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The vegetation of Manyara

Scale-dependent states and transitions in the African Rift Valley

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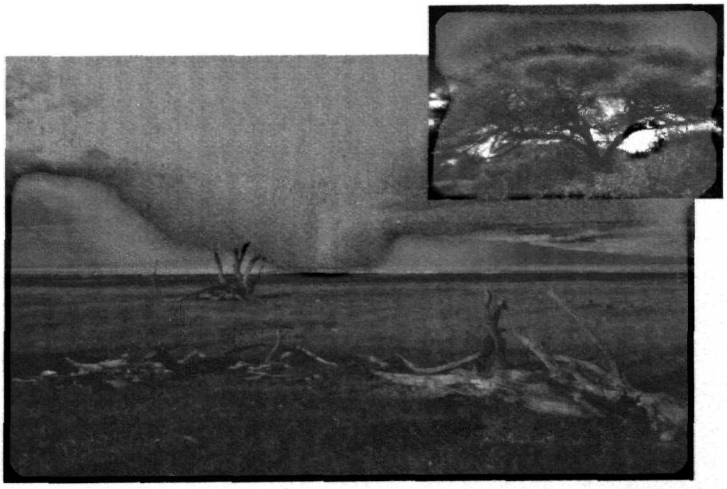
The vegetation of Manyara

Scale-dependent states and transitions in the African Rift Valley

Paul E. Loth



Abstract

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This study focuses on scale dependency, both temporal and spatial, of vegetation changes. At different spatial levels, starting from the level of the individual plant, via patch or stand, plant community, and, finally, at the level of ecosystems, the changes in the vegetation of an East African savanna in the Rift Valley are related to the time span considered. The dominant tree *Acacia tortilis* in Lake Manyara National Park was taken as a typical case in this respect.

A. tortilis seed germination and seedling establishment is most successful on bare patches, in the absence of other vegetation. For the reconstruction of tree establishment in the past, allometric tree growth was studied. Changes in floristic composition between the 1970s and the 1990s were predominantly caused by changes in abiotic factors. The influence of herbivores on the vegetation appears to be minimal on the long-term. The structure of the herbivore assemblage in Lake Manyara National Park, however, is more likely to be determined by changes in the vegetation. Although faunistic and floristic changes occur, these changes must be considered as fluctuations within the ecosystem, and do not lead to a change of the ecosystem itself. It is proposed that scale, both temporal and spatial, must be incorporated in state and transition models.

Key words: temporal and spatial scale, vegetation dynamics, biotic and abiotic factors, *Acacia tortilis*

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Table of contents

	Abstract	i
	Acknowledgements	ii
1.	Introduction	1
2.	Spatial patterns in the landscape and vegetation of Lake Manyara National Park	9
3.	Vegetation changes in Lake Manyara National Park	33
4.	Germination strategy of *Acacia tortilis* in a heterogeneous East African savanna environment	51
5.	Establishment of *Acacia tortilis* seedlings in a heterogeneous East African environment: effects of water, shading and browsing	69
6.	Age cohorts in *Acacia tortilis* populations in East Africa	87
7.	A decade of change in the herbivore assemblage of Lake Manyara National Park	105
8.	Synthesis: Scale-dependent states and transitions in the African Rift Valley	117
	Summary	125
	Samenvatting	127
	Curriculum vitae	131

Chapter 1

General introduction

Changes in vegetation: a matter of scale?

The vegetation is the manifest expression of the land forming factors that make the landscape. In a sequence from more general influences to more local the land forming factors include climate, geology, geomorphology (=land form), soil, water, vegetation, fire, and animal populations. Man affects all these factors, from the local to the global scale. Time is the fourth dimension within which the landscape is formed (Zonneveld 1979).

Changes in vegetation can either be successional or directional, away from an initial stage (Van Andel *et al.* 1993), or reversible fluctuations (states and transitions, Westoby *et al.* 1989). When an immediate return to the initial situation is no longer possible, changes in vegetation may be catastrophic (Rietkerk *et al.* 1996, 1997; Van de Koppel *et al.* 1997). Currently, many empirical studies and models emphasize the impact of herbivory on vegetation dynamics (Crawley 1983, Lamprey 1983, Prins and Van der Jeugd 1993, Kielland and Bryant 1998, and various papers in Olff *et al.* 1999). Belsky (1995) suggests, however, that herbivores have only short-lasting effects on vegetation patterns, although species composition is altered by herbivores (Coughenour 1991). Belsky (1995) argues that vegetation quality and productivity is more likely to direct the behaviour of animals than that animals change the vegetation.

Changes in vegetation take place at different scales, both in time and space (McDowell 1990, Delcourt and Delcourt 1991; figure 1). At the scale of individual plants, the rate at which species are replaced depends on the life form. For instance, the distribution of annual species is determined by rainfall distribution within a season, and on local drainage conditions (Breman *et al.* 1980). On the level of a patch, where plants together form homogeneous areas, the resilience against changes is higher than for individual plants, because the dispersal distance of propagules is small. Within a plant community, the next level in the scaling-up of the landscape, plant species that show a definite association or affinity with each other, grow together, because they have similar requirements for existence (Kent and Coker 1994). Plant communities change when the environmental factors, such as light, temperature, drainage and soil conditions change. Ecosystems are defined at various scales, (*e.g.* Odum 1976, Werger and Westhof 1985, Begon 1996, Crawley 1997) but because ecosystem functioning includes the interactions between fauna and the vegetation and especially large herbivores move through several plant communities, ecosystems generally will encompass more than one plant community. Because ecosystem change does not depend on the change of one plant community only, ecosystem changes therefore occur on a larger time scale again. Tropical savannas, which are grasslands with often a significant tree component, are one of the major vegetation formation types, and are influenced by climatic changes and changes in environmental gradients. Within this spatial-temporal domain human cultural evolution has transformed natural landscapes into cultural ones (Delcourt and Delcourt 1991).

In the study presented in this thesis, both temporal and spatial scale dependency of changes in vegetation have been investigated in Lake Manyara National Park, situated in the Rift Valley in northern Tanzania (figure 2). Lake Manyara is one of the many lakes with internal drainage in the Rift Valley system of central and northern Africa.

Because Lake Manyara National Park is relatively undisturbed, it offers an unique opportunity to study such lake-bordering systems, also because much is known in terms of floristic and faunal data.

In particular I investigated to what extent changes in vegetation can be regarded as transitions, controlled either by the Park's herbivores, or by abiotic factors.

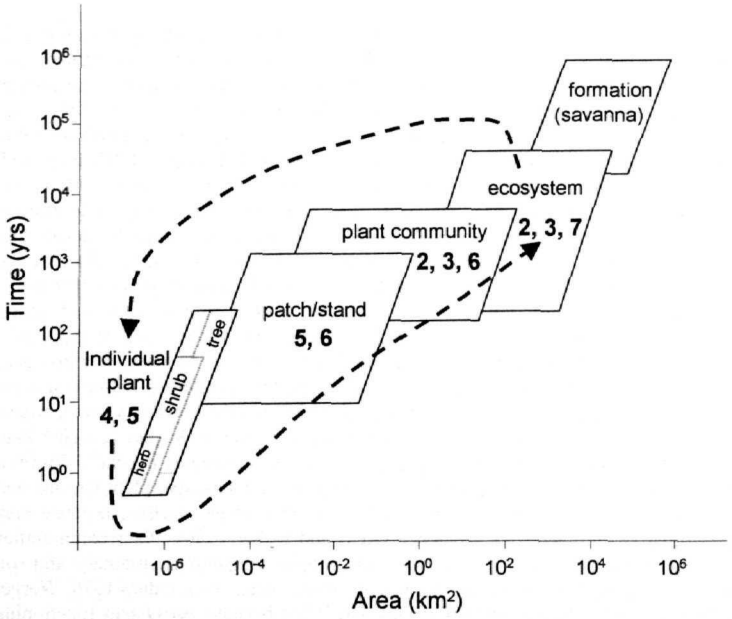

Figure 1. Spatial and temporal scales of vegetation patterns. Numbers in the figure refer to chapter numbers in this thesis. The study started at the landscap level (ecosystem and plant communities), investigated vegetation patterns on the individual level, and via patch/stand level and plant community level, returned at the ecosystem level (arrows). After Delcourt and Delcourt (1991).

Lake Manyara National Park

The study was carried out in Lake Manyara National Park (3°30'S, 35°45'E) in northern Tanzania. Lake Manyara National Park forms part of the Masai Ecosystem (figure 2), an area of about 35,000 km^2, defined by the watershed boundaries draining in the Lakes Manyara and Burunge and by boundaries between migratory large

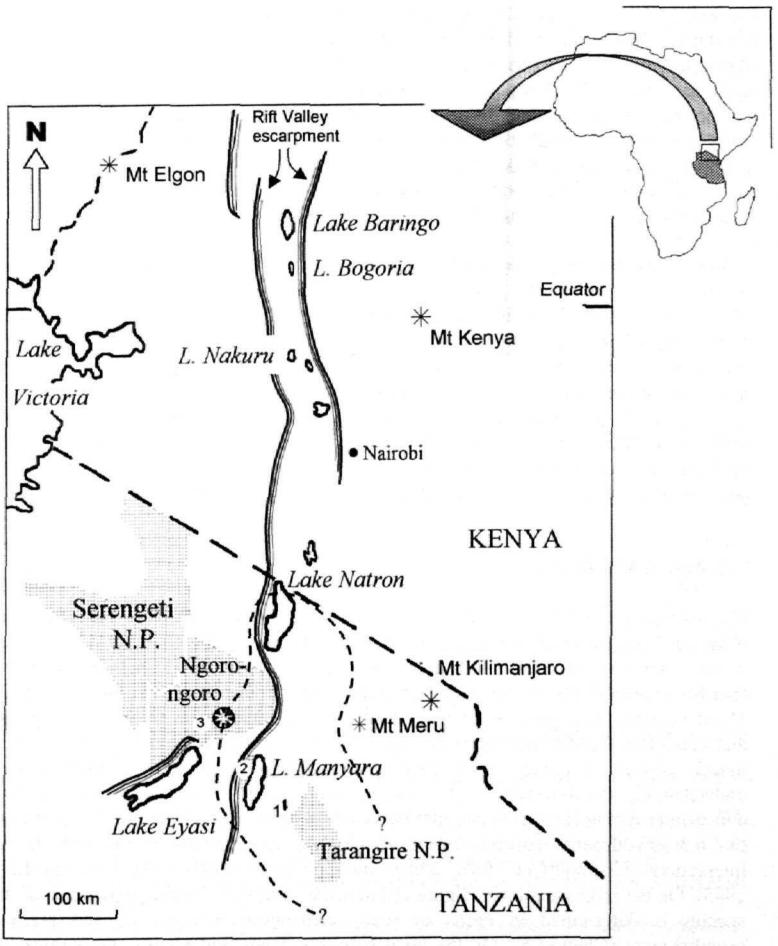

Figure 2. Lake Manyara in northern Tanzania as one of the soda lakes in the Great Rift Valley in East Africa. The approximate extent of the Masai Ecosystem is indicated by the broken line. Protected areas (National Parks and the Ngorongoro Conservation Area) are shaded. 1 = Lake Burunge, 2 = Lake Manyara National Park, 3 = Ngorongoro Crater.

mammals namely wildebeest *Connochaetes taurinus*, Burchell's zebra *Equus burchelli*, Thomson's gazelle *Gazella thomsoni*, and Grant's gazelle *G. granti*. These populations are concentrated in Tarangire National Park and to a lesser extent in Lake Manyara National Park (Prins 1987, 1996). The boundaries of the ecosystem to the north, east and south are not clearly defined, but the boundary to the west is marked by the occurrence of genetically different wildebeest populations in the Serengeti ecosystem and the Masai ecosystem. Based on the movements of plains game up and down the escarpment in Lake Manyara National Park, the water divide between Lake Manyara National Park and Lake Eyasi forms the western boundary. Elephant *Loxodonta africana* and buffalo *Syncerus caffer* are basically resident in the Park (Prins 1996).

Several studies have been carried out in the Park on botanical aspects (Greenway and Vesey-FitzGerald 1972, Douglas-Hamilton 1972, Weyerhaeuser 1982, Mwalyosi 1987, and a detailed description of the landscape patterns was available (Loth and Prins 1986, Chapter 2). The first animal census records date back to 1958 and have been regularly carried out since (Prins and Douglas-Hamilton 1990, Chapter 7). The small size of the Park (100 km^2, recently extended to 110 km^2) and its narrow width, between the steep escarpment and the lake, make it possible to carry out censuses of animals. Old-fields that have been incorporated at different times (1976 and 1990) in the Park area and additional abandoned fields in a farm south of the Park provided the opportunity to study vegetation succession and restoration in old fields.

Outline of the thesis

The starting point of this study is the landscape of Lake Manyara National Park (Chapter 2, figure 1). In the following chapter (Chapter 3), the changes that occurred in the vegetation since the 1960s are related to changes in abiotic factors, mainly as changes in groundwater level, and to changes in the number of herbivores (Chapter 7). These vegetation changes result from mortality and recruitment of the plant species that constitute the different plant communities. One of the dominant plant species is *Acacia tortilis*, a characteristic tree species of East African savannas. Hence, understanding the dynamics of this species is important for the understanding plant community dynamics. Of course, the study could have concentrated on other species too, but an additional reason to choose *A. tortilis* is its important role in plant-animal interactions (Coe and Coe 1987, Miller and Coe 1993, Miller 1994, Reid and Ellis, 1995). On the individual level (figure 1) microsite suitability for the persistence of this species is determined in terms of seed germination (Chapter 4) and seedling establishment (Chapter 5). On the level between stands and plant communities, the growth characteristics of established *A. tortilis* trees are studied in Chapter 6, and related to historical events. For the reconstruction of *A. tortilis* establishment in the past, a method to estimate tree age is introduced. Returning to the level of ecosystems, the changes in herbivores in Lake Manyara National Park are discussed in relation to changes in the landscape (Chapter 7). The synthesis in Chapter 8 puts the findings of the entire study within the perspective of scale-dependent changes in vegetation.

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Chapter 2

Spatial patterns of the landscape and vegetation of Lake Manyara National Park

This chapter is partly re-written from 'Spatial paterns of the landscape and vegetation of Lake Manyara National Park', by Loth and Prins, which appeared in the ITC Journal 1986 (2): 115 – 130. Especially the vegetation table (Table 2, *op. cit.*) has been partially modified and reproduced as a synoptic table.

Summary

This article describes the results of a vegetation survey of Lake Manyara National Park, Tanzania, and is accompanied by the 'Landscape ecological vegetation map of Lake Manyara National Park, Tanzania, scale 1 : 50,000'. The survey was based on aerial photographic interpretation and procedures defined as the 'ITC approach'. The area is subdivided into three main landscapes, each subdivided into several sub-landscapes which are characterized by both terrain and plant communities. Two properties of the vegetation are indicated separately: floristic composition and vegetation structure. The vegetation is classified into 38 communities in nine groups on the basis of floristic composition. The classification of vegetation structure is based on the cover by woody species (shrubs $\leq$ 5 m, trees > 5 m).

Introduction

The need for a vegetation map of Lake Manyara National Park, Tanzania, arose when the study on the relationship between the social organization and feeding strategies of the African buffalo *Syncerus caffer* was started in this area (Prins, 1996). One of the objectives of the study was to establish the preference of the buffalo for the different habitat types in the Park.

Although the vegetation of the Park had been extensively described by Greenway and Vesey-FitzGerald (1969), the only vegetation maps were rough, small scale sketch maps, showing only a few generalized vegetation types (Greenway and Vesey-FitzGerald 1969, Vesey-FitzGerald 1969, Douglas-Hamilton 1972).

Habitat choice by herbivores is related to forage availability (species composition), cover (vegetation structure), water availability and accessibility (terrain characteristics). Hence terrain characteristics are also indispensable for typification of the different habitat types. Our approach was therefore to analyze and describe the spatial patterns in the landscape with special emphasis on the vegetation. This resulted in a 1 : 50,000 scale landscape ecology vegetation map in which the units are delineated and described on the basis of landscape-forming factors such as climate, geology, geomorphology and soil characteristics - in addition to vegetation.

Lake Manyara National Park

Lake Manyara National Park, in northern Tanzania (centre of the Park at 3°30' S, 35°45' E), is situated between Lake Manyara and the steeply rising escarpment of the Great Rift Valley (fig. 1). The lake level, which fluctuates over the years (Prins and Loth, 1988), is at approximately 960 m altitude. The escarpment rises to a height of approximately 1200 to 1300 m in the northern part and to more than 1700 m at the southern end. The high plateau above the northwestern part of the Park is composed mainly of lava and layers of volcanic ash, overlying the basement rocks. Farther south, ancient crystalline rocks are exposed. The drainage system into the lake is closed. During the time of the survey, the Park occupied an area of 325 km^2, of which 225 km^2 was lake. A strip of land (10 km^2) adjacent to the Park to the south that was occupied by sugar cane plantations, was added to the Park in 1990 (see Chapter 3). Further extensions have been proposed, including the Marang Forest. Although human occupation within the Park has never been officially recorded, fires caused by man have modified the vegetation in some areas (Greenway and Vesey-FitzGerald 1969).

At present, the Park receives increasing interest among tourists (Prins, 1987).Immediately northeast of the Park are banana plantations adjacent to alkaline grasslands. These grasslands are used by large numbers of wild herbivores which move freely in and out the Park. To the west, on the volcanic soils of the plateau, are frequently-burned grasslands and scattered home-steads. Towards the south, the plateau becomes more hilly, with woodlands used for cattle grazing and some cultivated fields. The southern border is a line from the escarpment to the lake, while the eastern border runs through Lake Manyara.

Manyara is famous for its bird life and more than 350 species have been recorded here. Tens of thousands of pink pelicans *Pelcanus rufescens*, and African spoonbills

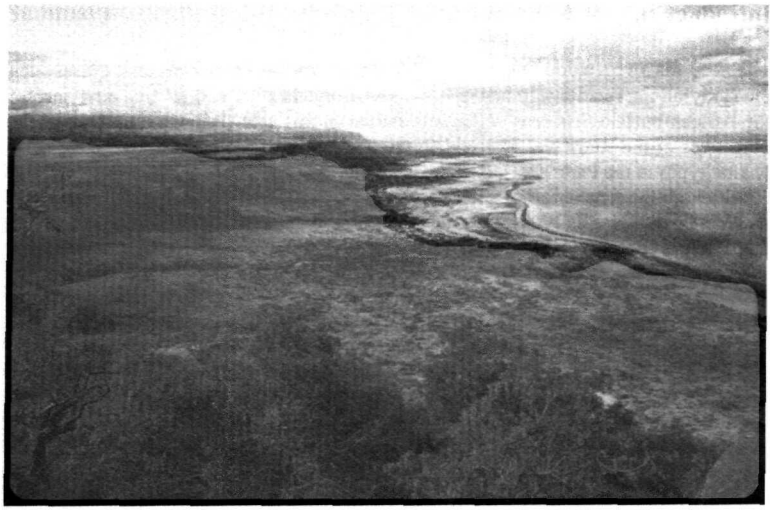


Figure 1. The Great Rift Valley in northern Tanzania facing north, with Lake Manyara, with lacustrine plains along the lake shore at the right-hand side. Faintly visible in the distance and partly obsured by clouds (left-hand side of photograph) are the highlands of the Ngorongoro Crater. The sandy dry river course of Ndala River is just visible at the foreground. Lake Manyara national Park lies between the escarpment and the lake.

Platalea alba, grey herons *Ardea cinera*, cormorants *Phalacrocorax africanus*, wood ibises *Ibis ibis* and sacred ibises *Threskiornis aethiopicus* nest in yellow-fever trees *Acacia xantophloea* and *A. albida* trees and in the groundwater forest. The lake also offers feeding grounds for flamingoes which in some years may number up to several hundreds of thousands. The presence of large flocks of lesser flamingoes *Phoenicopterus minor* is related to the high salinity of the lake.

Birds of prey include the African fish eagle *Haliaeetus vocifer*, augur buzzard *Buteo rufofuscus*, tawny eagle *Aquila rapax*, bataleur *Terathopius ecaudatus* and Verreaux's eagle *Aquila verraeauxii*.

In addition to its birds, Manyara is also well known for its large mammals. Population estimates for the large herbivores are given in Table 1 in Chapter 7. Total herbivore biomass is estimated at 177 kg ha^{-1} (mostly elephant and buffalo), which is one of the highest of the world.

Predators include lion *Panthera leo*, leopard *P. pardus*, spotted hyena *Crocuta crocuta*, black-backed jackal *Canis mesomelas*, bat-eared fox *Otocyon megalotis* and - occasionally - visiting cheetah *Aciconyx jubatus* and some golden cat *Felis aurata*. Small predators are serval *Felis serval*, African wild cat *F. silvestris*, honey badger *Mellivora capensis*, African civet *Viverra civetta*, genets *Genetta* spp. and several mongoose species.

Climate

The mean annual rainfall recorded over a 26-year period (1958 to 1984) is 630 mm, divided over a short rainy season (November through January), and a long rainy season (February through April), with a prolonged dry period from June through October. Rain in October and November is erratic, sometimes even absent, and the onset of the short rains may be delayed. The long-term variation in rainfall patterns results in fluctuation of the lake level (see Chapter 3). The mean annual temperature is approximately 22° C and the mean monthly temperatures do not deviate more than 3° C from the yearly mean.

Physiography

The main outlines of the landscape are to a large extent the result of three major geological events. The Mbulu Plateau is a remnant of old erosional surfaces which extend from the Sudanese-Ethiopian border in the north to the Mozambican border in the south. The underlying rocks belong to the Mozambique Belt which is a part of the crystalline basement complex in which a wide variety of sedimentary and volcanic rocks have been subjected to a similar metamorphic history (Safferson 1972). The crystalline basement complex in the area consists mainly of Precambrian gneisses, banded with quartzo-feldspathics (Mineral Resources Division 1965). The erosional surfaces were formed in the Tertiary (70 to 3 million years ago).

The second important series of events was the formation of the Rift Valley, which, with the major fault scarps, was formed in the Late Tertiary. Whereas the Great Rift Valley at most places is delineated by both western and eastern rift walls, in this area only the western side is bordered by an escarpment. At the eastern side, the Masai Steppe gently dips to the west, forming a depression at the foot of the fault scarp where the lake has settled at the lowest point.

Volcanic activity, the third important event, was associated with the Rift Valley formation. Most of the present volcanic forms, however, were formed during the Pleistocene up to recent times. In northern Tanzania, Mt Kilimanjaro, Mt Meru and the Ngorongoro caldera were formed during the Pleistocene (Berry 1972). In this century, Oldonyo Lengai, approximately 100 km north of the Park, erupted in 1917, 1942 and 1960, and was slightly active in 1983 and in 1995. As a result of Pleistocene volcanic activity, the northern part of the Mbulu Plateau is covered with lava. The Rift Valley filled with sediments (to its present form) during the last 10,000 years (Berry 1972).

The occurrence of volcanic lava and ash also accounts for the high alkalinity of the area. The sodium-rich volcanic material is easily weathered chemically and releases large quantities of sodium. The high phosphate concentration in soil samples from the northern lake bed is remarkable. Since the drainage system of Lake Manyara is closed, the alkalinity of the water becomes so high by evaporation that soda crystals form on the lake bed where the water retreats in the dry season (Beadle 1974).

Survey methods

Panchromatic black-and-white aerial photographs of the Park (scale 1:20,000, enlarged to an approximate scale 1:5,000) made in October 1976 provided the starting point for the survey. The quality of the 1976 photographs was rather poor and approximately 20% of the area was not covered because of gaps between the runs. In the stereo coverage (± 60% overlap) of the area, some 350 photographs were available. To have an overview of the terrain, an uncontrolled photo mosaic was made and reduced to a scale of approximately 1:20,000. This photo mosaic was interpreted monoscopically, while sample areas of the different terrain units, as distinguished on the photo mosaic, were examined stereoscopically at scale 1:5,000.

