatment wetland, was used as the main effect and transects were the replicates.

The Greenhouse-Geisser adjusted *P* value (G-G adj. *P*) rather than the unadjusted *P* was used to test the within-subjects effects (interaction between the main effects and time) in the RM-ANOVA analyses in order to correct for temporal correlation between the repeated measures. All hypotheses were tested at a Type I error rate of 0.05 unless mentioned otherwise. Residuals for each ANOVA were tested for homogeneity of variance and normal distribution. When needed, an appropriate transformation was derived using Taylor's Power Law (Legendre and Legendre, 1998). All analyses were conducted in SYSTAT 11 (Systat Software Inc., 2004).

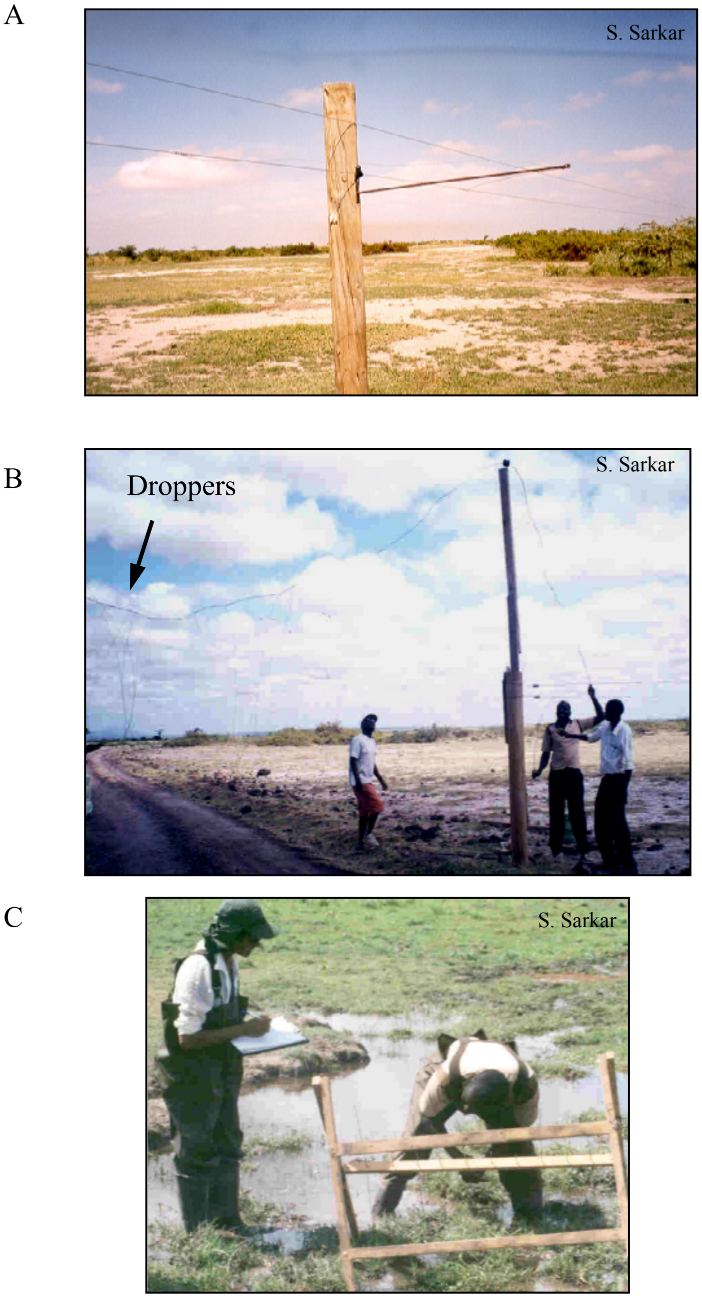

Figure 3.2. (A) The electric fencing used to enclose the treatment wetland at Ilmerishari in the Amboseli National Park, southern Kenya and the electrically charged rods (outriggers), which discourage elephants from knocking down the fence posts, (B) the electrically charged droppers that prevent elephants from entering the enclosure through the roadway, and (C) the slanted pin-frame used to estimate above-ground biomass of vegetation.

Species composition data were subjected to Correspondence Analysis (CA) to visualize any patterns in species composition over time since this method was most suited to the data. The data contained a large number of zeros and since no corresponding environmental data matrix was collected, CA was the best option for the desired analysis (Legendre and Legendre, 1998). Separate analyses were conducted for the control and treatment wetlands. Biplot scaling was applied to the inter-sample distances and rare species were not down-weighted. A sample was the number of hits on the pin frame for a species per sampling date. Analyses were conducted in CANOCO for Windows, version 4.5 (ter Braak and Smilauer, 2002). Separate Spearman's rank correlation analyses between sample scores for axis 1 and axis 2, and time were conducted in SYSTAT 11 in order to determine if there was a directional change in species composition over time.

3.4 Results

3.4.1 Seasonal Trends in the Control Wetland

Measurements of depth to the water-table were not successful because the copper rods were stolen and the wooden stakes, used in the subsequent year, were not easily extracted. Only one rod from the control was retrieved at the beginning of January 2003, before the onset of the rains, and one stake from the treatment wetland was extracted in mid-January 2004 (Figure 3.3). The top of the water table was measured at approximately 0.3 m and 0.5 m below the surface at the southeastern edge of the control and the treatment wetland, respectively.

Except for 2002-2003, where sufficient rainfall fell in the expected months, the short-rains of 2004 and 2005 were insufficient and caused drought conditions in the following dry seasons (Figure 3.3). The 2004-2005 drought, however, latest longer (Figure 3.3). This is likely because the 2004 long wet season (from March to May) did not receive much rain, which meant that the small amount of rain received in the short-wet season of 2004 (November to December) was insufficient for the vegetation that had already experienced 4 months without rainfall (Figure 3.3).

Depth of water in the wetland was often not measured due to time constraint, so the data were too few for an RM-ANOVA to be conducted. However, some basic observations can be made about the wetland between November 2002 and January 2003, and between December 2003 and January 2004.

At the start of the study, transect 3 was the wettest, followed by transect 2 and transect 1 (Figure 3.4a). However, in February 2003, when average rainfall had fallen below 30 mm, the depth of water in all three transects decreased sharply Figure 3.4a). The next sampling was conducted in December, 2003, when average rainfall was 30 mm and the drought was coming to an end. Interestingly, the depth along transect 2 and 3 had increased, but transect 1 had decreased further (Figure 3.4a). No water was seen along transect 1 in January 2004 in spite of the rains (Figure 3.4a), which might indicate the role of evaporation during this time.

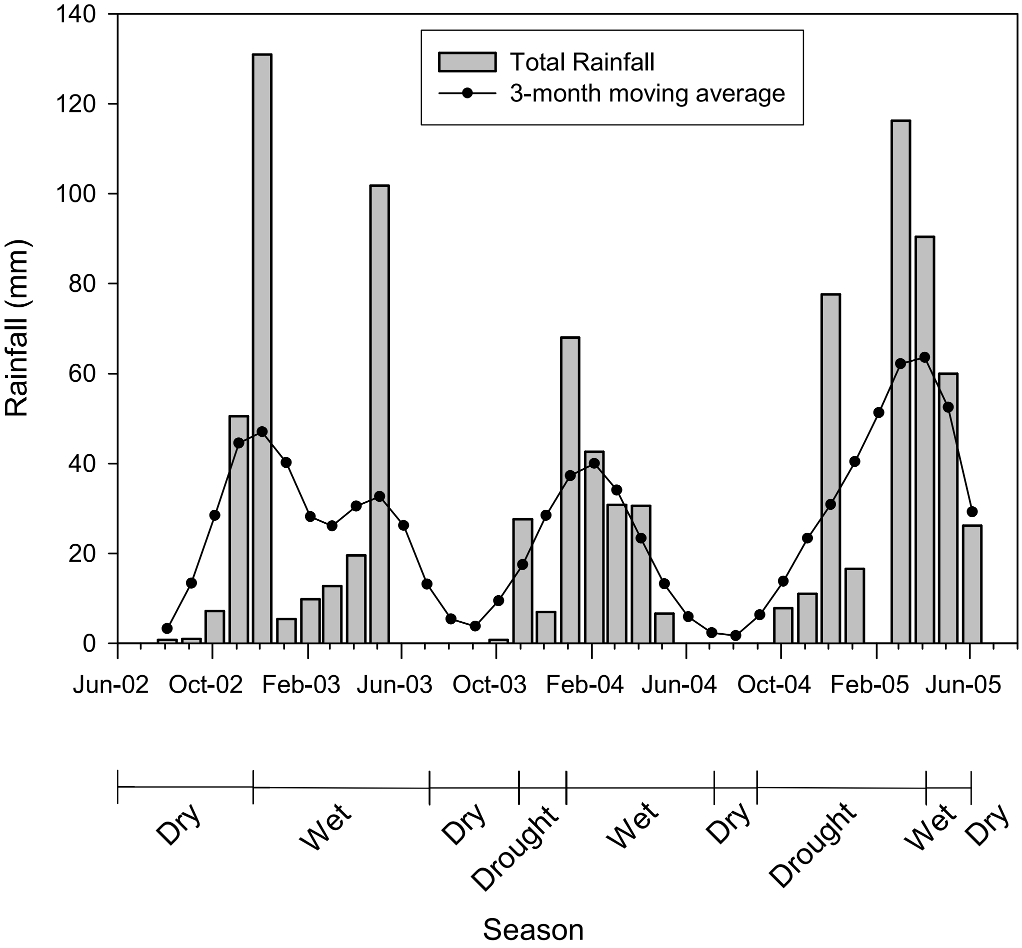

Figure 3.3. Monthly rainfall (bars) and the 3-month moving average rainfall (line) for the Amboseli National Park, southern Kenya, collected at the Ol' Tukai Weather Station (02°43'S, 37°23'E). Seasons, as determined using greenness and biomass deviations in the bushland plots to the north of the park have been included below the plot for comparison.

The data for the depth of water at each zone indicated that zone 1, which is the southeastern edge of the control wetland, was the driest at each sampling date (Figure 3.4b). The depth of water in zone 3, which was at the northwest edge of the control wetland decreased over the sampling period and can be considered as being intermediate between zone 1 and zones 2 and 4 primarily because of the presence of a permanent pool of water at transect 3 (Figure 3.4b). The pool had a mean depth of 44 (± 3.9) cm over the time sampling was conducted. If the data for this pool are removed from the calculation for water depth at zone 3, then zone 1 had more water than zone 3 towards the end of the sampling period (data not shown). Zone 2, which was at the centre of each transect between zone 1 and 3, was the wettest of the zones except at the beginning of the study (Figure 3.4b). Zone 4, which was at the northwest end of transect 3 that traversed the protrusion of the control wetland was not significantly different from zone 3 in the first 3 sampling dates (Figure 3.4b). However, between December 2003 and January 2004 zone 4 had significantly more water than zone 3. Zone 3 data included the measurements from the open pool, which might explain the similarity between zones 3 and 4.

Taken together, transect and zone data indicate that the wetland, as expected, was always permanently inundated in the centre, whereas the southeast and northeast edges were inundated only during times of sufficient rainfall and most likely low evaporation rates. Hence, the wetland was wettest from the centre towards the northwest.

Conductivity in the wetland ranged from below 100 to above 1300 $\mu S\ cm^{-1}$, but on average it was around 700 $\mu S\ cm^{-1}$ between October 2002 and May 2003, and in December 2003, the dates when sampling occurred (Figure 3.5a). There was a significant interaction between time and transect ($F_{12,\ 90} = 7.96$, Greenhouse-Geisser (G-G) adjusted $P < 0.001$), and time and zone ($F_{18,\ 90} = 7.98$, G-G adjusted $P < 0.001$) for the conductivity data.

Conductivity along transect 1 was the highest, with an average over time of 1057 $\mu S\ cm^{-1}$. However, transect 1 was only significantly different from transects 2 and 3 in November and December 2002 and March 2003 (Figure 3.5a). At the beginning of the study and in May and December 2003, transect 1 and 2 had similar mean conductivity (Figure 3.5a). Transect 2 had an average conductivity of 780 $\mu S\ cm^{-1}$ over time and the conductivity along this transect changed the most in November 2002. Conductivity in transect 2 was not significantly different from transect 3 in December 2002 and March 2003 (Figure 3.5a). Transect 3 was the freshest of the three transects with an average value over time of 453 $\mu S\ cm^{-1}$ that did not change a lot over time (Figure 3.5a).

Mean conductivity over time in zone 1 was the highest (929 $\mu S\ cm^{-1}$) followed by zone 4 (855 $\mu S\ cm^{-1}$), whereas zones 2 (614 $\mu S\ cm^{-1}$) and 3 (601 $\mu S\ cm^{-1}$) had similar mean conductivity values. Mean conductivity in zone 1 was significantly higher than that in the other zones only at the start of the study (Figure 3.5b). Conductivity in all zones increased in November 2002, albeit zone 1 changed the least. At the start of the wet season, all zones showed a decrease in conductivity with the advent of rain. However, once again zone 1 saw a smaller reduction in mean conductivity compared to the other zones (Figure 3.5b). Following the December 2002 sampling, each successive sample showed less change in conductivity in each zone, and conductivity remained below 1000 $\mu S\ cm^{-1}$ even in December 2003 (Figure 3.5b).

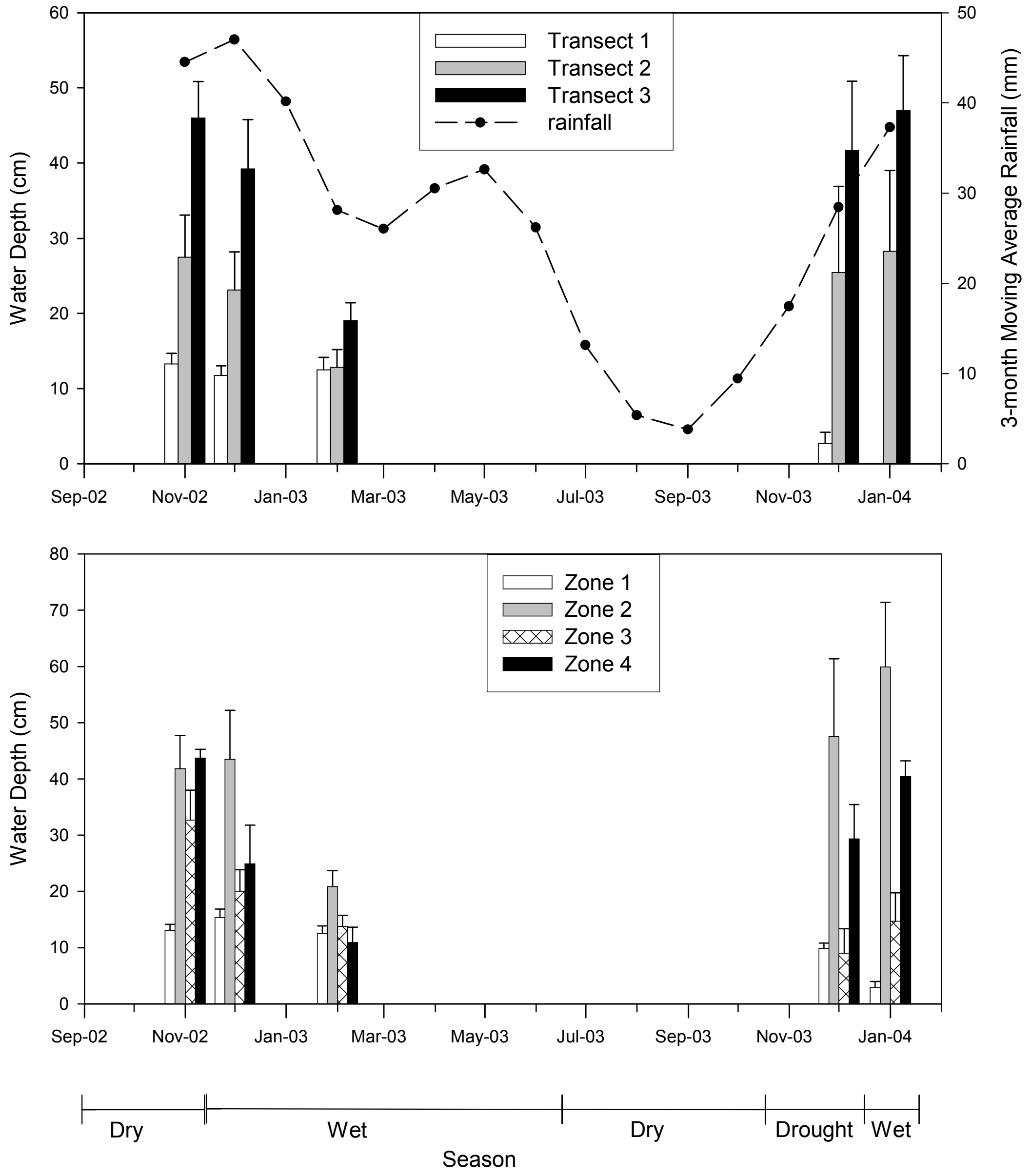

Figure 3.4. Depth of water measured using a meter rule in the control wetland at Ilmerishari, Amboseli National Park, southern Kenya. (A) Data averaged for each transect (bar) along which sampling was conducted, with the 3-month moving average rainfall also shown (line) and (B) data averaged for each zone (point of sampling) along the three transects. The error bars represent standard errors. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park.

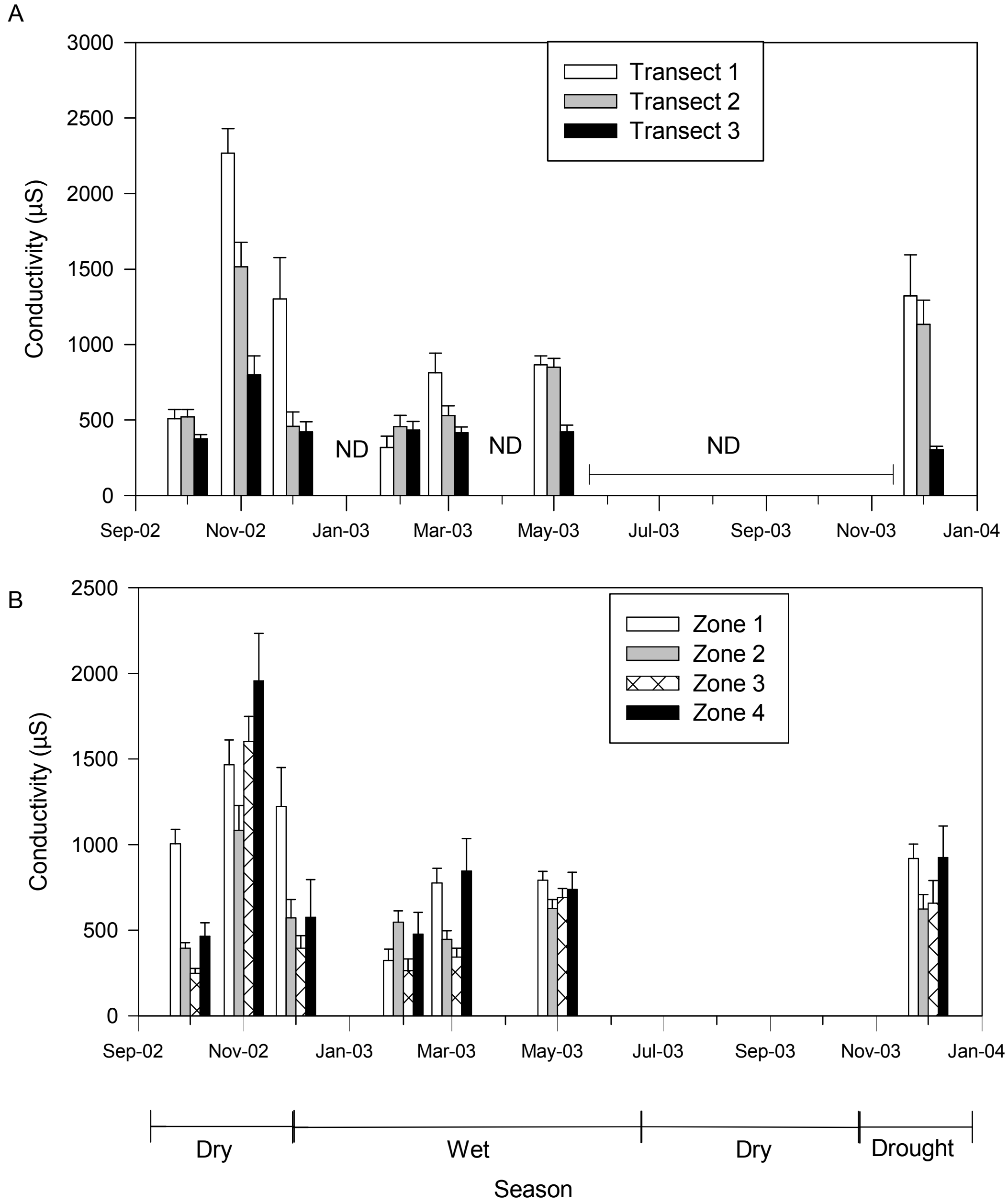

Figure 3.5. Conductivity for (A) each transect, and (B) each zone (sampling point) along transects of the control wetland at Ilmerishari, Amboseli National Park, southern Kenya. ND – no data was collected during these months. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park. Error bars indicate the standard error of the mean calculated using the mean standard error from an RM-ANOVA.

Total and green biomass did not vary with time along the three transects, but there were significant differences among transects (total biomass: $F_{2, 34} = 3.56$, $P = 0.04$; green biomass: $F_{2, 34} = 4.25$, $P = 0.02$). However, there was a significant interaction between time and transect for total biomass ($F_{42, 476} = 1.83$, G-G adjusted $P = 0.03$), and green biomass ($F_{42, 476} = 1.97$, G-G adjusted $P = 0.01$). Since there was little difference in the results for total and green biomass (Figure 3.6) I will focus on green biomass since herbivores tend to select for green vegetation (McNaughton, 1985).

Green biomass along transect 2 (51 g DW m^{-2} ± 5.9) was significantly higher than along transect 1 (31 g DW m^{-2} ± 4.0) and 3 (33 g DW m^{-2} ± 3.3), which were not significantly different. Green biomass, however, was not consistently higher in any one zone over time (Figure 3.6b), although zone 2 did have the highest biomass over most of the study period, followed by zone 4. Zone 4, however, was not significantly different from zones 1 and 3 during most months of sampling (Figure 3.6b). Zones 2 and 4 had especially higher biomass in the dry and drought months of 2002, 2003 and 2004. The data for January 2005 shows that biomass in zones 2 and 4 decreased to the level of zones 1 and 3 and, interestingly, all the zones except zone 4 were able to increase biomass after the rains had begun (Figure 3.6b). Zone 2 recovered the fastest compared to zones 1 and 3. Zones 1 and 3 were able to catch up to the biomass of zone 4 during the wet seasons, and in the May 2004 the biomass in zones 1 and 3 were not significantly different from zone 2 either (Figure 3.6b).

Height of the vegetation per transect did not change significantly over time ($F_{26, 442} = 1.42$, G-G adjusted $P = 0.17$). However, there was a significant interaction between time and zone ($F_{39, 442} = 2.50$, G-G adjusted $P < 0.01$). The vegetation in zone 2 was the tallest throughout the experiment, except in November 2002 (Figure 3.7). In December 2002, March 2003, May 2004 and April 2005, all representing portions of the rainy season, heights in zone 2 were similar to heights in zone 4. Towards the end of the study, in April 2005, zone 4 showed a sharp increase in height, but height decreased again in July, which is different from the results for biomass in zone 4 during this time (Figure 3.6b; Figure 3.7). Zones 1 and 3 that represent the edges of the wetland had shorter vegetation that showed some increase in height during the wet seasons, but during the dry seasons, height was never more than 5 cm (Figure 3.7).

The species composition of the control wetland did not change in any one direction over time. However, there were some changes within zones 1, 2 and 3. The data from the correspondence analysis was, therefore, split into zones and within each zone the sample scores for each transect were used to construct the biplots presented in Figure 3.8.

Zones 1 and 3, which covered the southeastern and northwestern edges of the wetland, respectively, both showed an increase in *Cynodon dactylon* over time. In zone 1 (Figure 3.8a), the change occurred most strongly on transect 3 (Spearman's correlation coefficient (r_s) for axis 1 sample scores and time = - 0.47; r_s for axis 2 sample scores and time = 0.42). In zone 3 (Figure 3.8c), the increase in *C. dactylon* was most evident on transect 2 (r_s for axis 2 sample scores and time = 0.62). Zone 1 was dominated by *Digitaria scalarum* (total biomass over entire study period = 663 g DW m^{-2}), followed by *C. dactylon* (457 g DW m^{-2}), whereas the reverse was true for zone 3 where *C. dactylon* had twice the biomass (570 g DW m^{-2}) of *D. scalarum* (275 g DW m^{-2}). The biplot for Zone 3 also shows floating *Azolla* spp. and *Pistia stratiotes* L. (Figure 3.8c). These species were only found in the open pool of water along transect 3. As a result of these species, zone 3 had more species overall than zone 1.

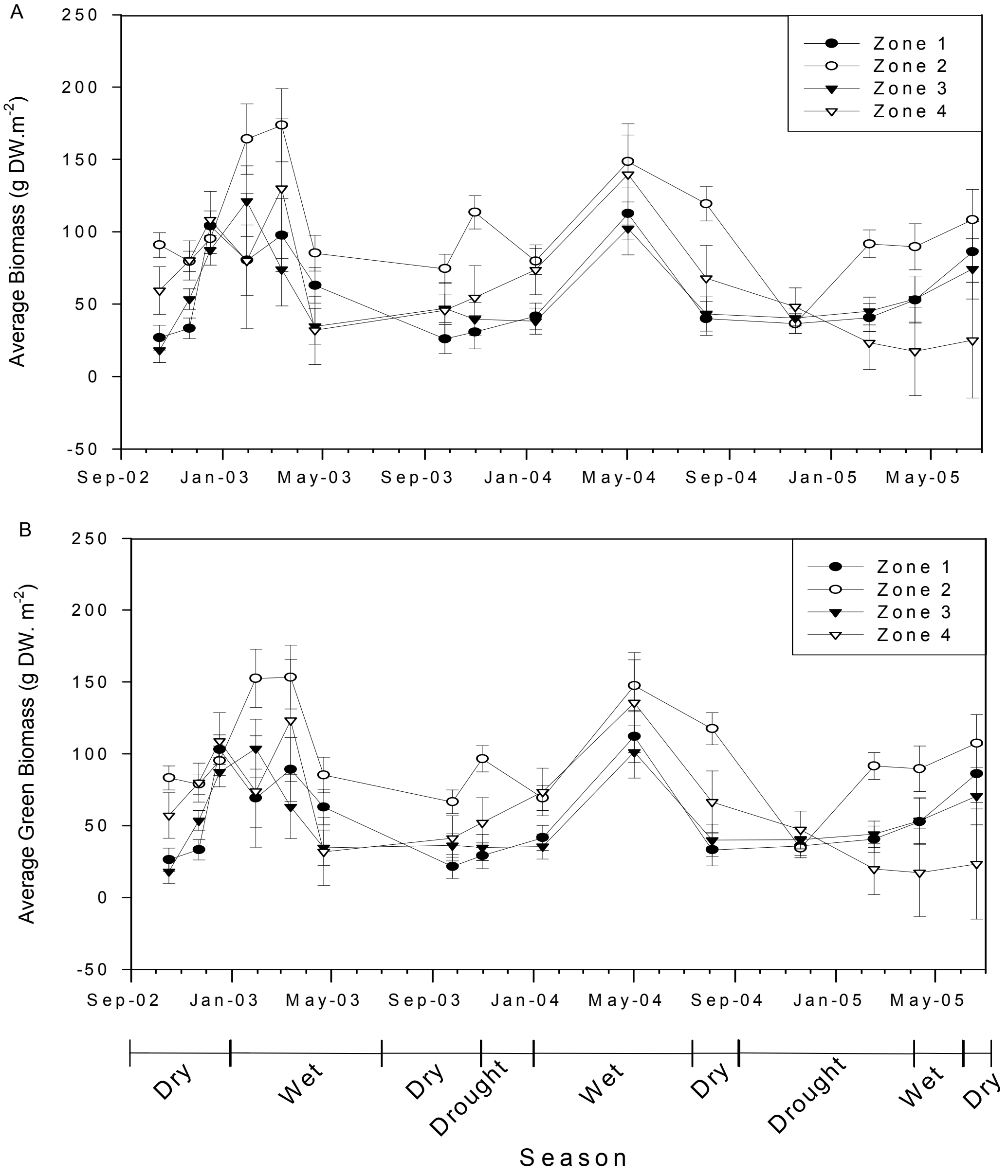

Figure 3.6. Total (A) and green (B) plant biomass for each zone (sampling point) along transects in the control wetland at Ilmerishari, Amboseli National Park, southern Kenya. Error bars indicate the standard error of the mean calculated using the mean standard error from an RM-ANOVA. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park.

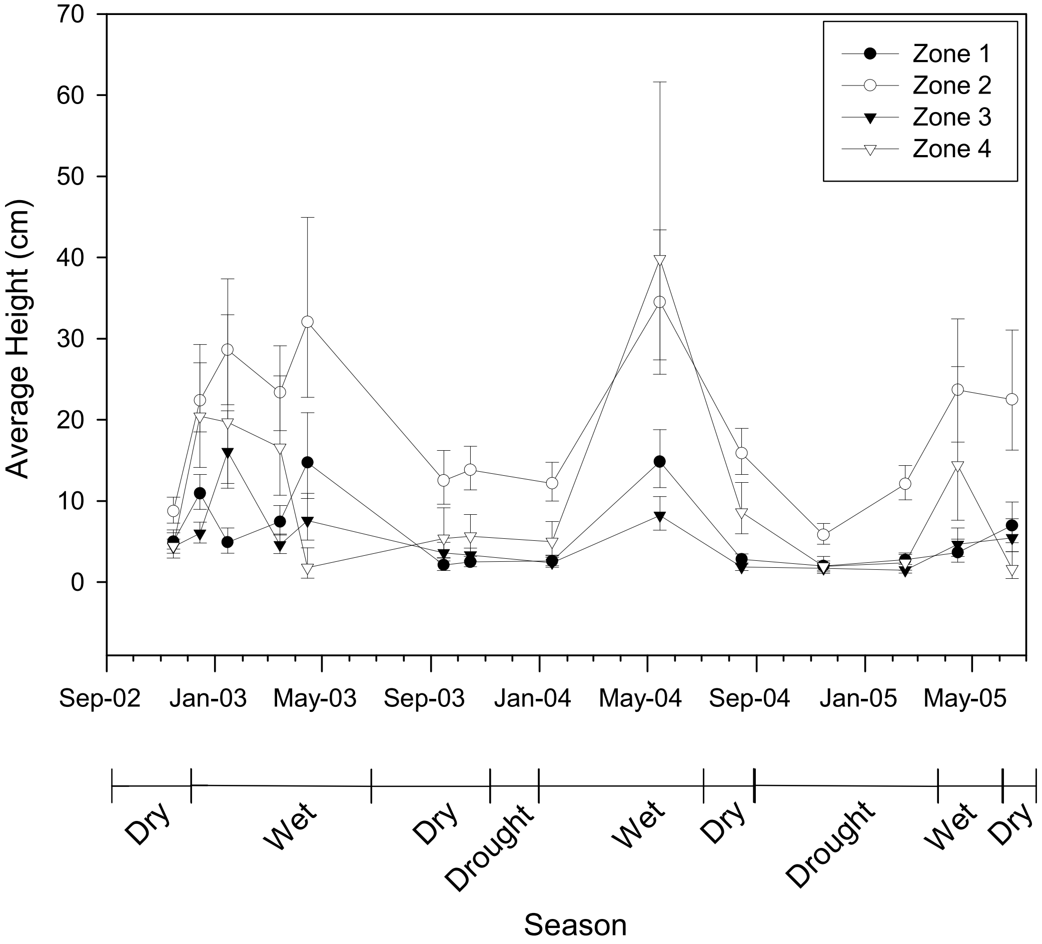

Figure 3.7. Height of vegetation for each zone (sampling point) along transects in the control wetland at Ilmerishari, Amboseli National Park, southern Kenya. Error bars indicate the standard error calculated using the mean standard error from an RM-ANOVA. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park.

Zones 2 and 4 were dominated by *D. scalarum* followed by *C. laevigatus*. However, in zone 2 the difference in total biomass over the study period between these two species was small (532 g DW m^{-2} for *D. scalarum* and 439 g DW m^{-2} for *C. laevigatus*), whereas in zone 4 the biomass of *D. scalarum* (1637 g DW m^{-2}) was almost three times higher than that of *C. laevigatus* (444 g DW m^{-2}). *Cyperus* *immensus* was also present in zone 2 at a biomass almost equal to that of *C. laevigatus*. Zone 4 had more floating macrophyte species, as well as herbaceous species, such as *Hydrocotyle ranunculoides* L.f. and *Ludwigia stolonifera* (Guill. & Perr.) Raven., commonly seen growing on floating vegetation mats. However, zone 2 still had more species overall compared to zone 4. Sample scores of both axes for zone 2 on transect 2 (Figure 3.8b) were highly correlated with time (r_s for axis 1 sample scores and time = -0.88; r_s for axis 2 sample scores and time = 0.93). This indicated the decrease in *D. scalarum* and the increase in *H. ranunculoides* and *L. stolonifera* over the duration of the study. Zone 4, which was only present along transect 3, did not show any directional change in species composition over time (Figure 3.8d).

Overall, it is apparent that the wetland is complex and the changes in biomass of each species over time were uniform neither between nor within zones. However, I collapsed these data into the total biomass for vegetation types over time for the *C. dactylon*/*D. scalarum* – dominated edge (zones 1 and 3) and the *D. scalarum*/*C. laevigatus* – dominated centre (zones 2 and 4) of the wetland in order to get a more general idea of the changes in vegetation.

At the beginning of the study, though grasses had the highest biomass on the edges of the wetland, they were only about twice as abundant as sedges (Figure 3.9a). However, in the first rainy seasons (2002 to 2003) grasses tended to increase in biomass, whereas the sedges did not show this same trend until later. Sedges still had a lower biomass than grasses even after the increase in February 2003. By September 2003, sedges were definitely rare and though at times the biomass matched that of the first sampling period, grasses were definitely becoming more than twice as abundant as sedges (Figure 3.9a). Forbs were not commonly seen along the edge and the biomass of forbs per sampling period remained below 30 g DW m^{-2} (Figure 3.9a).

The presence of herbivores, as represented by the total number of dung piles counted per location, indicated that in the dry season there were more animals present around the wetland habitats than in the surrounding savanna habitat (Table 3.1: see the row for total number of dung piles per location). However, this trend was reversed during the wet season. Furthermore, there were more animals on the east side of the enclosure than on the west side (Table 3.1).

There was four times as much dung found in the dry season (2955 piles) compared to the wet season (672 piles) for the area covered by the study (Table 3.1). There were four times more zebra, wildebeest and cattle dung piles than buffalo and elephant dung piles in the study area during the dry season (Table 3.1: see the column for total number of dung piles per species). However, in the wet season the numbers of dung piles from zebra and wildebeest decreased by 14 and 5 times, respectively, from dry season numbers whereas cattle numbers decreased by 31 times and buffalo numbers decreased by half (Table 3.1). Elephant dung increased a little in comparison. Overall, gazelles and giraffe were poorly represented in both seasons, though they were fewer in the wet than the dry season (Table 3.1).

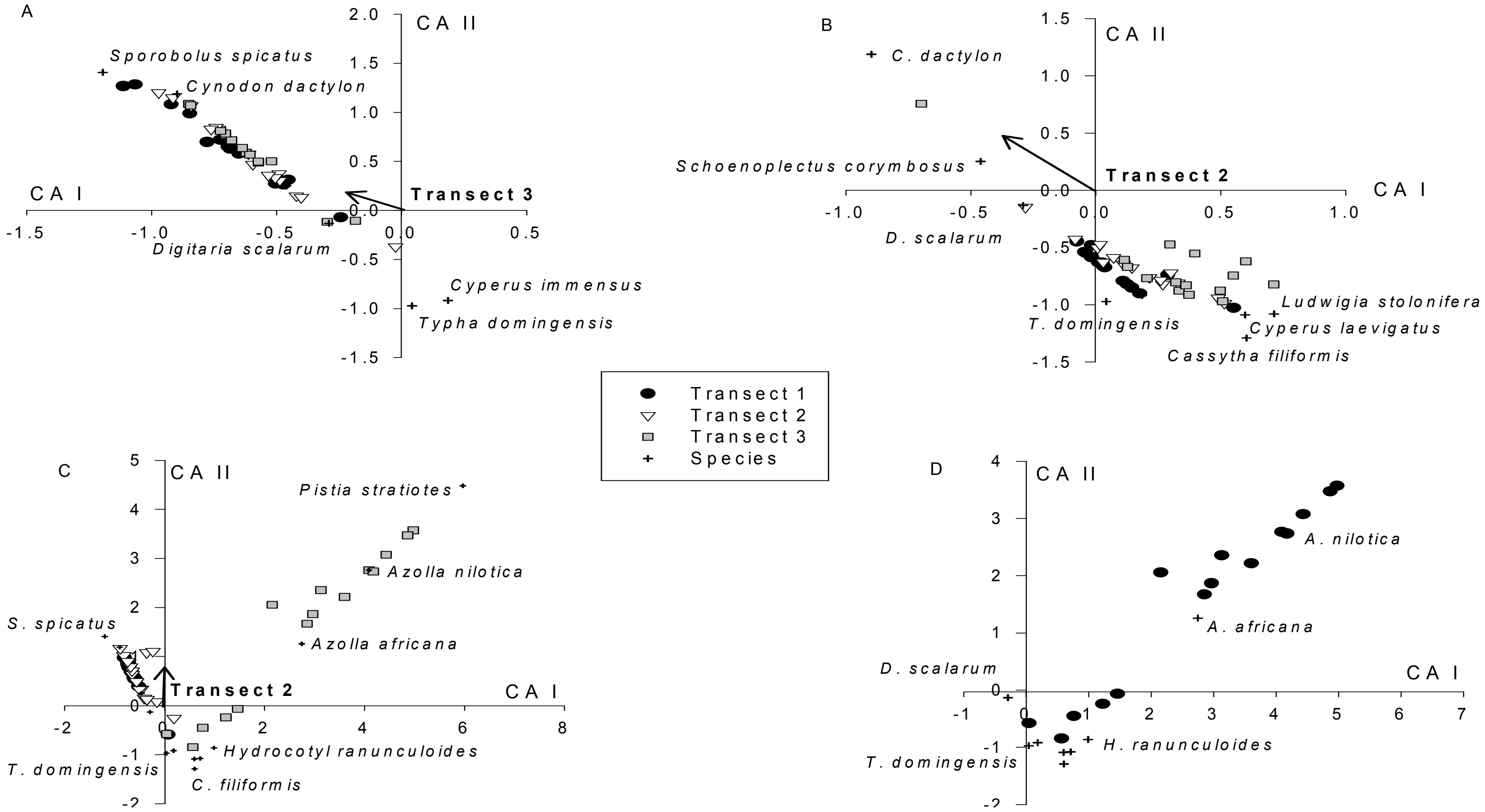

Figure 3.8. Biplots constructed from a single correspondence analysis showing the sample scores for each transect in (A) zone 1, (B) zone 2, (C) zone 3, and (D) zone 4 (only present in transect 3), as well as the species observed at the control wetland in Ilmerishari, Amboseli National Park, southern Kenya. Samples scores represent sampling dates. Arrows show the scaled correlation between the sample scores for each axis and time for the transect indicated in bold. The angle of the arrow indicates the direction of change in species composition along a specific transect over time, and the length of the arrow indicates the amount of correlation between axes scores and time.

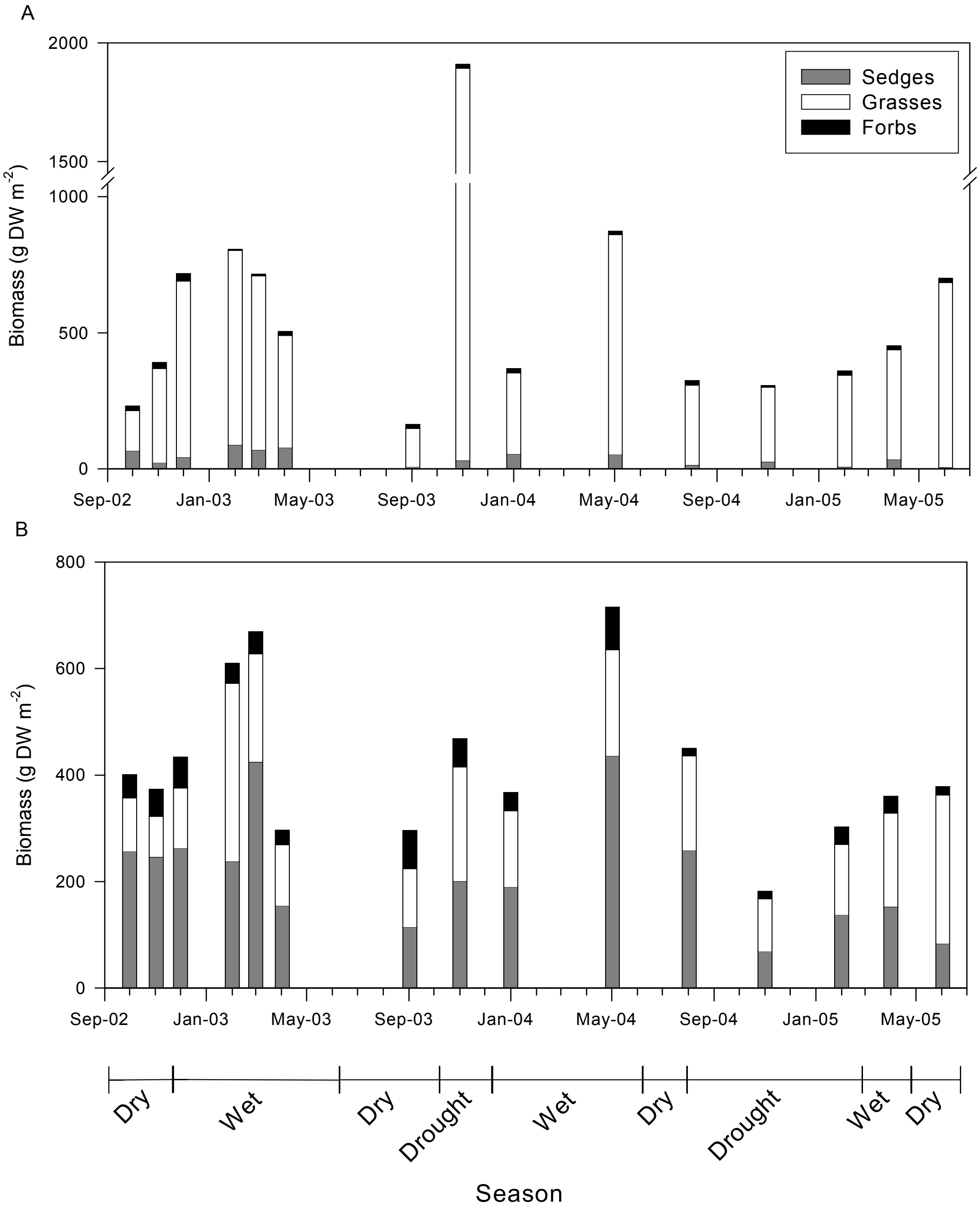

Figure 3.9. Total biomass of each vegetation type (sedges in grey, grasses in clear, and forbs in black) in the (A) edge and (B) centre of the control wetland at Ilmerishari, Amboseli National Park, southern Kenya. Sedges included *Cyperus immensus*, *C. laevigatus*, *Typha domingensis* and *Schoenoplectus corymbosus*. Grasses included *Cynodon dactylon, Digitaria scalarum*, and *Sporobolus spicatus*. Forbs included *Cassytha filiformis*, *Hydrocotyle ranunculoides*, *Ludwigia stolonifera*, *Pistia stratiotes*, *Azolla nilotica* Dcne.; Mett. and *A. Africana* Desv.

In the control wetland, wildebeest, zebra, and cattle dung was most abundant in the dry season, followed by elephant and buffalo dung (Table 3.1). However, in the wet season cattle dung was not present and elephant dung had the highest frequency of occurrence, followed by the occurrence of wildebeest, zebra, and buffalo dung. The gazelles and giraffe were poorly represented in both seasons, but they did appear to use the wetland more in the dry than in the wet season, since frequencies of dung occurrence were higher even though the total number of dung piles was also higher. Hippos went from 0.28% in the dry to 1% representation in the wet season, but in this case the increase was not the result of more hippos being present. Hippos leave evidence of vegetation "marking" rather than dung piles, and only one such marking was counted on 6 out of 8 sampling dates. In the dry season, when the number of dung piles counted in the control decreased to 197 from 1088, the relative occurrence of hippo dung increased. So in this case, in particular, an increase in percent occurrence was not the result of more markings or dung counted. This, however, was not the case for the other species.

3.4.2 Comparison of Control and Treatment wetland

The differences between the wetlands were obvious within one year (Figure 3.10). Other than the change in density of the sedges in the centre of the treatment wetland (Figure 3.10a and b), there was an increase in *A. xanthophloea* seedlings along the edges of the wetland. In comparison, there was little change in the control wetland (Figure 3.10c and d)

When the biomass, both total and green, in the control and treatment wetland were compared in an RM–ANOVA there was a significant time by location (control or treatment wetland) interaction for the edges of the wetlands (Total biomass: $F_{13, 793} = 8.11$, G. G. adjusted $P < 0.001$; Green biomass: $F_{13, 793} = 9.50$, G. G. adjusted $P < 0.001$), as well as for the centre of the wetlands (Total biomass: $F_{13, 390} = 2.66$, G. G. adjusted $P = 0.04$; Green biomass: $F_{13, 390} = 3.39$, G. G. adjusted $P < 0.01$). The interaction of location and time is indicative of a difference in response over time for the two wetlands. Since there was little difference in the results for green and total biomass, I will focus on the results for the former.

Green biomass on the edges of both wetlands peaked during the wet season and decreased during the dry seasons as expected (Figure 3.11a). However, it is interesting that, although a month may be indicated as a drought month by the classification based on vegetation in the bushland plots along the northern periphery of the park, the biomass in the wetlands is able to respond quickly to any small amount of rainfall (Figure 3.3; Figure 3.11a). This further emphasizes the importance of these wetland habitats to the ecosystem.

At the beginning of the study, the biomass on the edges of both wetlands was similar (Figure 3.11a) even though the mean for the treatment wetland was higher than the control. The biomass on the edges of the treatment wetland, however, very quickly became significantly higher than in the control as the wet season started and remained significantly higher even during the dry months throughout the study (Figure 3.11a). Typically, the biomass on the edge of the treatment wetland was about twice as high as in the control, except for May 2004 when the biomass in the control was slightly higher than in other wet seasons and the biomass in the treatment wetland was slightly lower.

Table 3.1. Frequency of dung piles counted (%) per location during the wet and dry seasons. Locations include the area around the Control and treatment (enclosed) wetlands and savanna habitat to the east and west of the Enclosure. Frequency of dung occurrence per species was calculated as the percent ratio between the number of dung piles counted per species per location over the total number of dung piles counted in that location

Seasons and Sampling Dates	Herbivores	Control Wetland	Inside Enclosure	East of Enclosure	West of Enclosure	Total No. of dung piles
Dry	Zebra	31	28	38	33	930
	Wildebeest	30	28	29	21	852
10/16/2002 11/22/2002 9/26/2003 12/12/2003	Cattle	24	30	17	40	745
	Buffalo	2	13	7	3	209
	Elephant	10	0.0	7	3	163
	Grant's Gazelle	1	1	1	0.0	31
	Thomson's Gazelle	1	0.0	0.3	0.0	13
	Hippopotamus	0.3	0.3	0.0	0.0	6
	Giraffe	0.4	0.1	0.0	1	6
	Total No. of dung piles	1088	1033	703	131	2955
Wet	Grant's Gazelle	1	5.	1	0.0	262
	Elephant	65	0.0	35	100	186
	Buffalo	8	55	14	0.0	120
12/18/2002 1/31/2003 3/14/2003 5/14/2003	Giraffe	0.0	0.0	0.0	0.0	67
	Cattle	0.0	0.0	7	0.0	24
	Wildebeest	15	39	32	0.0	11
	Hippopotamus	1	0.0	0.0	0.0	2
	Zebra	11	1	12	0.0	0
	Thomson's Gazelle	0.0	0.0	0.0	0.0	0
	Total No. of dung piles	197	99	370	6	672

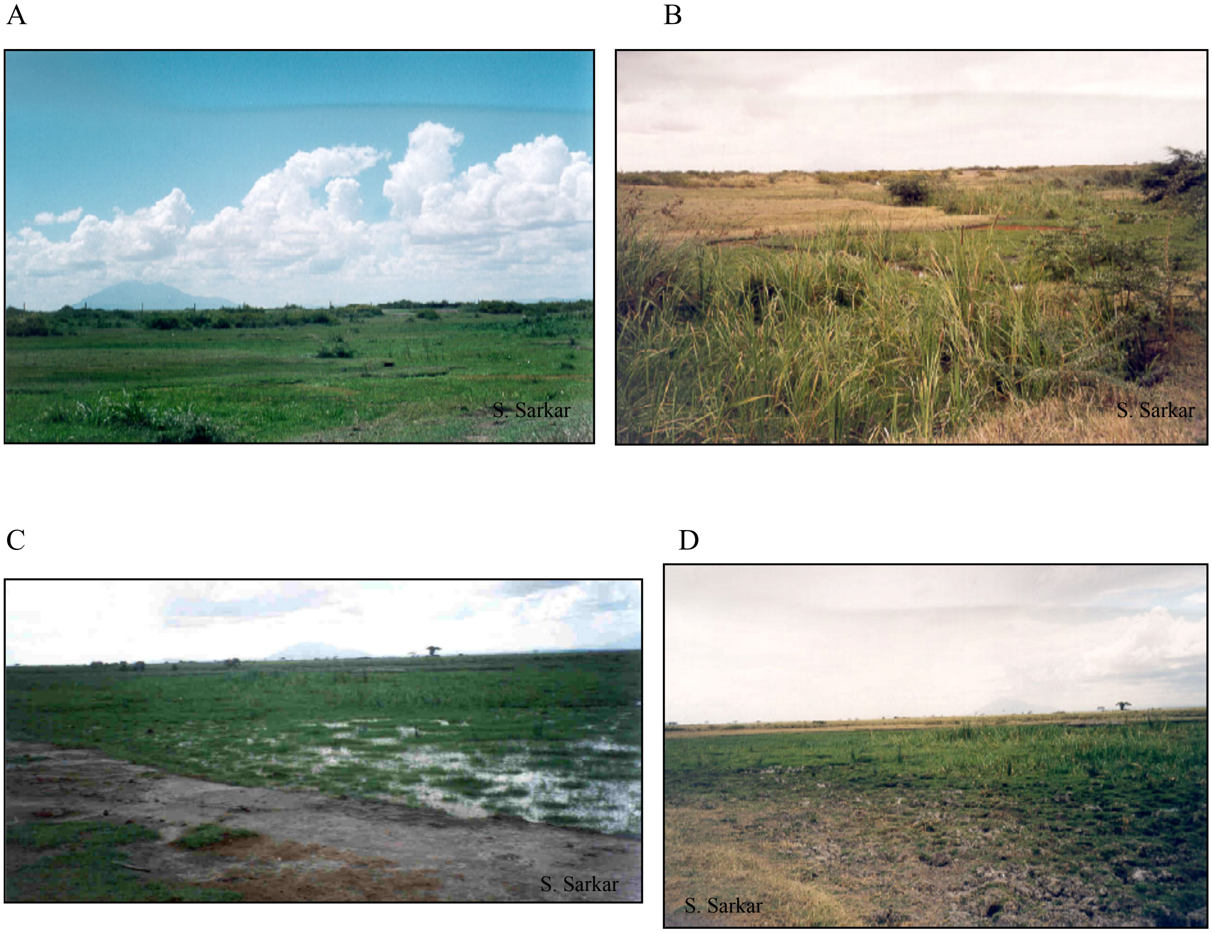

Figure 3.10. A view, facing northwest, of the treatment (A and B) and control (C and D) wetlands in November 2002 (A and C) and 2003 (B and D). The pictures, for the treatment wetland, were taken between transect 3 and transect 4. Notice the increase in sedge and *A. xanthophloea* in the later picture. The pictures of the control were taken at transect 2. The arrows in each set of pictures indicate reference points that were used to repeat the pictures in 2003.

Differences in green biomass in the centre of the two wetlands were more complicated. Biomass increased in the wet seasons as was the case on the edges of both wetlands. However, biomass in the centre of the control wetland did not appear to increase as much as the treatment wetland (Figure 3.11b). From October 2002 (end of dry season) to January 2003 (short wet season), biomass in both wetlands was similar. Following this period, biomass in the centre of the treatment wetland was higher than that in the control (Figure 3.11b). In May 2004 the biomass in the centre of the treatment wetland was almost double that in the other wet months, whereas there was no such major increase in the control (Figure 3.11b). Following this peak, the biomass in the treatment wetland plummeted by the start of the dry season, in August 2004, at which point the biomass in the two wetlands were no longer significantly different. Until the next wet season biomass did not differ in the centre of the two wetlands (Figure 3.11b). From the previous section, we know that the centre of the control (zone 2) had the highest biomass throughout the study period and was the fastest to recover from the dry seasons (Figure 3.6b). However, the treatment wetland responded even more strongly (Figure 3.11b).

Heights of the vegetation on the edge and in the centre of the two wetlands were very similar over time, albeit there was more variation in these data than in the biomass data. On the edge, heights in the two wetlands were similar up until the start of the 2003 wet season, at which point the treatment wetland showed a dramatic increase in height whereas the control showed a slight decrease (Figure 3.12a). Height on the edge of the treatment wetland increased to almost twice that in the control each wet season and decreased to almost the same the control during each dry and drought season (Figure 3.12a). At the end of the study, the height in the treatment wetland continued to increase even though the dry season had begun, which may be the result of continuing rainfall through to June 2005 (Figure 3.3).

A similar seasonal trend was observed in the centres of the two wetlands. The major difference is that the heights in the centres of the two wetlands were similar more often during the study (Figure 3.12b) than was the case for the edge (Figure 3.12a). However, the centre of the treatment wetland did have taller vegetation than the centre of the control wetland.

The eastern edge (zone 1) of the treatment wetland was dominated by *C. dactylon*, which had a total biomass over the study period of 4325 g DW m^{-2}. This species had twice the biomass of *C. laevigatus* (2214 g DW m^{-2}) and 8 times the biomass of *D. scalarum* (547 g DW m^{-2}), which were also found on the eastern edge. The results from a Spearman's rank correlation between the axes 1 and 2 sample scores for each transect, from the correspondence analysis for the treatment wetland, and time indicate that there was a significant change in the species composition of zone 1 from a *D. scalarum* and *C. laevigatus* dominated community to one that was dominated by *C. dactylon* (Figure 3.13a). There was a negative correlation (-0.53) between axis 1 sample scores and time, whereas there was a positive correlation (0.52) between axis 2 sample scores and time for the transects analyzed together.

On the other hand, on the western edge (zone 3) of the wetland *C. laevigatus* (1892 g DW m^{-2}), *Cyperus immensus* (1579 g DW m^{-2}), and *C. dactylon* (1491 g DW m^{-2}) had the highest biomass overall. Zone 3 on transect 2 (Figure 3.13b) had a weak negative correlation between axis 1 sample scores and time ($r_s = -0.31$) and a weak positive correlation between axis 2 sample scores and time ($r_s = 0.39$). Zone 3 on transects 4 and 5 also had weak negative correlations for axis 1 sample scores and time ($r_s = -0.49$, and -0.47, respectively), but stronger correlation between time and axis 2 sample scores (r_s of 0.86 and 0.95, respectively). This meant that the composition of the community in these areas changed over time from a *C. laevigatus* and *D. scalarum* dominated community towards a more *C. dactylon* dominated community in transects 2 and 4, and a *Sporobolus spicatus* dominated community in transect 5 (Figure 3.13c). Transect 3 had a weak positive correlation between time and axis 1 sample scores ($r_s = 0.34$), and a stronger correlation between time and axis 2 sample scores ($r_s = 0.80$). Transect 3 seemed to be increasing in *S. spicatus* and *H. ranunculoides* and decreasing in *C. laevigatus* and *D. scalarum* (Figure 3.13c). In April 2005, transect 4 had more *Azolla* spp. than at any other time, which was also seen in the centre of the wetland, but not on the eastern edge of the treatment wetland (Figure 3.13).

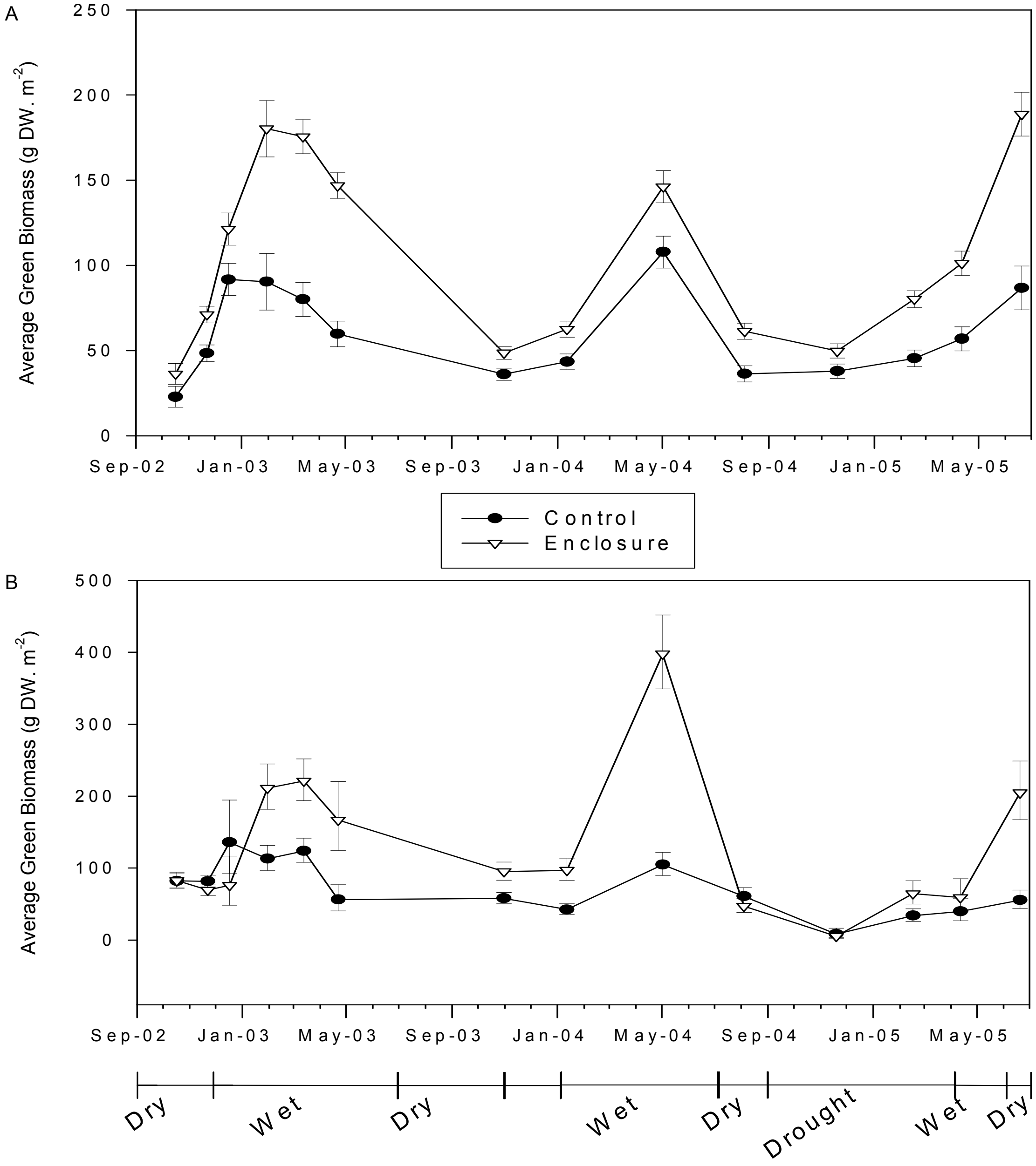

Figure 3.11. Average green biomass (A) on the edge and (B) in the centre of the control (filled circle) and treatment (open inverted triangle) wetlands in the Ilmerishari area of the Amboseli National Park, southern Kenya. Note the difference in scale between (A) and (B). Error bars indicate standard error of the mean derived from the mean standard error from a Repeated Measures ANOVA. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park.

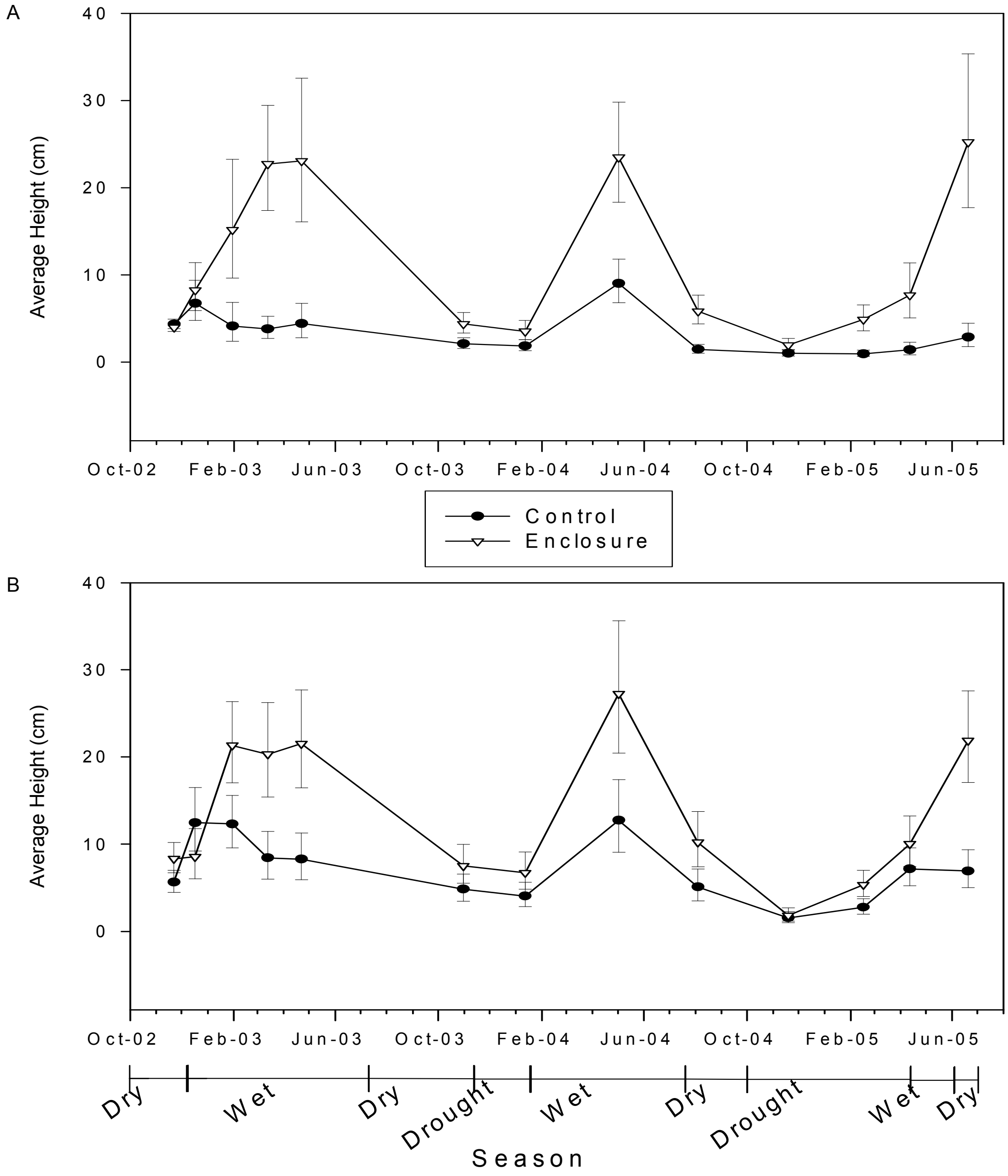

Figure 3.12. Average height (A) on the edge and (B) in the centre of the control (filled circle) and treatment (open inverted triangle) wetlands in the Ilmerishari area of the Amboseli National Park, southern Kenya. Error bars indicate standard error of the mean derived from the mean standard error from a Repeated Measures ANOVA. Seasons are derived from a combination of greenness index and biomass deviation of the bushland vegetation along the northern periphery of the park.

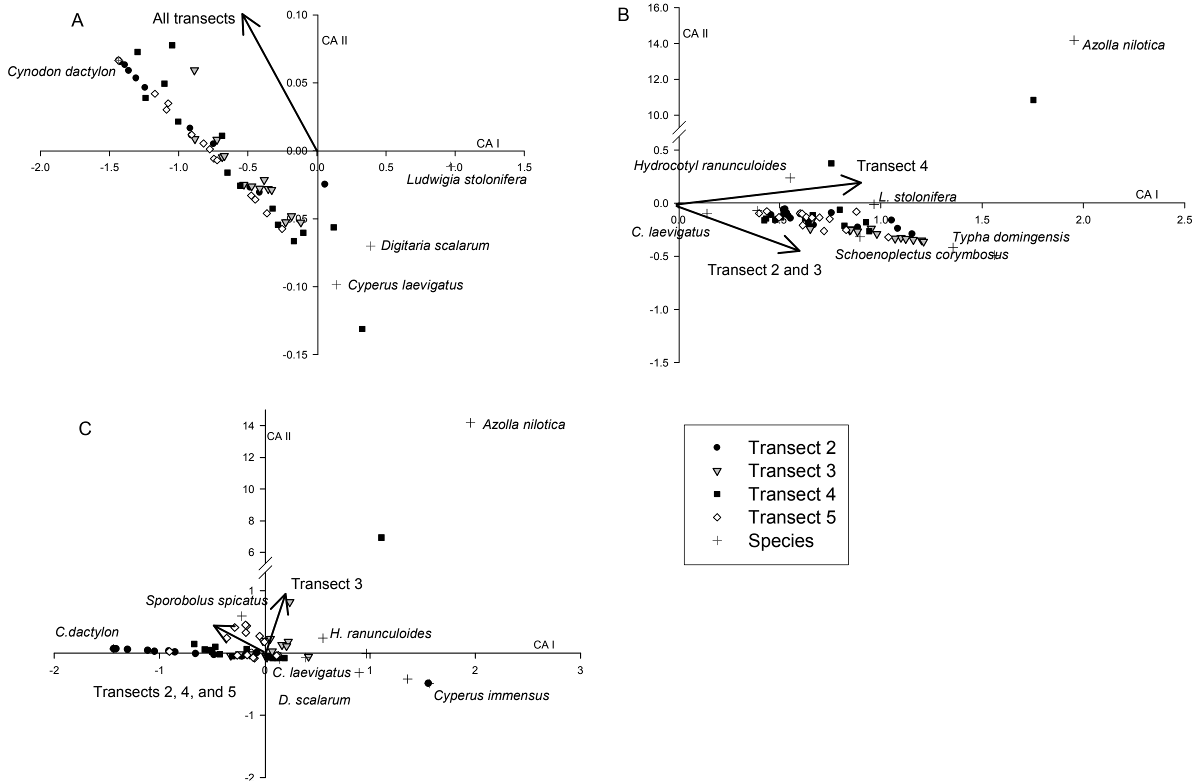

Figure 3.13. Biplots of plant species and sample scores for the three zones in the treatment wetland at Ilmerishari in the Amboseli National Park, southern Kenya where (a) zone 1, is the eastern edge, (b) zone 2, is the centre, and (c) zone 3, is the western edge of the treatment wetland. All scores were produced from a single correspondence analysis. Arrows show the scaled correlation between the sample scores for each axis and time for the transect (s) indicated in bold. The angle of the arrow indicates the direction of change in species composition along a specific transect over time, and the length of the arrow indicates the amount of correlation between axes scores and time, except in (A) where the Axis II scale was too small.

In the centre (zone 2) of the wetland the sedges *C. laevigatus* (2902 g DW m^{-2}) and *C. immensus* (2860 g DW m^{-2}) had the highest biomass overall, followed by a mix of *D. scalarum* (1610 g DW m^{-2}) and *L. stolonifera* (1218 g DW m^{-2}). Along transects 2 and 3, there was a positive correlation between axis 1 sample scores and time ($r_s = 0.75$ and -0.54, respectively) and a negative correlation between axis 2 sample scores and time ($r_s = -0.70$ and 0.53). This indicated a shift from a *D. scalarum* to a *C. immensus* dominated community (Figure 3.13b). Transect 4 had the strongest axis 1 sample score and time correlation co-efficient ($r_s = 0.80$), but a weaker positive axis 2 sample score and time correlation ($r_s = 0.31$). This indicated a shift from *C. laevigatus* and *D. scalarum* to *L. stolonifera*, *H. ranunculoides* and *Azolla* spp. (Figure 3.13b). On the other hand, transect 5 had the weakest correlations between both axis 1 ($r_s = -0.002$) and axis 2 ($r_s = -0.12$) sample scores and time, and did not change over the period of the study. It remained a mixed community of *D. scalarum*, *C. laevigatus, Schoenoplectus corymbosus* (Roth ex Roem. & Schult.) J. Raynal, *C. immensus* and *L. stolonifera*.