Preliminary interpretation of these photographs formed the basis for stratified field sampling. Survey procedures were according to the ITC approach of vegetation classification (Zonneveld *et al.*, 1979). Two sets of earlier photographs were not available until after the field survey. These included good quality photos, scale 1:50,000, which were interpreted later for the general terrain forms. Detailed information concerning terrain forms inside the Park was acquired from very good quality 1972 black-and-white photos, approximately scale 1:10,000. The interpretation of the 1972 photographs revealed information which did not appear on the 1976 photos, especially concerning soil moisture conditions. In addition to differences in quality, the time of the year at which the photographs were taken may have influenced the details visible on the photographs with respect to soil moisture. The 1972 photos were taken in early June, at the beginning of the dry season, whereas the 1976 photographs were taken at the end of the dry season, in October.

Since the field sampling programme was based on the preliminary interpretation of the 1976 photos, it was inevitable that some of the sampling points were inadequately chosen when plotted on the 1972 interpretation map.

The field survey was carried out between May and July 1982 with the invaluable assistance of two Park Rangers. One of these Rangers had also assisted Vesey-FitzGerald and was able to identify most of the tree and shrub species (with their scientific names) and many of the herb species. This information was checked against specimens kept in the herbarium at Ndala Research Camp. The camp contained a small but well-equipped laboratory and identification of plant species and processing of soil samples could be carried out immediately.

The sample plots (relevés) were located in each legend unit of the preliminary interpretation map (stratified field sampling). Within each legend unit, the sample was placed in a representative location determined by photo features. After reaching the sample point in the field, the location was briefly scanned to find a representative location for the actual relevé.

Variation in the vegetation cover caused by small-scale mosaics in the vegetation was dealt with by using relatively large sample plots. In a homogeneous grass vegetation, a plot size of 5 x 5 m appeared to be sufficient, whereas in vegetation types with a mosaic pattern, a plot size of 25 x 25 m usually covered a representative part of the vegetation. For woodlands and bushlands, three different plot sizes were used in the same location (Westhoff and van der Maarel 1973): 100 x 100 m for the trees, 50

x 50 m for the shrub layer and 5 x 5 m to 25 x 25 m for the herb layer. When more than one plot size was used, the plot had one common corner point and two common sides; this was considered as one relevé.

Data collection

Data collected per sample plot were entered on standard relevé sheets. These included:

(i) Terrain characteristics - information concerning (among other) slope type and slope steepness, hydrology, drainage and surface rockiness.

(ii) Soil characteristics - in principle, the soil was augered to a depth of 100 cm. Soil samples at depths of 25, 50 and 100 cm were collected and pH and conductivity were measured. The pH (2.5) was measured in a 1 : 2.5 soil-water suspension with an Orion pH meter. The suspension was then further diluted to 1:5 soil-water and the electrical conductivity (EC_5) was measured with a Cenco conductivity meter. Demineralized water was used for the dilution of the samples. Soil texture was estimated manually and classified according to ILACO (1981). Soil colours were determined by comparison with Munsell colour charts (Munsell Color 1973).

(iii) Vegetation data, including both structure and floristic composition.

Vegetation structure

The vegetation was divided into four strata :

- tree layer, woody species taller than 5 m
- high shrub layer, woody species between 2 m and 5 m
- low shrub layer, woody species lower than 2 m
- herb layer

The herb layer was further divided into four groups:

- perennial grasses
- annual grasses
- perennial forbs and climbers
- annual forbs and climbers

To distinguish between woody species and herbs, as well as between annuals and perennials, the annotated checklist of the vegetation of the Park (Greenway and Vesey-FitzGerald 1972) was used. If this checklist did not mention the life form of the species, the *Flora of Upland Kenya* (Agnew 1974), *Kenya Trees and Shrubs* (Dale and Greenway 1961), *A Revised List of Kenya Grasses* (Bogdan 1955) and *Parts I and II (Gramineae) of the Flora of Tropical East Africa* (Clayton 1970, Clayton *et al.* 1974) were accepted as authority. The percentage cover of the strata/groups was estimated, whereby the percentage of bare soil was also estimated in the 100 x 100 m plots. The number of dead trees and their species names were noted. The cover of each plant species was estimated per stratum or group according to a decimal scale (Londo 1976).

Floristic composition

All plant species in the field sample plots were recorded, when possible by their botanical names - or KiSwahili or KiSukuma names as identified by one of the Rangers. Plant species which could not be identified in the field were given a code, collected and labelled. These specimens were compared with herbarium material from earlier studies by Vesey-FitzGerald and Greenway. The herbarium was incomplete and

additional identification was done with the available floras. Plant species which could not be named were identified by the East African Herbarium in Nairobi.

(iv) Finally, all large herbivores known to use the sampled area were listed; these data are available on request.

Data processing and final map compilation

Vegetation composition and structure

The data from the field data sheets (relevé sheets) were compiled in a matrix format of the plant species (rows) versus relevés (columns). Both were rearranged so that a matrix was obtained with clusters of species (sociological species groups) and clusters of relevés (plant communities). The clusters were ordered so that the final matrix shows, as far as possible, a diagonal pattern. The principle of this tabulation-cluster technique is explained fully elsewhere (Mueller-Dombois and Ellenberg 1974).

During the field survey, a total of 480 plant species were identified in 127 relevés. Only species occurring more than three times, or occurring only two or three times within only one plant community, were used for the classification. The vegetation samples were classified according to their floristic composition. Groups of species (sociological groups) which showed a similar pattern in the relevé matrix could be distinguished. The plant communities were characterized by these sociological species groups.

Since a generally accepted syntaxonomic classification of the vegetation of East Africa has not yet been developed, the word 'community' is used here as a term which is not directly associated with a syntaxonomic status of the described vegetation. The term 'community' is defined here as a group of plants which typically occur together in repetitive groups of associated plants (Mueller-Dombois and Ellenberg 1974). In naming the communities, those species which are characteristic of the described communities were preferably used. Such species are not necessarily the most dominant species of the communities.

The estimated percentage canopy cover per vegetation stratum was used to describe the structure of the vegetation. Estimates obtained in the field were compared with planimetered tree canopy and shrub cover on the 1976 (1 : 5,000) aerial photographs. Although sometimes apparently healthy trees on the 1976 photographs appeared to be dead during the 1982 field survey, the number affected did not cause shifts between vegetation structure classes. The vegetation structure is indicated on the accompanying map by hatching (see also 'Key to vegetation structure' on map sheet).

Only the cover of woody species is included in this scheme. The cover by trees is plotted on the abscissa, while the cover of shrubs (woody species lower than 5 m) is plotted on the ordinate. Starting from grassland (**G**) with total cover of woody species less than 2%, an increase of shrub cover leads via bushed grassland (**BG**, total cover of woody species 2 to 20%, predominantly shrubs), bushland (**B**, 20 to 40%, also predominantly bush), dense bushland (**Bd**, 40 to 80%) to bush thicket (**Bt**, more than 80%). A total cover exceeding 100% is possible if some trees also occur; similarly, increase in cover predominantly by trees leads from grassland via wooded grassland

(**WG**), woodland (**W**), dense woodland (**Wd**) to forest (**F**, more than 80%). If the proportion of shrubs and trees in the total cover was approximately equal, the sequence from grassland became wooded and bushed grassland (**WBG**), wooded bushland (**WB**), dense wooded bushland (**WBd**) and wooded bushland thicket (**WBt**). When the total cover exceeded 100%, the cover by trees approximated a closed canopy and was therefore classified as forest (van Gils and van Wijngaarden 1984).

Terrain and soil

The physiography of the terrain outside the surveyed area was determined by aerial photograph interpretation only, and the terrain characteristics in those areas are therefore approximations. Slope steepness was classified according van Zuidam and van Zuidam-Cancelado (1979). In the surveyed area, other terrain characteristics, such as water availability, drainage conditions and surface stoniness, were estimated in the field.

Several types of water erosion were recognized. Rills ($\leq$ 50 cm) cannot be recognized as such on aerial photographs, but local differences in vegetation structure and tonal differences indicate their occurrence. Gullies (50 to 300 cm deep) generally could be recognized clearly as linear features. The rate of dissection by rills and gullies was estimated and the rate of dissection by rivers calculated from the 1958 photographs.

The soil classification was based on the FAO-Unesco (1974) soil classification system.

Composition of the legend units

The final classification into landscape ecological units was made by integrating the characteristics of the vegetation and the terrain. The terrain characteristics were obtained from the field data sheets and photographic features.

Relationships between vegetation and environment (terrain) were examined to obtain a tentative explanation of the occurrence and/or absence of vegetation communities. Distance to the lake (salinity), water availability, altitude, the occurrence of fire and the impact of animals proved to be the key environmental factors for differentiating vegetation communities within the surveyed area.

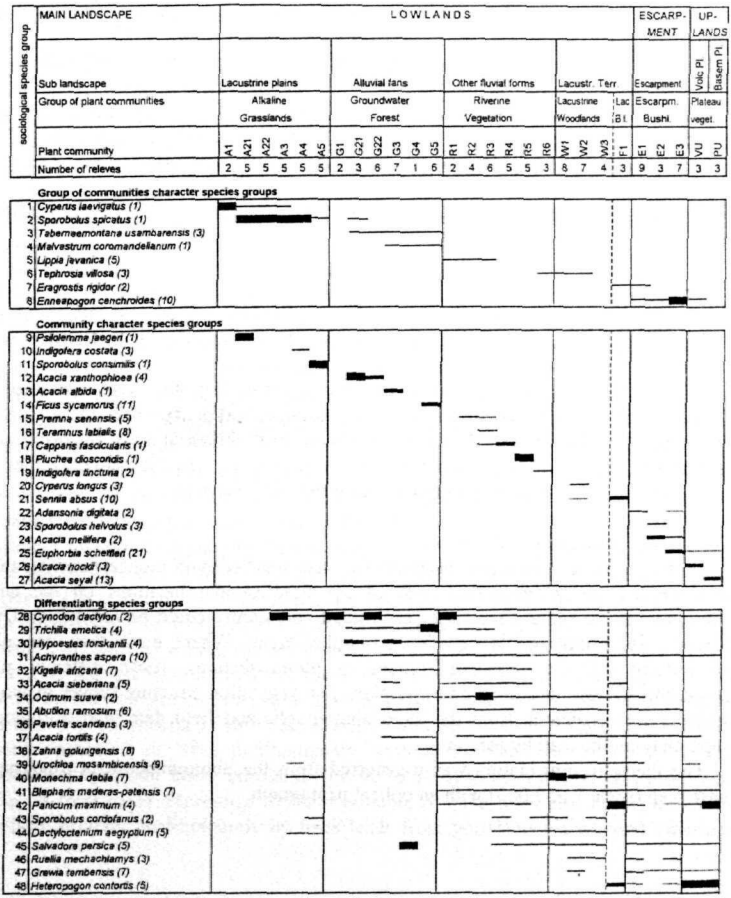
Final map compilation

The relevés, grouped in plant communities, were labelled with a code denoting those communities. By plotting this code of the field sample locations on the aerial photographs, the photo features of each plant community could be identified. These features were used to classify the unsampled areas. Where more than one plant community did not show differences in photo features, those different plant communities were described as a complex. The vegetation structure (cover of woody species) was estimated from the 1976 photographs and field data, and is indicated separately on the map by hatching.

The thematic information was transferred from the photographs to a topographic base map (scale 1 : 50,000) with an optical pantograph.

Table 1. Bar diagram summarizing the relationship between sociological species groups (rows) and vegetation types (= plant communities: columns) in Lake Manyara National Park, Tanzania (after Table 2, Loth and Prins 1986). Group of community species groups (1–8) define groups of plant communities, community character species groups (9–27) have a distribution almost exclusively limited to one plant community or their maximal occurrence is found in one plant community only. Differentiating species groups (28–48) indicate specific environmental conditions not limited to one (group of) plant communities.

▬ species must occur (≥ 75% of positions filled), combined outer cover of species > 20%; ▬ species must occur (≥ 75% of positions filled);— species should occur (25 – 75% of positions filled); ---- species may occur (10 – 25% of positions filled). Number of positions = row (number of species) times column (number of relevés). Between brackets: number of species in species groups. In Appendix 1 the plant species are listed that belong to the different species groups.



The draft final version of the vegetation map was drawn after interpretation of the 1958 and 1972 photographs and reinterpretation of the 1976 photographs. This final draft was again field-checked in 1984 and some minor adjustments were made.

Hierarchic organization of the legend

The hierarchy of the legend is based first on the main geologic landforms (main landscapes). The main landscapes are subdivided into sub-landscapes. The vegetation is classified in groups of communities which in general coincide with the sub-landscapes. Floristically, a group of communities is generally characterized by 'group of communities character species groups', *i.e.*, group(s) of species which occur exclusively together (see Table 1). The groups of communities are furthermore characterized by combinations of 'differentiating species groups'; the differentiating species groups, however, are not themselves characteristic of a group of communities. The plant communities are characterized by 'community character species groups' which are groups of species occurring only in a particular community. In some cases, variants of a plant community are distinguished. The same species are present within the variants of one plant community, but the cover of these species is different, which may result in a different vegetation structure.

The vegetation of areas which were poorly or not sampled during the 1982 field survey are, where possible, characterized by listing the species which were mentioned by Greenway and Vesey-FitzGerald (1969). In the legend, such communities are indicated as undifferentiated (U), and presumably dominant species are mentioned as the characteristic species.

The vegetation structure of each plant community is indicated separately. Finally, a short description of the physiography is given in the last column.

The landscape

In accordance with the main geological divisions, the area is divided into three main landscapes:

- the rift valley bottom or lowlands
- the escarpment, including the footslopes
- the uplifted Mbulu plateau or uplands.

Within each main landscape, several sub-landscapes were distinguished. Each sub-landscape generally could be characterized by a group of plant communities. These main landscapes with their sub-landscapes, groups of plant communities and plant communities, are presented hierarchically in the map legend.

Lowlands

The rift valley bottom has been filled in with weathered material from the uplands. The material is of alluvial and colluvial origin, and both the aerial photographs and the soil descriptions indicate that the material subsequently has been rearranged and modified by the lake. For this reason, the plains between the escarpment and the lake are called 'lacustrine plains' or 'lacustrine terraces'. The distinction between the

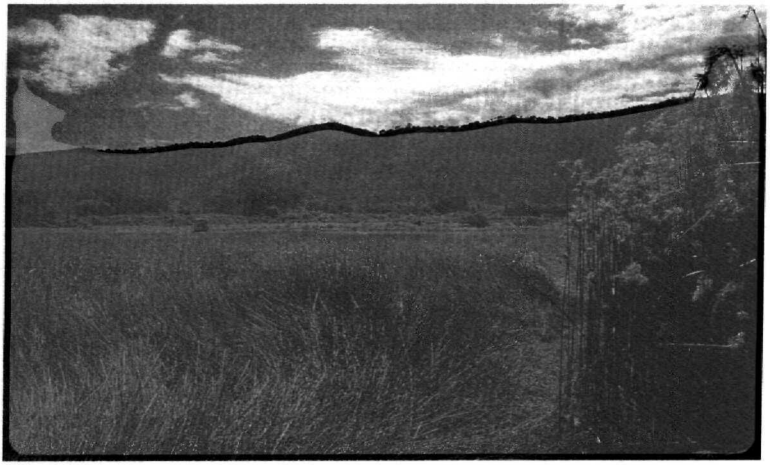


Figure 2. Lacustrine plain near Endabash River. At the right-hand side flowering *Typha angustifolia*, and in the center of the picture *Cyperus laevigatus* swamp (**A1** community). In the background, where the vehicle is parked, *Sporobolus spicatus* (**A2**) grassland is visible.The low shrubs in the background is *Capparis tomentosa – Pluchea dioscoridis* (**R5**) bushland. In the distance the steep escarpment with Marang Forest on plateau above (not visible).

lacustrine plains and the lacustrine terraces is made because the former are still under the influence of the lake, while the latter are not. The small deltas at the mouths of the rivers are liable to flooding by the lake and are therefore included in the sub-landscape of the lacustrine plains.

In the north, several fans of weathered sodium-rich volcanic material have been formed. These fans are partially flooded with water coming from springs at the foot of the escarpment. Other fluvial forms, such as flood plains, river terraces, back-swamps and small deltas, are most clearly developed in the southern Endabash area, but are also found along the other major rivers in the Park. The back-swamps and low terraces are regularly flooded during the wet season, the higher fluvial terraces only exceptionally. This sub-landscape also includes small alluvial fans and ravine bottoms.

Lacustrine plains

Based on frequency of flooding by the lake, three levels of lacustrine plains could be distinguished. The lowest lacustrine plains are frequently flooded (approximately once every two years). These plains may vary in extent from virtually non-existent when submerged to very large in dry periods when the whole lake has dried up. The middle lacustrine plains are regularly flooded (estimated as approximately once every 10 years by comparison of 1958, 1972 and 1976 photographs and field surveys in 1982). High lake levels are related to periods of years which are on average wetter than the long-term mean (see Chapter 3). The middle lacustrine plains vary in width from only

a few meters where the lake almost borders the escarpment, to maximally a few hundred meters where the transition from the escarpment to the lake is gradual. The size of of these plains does not vary much in time. At some places in the middle lacustrine plains, permanently swampy areas caused by seepage are found.

Transitional zones to higher terrain and locally occurring sandy beach ridges in the middle lacustrine plains are rarely flooded (approximately once every 30 years). The highest lacustrine plains may be flooded on exceptional occasions.

The alkaline grasslands occur on alkaline and saline, mostly clayey soils on recent lake deposits (lacustrine plains). The distribution of the plant communities of the alkaline grasslands is related to the frequency of flooding by strongly alkaline and saline water (pH = 10.5, conductivity = 6000 to 8000 mho). After flooding, appreciable desalinization of the soil by rain occurs in sandy soils only (*Sporobolus spicatus - Dactyloctenium aegyptium* (**A4**) community), or in seepage zones where almost salt-free groundwater emerges (*Cyperus laevigatus* (**A1**) community (see also Chapter 3; fig. 2).

In other areas, salts accumulate in the soil because of high evapotranspiration during the dry season. The *Sporobolus consimilis* (**A5**) community occurs on the highest parts of the lacustrine plains, the *Sporobolus spicatus - Cynodon dactylon* (**A3**) community on the intermediate parts, and the *Sporobolus spicatus* (**A2**) and the *Cyperus laevigatus* (**A1**) communities occur on the lowest parts. Bare mud flats (**A0**) are found close to the lake. These areas are dry only during the dry periods and are extremely saline. When the mudflats are not flooded for a long period, the grasses *Sporobolus spicatus* and *Psilolemma jaegeri* (syn.*Odyssae jaegeri*; **A2** community) may colonize these areas (Pielou 1952).

In the north, at the eastern side of the Simba River, the alkaline grasslands extend along the lake. These *Sporobolus spicatus - Cynodon dactylon* dominated grasslands (**AU**) are probably similar to the area at the western side of the Simba River. Since no aerial photographs were available of this area, it could not be ascertained how the different plant communities (**A2** and **A3**) are distributed in this area.

Alluvial fans

In the north, at the foot of the escarpment, the major rivers form large alluvial fans which have not been modified by the lake.

The *Croton macrostachyus* group of communities is found on nearly salt-free to slightly saline, moderately alkaline loamy and clayey soils on these alluvial fans which consist mainly of alluvial/colluvial deposits derived from predominantly volcanic rocks. In this area, special hydrologic conditions exist because of the presence of perennial (slightly alkaline and nearly salt-free) springs emerging at the foot of the escarpment. The distribution of the floristic communities are (causally) related to variation in hydrologic conditions.

Close to the spring heads on the upper part of the alluvial fans, the soils are kept nearly salt-free by perennial overland flow with fresh water from the springs. Here the real groundwater forest (*Croton macrostachyus - Cordia africana* (**G5**) community; fig. 3) occurs. In locally better drained areas, this forest is replaced by bushlands of the *Croton macrostachyus - Salvadora persica* (**G4**) community, which shows floristic affinity with the lacustrine woodlands.

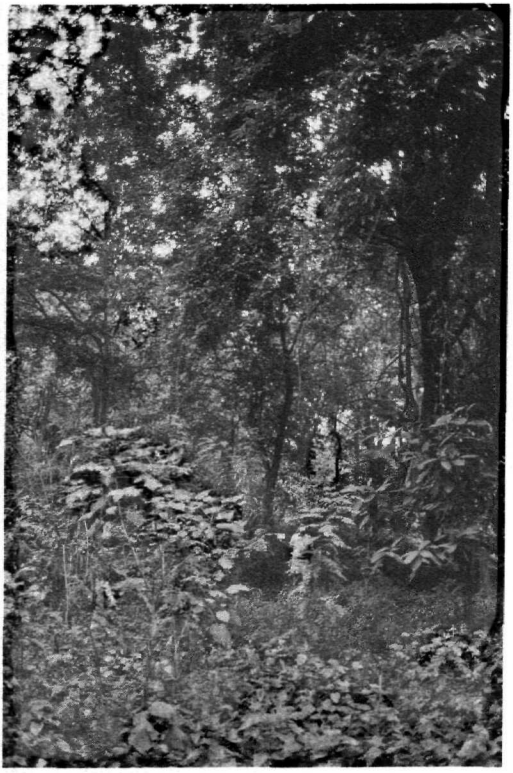


Figure 3. Grondwater forest **G5** in the northern part of the Park.

Farther away from the springs on the lower parts of the alluvial fans, the water has infiltrated into the soil. Because of evapotranspiration, the clayey soils have become slightly saline. The *Croton macrostachyus - Acacia albida* (**G3**) community is found here. On the lowest, nearly flat zones at the perimeter of the alluvial fans, the soils are slightly to strongly saline and strongly alkaline. The layers of different textural classes and the occasional occurrence of shell fragments in the soil indicate that this area was formerly submerged by the lake, which might be the explanation for the relatively high salinity and alkalinity of the soil. The *Croton macrostachyus – Phoenix reclinata* (**G2**) community occurs here in two variants (*viz.* the *Chloris gayana* variant and the *Rauvolfia caffra* variant).

In depressions between the alluvial fans, water from the springs stagnates. The groundwater table is permanently within 100 cm of the surface, and the soils are more

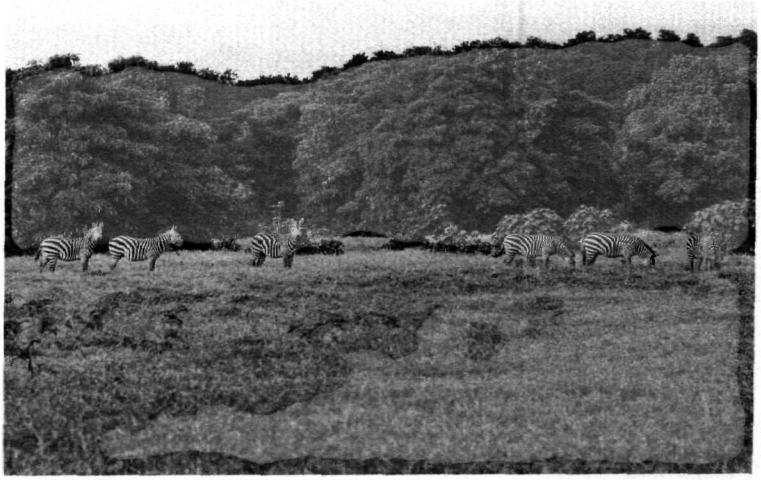


Figure 4. Burchell's zebra grazing *Cynodon dactylon* in a forest glade **G1.**

or less neutral and nearly salt-free. The *Croton macrostachyus* - *Cynodon dactylon* (**G1**; fig.4) community is characteristic of these areas.