When I condensed the species data into vegetation types, as I had done for the control wetland, I found that total biomass of grasses, over the study period, was almost equal to that of the sedges on the edges of the treatment wetland (Figure 3.14a), which is unlike the edges of the control wetland where grasses made up most of the biomass (Figure 3.9a). In the treatment wetland, sedges had almost twice as much biomass as grasses on the first sampling date. However, during the wet season, grass biomass increased and by the middle of the season became slightly higher than sedge biomass. This did not last long as grass biomass fell below sedge biomass in the next month (Figure 3.14a). Following the dry and drought months of 2003-2004, grass biomass more than doubled in May 2004. Grasses then became the most abundant vegetation type until the early dry season month of June 2005 when final sampling was conducted and sedges had recovered (Figure 3.14a). Forb biomass was almost never over 70 g DW m^{-2} on the edges, which is similar to the edge of the control wetland (Figure 3.14a).

On the other hand, sedges remained the dominant vegetation type throughout the study in the centre of the treatment wetland (Figure 3.14b), which is not the same as the case with the control wetland (Figure 3.9b). In the treatment wetland sedge biomass increased during the wet seasons and decreased during the dry seasons (Figure 3.14b). Grasses also showed a similar pattern, but were unable to take advantage of the decreases in sedges during the dry seasons, as was the case from May 2005 onwards on the edges of the wetland (Figure 3.14a). Sedges biomass was over three times that of grass and forb biomass, though the latter were definitely more abundant in the centre than the edge of the wetland.

Dung counts for the treatment wetland indicate that there was more usage by herbivores in the dry seasons than the wet seasons, as was the case around the control wetland (Table 3.1: see the rows for total number of dung piles). In the dry seasons, wildebeest, zebra and cattle dung were present in relatively high frequencies, followed by buffalo dung. In the wet season the frequencies of buffalo dung occurrences, followed by wildebeest dung occurrences, were the highest, while those of zebra and cattle decreased sharply relative to the dry seasons (Table 3.1). Hippo markings were counted three times in the dry season but not encountered in the wet season. This is not to say that there were no hippos, as the hippos may not have marked the vegetation along the transects in the wet season as they had in the dry season. However, there was a pool at the northern end of the treatment wetland

(500 m east of the control) in which the hippos tended to stay when the water levels were high. Gazelles were not well represented in either of the seasons. This was the same as in the control, suggesting that the gazelles do not frequent this section of the park (Table 3.1).

The relative frequency of dung occurrences of each species in the two wetlands summed over dry and wet seasons were then compared using Chi-square analyses (Table 3.2). In the dry seasons, the total number of dung piles for all species and for all species except elephants were not differently distributed between the treatment and control wetlands (Table 3.2). However, there were more buffalo and Thomson's gazelle dung piles in the treatment wetland than the control, whilst there was no difference in the number of wildebeest, zebra and cattle dung piles in the two wetlands (Table 3.2). As expected, elephants and giraffe were not present in the enclosure.

In the wet season, the total number of observed dung piles decreased in both wetlands and the control had significantly more dung piles than the enclosure (Table 3.2). However, when data for elephants were removed from the total, the enclosure had a significantly higher number of dung piles than the control (Table 3.2). The distribution of buffalo dung was still skewed towards the enclosure and there was no difference for the wildebeest dung. Zebra dung distributions did shift towards the control wetland in the wet season (Table 3.2). I took a closer look at the relative frequencies of dung occurrences of each species between the two wetlands over time in order to determine if in fact there had been a shift in their preference for one of the wetlands over time (data not shown). The data suggest that buffalo preferred the treatment wetland towards the end of the dry and the middle of the wet seasons, and they did not show preference for one or the other wetland in the early and late wet seasons. The other species did not show any distinct preference for either wetland.

3.5 Discussion

The control wetland at Ilmerishari showed seasonal changes in plant height and green biomass, conductivity and water depth, and use by animals. In general, the wetland was driest along the southeastern to northeastern edges and wettest at the centre. The centre also showed the least amount of change in water depth. Conductivity tended to be lowest in the permanently inundated centre and highest in the seasonally-inundated edges. The centre was dominated by a grass-sedge community of *D. scalarum* and *C. laevigatus,* with some *C. immensus*, whereas the edges were dominated by a mixed-grass community of *C. dactylon* and *D. scalarum*. *Cynodon dactylon* became more abundant along the edges of the wetland over the period of study. Throughout the wetland, green biomass and height decreased in the dry season and increased in the wet season. However, the vegetation at the centre of the wetland was almost always taller and greener than the vegetation on the edges. There was a seasonal pattern in the use by animals, based on the occurrence of dung. Dung from species such as wildebeest, zebra, gazelles, and giraffe was mostly seen in the dry season. Cattle dung was not present at all during the wet season. However, elephant dung was found around the control wetland in both dry and wet seasons.

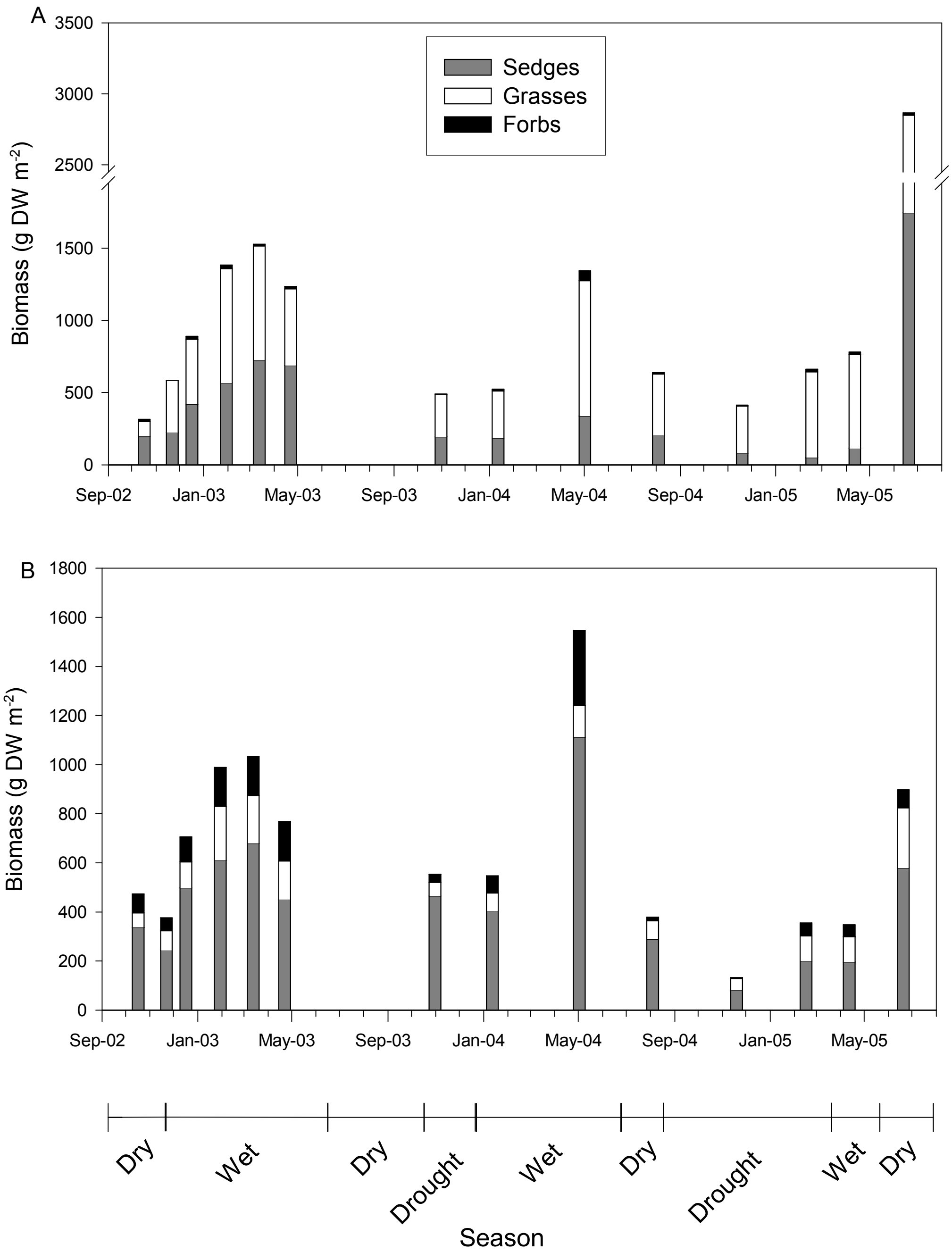

Figure 3.14. Total biomass of each vegetation type (sedges in grey, grasses in clear, and forbs in black) in the (A) edge and (B) centre of the treatment wetland at Ilmerishari, Amboseli National Park, southern Kenya. Relative abundance was calculated in the same way as in figure 1.9 and the species were also separated in the same way. However, the treatment wetland had two additional species that were included in the forbs, *Aptosimum pumilum* Benth. and *Commelina diffusa* Willd. Ex Kunth.

Table 3.2. Total number of dung piles counted around the control wetland and inside the enclosure at Ilmerishari, Amboseli National Park, southern Kenya, and the results of chi-square analyses comparing the relative frequencies of dung per species found around the wetlands in each season.

Seasons	Herbivores	Control Wetland	Inside Enclosure	Total	Expected	Chi-square (χ^2)	*P-value*
Dry	Zebra	333	289	622	311	3.1125	>0.05
	Wildebeest	329	290	619	309.5	2.4572	>0.1
	Cattle	264	308	572	286	3.3846	>0.05
	Buffalo	26	131	157	78.5	70.2229	**<0.005**
	Elephant	108	0	108	54	108.0000	**<0.005**
	Grant’s Gazelle	10	11	21	10.5	0.0476	>0.1
	Thomson’s Gazelle	11	0	11	5.5	11.0000	**<0.005**
	Hippopotamus	3	3	6	3	0.0000	>0.1
	Giraffe	4	0	4	2	4.0000	**< 0.05**
	Total	1088	1033	2121	1060.5	1..4262	> 0.1
	Total - no elephants	980	1033	2013	1006.5	1.3954	> 0.1
Wet	Elephant	128	0	128	64	128.0000	**<0.005**
	Buffalo	15	54	69	34.5	22.0435	**<0.005**
	Wildebeest	29	39	68	34	1.4706	>0.1
	Zebra	21	1	22	11	18.1818	**<0.005**
	Grant’s Gazelle	2	5	7	3.5	1.2857	>0.1
	Hippopotamus	2	0	2	1	2.0000	>0.1
	Thomson’s Gazelle	0	0	0	0	-	-
	Giraffe	0	0	0	0	-	-
	Cattle	0	0	0	0	-	-
	Total	197	99	296	148	32.4459	**< 0.005**
	Total - no elephants	69	99	168	84	5.3571	**< 0.01**

From my observations, rainfall had a role in determining the depth of water in the drier edges of the wetland that were only seasonally inundated. This is similar to the observations by Irungu (1992), who concluded that the seasonal extents of the wetlands were determined by local precipitation and run-off. The main factor determining water levels in the permanently inundated parts of the wetland, on the other hand, is groundwater inflow (Irungu, 1992). Although, only two measurements of the depth to the water table were collected, they indicated that the top of the water table was not far below the surface even at the end of the dry season.

The average conductivity of the control wetland (700 $\mu S\ cm^{-1}$) was higher than what is reported for the ground water that is thought to be its source. Irungu (1992) reports that the Ilmerishari wetlands are fed by volcanic aquifers that have an average electrical conductivity of 250 $\mu S\ cm^{-1}$ (measured from a borehole). This difference is likely the combined effect of higher evapotranspiration due to the presence of vegetation and the larger size of the wetland, as well as its shallower depth compared to the borehole.

The variability in conductivity over the study period is interesting. Following the rains in November 2002, there was a spike in conductivity for both dry and wet parts of the wetland. In the dry edges of the wetland rain could have re-dissolved salts accumulated in the soil over the dry season, causing a spike in conductivity in the water that, as it mixed with the waters in the wetter centre, would have caused the conductivity readings in these parts to increase as well. Since zone 4 is connected through a small channel to the main wetland, this explanation is relevant for this area as well. Run-on from the higher ground to the southeast of the control wetland may also influence the salinity of the wetland. The dominance of the halophytic sedge *C. laevigatus* (Thompson, 1985) in the centre of the control wetland further suggests that water can become highly saline in the wetland. A similar scenario was observed in shallow water holes around the southern plains of Serengeti (Wolanski and Gereta, 2001). Here, during the dry season, water would evaporate leaving behind salts that would be re-dissolved at the onset of the rains and cause a spike in the salinity of the water (Wolanski and Gereta, 2001).

The subsequent reduction in conductivity after the rains of November 2002 could be the result of freshening of the water by consistent, albeit low, amounts of rainfall. There was no above-ground drainage channel that would have lead to the loss of saline waters downstream away from the wetland, but there may be some reduction in salinity during periods of heavy flooding. Flooding beyond what I determined to be the edges of the wetland, however, was not observed when conductivity measurements were being collected.

Hydrology is considered one of the most important determinants of abiotic and consequently biotic conditions of a wetland (Mitsch and Gosselink, 2000). The salinity of the water influences the species that are able to establish themselves in the wetland (Otte, 2001). However, the presence of continuous moisture also ensures that the vegetation is kept in a growing state throughout the year (Howard-Williams and Gaudet, 1985). In the control wetland, the centre had higher amounts of green biomass and taller vegetation through most of the study period. The difference between this part of the wetland and the drier edges was greatest during the dry season, which indicated the importance of a continuous water supply to the maintenance of growth.

During the drought of 2004-2005, however, biomass and height in the inundated parts of the control wetland did decrease to the same levels as the rest of the wetland. This decrease was not entirely due to die-off since total biomass, which is the sum of green and brown biomass, was almost identical to green biomass. Instead, biomass was being removed. Hence, it is likely that as the drought progressed, the water levels in the permanently inundated parts of the wetland likely decreased sufficiently to allow grazers to move right into the middle of the wetland to feed. During the dry seasons, there were more herbivore dung piles around the wetland than in the wet season. Normally, animals such as wildebeest and zebra will not utilize the deeper parts of a wetland as they are not adapted to the environment (Howard-Williams and Gaudet, 1985). However, it is not entirely impossible that if conditions in the permanently inundated parts of the wetland changed, that the animals would take advantage of the vegetation when conditions were especially harsh in the surrounding savanna habitat.

The seasonally inundated edges of the wetland maintained a low amount of biomass of low height during the dry seasons, when animals were congregating around the wetland. However, both biomass and height recovered slightly during the wet season, when animals were moving away from the wetland. Because sampling was not conducted every month, it is not possible to determine how quickly the vegetation responded to rainfall. The only time sampling was almost monthly was between January and May 2003, when only the vegetation in zone 2 appeared to respond quickly to the onset of the rains.

Based on the data collected from the control wetland, the edge is a seasonal wetland habitat dominated by *C. dactylon* and *D. scalarum*, whereas the centre of the wetland is a *C. laevigatus* and *D. scalarum* dominated shallow wetland with some *C. immensus*. On the classification map presented in Chapter 2 (Figure 2.10), the Ilmerishari wetlands are classified as *C. immensus* and *C. dactylon* dominated shallow water wetlands partly surrounded by *C. laevigatus* dominated seasonal wetland habitat and partly by open grassland. The control wetland is spatially complex and appears to be a combination of all these classes, with the shallow wetland habitat occurring in the centre, in particular at zone 2 of transect 2, the seasonally inundated wetland habitat occurring around zone 2 of transects 1 and 3, and the open grassland, in this case dominated by *C. dactylon*, occurring along the drier southeastern and northeastern edges of the wetland. The fact that the edges were dominated by *C. dactylon*, which is both flooding and grazing-tolerant, indicates that this area experiences consistent grazing pressure and flooding (McNaughton, 1984). In Amboseli, wildebeest (Andere, 1981) and elephant (Western and Lindsay, 1984; Koch *et al.,* 1995) have been shown to graze in the *C. dactylon* dominated grasslands in the park.

The results from dung counts indicate that elephants used the control wetland year-round between 2002 and 2004. This is interesting since the aerial counts presented in Chapter 2 that showed that elephants were spending more time around the wetland habitats in the park is observable even at a smaller scale.

On comparing the control and treatment wetland, especially along the edges, it becomes clear that the elephants do in fact have a significant effect on biomass and height of vegetation in the control throughout the year. The biomass and height on the edges of the control do not show major changes between seasons when compared to the treatment wetland. During the dry season grazing by animals other than elephants is the driving force determining the biomass and height of the vegetation on the edges of the wetlands, since both plant biomass and height in the treatment wetland plummet to levels similar to the control. Green and total biomass for the enclosed wetland was not different for this period (data not shown) indicating that green biomass was not being converted to brown biomass as a result of die-off. However, the major impact of elephants was seen in the wet season when the data from the two wetlands are compared. The protected vegetation along the edges of the treatment wetland was better able to take advantage of the rains than was the vegetation on the edges of the control. Both biomass and height of the edge vegetation of the treatment wetland increased by almost twice compared to the edge vegetation of the control.

Biomass and height of vegetation in the central portion of the treatment wetland was significantly higher than for the control during the wet seasons, once again indicating the negative effect of elephants on vegetation at this time. The 2004-2005 dry-drought period caused vegetation in both the control and treatment wetlands to decrease to similar values, however, the treatment wetland showed a more dramatic decrease. This may indicate that the treatment wetland was more heavily used by other animals during this period. Unfortunately I do not have dung counts for this period and cannot confirm this.

The eastern edge of the treatment wetland was dominated by *C. dactylon*, whereas the western edge was dominated by *C. laevigatus*, *C. immensus*, and *C. dactylon*. The centre had the same sedge species dominating the community as the western edge of the wetland. However, along the edges there was shift towards a grass community dominated by *C. dactylon*, a result that is mirrored along the edges of the control wetland. Sedges were still present along the edges of the treatment wetland at the end of the study, which was not the case in the control. Based on the classification in Chapter 2, the eastern edge is open grassland and the western edge was initially a mix of seasonal and shallow water wetland habitat. The centre is also a mix of seasonal and shallow water wetland habitat.

A study on nutria (*Myocastor coypus* Molina) grazing and water management on wetland plant production and stand structure of coastal marshes in Louisiana, USA, reported that both a decrease in water levels and increased nutria grazing negatively affected production of the sedge *Schoenoplectus americanus* and, hence, changed stand structure towards a more erosion-prone system (Johnson Randall and Foote, 2005). In the wetlands I consider in this study, the poor rainfall conditions could have favoured grasses in both wetlands, but grazing could have selected for the more grazing-tolerant species, in this case *C. dactylon*.

The changes observed in the treatment wetland were towards more deep-water sedge than grass, which is also different from the control that moved towards more grasses. This might indicate that grazing was less heavy on the centre of the treatment wetland, but it might also be caused by differences in hydrology of this wetland relative to the control. The treatment wetland had more forbs, mostly floating macrophytes, which also indicates that this wetland was always wetter in the centre than the control. Furthermore, the treatment wetland was larger and, hence, on a proportion basis, the centre zone was better represented. However, in spite of these differences, the fact that sedges were still better able to maintain their position in the community versus the case in the centre of the control, indicates that grazing must have been a determining factor as well. The removal of elephants from the enclosed wetland may have allowed the sedges to maintain a strong hold on the community throughout the year as smaller herbivores do not eat poor quality sedges, unlike elephants that are better able to feed on this types of vegetation (Koch *et al.,* 1995; Western and Lindsay, 1984). This is further supported by the fact that the enclosure had more dung piles during the wet season than the control and was still able to maintain its biomass, height and sedge-dominated community.

The changes in vegetation that were observed in the treatment wetland were expected based on the prior knowledge on the ability of elephants to alter habitats. Hence, these observations are less likely the result of chance even though the treatment wetland was not replicated.

The treatment wetland experienced shifts in the dominant species. However, there were no major changes in the species composition over time. This is similar to the results of Mulhouse *et al.* (2005) who report that sedge/grass dominated wetlands of the Carolina Bay did not change as much in species richness as compared to pond/meadow wetlands dominated by aquatic species, because the former had less exposed sediment of which new species could take advantage. This is similar to the conditions in the Ilmerishari wetland. In combination with grazing, the communities in these wetlands appear to be undergoing pulse stable development in that, overall, the system is more or less a stable, mature system that responds to pulses of energy, in this case rain and grazing pressure, by short-term increases or decreases in one plant species over another (Mitsch and Gosselink, 2000). Once the pulse is removed, the community has the ability to shift back to a previous state based on the seed bank and rhizomatous/clonal vegetation.

The results from this study are not sufficient to prove or disprove the hypothesis that a removal of elephants will change the use patterns of the wetland by other species, since they only include counts over one year. However, within this time period, there was no evidence of a change in use by other herbivores. Buffalo appeared to have preferred the enclosure between 2002 and 2004, however, in the dry season Thomson’s gazelles were also better represented around the treatment than the control wetland. This was not expected since one would imagine the increase in growth inside the enclosure that could be potential hiding spots for carnivores would deter smaller herbivores. The use of both wetlands was about equal during the dry seasons, further indicating that the removal of elephants did not negatively impact use of the treatment wetland by other herbivores. However, the treatment wetland did become noisier each successive field trip as a result of an increase in the number of nesting birds in the sedge communities in the central region of the wetland. A study was being conducted on the bird diversity of Amboseli during the period my study was being conducted, but the results for the bird study have not yet been published

Overall, the control wetland showed seasonal changes in vegetation, water depth, conductivity and use by herbivores. Although the study period was quite dry, it was observed that the permanently inundated and seasonally inundated parts of the wetland differed in their characteristics and seasonal changes. The permanently inundated centre tended to change less than the seasonally inundated edge. The vegetation in the latter appears to be greatly influenced by grazing and the vegetation in the former may be influenced more by the salinity of the water. The location of this wetland at the southwestern edge of the park might make it more prone to continual grazing pressure as animals migrate in and out of the park. Furthermore, its shallow depth may make it more prone to steep draw-downs and increased salinity than the larger wetlands in the park, which suggests that the species composition, especially in the centre of the wetland, may not be exactly the same as in the other wetlands in the park. This is, however, expected since wetlands are by nature diverse, which is why classification of wetlands in one region can be a challenging task (Mitsch and Gosselink, 2000).

Elephants did appear to have a profound impact on the biomass and height of wetland vegetation in the Ilmerishari wetlands, especially during the wet season. This might be an added stress on this ecosystem that would be exaggerated by the grazing impacts of other species during dry years, such as was experienced during this study. Even though these results are from 2 small wetlands that may have different seasonal variations in hydrology compared to the larger wetlands in the park, the results do imply that elephants may have had a role in the opening-up of the wetland habitat as was proposed in Chapter 2.

The dry conditions experienced through most of the study may have caused the shift in dominance along the edges of both wetlands towards grazing-tolerant vegetation because grazing pressure is higher in dry seasons. However, except for the obvious benefits to the species that thrive in sedge-dominated wetlands, there was no evidence that the use of the control wetland by elephants or the removal of elephants from the treatment wetland was negatively affecting other herbivore species during the predominantly dry study period.

Elephants are important for the removal of tall, dense, low-quality vegetation that then gives rise to higher quality new growth of which other species in the grassland savanna ecosystem can take advantage (Western and Gichohi, 1993b). The role of elephants may be similar in the wetlands of Amboseli. From Chapter 2, there is some evidence that the tall, dense *C. papyrus* sedge community of the 1970's is not currently dominant in the ecosystem and although *C. immensus* is found in the vast shallow water wetlands habitat the vegetation is does not form tall, dense communities (see Figure 2.1). In the present chapter, the removal of elephants encouraged the growth of dense stands of *C. immensus* sedge in the centre of the wetland within one year, lending support to the hypothesis that elephants are responsible for the opening up of the wetlands of the Amboseli National Park.

If habitat diversity, which is considered to be the reason for the high animal diversity in the park (Western, 1994), was to be reintroduced into the Amboseli wetland ecosystem by the improvement of the sedge-community, then elephants have to be prevented from using all the wetlands all of the time. This can be achieved either by fencing certain wetlands even for a few years as is evident in this study, or by ensuring safe migration routes for the elephant population that would reduce the wet-season pressure on the wetlands. However, elephants cannot and should not be completely excluded from the wetlands of Amboseli as their role in maintaining low sedge and grass communities is also important for sustaining heterogeneity in the wetland habitats.

Chapter 4

Grazing in the Amboseli Wetlands

4.1 Introduction

In the African savanna grasslands numerous studies have been conducted on the responses of grasses to grazing pressure, such as in the Serengeti (McNaughton, 1979a; McNaughton, 1985) and Amboseli (Georgiadis *et al.,* 1989; also see Skarpe, 1991). The "grazing optimization hypothesis" (McNaughton, 1979b) that states that there is a maximization of above-ground productivity at moderate grazing levels, was constructed from grassland studies. The reasons for the improved productivity in grasslands under moderate grazing are thought to be: enhanced photosynthetic capacity; increase in leaf cell division and elongation, as younger, faster growing parts of the plant are maintained; more efficient light use, due to reductions in mutual shading; promotion of tillering as a result of hormone redistribution; reduced rate of leaf senescence; nutrient recycling accompanying herbivory; and stimulatory effects of herbivore saliva (McNaughton, 1979a). Furthermore, simulated grazing studies conducted using transplanted *Sporobolus kentrophyllus* [K. Schum.] in Amboseli National Park (Georgiadis *et al.,* 1989) and *Kyllinga nervosa* Steud. from the Serengeti ecosystem (McNaughton, 1979b) have reported that when plants have a moisture deficit, they benefit more from clipping at moderate levels than when moisture is not a limiting factor.

In any grazing ecosystem, such as the semi-arid savannas, degradation due to over-grazing is a important issue. Most studies looking at the effect of over-grazing by livestock have shown that there is a change in the plant species composition from palatable to non-palatable grasses when grazing intensities are severe (Skarpe, 1991). The reason for this change is an interaction between selective grazing for palatable species, which results in the reduction in biomass of these species, and the increased competitive advantage for the non-palatable species if present in the vicinity. There are also the effects of trampling and reduced vegetation cover that tend to reduce the available soil moisture, which, depending on tolerances, impacts different plant species in different ways (Skarpe, 1991). Hence, different grazing levels and ways in which grazers interact with the plant layer have been shown to cause heterogeneity above what plant-soil interactions would have dictated in a grazing ecosystem (Adler *et al.*, 2001).

There have been studies on the impacts of livestock grazing in African wetland systems (Scoones, 1991; Hongo and Masikini, 2003). These generally agree that under moderate stocking rates, traditional grazing regimes that use wetland vegetation only in the dry season help to maintain wetland vegetation in a highly productive state. However, with increasing grazing pressure there was a resultant decrease in productivity and a change in species composition. This was similar to the results from studies done on the impacts of the lesser snow geese on both Arctic salt marshes and the Bylot Island wetlands, where a decrease in vegetation and increase in soil erosion resulted from an increasing goose population (Gauthier *et al*., 1996; Jefferies and Rockwell, 2002). There is also evidence from a coastal wetland on Lake Erie that plant species richness can be decreased in otherwise species-rich communities as a result of sediment disturbance due to herbivore activity

(Barry *et al*., 1998). On the other hand, the removal of exotic plant species from Californian vernal pools as a result of heavy cattle grazing increased plant diversity (Marty, 2005). There is one study that reports that the type of wetland habitat also dictates the response to grazing. In this study, perennial herbaceous marshes showed less sensitivity to grazing in terms of species composition than the creek vegetation, several metres away, that showed an increase in diversity under moderate grazing (Jackson and Allen-Diaz, 2006). Annual total herbaceous cover in both, however, decreased over time under moderate grazing, but increased with light or no grazing.

The literature on the impacts of grazing on wetlands suggest that increasing grazing pressure causes a decrease in plant diversity and productivity directly through its impacts on the vegetation, and also indirectly through its affects on the integrity of the sediment and seed banks. The changes in species composition, however, depend on the inherent dynamics of the wetland habitat.

The rich diversity of the Amboseli National Park and the surrounding savanna ecosystem is primarily reliant on the wetlands (Western, 1994). The change in seasonal migration of elephants due to the threat of poachers in the 1970's and the almost doubling of the elephant population from the 1960's to 1999 (Western and Lindsay, 1984; Koch *et al.,* 1995; Moss, 2001) have meant an increased pressure on the park ecosystem. This has been shown to have contributed significantly to the loss of the dense and open *A. xanthophloea* woodlands that bordered the southern edges of the wetlands (Western and Maitumo, 2004). The elephants have also been using the permanent wetland habitats in the park through out the year, which was evident in the long-term data presented in Chapter 2. This increased use is thought to have contributed to the reduction in tall, dense sedge communities and the dominance of shorter, floating mat communities in the park wetlands (see Chapter 2 and Chapter 3). These studies looked at the gross effects of grazing, especially by elephants, on seasonal biomass and height of vegetation. There is, however, a need to look at the effect of grazing on these wetland habitats at a finer scale to determine how they react to grazing pressure.

In this study I explored grazing and its effects on vegetation in a reference wetland in the Amboseli National Park. The study began by quantifying the effects of natural grazing on the edges and in the permanently inundated centre of the wetland over one year. Changes in grazing level over the year and the resultant effects on vegetation biomass, growth and species composition were investigated using temporary (mobile) and permanent (stationary) cages that excluded medium to large herbivore grazing (rodent and invertebrate grazing was not controlled). I hypothesized that, although vegetation biomass would be decreased by grazing, growth rate and species composition would not. I also hypothesized that grazing levels would not vary over the year based on the assumption that the large herbivores were remaining in the park over much of the year, but there would also be a seasonal effect on biomass, growth rates and species composition of vegetation on the drier edge of the wetland more so than in the wetter centre.

The second component of the study was to observe the effects of varied levels of artificial grazing on biomass and growth of the vegetation in the two zones. High, moderate and low grazing levels were simulated by manually cutting inside cages in each zone. The hypothesis tested was that moderate levels of grazing would have positive effects on growth in both zones.

4.2 Study Area

The experiments were conducted at the northwest of Longinye wetland (Figure 4.1a). The experiment was set up on the south-facing edge of the wetland near a permanent enclosure that had been built in 1985 as part of a woodland restoration and aesthetic project (Western and Maitumo, 2004). The edge of the wetland, referred to as CDE from here on, was dominated by *C. dactylon* (Figure 4.1b) and would be part of the open grassland habitat that fringes the wetlands shown in Chapter 2. This part of the wetland is only inundated during heavy rainfalls when the wetlands expand, and during this study the CDE zone was never inundated. The grasses had an average height of 37.7 cm, as measured using a meter rule from ground level. *Cyperus laevigatus* dominated mats and floating *Azolla* and *Pistia stratiotes* covered most of the permanently inundated centre, which will be referred to as CLC from here on (Figure 4.1c). Deep channels in the wetland's sediment were indicative of hippos and dung piles on the edge of the wetland indicated the presence of elephants, wildebeest and other herbivores.

4.3 Materials and Methods

4.3.1 Cage Description and Set-Up

Ten cages made of 1" steel mesh measuring 1m x 1m x 1m were initially built for use in the first experiment. Five cages were placed in the CDE zone and five in the CLC zone. The cages were held down with iron pegs. However, these were not sufficient to keep elephants from overturning the cages once in a while. Hence, for the second experiment the cages were cut down in height to 50 cm so that they would be less visible to the elephants. The vegetation was never taller than the cages at the start of an experiment.

In each zone, the cages were distributed so as to include as much of the obvious visual heterogeneity between the patches of vegetation, in terms of height and fullness, in order to account for these differences in the plants' responses to grazing pressure. The cages in the CLC zone were placed on the floating mats (Figure 4.1c).

4.3.2 Estimation of Above-Ground Biomass

Above-ground biomass (referred to as biomass from here on) was estimated using the slanted pin-frame also used in Chapter 3. The number of hits per pin per species per cage was recorded for the first experiment and this number was averaged from a total of 4 frames (20 pins). In the second experiment the hits were not separated by species as it was considered unnecessary based on the results from the first experiment. In this case the hits per pin per cage were averaged from 3 frames (15 pins).

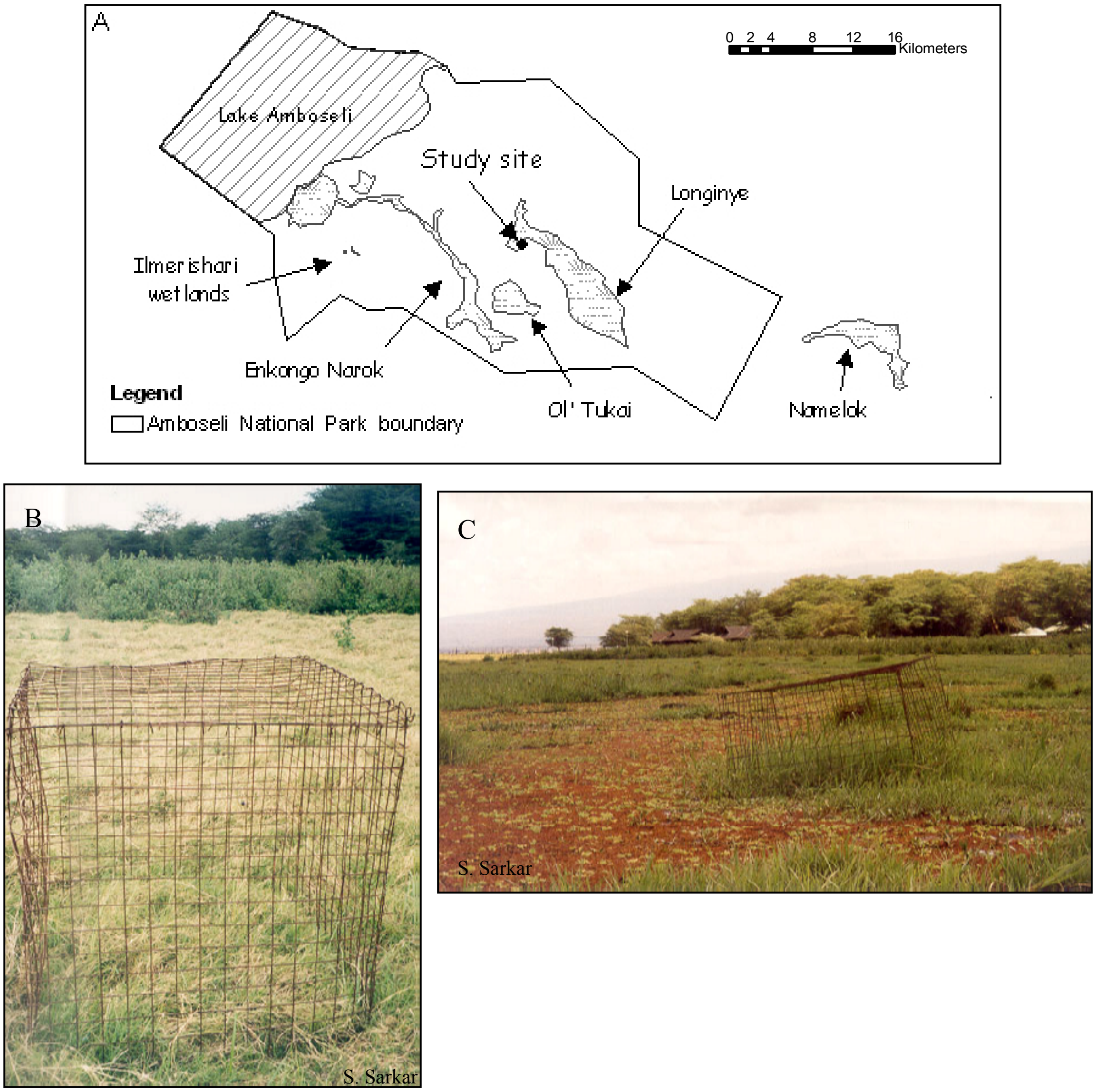

Figure 4.1. Location of the study site on the northwest end of the Longinye wetland (02°39'S, 37°16'E) in the Amboseli National Park, southern Kenya, with close-up photographs of the *Cynodon dactylon* dominated edge (B), and *Cyperus laevigatus* dominated centre (C), of the wetland.

4.3.3 Experiment 1 – Natural Grazing

This study commenced on January 29, 2003 and sampling was conducted in the middle of March, April, June, September and November 2003, and January 2004. The method used for this experiment is a modification of McNaughton's method that was used to study grazing dynamics in the Serengeti plains (McNaughton, 1979b; McNaughton, 1985). McNaughton (1985) built a permanent enclosure at the beginning of the study period as well as adjacent temporary enclosures to measure short-term re-growth following grazing events. He moved these temporary enclosures according to the grazing patterns of the three ungulates he was studying. This was necessary in his case because the animals are known to move out of the plains during the dry season.

In my study, biomass inside (B_i) and outside (B_o) each cage was estimated for each of the five cages in each zone at the time the cages were put in place (initial sampling). They were then left in place for a variable amount of time (one to three months) and then biomass was re-measured (final sampling). Three of the cages were moved to a new position and the process was repeated. These cages will be referred to as the mobile cages. The cages were not moved in accordance with grazing patterns as I wanted to monitor growth and grazing over both the wet and dry seasons. The two remaining cages were sampled at the start of the experiment and then each time the mobile cages were sampled. However, they were not moved to a new location. These cages will be referred to as the stationary cages.

A General Linear Model-ANOVA (GLM-ANOVA) with fixed effects was used to test the effect of protection from grazing, time and an interaction of the two on the growth of vegetation, represented by biomass, in the mobile cages. Separate analyses were conducted for the initial and final samples. The same effects were tested for the stationary cages using Repeated Measures ANOVA (RM-ANOVA) where the within-subject effect was time and the between-subject effects was grazing. Changes in biomass between each set of sampling dates for the inside and outside of the cages were also calculated and subjected to the above tests.

McNaughton (1979b) calculated grazing intensity (GI) as $1\text{-}g/ng$, where g was the biomass, as measured using the canopy intercept method (McNaughton, 1979a), in grazed areas that were not protected by fencing, and ng was the biomass inside the permanent fenced enclosures that had been set up the beginning of the study. When growth of vegetation under grazing pressure (as represented by g) is the same as that of the vegetation that is protected (ng), then GI will equal zero; as grazing increases the value of GI will approach one. To calculate GI for my experiment I substituted g with B_o and ng with B_i for each mobile cage on each of the initial and final sampling dates. Grazing intensity was not calculated for the stationary cages because the data are cumulative and would not represent actual grazing intensity over each sampling period.

The effects of time and the difference between GI from the initial versus the final samples from the mobile cages were tested using a GLM-ANOVA model with an interaction term. The initial measurements from January 2003 were dropped as they introduced high amounts of variation to the analyses.

In all statistical analyses, a cage effect was included to remove variance due to the location of the cage since the cages were placed such that the visual heterogeneity of the site was included as explained above. All hypotheses were tested at a Type I error rate (*P*) of 0.05 unless mentioned otherwise. The Greenhouse-Geisser adjusted *P* value (G-G adj. *P*) rather than the unadjusted *P* was used to test the within-subjects effects in the RM-ANOVA analyses in order to correct for temporal correlation between the repeated measures. Residuals for each ANOVA were tested for randomness, equality of variance, and normal distribution; when needed an appropriate transformation was derived using the Taylor's Power Law (Legendre and Legendre, 1998). All analyses were conducted in SYSTAT 11 (Systat Software Inc., 2004).

Species composition data recorded from the stationary cages were subjected to Correspondence Analysis (CA) to visualize any patterns in species composition inside and outside the cages during the entire sampling period. Separate analyses were conducted for the CDE and CLC zones. Biplot scaling was applied to the inter-sample distances and rare species were not down-weighted. Analyses were conducted in CANOCO for Windows, version 4.5 (ter Braak and Smilauer, 2002).

4.3.4 Experiment 2: Simulated Grazing

The cages from experiment 1 were moved to new, fixed positions in their respective parts of the wetland at the start of experiment two. Each of the ten cages were divided into four 50 cm by 50 cm portions and randomly assigned to one of three simulated grazing levels or the control (NO). The three grazing levels, high (HI), medium (ME), and low (LO), were simulated by cutting back the vegetation using pruning shears. Since I was using the canopy intercept method to measure biomass, the plants were cut off as close to the soil layer as possible so that they would not be detected by the pin-frame (Figure 4.2). The nominal treatments were intended to be 100% (HI), 66% (ME), and 33% (LO).

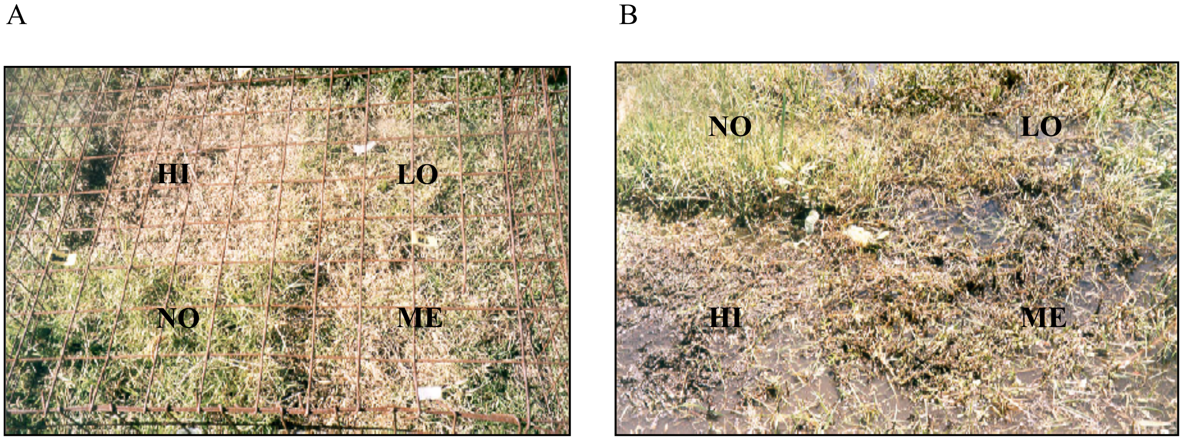

Figure 4.2. Simulated grazing treatments on the, (A) *Cynodon dactylon* dominated edge, and (B) *Cyperus laevigatus* dominated centre of the Longinye wetland, Amboseli National Park, southern Kenya. NO is the control, whereas, LO, ME, and HI correspond to nominal treatments of 33% grazed (low), 66% grazed (medium), and 100% grazed (high), respectively.

Over the span of the experiment, the actual percentage biomass removed varied from month to month, though there was always a difference between the treatments for the CDE zone. This was not, however, the case in the CLC zone. The instability of the floating mats hindered the cutting and measurement of the vegetation. Hence, the percentage biomass removed as measured using the pin-frame was lower than I had intended for each treatment. The percentage of actual vegetation removed at each treatment level in the two zones is shown in Table 4.1.

Table 4.1. Above ground biomass removed at each treatment level of the simulated grazing experiment in the Longinye Wetland, Amboseli National Park, southern Kenya, expressed as a percentage of the biomass initially present.

	Treatment					
	CDE (Edge)			CLC (Centre)		
Sampling Date	LO	ME	HI	LO	ME	HI
January 2004	39	57	89	20	25	43
April 2004	24	53	84	37	52	63
June 2004	41	58	87	46	56	57
August 2004	41	40	69	21	29	44
September 2004	24	38	67	21	39	44
November 2004	39	54	86	28	42	62
February 2005	36	67	90	23	33	43
April 2005	36	55	88	39	55	58
Average biomass removed (%)	**35**	**53**	**83**	**29**	**41**	**52**

The study commenced on January 22, 2004, following which data were collected in the beginning of April, June, and August, on September 22nd, and November 12th, of 2004, and on February 14th, April 5th and June 13th, of 2005. This time-span covered wet, dry, and drought seasons for 2004-2005, as determined using the greenness and biomass deviation values from the bushland plots on the northern periphery of the park (Figure 4.3). For the first two months of sampling, treatments were applied to all ten cages, however, from June onwards two of each set of five cages were allowed to "grow out" in order to determine the effect of a short grazing period on the regeneration and consequent growth of vegetation. These cages will be referred to as short-term grazing (STG) cages. The other three of each set of five cages were sampled, treated, allowed to regenerate and sampled again each month. The same treatments were applied to the same portions of the cage to determine the effect of continuous HI, ME, LO or NO grazing on vegetation regeneration. These cages will be referred to as the long-term grazing (LTG) cages.

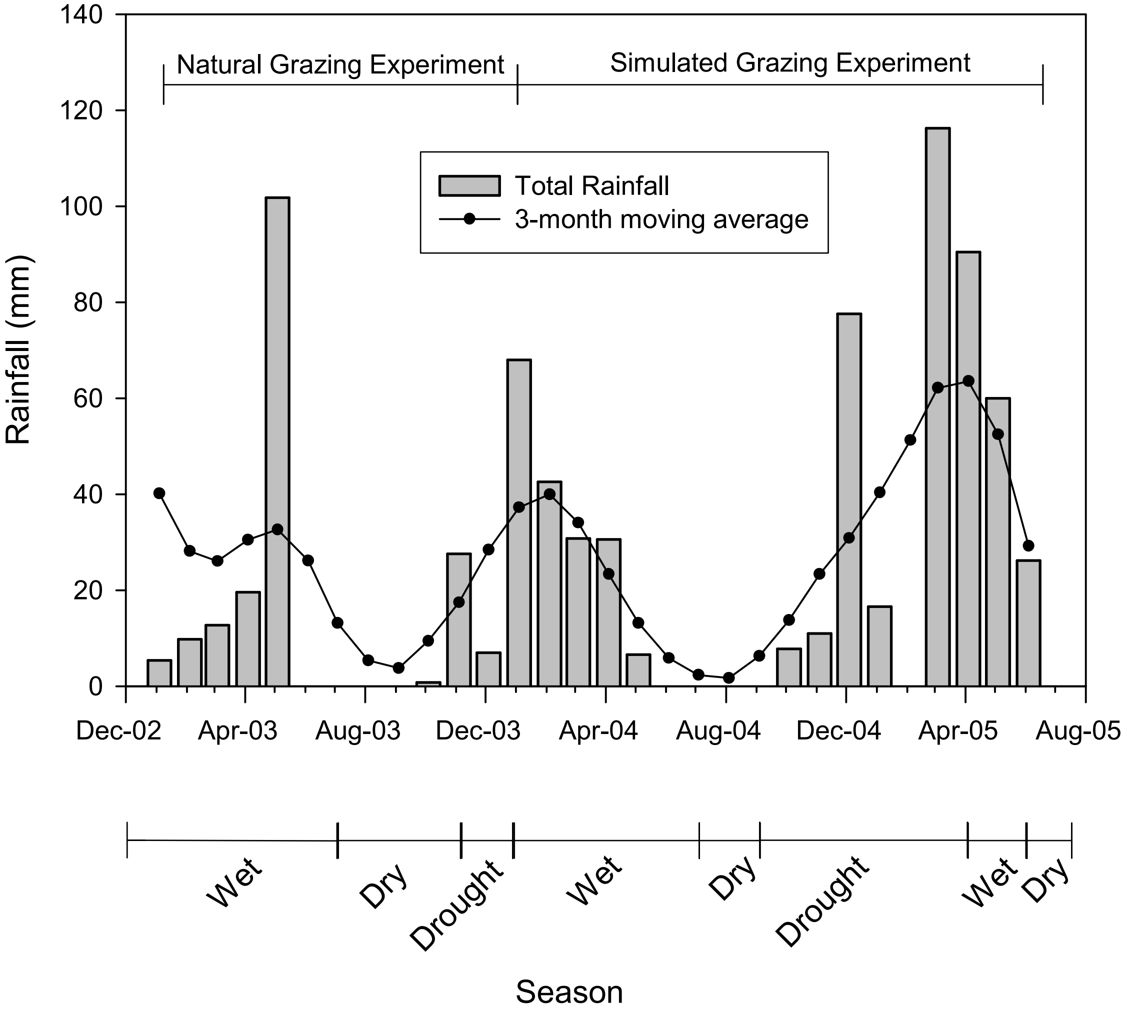

Figure 4.3. Monthly rainfall (bars) and the 3-month moving average rainfall (line) for the Amboseli National Park, southern Kenya, collected at the Ol' Tukai Weather Station (02°43'S, 37°23'E). Seasons, as determined using greenness and biomass deviations in the bushland plots to the north of the park have been included below the plot for comparison.

Growth rate was calculated for each of the three treatments in each of the LTG cages by subtracting the post-treatment biomass in the previous sampling date from the pre-treatment biomass in the current sampling date. This result was then divided by the number of days between the two dates. For the NO treatment in the LTG cages and for the STG cages there was no treatment applied on the sampling dates, but the same calculation was used to determine seasonal growth patterns under no grazing.

Since the cages were in a fixed position throughout the experiment, RM- ANOVA was applied to the data on growth rate for the LTG and STG cages in each of the two zones. Treatment and cage were the between subjects effects (main effects), whereas time was the within subjects effect (interaction effects). A *P*-value of 0.05 was used to test the hypotheses, unless otherwise stated, and residuals were tested to ensure that they complied with the assumptions. All analyses were conducted in SYSTAT 11.

4.4 Results

4.4.1 Experiment 1: Natural Grazing and its effects on Vegetation Growth and Species Composition

In the CDE zone, final measurements of biomass inside (B_i) and outside (B_o) the mobile cages differed significantly. Mean biomass inside (297 g DW m^{-2}) was significantly higher, by 13.5%, than mean biomass outside (257 g DW m^{-2}) the cages ($F_{1, 22} = 13.50$, $P = 0.001$). There was also a significant date effect ($F_{5, 22} = 41.60$, $P < 0.001$) with both B_i and B_o increasing from March to May then decreasing over the remainder of the year (Figure 4.4a). When the cages were first put in place (Initial) in the CDE zone, however, there was no difference in biomass between the inside and outside of the cages. There was a significant effect due to date ($F_{6, 26} = 81.61$, $P < 0.001$), which can be seen in Figure 4.4a.

Mean change in biomass was negative for both the inside (-0.24 g DW m^{-2} d^{-1}) and the outside (-0.81 g DW m^{-2} d^{-1}) of the mobile cages in the CDE zone, and these values were significantly different from each other ($F_{1, 10} = 6.21$, $P = 0.032$). There was also a significant time period effect ($F_{5,10} = 35.77$, $P < 0.001$) as seen in Figure 4.4b and a time period by cage interaction ($F_{10, 10} = 3.74$, $P = 0.025$) as a result of one cage having a more positive change in biomass compared to the other two cages in the first two time periods.

In the CLC zone, the difference in biomass between the inside and outside of the mobile cages at re-sampling (Figure 4.5a) was statistically significant ($F_{1, 22} = 19.16$, $P < 0.001$). Mean final biomass inside (492 g DW m^{-2}) was three times greater than mean final B_o (166 g DW m^{-2}) mainly because of the high B_i recorded in November 2003, when B_i was 13 times higher than B_o (Figure 4.5a). There was also a significant date effect ($F_{5, 22} = 6.17$, $P = 0.001$), with peaks in B_i observed in June and November 2003, and one peak in B_o observed in June 2003 (Figure 4.5a), which coincided with the peaks in rainfall over the study period. However, statistically, the peaks in biomass inside and outside the cages in June 2003 were not significantly different for the initial or the final measurements. There was a significant cage effect ($F_{2, 22}= 7.18$, $P = 0.004$), as one cage had consistently higher biomass than the others. There was also a significant cage effect in the results of the initial biomass measurements ($F_{2, 24} = 17.03$, $P < 0.001$). This is a reflection of the positioning of the cages in a way that accommodated for the visual heterogeneity of the site, as described earlier. There was no difference in biomass inside and outside the cages ($F_{1, 24} = 2.63$, $P = 0.118$) at the start of each sampling period in the CLC zone (Figure 4.5a). The ANOVA results, however, did indicate a significant date effect ($F_{6, 24}= 6.06$, $P < 0.001$), which is not apparent in Figure 4.5a due to the scale.

The mean change in biomass inside the mobile cages of the CLC zone was higher (13 g DW m^{-2} d^{-1}) than mean change in biomass outside the cages (3 g DW m^{-2} d^{-1}). In this zone, only the change in biomass inside the cage was significantly different from zero ($t = 2.76$, $df = 17$, $P = 0.013$) and this may be due to the large positive change that occurred between September and November 2003 (Figure 4.5b). The change outside the cages was positive only between April and June 2003 and September and November 2003. In the former, the change was similar to that inside the cages and in the latter the amount of change was close to zero (Figure 4.5b). The effect due to time period was not significant, but *P* was close to 0.05 ($F_{5,\,10} = 3.22$, $P = 0.055$).

Grazing intensity (GI) did not change significantly with time ($F_{5,\,22} = 1.10$, $P = 0.389$) in the CDE zone (Figure 4.6a), but there was a significant difference between the initial and final measurements ($F_{1,\,22} = 14.54$, $P < 0.001$). Mean GI for the initial samples was -0.22, which was not significantly different from zero ($t = 0.368$, $df = 17$, $P = 0.368$) as would be expected since initial B_i and B_o were not significantly different. These results confirm that there was no difference between the inside and outside of the cages initially and that any grazing measured in the final sampling on each date was a result of actual removal of vegetation between this and the previous date. Mean GI for the final samples was 0.13 and this was significantly different from zero ($t = 4.09$, $df = 17$, $P < 0.001$).

In the CLC zone, initial GI (0.11) was consistently lower than final GI (0.44) and this difference was statistically significant ($F_{1,\,21} = 6.46$, $P = 0.019$). Furthermore, final GI was significantly different from zero ($t = 3.329$, $df = 17$, $P = 0.004$), whereas initial GI was not ($t = 0.633$, $df = 16$, $P = 0.535$). Grazing intensity in the initial and final samples also showed a significant date effect ($F_{5,\,21} = 11.87$, $P < 0.001$). This is most likely because of the significantly lower GI in June 2003 (Figure 4.6b) that was the result of measured value for B_o being higher than B_i when the cages were sampled in June (Figure 4.5a), even though statistically these values were not significantly different (as mentioned above). Hence, without the negative GI from June 2003, there would most likely be no difference in GI over time.

For the stationary cages from both the CDE and CLC zones RM-ANOVA resulted in residuals that violated the assumption of normal distribution even after transformation. Hence, the RM-ANOVA results have to be viewed with caution. However, there was a difference in biomass between treatments in the CDE zone ($F_{1,\,1} = 331.390$, $P = 0.035$) as seen in Figure 4.7a. Biomass inside the cages (344 g DW m^{-2}) was significantly higher than biomass outside the cages (263 g DW m^{-2}). Figure 4.7a also shows a trend through time, which was significant only at $P = 0.1$ ($F_{6,\,6} = 54.64$, G-G adj. $P = 0.086$). The mean change in biomass inside the stationary cages was not significantly different from mean change in biomass outside the cages ($F_{1,\,1} = 0.193$, $P = 0.736$).

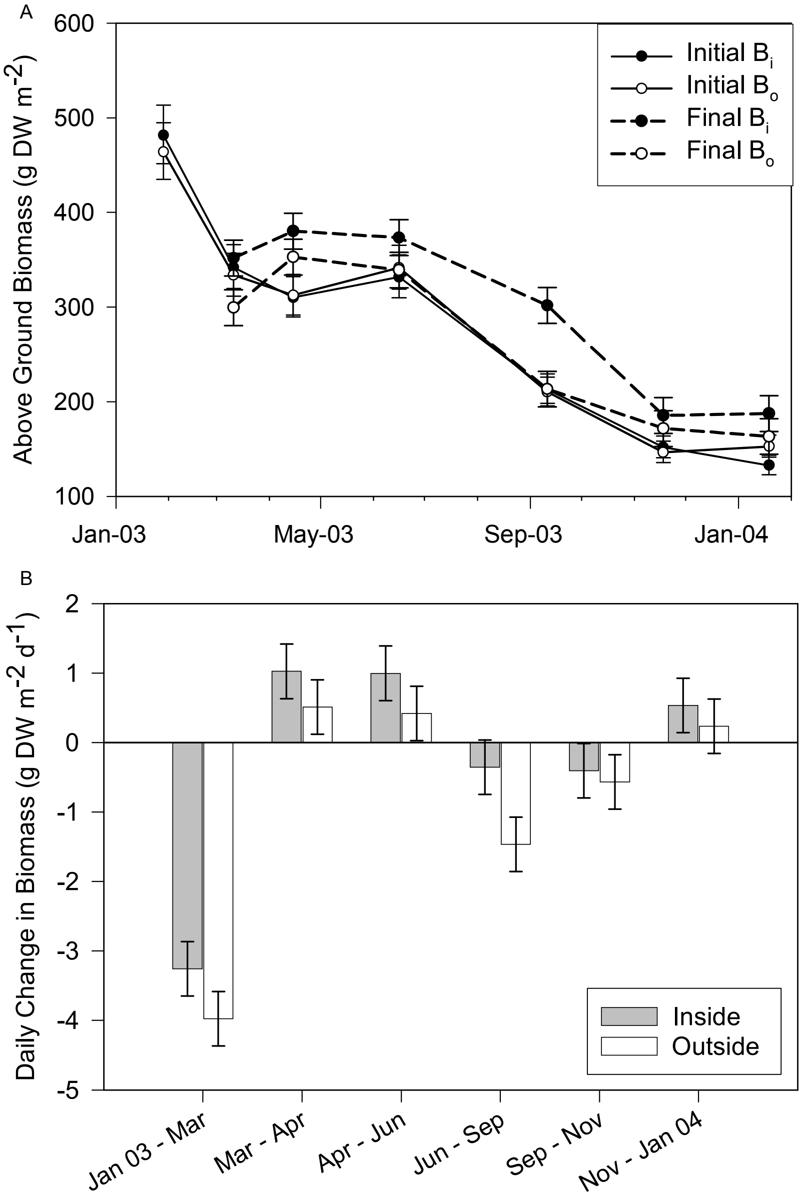

Figure 4.4. (A) Above ground biomass inside (B_i) and outside (B_o) the mobile cages from the natural grazing experiment, placed in the *Cynodon dactylon* dominated edge (CDE) of Longinye wetland, Amboseli National Park, southern Kenya, when the cages were first put in place (initial) and after they had been left in place for a period of time (final). (B) Daily change in biomass on the inside and outside of the same mobile cages in the CDE zone over each time period between sampling. Means were derived from n =3 samples and the standard error of the means are shown by the error bars.

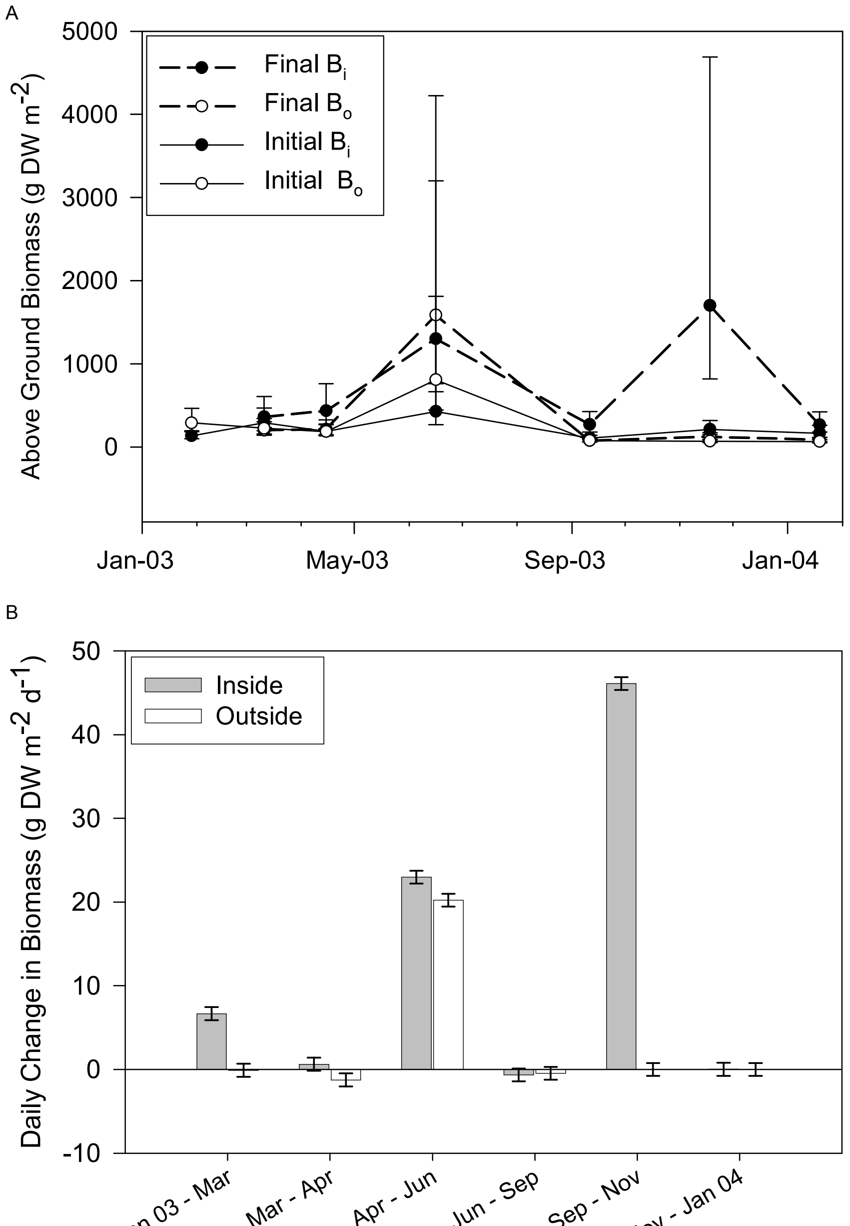

Figure 4.5. (A) Above ground biomass inside (B_i) and outside (B_o) the mobile cages from the natural grazing experiment in the *Cyperus laevigatus* dominated centre (CLC) of Longinye wetland, Amboseli National Park, southern Kenya, measured initially, when the cages were put in place and after the cages had been left in place a period of time (final). (B) Daily change in biomass on the inside and outside of the same mobile cages in the CLC zone over each time period between sampling. Means were derived from n =3 samples and the error bars represent the mean ± standard error of the mean in (A) and the standard errors of the means in (B).

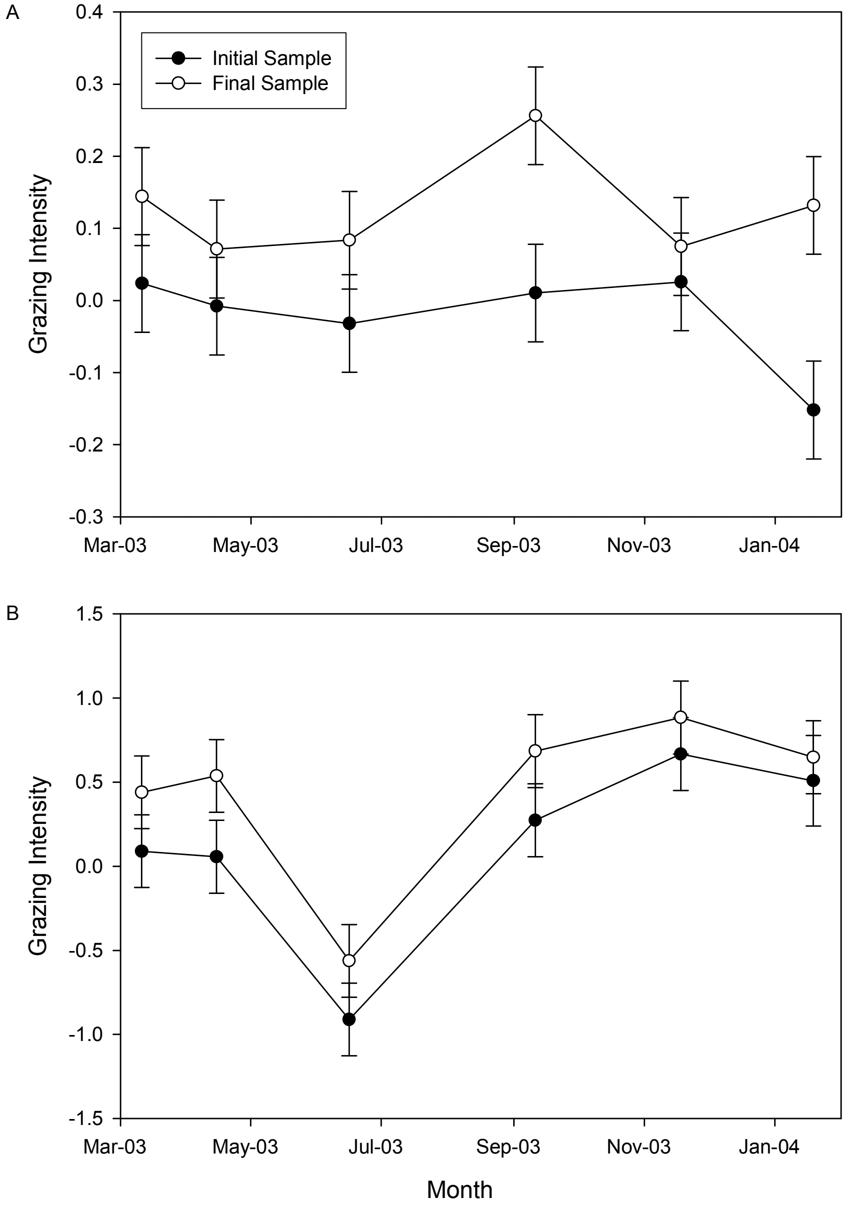

Figure 4.6. Grazing intensity for (A) the *Cynodon dactylon* dominated edge (CDE), and (B) the *Cyperus laevigatus* dominated centre (CLC) of Longinye wetland calculated at each sampling time for the natural grazing experiment. Each point on the graph is a least square mean from n = 3 and the error bars represent the standard error of the mean.

In the stationary cages of the CLC zone there appeared to be a date by treatment interaction (Figure 4.7b). However the Greenhouse-Geisser adjusted *P* was not significant ($F_{6,6} = 8.55$, $P = 0.210$). There were no significant effects due to treatment, though mean B_i (1386.5 g DW m^{-2}) was twice as high as mean B_o (622.72 g DW m^{-2}). This was probably the result of the B_i in November 2003, which was 24 times higher than B_o (Figure 4.7a). There was also no significant trend through time. Mean change in biomass inside and outside the stationary cages was not significantly different ($F_{1, 1} = 2.23$, $P = 0.376$).

There was little evidence from the stationary cages of major changes in species composition in either zones (Figure 4.8a; Figure 4.9a). In the CDE zone, as expected, *Cynodon dactylon* was the most dominant species present throughout the experiment (Figure 4.8b). *Digitaria scalarum* was first recorded both inside and outside the cage in April 2003, but by June 2003 there was more of it inside than outside the cages (Figure 4.8a and b). It eventually disappeared from the outside in September while it was reduced inside, following which the species was detected neither inside nor outside the cages (Figure 4.8b). *Cyperus laevigatus* on the other hand was only first recorded in September (Figure 4.8a and b). This may be an artifact of my sampling frequency since the high amount of rainfall in June may have prompted growth of this species, but I did not see it until the next time sampling took place. Furthermore, there was a higher biomass of this species inside compared to outside the cage, but within the next two months this species was no longer seen inside the cages and finally none was recorded on either side of the cages (Figure 4.8a and b).

In the CLC zone, species composition was much richer than that in the CDE zone and there were more changes inside and outside the cages in the CLC than in the CDE zone (Figure 4.9a). Furthermore, the total biomass of vegetation inside the cages was about 16 times higher than outside the cages (Figure 4.9b). In January of 2003 both the inside and outside of the cages had a similar species composition with a mixture of the wetter species, especially *D. scalarum* (Figure 4.9a), though it is difficult to discern this from Figure 4.9b due to the scale. In March, April, September and November 2003 the composition inside the cages tended more towards *C. laevigatus* compared to the outside because although the amounts of both *C. laevigatus* and *D. scalarum* were increasing inside the cage the former increased in biomass by ten times more than the latter (Figure 4.9b). The biomass of both of these species outside the cages did not change much through the study. *Cynodon dactylon* was observed in large amounts inside the cages only in April 2003 and hence, for that month the inside of the cages were closer to *C. dactylon* in the ordination (Figure 4.9b). In January 2004, once again the inside and outside of the cages were found close to each other in Figure 4.9a because of a sudden reduction in biomass of both *C. laevigatus* and *D. scalarum* inside the cages (Figure 4.9b). This may have been the result of the crowded conditions inside the cages or some disruption to the cage by elephants in between December and January. *Schoenoplectus corymbosus* was observed outside the cages in January, March and April 2003 and *C. immensus* in all months except September. This may be an artifact of cage placement since these species grow in deeper water and are seldom seen in the centre of the floating mats, which is were the cages were placed.