The valley bottom around the village of Mto-wa-Mbu, east of the Simba River, is used mainly for irrigated banana plantations. Maize and beans are also important crops. A few decades ago this area was cleared of its original vegetation, and this clearing is still in progress. According to local information, the vegetation was mainly like the Croton macrostachyus group of communities.

River terraces, back-swamps and flood plains

In general, riverine vegetation occurs on salt-free, neutral loamy sands on fluvial terraces and back-swamps along rivers and ephemeral streams. There is excessive moisture during the wet season, but not during the dry season. Locally, where these areas are also flooded by the lake at extreme high lake levels, slightly saline and slightly alkaline soils are found. Differences in hydrological conditions are probably responsible for the distribution of the communities in this area.

The sandy flood plains of the major rivers are frequently flooded during the wet season and have a good water supply during the dry season. The *Capparis tomentosa* - *Triumfetta rhomboidea* (**R1**) community is found here. The *Capparis tomentosa* - *Hippocratea paniculata* (**R2**) community is characteristic of the low alluvial terraces and back-swamps which are regularly flooded during the wet season. The groundwater table probably is within rooting depth throughout the year (see also Chapter 3). Closer to the lake, where such areas are flooded at extreme high lake levels, salts have accumulated in the soil -at least within augering depth. Fresh groundwater, however,

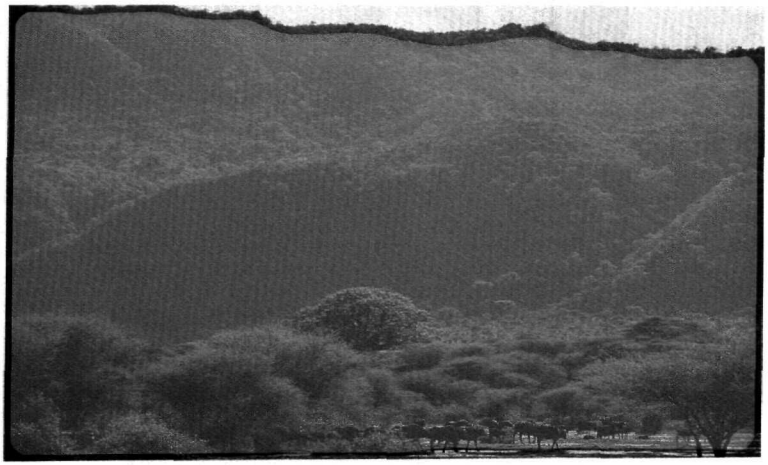


Figure 5. Buffalo in **W1** woodland with a tall baobab tree, *Adandonia digitata*, emerging above the *Acacia tortilis* canopies. At the foreground the alkaline grasslands are just visible. Regenerating *Acacia* are growing at the transitions from the alkaline grasslands to the lacustrine terraces.

probably is within rooting depth throughout the year. The characteristic community is *Capparis tomentosa - Pluchea discoridis* (**R5**). On the higher fluvial terraces and the lacustrine terraces along major rivers where the groundwater rises within 100 cm during the wet season and along the ephemeral streams, moisture availability is relatively high during the wet season but only marginal during the dry season. Here the *Capparis tomentosa – Acacia sieberiana* (**R3**) community occurs. Apart from the areas where the lake has flooded these higher fluvial terraces, salt accumulation can also be found in the former river beds which are only exceptionally flooded by the river. The *Capparis tomentosa - Capparis fascicularis* (**R4**) community is found on such slightly alkaline soils.

The *Ficus wakefieldii* dominated community (**RU1**) is found on the small colluvial/alluvial fans at the foot of the extremely steep escarpment south of the Endabash River. *Croton megalocarpus - Garcinia livingstonei* dominated gallery forest (**RU2**) occurs at the bottom of the ravines also, as a narrow interrupted fringe of gallery forest, along the perennial streams from the escarpment (not mapped separately).

Lacustrine terraces

The low lacustrine terrace and the high lacustrine terrace are located between the escarpment and the lacustrine plains. The flat low lacustrine terrace is separated from the gently sloping high lacustrine terrace by a small steep slope, clearly visible on

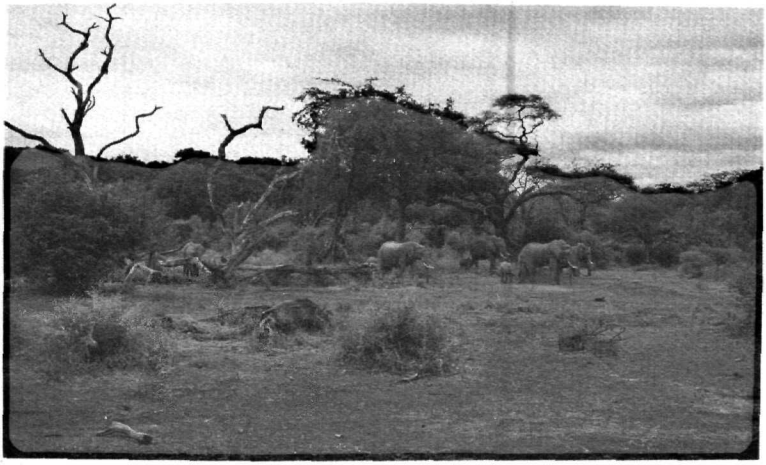


Figure 6. Elephant in *Acacia tortilis* woodland (**W1** plant community). Note the remnants of dead *Acacia* trees.

aerial photographs. The position of this transitional slope, parallel to the lake, indicates a former lake level. The texture of the soil of the lacustrine terraces is not uniform through the profile, indicating former rearrangement of the material by action of the lake.

The lacustrine woodlands and lacustrine bushlands occur on non-saline, neutral to slightly acid, well-drained loamy sands or sandy loams of the lacustrine terraces, where moisture depends mainly on rainfall. The distribution of the floristic communities is related to differences in soil depth and soil drainage conditions.

Well drained, deep soils occur on these lacustrine terraces. Two communities can be distinguished here. On the low lacustrine terrace, the soils are more-or-less neutral loamy sands, and the *Acacia tortilis - Chloris virgata* (**W1**) community is found (figs. 5 and 6). The lacustrine bushlands (*Sporobolus pyramidalis - Rhynchosia sublobata* community (**F1**; fig. 7) and *Sporobolus pyramidalis - Vernonia cinerascens* dominated community (**FU**)) occur in the Endabash area only on slightly acid soils. The floristic composition of these bushlands is allegedly influenced by past occurrence of fires in this area (Greenway and Vesey-FitzGerald 1969).

The soils of the sloping to moderately steep high lacustrine terrace are shallow to moderately deep, gravelly loamy sands. On these somewhat excessively drained soils,the *Acacia tortilis - Vernonia cinerascens* (**W2**) community prevails. At some places at the foot of the escarpment where run-off from the escarpment face is concentrated in gullies, the *Acacia tortilis - Hypoestes verticillaris* (**W3**) community

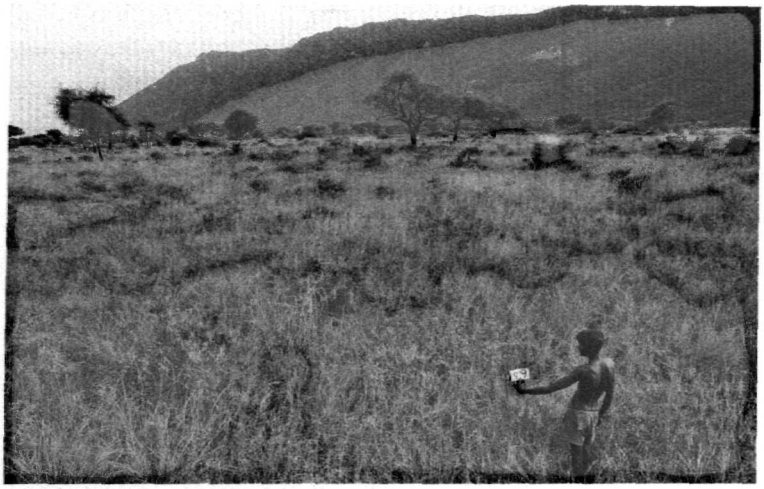


Figure 7. **F1** wooded bushland in the Endabash area. Note the dense grass sward and the low density of trees.

can be found; here typical elements of the riverine bushlands occur in addition to species of the woodlands.

Escarpment and footslopes

The escarpment separating the lowlands from the uplands is very steep to extremely steep, and where the escarpment rises to its greatest height (700 m above the valley floor), cliffs of bare rock frequently occur. In the north, where volcanic ash overlies the basement complex, the escarpment has an irregular slope form. The presence of infilled terraces indicates irregular uplifting along the scarp zone here. The concave steep footslopes with shallow soils are separated from the sloping to moderately steep upper lacustrine terraces, which have in general a straight slope form. A prominent feature in the northern part of the escarpment is the presence of a number of springs. These springs probably indicate the contact zone of two different rock types the volcanic rocks with a higher porosity than the granites of the underlying basement complex. Several large ravines incise the escarpment.

The escarpment bushlands occur on the moderately steep to steep colluvial footslopes and on the very steep escarpment face. The soils are shallow to very shallow, gravelly to stony loamy sands. The *Grewia tembensis – Justicia cordata* (**E1**) community is found on the somewhat excessively drained steep footslopes.

As far as the escarpment itself was sampled, the parent material from which the soils are derived is mainly volcanic rock, resulting in moderately alkaline soils. Two communities can be distinguished here. The *Grewia tembensis - Euphorbia scheffleri* (**E3**) community is found on the excessively drained shallow stony loams of the

escarpment, while the *Grewia tembensis - Cadaba farinosa* (**E2**) community is typical for the infilled valleys in the scarp zone which have deep, poorly drained, moderately saline black cotton clays.

The *Grewia tembensis - Terminalia brownii* dominated bushland (**EU1**) occurs on the exposed parts of the escarpment which are susceptible to fire, whereas the *Grewia tembensis - Commiphora* spp. (**EU2**) dominated bush thickets occur where the vegetation has been protected by the rocky terrain on steep slopes or in the valleys (Greenway and Vesey-FitzGerald 1969). Observations of aerial photographs revealed that in addition to fire, the vegetation structure is also greatly influenced by elephant. On the less steep parts of the escarpment with a rather smooth surface (**EU1** community), elephant are able to mount slopes of up to 60° by making continuous zigzags. During their passage, they feed on the shrubs and trample the herb layer. The effect of the passage of elephant - and other animals in succession – along such a slope becomes clear during the dry season, when the trotted paths become bare and a typical, dotted pattern shows up on aerial photographs. Where the terrain is too steep or too rough for the elephant to pass, the shrubs are able to form an almost closed layer (wooded bush thicket, **EU2** community).

The physical conditions of the lowland and escarpment main landscapes are summarized in Table 2. Lack of field data of the upland main landscape prevented inclusion of this landscape in this Table.

Uplands

Within the main landscape of the uplands, two sub-landscapes are distinguished. In the north, a flat to almost flat volcanic plateau is formed by lava and volcanic ash. Towards the south, the plateau is formed by the outcropping basement complex with more undulating topography. The classification of the vegetation is based mainly on differences in vegetation structure as observed from aerial photographs. Characteristic species are derived from Greenway and Vesey-FitzGerald (1969) with additional sightings made during the fieldwork.

Volcanic plateau

In the northern and western part, sheets of lava and volcanic ash overlie the basement complex, thus forming the volcanic plateau with an altitude of 1200 to 1300 m a.s.l. The terrain is almost flat with a general dip in the northern direction where a depression is filled in with sediments. The occurrence of small, smooth scarps may indicate minor tectonic movements after the ash was deposited, resulting in steps in the plateau. Where deep incisions have formed ravines, the edges have a gentle sloping concave surface and are subject to rill and gully erosion.

The vegetation of the annually burned volcanic plateau consists of *Themeda triandra* dominated grasslands (**VU1**), except where the terrain is irregular. Bushlands, for example, occur on the small slopes that form the transition between steps in the terrain. At the edges of the plateau where rill and gully erosion occurs, trees grow along the drainage lines. Although fire is known to occur in these areas, no fire patterns were observed on the aerial photographs. Hence it is assumed that these areas are irregularly and infrequently burned. Lack of field data and characteristic photo features prevented a systematic separation of these two communities. Whereas the

Themeda triandra dominated grasslands (**VU1**) occur on the better drained parts, the *Pennisetum mezianum* dominated grasslands (**VU2**) occur in the infilled depression with only impeded drainage. These grasslands are burned annually and are exclusively used for grazing by cattle and game. On the well-drained parts of the volcanic plateau, dry land subsistence farming (**Cv**) occurs with maize as the main crop, but beans are often interspersed between the rows of maize. Other crops are wheat, barley and millet.

Basement complex plateau

On the basis of terrain form, the basement complex plateau can be divided into three forms with which the distinguished communities coincide. First, a gently sloping, moderately dissected rolling higher part (above 1500 m a.s.l.) with a rectangular drainage pattern is found in the south. This area is occupied largely by a Forest Reserve, the Marang Forest (**MU**). The crowns of the trees form an uninterrupted closed canopy, except where open glades occur on permanently swampy areas along streams. Within the **MU** community, the Forestry Division of Tanzania (1968) recognized three types of forest, namely the Buger type (dominated by *Olea* spp.), the Daudi type (dominated by *Albizzia* spp.), and the Kansai type (dominated by *Podocarpus* spp.).

Table 2. Summary of physical conditions of the lowland and escarpment plant communities.

Community	Lithology	SOIL CHARACTERISTICS					Other features	Vegetation structure
		pH	Salinity	Depth	Texture	Drainage		
AO	unconsolidated	9.5	5	3	var	- -	frequently flooded by lake	bare
A1	lacustrine	8.0	3	3	var	- - -	regularly flooded by lake: seepage	G
A2	sediments	8.5	3	3	var	-	regularly flooded by lake	G
A3		9.4	4	3	var	-/+	rarely flooded by lake	G
A4		7.6	1	3	sand	+	*exceptionally flooded by lake*	G,BG
A5		8.9	4	3	var	-	exceptionally flooded by lake	G
G1	all sediments	7.5	1	3	clay	- -	seasonally waterlogged	G
G2.1	lacustrine	9.5	3	3	var	-/+	exc flooded by lake where	G,WBG
G2.2	sediments	9.5	2	3	var	-/+	marginal to alk grasslands	B,Bd,Bt,WB
G3	all, sediments	8.3	2	3	loam/clay	-		B,Bd,WB
G4	of weathered	8.0	1	3	clay	+		B,Bd
G5	volc rocks	8.0	1	3	clay	- -	perenn overland flow springs	WBd,F
R1	alluvial	?	(0)	(3)	(sand)	- -	seasonally flooded	G,BG
R2	sediments	7.1	0	3	loam	-	seasonally flooded	Bt,WBt
R3	of	6.7	0	3	loams	-/+		Bd,Bt
R4	predominantly	7.7	1	3	clay-loam	+	exceptionally flooded by lake	B,Bd
R5	weathered	8.0	2	3	s-l/cl-l	-	exceptionally flooded by lake	Bd,Bt,WBt/F
R6	*gneisses*	7.4	3	3	var	-/+		*BG*
W3	coll/all	7.2	0	2-3	loamy sand	+	concentration of run on	Bd,WB
W1	deposits of	7.0	0	2-3	l-s/s-l	+/++	local run on	WBG,WB,WBd
W2	weathered	7.0	0	2	loamy sand	++	sloping/mod steep; gravelly	BG,WBG,B
B1	gneisses	6.2	0	3	sandy loam	+		BG,B,Bd
E1	weath bas compl	7.5	0	1	loamy sand	++	steep/very steep; gravelly/stoney	B,Bd
E2	all volc sedim	8.0	2	3	clay	- -	seasonally waterlogged	G,BG
E3	weath volc rock	8.1	1	1	loam	+++	extremely steep; stoney	B,Bd

Abbreviations: All = alluvial; coll = colluvial; weath = weathered; bas comp = basement complex; volc = volcanic; var = variable; s-l = sandy loam; c-l = clayey loam; exc = exceptionally; perenn = perennial. Salinity classes: 0 = salt-free; 1 = slightly saline; 2 = moderately saline; 3 = saline; 4 = very saline; 5 = extremely saline. Soil depth: 3 = deep; 2 = moderately deep; 1 = shallow. Drainage classes: - - - = very poor; - - = poor; - = imperfect; + = well drained; ++ = somewhat excessive; +++ = excessive

Second, north of the Marang Forest, a complex of concave infilled valleys and moderately dissected, gently sloping terrain with a dendritic drainage pattern (1200 to 1500 m a.s.l.) is found. The *Acacia tortilis – Sporobolus pyramidalis* dominated woodlands (**PU1**) that occur here have been much degraded by fire (Greenway and Vesey-FitzGerald 1969).

Hilly outcroppings of the basement complex, often covered with loose surface rocks, made up the third terrain form. The *Combretrum molle - Commiphora* spp. dominated bushland (**PU2**) which occur here are partly modified by fire (Vesey-FitzGerald 1969). Small plots of dryland subsistence farming (**Cb**) occur throughout the basement complex plateau on the level parts. Maize and beans are the main crops.

Concluding remarks

The classification of the vegetation in sociologic groups versus relevés according to the method used here results in a matrix which shows as much as possible a diagonal pattern. At closer inspection, the build-up of the vegetation table in this study shows some discrepancies with regard to this principle. For example, the lacustrine bushlands (**F** group of communities) show less floristic affinity with the lacustrine woodlands (**W**) than with the escarpment bushlands (**E**). The position of the lacustrine bushland group of communities in the vegetation table, however, is not dictated by only floristic composition but also by terrain characteristics. On the basis of these characteristics, the lacustrine terraces are part of the lowland main landscape rather than of the escarpment and footslopes main landscapes. Such discrepancies are thus a consequence of the approach which was adopted for this survey, namely to analyze and describe the spatial patterns in the landscape of Lake Manyara National Park.

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Appendix 1. Annotated list of plant species used in the compilation of Table 1. grp = sociological species group, freq = total number of occurrences. For life forms, see end of list. Synonyms used in 1982, nomenclature updated by National Herbarium of Tanzania in 1996.

grp	life form	species	freq
1	pg	*Cyperus laevigatus*	13
2	pg	*Sporobolus spicatus*	29
3	ah	*Acalypha indica*	21
3	pg	*Cyperus alternifolius*	8
3	hs	*Tabernaemontana ventricosa* syn *T. usambarensis*	23
4		*Malvastrum coromandelianum*	8
5	ah	*Ageratum conyzoides*	5
5	hs	*Harrisonia abyssinica*	12
5	hs	*Lippia javanica*	20
5	ah	*Tagetes minuta*	9
5	hs	*Triumfetta rhomboidea*	9
6	ph	*Commelina benghalensis*	13
6	ah	*Euphorbia hirta*	3
6	ah	*Tephrosia villosa*	17
7	ls	*Microglossa pyrrhopappa* syn *Conyza p.*	7
7	pg	*Eragrostis rigidior*	10
8	ls	*Acacia schweinfurtii*	16
8	h	*Acalypha ornata*	6
8	ls	*Barleria eranthemoides*	20
8	h	*Becium* indet.	14
8	ah	*Cyathula orthacantha*	13
8	hs	*Ehretia amoena*	13
8	pg	*Enneapogon cenchroides*	15
8	pg	*Enteropogon macrostachys*	18
8	ah	*Melhania velutina*	17
8	t	*Terminalia brownii*	5
9	pg	*Psilolemma jaegeri* syn *Odyssea j.*	6
10	ah	*Corchorus tridens*	8
10	ag	*Cyperus teneriffae*	6
10	ah	*Indigofera costata*	10
11	pg	*Sporobolus consimilis*	9
12	t	*Acacia xanthophloea*	13
12	pg	*Chloris gayana*	19
12	t	*Phoenix reclinata*	10
12	ph	*Phyla nodiflora*	4
13	t	*Acacia albida*	15
14	t	*Acacia robusta* syn *A. clavigera*	6
14	ls	*Albizia zimmermannii*	4
14	t	*Antiaris toxicaria*	4
14	pc	*Asparagus setaceus*	4
14	ph	*Centella asiatica*	4
14	t	*Cordia africana*	5
14	t	*Ficus natalensis*	8
14	t	*Ficus sycomorus*	8
14	pc	*Hydrocotyle ranunculoides*	3
14	ph	*Justicia betonica*	4
14	pc	*Christella dentata* syn *Thelypteris d.*	3
15	ah	*Bidens schimperi*	9
15	t	*Bridelia micrantha*	4
15	pc	*Ipomoea obscura*	12
15	pc	*Premna senensis*	7
15	pc	*Thunbergia alata*	3
16	t	*Maclura africana* syn *Cardiogyne a.*	11
16	t	*Croton megalocarpus*	4
16	ah	*Crotalaria polysperma*	16
16	pc	*Dalechampia ipomoeifolia*	8
16	ph	*Enicostema axillare*	6
16	ag	*Eragrostis aspera*	8
16	h	*Teramnus labialis*	8
16	ah	*Wissadula periplocifolia*	10
17	hs	*Capparis fascicularis*	11
18	hs	*Pluchea dioscoridis*	7
19	ah	*Dicoma tomentosa*	4
19	hs	*Indigofera tinctoria*	10
20	pg	*Cyperus longus* ssp. *tenuifolius*	5
20	ah	*Digeria muricata*	9
20	ah	*Oxygonium sinuatum*	5
21	ph	*Analeima petersii*	5
21	ph	*Boerhavia diffusa*	6
21	ah	*Chamaecrista absus* syn *Cassia a.*	4
21	ah	*Chamaecrista mimosoides* syn *Cassia m.*	3
21	ph	*Hermannia glanduligula*	10
21	ph	*Justicia flava*	6
21	ls	*Lantana viburnoides*	4
21	h	*Rhynchosia sublobata*	4
21	h	*Sesamum angolense*	5
21	ph	*Tephrosia uniflora*	10
22	t	*Adansonia digitata*	7
22	ah	*Justicia heterocarpa*	12
23	ah	*Leonotis nepetifolia*	4
23	[g	*Pennisetum mezianum*	3
23	pg	*Sporobolus helvolus*	3
24	t	*Acacia melifera*	12
24	t	*Maerua angolensis*	9
25	h	*Abutilon hirtum*	7
25	pc	*Asparagus aethiopicus*	4
25	h	*Barleria submollis*	11
25	hs	*Canthium setiflorum*	9
25	pc	*Cissus quadrangularis*	6
25	hs	*Croton dichogamus*	4
25	ph	*Cynanchum tetrapterum*	5
25	hs	*Dombeya kirkii*	4
25	pg	*Eleusine jaegeri*	6
25	hs	*Euphorbia scheffleri*	5
25	ah	*Farsetia stenoptera*	6
25	hs	*Grewia bicolor*	6
25	hs	*Grewia villosa*	5
25	ah	*Leucas neufizeana*	10
25	ls	*Opilia campestris*	6
25	ph	*Sansevieria robusta* syn *S. ehrenbergii*	3
25	ag	*Setaria verticillata*	11
25	ag	*Tetrapogon cenchriformis*	10
25	ag	*Tetrapogon tenellus*	5
25	ls	*Triumfetta flavescens*	7
26	t	*Acacia hockii*	3
26	ls	*Hermannia uhligii*	3
26	ph	*Solanum setaceum*	6
27	t	*Acacia seyal*	3
27	hs	*Agave 097*	2
27	t	*Combretum molle*	2
27	t	*Zanthoxylum chalybeum* syn *Fagara c.*	3
27	t	*Ficus glumosa*	2
27	t	*Ozoroa insignis* syn *Heeria reticulata*	2
27	h	*Labiatae indet.*	4
27	t	*Lannea schweinfurthii* syn L. stuhlmannii	3
27	t	*Lonchocarpus eriocalyx*	3
27	t	*Pappea capensis*	4
27	t	*Rhus natalensis*	2
27	c	*Secamone punctulata*	3
27	pg	*Themeda triandra*	3
28	pg	*Cynodon dactylon*	59
28	pg	*Cynodon plectostachyus*	52