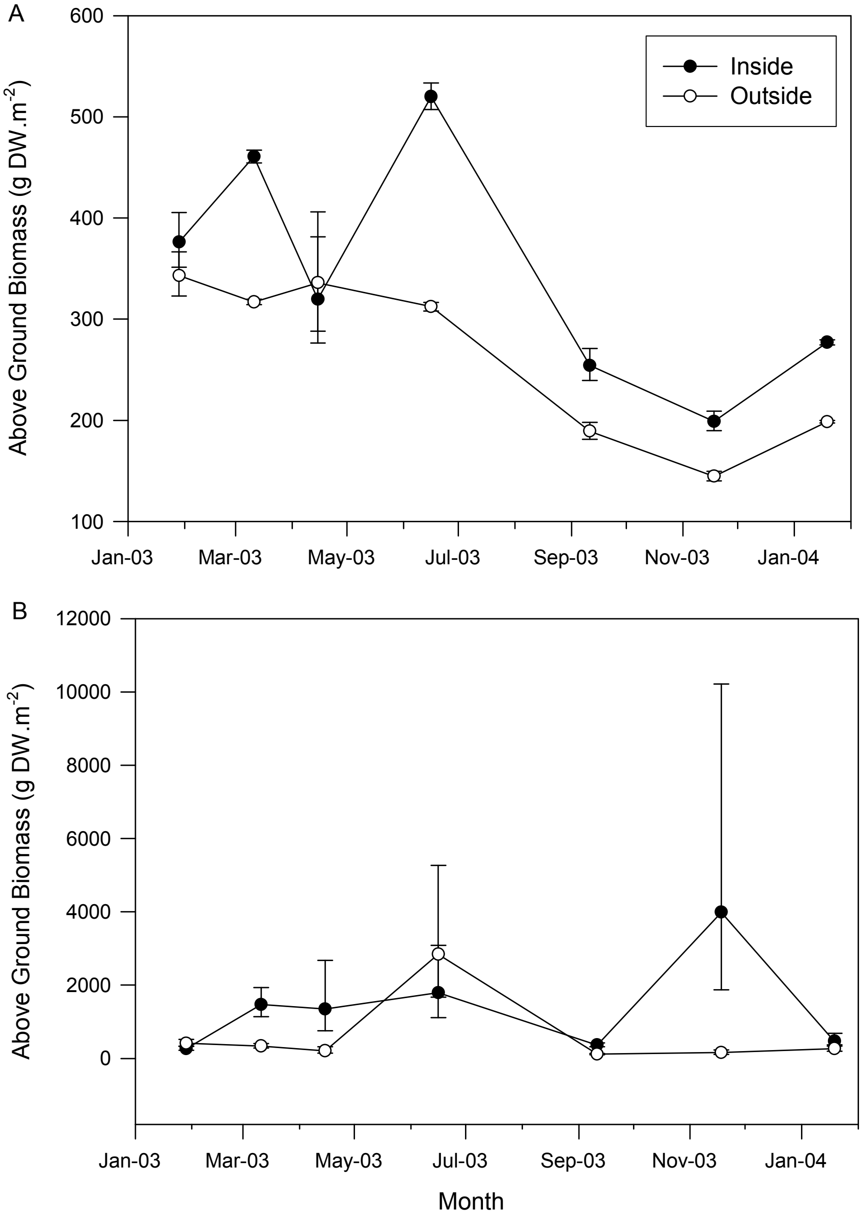

Figure 4.7. Above ground biomass in the stationary cages from the natural grazing experiment measured in (A) the *Cynodon dactylon* edge (CDE), and (B) in the *Cyperus laevigatus* centre (CLC) of the Longinye wetland, Amboseli National Park, southern Kenya. Each point represents the least square mean biomass derived from n = 2 and the mean ± standard error of the mean are represented by the error bars.

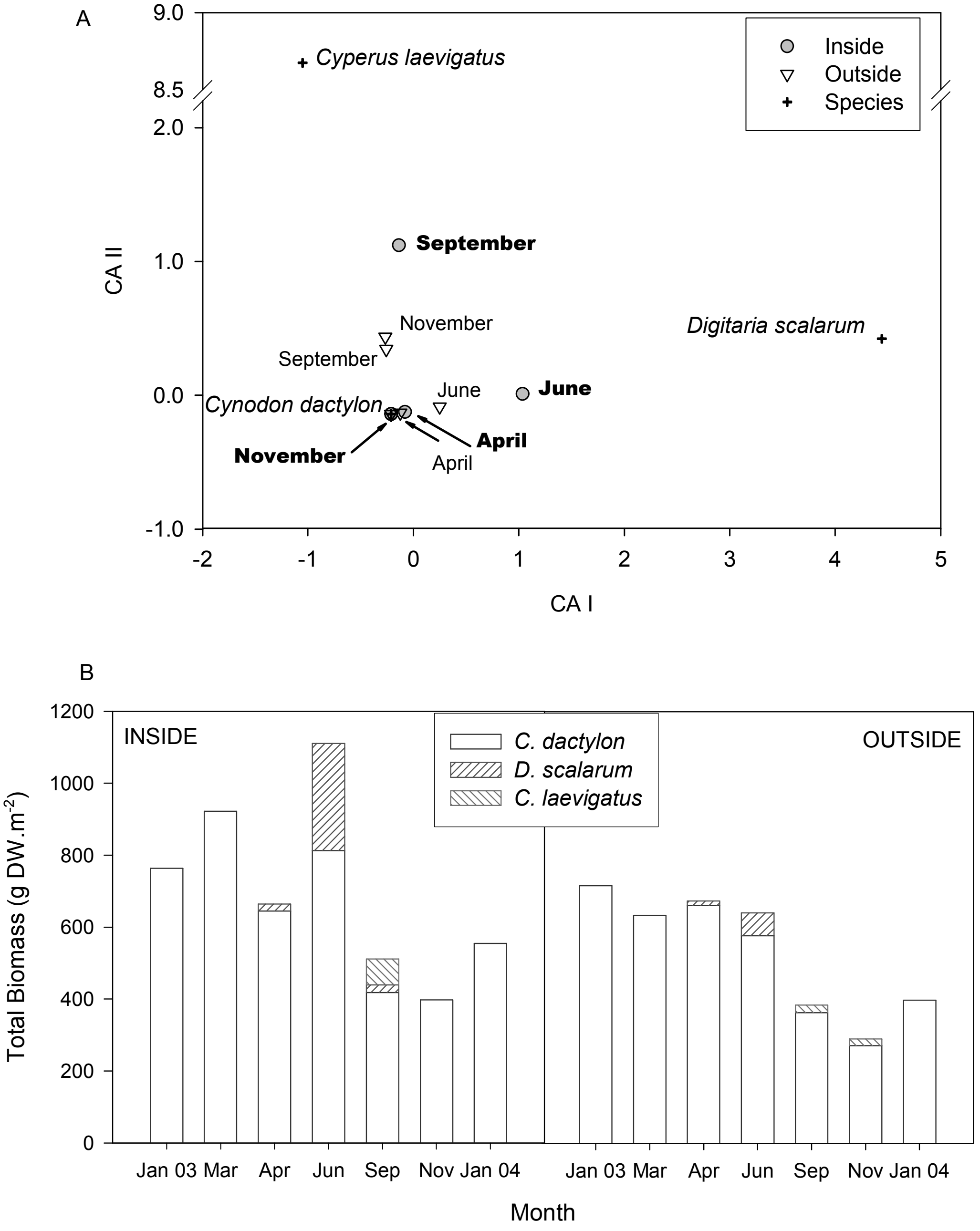

Figure 4.8. (A) Biplot of the stationary cages, from the natural grazing experiment placed in the *Cynodon dactylon* dominated edge (CDE) of the Longinye wetland, Amboseli National Park, southern Kenya, constructed using correspondence analysis (CA) scores. Months presented in bold type indicate CA scores for the inside of the cages in those months. (B) Total above ground biomass of the main species observed inside (left) and outside (right) the stationary cages during the study.

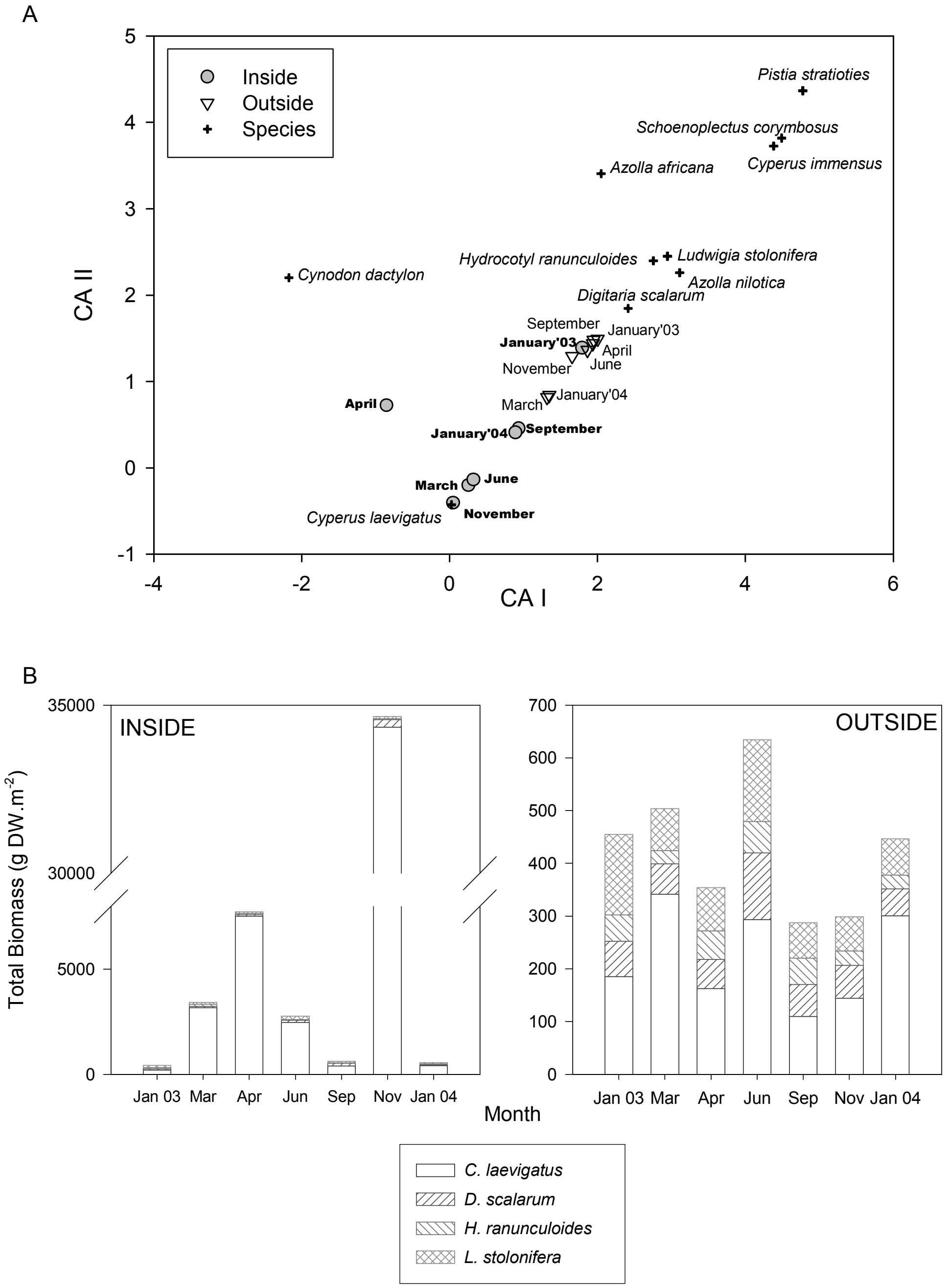

Figure 4.9. (A) Biplot of the stationary cages from the natural grazing experiment placed in the *Cyperus laevigatus* dominated centre (CLC) of the Longinye wetland, Amboseli National Park, southern Kenya, constructed using correspondence analysis (CA) scores. Months presented in bold indicate CA scores for the inside of the cages in those months. (B) Total above ground biomass of the species observed inside (left) and outside (right) the stationary cages during the study. Note the difference in scales of the two biomass plots.

4.4.2 Experiment 2: Effects of Simulated Grazing on Vegetation Growth

Long-term simulated grazing had a significant effect on growth in both zones (Figure 4.10a; Figure 4.11a). At the start of the experiment, in January 2004, the biomass for each treatment was about the same. However, each treatment subsequently altered the growth rate of the vegetation to varying degrees over the period of the experiment (Figure 4.10a; Figure 4.11a), which is captured in the growth rate analyses presented in Figure 4.10b and Figure 4.11b.

There was a significant effect of grazing treatment on growth rate in the long-term grazing (LTG) cages of the CDE zone ($F_{3,6} = 66.666$, $P < 0.001$). Growth rate in the control (0.03 g DW m^{-2} d^{-1}) was significantly lower than for all other treatments when averaged over the entire study period (Figure 4.10b). Low and medium grazing levels resulted in statistically similar mean growth rates (0.3 g DW m^{-2} d^{-1}), whereas a high grazing level resulted in the highest mean growth rate (0.4 g DW m^{-2} d^{-1}).

There were also significant cage ($F_{2,6} = 8.081$, $P = 0.020$) and time period ($F_{7,14} = 8.001$, G-G adj. $P = 0.020$) effects on growth rate, as well as a weak time period by cage interaction ($F_{14,42} = 2.586$, G-G adj. $P = 0.063$). The cage effect and weak interaction were due to one cage having lower growth rates when compared to the other cages primarily between June and August 2004 and February and April 2005. The time period effect was a result of growth rates between June and August 2004, and August and September 2004 being lower than all other time-periods except February to April 2005 (data not shown). The latter was not significantly different from any other time-period. The former two time-periods correspond to the dry season and hence, the reduction in growth rates could be a direct result of a lack of water. However, the growth rates for both the HI and ME treatments were positive, whereas for the control they were negative over those four months. Between February and April 2005 rainfall was increasing. However, the control still had negative growth rates, which brought the average growth rate for this time period down.

There was a significant effect of treatment ($F_{3,3} = 29.692$, $P = 0.010$) on the growth rates in the short-term grazing (STG) cages of the CDE zone (Figure 4.10b). The growth rate under high simulated grazing (0.2 g DW m^{-2} d^{-1}) was twice that under medium simulated grazing levels (0.1 g DW m^{-2} d^{-1}) and approximately four times that under low simulated grazing levels (0.04 g DW m^{-2} d^{-1}) and the control (0.05 g DW m^{-2} d^{-1}).

There was also a time period effect ($F_{7,7} = 39.242$, G-G adj. $P < 0.001$) and a time period by cage interaction ($F_{7,21} = 8.746$, G-G adj. $P = 0.017$). The most significant difference in growth rate over time occurred between August and September 2004 where it was negative in both the STG cages in the CDE zone (data not shown). This was a result of negative growth in all treatments and the control and hence indicates that at the end of the growing season, the early simulated grazing treatments did not have a lasting effect. However, over all of the time-periods the highest grazing level did maintain the least negative or more positive growth rate. The time period by cage interaction was most probably caused by one cage that had a negative growth rate between February and April 2005. This time period and that between August and September had growth rates that were significantly different from the rates in the other time periods when the data were subjected to a multiple paired-t comparison with Bonferroni corrections.

The results from the simulated grazing experiment for the LTG cages in the CLC zone (Figure 4.11) indicate significant interactions between time period and treatment ($F_{21, 42} = 3.816$, $P = 0.010$) and, therefore, the average growth rate per treatment for each time period in the CLC zone is shown here (Figure 4.11b). The only time periods in which there were strong significant differences between grazing levels were January to April 2004 (first time period), April to June 2004 (second time period), September to November 2004 (fifth time period), and November 2004 to February 2005 (sixth time period) as indicated by asterisks in Figure 4.11b. There was only a weak difference ($t = -3.253$, $df = 2$, $P = 0.083$) between the control and high grazing levels in June to August 2004 (third time period), that is, during the dry season (Figure 4.11b).

The highest simulated grazing treatment had similar growth rates to the low and medium treatments in the first, second and third time periods, which was expected since the actual percentage of vegetation removed for each treatment (Table 4.1) were very similar (Figure 4.11a). However, in the fifth and sixth time periods, the highest grazing treatment did cause significantly higher growth rates. Growth rate for the control was negative in the second, third, fifth and sixth time-periods, but only in the second and fifth was it significantly lower than growth rates for the other treatments. Over the entire study period, low and medium grazing treatments resulted in growth rates that were not significantly different, which is probably because the percentage of vegetation removed for these treatments were very similar (Table 4.1). The growth rates in each of the LTG cages in the CLC zone varied with time as indicated by a significant time period by cage interaction ($F_{14, 42} = 11.53$, $P < 0.001$). However, it was not possible to test for cage by treatment interaction because of insufficient degrees of freedom and hence I assumed that although the mean growth rates varied with time in each cage, the relative effects of the treatments were the same in all three cages.

The response of the vegetation in the STG cages of the CLC zone was highly variable. There was only a weak effect of simulated grazing on growth rate in the STG cages of the CLC zone ($F_{3, 3} = 6.880$, $P = 0.074$). However, there was a significant time period effect ($F_{7, 7} = 8.278$, G-G adj. $P = 0.037$) and time period by cage interaction ($F_{7, 21} = 9.934$, $P = 0.028$). The latter was the result of the two cages having completely opposite growth rates to one another between fourth and fifth time periods (August to November 2004) suggesting that there is inherent variability within the zone. Figure 4.12 shows the mean growth rate per time period for the STG cages. Growth rate was significantly lower between June and August 2004 (third time period), November 2004 and February 2005 (sixth time period), and February and April 2005 (seventh time period). In the third and sixth time periods the growth rates for each treatment (not shown) were negative, which is unlike the results from LTG cages in the CLC zone (Figure 4.11b; Figure 4.12). It is apparent that in the CLC zone the effects of short-term simulated grazing treatments did not last even at the highest simulated grazing level. This is probably because the actual amount of vegetation removed in January and April 2004 from the STG cages for the highest simulated grazing treatment in the CLC zone was similar to the amount taken from the medium simulated grazing treatment in the CDE zone. The medium grazing treatment in the STG cages of the CDE zone did not show lasting effects on growth rate, either (Table 4.1; Figure 4.10b).

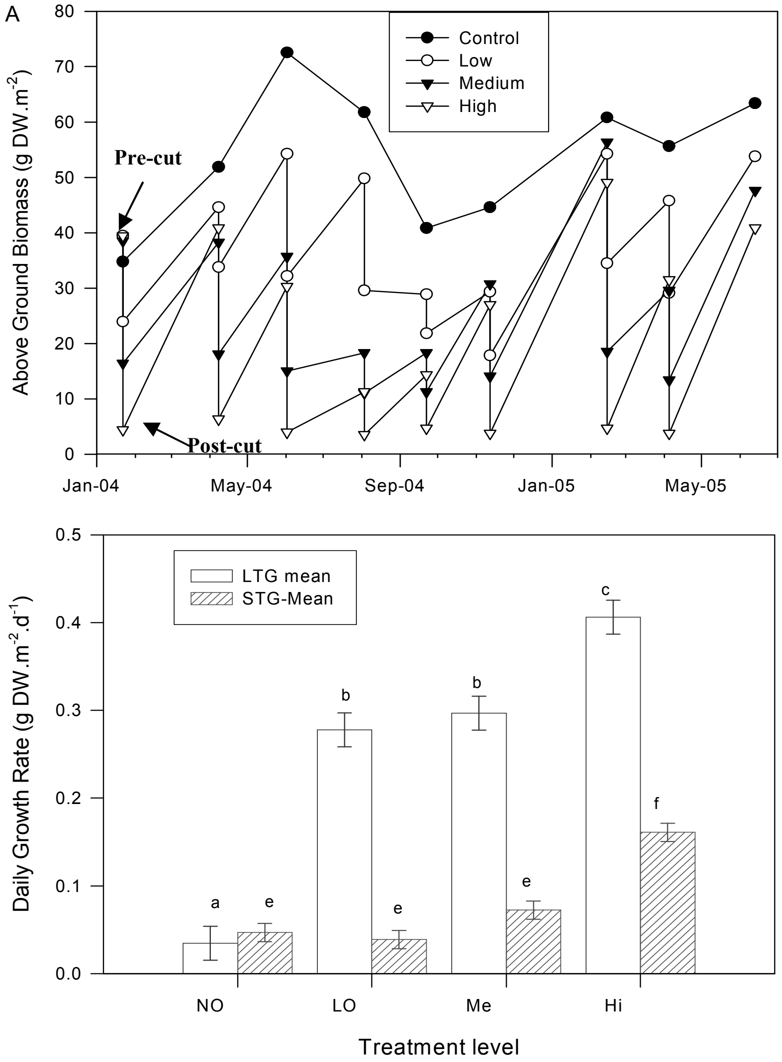

Figure 4.10. (A) Above ground biomass measured in the long-term grazing (LTG) cages prior to cutting (pre-cut) and after growth had occurred (post-cut) on each sampling date for each simulated grazing treatment in the *Cynodon dactylon* dominated edge (CDE) zone in the Longinye wetland, Amboseli National Park, southern Kenya. (B) Growth rates, expressed in biomass per day, resulting from three levels of simulated grazing (LO – low; ME- medium; HI- high) and a control (NO) in the LTG and short-term grazing (STG) cages. Small case letters indicate results of paired t-tests at *P* of 0.05 done on each set of data, i.e. LTG and STG, separately. LTG means were derived from n = 3 and STG means from n = 2. Error bars represent the standard error of the mean.

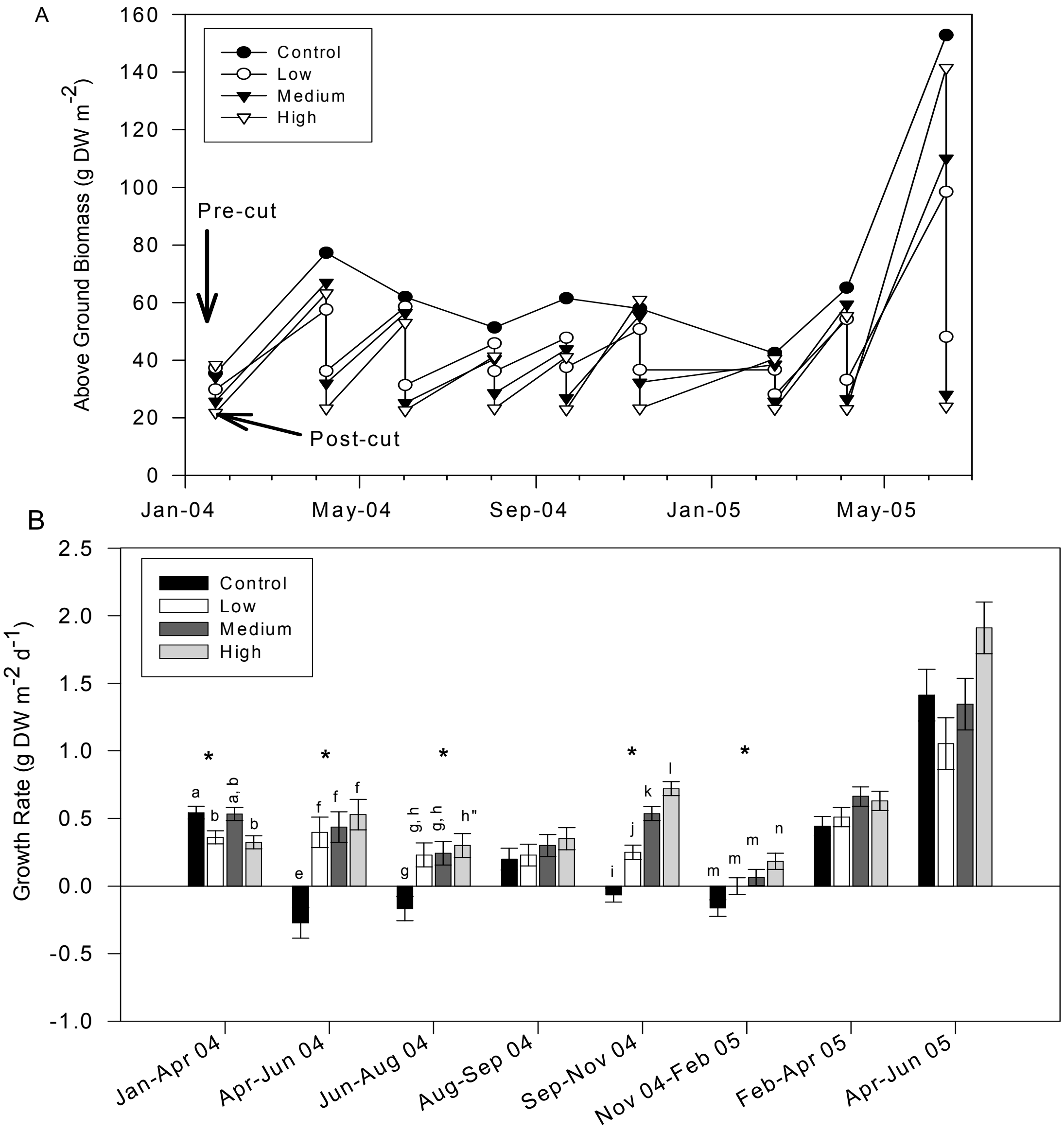

Figure 4.11. (A) Above ground biomass measured in the long-term grazing (LTG) cages prior to cutting (pre-cut) and after growth had occurred (post-cut) on each sampling date for each simulated grazing treatment in the *Cyperus laevigatus* dominated centre (CLC) zone of the Longinye wetland, Amboseli National Park, southern Kenya. (B) Growth rates, expressed in biomass per day, resulting from simulated grazing in the LTG cages. Asterisks (*) indicate those time periods when treatment effects were significant, and the letters indicate the results of t-tests conducted for each time-period separately at $P = 0.05$, except where the single quotation mark (“) is used, which indicated significance at $P = 0.1$. Means were derived from n = 3 and error bars represent standard error of the mean.

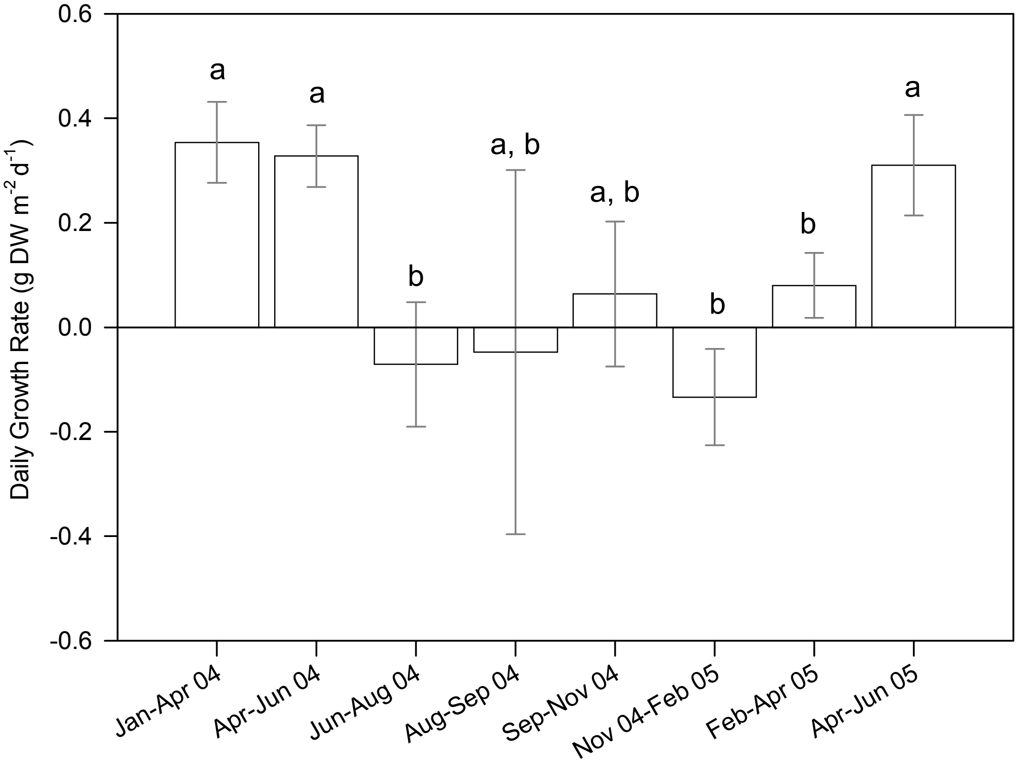

Figure 4.12. Growth rates, expressed in biomass per day, resulting from simulated grazing in the short-term grazing (STG) cages in the *Cyperus laevigatus* dominated centre (CLC) zone of the Longinye wetland, Amboseli National Park, southern Kenya. Small case letters indicate the results of paired t-tests conducted at $P = 0.05$. Means are derived from n = 2 and standard error of the mean are represented by the error bars.

4.5 Discussion

The significant difference between biomass inside and outside the mobile cages in the CDE zone upon re-sampling indicates that grazing was occurring in this zone. As expected, biomass and growth rate (change in biomass) in the mobile cages were changing with time rather than with grazing intensity, which itself did not change over time. The intensity of grazing measured in the CDE zone (0.13) was low compared to the value of 0.49 reported by McNaughton (1985) to cause the most stimulation of above-ground productivity in grazed plots in grasslands of the Serengeti. This is further corroborated by the fact that when the experiment was started, the grasses in the CDE zone were 37.7 cm tall and showed less densely packed growth characteristics, which have been reported to occur in less heavily grazed areas of the Serengeti ecosystem (McNaughton, 1984). Hence the level of grazing experienced by the vegetation in the CDE zone may not have been high enough to cause an increase in growth rate as has been reported in other studies (McNaughton, 1979a). Other wetland edge sites that are under higher grazing intensities might have responded differently under the same circumstances.

As expected, however, the biomass and growth rate of the vegetation changed with time and this may be the effect of rainfall and subsequent soil water availability, which is one of the critical environmental factors that Georgiadis *et al.* (1989) emphasize should be taken into account when looking at the effects of grazing on plant productivity. In the current study, the overall decrease in biomass over the period of the study may have been the result of the decline in average precipitation that fell between January 2003 and January 2004, with the exception of a peak in May 2003 (Figure 4.3). Furthermore, growth rate was positive when rainfall was high, such as between March and June 2003, and between November and January 2004 (Figure 4.3). McNaughton (1985) does report that there is a linear relationship between precipitation and productivity of grasslands in Serengeti.

Results from the stationary cages in the CDE zone also show a difference between biomass inside and outside the cages and a decrease in overall biomass over time, albeit not a statistically significant one. Growth rate was not different inside and outside the cages. Taken together, this confirms that during the study period biomass was decreased due to grazing and there was no long-term compensatory growth. However, the results for species composition do suggest that *D. scalarum* was being removed selectively between June and September 2003 since it was the only species that was present inside but not outside the cages in September. Byenkya (2004) reports that cattle tended to favour *D. scalarum* in the wet season, which in the present study included June and July.

Studies have reported that grazing in semi-arid ecosystems does not affect species diversity as it does in humid ecosystems (Belsky, 1988; Milchunas *et al*., 1988) The reason being that vegetation in semi-arid ecosystems need to be drought tolerant and even if there is a decrease in inter-species composition by the reduction of one species, there may not be an increase in another species unless it is tolerant to the environmental conditions. Hence, the lack of change in species composition in my study may be another example of the lack of change in a semi-arid ecosystem.

In order to compare the results of the natural grazing experiment with the simulated grazing experiment, I calculated approximate GI (1-g/ng) values for each of the grazing treatments in the latter by substituting g with control biomass and ng with biomass from a treatment. The highest simulated grazing level had a consistent GI of 0.9, while the lowest simulated grazing level had an average of 0.5 (range: 0.3 to 0.6) and the medium simulated grazing level a value of 0.7 (range: 0.5 to 0.8). These values were much higher than those encountered during the natural grazing experiment and those reported in McNaughton (1985) to induce positive growth.

When GI was increased through simulated grazing treatments, positive effects on growth were induced. In addition, the highest and medium grazing treatments increased plant growth rate relative to the low grazing treatment and control during the dry season, and the highest grazing treatment, when applied only twice as was the case in the STG cages, was able to generate a persistent positive effect on growth. This suggests that if grazing levels are high enough then above-ground productivity can be stimulated, in particular during periods of low soil water potential as was observed by Georgiadis *et al.* (1989).

Cynodon dactylon is rhizomatous and, hence, grazing tolerant (Thompson, 1985). It is present in much of the seasonally inundated and shallow wetlands, as well as the grasslands fringing the wetlands of Amboseli National Park, as shown in chapter 2 and chapter 3, which is predominantly a grazing ecosystem. Hence, the increased growth rate shown under high levels of stimulated grazing might in fact indicate the resilience of this grass to grazing. However, the simulated grazing experiment, did not take into account the effects of trampling on soil water availability, which has been shown to greatly impact grasslands under heavy grazing (Skarpe, 1991). Although moisture may not be limiting in the CDE zone, since it is part of the floodplain of the wetland and likely overlies a shallow water table, rain water that follow periods of drought may not infiltrate into the soils as easily in heavily trampled and compacted soils as it would if the soils had larger pore spaces. The results from the simulated study must, therefore, be viewed with caution.

Natural grazing in the CLC zone significantly reduced biomass outside the mobile cages relative to the inside of the cages as expected. Furthermore, neither biomass nor growth rate, which was positive inside the cages and negative outside the cages, varied with GI. Both variables had a significant date effect that appeared to follow cumulative rainfall as was the case in the CDE zone. GI did not vary over time if the results from June are discarded, since B_o was not significantly different from B_i in June. This lends further support to the assumption that grazing, albeit at low levels, is consistent throughout the year in this wetland.

Results from the stationary cages do not correspond to those from the mobile cages. This may be a result of the complexities associated with a more diverse community and the local environment in the CLC zone. However, the results of the correspondence analysis do suggest that when protected from grazing *C. laevigatus* became more dominant at the expense of the other species. This suggests that the species composition of the wetter centre of the wetland can be affected by grazing, in that grazing may maintain greater diversity. This has been suggested in other humid terrestrial ecosystems (Milchunas *et al*., 1988).

The GI calculated from the natural grazing experiment in the CLC was close to the average McNaughton (1985) found to stimulate the most compensatory growth in the Serengeti grasslands. However, there was no measurable increase in growth under natural grazing in the CLC zone. This may be due to the differences in the vegetation and the conditions of the two studies, McNaughton's study being in a dry grassland and the current study being in a permanently inundated wetland. It may, however, indicate that natural grazing has negative effects on vegetation growth in floating mat communities.

When GI for the simulated grazing experiment was calculated for the CLC cages, the highest simulated grazing level had a mean GI of 0.6 (range: 0.4 to 0.8), the lowest simulated grazing level had a mean GI of 0.4 (range: 0.2 to 0.7) and the medium simulated grazing level had a mean GI of 0.5 (range: 0.3 to 0.8). These values are lower than that from the CDE under simulated grazing treatments due to the difficulties in setting up the treatments in the water. However, they are similar to the GI calculated from the natural grazing experiment in the CLC zone, which was estimated at 0.44.

Simulated grazing treatments in the LTG cages of the CLC zone did increase growth, though the effects varied with time. When rainfall was decreasing or when no rainfall was recorded, the growth rate in the control (NO) was significantly lower than the other treatments. This suggests that vegetation growing on the floating mats does respond positively to removal of above ground biomass when rain is scarce. The growth rates from the highest grazing level were significantly higher than the growth rates from the other treatment levels only when rainfall was increasing. This indicates that the vegetation in the mats was quickly able to respond to rain when grazed down. These results suggest that grazing reduced drought stress on the clipped plants compared to the control, giving them a competitive advantage in times of drought and at the onset of rains, as is the case in dry grasslands (Georgiadis *et al.,* 1989; McNaughton, 1979b). However, moisture should not be an issue for floating mats as they overlie a permanent source of water. It has been shown that cold rain water encourages the mixing of water layers below the floating mats, which in turn increases the oxygen content of the water (Howard-Williams and Gaudet, 1985). This mixing and oxygenation of the layers may increase nutrient availability that a growing plant can take better advantage of then a senescing plant.

The fact that GI was similar in both the natural grazing experiment and the simulated grazing experiment in the CLC zone, but effects on growth were not, suggests that there may be a damaging effect of natural grazing on the vegetation mats that could be affecting growth under natural conditions. It is possible that the manner in which the vegetation was clipped did not damage the mat and hence, positive growth rates occurred under simulated grazing but not under natural grazing.

By the end of the dry season in Amboseli, the wetlands become the main source of food and water for the herbivores (Andere, 1981; Western and Lindsay, 1984). It is therefore conceivable that the floating mats inside the wetlands are being damaged through the movement and grazing activities of these herbivores at a time when the plants are also the most stressed. Hence, the positive effects of grazing are not obvious in the natural grazing experiment, but are seen when the vegetation is clipped without damage.

In the short-term grazing cages of the CLC zone, growth was negative in all treatments during the dry season, which suggests that there were no long-term effects of grazing treatments as was the case in the CDE zone. Furthermore, growth rates were negative from November 2004 to April 2005, which is most likely the result of overcrowding in these cages.

With the increase in the elephant population and changes in their migratory patterns in the Amboseli basin the wetlands are coming under immense pressure. This makes research on the impacts of natural grazing levels on wetland vegetation in Amboseli National Park critical so that management strategies aimed at the wetlands can be developed. My study showed that grazing levels on the edge and in the centre of the Longinye wetland remained consistent throughout the year and that plant growth rate and biomass varied with seasons and not grazing intensity under natural grazing regimes. When grazing intensity was increased using simulated grazing treatments on the *C. dactylon* dominated edge community, growth rate was positively affected especially during the dry season. In the centre, on the other hand, grazing intensity was not increased above that recorded under the natural grazing regime however the growth rates increased. Simulated grazing treatments do not mimic the effects of natural grazing, such as the compaction of soil on the edges of the wetland or the removal of root biomass or damage to the meristem in the floating mat community. In this study, the positive growth under simulated grazing suggests that the vegetation is capable of responding positively, in terms of biomass and growth, to grazing. However, since simulated grazing does not take into account all of the impacts of grazers, the actual effects of increasing grazing pressure on the vegetation of the Amboseli wetlands may be detrimental in the long-run.

Chapter 5

Current Vegetation and Long Term Changes in the Namelok, Kimana, Lenkir and Esoitpus Wetlands of the Amboseli Ecosystem, Southern Kenya: The Impacts of Land-Use

5.1 Introduction

Wetlands are spatially and temporally complex, diverse, and dynamic ecosystems (Mitsch and Gosselink, 2000), which have been used for centuries as agricultural and grazing lands because of their particular characteristics in many parts of the world (Hughes, 1996). In semi-arid ecosystems in particular, wetlands become an even more precious and stable source of water and fertile soils because of the insufficient and highly variable rainfall in these areas (Hughes, 1996). These wetlands not only act as reservoirs for surface water but some may also recharge aquifers (Mitsch and Gosselink, 2000), which are then tapped in various other parts of the arid region (Howard-Williams and Thompson, 1985; Irungu, 1992). Although there is debate as to the impact of wetland vegetation on evaporative loss of water, Jones and Humphries (2002) report that *Cyperus papyrus,* a C_4 emergent sedge, reduced water loss along the fringes of Lake Naivasha, Kenya, as a result of a more efficient photosynthetic system. Hence, depending on the plant community structure, wetland vegetation may help reduce loss of water through evaporative processes in a climate where potential evapotranspiration greatly exceeds rainfall (Hughes, 1996). Aquifer-fed wetlands that undergo seasonally fluctuations in extent and those fed by rivers and streams also trap fertile sediment during floods, providing areas that are continually re-fertilized, which makes wetlands attractive places for continuous agriculture to be conducted (Howard-Williams and Thompson, 1985).

In East Africa, wetlands have traditionally been a seasonal source of water for livestock, wildlife, and small-scale agriculture and fisheries, as well as a source for plant materials used for medicinal and building purposes (Chapman *et al.*, 2001). Some communities, such as the Pokomo and Wardei of the Tana River District, Kenya, continue to use the wetland habitats in traditional ways. They allow the wetland vegetation to regenerate during the wet seasons immediately following dry-season cultivation (Terer *et al.*, 2004). However, other communities have moved towards year-round use rather than dry-season use of the wetlands (Chapman *et al.*, 2001; Terer *et al.*, 2004). In Burkina Faso, increasing population density and decreasing rainfall has meant that the relative cost of clearing dense wetland vegetation for cultivation is much lower compared to the returns from rain-fed cultivation (Scoones, 1991). This has prompted a rapid increase in agricultural activities inside the wetlands. In Kenya, the colonial government encouraged draining of wetlands for agriculture, as was the global view during that period (Thenya, 2001). However in more recent recommendations (1989 to 1993 and 1994 to 1996) for the Laikipia District, a semi-arid area to the north of Nairobi city, draining of wetlands was still being recommended (Thenya, 2001).

In the semi-arid Amboseli ecosystem, wetlands (Figure 5.1) have always been key resources in the dry seasons for the nomadic pastoralist Maasai community. The Maasai have moved their livestock towards the wetlands in the dry seasons and then moved away from the wetlands to use the larger area of pasture in the surrounding ecosystem in the wet season for hundreds of years (Western, 1994). Although cultivation took place on the slopes of Mt. Kilimanjaro to the south of the ecosystem and in areas suitable for rain-fed production starting in the 1930's, it was not practiced to a great extent in the wetlands of Amboseli.

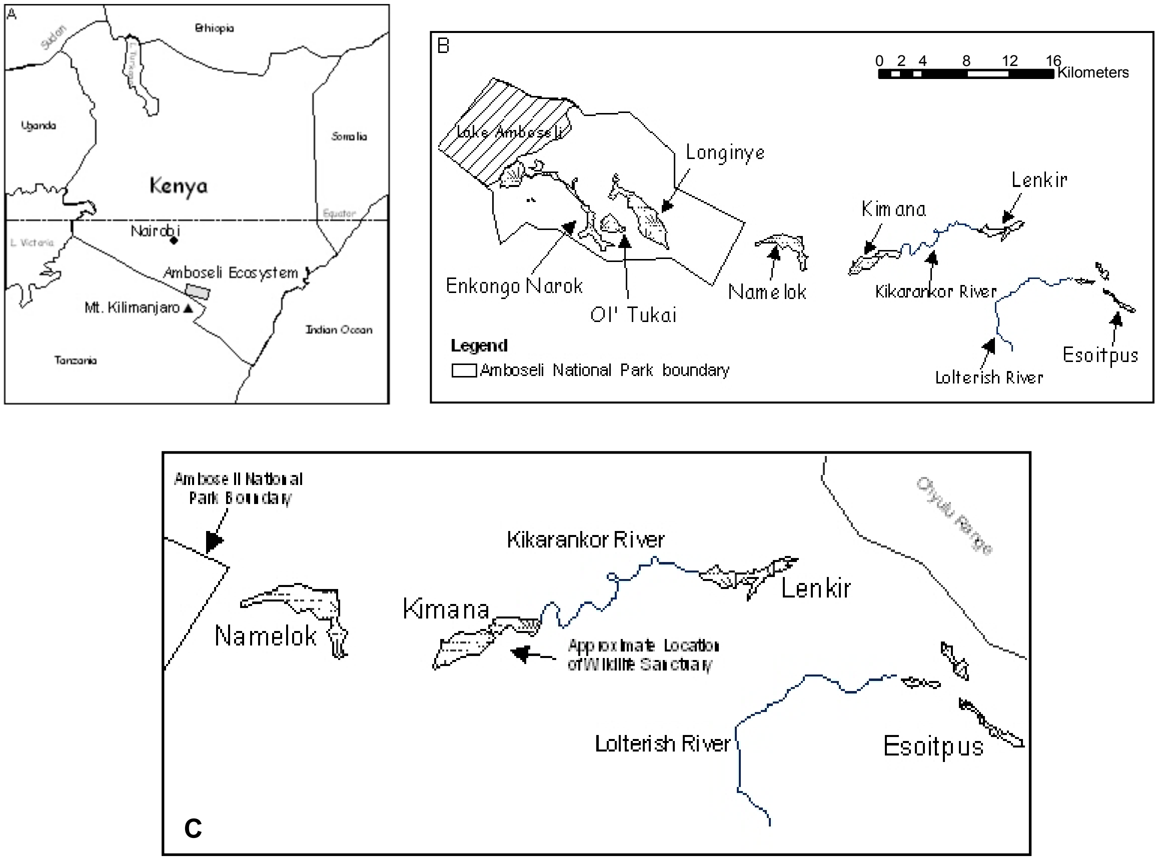

Figure 5.1. Location of the Amboseli Ecosystem (shaded area) in southern Kenya (A), the layout of the wetlands in the ecosystem (B), and the wetlands under human use to the east of the Amboseli National Park (C). Notice the location of Mt. Kilimanjaro, which feeds the springs that discharge into the Amboseli wetlands.

The loss of two of the main wetlands, Enkongo Narok and Longinye (Figure 5.1b) that were traditionally used for dry-season forage and water for livestock to the Amboseli National Park, as well as numerous drought years in the 1970's, forced some Maasai to supplement their pastoralist lifestyles with agriculture (Western, 1994). Increasing human populations, primarily driven by post-independence immigration of agrarian communities of Kikuyu and Kikamba people (Western, 1994; Southgate and Hulme, 2001), as well as land-tenure concerns amongst the Maasai (Western, 1994), also drove an advance of farming and sedentary lifestyles along the wetter margins of rivers and into the wetlands outside the Amboseli National Park (Campbell *et al.*, 2000). The irrigation activities are still predominantly small-scale, low-cost operations requiring furrow set-ups (Githaiga *et al.*, 2003), but the area under irrigation is increasing. The percentage of Maasai who are now involved in cultivation increased from 20% in 1977, when irrigated agriculture around the wetlands was in its early stage, to 37% in 1999 (Campbell *et al*, 2000). Irrigation has allowed year-round cultivation to be conducted and furthermore, large amounts of water from some of the rivers that feed these wetlands have been diverted for use in industry (Githaiga *et al.*, 2003).

Each of the wetlands under human use (Figure 5.1c) has undergone slightly different histories, which may have translated into different plant communities. However they all receive water either through underground springs or over-ground rivers that are fed by rainfall from the forested regions found between the 2000 to 2500 m isoclines of Mt. Kilimanjaro (Kaser *et al.*, 2004). These regions have been experiencing decreases in annual precipitation of up to 36% for the period between 1922 and 2002 (Hemp, 2005). This has probably translated into less water flowing into the wetlands in the Amboseli ecosystem, even though the annual rainfall in the Amboseli basin does not show any directional trend over a 25-year period (Altmann *et al.*, 2002). Hence, we are considering wetlands that are being increasingly used by humans, and which have also likely experienced decreasing amounts of source water from the forests of Mt. Kilimanjaro. However, except for a single ground survey that was conducted by Githaiga *et al.* (2003) in particular locations around these wetlands for a water quality study, there is little information about the vegetation of these wetlands now, let alone prior to and during, the advent of agricultural activities.

This study had two objectives. The first objective was to document the current vegetation communities in these wetlands and the second was to study the changes in vegetation cover in the wetlands over four decades (1970's, 1980's, 1990's and 2000's), in an attempt to understand the impacts of land-use on natural wetland vegetation. Supervised classification and Normalized Difference Vegetation Index (NDVI) change detection analyses on satellite imagery were used to accomplish these objectives, as was the case in Chapter 2. Details on the efficacy of these methods in wetland studies were presented in Chapter 2 and will not be repeated here.

5.2 Materials and Methods

5.2.1 Image acquisition

LANDSAT images from 1976, 1987, 1993/5, and 2002 that included the wetlands of interest for this study were acquired from the Regional Centre for Mapping and Resource Development (RCMRD) based in Nairobi, Kenya, along with the images used in Chapter 2. In 1976 (path 180, row 62) all the wetlands including those inside the park were captured on one scene, and in 1987 (path 168, row 62) the Namelok and Kimana wetlands were captured on the same scene as the park wetlands. The path 168 row 62 image scenes from 1993 and 2002 captured Namelok along with the park wetlands and, hence, Namelok was subset from these images after pre-processing and classification was completed. The path 167, row 62 image scenes from 1995 and 2002 captured the Kimana, Lenkir, and Esoitpus wetlands. The selection criteria for these images were the same as those for the park wetlands; that is, they were based on availability, cloud cover, and cost, and dry-season images were given priority. All the images used were from February except for the 2002 image that captured the Kimana, Lenkir, and Esoitpus wetlans (path 167), which was captured in July. Since July is normally the first month of the long dry season following the long wet season, and February is the end of the short wet season, it was assumed that the vegetation does not differ drastically between these two months.

5.2.2 Image pre-processing

Details of image pre-processing are the same as described in Chapter 2 of this thesis and will not be repeated here. However, along with the 1993 image, the 1995 image also needed geo-correction. This was done using the geo-correction procedure explained in Chapter 2, except that 13 ground control points (GCPs) were used to correct the 1995 image to within 0.38 pixel (10.83m) of the 2002 path 167 image. Geo-correction of this image was more difficult than the correction of the 1993 image due to the poorer quality of this image, which made finding GCPs challenging. Image masking, sub-setting, and NDVI calculations were conducted on the path 167 images in the same manner as for the path 168 images.

5.2.3 Image classification

As described in Chapter 2, spectral bands 2, 3, 4, and 5, which cover the green to middle infrared portions of the electromagnetic spectrum, were used to conduct an unsupervised classification on the 2002 image from path 167. As was done for the 2002 image from path 168 in Chapter 2, the raw 2002 image from path 167 was separated into 20 classes using 100 iterations of the K-means clustering algorithm in FOCUS. These classes were then used to identify ground truth sites that would be used in a supervised classification.

Ground truthing for Namelok to Esoitpus was conducted at the same time as the park wetlands. Details of this exercise are given in Chapter 2. A sample of the photographs showing some of the wetland classes and irrigated areas are presented in Figure 5.2. More information was collected for the 168 scene that included the Amboseli National Park wetlands and the Namelok wetland than for the other three wetlands in the 167 scene. As a result, the classification of the 168 scene and, hence, Namelok, was more detailed than that of the 167 scene.

The ground truth information was used in the same way as in Chapter 2 in order to create training classes. The training classes were tested for separability using the Bhattacharrya distance statistic and the class histograms were examined for normal distributions (Campbell, 2002). When classes were not spectrally separable, they were merged and re-tested. Wetland habitats, however, were not merged whenever possible since they were the focus of this study. The Maximum Likelihood algorithm with the null class option was used to conduct the supervised classification of the 2002 image from path 167 in the same way as the image from path 168. An accuracy assessment was conducted on the classified image. This was more challenging for the wetlands outside the park than for the wetlands inside the park since there is very little literature on the status of their vegetation at present. The vegetation classes in Namelok, however, are probably more accurate since they were derived from a larger amount of data from the park wetlands. This is because Namelok was classified in the same image as the park wetlands.

5.2.4 NDVI change detection

As in Chapter 2, spectral bands 2 and 4 of the 1976 image (Lee and Marsh, 1995) and bands 3 and 4 of the images of the remaining years (Campbell, 2002) were used to calculate NDVI for each image . The bands from the image of a later year were corrected using matching bands from the previous year using the MATCH and LUT algorithms before NDVI images were calculated for each year. This was done for each set of comparisons (1976 to 1987, 1987 to 1993/5, and 1993/5 to 2002).

The NDVI of the previous year was subtracted from that of the later year in order to create NDVI change detection images that were then exported to ArcMap. The positive and negative changes in NDVI were displayed using the mean NDVI ± 2 standard deviations.

5.3 Results

5.3.1 Current status of vegetation: 2002 image classification

5.3.1.1 Namelok Wetland

During classification a total of 15 classes were identified for the 168 scene that included the Namelok wetland. For simplicity of presentation the classes not related to wetland-type vegetation, such as the dry grasslands and scrubland, were aggregated, where suitable, to obtain the 9 classes shown in Figure 5.3. Since this wetland was classified in the same image as the park wetlands, the accuracy assessment was the same. An overall Kappa index of 0.525 ± 0.004 and an overall accuracy of 60% was obtained for this map. The percent of the area that was not classified into an information class (null) for the whole image was about 3%, of which 2.45% was classified as null around the Namelok wetland (Table 5.1).

Separability of between the riverine vegetation class and the open scrubland class was the lowest (Bhattacharrya distance of 1.4). However, as explained in Chapter 2, these classes were not aggregated because it was decided that the lack of good separation was a result of mixed pixels, since these two vegetation classes appear close to one another (Figure 5.3). The *C. laevigatus* dominated seasonal wetland class, the *Cyperus* dominated deep water wetland class, and the *C. immensus*/*C. dactylon* shallow water wetland class did not have good separability between them. Aggregating them into one class, as mentioned in Chapter 2, did not improve their separability measure. Hence, I assumed that since these vegetation types are found close together, mixing of pixels might also be causing a reduced separability. These classes were not aggregated. However, it is important, therefore, to keep in mind that the percent coverage of these classes may have been either under- or over-estimated in the classification map (Figure 5.3; Table 5.1).

Figure 5.2. Typical vegetation scenes in (A) *Cyperus* dominated deep water wetland (in the background) and grass dominated seasonal wetland (in the fore ground) habitats, and an irrigated maize (B) and vegetable (C) field found to the east of Amboseli National Park, southern Kenya.

The open grassland community inside the park differed in species composition from the grassland community around Namelok, but they were not spectrally different enough to retain them as separate classes during classification. Instead the differences in the species can be seen by comparing the tables (Table 2.1; Table 5.1). The grassland community around Namelok has more shrub species and is less common than inside the park. Around Namelok, riverine, grassland, and scrubland communities are equally represented (Table 5.1).

The results of supervised classification indicate that Namelok has a minimal sedge-dominated deep water wetland (Figure 5.3; Table 5.1). The area of both the *Cyperus* dominated deep water wetland and *C. immensus*/*C. dactylon* shallow wetland is represented by less than 0.05% of the classified image (Table 5.1). No open water (vegetation class 1 in Chapter 2 Table 2.1) was captured in this part of the image by the classification (Figure 5.3) even though Githaiga *et al.* (2003) reports that water from the source springs feeds into a large *C. papyrus* wetland. However, there is a well-developed *C. laevigatus* dominated seasonal wetland, as well as a riverine community dominated by a mixture of grasses and herbaceous vegetation along with scattered tree and shrub species (Figure 5.3; Table 5.1). Both these classes cover between 8 to 9% of the area classified and appear to be widely distributed even at large distances from the wetland (Figure 5.3). This wide distribution might be the result of misclassification based on the separability measures. The grassland community in the centre of Namelok wetland (Figure 5.3) was dominated by *C. dactylon*, whereas the other species listed for the grassland vegetation class in Table 5.1 were dominant to the west of the wetland (Figure 5.3).

About 2% of the classified area was covered by irrigated agricultural fields (shambas) and less than 1% was abandoned shambas (Figure 5.3; Table 5.1). Most of the irrigated fields were situated along the southern boundary of the wetland though some pixels were classified as shambas in the north as well. The shambas that were abandoned occur inside the boundaries of the estimated extent of the wetland, and these were abandoned in 2006 as a result of flooding which demonstrates that agriculture does occur in the wetland as well as along it (Figure 5.3).

5.3.1.2 Kimana, Lenkir, and Esoitpus Wetlands

The Kimana, Lenkir, and Esoitpus wetlands were classified separately from the Namelok wetland because they were captured on a different scene at a different time in the year. The ground truthing exercise, which was carried out in February, may have included more error in the classification of these wetlands, which were captured in July, than for Namelok that was captured in February. However, the overall Kappa index for the Kimana to Esoitpus (K-E) classification was 0.628 ± 0.007 and the overall accuracy was 73%. These results are more than likely the result of having fewer classes at the start of the classification, which is known to both improve accuracy and Kappa index (McCarthy *et al.*, 2005). The null class was still about 3% of the image, which was not unlike the case for Namelok (Table 5.1; Table 5.2).

The largest vegetation class for the K-E scene was the *Acacia tortilis* and *Commiphora* woodland (Table 5.2) and overall this area appears to have a lot more woody vegetation than did Namelok (Figure 5.3; Figure 5.4). However, the percentage of woody vegetation attributed to riverine vegetation was small (1.92%) in K-E and most of this class was identified as being in the Esoitpus wetland (Figure 5.4; Table 5.2). The *Cyperus* dominated deep water wetland class and the *C. laevigatus*/*C. dactylon* dominated seasonal wetland class covered 0.56% and 1.36%, respectively (Table 5.2), with all of the former in Kimana, and most of the latter in Lenkir (Figure 5.4). The riverine vegetation class and the *C. laevigatus*/*C. dactylon* dominated seasonal wetland class had the poorest separability, with a distance of 1.1. These classes are both dominated by *C. dactylon*, the main difference between these two classes being the denser herbaceous layer.

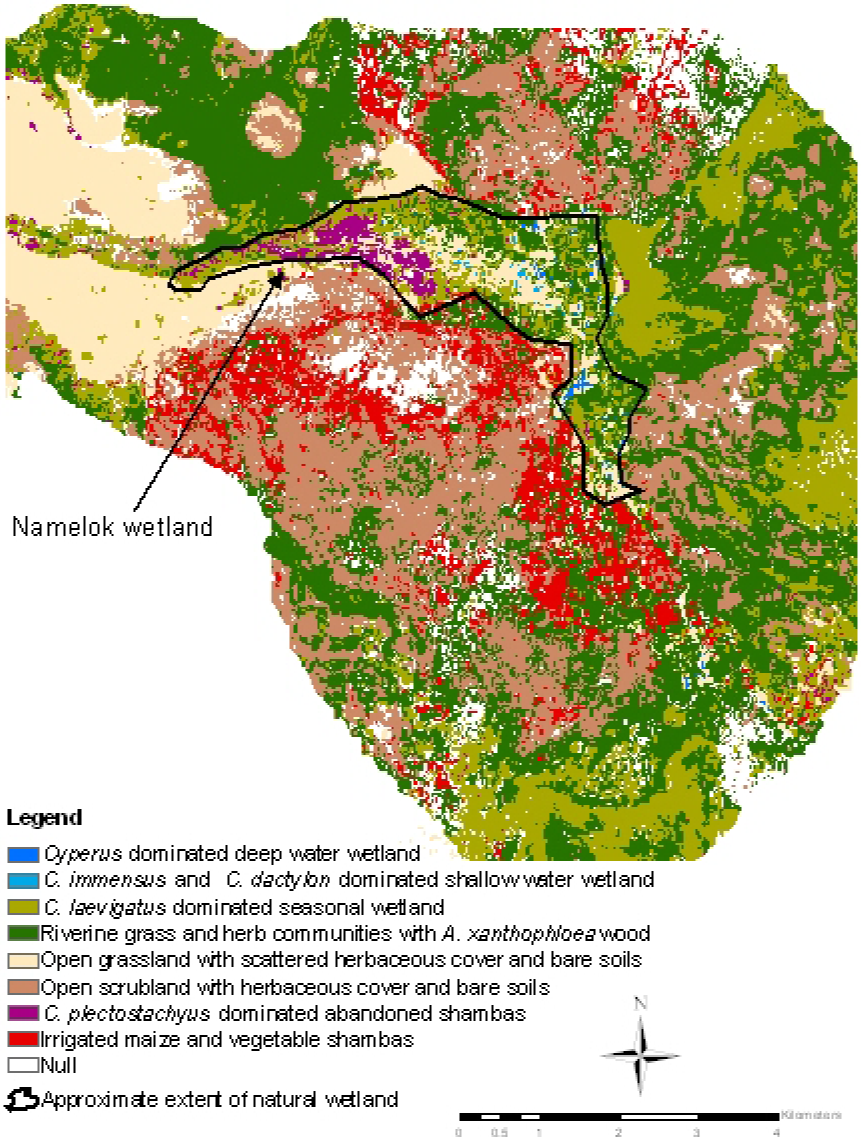

Figure 5.3. The main vegetation classes found in and around the Namelok wetland found to the east of Amboseli National Park, southern Kenya, that was derived from a supervised classification using bands 2 to 5 of a February 2002 LANDSAT ETM+ image.

Table 5.1. Species that were included in the vegetation classes from the supervised classification of the Namelok wetland area found to the east of Amboseli National Park, southern Kenya, along with the approximate area covered by each class as a percentage of the total classified area.

	Vegetation Class	**Area (%)**	**Dominant Species**	**Other Species**
1.	*Cyperus* dominated deep water wetland (permanently inundated)	< 0.05	*Cyperus immensus, Cyperus laevigatus*	*Azolla spp., C. dactylon*
2.	*C. immensus* and *C. dactylon* dominated shallow water wetland (mostly inundated)	< 0.05	*C. immensus, Cynodon dactylon*	*Solanum incanum, Withania somnifera, Phoenix reclinata*
3.	*C. laevigatus* seasonal wetland (inundated during periods of high rainfall)	7.80	*C. laevigatus*	*Digitaria scalarum, Sporobolus spicatus, C. dactylon*
4.	Riverine grass and herbaceous community with *A. xanthophloea*	8.25	*Cyathula erinacea, Dactyloctenium aegytium, Cyperus merkeri, Sporobolus fimbriatus*	*Acacia xanthophloea, Azima tetracantha, Eriochloa nubica*
5.	Open grassland with scattered herbaceous cover and bare soils	6.08	*Psilolema jaegeri, Sporobolus species, Cynodon plectostachyus, Pennisetum mezianum*	*Chloris roxburgiana*, *Sericocompsis hildebranti*, *S. incanum*
6.	Open scrubland with herbaceous cover and bare soils	6.16	*Tribulus terristris, Suaeda monoica, Salvadora persica*	*Balanites aegyptiaca, Acacia tortilis, Justicia uncinulata,*
7.	*C. plectostachyus* dominated abandoned agricultural fields (shambas)	0.32	*C. plectostachyus*	*Setaria verticillata, Amaranthus graecizans, Leonotis nepetifolia, A. xanthophloea, A. tetracantha*
8.	Irrigated maize and vegetable shambas	2.01	*Maize*	*Bananas, Tomatoes, Onions*
9.	Null – areas not assigned to a class	2.45		

About 11% of the area was classified as being under irrigated agriculture, with most of the activity around Kimana, followed by Lenkir and the edges of the Kikarankor and Lolterish Rivers (Figure 5.4; Table 5.2). The area under irrigation to the south of Kimana is suspect as this area is a wildlife sanctuary (Figure 5.1c). This is more than likely a misclassification because the irrigated shamba class had separability distances of between 1.4 and 1.6 with the woody vegetation classes 3, 5, and 7 in Table 5.2. The fact that the shambas are usually in wooded areas as seen in Figure 5.2 b and c, is likely the reason for this confusion. However, with the information available to me, I was neither able to improve these distance values nor aggregate the classes. Hence, the area under irrigation is more than likely over-estimated especially around Kimana and to the east of Esoitpus (Figure 5.4).

5.3.2 Temporal change in vegetation: 1976 to 2002 NDVI change detection

In 1987, 3.5% of the Namelok-Kimana area used for change detection had a lower NDVI than in 1976, and 3.0% had a higher NDVI in 1987 than in 1976 (Figure 5.5a). Most of the decrease appears to have occurred around the northeastern edge of Kimana (on the right of the figure), whereas most of the increase happened within the boundaries of the Namelok wetland (Figure 5.5a). Below the southeastern arm of Namelok there were a few pixels that showed a positive change in NDVI (Figure 5.5a). Similarly, to the southwest of Kimana there are scattered pixels of positive change (Figure 5.5a). These areas may indicate irrigated fields.

Since the NDVI is a measure of greenness, local rainfall patterns from the period in which a satellite image is captured must be accounted for as rainfall plays a major role in plant growth, especially in arid areas. As in Chapter 2, I used rainfall for the 4 preceding months from the date of image capture to compare the two images used in a vegetation change detection analysis. This meant that most of the rainfall values used came from October to February except for the 167 scene from 2002 that covered March to July (Table 5.3).

Based on this criterion the period in 1976 was much drier than in 1987 (Table 5.3). Hence not all the increases in NDVI, especially outside the wetlands, can be attributed to the presence of irrigated fields. The decrease in NDVI seen inside the southeastern arm of the Namelok wetland is interesting, however, and might indicate loss of vegetation resulting from harvesting of either wetland plants or irrigated crops or from the formation of open pools of water in 1987.

Table 5.2. Species that comprise the vegetation classes from the supervised classification of the Kimana, Lenkir and Esoitpus wetlands found to the east of Amboseli National Park, southern Kenya, and the area covered by each class as a percentage of the total classified area

	Vegetation Class	Area (%)	Dominant Species	Other Species
1.	*Cyperus* dominated deep water wetland with *C. papyrus* islands	0.56	*Cyperus papyrus*, *Cyperus immensus*	*Cyperus laevigatus, Ludwigia stolonifera*
2.	*C. laevigatus* and *C. dactylon* dominated seasonal wetland	1.36	*C. laevigatus and Cynodon dactylon*	*Acacia xanthophloea, Pluchea ovalis*
3.	Riverine vegetation with *C. dactylon*, *A. xanthophloea* and scrub	1.92	*C. dactylon*	*Solanum incanum, Amaranthus hybridus, A. xanthophloea*
4.	*S. kentrophyllus* grassland with scattered trees and scrub	6.08	*Sporobolus kentrophyllus*	*Cynodon plectostachyus, A. hybridus, Dicliptera albicaulis, Salvadora persica, Balanites aegyptiaca*
5.	*A. mellifera* and *Cucumis* shrub with herbaceous understory	11.10	*Acacia mellifera, Cucumis spp.*	*B. aegyptiaca, Ipomea spp., Setaria acromelana, Heliotropium spp., S. incanum, Lycium europeum*
6.	*A. tortilis* and *Commiphor*a dominated open woodland with herbaceous understory	54.51	*Commiphora africana, A. tortilis, Cyathula erinacea, Tribulus terristris*	*Eragrostis spp., Sporobolus nervosa, Sericocomopsis pallida, Pennisetum stramineum, B. aegyptiaca, A. mellifera*
7.	Forested areas	110.08	*Acacia spp., Commiphora spp.*	Unknown
8.	Irrigated maize and vegetable agricultural fields (shambas)	10.51	Maize	Beans, Bananas, Tomatoes, Onions, Kale, Cabbage
9.	Null – areas not assigned to a class	2.88		

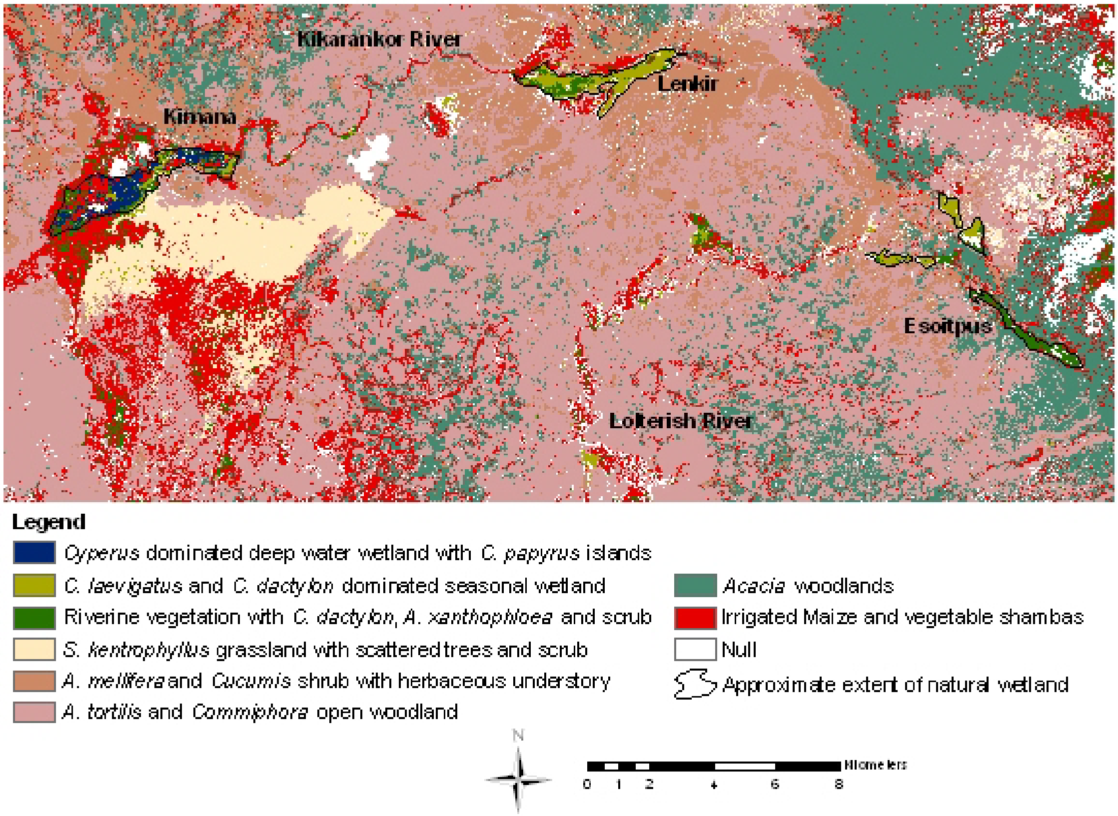

Figure 5.4. Results for the Kimana, Lenkir and Esoitpus wetlands found to the east of Amboseli National Park, southern Kenya, showing the main vegetation classes derived from a supervised classification on bands 2 to 5 of a July 2002 LANDSAT ETM+ image.

From 1987 to 1993, 5.8% of the area used for change detection showed an increase in NDVI and only 1.7% showed a decrease (Figure 5.5b). Most of the increase occurred in the surrounding areas (Figure 5.5b), which is consistent with the rainfall data for January 1993 (Table 5.3). However, the area of decrease in NDVI was mostly inside the Kimana wetland and to a much lesser extent the centre of Namelok wetland (Figure 5.5b). This may indicate an increase in open water, which would reduce NDVI values.