Appendix 1, continued.

grp	life form	species	freq
29	hs	*Cordia goetzei*	23
29	t	*Croton macrostachyus*	31
29	t	*Rauvolfia caffra*	22
29	t	*Trichilia emetica*	29
		syn *T. roka*	
30	hs	*Cordia sinensis*	29
30	t	*Hyphaene ventricosa*	7
30	ph	*Hypoestes forskahlii*	49
		syn *H. verticillaris*	
30	ph	*Justicia glabra*	41
31	ph	*Abutilon mauritianum*	63
31	ah	*Achyranthes aspera*	73
31	pg	*Cenchrus ciliaris*	43
31	hs	*Cordia monoica*	61
		syn *C. ovalis*	
31	ah	*Crotalaria incana*	16
31	g	*Digitaria abyssinica*	7
		syn *D. scalarum*	
31	hs	*Hoslundia opposita*	38
31	h	*Portulaca quadrifida*	17
31	ah	*Sida alba*	30
31	ls	*Withania somnifera*	10
32	hs	*Senna didymobotrya*	19
		syn *Cassia d.*	
32	hs	*Dovyalis xanthocarpa*	29
32	t	*Ekebergia capensis*	9
32	t	*Hippocratea paniculata*	11
32	t	*Kigelia africana*	24
32	hs	*Vangeria madagascariensis*	29
		syn *V. acutiloba*	
32	t	*Ziziphus pubescens*	23
33	t	*Acacia sieberiana*	23
33	hs	*Capparis tomentosa*	28
33	h	*Dicliptera verticillata*	20
33	ls	*Hibiscus lunariifolius*	13
33	ph	*Sphaeranthus ukambensis*	31
34	t	*Gardenia ternifolia*	50
		syn *G. jovis-tonantis*	
34	ls	*Ocimum suave*	61
35	ls	*Abutilon ramosum*	29
35	ah	*Boerhavia erecta*	15
35	ag	*Digitaria velutina*	40
35	ah	*Hibiscus vitifolius*	16
35	ph	*Ruellia prostrata*	21
35	ah	*Zaleya pentandra*	28
36	ls	*Acalypha fruticosa*	56
36	ah	*Bidens pilosa*	35
36	hs	*Pavetta scandens*	49
37	t	*Acacia tortilis*	54
37	ls	*Hibiscus calyphyllus*	38
37	hs	*Maerua triphylla*	67
37	ls	*Thylachium africanum*	50
38	t	*Blighia unijugata*	4
38	t	*Celtis zenkeri*	5
38	c	*Cuscuta kilimanjari*	6
38	hs	*Diospyros abyssinica*	8
38	h	*Phaulopsis imbricata*	4
38	pg	*Setaria homonyma*	9
38	hs	*Tragia benthamii*	5
38	t	*Zanha golungensis*	7
39	t	*Balanites aegyptiaca*	34
39	ah	*Senna occidentalis*	9
		syn *Cassia o.*	
39	pc	*Cucumis figarei*	17
39	ah	*Indigofera colutea*	27
39	ls	*Phyllanthus sepialis*	21
39	ah	*Tephrosia pumila*	15
39	ph	*Tephrosia rhodesica*	24
39	ah	*Trichodesma zeylanicum*	23
39	pg	*Urochloa mosambicensis*	48
		syn *U. pullulans*	
	ag	*Chloris virgata*	40
40	ph	*Sida ovata*	56
40	ah	*Gutenbergia cordifolia*	50
		syn *Erlangea c.*	
40	h	*Indigofera arrecta*	40
40	ah	*Monechma debile*	68
40	ah	*Ocimum basilicum*	45
40	ah	*Peristrophe bicalyculata*	52
41	ph	*Blepharis maderaspatensis*	39
41	ph	*Boerhavia coccinia*	36
41	hs	*Cadaba farinosa*	24
41	ah	*Gynandropsis gynandra*	15
41	ph	*Hibiscus micranthus*	41
41	ah	*Pupalia lappacea*	27
41	h	*Solanum incanum*	46
42	ag	*Eragrostis cilianensis*	10
42	pg	*Eragrostis superba*	25
42	pg	*Panicum maximum*	34
42	pg	*Sporobolus pyramidalis*	21
43	h	*Alternanthera repens*	29
43	ag	*Sporobolus cordofanus*	19
44	h	*Abutilon bidentatum*	18
44	ah	*Asystasia mysorensis*	12
		syn *A. schimperi*	
44	ag	*Dactyloctenium aegyptium*	38
44	h	*Priva adhaerens*	18
		syn *P. cordifolia*	
44	ah	*Tribulus terrestris*	21
45	ag	*Aristida adscensionis*	41
45	ag	*Brachiaria deflexa*	23
45	hs	*Justicia cordata*	30
45	hs	*Salvadora persica*	49
45	hs	*Vepris uguenensis*	28
46	ag	*Setaria sagittifolia*	14
		syn *Cymbosetaria s.*	
46	ah	*Phyllanthus odontadenius*	11
46	ls	*Ruellia megachlamys*	28
47	pg	*Chloris roxburghiana*	19
47	hs	*Grewia tembensis*	21
47	ph	*Heliotropium subulatum*	16
47	ah	*Phyllanthus maderaspatensis*	14
47	ah	*Portulaca oleracea*	2
47	ag	*Tragus berteronianus*	11
47	ls	*Vernonia cinerascens*	13
48	pg	*Botriochloa radicans*	17
48	pg	*Heteropogon contortus*	21
48	pg	*Hyparrhenia filipendula*	4
48	ls	*Maerua decumbens*	6
		syn *M. edulis*	
48	t	*Sclerocarya birrea*	5

Life form:

t	tree (woody species > 5m)
hs	high shrub (woody species 2 - 5 m)
ls	low shrub (woody species < 2 m)
ph	perennial forbs
ah	annual forbs
h	forb
pg	perennial grass
ag	annual grass
pc	perennial climber
ac	annual climber
c	climber

Chapter 3

Vegetation changes in Lake Manyara National Park, Tanzania

Summary

The vegetation composition of Lake Manyara National Park below the western side of the Gregory Rift in northern Tanzania reflects the lessening influence of the alkaline lake, Manyara, along an altitude gradient from east to west. Close to the lake edaphic conditions are perpetuated by the sodic water of the lake. The distribution of the two dominant grass species, *Sporobolus spicatus* and *Psilolemma jaegeri* is related to soil texture and colonization after flooding. Between 1982 and 1996 the cyperus grass *Cyperus laevigatus*, characteristic of up-welling groundwater in the lake shore, has disappeared in the northern part of the park, but large swards still exist further south. The disappearance of the cyperus grass swards is attributed to land clearing that started in the 1940s and resulted in reduced infiltration, resulting in less upwelling of groundwater.

Although the composition of the herbivore assemblage has changed over time, the changes did not appear to have a significant impact on the composition of the vegetation. In the recent past elephants opened up the acacia woodlands. The increase of the 'regeneration class' of *Acacia tortilis* is attributed to the opening up of the woodlands. The distribution of three most common *Acacia* spp is related to groundwater depth, whereby *A. tortilis* tolerates the greatest variance in groundwater depth. The presence of numerous dead A. sieberiana trees in the center of the Park, where also the cyperus grass marsh has disappeared, may be an indication that the ground water table is dropping.

Introduction

Herbivores play an important role in the dynamics of African savannas (Norton-Griffiths 1979, Pellew 1983, Dublin 1991, 1995). At high densities, elephants kill trees, resulting in reduced woody cover (Van Wijngaarden 1985, Mwalyosi 1987, Buss 1990). When seedling establishment is limited by light, tree canopy removal may enhance seedling establishment (Hoffmann 1996). Grazing enhances the establishment of woody species by reducing the grass cover, so that light conditions are favourable for seedling establishment (Belsky and Blumenthal 1997). Woodland regeneration is prevented by selective browsing of seedlings (Prins and Van der Jeugd 1993), or by associational grazing (Olff *et al.* 1999; see also Chapter 5).

Lake Manyara National Park in northern Tanzania has one of the highest herbivore densities in Africa (Drent and Prins 1987). Although the total herbivore biomass has remained fairly constant since the first counts in 1958, the composition of the herbivore assemblage in the park has changed over time. For instance, Prins and Douglas-Hamilton (1990) found that elephant and buffalo were competitors, but recently, wildebeest appear to have replaced elephant as the major competitor of buffalo (Chapter 7). Grazers are likely to differ in body size for coexistence to occur (Prins and Olff 1998, Van de Koppel and Prins 1998) because diet selectivity and efficiency of digestion are a function of body size (Gordon and Illius 1996, Perez and Gordon 1999). A change in herbivore guild composition may therefore lead to, or is induced by, a change in vegetation.

During the dry season, a large proportion of the Park's grazers is supported by the alkaline grasslands, which then provide sufficient bulk of good quality forage (Prins and Beekman 1989). The extent of the grasslands in close proximity to the lake depends on the level of the lake. The lake has no outlet, so that in periods of above average rainfall the lake fills up, while during periods of drought the lake dries out. Consequently, the extent of the grass swards may vary over the years (Vesey-FitzGerald 1963, 1970), and competition between grazers utilising the grasslands in particular may vary with varying lake levels (Prins and Douglas-Hamilton 1990). Because grazing and changes in grazing intensity modify grassland species competition (Walker *et al.* 1981, Berendse 1985, Bergelson and Crawley 1992, Olff *et al.* 1997, Silvertown *et al.* 1994), changes in grazing intensity likewise can alter the species composition of the alkaline grasslands.

Flooding by the alkaline lake alters the physical conditions of the areas that are submerged, due to the salinity of the alkaline lake water. The latest floods submerging the highest lacustrine plains was in 1970, and recently in 1998 (H.H.T. Prins, pers. comm.). Desalinisation of the soils of the lacustrine plains takes place after the lake water has receded. The rate at which floristic elements from the lacustrine terraces invade these areas are thus expected to represent the desalinisation rate of these areas.

It was found that the presence of certain plant communities such as the groundwater forest, the alkaline grasslands and marshes of the cyperus grass *Cyperus laevigatus*, was related to groundwater level and groundwater quality (Loth and Prins 1986). The species composition of groundwater related plant communities could therefore be expected to change with changing groundwater levels.

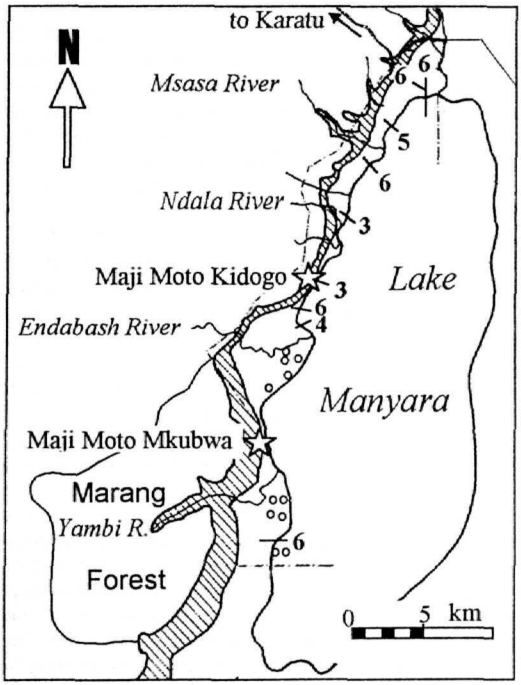

Figure 1. The location of surveyed transects (lines) with the number of boreholes per transect in Lake Manyara National Park. The escarpment of the Rift Valley is hatched. o additional bore holes, not located along a transect, ☆ hot spring, ------ Park boundary.

Hence, there are two hypotheses: 1) changes in vegetation are due to herbivores, and 2) changes in vegetation are due to changes in abiotic factors, in particular in groundwater level. In this paper I describe which changes took place in the vegetation since the 1960s, with emphasis on changes in species composition of alkaline grasslands and changes in the occurrence of *Acacia tortilis* in the lacustrine woodlands (**W group of plant communities, chapter 2**).

Methods

Data collection

In 1982 the vegetation of Lake Manyara National Park in northern Tanzania was described and mapped for the area north of Endabash River, and extrapolated to the entire park (Loth and Prins 1986). The present study describes the area south of Endabash River as well.

For the alkaline grasslands I compared the floristic composition in relation to abiotic factors over time. Changes in the *Acacia* woodlands were studied in four ways. Firstly, the abundance of *A. tortilis* in three phases of establishment in relation to environmental variables was compared between 1982 and 1996; secondly, the demography of the *A. tortilis* population in 1996 was compared with that of 1968 and 1981; thirdly, the degree of tree damage in 1996 was compared to that in 1981, and lastly, the condition and the mortality rate of *A. tortilis* trees since 1968 was determined along a fixed transect. Changes in *Acacia* woodlands are compared with changes in the herbivore assemblage.

Floristic composition in 1982 and in 1996

In 1982 the relationship between plant communities and groundwater depth beyond 1.25 m, the maximum auguring depth, was inferred from terrain characteristics. In 1996 a soil auguring project was carried out to substantiate this presumed relationship between groundwater depth and the distribution of plant species. Near each bore hole site, two vegetation descriptions were made. The maximum auguring depth was 20 m.Forty-six borehole sites were situated along 9 transects form the lake towards the escarpment (fig 1). The elevation of the transect sampling points relative to the lake level was surveyed at regular intervals along the transect with a theodolite, varying between 50 and 100 m depending on the slope of the terrain. The transects were selected in such way that as many different vegetation types as possible were traversed. The landscape ecological vegetation map of Lake Manyara National Park at scale 1:50,000 (Loth and Prins 1986) and 1988 aerial photographs at scale 1:20,000 were used to position the transects. In addition, 13 boreholes were augured that were not laid out along a transect; the elevation of these boreholes was not measured. Bore holes were manually augured in distinct plant communities until the groundwater table was reached. Groundwater samples were taken to the laboratory to determine pH (Eijkelkamp pH meter, type 18.36) and electric conductivity (EC; Hach 1725 electric conductivity meter). Samples with a conductivity exceeding the meter's range were diluted 9 times with distilled water (pH = 7.0, EC = 32 $\mu mho.cm^{-1}$). Plant species composition was sampled in standard plot sizes of 10 x 10 m in homogeneous grass vegetation, whereas in vegetation types with a mosaic pattern a plot size of 25 x 25 m usually covered a representative part of the vegetation. In shrubby vegetation and in woodlands the plot size was 50 x 50 m for woody species, and 5 x 5 m to 25 x 25 m for the herb layer. When more than one plot size was used, the plots were considered to form one relevé. For the vegetation structure, the same four strata as in 1982 were used: trees (> 5 m), high shrubs (2 – 5 m), low shrubs (woody species < 2 m), and herbaceous layer (Loth and Prins 1986; Chapter 2). The percentage cover of each plant

species within the plot was estimated. Species that could not be named in the field were collected for identification in the National Herbarium of Tanzania in Arusha.

Terrain characteristics were entered on standard relevé sheets, following Loth and Prins (1986). Only two slope steepness classes were distinguished: flat to almost flat (slope < 2%) and gently sloping (2-5%); steeper slopes were not encountered during this study along the chosen transects. Drainage was subjectively classified in 5 classes, ranking from very poorly drained (1) to well drained (5); other terrain characteristics, such as rock outcrop and surface stoniness, fell within one class. In each sample plot the soil was augured 1 m deep and soil descriptions were made at 20, 50 and 100 cm. Soil texture was ranked in 5 categories from coarse (sandy) soils to fine (clayey) soils. Calcium carbonate content was determined in the field using a 10% HCl solution and classified in 4 classes: traces, low, medium and very high (International Land Development Consultants 1981). Soil samples from the three depths were taken for analysis of $pH_{2.5}$ (1:2.5 soil water suspension) and EC_5 (1:5 soil water suspension).

The 1996 distribution of the three main *Acacia* species, *A. xanthophloea, A. sieberiana,* and *A. tortilis,* was determined in relation to groundwater depth.

Acacia woodland dynamics

The abundance of *A. tortilis* in the 1982 and 1996 relevés in the three height classes, low shrub (<2 m), high shrub (2 – 5 m) and trees (>5 m), were considered to represent three establishment phases of this species. The abundance of the different establishment phases was related with environmental variables for the two years.

Weyerhaeuser (1982) presented *A. tortilis* size class distributions within the *A. tortilis* woodlands between Maji Moto Kidogo (small hot springs) and Msasa River (fig 1) for 1968 (derived from Douglas-Hamilton 1976) and 1981. In these years the data had been collected in 6 areas varying in size from 4.2 to 56.0 ha. In 1996 stem diameter and tree height of *A. tortilis* trees was determined in 52 randomly selected 0.25 ha blocks in the same general area as 1981, as the exact location of the 1981 plots could not be determined. The size classes were based on girth at breast height (cm) in 1968, and in 1981 and 1996 on diameter at breast height (cm), with a further distinction in tree height < 1 m and > 1 m for the smallest diameter class (< 5 cm).

In 1981 damage to the two largest tree classes was classified in four categories: 1) undamaged, 2) < 50% of stem debarked, 3) > 50% of stem debarked, 4) dead trees (Weyerhaeuser 1982). In 1996 the same classes were used, but apart from damage to bark, also damage to the tree canopy was included. A comparison was made with the 1968 and 1981 data for the two largest tree size classes.

In addition, the condition (damaged or undamaged) of marked *A. tortilis* trees along a transect established in the *Acacia* woodlands near Ndala River back in 1968, was surveyed again in 1996. These observations were compared with those made in the period 1968 – 1987, derived from Weyerhaeuser (1982) and Prins (unpubl. data).

Data analysis

Comparison floristic composition 1982 and 1996

To explore to what extent changes in floristic composition between 1982 and 1996 could be explained by changes in environmental factors, multivariate ordination techniques were used. After the 1982 and 1996 data sets were combined, detrended

correspondence analysis (DCA) was used to determine whether the species response to environmental factors was best described by a linear (principal component analysis, PCA) or by an unimodal model (correspondence analysis, CA; Ter Braak 1995). The data showed that the length of the first gradient was sufficiently long to describe the response model as unimodal (ter Braak and Šmilauer 1998). Detrended correspondence analysis was used because preliminary analysis without detrending had revealed a strong arch effect (Kent and Coker 1994, Ter Braak 1995). In 1996 279 species were found in 94 relevés. In the combined data set (1982 and 1996) 237 species in 139 relevés were used in the analyses: rare species, which were found only once or twice, were omitted. Species cover was square root transformed.

Preliminary examination of the soil data revealed that the soil characteristics of the three soil depths were strongly correlated with each other, except for texture of sites in the alkaline grasslands. For the multivariate analysis only soil data at 20 cm depth were used, because soil data at this depth were available for all sites. Electric conductivity was logarithmically transformed to reduce the influence of extreme high values.

The distribution of the three *Acacia* species, *A. tortilis, A. sieberiana* and *A. xanthophloea*, in relation to groundwater level was determined by logistic regression, based on presence/absence data (Jongman *et al.* 1995). Sigmoid and Gaussian logit curves were fitted (Advanced Graphics Software 1995).

Acacia woodland dynamics

To analyse to what extent the measured environmental factors influenced *A. tortilis* establishment, multivariate ordination was used for the 1982 and 1996 data sets separately. Direct gradient analysis (canonical correspondence analysis, CCA; Kent and Coker 1994, Ter Braak 1995) was applied to the data in the computer programme CANOCO (Ter Braak 1988), with the same environmental factors entered for both years.

For the comparison of the demography of the *A. tortilis* populations between 1968, 1981, and 1996, the trees were classified in 5 age/size classes as presented in Table 1. Because the areas in which the trees were measured in 1968 and 1981 varied in size, weighted means were used for the comparison with the 1996 data. Tree density data were logarithmically transformed, adding unity to allow inclusion of zero counts for particular size/damage classes, in order to obtain homogeneity of variances for analyses of variance.

Table 1. Classification of *A. tortilis* trees in age/size classes. gbh = girth at breast height (cm), dbh = diameter at breast height (cm), h = tree height (m), - = no height criterium.

Class	1968	1981 and 1996	
	gbh	dbh	h
I	0-10	<5	<1
II	10-20	<5	>1
III	20-30	5-10	-
IV	30-90	10-30	-
V	>90	>30	-

Tree damage scores were expressed as number of affected trees per hectare. For the 1981 data, weighted means were used. Analyses of variance for differences in tree densities were carried out on log-transformed density data.

The first date for which transect data had been presented in 1968 (Weyerhaeuser 1982) was taken as day one, and the consecutive dates were represented as the day number since day one. The numbers of days were expressed in years by division by 365. In scatter plots exponential functions were fitted with year and elephant densities to determine tree mortality rate.

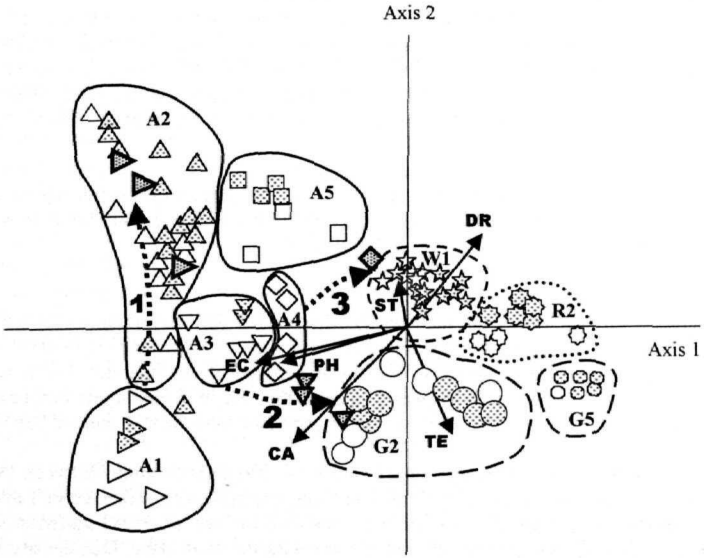

Figure 2. Ordination diagram (DCA) of 139 relevés in Lake Manyara N.P. made in 1982 and 1996, showing sample plots along environmental gradients (arrows). Closed lines encircle relevés belonging to the same plant community, the shape of the symbols indicate to which plant community the sample plots belonged in 1982. Open symbols: 1982, shaded symbols: 1996, changed sample plots thick lines. Numbered arrows indicate changes: 1 change in drainage conditions (groundwater table) (A1 replaced by A2); 2 desalinization of recent sandy deposits on lacustrine plains:(A3 → G2); 3 desalinization of sandy beach ridges (A4 → W1). ST = slope steepness, DR = drainage class, TE = soil texture, CA = $CaCO_3$ content, EC = electric conductivity, PH = soil pH. For clarity, sample plots in plant communities that did not show changes have been omitted. For presentation purposes, the origin of the axes coincide with the origin of the vectors of environmental factors. Length of the first axis = 6.58, length of the second axis = 4.93.