Namelok did not change much between 1993 and 2002. However, 4.1% of the area covered in the change detection showed a decrease in NDVI and 1.8% showed an increase (Figure 5.5c). Most of the increases occurred in the areas classified as grasslands in Figure 5.3, whereas the decreases occurred in areas classified as *C. laevigatus*/*C. dactylon* seasonal wetland or riverine vegetation (Figure 5.3; Figure 5.5c). Total rainfall that fell in the 4 months preceding the date of image-capture was higher in 1993 than in 2002, primarily due to the January 1993 rain event (Table 5.3). This should have caused NDVI to decrease in the grasslands. However, rainfall in December 2001 was high, which would have caused greening in this area and the resultant increase in NDVI observed in the image (Figure 5.5c). The decrease in NDVI in the seasonal wetland and riverine communities is interesting, since they did not increase in greenness in response to the January 1993 rain event as shown by a lack of change in these areas between 1987 and 1993 (Figure 5.5b). Two possible explanations exist. The first is that there were lingering pools of water left from the December 2001 rains that would decrease NDVI. The second possibility is that the vegetation in these areas was removed. Inaccuracies in the change detection process, however, cannot be ignored either.

Kimana showed increased NDVI in the centre, the western edge, and the southwestern edges between 1995 and 2002 (Figure 5.5d). This increase, however, only constituted 0.7% of the total area used in the change detection analyses. Over 7% of the area showed a decrease in NDVI between 1995 and 2002 (Figure 5.5d). The period between October and February of 1995 was wetter than the period from March to July in 2002, since the 2002 path 167 scene was captured in July (Table 5.3). Hence, there was less moisture available to the grass and woody vegetation in 2002 than there was in 1995, which may have resulted in the large area that shows decreased NDVI. Most of the increases in NDVI appear to have occurred in areas that were classified as being under irrigation or having *C. laevigatus* and *C. papyrus* communities (Figure 5.4). This does concur with the fact that, whereas there was less moisture available to all the other vegetation experiencing the middle of the long-dry season in the Amboseli ecosystem, the wetland and agricultural plants were being provided with sufficient moisture to maintain vigor.

The Lenkir (top left of Figure 5.6a) and Esoitpus (bottom right of Figure 5.6a) wetlands did not give the same results in the 1976 to 1987 change detection analysis. There was a decrease in NDVI over 1.6% of the area analysed, and most of this seemed to occur around the periphery of Lenkir wetland (Figure 5.6a). On the other hand, 4.1% of the area showed an increase in NDVI and this was centered at the Lolterish River (Figure 5.1c) and Esoitpus wetland (Figure 5.6a). As described already, 1987 was wetter than 1976 and, hence, we should have seen an increase in NDVI around Lenkir as well as in Esoitpus. The decrease in NDVI around Lenkir therefore, might indicate removal of vegetation or areas of flooding.

Between 1987 and 1995, 3.5% of the area analysed showed a decrease in NDVI whereas 2.1% showed an increase in NDVI. These changes mostly occurred around the wetlands and Lolterish River (Figure 5.6b). Overall, the 4 months preceeding the date of capture for the 1995 image was wetter than the same period for the 1987 image (Table 5.3). The areas of decreased NDVI in the wetlands and on the margin of Lolterish River might correspond to pools of open water and areas of flooding. On the other hand, areas of increased NDVI in the areas outside the wetland boundaries are more likely due to the new vegetation growth in response to higher rainfall.

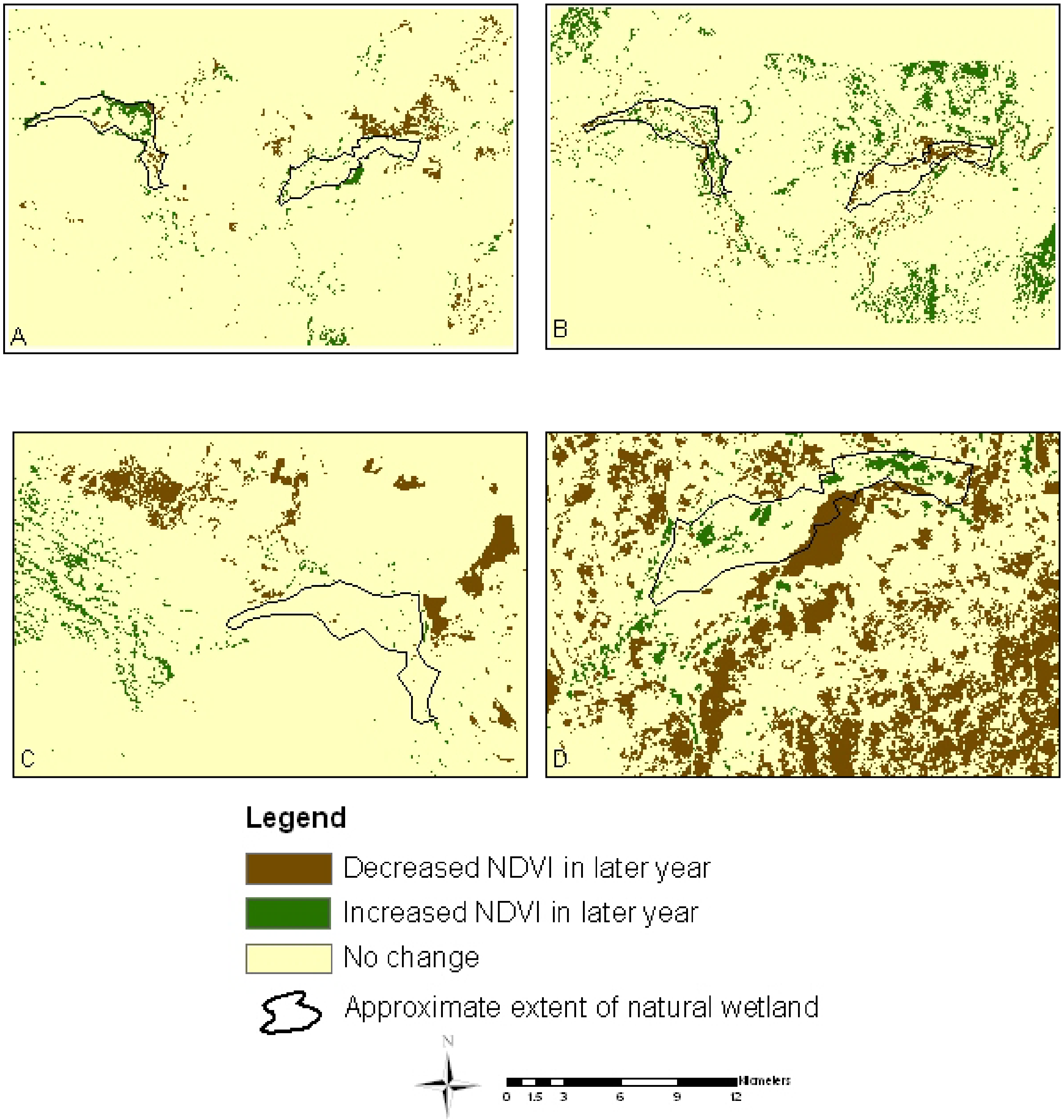

Figure 5.5. Detection of change over four decades in the Normalized Differential Vegetation Index (NDVI) for the Namelok (on left) and Kimana (on right) wetlands in Kajiado District, southern Kenya, where (A) is the difference image for 1976 to 1987, (B) is the difference image for 1987 to 1993, (C) is the difference image for Namelok for 1993 to February 2002, and (D) is the difference image for Kimana for 1995 to July 2002. The difference images were derived by subtracting the NDVI values of the previous year from those of the current year so that an increase in NDVI indicates more vegetation vigor in the current decade as compared to the previous decade.

Table 5.3. Monthly rainfall values for the 4 months preceding the month in which an image was captured for the years used in an NDVI change detection analyses for the Amboseli wetlands found to the east of Amboseli National Park, southern Kenya. The two images from 2002 were captured at different times of the year. The scene from path 168 covers the Namelok wetland and was captured in February like the 1976 to 1995 images, whereas the scene from path 167 that covers the Kimana, Lenkir and Esoitpus images was captured in July.

Month	**1976**	**1987**	**1993**	**1995**	**2002 Path 168**	**2002 Path 167**
October	7	59	0	23.4	24.0	-
November	46	93	4	82.2	50.5	-
December	44	43	37	97.4	130.9	-
January	0	28	264	21.0	61.0	-
February	28	4	15	121.0	0.0	-
March	-	-	-	-	-	43.4
April	-	-	-	-	-	58.0
May	-	-	-	-	-	48.8
June	-	-	-	-	-	0.0
July	-	-	-	-	-	0.0
Total	125	227	320	345	266.4	150.2

As explained above with respect to NDVI change in the Kimana wetland, 1995 was wetter than 2002 and this is reflected in the NDVI change detection analysis for the Lenkir and Esoitpus wetlands. The area of decreased NDVI is 2.4% and the area of increased NDVI is 1.8%. Most of the increase is around Lolterish River and to the east of Esoitpus, though some occurred to the north and west of Lenkir (Figure 5.6c). These areas were classified as irrigated agriculture and woodland (Figure 5.4). The increase in greenness in areas classified as woodland is interesting since the 2002 image is from the middle of the long-dry season and hence, one would expect lower vigor in the wooded areas. However, as was the case in the Kimana image, the increased NDVI might be the residual effect of the December 2001 rainfall (Table 5.3). Areas of irrigated agriculture, however, would remain green due to the continuous supply of water from the irrigation system. The decreases in NDVI occurred around the northeastern to southeastern edges of Lenkir (Figure 5.6c), which have been classified as *A. mellifera* and *Cucumis* shrub (Figure 5.4). This corresponds better to the fact that the period from which the 2002 path 167 scene was captured was dry. However, the difference in response of these communities and that of the woodlands is interesting.

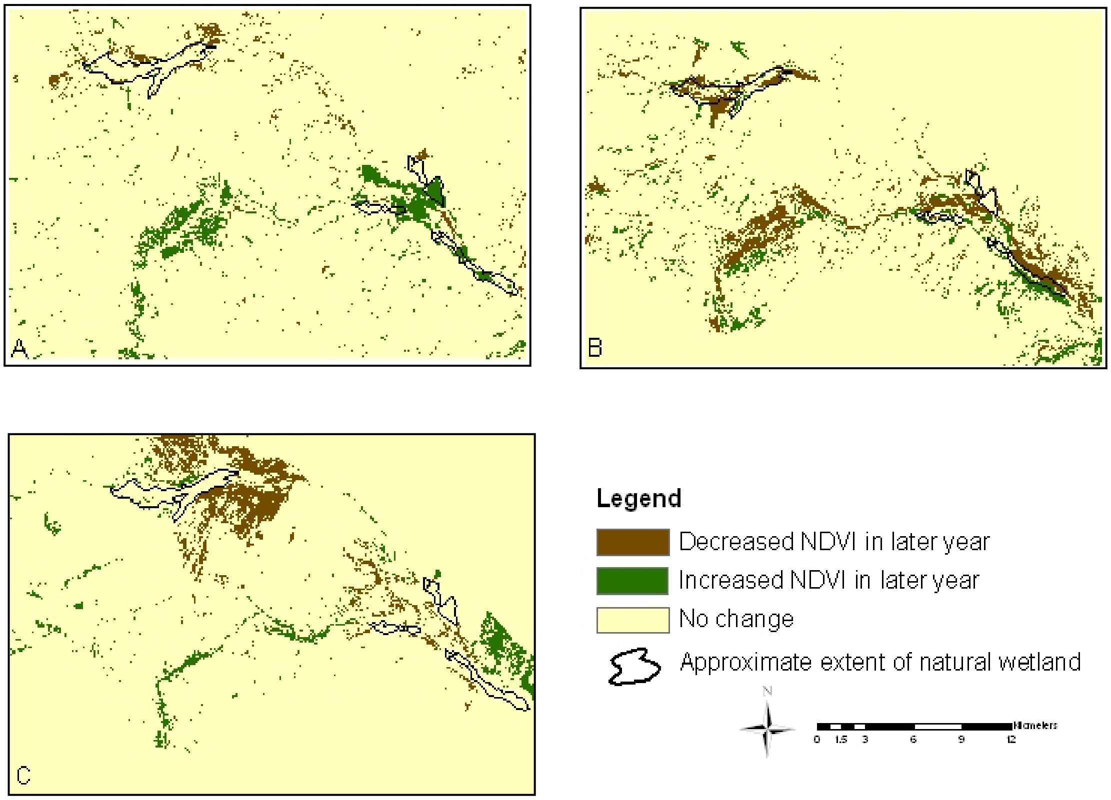

Figure 5.6. Detection of change over four decades in the Normalized Differential Vegetation Index (NDVI) for the Lenkir (top left) and Esoitpus (bottom right) wetlands found to the east of Amboseli National Park, southern Kenya, where (A) is the difference image for 1976 to 1987, (B) is the difference image for 1987 to 1995, (C) is the difference image for 1995 to July 2002. The difference images were derived by subtracting the NDVI values of the previous year from those of the current year so that an increase in NDVI indicates more vegetation vigor in the current decade as compared to the previous decade.

5.4 Discussion

Currently, the Namelok, Lenkir and Esoitpus wetlands outside the boundaries of Amboseli National Park in Kajiado District, southern Kenya, appear to have poorly developed deep or shallow water wetland communities but large areas of *C. laevigatus* sedge and grass-dominated seasonal wetland and riverine communities. Kimana, on the other hand, has a deep water sedge community along with small seasonal wetland and riverine communities. Irrigated fields are not the most extensive class, but appear to occupy much of the edges of the wetlands (except Esoitpus) and the major rivers in the area. Irrigated fields appear to be more extensive in Kimana and Namelok, less so in Lenkir, and likely also less common around Esoitpus than indicated because of misclassification. These differences in wetland communities and areas under irrigation are probably the result of the histories of each of these wetlands.

Namelok went from minimal agriculture in 1971 to an explosion of irrigated agriculture between 1983 and 1984 (Lindsay, 1987). The area surrounding Namelok was fenced in 1999 in order to reduce damage to crops by wildlife (Worden *et al*., 2003). The occurrence of a large area of irrigated agriculture and the presence of abandoned fields in this area is, therefore, consistent. Furthermore, Githaiga *et al.* (2003) report that water from an underground stream is now captured in a concrete tank for domestic use, following which it is channeled into a *C. papyrus* wetland that in turn feeds into irrigation canals that are used in maize, tomato, onion and banana cultivation. The exact location of the stream was not given by the authors. The small area within the boundary of Namelok wetland that was classified as *Cyperus* dominated deep water wetland (Figure 5.3) might correspond to the *C. papyrus* wetland mentioned in Githaiga *et al*. (2003).

The hydrological condition of a wetland is one of the main factors that influence its plant community structure and development (Mitsch and Gosselink, 2000). The dominant presence of *C. dactylon* grasslands and *C. laevigatus* seasonal wetland habitats in the Namelok wetland are indicative of dry conditions within the wetland. Both these species are tolerant of seasonal inundation and are common on margins of wetlands rather than in deep water (Thompson, 1985), as was seen in the Ilmerishari and Longinye wetland edges in chapter 3 and 4, respectively. Since irrigated agriculture has been well established in this area since 1984, it is possible that the water levels in the wetland have steadily decreased and allowed for the expansion of the seasonal wetland and grassland communities.

Succession models constructed for the Carolina Bay wetlands have shown that draw-down in deep-water wetlands results in the establishment of a more diverse community, in particular of non-wetland plants, compared to the results of draw-down in grass/sedge marshes (Mulhouse *et al.,* 2005). The authors suggest that the open structure of the deep-water wetland community provides bare soils in which non-wetland plants can establish during periods of draw-down. In dense grass/sedge marshes, however, the community is more robust and less bare soil is accessible for establishment of new species (Mulhouse *et al.,* 2005). The nature of succession, that is, whether it is cyclical or directional, is dependent on the factors acting on the community (Mitsch and Gosselink, 2000; Mulhouse *et al.*, 2005). Activities such as burning or grazing of vegetation have the potential to alter succession, however, an alteration in the hydrological condition of the wetland is normally the overwhelming factor that drives succession (Mitsch and Gosselink, 2000; Otte, 2001).

The results of NDVI change detection for Namelok shows a positive change in NDVI within the seasonal wetland community inside the wetland between 1976 and 1987. Although rainfall was higher in 1987 than 1976, the surrounding habitat did not show a similar increase in NDVI. Taken together, these results may suggest the development of the seasonal wetland community between 1976 and 1987 that is characteristically capable of responding to small amounts of rainfall quickly (Swift *et al*., 1996). If this is an accurate assessment, the results concur with the development of agriculture in Namelok that favoured the formation of seasonal wetland communities. However, ground information from those years is required to confirm this conclusion.

The expansion of agriculture around Namelok was harder to determine using the NDVI images because of the effect of rainfall. The only time period when irrigated fields could be identified with some certainty was between 1993 and 2002, since the later year was drier. The areas of positive change also corresponded to the areas classified as irrigated agriculture in the 2002 classification, which confirms the NDVI results.

The Lenkir wetland appears to be comprised almost completely of seasonal wetland and some riverine vegetation communities, with no open or deep water wetland communities. Furthermore, irrigation occurs on its northern and southern edges and all along the Kikarankor River, which connects Lenkir to the Kimana wetland. Githaiga *et al.* (2003) report that irrigation is common in this area and that the eastern end of the wetland is used for livestock grazing. However, a large irrigation scheme that was situated just to the southwest of the wetland was abandoned in the late 1990's as a result of a decrease in water within the wetland (Southgate and Hulme, 2001). This lends support to the classification, in that there is no longer open water or a deep-water wetland community in this area.

The NDVI change detection results for Lenkir were not informative. Unlike in Namelok, there did not appear to be a fast growing community present within the wetland between 1976 and 1987. There was very little change within the wetland boundaries and the only time there was a change it was a decrease in NDVI. These decreases were more than likely the result of flooding caused by wetter conditions in 1995. In the 1995 to 2002 change detection image the decrease in NDVI around the *A. mellifera* and *Cucumis* scrub along the northeast to southeast periphery of Lenkir was indicative of the lower rainfall of 2002 compared to 1995. This same community also occurs on the western edge of the wetland near to the entry point of the Kikarankor River; however, there was no decrease in NDVI here. This is interesting and might be the result of higher soil moisture as a result of the proximity to the river. The advance of irrigated agriculture was not visible from the change detection images for Lenkir. It was also not possible to infer when there might have been a change in vegetation community, if in fact there had ever been one. The evidence on the hydrological status of the wetland from the literature does suggest that a change in community should have occurred. However, to my knowledge, there have been no detailed vegetation surveys in this area. Hence, results from my classification cannot be compared in order to determine if vegetation has changed since the advent of irrigated agriculture around the wetland.

The Esoitpus wetland has been almost completely drained as a result of its source, the Lolterish River, being diverted through water pipelines to the Export Processing Zone (EPZ) based in Kitengela north of the Amboseli ecosystem (Githaiga *et al*., 2003). However, irrigated agriculture, as well as water extraction for livestock and domestic use, occurs around a meager spillway downstream of the pipeline (Githaiga *et al.*, 2003).

Irrigated fields were identified along Lolterish River in the 2002 classification in the present study. However, spectrally this class was not separable from the woodland class and caution must be taken in concluding that all the area classified as irrigated agriculture along the Lolterish River is in fact irrigation and not woodland communities. More ground information is needed to improve separability of these classes. The dominant riverine community and small area of seasonal wetland community that occupies the Esoitpus wetland are most likely the result of the massive drawdown after the construction of the pipeline. As explained for Namelok, seasonal wetland communities are present only where water levels are low or inundation is temporary. The presence of a riverine community that has *A. xanthophloea* is indicative of a shallow water table (Western and Sindiyo, 1972).

The NDVI change detection results for Esoitpus were also not very informative. The initial increase in NDVI between 1976 and 1987 indicates the presence of a vegetation community that can quickly respond to rainfall. Change detection results from the two following decades indicate an increase in flooded areas around the river margins and the wetland in 1995, followed by the occurrence of agriculture along the margins of Lolterish in 2002. The latter corresponds to the classification results.

The Kimana wetland is used not only by livestock, humans, and for water for agriculture, but the creation of the Kimana Community Wildlife Sanctuary in the 1998 means that wildlife also have access to the southern edge of the wetland (Worden *et al*., 2003). The area where the sanctuary is located was classified as grassland with scattered shrubs and trees, but also as irrigated fields. These are probably wooded areas that were erroneously classified

Kimana has the largest area of *Cyperus* dominated deep water wetland habitat. The occurrence of this habitat in Kimana might be the result of better management of the wetland by the community. The creation of the community-based “Furrow Groups” that govern the use of water from the wetland by its members (Southgate and Hulme, 2001), imply that this scenario could be possible. However, because long-term vegetation data are not available, it is not possible to rule out that Kimana was always the deeper of the wetlands and, hence, more likely to have a deep water wetland community.

The springs that feed Kimana are located to the southwest of the wetland, and this area is used to provide water for domestic use, livestock, wildlife and for the Kimana irrigation scheme (Githaiga *et al.,* 2003). The areas under irrigation are clearly seen in the lower region, below the Kimana wetland, of the Namelok-Kimana classification image in the present study. Irrigated agriculture around the periphery of the Kimana wetland did not become established until the mid 1990’s when more herders decided to diversify into agricultural practices (Campbell *et al.*, 2003). Due to its proximity to a major rural road, agriculture intensified rapidly (Worden *et al.*, 2003). Most of this area is also clearly defined in the current classification.

Kimana has changed the least in terms of NDVI, which suggests that for the times covered in this analysis, there have been no drastic changes in the hydrology of the wetland as has been the case in the other wetlands. This is also shown by the fact that areas within the Kimana wetland that showed a decrease in NDVI in 1995, which was a wetter year than 1987, were greener in the drier year of 2002.

In contrast, the vegetation in the surrounding dry land saw a reduction in NDVI in 2002. This suggests that the wetland vegetation had enough water to maintain its vigour. The NDVI decrease between 1987 and 1995 was most likely the effect of flooded areas. The detection of irrigated fields was only possible in the 1995 to 2002 image, as they corresponded to the classification image.

The habitat surrounding all of the wetlands was predominantly wood and shrub vegetation, which is in stark contrast to the grass and scattered scrub vegetation that surrounds the wetlands of the Amboseli National Park presented in Chapter 2 (Figure 2.10). This phenomenon has been observed in other ecosystems in East Africa, where the protected areas have lost their woody vegetation and browsing fauna, whereas the ecosystem outside the protected area has become more wooded but has lost its grazer population (Western and Gichohi, 1993b). Based on an ecosystem-wide count of wildlife around the wetlands of Amboseli, including the park wetlands, Namelok had the highest density of the browser species gerenuk (*Litocranius walleri* Brooke) and giraffe (*Giraffa camelopardis* L.), which do not need to be close to a water source at all times and, hence, are not affected by the fencing of the wetland. Kimana wetland was the only one that had the full suite of mammalian herbivores, that is, grazers, browsers, and mixed feeders (feed on both graze and browse), but at a lower density than the park. The park was dominated by the common grazing ungulates and elephants, but had few browsers (Worden *et al*., 2003). As the authors of that study noted, some of the species are rare and difficult to count, and further it was a single count. Some differences between the wetlands may not, therefore, be accurate, but overall the trend seems to concur with the habitat distribution across the ecosystem.

Namelok, Lenkir, and Kimana wetlands are under the larger threat of increasing levels of fertilizer and pesticide use that occurs as agriculture intensifies. Preliminary results from Githaiga *et al.* (2003) indicate that water leaving the irrigated fields fed by the Amboseli wetlands have 7 times the nutrients and higher COD, BOD, dissolved and suspended solids, electrical conductivity and pH than water from the source springs. Githaiga *et al.* (2003) also report that the irrigation canals are already choked with algal scum, which is a sign of eutrophication. If agriculture continues to grow around the wetlands their capacity to assimilate nutrients may be overloaded and this could have negative effects on the quality of water and the wetland vegetation community, and the animal species that rely on them. Invertebrate species are also potentially at risk from a change in wetland hydrology and vegetation communities (Chapman *et al.*, 2001).

The Namelok wetland represents long-term extraction of water for irrigation, whereas Kimana represents more recent, but intense irrigation activity along with use by livestock and wildlife. Esoitpus represents a wetland that has been essentially drained, whereas Lenkir may be similar to Namelok in terms of the dominance of agricultural use. Namelok, Eositpus and Lenkir all have vegetation communities that are more common in shallow waters or seasonally inundated floodplains, whereas Kimana is dominated by a deep water wetland community. Although it is tempting to say that Kimana's diverse use and the inclusion of wildlife conservation has resulted in this community, the lack of hydrological and historical ecological data for all these wetlands prevents such a conclusion. However, at the same time it is not likely that agriculture has not had an impact on the hydrology and vegetation of the Namelok, Lenkir, and Kimana wetlands and that the draining of Esoitpus did not change its vegetation community.

If rainfall in the forests of Mt. Kilimanjaro continues to decrease, the wetlands of Amboseli may experience lower recharge rates. This may have negative impacts on the farmers, herders, and wildlife. The conservation efforts of the Kimana community are the only published example for these wetlands. It is essential that conservation and management plans be developed for all of the wetlands since it is unlikely that the communities will return to a predominantly nomadic pastoralist lifestyle. Hence, the use of traditional land-use practices, like the example of the Pokomo-Wardei people of the Tana River District (Terer *et al.*, 2004), is not an option for conservation. With the recent move in Kenya towards acknowledging the importance of protecting habitats (Wamukoya and Situma, 2000), it is hoped that conservation plans for these wetlands that includes human use are developed. In any conservation and management plan that is developed for these wetlands, however, water conservation efforts must be a major focus, since hydrology greatly influences a wetland ecosystem.

Chapter 6

General Discussion and Future Work

6.1 General Discussion

The wetlands in the semi-arid savanna ecosystem of Amboseli are a fundamental component in this spatially and temporally variable ecosystem and are important determinants of the ecological patterns and processes within it (Worden *et al*., 2003). The heterogeneity they introduce into the ecosystem and their role as perennial water sources have been linked to the rich diversity of wild mammals that are found in Amboseli (Western, 1994). They are also critical for the growing human population of the area and have been so for many centuries (Western, 1994).

The conservation of these wetlands is dependent of having good knowledge on their structure and function. This was the underlying reason for this thesis. However, two major perturbations in the ecosystem that have been present for over 3 decades have likely altered the wetland habitat to what it is today. The perturbations include the modification of wet season migration of the Amboseli elephant population due to the threat of poaching (Koch *et al.*, 1995), and the change in land use around the wetlands outside of the park from predominantly livestock and wildlife watering and grazing pastures to irrigated agriculture (Worden *et al*., 2003). In order to understand the wetlands, therefore, an examination of the effects of these perturbations on the structure and function of the wetlands had to be attempted.

The plant species encountered in the classification of the wetlands within the park boundary and those under human use were similar. *Cyperus laevigatus* and *C. immensus* were common in the wetlands inside and outside the park. *Cyperus immensus* was commonly part of the shallow and deep water wetland habitats, whereas *C. laevigatus* was common in all the wetland habitats, but dominated the seasonally inundated habitat. The only wetlands where a *C. papyrus*-dominated wetland habitat was identified were the Enkongo Narok wetland inside the park and the Kimana wetland to the east of the park. The grazing and flood tolerant grass, *Cynodon dactylon*, was ubiquitous in the shallow and seasonally-inundated habitats of all the wetlands, as well as in the grasslands fringing the wetlands. The park wetlands consisted of the different wetland habitats; open water, deep and shallow water, and seasonally inundated. These wetlands are larger and, hence, more likely to have greater diversity. On the other hand, the wetlands under human use mostly consisted of seasonally inundated wetland habitat or riverine communities and, except for Kimana, have less shallow or deep water wetland communities.

These results imply three things. First, grazing by elephants, which is currently high especially in the permanently inundated wetland habitat, favours shorter sedges. Second, human use, which is currently centered on water extraction for agriculture and industry, favours the creation of shallower wetland communities. The third implication is that grazing pressure in the shallower habitats is or has been consistently present, although not necessarily heavy, which has selected for grazing tolerant species such as *C. dactylon*.

The impact of elephants on the woodlands of semi-arid ecosystems is widely known, and is also obvious in the southern part of Amboseli National Park. The vegetation classification of the ecosystem also revealed differences between non-wetland habitats inside and outside of the park, and supports the theory that elephants are the key driving force in the loss of woodland from the park ecosystem. Another major difference between the inside and the outside of the park was the presence of large areas inside and around the wetlands under human use that were classified as riverine vegetation that had *Acacia xanthophloea* woodland and *C. dactylon* grass. While I did not include impacts of elephants on *A. xanthophloea* in my work, the recruitment of this species within the enclosure created for the study presented in chapter 3 was remarkable.

The reduction in woodlands to the south of the wetlands inside the park seemed to correlate with the increase in the extent of all the wetlands in this part of the ecosystem, as shown by the hand-drawn illustrations from 1950 to 1976. In addition to this increase, the seasonal changes in the extents and flooding patterns of the Longinye wetland were highly dynamic. Some of these changes did not coincide with local rainfall, though rainfall is reported to greatly influence wetland dynamics (Irungu, 1992). Hence, either the impact of vegetation or the creation of channels by elephants and hippos may be responsible for the changes in pattern observed. Another aspect that cannot be confirmed is the effect of changing rainfall in the forests of Mt. Kilimanjaro, which feed the springs of the Amboseli wetlands.

The impacts of elephants on wetland vegetation was shown when the control and treatment (enclosed) wetlands of Ilmerishari in the Amboseli National Park were compared. The control wetland showed seasonal changes in vegetation biomass and height, as well as use by herbivores. The wet season brought about an increase in plant growth, albeit muted compared to the treatment wetland, and the dry season saw a decrease in growth. A larger number of species of herbivores, except elephants, used the control wetland more in the dry season than in the wet season, which implies that herbivores other than elephants still move away from the wetlands in the wet season. These data are supported by the long-term permanent plot study on grazing damage on edge vegetation. These data showed that the wet season use of this habitat has not been increasing year-round, even though one of the plots was favoured more than the other, most likely due to the differences in plant species in the two plots.

Elephant dung was present around the control wetland throughout the year. This reliance on the wetland habitat by elephants was also seen on a larger scale from the long-term aerial count data. From these data it was apparent that elephants have been increasingly relying on the wetland habitats year-round since 1975, which coincides with the period when elephants are thought to have stopped migrating out of the park during the wet season (Koch *et al.*, 1995). Why the elephants have continued their use of the wetland habitats year-round may be the combined effect of an increasing population and unsafe or blocked migratory routes that forces them to stay within the park continually.

The results from the 3-year comparison study of the wetlands further showed that elephants greatly reduced both height and biomass of vegetation in the control wetland when compared to the treatment wetland that was protected from elephant grazing. The difference between the wetlands was most obvious in the wet season.

The edges of the two wetlands were similar in the dry seasons, which indicated that the other herbivores, such as wildebeest, zebra, buffalo, and cattle, had a major influence on the vegetation in this season. However, in the wet season, the biomass and height of the edges was greater in the treatment than the control wetland. This suggests that the elephants maintain the vegetation at a low biomass and height throughout the year, but that other grazers exacerbate the conditions when they concentrate around the edges in dry seasons or during droughts.

The edges of both Ilmerishari wetlands were covered with herbaceous vegetation throughout the study, even during the drought conditions. The edges of the two wetlands were dominated by *C. dactylon*. The fact that this species was maintained even under the heavy grazing that would have occurred during the drought, this being inferred from the expected movement of herbivores since dung counts were not available for the drought periods, implied its ability to withstand heavy grazing. This ability was also seen in the one-year simulated grazing experiment conducted along the edge of the Longinye wetland. However, heavy grazing by an increasing snow goose population has shown to cause erosion of the edges of arctic salt marshes through the damage and removal of plant material (Jefferies and Rockwell, 2002) and the effects of trampling and compaction of the soil have also been linked to poor plant growth under heavy grazing pressure in savanna grasslands (Skarpe, 1991). These effects were not studied in the Amboseli wetlands and the simulated grazing experiment did not damage the soil in the same way as herbivore activity would. Hence, the results have to be viewed with caution.

In the control wetland, grasses were more common than sedges throughout the wetland, whereas sedges were more abundant in the treatment wetland. These differences may have started off as a result of the differences between the hydrology of the wetlands, however, the increased height and biomass of vegetation produced in the centre of the treatment wetland after elephants were excluded was unmistakable, even though the experiment was unreplicated. *Cyperus immensus* became the dominant sedge in the treatment wetland and was maintained in tall, mono-specific stands that invaded the edges of the wetland towards the end of the study. The presence of herbivores other than elephants, as represented by dung counts, was not different from that around the control wetland, and was in fact higher in the treatment than the control in the wet seasons. The fact that tall, dense stands of *C. immensus* were still able to take over much of the treatment wetland suggests the impacts of elephants on wetland vegetation. Going back to the classification of the Amboseli National Park wetlands presented in chapter 2, the role of elephants in opening-up the wetlands of the park, as suggested by Western (1997), but not formally documented, is more likely.

The impacts of grazing on the floating vegetation mats dominated by *C. laevigatus* in the permanently inundated centre of the Longinye wetland indicate that this habitat can benefit from grazing if it is done without damage to the integrity of the mat itself. When grazing was simulated, growth rate increased even though the intensity of grazing was lower than that experienced by the vegetation when under natural grazing. This suggested that natural grazing may damage or disrupt the mats, which in turn reduces the beneficial effects of grazing observed when grazing was simulated. Under the latter treatments, grazed plants were able to take advantage of rain, most likely as a result of improved oxygen and nutrient status of the water underlying the mats, quicker than un-grazed vegetation.

Overall, increased grazing pressure by elephants on the wetland habitats is more than likely responsible for the loss of tall, dense sedge communities that were dominated by *C. papyrus* in the 1970's. The short-term studies also suggest that, although the wetland vegetation can sustain grazing and, in fact, can benefit from it through increased growth rates, continued grazing pressure on wetland habitats may, ultimately, have damaging effects to the vegetation. The current mix of wetland communities that make up the wetlands of the Amboseli National Park have not been linked to animal extinctions from the park as has the loss of woodlands. However, there has been an observed reduction in the bird population that may be at least partly related to the loss of tall sedge communities.

In the wetlands under human use, the extraction of water for irrigated agriculture and industrial use seems to have resulted in draw-down that has favoured the development of communities commonly found in shallower and fringe wetlands. The exception is the Kimana wetland, which still has dense stands of *C. papyrus* interspersed in a *C. immensus* deep water wetland. Large areas around Kimana, like Namelok and Lenkir, are under irrigated agriculture. The only difference between these wetlands is that in Kimana there has been a community-based group that has dictated water-use by its members. Due to the lack of historical information on the vegetation and hydrology of the wetlands, it is unwise to conclude that the management of Kimana is the reason it has deeper wetland habitats than the other wetlands, even though this is implied by the evidence on the history and extent of land-use in the wetlands. The Esoitpus wetland has been almost entirely drained as a result of the pipeline that transports its spring waters to the Export Processing Zone just south of Nairobi. The resultant community is dominated by *A. xanthophloea* riverine communities and some seasonal wetland habitat. However, there is no historical record of the ecology and hydrology of this wetland to confirm the current community is the result of draw-down. The results from the wetlands outside the park are useful in giving the current status of the wetlands but, unfortunately, the long-term vegetation change analyses were not useful in identifying the historical changes in wetland vegetation from the period when irrigated agriculture first started to its current status as a dominant part of the areas surrounding the wetlands.