Results

Floristic composition in relation to environmental factors

DCA of the sample sites of both years revealed that the first axis explained 31.5% of the variation and the second axis 9.4%. The ordination values of the first axis were negatively correlated with the logarithm of EC ($R^2 = 0.55$), and hardly with pH ($R^2 = 0.37$) or calcium carbonate content ($R^2 = 0.24$), whereas and positive with drainage ($R^2 = 0.15$), and, very weakly, with soil texture ($R^2 = 0.04$). The ordination values of the second axis were negatively correlated with soil texture ($P < 0.001$, $R^2 = 0.10$), and furthermore, only weakly with EC ($R^2 = 0.08$) and pH ($R^2 = 0.07$). In the ordination diagram vectors (fig 2) represent these influences of the environmental factors. The sample plots taken in the alkaline grasslands, in close proximity to the lake, are at the lower end of the first axis in the ordination biplot, reflecting high pH and high electric conductivity (EC) of these soils. The relevés taken on the lacustrine terraces, with salt free, neutral soils were at the high end of the first axis. The position of the relevés along the second axis is attributed to soil texture and drainage characteristics. The relevés taken in the alkaline grasslands showed a high degree of spread along the second axis, in contrast to the relevés of other groups of plant communities. The *Cyperus laevigatus* plant community with high groundwater table occurs at low values of the second axis, corresponding with poor drainage conditions. Along this axis, relevés, where *Sporobolus spicatus* and *Psilolemma jaegeri* were co-dominant, had intermediate values between the *C. laevigatus* dominated plant communities and those dominated by *P. jaegeri*. Since soil texture is negatively correlated with the values of the 2nd axis, the high values for sample plots with *P. jaegeri* as the dominant species in the alkaline grasslands are indicative for sandy soils. Indeed, on the lacustrine plains close to the lake where *S. spicatus* and *P. jaegeri* both were found with low cover, *P. jaegeri* was found on small, sandy elevations (0.1 m high), while *S. spicatus* was found on the lower terrain in between these slightly elevated sandy patches.

All environmental variables, except soil texture, were significantly correlated with each other (Table 2).

Table 2. Pearson's correlation coefficients for environmental factors in Lake Manyara National Park. Data for 1982 and 1996 combined. Note, that the plant communities (PL_COM) also showed strong and significant correlations, because the sequence of the plant communities are ranked along altitude (see map, Loth and Prins 1986). DR drainage class, TE soil texture, ST slope steepness, EC electric conductivity, PH soil pH, CA $CaCO_3$ content, PL_COM plant community. Important correlations are printed in bold. *: $P < 0.05$, **: $P < 0.01$.

	DR	TE	ST	EC	PH	CA	PL_COM
DR	1.000						
TE	-.237**	1.000					
ST	.349**	-.354**	1.000				
EC	-.459**	.211**	-.408**	1.000			
PH	-.300**	.176*	-.338**	**.848****	1.000		
CA	-.233**	.314**	-.287**	**.752****	**.787****	1.000	
PL_COM	**.524****	-.216**	.459**	**-.830****	**-.744****	**-.676****	1.000

Comparison floristic composition 1982 and 1996

Sites, with *C. laevigatus* as dominant species in 1982, had higher 2nd axis values in 1996, and are now dominated by *S. spicatus* and *P. jaegeri* (arrow 1 in fig 2). In 1996 extended *C. laevigatus* swards were only found south of Endabash River and at the mouth of Simba River in the north.

In the transition zones from lacustrine plains to lacustrine terraces the relevés had higher 1st axis values in 1996 (arrows marked 2 and 3 in fig 2). On the alluvial deposits on the lacustrine terraces (A3), A. *xanthophloea* was found on the transition to the groundwater forest, while *A. tortilis* was prominently found on the sandy beach walls (A4). Since electric conductivity and pH were negatively related to the ordination values of the first axis, this suggests that the shift to higher values along axis 1 meant that soils had become less saline and less sodic.

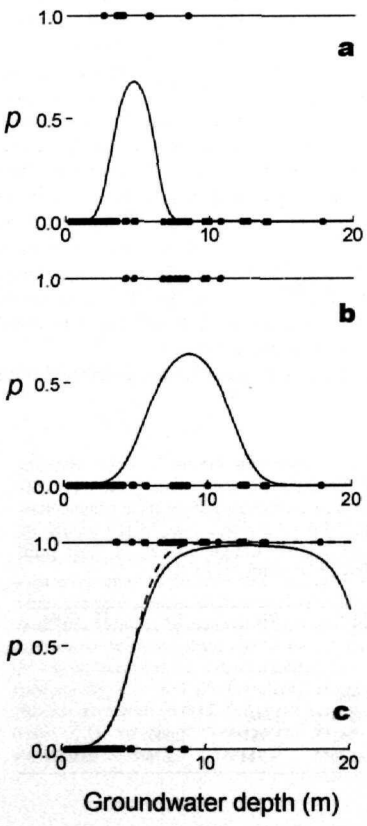

Figure 3. Response curves for three *Acacia* species to groundwater depth in Lake Manyara National Park, Tanzania. Gaussian logit curve fitted by logit regression of the presences (● at $p = 1$) and absences (● at $p = 0$) for *A. xanthophloea (a)*, *A. sieberiana (b)*, and *A. tortilis (c)*. For *A. tortilis* also a sigmoid curve was fitted. Gaussian logit curve is defined as

$$p = c \exp(-0.5 (x - u)^2 / t^2) / [1 + c \exp(-0.5 (x - u)^2 / t^2)],$$

where u = optimum and t = tolerance (Jongman *et al.* 1995).

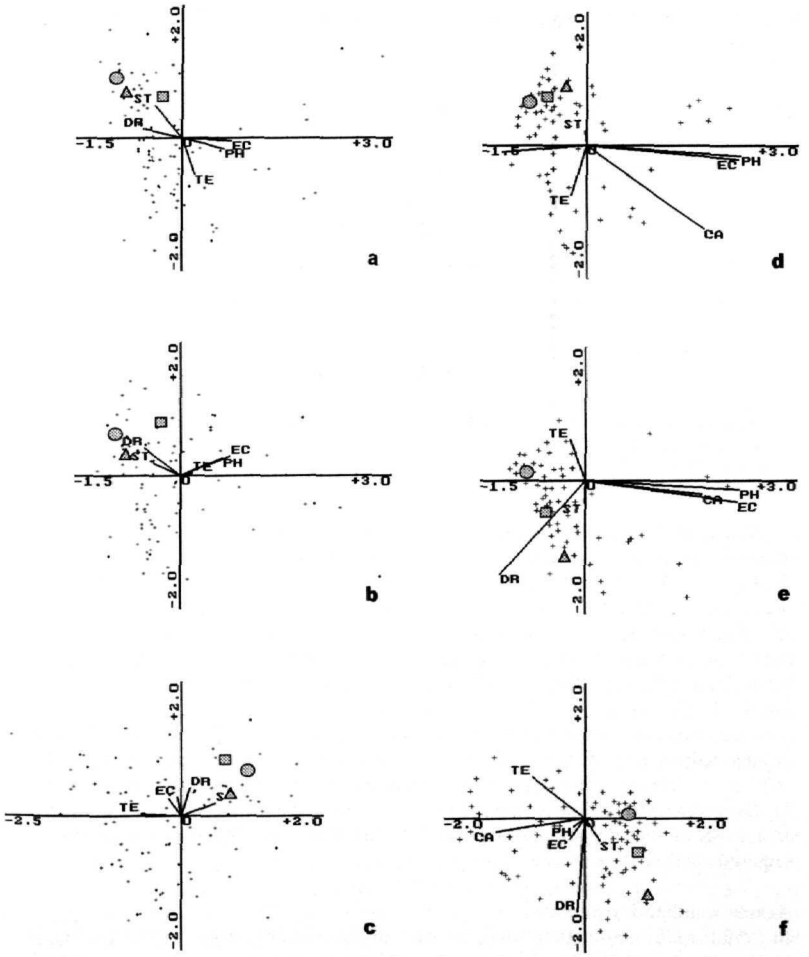

Figure 4. Canonical corresponcence ordination of species-environment relationships in Lake Manyara N.P. in 1982 (*a-c*) and 1996 (*d-f*). Environmental factors are represented by lines; species by +, and *A. tortilis* establishment phases: low shrub, < 2m (Δ), high shrub, 2 – 5 m (□), tree, > 5 m (○). *a, d:* axes 1 and 2; *b, e:* axes 1 and 3; *c, f:* axes 2 and 3. ST = slope steepness, DR = drainage class, TE = soil texture, CA = $CaCO_3$ content, EC = electric conductivity, PH = soil pH.

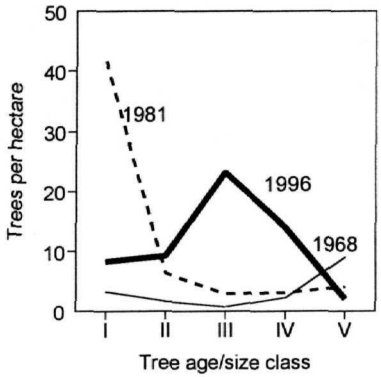

Figure 5. Tree densities per age/size class in *A. tortilis* woodlands in Lake Manyara National Park between Maji Moto Kidogo and Director's Stream in 1968, 1981, and 1996. See Table 1 for definitions of the age/size classes.

More than 90% of all sample plots had a slope < 2%, and only 10 relevés, 8 of which in the *Acacia* woodlands (W1 plant community), were classified as gently sloping (2 - 6%). The 1982 sample sites had somewhat steeper slopes than the 1996 sites ($F_{1,14} = 21.0$, $P < 0.01$), but no difference was found in soil texture ($F_{1,14} = 0.6$, NS). The slight shift in position of the *Acacia* woodlands in the ordination biplot may reflect the fact that the soils of the sample plots in 1982 were classified as slightly better drained than in 1996, due to better run off on the slightly steeper slopes ($F_{1,14} = 4.2$, $P = 0.06$).

A. xanthophloea had its optimum at high groundwater table (4.7 m), *A. sieberiana* at intermediate groundwater table (8.7 m) , and *A. tortilis* at low groundwater table (12.9 m, or deeper), although *A. tortilis* was also found at high groundwater tables (fig 3). The occurrence of dead *A. sieberiana* trees without visible damage in the Endabash area suggests that the groundwater table in this area may have dropped below the required depth for this species.

Acacia woodland dynamics

In 1982 the CCA ordination values for each of the first three axes of the three height classes of *A. tortilis* were fairly similar, and the position in the biplots was mainly determined by drainage and slope steepness (fig 4a-c). In 1996 the three size classes are ranked according to their ordination values in each of the biplots (fig 4 d-f). The relative positions of the different size classes along the first axis (fig 4d) coincide with soil electric conductivity and soil pH, whereby low shrubs were positioned at relatively high values, and mature trees at the lowest. Along the second and third axes (fig 4e, f) the different life stages can be ranked according to texture and drainage respectively, with the youngest life stage placed at low texture values (coarse soils)

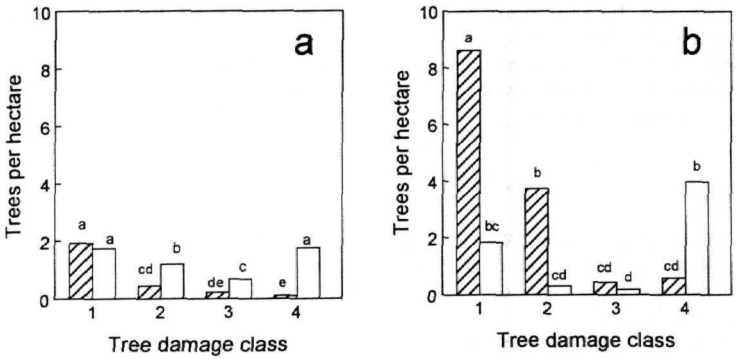

Figure 6. *A. tortilis* tree density and tree condition in the *A.tortilis* woodlands in Lake Manyara National Park in 1981 (a) and 1996 (b). Tree damage absent (1), affecting less than half the tree canopy and/or bark removed (2), damage to more than half the tree canopy and/or bark removed (3), and dead trees (4). Left bars: large trees (class IV), filled bars: mature trees (class V).

and high drainage values (relatively better drained soils). This defines the sandy soils of beach walls and the alluvial deposits on the lacustrine plains, where the coarsest material has been deposited.

More than 90% of all sample plots had a slope < 2%, and only 10 relevés, 8 of which in the *Acacia* woodlands (W1 plant community), were classified as gently sloping (2 - 6%). The 1982 sample sites had somewhat steeper slopes than the 1996 sites ($F_{1,14} = 21.0$, $P < 0.01$), but no difference was found in soil texture ($F_{1,14} = 0.6$, NS). The slight shift in position of the *Acacia* woodlands in the ordination biplot may reflect the fact that the soils of the sample plots in 1982 were classified as slightly better drained than in 1996, due to better run off on the slightly steeper slopes ($F_{1,14} = 4.2$, $P = 0.06$).

In 1968 about half of the *A. tortilis* population consisted of mature trees (class V), and younger trees had been found in much lower densities (fig 5). In 1981 the number of youngest trees (class I) had increased about ten fold, in classes II and III more than doubled, in class IV increased slightly, while the number of mature trees (class V) had more than halved. The differences between 1968 and 1981 are actual, because in both years the same areas had been counted. In 1996 class III trees had been found most frequently, while class V had the lowest number of trees. Using the number of mature trees at the different years and the elapsed time, the mortality rate of mature trees between 1968 and 1981 was calculated as 9.3% yr^{-1}, and between 1981 and 1996 2.9% yr^{-1}.

In 1996 more dead trees were found than in 1981, and especially the number of dead mature trees had increased considerably (fig 6a and 6b). The number of damaged mature trees had decreased, while more class II trees were damaged, although the inflicted damage in most cases was not considered to be lethal. The mortality rate of

the trees along the transect was 11.9% yr^{-1} ($F_{2,2} = 782.4$ $P < 0.001$, $R^2 = 0.997$; fig 7a). Inclusion of elephant density as covariate in the general linear model did improve he model. When the fraction of undamaged trees of the total number of alive trees was regressed upon elephant density, a strong, negative trend ($F_{1,3} = 7.74$, $P = 0.069$, $R^2 = 0.63$) was apparent (fig 7b).

Discussion

In Lake Manyara National Park the vegetation between the lake and the escarpment is unmistakably defined by a gradient, from very alkaline and saline, poorly to imperfectly drained soils close to the lake, to neutral and salt free, well-drained soils higher up the shore.

Within the alkaline grasslands the distribution of the dominant grass species, *Sporobolus spicatus* and *Psilolemma jaegeri*, depends on soil texture and on the way these two species recolonize the lake bed after recession of lake water recedes following flooding by the lake (Vesey-FitzGerald 1963). Desalinization of these soils requires above-average rainfall, which will result in higher lake levels and subsequently the soils are flooded again. Fluctuations in lake level not only cause changes in the vegetation composition of the alkaline grasslands, but also perpetuate the extreme physical conditions.

In the northern part of the Park the *C. laevigatus* swards had almost completely disappeared in 1996, with the exception of the small hot springs and at the mouth of Simba River. Extended *C. laevigatus* swards were still present along the lakeshore south of Endabash River. Since these marshes occur in seepage zones (Loth and Prins 1986), the lower groundwater tables found in the northern part of the park suggest that the amount of seepage has diminished. The extended *C. laevigatus* swards were only found below the Marang Forest Reserve that covers the catchment area that drains into the lake. In the areas north of the hot springs, the vegetation on the plateau had been removed during the Second World War, as part of the War Effort (pers. comm. M. Kullander). I suggest, therefore, that the seepage zones are fed by aquifers that are recharged from the plateau, westerly of the lake. The replacement of natural vegetation by arable fields in the north has resulted in increased run off and, consequently, decreased infiltration. The effect of reduced recharge of aquifers in turn has on the long term apparently resulted in drying up of seepage zones in the alkaline grasslands, where the cyperus grass *C. laevigatus* once thrived.

The increase in the number of dead trees found between 1981 and 1996 is not necessarily an indication of an increased mortality rate. Dead trees can remain available for a very long period. The time of death of *Acacia* trees is difficult to assess, except for trees that had died recently, because fine twigs and branches become dis-attached within two to three years. Remnants of *Acacia* trees killed by the 1970 lake flood, were still standing along the lake shore in 1996, so that it is possible that some of the trees that had been scored as dead trees in 1981, had been scored again as dead trees in 1996. At the other hand, Park's personnel collect dead wood as fuel wood, and consequently, the disappearance rate is accelerated. No conclusions can therefore reliably be drawn from the number of dead trees found in the park.

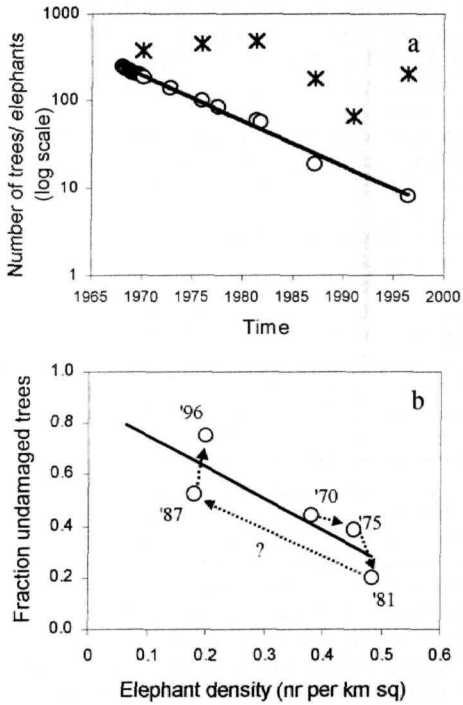

Figure 7. Number and condition of marked *A. tortilis* trees along a transect in Ndala area in Lake Manyara National Park in relation to elephant population size. *a)* Number of marked trees (black dots) and total elephant population in the Park (asterix). Slope of regression line of $\log_e$ transormed tree numbers on year = −0.119 ($F_{1,3} = 182.7$, $P < 0.001$, $R^2 = 0.978$). *b)* Tree damage in relation to elephant density. Regression line of fraction undamaged trees on elephant density: $y = 0.875 - 1.22\ x$ ($F_{1,3} = 7.74$, $P = 0.069$, $R^2 = 0.63$). Transect data 1968 – 1981 from Weyerhaeuser (1982) 1987 and 1991 from Prins (unpubl. data) and 1996 this study. Elephant census data from Prins and Douglas-Hamilton (1990), Prins and Van Der Jeugd (1993) and this study.

Along the lakeshore, remnants of *A. tortilis* trees marked the extreme high lake level of 1970 that had killed the trees. After 12 years, these sites were still dominated by floristic elements of the alkaline grasslands. In 1996, 26 years after these extreme high lake levels, *Acacia* woodland species, including *A. tortilis*, were found on the sandy beach ridges. On the sandy river deltas also *A. xanthophloea* had established. Salts were leached from the sandy soils, but as soon as the soil becomes finer textured, the percolation rate of salts decreases. The *Sporobolus consimilis* plant community

was found on places of the lake bed that had not been flooded since 1970. The pH and salinity of these loamy soils had not changed in the period between 1982 and 1996. On aerial photographs the tall bunch grass *S. consimilis*, characteristic these loamy soils, has been present on the same places since 1958, and , according to A. Seif (pers. comm.), these patches with *S. consimilis* also existed in 1936.

The floristic composition and the extent of the alkaline grasslands is determined by the physical conditions, caused by the proximity of the lake, and by changing groundwater levels. Apparently, changes in the herbivore assemblage have no effect on the alkaline grasslands.

In 1968 mature trees dominated the *A. tortilis* population in the northern part of the Park. The high mortality rate of 9.3% per annum of mature trees between 1968 and 1981 was attributed to debarking behaviour of elephants (Vesey-FitzGerald 1970, Douglas-Hamilton 1972, Mwalyosi 1987). The low abundance of young adult trees, the recruitment class for mature ones, may also have caused a low mortality rate in the period between 1981 and 1996. The decrease in the number of mature trees damaged by elephants at the cost of young adults suggests, that elephants select younger trees above mature trees, as was also concluded by Mwalyosi (1990). The decline in damage to mature trees resulted from a drastic reduction in elephant population due to poaching (Chapter 7), but also because elephants selected trees of a younger age.

The analysis of the transect data should be interpreted with caution, since no replicas are available. However, the data suggest that the relatively high mortality rate of the transect trees remained constant between 1968 and 1996. The mortality rate among the transect trees was not explained by the total number of elephants in the park, although there is a tendency that a higher proportion of trees was damaged at moments when the density of elephants was higher. The current increase in elephant density is not expected to affect tree damage in the transect, since only the largest tree classes are included in the transect, and such trees are no longer selected by elephants.

In conclusion, the distribution of the two dominant alkaline grassland species, *S. spicatus* and *P. jaegeri*, is determined by local differences in soil texture. The cyperus grass, *C. laevigatus*, is found on places within the alkaline grasslands with high groundwater tables. Since 1982, the groundwater table in the northern part of the Park appears to have fallen, resulting in the displacement of the cyperus grass with the other alkaline grass species. High lake levels in the 1970s submerged transition zones between the lakeshore and the lacustrine terraces. In 1982 few species of the lacustrine terraces were present, but in 1996 more species, including *A. tortilis*, from the lacustrine terraces were found on the lightest soil types, due to sufficient leaching out of the salts. Elephants had opened up the woodlands since the 1960s. The proportion of trees damaged by elephants depends on elephant density.

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Chapter 4

Germination strategy of *Acacia tortilis* in a heterogeneous East African savanna environment

Summary

In savanna ecosystems, water availability in the upper soil layers is highly variable, but once established, trees have access to deeper, permanently moist soil layers. In the Rift Valley in Tanzania, *Acacia tortilis* occurred abundantly as a tree in recently abandoned arable fields, and in gaps in existing *Acacia* woodland canopy, but not in perennial grasslands or underneath the parent canopy. Whether such regeneration patterns can be regarded as a reflection of the germination strategy of *A. tortilis* was determined by examining the germination success of *A. tortilis* under field conditions and by investigating the physiological conditions that provoke seed germination in laboratory experiments.

In field experiments in Lake Manyara National Park in northern Tanzania, *A. tortilis* seed germination was highest in bare soil patches that were not shaded by vegetation, followed by patches in perennial grass swards and lastly, under tree canopies. Seeds placed on top of the soil rarely germinated, while seeds covered by elephant dung or buried 1 cm deep in the soil showed no difference in germination success.

In laboratory experiments these differences could be attributed to temperature related water absorption rates by the seeds, although an optimum temperature of 22 to 24 °C was found for the actual germination. Seeds that had absorbed water became spoiled when kept at temperatures above 35.5 °C. The absence of light did not have a significant effect on germination success.

Seed water absorption rate was found to be related to seed moisture content, with a threshold water content of 6.5%, below which the water absorption rate had become infinitesimal. These seeds are added to the seed bank. Seeds with low water contents did, however, absorb water and germinated after being exposed to dry heat of 150 to 450 °C.

Although the best germination results occurred in bare sites away from the parent tree, *A. tortilis* does not actively disperse the seeds. *A. tortilis* regeneration from the seed bank outside tree canopies and in gaps formed by the death of mature trees in *Acacia* woodland in Lake Manyara National Park was substantial. The tree's regeneration potential thus depends on the state of the vegetation.

Introduction

Plants in savanna ecosystems have to be adapted to highly variable environmental conditions, both spatially and temporally. A number of factors cause this variability. First, rainfall is unpredictable. For instance, Prins and Loth (1988) have shown for northern Tanzania that superimposed on large-scale cyclic trends in annual rainfall, the annual amount of rainfall recorded at individual locations had random variation. Secondly, the occurrence of fire, and the temperature regime of fires, is unpredictable. Norton-Griffiths (1979) and Pellew (1983) reported that fire prevents the growth of trees smaller than one meter in East African savannas, but fire may also stimulate seed germination of woody species (Mucunguzi and Oryem-Origa 1996, Sabiiti and Wein 1987; in Australia: Hodgkinson 1991). Thirdly, the interaction between browsers and plants (Chapter 3, 5 and 7) may ensue in vegetation changes that are often the result of transitions between vegetation states (Westoby *et al.* 1989) that are apparently well described by mathematical catastrophe theory (Rietkerk *et al.* 1996). Competitive interactions between grasses and trees (Belsky 1994, Knoop and Walker 1985, Stuart-Hill and Tainton 1989, Smith and Goodman 1987, Walker and Noy-Meir 1982) complicate matters further, with the result that vegetation states dominated by trees or grasses, respectively, may develop in the landscape unpredictably (Van de Koppel and Prins 1998). Removal of aboveground biomass by fire may shift the balance between competing species (Defosse and Robberecht 1996), but may cause similar catastrophic vegetation shifts as herbivores.

Plants have evolved different strategies to cope with such highly variable, competitive or stress-full environments. In contrast to animals, plants once established cannot move. Long-lived species may thus have secondary plant components to deter browsers (reviewed in Owen-Smith and Robbins 1993) or thick bark to withstand heat damage (Pinard and Huffman 1997). However, from the point-of-view of locations that are ever-changing between states that are (potentially) well-suited for the growth of a particular plant species to circumstances that are ill-suited for the same species, seed dispersal and seedling establishment is of crucial importance to understand the dynamics of savanna ecosystems. Indeed, the evolution of life histories of these plant species must have been subjected to selective forces that determine whether a young plant of a given species is at the right time at the right spot to develop into an adult which can reproduce in time before it dies. Dormancy (Skordilis and Thanos 1995) and dispersal (Miller 1994a,b) enable escape from unfavourable conditions in time and space.

Many East African savannas are dominated by *Acacia tortilis* (Forssk.) Hayne and some other *Acacia* species. These trees may reach an age of some 150 years (Prins and Van der Jeugd 1993) and in Lake Manyara National Park in northern Tanzania death of adult trees is to a large extent the result of utilisation by elephants (*Loxodonta africana* Blumenbach) (Douglas-Hamilton 1972, Weyerhaeuser 1982), submergence when lake levels are high (Douglas-Hamilton 1972, and *pers. obs.*), and perhaps droughts (Chapter 3). The central question in the dynamics of savannas is perhaps not so much what terminates the lives of these trees as what determines where new stands of trees such as *Acacia* may emerge. *Acacia* regeneration does not occur underneath the parent canopy (Mwalyosi 1990, Smith and Goodman 1986; Smith and Shackleton 1988, Vesey-FitzGerald 1973). This was also observed in the study area, Lake Manyara National Park (Tanzania), while in nearby,

recently abandoned arable fields, where a perennial herbaceous layer had not yet established, *Acacia* establishment was often abundant (*pers. obs.*). The objective of this study is to determine whether the species' germination strategy is reflected in these regeneration patterns. Field experiments where conducted to establish (1) where and under what conditions seeds germinate. The physiological conditions that provoke seed germination were examined under laboratory conditions, specifically (2) the effect of temperature and light on germination and (3) the effect of temperature on seed loss. Furthermore, seeds were (4) subjected to dry heat treatments to simulate the effect of fire on the germination characteristics.

Study site and species

The field experiments were conducted in the part of Lake Manyara National Park, in northern Tanzania (centred at 3°30' S, 35°45'E) which lies between Lake Manyara to the east and the steep rising escarpment of the Great Rift to the west. The Park below the escarpment consists of various lacustrine terraces adjacent to the lake alkaline grasslands, which are liable to flooding by the lake. Except where in the northern part of the park seepage sustains a broad-leafed forest dominated by *Trichilia emetica* Vahl, the terraces which are not flooded by the lake are characterized by the occurrence of *Acacia* woodlands, dominated by *A. tortilis*. The zone with the *Acacia* woodlands varies in width from about 300 m to 3 km (Loth and Prins 1986). The mean annual rainfall is 650 mm, with a bimodal distribution pattern. The mean annual temperature is 21°C, and the mean monthly temperatures do not deviate more than 3°C from the yearly mean (Loth and Prins 1986).

Acacia tortilis (Forssk.) Hayne ssp. *spirocarpa* (A. Rich.) Brenan is a leguminous tree with an umbrella shaped canopy. Canopies of mature trees may reach a diameter of over 30 meters. The main flowering period occurs between May and July (*pers. obs.*), although incidental 'out-of season' flowering has been observed, as is also reported by Haro and Oba (1993) for the Turkwell River floodplain in Kenya. The flowering period is followed by pod formation and seed filling, and a period of ripening. After some 150 days the mature, indehiscent pods fall on the ground (Lamprey *et al.* 1974), on which they can be found in large numbers between October and December (*pers. obs.*). When unripe, the pods as well as the seeds are green. Unripe seed coats are soft, becoming hard upon ripening.

A. tortilis seeds were collected from freshly fallen pods over a four-month period (July 1995 - November 1995). Fully-grown seeds were visually inspected on signs of insect damage, and only seeds that did not show any markings on the seed coat were retained for the germination experiments. Seeds collected throughout the entire period were pooled. To avoid losses of stored seeds by bruchid beetles infestation as reported by Ernst *et al.* (1990), Lamprey *et al.* (1974) and Vir and Jindal (1994), the collected seeds were sprayed with a household insect killer (Doom, produced by Twiga Chemical Industries Ltd for Reckitt & Colman Industries Ltd, Nairobi. Working ingredients: 0.19% pyrethrum, 0.105% permethrin (25:75 cis:trans isomers), 0.5% dichlorvos and 0.5% piperonyl butoxide), and kept in closed tin containers.

Methods

Data collecting

Field experiments

The effect of habitat type and micro site on seed germination was investigated in a field experiment with a full factorial design. Three treatments were applied to the seeds: seeds were placed on top of the soil, covered with a 5 cm thick layer of elephant dung, or the seeds were buried 1 cm deep in the soil. The experiment was carried out in duplicate in three different habitat types: bare soil without shading, within swards of the perennial grass *Cenchrus ciliaris* L., and under mature *Acacia* canopy with herbaceous undergrowth. Each experimental site consisted of nine PVC rings of 3 cm high, with a diameter of 10 cm. The treatments were randomly assigned to the rings in a Latin square design. Twelve seeds were placed in a regular pattern in each ring. Chicken wire with 1.5 cm maze width was placed around the sites to prevent seed predation by baboons (*Papio cynocephalus anubis* Lesson), and small rodents. Every four days the number of emerging seeds as identified by the cracking or the elevation of the soil and the number of newly emerged seedlings was recorded. The experiment was rain fed and ran from 15 February 1996 to 28 August 1996, for a total of 105 days. The latest rainfall was recorded on 26 May 1996. The amount of light reaching the soil surface at each location was determined as the fraction of current (mV; Dynatek 9050 Digital Multimeter) generated by a 0.5 m linear integrating light meter (TDFL, Wageningen, The Netherlands), whereby the current reading in direct sunlight was used as the reference value. In perennial grass swards about 65% (n=34) of the light was intercepted and under *Acacia* canopies more than 90% (n=40).

The effect of shading on soil temperature was measured in a sandy soil in full sun and covered with guinea-sacking cloth, resulting in a 95% reduction in incoming radiation. On 37 days during a three-month period (1 June - 11 August 1995) the temperature at 5 cm above the soil and at 1 cm in the soil was measured daily at two-hourly intervals between 7.00 and 17.00 h.

The allelopathic effects of the parent tree on seed germination was assessed by placing seeds under the canopies of *A. tortilis* (n=20) and *Gardenia ternifolia* (Schum. & Thonn. (n=8) trees, and under two shrub species, *Cadaba farinosa* Forssk. *Acalypha fructicosa* Forssk. (n=13 for the two species combined). This was aimed at separating the effect of the parent tree from that of lack of light. The amount of light reaching the ground as measured with the linear integrating light meter did not differ among the two tree species ($P>0.05$), but underneath shrubs less light was intercepted by the canopy (shrub: 84%, *Acacia*: 93%, and *Gardenia*: 94%; $F_{2,39} = 8.586$, $P < 0.001$). Under each canopy, two 3 cm high PVC rings with a diameter of 10 cm were placed one cm deep into the soil. Twelve *Acacia* seeds were buried at 1 cm depth with regular spacing in each ring. These experimental sites were screened off with chicken wire to prevent seed predation. Germinated seeds were scored as above. The experiment started in December 1995 and continued until two weeks after the last rainfall event, on 26 May 1996. The experiment was rain fed and no additional water was supplied.

Climate chamber experiments

The climate chamber experiments were carried out between July and September 1997, about two years after seed collecting. The effect of temperature on seed germination characteristics (water absorption by the seeds and seed germination) was experimentally assessed by placing six petri-dishes containing 20 seeds each at 17, 21, 25, 29, 33 and 41 °C and under 12 h light/dark conditions in Weiss climate chambers. The effect of light on seed germination characteristics was investigated by covering six additional petri-dishes with 20 seeds each with aluminium trays to block out the light at 17, 25, 33 and 41 °C. The petri-dishes had permanent moist tissue on the bottom. The relative humidity in the climate chambers was kept at 80%. The numbers of swollen seeds and germinated seeds were scored daily on weekdays for a period of 60 days (17, 25, and 33 °C), 38 days (21 and 29 °C) and 12 days (41 °C). The duration at 41 °C was limited, because seeds did not germinate and appeared to be spoiled after only a few days. Seeds were considered to have germinated when the radicle was clearly visible. Swollen seeds that had not germinated but had been covered with fungi for at least five days were considered spoiled. This was confirmed afterwards by evaluating the viability of embryos of such seeds after staining for 24 hours in triphenyltetrazoliumchloride (Moore, 1973). These, and germinating seeds were removed from the seed coat to determine whether the seeds had been infested with bruchid beetle larvae.

Because germination can only take place after the seeds have absorbed water, the seed germination rate could be expected to depend on the rate at which the seeds absorbed water. The effect of temperature on the germination rate, independently of the water absorption rate, was determined in seeds which, after treatment, had absorbed water within 24 h. The treatment consisted of immersing the seeds in hot water (80 °C), which was allowed to cool and soaking the seeds for 24 h (Mbuya *et al.* 1994). Seeds that had absorbed water after 24 hours were equally divided over 5 (17, 25 and 33 °C), 6 (21, 29, and 41 °C) and 8 (11 °C) petri-dishes with moist tissue on the bottom. The average number of seeds per petri-dish, corrected for insect infestation, was 9.1. The number of germinated seeds was counted for eight days, every 12 hours during the first two days and daily thereafter.

The effect of seed water content on the probability that seeds absorbed water was examined by comparing the water content of seeds which had not absorbed water during the course of the experiments detailed above. The water content of two samples of ten seeds that had not absorbed water after 60 days at 17, 25 and 33 °C, and six samples of ten seeds each from the seed stock, was determined by weighing the samples before and after five days drying at 70 °C. The water content of the seeds was regressed upon the proportion of the seeds that had not taken up water.

For the determination of the effect of dry heat on seed germination seeds were used, which had not swollen after 60 days at 17, 25 or 33 °C. Air-dried seeds were either placed in petri-dishes with moist tissue on the bottom without further treatment, or after being put for 15 seconds in a stove kept at 150, 300 and 450 °C. For each temperature treatment, 6 batches of 20 seeds were prepared by placing 10 seeds per ceramic cup in the oven; the seeds were allowed to cool down for 30 minutes afterwards. For the treatment at 450 °C, the ceramic cups were filled with fine sand,

and the seeds placed on top of the sand, after it appeared during an earlier attempt that during the cooling down period the seeds attained burnt marks and several seeds had popped. The number of swollen and germinated seeds at 29 °C was scored daily for twelve days.

Data analysis

Field experiments

In the experiment in which germination success between different habitat types and microsites was compared, two-way Anova of arcsine transformed data showed that there was no block effect of the replicas ($F_{1,36} = 1.90$, $P > 0.1$), and the replicas were lumped for further analysis. The germination success at the end of the experiment was determined by Analysis of covariance, with site and treatment of the seeds as categorical variables, and time as covariate.

Climate chamber experiments

A number of swollen and germinated seeds appeared to have been infested by bruchid larvae. These seeds were excluded from the analyses. The data were transformed when the variances were not homogeneous. Proportional data were arcsine transformed.

A seed, which has absorbed water or germinated at time t has a status $S(t)=1$, while unchanged seeds have status $S(t)=0$. The proportion of all transmuted (swollen or germinated) seeds (p_1) is related to time (t) and any other independent variable. A predictor for proportional data is provided by the logit transformation of (p_1): $\ln (p_1/(1-p_1)) = a + b_1x + .. + b_nx^n$ (Jongman *et al.* 1995, Sokal and Rohlf 1995). Both the probability that a single seed will change from $S=0$ to $S=1$, and the cumulative proportion of transmuted seeds can be described by the model. The linear predictor for the probability for seed transmutation is given by:

$$\ln[(n_{1,t})/(N - \sum_{i=1}^{t} n_{1,i})]$$

where $n_{1,t}$ is the number of changed seeds at time t, N is the total number of seeds and $\sum_{i=1}^{t} n_{1,i}$ is the cumulative number of transmuted seeds at time t. In the model describing the cumulative proportion of transmuted seeds, the numerator is replaced by the term: $\sum_{i=1}^{t} n_{1,i}$

In the logistic regression model the light treatment was entered as describing the cumulative proportion of transmuted seeds, the numerator is replaced by categorical variable (light/dark regime and continuously dark) in addition to the covariates time and temperature. Higher order interactions were included in the model, because optimum responses were expected within the range of the independent variables. Since a seed at any one time can only have two, mutually exclusive states (0 or 1), the dependent variable is binomially distributed. The best fit for the logistic regression is obtained when those parameters are included in the model, for which the statistic $-2LL$ is minimized (where LL stands for the $\log_e$ of the likelihood). For inclusion of additional parameters in the model, the significance of the reduction of the quantity $-2LL$ of the old model has a χ^2 distribution with the number of degrees of freedom equal to the difference in the number of parameters between the models (Huisman *et*

al. 1993). A large value for the statistic *–2LL* does not necessarily imply a poor fit of the model (McCullagh and Nelder 1989 in: Huisman *et al.* 1993). The model with the highest explained variation was accepted (Huisman *et al.* 1993), which for both for water absorption and germination appeared to be the model based on probabilities (table 1). The logistic regression analysis was carried out with the SPSS (SPSS Inc. 1995) statistical package.

The predictions from the logistic regression model for seed germination were compared with the analyses of a second germination experiment, where seeds which had been subjected to a heat treatment were placed at various temperatures for germination. The optimum germination rate was established by plotting the half time values, i.e. the number of hours required for half of the seeds of the total number of germinated seeds to have germinated within an eight-day period, against temperature. A second order polynomial curve, rather than a Gaussian response curve was fitted through the data, because an optimum temperature was expected within a distinct temperature range, beyond which germination is impossible. The effects of temperature and light treatment on seed spoilage was examined for each petri-dish (n=54) at the temperature range from 17 to 33 °C. For each petri dish the number of spoiled seeds within 35 days were scored and calculated as the percentage of swollen seeds which had not been infested by bruchid larvae. Seed spoilage at 41 °C was omitted, because all swollen seeds became spoiled after only a few days. Multivariate analysis of variance, with light treatment as categorical variable, and temperature as covariate was carried out rather than logistic regression analysis, because seed spoilage could not be related to the day at which the seeds had absorbed water.

Table 1. Variance explained (R^2) for logistic regression models for water absorption and germination, based on proportional and cumulative data. Degrees of freedom (d.f.) denotes the number of parameters included in the models with the lowest *–2LL*.

Model	R^2	*d.f.*
Proportional:		
Water absorption	0.69	3
Germination	0.65	4
Cumulative:		
Water absorption	0.37	4
Germination	0.22	5

Results

Field experiments

The main effects, site ($F_{2,45} = 4.19$, $P < 0.05$), treatment of the seed ($F_{2,45} = 51.82$, $P < 0.001$), and their interaction ($F_{4,45} = 2.95$, $P < 0.05$) had a significant effect on germination success. One-way Anova of the grouped variates showed that seeds placed on top of the soil had significantly lower germination success than the other treatments (fig 1). Seeds placed on top of the soil failed to germinate in all but two seeds in the

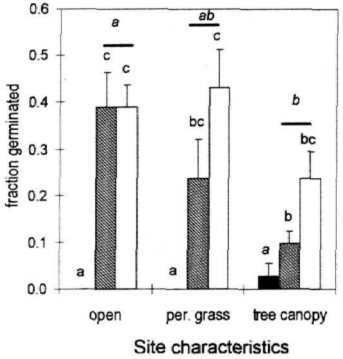

Figure 1. *A. tortilis* germination in open sites, in perennial grass sward and under *Acacia* canopy with different treatments of the seeds. ▨: seeds placed on top of the soil, ▧: seeds covered with 5 cm thick layer of elephant dung, □: seeds placed 1 cm deep into the soil. Means calculated for 18 plots per treatment, with 12 seeds each. Bars indicate 95% confidence limit. Letters denote significant differences at $\alpha = 0.05$ for all treatments, italic letters for buried and dung covered seeds combined (Bonferroni multiple comparison test).

same ring under *Acacia* canopy. Obviously, seeds rarely germinated when placed on top of the soil. When these seeds were omitted from the analysis, there was no significant difference in germination success between buried seeds and seeds covered by elephant dung ($F_{1,34} = 3.30$, $P > 0.05$), and only seeds under canopies had definitely lower germination success than seeds placed in the other sites ($F_{2,33} = 5.509$, $P < 0.01$); the interaction term was no longer significant ($F_{2,30} = 1.14$, $P > 0.1$). When temperature measurements immediately following rain showers were excluded, the mean soil temperatures in exposed situations was 8.3 °C (95% C.I. = 0.72, n = 179) higher than in shaded soils. The drop in temperature after soil wetting depended on the soil temperature before wetting in a linear fashion ($T_{after} = 0.41 * T_{before} + 12.3$; $F_{1,47} = 85.9$, $P<0.001$, $R^2=0.64$).

The proportion of the seeds that germinated was not significantly different whether planted under trees or under shrubs, and the proportion of germinated seeds did not depend on the amount of light reaching the soil ($F_{3,78} = 0.640$, $P > 0.1$). Thus, it can be concluded that there is no effect of the parent tree on the germination ability of *Acacia* seeds which are placed one cm deep in the soil underneath it's canopy.

Climate chamber experiments

At all temperatures more than half of the total number of seeds that absorbed water did so during the first 10 days (figure 2a). Although the water absorption rate was highest at 41 °C, none of the seeds subsequently germinated when kept at this temperature (figure 2b). Inclusion of light treatment in the logistic regression analysis for water absorption did not significantly improve the model ($\chi^2 = 0.17$, df=1, $P > 0.1$). Time and the temperature at which the seeds were placed during the experiment both had a significant effect on the probability that seeds absorb water ($\chi^2 = 717.2$, df = 2 , P <

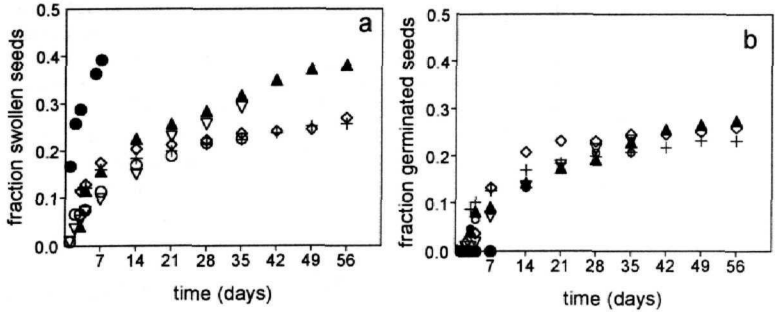

Figure 2. Daily and weekly cumulative fraction of *A. tortilis* seeds, kept at different constant temperatures that had absorbed water ('*swollen*'; a), or had germinated (b). The results of the germination experiments carried out under 12-hourly light/dark and continously dark conditions were combined. The fractions have been corrected for seeds that were infested by bruchid beetles. ◇ seeds kept at 17 °C, ○ : 21 °C, + : 25 °C, ▽: 29 °C; ▲ 33 °C, ● : 41 ° C.

0.001), but not the interaction between time and temperature (χ^2 = 1.84, df = 1, P > 0.1). Inclusion of the quadratic term for temperature significantly decreased the log likelihood (χ^2 = 68.9, df = 1, P < 0.001). Consequently, the model predicts that some *Acacia* seeds absorb water immediately after the seeds have been placed in moist environment, while the probability that the remaining seeds absorb water declines with time to approach 0 after sixty days (figure 3a). Above 25 °C the water absorption rate increased exponentially with temperature. Thus it appears to be logical to conclude that the absorption *rate* per seed increases in the same way. The presence or absence of light did not have a significant effect on seed germination, although just barely so (χ^2 = 5.548, df = 2, P>0.05). Time did not have a significant effect on the probability of seed germination *per se* (χ^2 = 0.691, df = 1,P > 0.1), but the interactions of time with temperature and the square of temperature are significant (for both terms P<0.001), resulting in a decrease in the probability of remaining seeds to germinate with time (figure 3b). The logistic regression model for seed germination predicts that the optimum temperature for seed germination is at around 21 °C. In the germination experiment no germination occurred at a temperature of 41 °C if the seeds were kept longer than 2 days at this temperature.

Linear regression analysis showed that the mean water content of the seeds, which had not absorbed water after the germination experiments, was significantly lower as a smaller proportion of the seeds remained unchanged (y= 5.639 + 1.836 * (1-x), where x = fraction of swollen seeds; P < 0.001; R^2 = 0.64). This indicates that seeds with a high moisture content absorbed water sooner than seeds with a lower moisture content. Most seeds, which were swollen after immersion in hot water, germinated between 17 and 25 °C (figure 4), with an optimum temperature of 22.4 °C as derived from the fitted polynomial curve. This model was preferred above a Gaussian response curve,

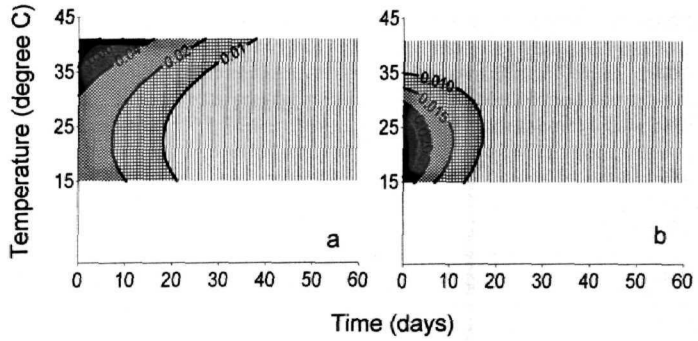

Figure 3. Probabilities that (a) seeds from a seed lot swell as a result from water aborption or that (b) swollen seeds germinate at different temperatures in climate chamber experiments. The fitted regression model for (a) is: $p=1/(1 + \exp(1.5698 + 0.0644*DAY + 0.1684*TEMP - 0.0038*TEMP^2))$, and for (b): $p=1/(1+\exp(6.5545-0.2916*TEMP+0.0069*TEMP^2 + 0.0074*DAY*TEMP - 0.0002*DAY*TEMP^2))$; *TEMP stands for temperature. Note the differences in the* probability intervals.

because it was expected that the chances that swollen seeds would survive, and germinate after eight days, would be actually zero above a critical temperature. The model predicts that no seeds germinate at constant temperatures below 8.7 or above 35.5 °C. Seeds that had not absorbed water after being placed in a wet environment for 60 days, did so after a short exposure to dry heat. The difference in germination success between similar seeds not exposed to dry heat and those exposed to dry heat was significant ($F_{3,20} = 7.441$, $P < 0.01$; figure 5). At the highest temperature, a quarter of the seeds that absorbed water, was killed, while at the other temperatures and in the control almost no seeds were lost, but the effect of heat on seed spoilage was not significant ($F_{3,15} = 2.264$, $P > 0.1$).