The impact of herbivores on the structure and species composition of the wetlands implies strong top-down effects. With increased use of wetlands by elephants come increased faecal deposits and increased churning of the water and sediment. These provide conditions of increased potential nutrients and increased aeration. The result on the trophic cascades within these wetlands can have immense impacts on the vegetation and micro-habitats of the wetlands. The results presented on elephant effects are from shallow water wetlands. The dynamics of the vegetation may be very different in the deeper wetlands where churning of the water and sediments may have even more far-reaching impacts on the vegetation.

In effect, the herbivores act as a functional group with respect to the wetland vegetation much like they do in the Serengeti grasslands (Blondel, 2003). However, there is also the chance that the changes in hydrology that are expected from the types of human activities around the wetlands outside the park and potential changes in hydrology within the park have some bottom-up effects on the kinds of vegetation that can be present. *Cyperus papyrus* is suited to draw-downs, but is in the best condition when its roots are submerged (Thompson, 1985). Hence, the loss of this species in the wetlands may be the direct result of draw-down in the wetlands outside the park, but a combination of elephant activity and hydrological alterations in the wetlands inside the park.

The fact that the sedge community was able to rebound when elephant grazing pressure was removed from a park wetland indicates that the system is not an alternate stable state. One option for keeping elephants out of wetlands for short periods of time to allow the re-establishment of tall sedge communities is the building of enclosures. These are relatively inexpensive, but they do require constant monitoring and some maintenance. In the comparative study of the two Ilmerishari wetlands, the vegetation in the treatment wetland responded dramatically within one year, even though the conditions were drier than normal. The dung count results from one year of the comparative study also suggested that medium and small herbivores were not deterred from the denser vegetation inside the treatment wetland. This implies that increasing denser sedge communities may not take away habitat from other herbivores. However, these results are short-term and from a drier time period, and may not, therefore, be representative of conditions over longer or wetter years.

If rainfall in the forests of Mt. Kilimanjaro that feeds the wetlands of Amboseli continues to decrease as reported by Hemp (2005), the wetlands may experience lower recharge rates. This may have negative impacts on farmers, herders, and wildlife. Conservation plans for the wetlands outside the park must, therefore, consider water conservation as the primary issue since land-use is not going to revert from irrigated agriculture back to traditional pastoralism. The wetlands in the park, on the other hand, may have benefited from the loss of the *A. xanthophloea* woodlands that were likely extracting some if not a lot of water from the aquifers that feed the wetlands. The current diversity in the types of wetland habitat implies that the wetlands have different ecotones that are important for the maintenance of invertebrate and vertebrate communities (Chapman *et al.*, 2001). Any management plans for the wetlands in the park must strive to maintain this diversity. It is, therefore, important that the other herbivores be free to migrate as well, as they also impact the wetlands and may exacerbate the effects of elephants. In order for migration routes to be safe and accessible in an ecosystem that is experiencing large increases in sedentary human populations, the human community has to be a part of the plan. They have to benefit from the plan and be provided with securities against damage by wildlife. Fortunately, there are numerous grass-roots projects that are attempting to put these plans in place, so it is possible to be optimistic about the future of the Amboseli ecosystem and its wildlife.

6.2 Future Work

The hydrological condition of a wetland is the driving force for both the abiotic and biotic components. Hence, it is critical that an in-depth hydrological study be conducted for all the Amboseli wetlands. The only study thus far (Irungu, 1992) covers a few of the wetlands, concentrating mostly on the park wetlands. Presently, the wetlands outside the park are being used without any knowledge of the hydroperiod or recharge rates of the wetlands. Without this information they are likely to be over-used, and that will eventually lead to the complete loss of the wetland habitat. Amboseli is a semi-arid ecosystem and evapotranspiration far exceeds rainfall. This has overarching consequences on the sustainable use of water from the wetlands for irrigation and calls for studies on ways in which water can be conserved in a manner that is suitable to the people living around the wetlands. A hydrological study will also help to better understand the dynamic wetlands, such as Longinye, as well as the impacts of herbivores, in particular elephants, on vegetation from a different perspective. The impacts of road development across the wetlands and the impact of these on the flooding patterns of the wetlands should be considered.

Some studies should be conducted on the impact of elephants on the trophic cascade and the relative differences in response between shallow and deep water wetlands should be considered. The relative importance of vegetative propagation versus germination from the seedbank needs to be assessed along with the effect of herbivore activity on sediment and seedbank integrity. Since the wetlands seem to have the potential to regenerate when grazing pressure is elliviated it is important that the integrity of the seedbanks and sediment be maintained if the seedbank is the critical source of new growth. The impacts of changing vegetation communities on herbivores also require study. In this thesis the impacts of herbivores on vegetation was assessed. However, interactions between vegetation and herbivores go both ways (Hunter and Price, 1992), and, hence, interactions in both directions should be understood if the conservation process is going have better chances of success. This requires that a more detailed natural grazing experiment that involves frequent sampling over the growing and dry seasons of both vegetation parameters and herbivore density be conducted.

Although this thesis has provided some basic knowledge of the wetlands of the Amboseli savanna ecosystem, there is still a lot more work required that will help towards a better understanding of the wetland ecosystem.

Appendix A
Calibration of the Slanted Pin-Frame

Calibration of the pin frame was carried out as outlined in Western and Gichohi (1993a). As recommended, the variation due to season, and vegetation type and density was included in the calibration exercise. This was accomplished by, firstly, collecting samples from two seasons, the short-wet (December 2002) and late dry seasons (October 2003). Secondly, at least 3 replicate quadrats were placed in areas ranging from dense to sparse and tall to short vegetation to take into account the different biomass levels. Thirdly, separate calibration equations were derived for the vegetation on the grass-dominated edges and the floating mats in the centre of the wetland.

The Ilmerishari (control and enclosed) wetland, which is where data for chapter 3 were collected, was used for the calibration of the pin frame. The vegetation in this area was very similar to that in the area around the Ol' Tukai wetland that was the focus of chapter 4. Hence, a separate calibration exercise was not conducted for the latter wetland.

A 50 cm x 50 cm quadrat was used in the calibration. It was placed at random within a vegetation community of a particular biomass level and the total number of hits per pin was recorded. Five pins were used in the frame, as this was considered sufficient for the relatively low diversity and biomass observed in this area. Complete coverage of the quadrat was achieved with 3 placements of the frame. Once the hits were recorded the vegetation was cut from the base (at ground level for the edge, and mat level for the centre), stored in black plastic bags to reduce water loss prior to weighing, and labeled. Then the samples were weighed using an Ohaus dial-o-gram, 1600g capacity scale (Ohaus Scale Corporation, Union, NJ)), transferred to a brown paper bag, labeled and left undisturbed to air-dry. Air-drying took between 1 and 2 months, depending on the humidity and temperature. The samples were re-weighed when possible until there were no longer changes of more than 10g from the previous weighing and this final weight was considered the dry weight for the sample. Ten grams was used as the cut-off point since the scale had an error of between 2 and 5 g. A total of 12 twelve samples were collected from the grass-dominated edge and 10 from the floating mats in the centre.

An equation was derived relating biomass expressed as g DW m^{-2} to the average hits per pin (total hits for the sample divided by 15, the total number of pins used per quadrat) using ordinary least squares regression. The equations derived for the two wetland vegetation types were as follows:

Grass-dominated edge: biomass = 31.693*h/p

Where, h/p = average hits per pin; $R^2 = 0.85$, $n = 12$, $P < 0.0001$

The intercept was not significantly different from zero and hence, was forced to zero (Figure A).

The relationship for floating mat vegetation at the centre of the wetland had a positive intercept (P = 0.003) with a linear fit, and was clearly non-linear (Figure A). Therefore a curvilinear regression was used:

Floating mat vegetation (centre of wetland): *Ln* (biomass) = 3.058 + (0.543*h/p)

$R^2 = 0.92$, n = 10, $P < 0.0001$

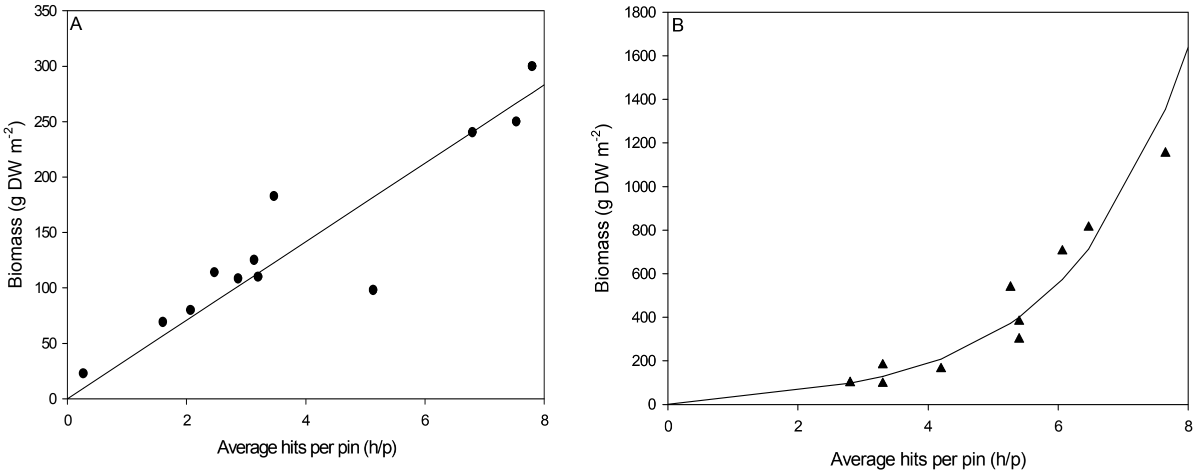

Figure A 1. Calibration of a slanted-pin frame for, (A) grass-dominated edge vegetation, and (B) floating mat vegetation in the centre of the Ilmerishari wetlands, Amboseli National Park, southern Kenya.

References

Adams, M. E. 1996. Savanna environments. *In* The physical geography of Africa. *Edited by* W.M. Adams, A.S. Goudie, and A.R. Orme. Oxford University Press Inc., New York, pp. 196-210.

Adler, P.B., Raff, D.A., and Lauenroth, W.K. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128 (4): 465-479.

Altmann, J., Alberts, S.C., Altmann, S.A., and Roy, S.B. 2002. Dramatic change in local climate patterns in the Amboseli basin, Kenya. African Journal of Ecology **40**: 248-251.

Andere, D.K. 1981. Wildebeest *Connochaetes taurinus* (Burchell) and its Food Supply in Amboseli Basin. African Journal of Ecology **19**: 239-250.

Arsenault, R. and Owen-Smith, N. 2002. Facilitation versus competition in grazing herbivore assemblages. Oikos **97** (3): 313-318.

Augustine, D.J. 2003. Spatial heterogeneity in the herbaceous layer of a semi-arid savanna ecosystem. Plant Ecology **167** (2): 319-332.

Barry, M.J., Bowers, R., and de Szalay, F.C. 1998. Effects of hydrology, herbivory and sediment disturbance on plant recruitment in a Lake Erie coastal wetland. The American Midland Naturalist **151 (3)**: 217-232.

Becht, R. and Harper, D.M. 2002. Towards an understanding of human impact upon the hydrology of Lake Naivasha, Kenya. Hydrobiologia **488**: 1-11.

Behrensmeyer, A.K. 1993. The taphonomic record of ecological change in Amboseli-Park, Kenya. Research & Exploration **9** (4): 402-421.

Belsky, A.J. 1988. Regional influences on small-scale vegetational heterogeneity within grasslands in the Serengeti National Park, Tanzania. Plant Ecology **74** (1): 3-10.

Belsky, A.J., Amundson, R.G., Duxbury, J.M., Riha, S.J., Ali, A.R., and Mwonga, S.M. 1989. The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya. Journal of Applied Ecology **26** (3): 1005-1024.

Belsky, A.J., Mwonga, S.M., Amundson, R.G., Duxbury, J.M., and Ali, A.R. 1993. Comparative effects of isolated trees on their undercanopy environments in high- and low-rainfall savannas. Journal of Applied Ecology **30** (1): 143-155.

Bennun, L.A. 2001. Long-term monitoring and the conservation of tropical wetlands: high ideals and harsh realities. Hydrobiologia **458**: 9-19.

Birkett, A. and Stevens-Wood, B. 2005. Effect of low rainfall and browsing by large herbivores on an enclosed savannah habitat in Kenya. African Journal of Ecology **43** (2): 123-130.

Blondel, J. 2003. Guilds or functional groups: does it matter? Oikos **100** (2): 223-231

Boar, R.R., Harper, D.M., and Adams, C.S. 1999. Biomass allocation in *Cyperus papyrus* in a tropical wetland, Lake Naivasha, Kenya. Biotropica **31** (3): 411-421.

Byenkya, G.S. 2004. Impact of undesirable plant communities on the carrying capacity and livestock performance in pastoral systems of south-western Uganda. Doctor of Philosophy thesis, Texas A&M University, USA.

Campbell, D.J. 1986. The prospect for desertification in Kajiado district, Kenya. Geographical Journal **152**: 44-55.

Campbell, D.J., Gichohi, H., Mwangi, A., and Chege, L. 2000. Land use conflict in Kajiado District, Kenya. Land Use Policy **17** (4): 337-348.

Campbell, D. J., Lusch, D. P., Smucker, T., and Wangui, E. E. 2003. Root causes of land use change in the Loitokitok area, Kajiado District, Kenya. LUCID working paper No. 19, International Livestock Research Institute, Nairobi, Kenya.

Campbell, J.B. 2002. Introduction to remote sensing. The Guilford Press, New York.

Catarino, L., Martins, E.S., and Diniz, M.A. 2002. Vegetation structure and ecology of the Cufada lagoon (Guinea-Bissau). East African Wildlife Journal **40**: 252-259.

Chapman, L.J., Balirwa, J., Bugenyi, F.W.B., Chapman, C., and Crisman, T.L. 2001. Wetlands of East Africa: biodiversity, exploitation, and policy perspectives. *In* Biodiversity in wetlands: assessment, function and conservation. *Edited by* B.Gopal, W.J.Junk, and J.A.Davis. Backhuys Publishers, Leiden, Netherlands, pp. 101-131.

Coe, M.J., Cumming, D.H., and Phillipson, J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. Oecologia **22**: 341-354.

Cumming, D.H.M., Fenton, M.B., Rautenbach, I.L., Taylor, R.D., Cumming, G.S., Cumming, M.S., Dunlop, J.M., Ford, A.G., Hovorka, M.D., Johnston, D.S., Kalcounis, M., Mahlangu, Z., and Portfors, V.R. 1997. Elephants, woodlands and biodiversity in southern Africa. South African Journal of Science **9**: 231-236.

Dangerfield, J.M. 1997. Abundance and diversity of soil macrofauna in northern Botswana. Journal of Tropical Ecology **13**: 527-538.

Denny, P. 1985. Wetland vegetation and associated plant life-forms. *In* The ecology and management of African wetland vegetation. *Edited by* P. Denny. Dr. W. Junk Publishers, Boston, MA. pp. 1-18.

Denny, P. 2001. Research, capacity-building and empowerment for sustainable management of African wetland ecosystems. Hydrobiologia **458**: 21-31.

Dottavio, C.L. and Dottavio, F.D. 1984. Potential benefits of new satellite sensors for wetland mapping. Photogrammetric Engineering and Remote Sensing **50** (5): 599-606.

Dublin, H. 1995. Vegetation dynamics in the Serengeti-Mara ecosystem: The role of elephants, fire, and other factors. *In* Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. *Edited by* A.R.E. Sinclair and P. Arcese. The University of Chicago Press, Chicago, U.S.A, pp. 71-90.

Dyer, M.I., Turner, C.L., and Seastedt, T.R. 1993. Herbivory and its consequences. Ecological Applications **3** (1): 10-16.

Ellery, W.N., McCarthy, T.S., and Dangerfield, J.M. 2000. Floristic diversity in the Okavango delta, Botswana as an endogenous product of biological activity. *In* Biodiversity in wetlands: assessment, function and conservation. *Edited by* B. Gopal, W.J. Junk, and J.A. Davis. Backhuys Publishers, Leiden, The Netherlands, pp. 195-226.

Fritz, H., Duncan, P., Gordon, I.J., and Illius, A.W. 2002. Megaherbivores influence trophic guilds structure in African ungulate communities. Oecologia **131** (4): 620-625.

Furley, P.A. 1999. The nature and diversity of neotropical savanna vegetation with particular reference to the Brazilian cerrados. Global Ecology and Biogeography **8** (3-4): 223-241.

Gaudet, J.J. 1979. Seasonal changes in nutrients in a tropical swamp: North Swamp, Lake Naivasha, Kenya. Journal of Ecology **67**: 953-981.

Gauthier, G., Rochefort, L., and Reed, A. 1996. The exploitation of wetland ecosystems by herbivores on Bylot Island. Geoscience Canada **23** (4): 253-259.

Georgiadis, N.J., Ruess, R.W., McNaughton, S.J., and Western, D. 1989. Ecological conditions that determine when grazing stimulates grass production. Oecologia **81**: 316-322.

Gibson, P.J. and Power, C.H. 2000. Introductory remote sensing: Digital image processing and applications. Routledge, New York.

Gichuki, C.M. 2000. Community participation in the protection of Kenya's wetlands. Ostrich **71 (1-2)**: 122-125.

Githaiga, J.M., Reid, R., Muchiru, A.N., and van Dijk, S. 2003. Survey of water quality changes with land use type in the Loitokitok area, Kajiado District, Kenya. LUCID working paper No. 35, International Livestock Research Institute, Nairobi, Kenya.

Grant, C.C. and Scholes, M.C. 2006. The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. Biological Conservation **130 (3)**: 426-437.

Haack, B. 1996. Environmental auditing: Monitoring wetland changes with remote sensing: an East African example. Environmental Management **20 (3)**: 411-419.

Harper, D. and Mavuti, K. 1996. Freshwater wetlands and marshes. *In* East African ecosystems and their conservation. *Edited by* T.R. McClanahan and T.P. Young. Oxford University Press, New York, pp. 217-239.

Harvey, K.R. and Hill, G.J.E. 2001. Vegetation mapping of a tropical freshwater swamp in the Northern Territory, Australia: a comparison of aerial photography, Landsat TM and SPOT satellite imagery. International Journal of Remote Sensing **22** (15): 2911-2925.

Hemp, A. 2005. Climate change-driven forest fires marginalize the impact of ice cap wasting on Kilimanjaro. Global Change Biology **11** (7): 1013-1023.

Holmgren, M., Stapp, P., Dickman, C.R., Gracia, C., Graham, S., Gutierrez, J.R., Hice, C., Jaksic, F., Kelt, D.A., Letnic, M., Limo, M., Lopez, B.C., Meserve, P.L., Milstead, W.B., Polis, G.A., Previtali, M.A., Richter, M., Sabate, S., and Squeo, F.A. 2006. Extreme climatic events shape arid and semiarid ecosystems. Frontiers in Ecology and the Environmental **4** (2): 87-95.

Hongo, H. and Masikini, M. 2003. Impact of immigrant pastoral herds to fringing wetlands of Lake Victoria in Magu district Mwanza region, Tanzania. Physics and Chemistry of the Earth **28** (20-27): 1001-1007.

Howard-Williams, C. and Gaudet, J. J. 1985. The Structure and Functioning of African Swamps. *In* The Ecology and Management of African Wetland Vegetation. *Edited by* P. Denny. Dr. W. Junk Publishers, Dordrecht. pp. 154-175.

Howard-Williams, C. and Thompson, K. 1985. The conservation and management of African wetlands. *In* The ecology and management of African wetland vegetation. *Edited by* P. Denny. Dr W. Junk Publishers, Boston, MA, pp. 203-230.

Hughes, F.M.R. 1996. Wetlands. *In* The physical geography of Africa. *Edited by* W.M. Adams, A.S. Goudie, and A.R. Orme. Oxford University Press Inc., New York, pp. 267-286.

Hughes, L. 2003. Climate change and Australia: Trends, projections and impacts. Austral Ecology **28** (4): 423-443.

Hulme, M. 1996. Climate change within the period of meteorological records. *In* The physical geography of Africa. *Edited by* W.M. Adams, A.S. Goudie, and A.R. Orme. Oxford University Press Inc., New York, pp. 88-102.

Hunter, M.D. and Price, P.W. 1992. Playing chutes and ladders - heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology **73** (3): 724-732.

Irungu, C.N. 1992. A Hydrogeological Study of the Amboseli Basin (Kenya). MSc thesis, ITC, Netherlands.

Jackson, R.D. and Allen-Diaz, B. 2006. Spring-fed wetland and riparian plant communities respond differently to altered grazing intensity. Journal of Applied Ecology **43** (3): 485-498.

Jano, A.P., Jefferies, R.L., and Rockwell, R.F. 1998. The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. Journal of Ecology **86** (1): 93-99.

Jefferies, R.L. and Rockwell, R.F. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. Applied Vegetation Science **5** (1): 7-16.

Johnson Randall, L.A. and Foote, A.L. 2005. Effects of managed impoundments and herbivory on wetland plant production and stand structure. Wetlands **25** (1): 38-50.

Jones, M.B. and Humphries, S.W. 2002. Impacts of the C-4 sedge Cyperus papyrus L. on carbon and water fluxes in an African wetland. Hydrobiologia **488** (1-3): 107-113.

Junk, W.J. 2002. Long-term environmental trends and the future of tropical wetlands. Environmental Conservation **29** (4): 414-435.

Kareri, R.W. 1992. The sociological and economic values of Kenya's wetlands. *In* Wetlands of Kenya. Proceedings of the KWWG seminar on wetlands of Kenya. *Edited by* S. A. Crafter, S. G. Njuguna, and G. W. Howard, National Museums of Kenya, Nairobi, Kenya, pp. 99-107

Kaser, G., Hardy, D.R., Molg, T., Bradley, R.S., and Hyera, T.M. 2004. Modern glacier retreat on Kilimanjaro as evidence of climate change: Observations and facts. International Journal of Climatology **24** (3): 329-339.

Kiai, S.P.M. and Mailu, G.M. 1998. Kenya country paper: Wetland classification for agricultural development in eastern and southern Africa. FAO SAFR website. .

Koch, P.L., Heisinger, J., Moss, C.J., Carlson, R.W., Fogel, M.L., and Behrensmeyer, A.K. 1995. Isotopic tracking of change in diet and habitat use in African elephants. Science **267**: 1340-1343.

Laws, R.M. 1970. Elephants as agents of habitat and landscape change in East-Africa. Oikos **21** (1): 1-5.

Le Maitre, D.C., Scott, D.F., and Colvin, C. 1999. A review of information on interactions between vegetation and groundwater. Water SA **25** (2): 137-152.

Lee, C. and Marsh, S. 1995. The use of archival Landsat MSS and ancilliary data in a GIS environment to map historical change in an urban riparian habitat. *In* Wetland and environmental applications of GIS. *Edited by* J.G. Lyon and J. McCarthy. Lewis Publishers, New York, NY, pp. 83-105.

Legendre, P. and Legendre, L. 1998. Numerical Ecology. Elsevier Science, Amsterdam.

Lindsay, W.K. 1987. Integrating parks and pastoralists: some lessons from Amboseli. *In* Conservation in Africa: people, policies and practice. *Edited by* D. Anderson and R. Grove. Cambridge University Press, New York. pp. 149-167.

Linzey, A.V. and Washok, K.A. 2000. Seed removal by ants, birds and rodents in a woodland savanna habitat in Zimbabwe. African Zoology **35** (2): 295-299.

Little, P.D. 1996. Pastoralism, biodiversity, and the shaping of savanna landscapes in East Africa. Africa **66** (1): 37-51.

Ludwig, F., Dawson, T.E., Kroon, H., and Berendse, F. 2003. Hydraulic lift in *Acacia tortilis* trees on an East African savanna. Oecologia **134**: 293-300.

Lyon, J.G. 2001. Wetland landscape characterization: techniques and applications for GIS, mapping, remote sensing, and image analysis. Ann Arbour Press, Chelsea, MI.

Maddock, L. 1979. The "migration" and grazing succession. *In* Serengeti, dynamics of an ecosystem. *Edited by* A.R.E. Sinclair and M. Norton-Griffiths. The University of Chicago Press, Chicago, pp. 104-129.

Marty, J.T. 2005. Effects of cattle grazing on diversity in ephemeral wetlands. Conservation Biology **19** (5): 1626-1632.

Mavuti, K.M. 1992. An account of some important freshwater wetlands of Kenya, *In* Wetlands of Kenya. Proceedings of the KWWG seminar on wetlands of Kenya. *Edited by* S. A. Crafter, S. G. Njuguna, and G. W. Howard. National Museums of Kenya, Nairobi, Kenya, pp. 23-35

McCarthy, J., Gumbricht, T., and McCarthy, T.S. 2005. Ecoregion classification in the Okavango Delta, Botswana from multitemporal remote sensing. International Journal of Remote Sensing **26** (19): 4339-4357.

McCarthy, J.M., Gumbricht, T., McCarthy, T., Frost, P., Wessels, K., and Siedel, F. 2003. Flooding patterns of the Okavango Wetland in Botswana between 1972 and 2000. AMBIO **32** (7): 453-457.

McNaughton, S.J. 1979a. Grassland-Herbivore Dynamics. *In* Serengeti: Dynamics of an Ecosystem. *Edited by* A.R.E.Sinclair and M.Norton-Griffiths. The University of Chicago Press, Chicago, U.S.A, pp. 46-81.

McNaughton, S.J. 1979b. Grazing as an Optimization Process: Grass-ungulate Relationships in the Serengeti. The American Naturalist **113** (5): 691-703.

McNaughton, S.J. 1984. Grazing lawns: Animals in herds, plant form, and coevolution. The American Naturalist **124** (6): 863-886.

McNaughton, S.J. 1985. Ecology of a Grazing Ecosystem: The Serengeti. Ecological Monographs **55** (3): 259-294.

McNaughton, S.J. 1990. Mineral nutrition and seasonal movements of African migratory ungulates. Nature **345**: 613-615.

Milchunas, D.G., Sala, O.E., and Laurenroth, W.K. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. The American Naturalist **132** (1): 87-106.

Mitsch, W.J. and Gosselink, J.G. 2000. Wetlands. John Wiley & Sons, Inc., New York.

Moss, C.J. 2001. The demography of an African elephant (Loxodonta africana) population in Amboseli, Kenya. Journal of Zoology **255**: 145-156.

Mosugelo, D.K., Moe, S.R., Ringrose, S., and Nellemann, C. 2002. Vegetation changes during a 36-year period in northern Chobe National Park, Botswana. African Journal of Ecology **40** (3): 232-240.

Mulhouse, J.M., De Steven, D., Lide, R.F., and Sharitz, R.R. 2005. Effects of dominant species on vegetation change in Carolina bay wetlands following a multi-year drought. Journal of the Torrey Botanical Society **132** (3): 411-420.

Mungai, P.M. 1992. Wetland and dry land management, *In* Wetlands of Kenya. Proceedings of the KWWG seminar on wetlands of Kenya. *Edited by* S. A. Crafter, S., G. Njuguna, and G. W. Howard. National Museums of Kenya, Nairobi, Kenya, pp. 167-171.

Ndiaye, D., Lensi, R., Lepage, M., and Brauman, A. 2004a. The effect of the soil-feeding termite Cubitermes niokoloensis on soil microbial activity in a semi-arid savanna in West Africa. Plant and Soil **259** (1-2): 277-286.

Ndiaye, D., Lepage, M., Sall, C.E., and Brauman ,A. 2004b. Nitrogen transformations associated with termite biogenic structures in a dry savanna ecosystem. Plant and Soil **265** (1-2): 189-196.

Ole Nkako, F.M. 1992. Wetland conservation in Kenya: KWS and Ramsar, *In* Wetlands of Kenya. Proceedings of the KWWG seminar on wetlands of Kenya. *Edited by* S.A. Crafter, S.G. Njuguna, and G. W. Howard. National Museums of Kenya, Nairobi, Kenya, pp. 91-98

Otte, M.L. 2001. What is stress to a wetland plant? Environmental and Experimental Botany **46**: 195-202.

Owen-Smith, N. and Novellie, P. 1982. What should a clever ungulate eat? The American Naturalist **119** (2): 151-178.

Pellew, R.A.P. 1983. The impacts of elephant, giraffe and fire upon the *Acacia tortilis* woodlands of the Serengeti. African Journal of Ecology **21** (1): 41-74.

Plisnier, P.D., Serneels, S., and Lambin, E.F. 2000. Impact of ENSO on East African ecosystems: a multivariate analysis based on climate and remote sensing data. Global Ecology and Biogeography **9** (6): 481-497.

Pratt, D.J., Greenway, P.J., and Gwynne, M.D. 1966. A classification of East African rangeland, with an appendix on terminology. Journal of Applied Ecology **3**: 369-382.

Prince, M.E. and Silva, M. 2002. On the determinants of census area: implications for mammalian macroecological patterns. Global Ecology and Biogeography **11**(5): 401-409.

Prins, H.H.T. and van der Jeugd, H.P. 1993. Herbivore population crashes and woodland structure in East Africa. Journal of Ecology **81**: 305-314.

Richards, J.A. and Xiuping, J. 1999. Remote sensing digital image analysis: An introduction. Springer-Verlag, New York.

Schuurman, G. 2006. Foraging and distribution patterns in a termite assemblage dominated by fungus-growing species in semi-arid northern Botswana. Journal of Tropical Ecology **22**: 277-287.

Scoones, I. 1991. Wetlands in drylands: key resources for agricultural and pastoral production in Africa. AMBIO **20** (8): 366-371.

Sinclair, A.R.E. 1995. Equilibria in plant-herbivore interactions. *In* Serengeti II: Dynamics, Management, and Conservation of an Ecosystem. *Edited by* A.R.E. Sinclair and P. Arcese. The University of Chicago Press, Chicago, IL, pp. 91-113.

Skarpe, C. 1991. Impact of grazing in savanna ecosystems. AMBIO **20** (8): 351-356.

Southgate, C. and Hulme, D. 2001. Uncommon property: The scramble for wetland in southern Kenya. *In* African enclosures? The social dynamics of wetlands in drylands. *Edited by* P. Woodhouse, H. Bernstein, and D. Hulme. Africa World Press Inc., Trenton, NJ, pp. 73-117.

Srivastava, D.S. and Jefferies, R.L. 1995. Mosaics of vegetation and soil-salinity - a consequence of goose foraging in an arctic salt-marsh. Canadian Journal of Botany **73** (1): 75-83.

Srivastava, D.S. and Jefferies, R.L. 1996. A positive feedback: Herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. Journal of Ecology **84** (1): 31-42.

Stiles, D. 2004. The ivory trade and elephant conservation. Environmental Conservation **31** (4): 309-321.

Swift, D.M., Coughenour, M.B., and Atsedu, M. 1996. Arid and semi-arid ecosystems. *In* East African ecosystems and their conservation. *Edited by* T.R. McClanahan and T.P. Young. Oxford University Press Inc., NY, pp. 243-272.

Systat Software Inc. 2004. SYSTAT 11. Systat Software Inc., Richmond, CA, USA.

ter Braak, C.J.F. and Smilauer, P. 2002. CANOCO for Windows. (4.5). Wageningen, The Netherlands, Biometris - Plant Research International, Wageningen University and Research Centre.

Terer, T., Ndiritu, G.G., and Gichuki, N.N. 2004. Socio-economic values and traditional strategies of managing wetland resources in Lower Tana River, Kenya. Hydrobiologia **527**: 3-14.

Thenya, T. 2001. Challenges of conservation of dryland shallow waters, Ewaso Narok swamp, Laikipia District, Kenya. Hydrobiologia **458**: 107-119.

Thirgood, S., Mosser, A., Tham, S., Hopcraft, G., Mwangomo, E., Mlengeya, T., Kilewo, M., Fryxell, J., Sinclair, A.R.E., and Borner, M. 2004. Can parks protect migratory ungulates? The case of the Serengeti wildebeest. Animal Conservation **7**: 113-120.

Thompson, K. 1985. Emergent plants of permanent and seasonally-flooded wetlands. *In* The ecology and management of African wetland vegetation. *Edited by* P. Denny. Dr. W. Junk Publishers, Dordrecht, The Netherlands, pp. 43-107.

Thresher, P. 1981. The present value of an Amboseli lion. World Animal Review **40**: 30-33.

Turner, C.L., Seastedt, T.R., and Dyer, M.I. 1993. Maximization of aboveground grassland production – The role of defoliation frequency, intensity, and history. Ecological Applications **3** (1): 175-186.

van de Koppel, J. and Prins, H.H.T. 1998. The importance of herbivore interactions for the dynamics of African savanna woodlands: an hypothesis. Journal of Tropical Ecology **14** (5): 565-576.

van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. Ecology **62** (3): 688-696.

Wamukoya, G.M. and Situma, F.D.P. 2000. Environmental management in Kenya: a guide to the environmental management and coordination act. Centre for Research and Education on Environmental Law, Nairobi, Kenya.

Western, D. 1973. The structure, dynamics, and changes of the Amboseli ecosystem. Pd. D. thesis, University of Nairobi, Nairobi, Kenya.

Western, D. 1975. Water availability and its influence on the structure and dynamics of a savannah large mammal community. East African Wildlife Journal **13**: 265-286.

Western, D. 1994. Ecosystem conservation and rural development: The case of Amboseli. *In* Natural Connections: Perspectives in community-based conservation. *Edited by* D. Western, R.M. Wright, and S.C. Strum. Island Press, Washington DC, pp. 15-52.

Western, D. 1997. In the dust of Kilimanjaro. Island Press, Washington, DC.

Western, D. and Gichohi, H. 1993a. An Ecological Monitoring Program for Kenya's Protected Areas. Wildlife Conservancy International, NY.

Western, D. and Gichohi, H. 1993b. Segregation effects and the impoverishment of savanna parks: the case for ecosystem viability analysis. African Journal of Ecology **31**: 269-281.

Western, D. and Lindsay, W.K. 1984. Seasonal herd dynamics of a savanna elephant population. African Journal of Ecology **22**: 229-244.

Western, D. and Maitumo, D. 2004. Woodland loss and restoration in a savanna park: A 20-year experiment. African Journal of Ecology **42**: 111-121.

Western, D. and Sindiyo, D.M. 1972. The status of the Amboseli rhino population. East African Wildlife Journal **10**: 43-57.

Wolanski, E. and Gereta, E. 2001. Water quantity and quality as the factors driving the Serengeti ecosystem, Tanzania. Hydrobiologia **458**: 169-180.

Worden, J., Reid, R., and Gichohi, H. 2003. Land-use impacts on large wildlife and livestock in the swamps of the greater Amboseli ecosystem, Kajiado district, Kenya. LUCID working paper No. 27, International Livestock Research Institute, Nairobi, Kenya.