Discussion

The capacity to overcome nutrient shortages during seedling growth is determined by the amount of reserves, and thus by seed size, although dormancy, dispersal and seed size are interdependent (Venable and Brown 1988). Seeds therefore do not germinate as a reaction to nutrient availability in the soil, but to suitable physical conditions. The highest rate of soil wetting and drying occurs at the soil surface and decreases with depth. Plant available moisture therefore becomes more predictable with increasing soil depth. In tropical savannas establishing plants need to secure access to moisture, and simultaneously germination strategies may provide escape opportunities from unfavourable conditions. Seed germination is governed by water absorption and subsequent cell division and elongation, and both processes are temperature dependent.The water absorption rate of the hard-coated seeds of tropical leguminous

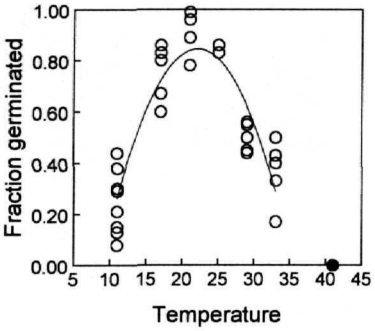

Figure 4. Proportion of seeds that, after water absorption, germinated at various temperatures within an eight-day period. Water absorption was forced by immersion of seeds in hot water and left soaking for one day. Fitted curve excluded complete failure of seeds to germinate at 41 °C (black dot): $y = -0.004705x^2 + 0.2081x - 1.4558$; $R^2 = 0.82$.

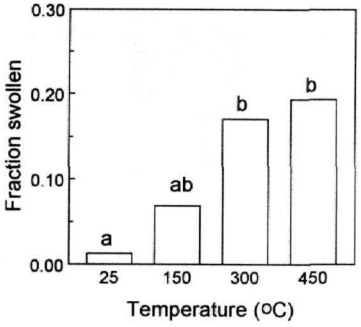

Figure 5. Fraction of seeds with a water content below the threshold value for water absorption (see text) that absorbed water after short (15 seconds) exposure to dry heat. The control did not receive heat treatment. Letters denote significant differences at $\alpha = 0.05$ (Bonferroni multiple comparison test).

trees depends on the water content of the seeds (Van Staden *et al.* 1989), and below a certain threshold water content (6.5% for *A. tortilis*, this study), the water absorption rate becomes infinitesimal. Such seeds are added to the seed bank, because *Acacia* seeds remain viable for a long time (Cavanagh 1980, Skoglund 1992). Above the minimum water content, the water absorption rate increases with temperature under sufficiently moist conditions. Therefore, seeds on top of the soil surface generally do not germinate, because a suitably moist micro-habitat is generally lacking for water absorption (Coughenour and Detling 1986). Although exposure to constant temperatures, as has been used in this study, does not normally occur, the amplitude of the daily temperature fluctuations is dampened with increasing depth.

Based on the results, *A. tortilis* seeds are expected to germinate better at sites with a large temperature amplitude, because high temperatures, above 25 °C, enabling rapid water absorption will be alternated by lower temperatures, suitable for germination. Such situations are found close to the bare soil surface where temperature fluctuations are highest. Germination success is therefore expected to be highest in sites that are fully exposed, and to decrease with increasing vegetation cover. The prolific germination and subsequent establishment of *A. tortilis* on freshly ploughed and recently abandoned fields (pers. obs.), because tillage causes increased soil temperatures, as is reported in the agricultural literature (Hayward 1980, Saran 1973, Lal 1986).

Because germination in the shade of parental trees is not optimal (see also Chapter 5), seeds must be transported away from the parent canopy. *A. tortilis* does, however,

not have an active seed dispersal mechanism. Ingestion by herbivores could result in the desired distribution, while dung in which the seeds are deposited provides the required water holding environment necessary for germination (Miller 1996; this study). The hard seed coats prevent destruction of the seed during the mastication process (Coe and Coe 1987, Miller 1994a), and seeds of indehiscent *Acacia* pods can withstand larger forces than dehiscent pods (Coe and Coe 1987). Since ingestion of seeds by large herbivores also lowers the infection rate of seeds by bruchids, Miller (1994a,b), and Miller and Coe (1993) suggested that *Acacia* seed characteristics evolved under the influence of bruchids and herbivores. Results from this study show that for optimal germination, seeds should be deposited by herbivores on bare spots. In the study area the density of elephant dung during the pod bearing season was, however, more than 30 times higher in *Acacia* groves than in adjacent perennial grasslands (Loth, unpubl. data). Dispersal of seeds by herbivores away from the parent tree may be less important than is claimed by Janzen and Martin (1982).

Seed germination of many hard coated legume seeds is stimulated by fire, and this study demonstrated that this is also the case for *A. tortilis*. The difference in seed coat

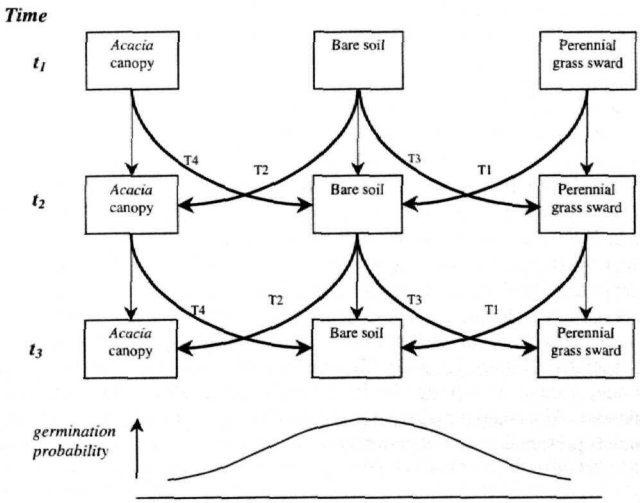

Figure 6. Vegetation states and transitions (solid lines) at a single location in time (t_1 to t_3). Stable states are indicated by thin lines, transitions by thick lines. Under heavy grazing pressure, states may remain permanent (bare soil), or may change from perennial grass sward to bare soil (T1). *Acacia* canopy can only establish on bare soil patches (T2). Under moderate grazing pressure, bare soil may change to perennial grass sward (T3), and perennial grass swards may remain permanent, or may be invaded by woody species (not indicated in figure). *Acacia* canopy reverts to bare soil (T4) due to senescence of the trees or death caused by elephants, or by

thickness of dehiscent and indehiscent pods may well have been developed as an adaptation against the impact of fire. In agreement with Dell (1980), it was found that treatment of impermeable seeds with dry heat caused such seeds to absorb water and germinate. Temperatures recorded in savanna fires at, or just above, soil surface may vary greatly, ranging from less than 70 °C to above 800 °C, but, due to the low thermal conductivity of soil, temperatures at 2 cm below the soil surface seldom exceed 35 °C (reviewed in Frost and Robertson 1987, Van de Vijver 1999). Thus, fires may stimulate the germination of impermeable seeds. Seeds in indehiscent pods can be expected to be exposed to higher temperatures when the pod burns than seeds from dehiscent pods. Seeds scattered on the soil are more likely to escape the heat of the fires in small cracks and other soil roughnesses than seeds enclosed by pods, so that seed coats of species with dehiscent pods do not need to be as thick as those with indehiscent pods.In Lake Manyara N.P. *Acacia* regeneration has been high on bare places where trees had died over the past 20 years (pers. obs.). Gaps in the *Acacia* canopy had not been colonized rapidly by perennials, presumably due to the high herbivore density (Chapter 7). It is conceivable that a seed bank existed on the spots vacated by the parent trees, from which regeneration resulted. The germination strategy could have evolved so as to enable self-replacement by the time the parent tree dies, since seed dispersal by herbivores to new locations appears to be less effective.

The probability that *Acacia* seed germinates appears to depend on the state of the vegetation (figure 6). In Lake Manyara N.P., the transition of unsuitable *Acacia* canopies to potentially suitable, exposed sites is effected by elephant impact, or by senescence of the trees; fire has not occurred in the Park since 1958. Perennial grasses may colonize gaps, or they may remain bare for a longer period. The transition from bare to grass sward, and subsequent transitions to shrub and woodland with species which are adapted to germinate under shaded conditions, may be regulated by grazing pressure. The herbivore density in Manyara is one of the highest in East Africa (Prins and Beekman 1989). Localized transitions from existing grasslands to bare soil can be brought about by animal activities, such as trampling. Seed germination of *Acacia* in elephant dung deposited in closed-sward *Urochloa mosambicensis* (Hack.) Dandy grasslands was found, although establishment of *Acacia* in these grasslands was rare over a 40-year period, as could be concluded from comparisons of aerial photographs (pers. obs., see also Chapter 2 and 3). The creation of temporary open gaps in grass swards by dung patches as reported by Brown and Archer (1987), thus may enhance seed germination from seeds in the dung. Seeds already present in the seed bank in such grasslands presumably do not germinate.

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Chapter 5

Establishment of *Acacia tortilis* seedlings in a heterogeneous East African environment: effects of water, shading and browsing

Summary

Tree establishment in savannas is modified by herbivores, either indirectly by changing resource availability, or directly, by the selective removal of seedlings. The occurrence of even-aged stands in East Africa of the tree *Acacia tortilis* has been attributed to windows in herbivore pressure due to epidemics. Seedlings must be permanently present in order to take advantage of gaps in herbivore pressure. In this study the conditions under which *A. tortilis* seedlings established was studied to test whether the conditions for seedling establishment are generally favourable. In a field experiment, seeds were sown in four different habitat types: bare soil, perennial grass swards, and under woody canopy, with, or without herbaceous under growth. As treatment root comprtition was excluded. Seedlings on bare soil patches survived longest, and exclusion of root competition resulted in longer seedling survival. Four rainfall periods were distinguished; seedling survival was positively correlated with the amount of rainfall that had fallen in the period during which the seedlings emerged. In a pot experiment plant growth was considerably reduced by shading, and also clipping resulted in reduced growth of both above-ground and below-ground plant parts. *A. tortilis* seedlings survived longer on bare patches where light competition and root competition was absent. For the survival of the dry season, roots must have reached permanent soil layers. The highest growth rates were attained in absence of competition for light and for water in the rooting zone. Seedling establishment therefore is best in bare soil patches, which can be expected to occur more frequently under high grazing pressure. *A. tortilis* population regulation by browsers could not be ruled out.

Introduction

In African savannas, the grassland – woodland dynamics are often considered to be mainly driven by disturbances caused by herbivores and fire (Pellew 1983, Dublin 1991, McNaughton 1992). Herbivores indirectly affect the composition of the vegetation by modifying resource availability (McNaughton 1983, Dublin *et al.* 1990, Ritchie and Tilman 1995, Hobbs 1996, Augustine and McNaughton 1998). The effect of herbivory on the vegetation can be direct by selective removal of palatable species (McNaughton 1983), and tree establishment can be prevented by browsing of seedlings, either by small mammals (Ostfeld and Canham 1993, Auld 1995, Crawley and Long 1995), or large herbivores (Prins and Van der Jeugd 1993).

In East African savannas *Acacia tortilis* is one of the dominant tree species. The prevalence of even-aged *A. tortilis* stands in these savannas has been explained by crashes in populations of browsing herbivores, like impala, resulting from the outbreaks of anthrax epidemics and rinderpest. A temporal alleviation of the browser pressure allows seedlings to escape predation by browsers, and trees can establish (Prins and Van der Jeugd 1993). Norton-Griffiths (1979) suggested that the widespread presence of trees, mostly *A. tortilis*, in the East African savannas resulted from the devastating impact of rinderpest on the grazer populations. Within two years after the introduction of rinderpest in East Africa before the turn of the century, the panepidemic wiped out over 95% of the wildebeest and buffalo populations. Erstwhile extended grasslands thereafter were invaded by trees.

Is then woodland regeneration in East African savannas suppressed by the presence of herbivores, both grazers and browsers alike? The occurrence of age cohorts of Acacia trees as a result of windows in herbivore pressure as proposed by Prins and Van der Jeugd (1993) means that Acacia seedlings are selectively removed. This presumes continuous presence of the trees as a seedling, so that seedlings can establish as soon as the browser population crashes. The establishment of trees after crashes of grazer populations could follow from three different scenarios. First, suppression of tree establishment may be mediated through associational preference for the seedlings of the grazers. Although grazers do not select for tree seedlings, they do not avoid them while grazing the grass sward. Second, in the absence of herbivores different competitive circumstances may come into existence favouring *A. tortilis* seedling establishment. Third, more intense and more frequent fires stimulate *Acacia* regeneration, because fuel load could built up after the epidemics among the grazers.

To test the hypothesis that the *A. tortilis* population is controlled by both grazers and browsers, I considered the conditions under which Acacia seedlings can establish. If Acacia seedlings can establish under a wide range of conditions, then control by browsers is likely, because seedlings will be continuously present. If, however, seedling establishment is limited by light and water, then grazers may control the *Acacia* population.

In Lake Manyara National Park in northern Tanzania, the study area, fire has been absent for at least half a century (Warden's Reports 1960 – present, A. Seif interviewed by H.H.T. Prins in 1991). Any changes in functional vegetation types in Manyara over this period may therefore be attributed to the interaction between

herbivores and vegetation (but see Chapter 3), although Caughley (1976) suggested that vegetation cycles in Luangwa Valley in Zambia, involving elephants, may be as long as 200 years.

In this study the conditions are investigated under which *A. tortilis* seedling growth and establishment is constrained. Under a tree canopy, air temperatures are lower and humidity is higher, so that transpiration requirements and evaporation losses are lower. Because more soil moisture is available, seedling survival is expected to be higher under tree canopies. Simultaneously, however, light as a resource for photosynthesis is reduced by the canopy (Holmgren *et al.* 1997). Under tree canopies the effects of competition may exceed those of facilitation. Light and soil moisture availability are therefore expected to be the major factors determining successful seedling establishment. This hypothesis was tested in a field experiment where, in absence and in presence of root competition, *A. tortilis* seedling survival was determined in different habitat types, which were characterized by the presence or absence of a herbaceous and the presence and absence of a woody stratum.

Additional experiments were carried out under controlled conditions to determine the effect of light interception on the growth of *Acacia* seedlings. Because browsing has been considered a main effect of seedling establishment (Prins and Van der Jeugd 1993), clipping treatments were applied in a controlled experiment to simulate the impact of browsing. It was expected that shading would reduce root growth and that exclusion of root competition in the top 30 cm would result in enhanced survival chances of the seedlings. Furthermore it was expected that clipping also would have a negative impact on seedling growth.

Study site and species

The field experiments were conducted in Lake Manyara National Park, northern Tanzania (centred at 3°30' S, 35°45'E), which lies between Lake Manyara to the east and the steep rising escarpment of the Great Rift to the west. The Park below the escarpment consists of various lacustrine terraces. The areas adjacent to the lake are liable to flooding by the lake and are characterized by the occurrence of alkaline

Table 1. Number of sites used in an experiment designed to measure growth and survival of *A. tortilis* seedlings, per functional vegetation type, and number of control plots and plots where root competition was excluded within each functional vegetation type in which seedlings emerged. Vegetation types are defined by the presence and absence of a herbaceous layer and a woody component. The presence of adult *A. tortilis* as woody species is indicated separately.

Vegetation type	Presence *A. tortilis*	Number of sites	Number of plots where at least 1 seedling emerged	
			Control	Root comp excluded
Bare soil	-	17	16	17
Perennial grass sward	-	15	14	14
Woody - bare	-	19	15	18
	+	8	7	6
Woody – understorey	+	13	11	13

grasslands. Lacustrine terraces, which are not flooded by the lake, are characterized by the occurrence of *Acacia* woodlands, dominated by *A. tortilis*, except where in the northern part of the park seepage sustains a broad-leafed forest dominated by *Trichilia emetica* Vahl. The zone with the *Acacia* woodlands varies in width from about 300 m to 3 km (Loth and Prins 1986). The mean annual rainfall is 650 mm, with a bimodal distribution pattern. The mean annual temperature is 21°C, and the mean monthly temperatures do not deviate more than 3°C from the yearly mean (Loth and Prins 1986).

The most important large herbivores in the Park are the African buffalo (*Syncerus caffer*) and the elephant (*Loxodonta africana*) (Prins and Douglas-Hamilton 1990). In the 1960s and 1970s elephants occurred at very high densities (4.5 elephants per km^2), but declined rapidly since the mid-1980s due to poaching, to reach a low of less than 1 elephant per km^2 in 1991 (Prins *et al.* 1994). Since then, elephant numbers have increased again (Turner 1995, Chapter 7). At high densities, elephants killed a considerable proportion of mature *A. tortilis* trees, resulting in the opening up of the Acacia woodlands (Douglas-Hamilton 1972,Weyerhaeuser 1982)

Acacia tortilis (Forssk.) Hayne ssp. *spirocarpa* (A. Rich.) Brenan is a leguminous tree with an umbrella shaped canopy. Canopies of mature trees may reach a diameter of over 30 meters. The main flowering period occurs between May and July (*pers. obs.*), although incidental 'out-of season' flowering has been observed, as is also reported by Haro and Oba (1993) for the Turkwell River floodplain in Kenya. Pod formation, seed filling, and a period of ripening follow the flowering period. After about 150 days the mature, indehiscent pods fall on the ground (Lamprey *et al.* 1974), on which they can be found in large numbers between October and December (pers. obs.). When unripe, the pods as well as the seeds are green. Unripe seed coats are soft, becoming hard upon ripening.

Methods

A. tortilis seeds were collected from freshly fallen pods over a four-month period (July 1995 - November 1995). Fully-grown seeds were visually inspected on signs of insect damage, and only seeds that did not show any markings on the seed coat were retained for the germination experiments. Seeds collected throughout the entire period were pooled. To avoid loss of stored seeds by bruchid beetles infestation as reported by Lamprey *et al.* (1974), Ernst *et al.* (1990), and Vir and Jindal (1994), the collected seeds were sprayed with a household insect killer (working ingredients: 0.19% pyrethrum, 0.105% permethrin (25:75 cis:trans isomers), 0.5% dichlorvos and 0.5% piperonyl butoxide), and kept in closed tin containers.

Effects of shade and root competition on seedling survival

Within the *A. tortilis – Chloris virgata* (W1) plant community mean (Loth and Prins 1986), experimental sites were chosen on the basis of presence and absence of a herbaceous and a woody layer. The sites consisted of bare patches, perennial grass swards, overhead woody canopy without undergrowth (< 10 % cover by herbs), and

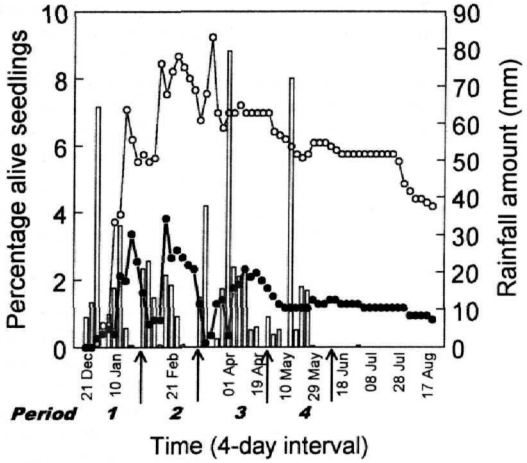

Figure 1. Number of alive *A. tortilis* seedlings counted at 4-day intervals, as percentage of total number of sown seeds in two treatments: ● control, O root competition excluded. Bars indicate amount of rain fallen between observations (4-day totals), arrows indicate limits of rainfall periods (Period 1-4; see text for explanation).

overhead woody canopy with undergrowth (> 10% cover by herbs, see table 1). The distance to the nearest herbaceous plants in bare patches was at least one meter. Perennial grasses were *Enteropogon macrostachyus* and *Cenchrus ciliaris*. The overhead woody canopy species were the trees *A. tortilis*, *Balanites aegyptiaca* and *Gardenia tenuifolia*, or the shrubs *Cadaba farinosa* and *Capparis fascicularis*.To determine the effect of root competition on *A. tortilis* seedling survival, seedlings were grown in paired plots. In the treated (TR_1) plots, root competition in the topsoil was excluded by placing a 30 cm long PVC pipe with a diameter of 10 cm into the soil. In the control (TR_0) plots, a 2 cm high PVC ring with the same diameter was placed 1 cm deep into the soil. The paired plots were situated within 30 cm of each other. The placement of fine-mazed chicken wire (maze width 1 cm) over the sites prevented disturbance by baboons and small rodents. Emerging herbs and grasses were not removed from the sites, unless they emerged from within the plots where root competition was excluded.

The effect of light competition on seedling survival was determined by using the fraction of sunlight reaching the soil at each site. The fraction of sunlight reaching the soil at each site was determined four times, from February to April 1996, as the fraction of current (mV; Dynatek 9050 Digital Multimeter) generated by a 0.5 m linear integrating light meter (TFDL, Wageningen, The Netherlands) held at ground level. The current reading in direct sunlight was used as the reference value. Each measurement was calculated as the mean of 5 readings at soil level divided by the

mean of two readings taken in direct sunlight, one taken at the start of the readings at soil level and one at the end. Equipment failure precluded light measurements after April 1996.

Twelve *Acacia* seeds were planted at 0.5 cm soil depth in each of two paired plots within a site. Each treatment was replicated at least eight times, with relatively more plots placed under woody canopy than in the other two habitat types, since it was expected that germination success would be less in sites with an overhead woody canopy than in plots without a woody canopy overhead (Chapter 4). Seedlings were counted as soon as the cotyledons were visible above the soil surface. Every four days the numbers of seedlings were counted; this interval was short enough to recognize seedlings that had emerged but subsequently died within the interval.

The experiment was rain fed and ran from mid-December 1995 to the end of August 1996. Rainfall was recorded daily. After the first rains of the following season had fallen, the plots were inspected again on 17 December 1996 to count the number of plants that had survived the dry season. The latest rainfall was recorded on 26 May 1996, and the first rain of the following season was recorded on 19 November 1996.

Data analysis

A period was considered dry when in at least three consecutive counting intervals of 4 days less than 5 mm rain had been recorded in each of the intervals. Four wet and dry cycles could thus be distinguished, and each cycle lasted about 40 days (fig. 1).

Seedling survival was analysed in a general factorial model, with root competition treatment and vegetation type as factors, and the total amount of rainfall recorded during the rainfall period (fig. 1) in which the seedling had emerged, as covariate. Since soil water availability was expected to vary with vegetation type, factor by covariate interaction was included into the model. Because light measurements were restricted to a limited period of time, light conditions could not be used as a covariate in the analyses. The mean values of the proportion of light reaching the soil surface were used to characterize the different vegetation types.

Seedling survival was the number of days that the seedling was recorded as being alive until the end of the experiment. For the statistical analysis natural logarithm of seedling survival was used.

For plots where two or more seedlings had emerged, Spearman's rank correlation coefficients were calculated for a two-tailed test that seedling age was not associated with the seed's germination rank number. Only plots in which two or more seedlings had emerged were used for the analysis ($N = 311$ seedlings).

The presence of *A. tortilis* as a woody canopy species had no significant effect on seedling age ($F_{1,121} = 0.0007$, NS). No distinction was therefore made hereafter whether or not *A. tortilis* was present as a woody species.

Effects of shade and clipping on growth

To determine the effect of light and clipping on the growth of various *A. tortilis* plant parts, an experiment with a factorial design was carried out. Clipping was meant to mimick browsing by ungulates. Water was not limiting. Three clipping regimes were applied before final harvest after 130 days: not clipped, clipped once (day 40), and clipped three times (days 15, 40 and 75). Each clipping regime was repeated in full sun

and underneath gunny sacking material, providing a 92% reduction in light. For the experiment six week old nursery plants were planted singly in a PVC pipe (Ø = 10 cm, height = 30 cm) with clear, perforated plastic lids fixed at the bottom. The pipes were filled with sieved river sand (mesh 4 mm), mixed 1:1 with loamy soil excavated from a termite mound. Six plants were used per treatment, and each treatment was replicated three times, bringing the total to 108 plants. One plant had died during the experiment due to insect damage to the roots.

Root length and plant height (in cm), and stem diameter (in mm) were recorded before planting. As a measure for the rate of root growth the cover by the roots of the plastic sheeting at the bottom was estimated in eight classes at regular intervals. When no roots were visible, a zero was scored. The clipped material was separated in stem and leaf material, air dried and weighed. The stem diameter and the total length of the clipped branches were measured for the clipped plants.

Table 2. Linear model describing the mean natural logarithm of seedling age with root competition treatment (Treatment) and vegetation type as factors, with the total amount of rainfall that had fallen in which seedlings had emerged (Rainfall) as covariate. The least square regression was weighted by the number of emerged seedlings per plot. N = 333 seedlings, R^2 = 0.24.

Source	df	*F*	Sig.
Treatment	1	36.7	.000
Vegetation type	3	8.5	.000
Treatment * Vegetation type	3	2.6	.049
Vegetation type * Rainfall	3	10.9	.000

Table 3. Analysis of variance for *A. tortilis* seedling survival in four vegetation types: bare soil, perennial grass sward, woody canopy without understorey, and woody canopy with understorey, for root competition (Tr_comp) and rainfall period during which seedlings emerged (Period) as factors. F-ratios and significance levels indicated: NS not significant, * P< 0.05, ** P < 0.01, *** P < 0.001.

Source	Df	Bare soil	Perennial grass sward	Woody - bare	Woody - underst.
R^2		0.26	0.07	0.34	0.16
Model	5	7.80^{***}	1.97^{NS}	12.46^{***}	2.93^{*}
Tr_comp	1	10.11^{**}	2.47^{NS}	35.03^{***}	2.47^{NS}
Period	2	13.91^{***}	1.92^{NS}	3.71^{*}	4.07^{*}
Tr_comp*Period	2	0.67^{NS}	0.84^{NS}	4.86^{*}	0.94^{NS}

Data analysis

First, analysis of variance was carried out on weights of plant parts to determine whether a block effect was present. No replica effect was found (root weights: $F_{2,81}=0.31$, NS; shoot weights: $F_{2,81}=0.86$, NS), nor in the interactions with the other factors. In the analysis, the replicas were therefore lumped. The natural logarithm of weights was used in the analysis to obtain normal distribution of the data.

Unclipped plants in the shade that were placed at the edge of the experimental setup clearly profited from additional light. Plants placed at the inner side of the edge had a significant lower production of the various plant parts than plants at the edge of the experimental field (roots: $F_{1,16} = 64.9$, $P < 0.001$, shoots: $F_{1,16} = 69.2$, $P < 0.001$). Since the amount of light interception at the edge was not quantified, the plants placed at the edge of the experimental field were excluded from further analysis. Regression analysis was carried out on $\log_e$ transformed root cover data, adding unity to allow transformation of the zero scores. The median values of the classes were used as the average cover by the roots.

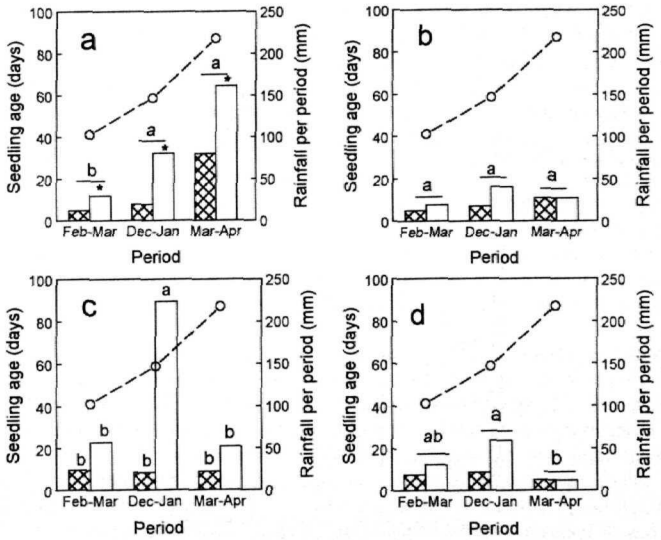

Figure 2. A. tortilis seedling age (days) in four vegetation types in relation to the period within which the seedlings emerged and total amount of rainfall recorded in each period. (a) bare soil, (b) perennial grass sward, (c) woody canopy with less than 10% cover by herbs, and (d) woody canopy with more than 10% cover by herbs. Hatched bars: control, open bars: root competition excluded. Letters denote significant differences and asterix indicates significant differences between root competition treatments at $\alpha = 0.05$ (Tukey's HSD test).

Stem growth was calculated as the increase in diameter relative to the initial diameter; in those instances that a smaller stem diameter had been measured at the latest date, the difference between the two measurements was set at zero. Prior to the statistical analysis the data were square root transformed for normalization.

Results

Effects of shade and root competition on seedling survival

Root competition, vegetation type and the period during which the seedlings emerged, had a significant effect on seedling survival (Table 2). In sites without a herbaceous layer seedling survival was higher in plots where root competition was excluded (Table 3, fig 2a,c). Seedlings in bare soil patches tended to survive longer when they emerged during a period with higher rainfall (fig 2a). No such trend was found in perennial grass swards (fig 2b). Under woody canopy without herbaceous understorey seedling age was unexpectedly high for those seedlings which emerged during the first period in plots where root competition was excluded (fig 2c). At the end of the experimental period, 17 seedlings were still alive in bare soil sites, and 4 under trees without herbaceous cover. Twelve seedlings in bare soil sites and all four underneath woody canopy were found in the sites where root competition was excluded. After the next rainy season had started, one plant was found under a *Gardenia tenuifolia* tree, and six plants were found on bare soil sites. All these plants were established in plots where root competition was excluded.

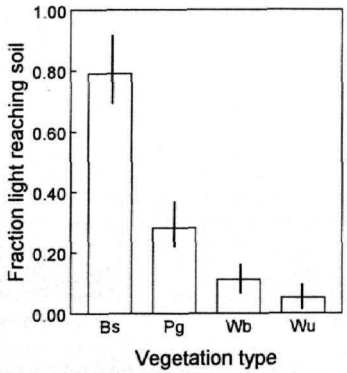

Figure 3. Mean fraction of light reaching the soil (± SE) for four functional vegetation types: Bs = bare soil, Pg = perennial grass sward, Wb = woody canopy without herbaceous understorey (cover by herbs < 10%), Wu = woody canopy with herbaceous understorey (cover by herbs > 10%). Means per vegetation type averaged for four measurement dates.

Table 4. Results of bivariate correlation analysis between age of *A. tortilis* seedlings grown in four vegetation types in a field experiment where root competition was either excluded or not interfered with, with date, rainfall per period, and rank number of seed emergence (seed rank nr). Only data for plots where at least two seedlings had emerged, were used. Spearman's rank correlation coefficients and two-tailed significance indicated: * $P < 0.05$, ** $P < 0.01$.

	date	Rainfall per period	vegetation type	root comp.	seed rank nr	seedling age
date	1.000					
rainfall	.288**	1.000				
veg. type	-.079	.041	1.000			
root comp.	-.087	.001	.086	1.000		
seed rank nr	.574**	.184**	-.095	.112*	1.000	
seedling age	-.106	.154**	-.037	.292	-.048	1.000

The mean fraction of sunlight reaching the soil was significantly different for the four vegetation types (fig. 3). The fraction of light reaching the soil was highest in bare soil sites, and lowest under woody canopy with a herbaceous understorey, and with root competition treatment, but not correlated with date, vegetation type and rank number of seedling emergence (Table 4).

Effects of shade and clipping on Acacia seedling growth

A. tortilis plant weights and dimensions at harvesting time were larger in sun-grown plants than in shade-grown plants, and plants were generally lighter and smaller under increasing clipping intensity (Tables 5 and 6). Light and clipping had a significant ($F_{5,93}$=91.4, $P < 0.001$; $R^2 = 0.82$) effect on the total above ground production, but the effect of clipping in sun-grown plants was more severe than in shade-grown plants (figure 4). Light had no effect on the root : shoot ratio, and although the effect of clipping on the root:shoot ratio was significant, the explained variance was very low (Table 5).

Analysis of variance of root cover showed that light and clipping as factors and seedling age as covariate, had a strong and significant effect on root growth rate ($F_{12,636}$=630, $P < 0.001$; R^2=0.92). The analysis was repeated for the two light treatments separately because the highest order interaction was significant ($F_{2,636}$ = 12.0, $P < 0.001$). When the analysis was repeated for the two light treatments separately, the interaction between clipping and seedling age was found to be significant in the shade ($F_{2,318}$ = 11.7, $P < 0.001$), but not in the sun ($F_{2,318}$ = 0.56, NS). Based on the statistical analysis, clipping in sun-grown plants resulted in a delayed growth of the roots, but the growth rate remained unchanged, while in the shade clipping resulted in a reduction of the root growth rate. The growth rate in sun-grown plants in unclipped and single clipped situation, however, may have been underestimated, because the basal root cover approached 100%, and therefore leading to an underestimation of the growth rate (see 100% cover line in figure 5). It seems therefore reasonable to conclude that clipping delays root growth (until equivalent

Table 5. Effect of light (2 levels) and clipping (3 treatments) on weights and dimensions of *A. tortilis* plants. Significance of F values for two-way analysis of variance are as follows: *** significant at $p<0.001$, ** $p<0.01$, * $p<0.05$, NS = not significant. For all factors n=99, except for stem diameter (n=98). Note that all interactions were significant, except for the root:shoot ratio where only clipping had a significant effect.

Treatment	Root weight	Shoot weight	Leaf weight	Stem weight	Stem diameter	Branch length	Root:shoot
Light	274.7^{***}	220.4^{***}	176.6^{***}	232.1^{***}	148.6^{***}	77.4^{***}	0.00^{NS}
Clipping	75.9^{***}	84.4^{***}	71.3^{***}	87.1^{***}	42.9^{***}	37.5^{***}	6.0^{**}
Light x Clipping	8.2^{**}	7.0^{**}	3.6^{*}	12.6^{***}	27.8^{***}	3.8^{*}	1.1^{NS}
Explained variance	0.83	0.82	0.79	0.83	0.76	0.65	0.08

Table 6. Mean weights of above and below ground plant parts, total branch lengths, and stem diameter increase of *A. tortilis* seedlings at final harvest, after 90 days under light and shaded conditions and under different clipping intensities. Mean values (± S.E.) have been back transformed from natural logarithm transformed data for weights and lengths, and square root data for stem diameter increase used in the Analysis of variance. Letters denote significant differences at $\alpha=0.05$ (Tukey's multiple comparisons test).

Treatment			Root weight	Shoot weight	Stem weight	Branch length	Increase stem	Stem weight per
Light	Clipping	N	(g)	(g)	(g)	(mm)	diameter (mm)	branch length ($g.m^{-1}$)
Sun	no clipping	17	8.97^{a} (±0.085)	7.65^{a} (±0.368)	4.40^{a} (±0.379)	887.3^{a} (±1.14)	1.49^{a} (±0.002)	4.95^{a} (±1.087)
	single clipping	18	4.76^{b} (±0.518)	3.72^{b} (±0.454)	1.79^{b} (±0.461)	610.1^{a} (±1.12)	1.06^{b} (±0.002)	2.93^{b} (±1.115)
	multiple clipping	18	1.26^{c} (±0.103)	0.89^{c} (±0.416)	0.41^{c} (±0.415)	190.9^{bc} (±1.16)	0.22^{de} (±0.001)	2.12^{b} (±1.092)
Shade	no clipping	10	1.28^{c} (±0.542)	1.29^{c} (±0.532)	0.58^{c} (±0.521)	253.0^{b} (±1.96)	0.67^{c} (±0.005)[1]	2.55^{b} (±1.547)
	single clipping	18	0.65^{d} (±0.473)	0.45^{d} (±0.465)	0.22^{d} (±0.443)	188.6^{bc} (±1.82)	0.28^{d} (±0.002)	1.31^{c} (±1.066)
	multiple clipping	18	0.41^{d} (±.0339)	0.28^{d} (±0.338)	0.16^{d} (±0.327)	111.2^{c} (±1.46)	0.10^{e} (±0.002)	1.42^{c} (±1.096)

[1] n=9

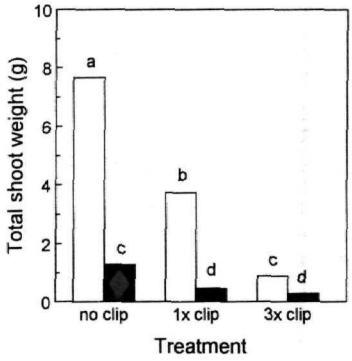

Figure 4. Total above-ground biomass production of *A. tortilis* plants grown under different light conditions and clipping regimes. Black bars: plants grown in shade, hatch bars: plants grown in full sun. Multiple clipped plants had been clipped three times before harvesting time. Letters denote significant difference at α=0.05 (Tukey's multiple comparisons).

amount of foliage present as at time of clipping), while shading reduces the root growth rate.

At the final harvest, the proportion of basal area covered by Acacia roots (=root density) showed a significant ($F_{1,51} = 133.7$, $P < 0.001$) relationship with the weight of the roots ($y = 0.328 + 0.216*\ln(W_{root})$; $R^2=0.72$). It can be stated, therefore, that heavier roots rooted to a greater depth.

Stem growth in sun-grown plants was always higher than that in shade, and in both light conditions the stem diameter increase was highest in unclipped plants. Although the interaction between the factors was significant ($F_{2,93} = 8.21$; $P < 0.001$), figure 5 suggests that in both light conditions clipping caused a considerable, and comparable delay in stem growth when the stems were more frequently clipped. Likewise, the stem weight per meter branch was significantly lower for plants which had been clipped at least one time, and sun grown plants had heavier stems than shade grown plants (for statistics, see Tables 5 and 6).

Discussion

In this study *A. tortilis* survival was assumed to be governed by light and soil moisture availability. Nutrients were not limiting plant growth in the loamy soils of Lake Manyara National Park, because the lacustrine soils of Lake Manyara originate in part from nutrient rich volcanic material mean (Loth and Prins 1986).

The field experiment was designed to determine whether light interception by overhead foliage or root competition for available moisture in the upper soil layers prevented the establishment of *A. tortilis* seedlings. *Acacia* seed germination rates not

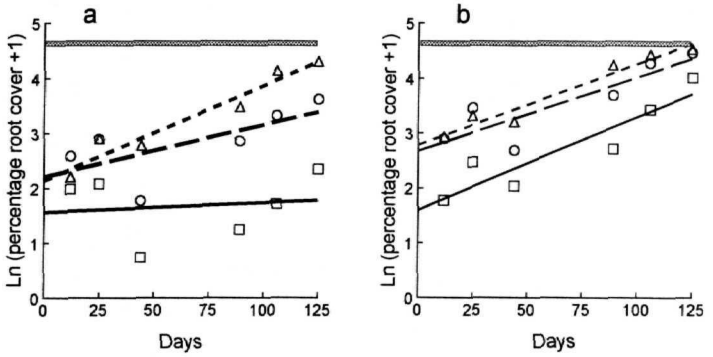

Figure 5 *A. tortilis* root growth rates in (a) full sun and (b) shaded conditions, subjected to different clipping frequencies. Abscissa shows the duration of the experiment (days), the ordinate represents the natural logarithm of root cover of the pot bottoms, and regression lines. Age of the plants at the start of the experiments about 45 days. The stippled line shows the 100% cover value. Triangles: no clipping, circles: single clipped plants, squares: multi-clipped plants.

only depend on environmental conditions, but also on seed characteristics, in particular on seed water content (Chapter 4). Consequently, since seedlings do not emerge at the same moment, the conditions under which emerging seedlings grow will not remain identical throughout the experimental period, even within the same plot. The growth rate of seedlings appeared to be independent of the sequence in which the seedlings emerged, suggesting that the intrinsic growth characteristic of early emerging seedlings were the same as those of later emerging seedlings.

Seedling survival in bare patches, where light is not a limiting factor, is only limited by moisture availability. In this study the survival period of the seedlings growing on bare patches was generally higher than that of seedlings growing in other sites. It was further found that the age of seedlings growing in bare sites was highest when the seedlings emerged during the period with the highest amount of rainfall. This is not surprising, because especially during the initial growth of a seedling after emergence, the water content of the top soil is critical. More free moisture will be available in the top soil for emerged seedlings with increasing rainfall amounts.

It had been assumed that root competition in bare soil sites will be absent, or at least considerably less than in grass swards. Yet, seedlings in plots where root competition was excluded in bare soil sites grew older than in the control plots. The effects of soil disturbance and exclusion of root competition possibly had not been adequately separated in the experiments, because superficial roots could have been present in bare soil sites. During the installation of the PVC pipe to exclude root competition, the soil inevitably was disturbed. I suggest therefore, that the positive effect that the treatment

will have had on the water holding capacity of the soil was greater than the effect of exclusion of root competition. In perennial grass swards root competition exclusion had no effect on seedling survival, while seedling survival was not enhanced by increased rainfall. Clearly, light as a resource had become a more limiting factor than water availability. In sites with a woody canopy, seedling survival in the control sites remained at a more-or-less constant, low level. In the treated plots, however, seedlings that emerged during the first period survived longest, whereas seedlings emerging during the period with the highest amount of rainfall, in the last period, tended to survive shorter. Possibly the overhead canopy of woody species had become more dense in the course of the season, thus reducing light as a resource even more.

The results of the experiment in which young *A tortilis* plants were grown under different light conditions and various clipping regimes, confirm that light is an important growth limiting factor, since the plants were grown while water was not a limiting factor. A second tentative conclusion may be that the plants maintain a constant shoot:root ratio, at least as a young plant. This conclusion ties up neatly with the findings of the field experiment, but more experiments are needed to find the causal link for this balance between root and shoot biomass. Although under tree canopies sufficient soil moisture may be available, especially in the treated plots, light for photosynthesis is constrained, so that root development is concordantly retarded. Root growth is however essential to reach the safe heaven of the deeper soil layers where water is available to cope with the dry season.

In the absence of a herbaceous layer, seedlings growing in the shade of a tree canopy may initially have a higher short-term survival chance. Under a canopy, moisture stress is reduced by lower temperatures and reduced wind velocities. Seedlings growing under a tree canopy therefore may be able to survive longer when a dry spell follows the moment that a seedling had emerged. Seedling survival in sites under trees with herbaceous undergrowth was not enhanced by exclusion of root competition. When a herbaceous layer is present underneath a tree canopy, the available soil moisture may be more rapidly depleted by transpiration, even though the initial soil moisture content may have been higher, because vegetation enhances the infiltration capacity of the soil (Van Wijngaarden 1985). In these sites the fraction of light intercepted by the total canopy was highest of all habitat types. For the reasons which will be explained below, the lack of light has been the cause of reduced seedling survival time.

Clipping removed part of the photosynthetic material, so that less photosynthates were produced after clipping. Although the root mass was highest in unclipped plants and decreased with increasing clipping intensity, the root:shoot ratio at harvesting time was lowest in unclipped plants. This means that after clipping a negative root growth may have occurred by reallocation of carbohydrates from the roots to the leaves, or that root formation is halted or strongly reduced until the root:shoot ratio has been brought into balance again. Consequently, browsing may have a detrimental effect on the establishment chances of *A. tortilis*, as is suggested by (Prins and Van der Jeugd 1993).

For successful establishment the roots of young *A. tortilis* plants must reach a depth where water remains available until the start of the next rainy season. *A. tortilis* requires permanent access to soil moisture, because, after the leaves are shed in the dry

season, new leaves are formed *before* the arrival of the new rains (pers obs). Without a transpiring leaf surface, the tension of the soil moisture must be sufficiently low during the flush of the new leaves. Within one soil type, the moisture tension in the top soil increases during the dry season due to (evapo) transpiration. Plant available water (PAW) in the soil becomes more reliable with increasing depth. When water was not limited, *A. tortilis* plants produced more roots and shoots in full sun than in shade. The production of photosynthates depends on the amount of photosynthetic active radiation (PAR) reaching the chloroplasts in the leaves. In two contrasting light conditions, the photosynthates in intact *A. tortilis* were equally allocated to the above-ground and below-ground plant parts. It is likely that the root:shoot ratio for intact plants during the establishment phase will be fairly constant, irrespective of the amount of PAR available to the plant. Roots of *Acacia* in the sun grew faster, and therefore reached deeper soil layers earlier than roots of *Acacia* growing in the shade. As soon as seedlings growing in exposed sites survive the early stages, they will therefore have a better chance to survive the dry season.

Seedling survival depends on the water availability in the top soil, where, in the presence of herbal vegetation, competition for moisture is strongest and seedling establishment poorest (Bertiller *et al.* 1996, Soriano & Sala in *ibid.*). At the same time, the presence of a canopy causes a reduction in evaporation, while vegetation improves the infiltration capacity of the, so that vegetated soils may have a higher moisture content than soils without vegetation (Van Wijngaarden 1985, Cerda 1997). *A. tortilis* establishment is best in the absence of a herbaceous layer, and competition for moisture appeared to be a key factor. Seedlings growing underneath tree canopies were capable to survive the first dry season, because of enhanced moisture availability under tree canopies. Despite their survival, the roots of such plants had not reached 'safe' soil layers, where permanent water is available to the plants. Plants growing underneath tree canopies thus cannot be considered to have successfully established after having survived their first dry season. More studies are needed to qualify and quantify moisture availability underneath tree canopies as a result of hydraulic lift, as well as the root growth rates of *A. tortilis*. Plants growing in shaded conditions were considerably weaker, and thus less resilient against disturbances than plants growing in exposed sites. In conclusion, the conditions favouring successful *A. tortilis* seedling establishment are in exposed, bare soil sites, where seed germination is maximal. Browsing causes delayed root growth, so that the chances for successful establishment are reduced after a seedling has been browsed.

Vegetation patterns can be explained by differences in seedling establishment (Olff *et al.* 1994, Schulze *et al.* 1996). The removal of adult *A. tortilis* trees in Lake Manyara National Park by elephants (Douglas-Hamilton 1972) resulted in gaps in the woodlands, which, possibly due to the high herbivore density in the park, were not overgrown by perennial grasses. These bare patches enabled successful establishment of *A. tortilis,* so that presently, a new generation *A tortilis* trees has taken position in the woodland gaps, created by the elephants. This conclusion does not exclude the possibility that *Acacia* regeneration is regulated by browsers, as proposed by Prins and Van Der Jeugd (1993). The prolific establishment of *Acacia* in recently abandoned arable fields confirms the conclusion that bare soil provides the optimal conditions for seedling establishment. When the abandoned fields were added to the park as an

extension, browsers did not colonize the area immediately. Five years after abandonment, only very few browsers (impala, bush buck) had taken residence. Hence, here suitable growing conditions coincided with the absence of a browser population.

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Chapter 6

Age cohorts in *Acacia tortilis* populations in East Africa

Summary

Acacia tortilis seedlings can establish when light is not limited and when browsing pressure is not too high. At increased grazing intensities, *Acacia* invades grasslands, because grazing reduces the grass biomass. Selective browsing of seedlings can prevent establishment of woody species. *Acacia* establishment has been linked with crashes in populations of browsers. Knowledge of tree development with age is a prerequisite for reconstructing tree establishment in the past. Growth rings have been used to determine the age of *Acacia* trees, but these are difficult to observe. Parenchyma band thickness of tree discs obtained from old-fields was found to vary along a radial gradient in a repeating pattern. The periodicity in parenchyma band thickness in stem discs was confirmed by spectral analysis, and was closely related with the number of years that had passed since the fields were abandoned. The growth rates found in this study were 2 to 4 times higher than those reported in other studies. In closed-canopy *A. tortilis* forests in 33 yr old-fields, density dependent stem growth was demonstrated to follow the –3/2 self-thinning rule. Other explanantions for the differences in stem growth rates are discussed. I conclude that periodicity in parenchyma band width in *A. tortilis* stem discs can be used to estimate the age of the trees, although more stem discs need to be analysed, particularly of trees growing in undisturbed soils, before this technique can be more broadly applied. The existence of tree stands as age cohorts as a result of crashes in herbivore populations could not be substantiated.

Introduction

Acacia tortilis is a characteristic tree species of East African savannas. Although the seed germinates underneath tree canopies, seedlings do not establish there (Vesey-FitzGerald 1973, Smith and Shackleton 1988, chapter 5). For many woody species competition for light is a limiting factor for successful establishment (Smith and Goodman 1987, Hoffmann 1996). Woody species may benefit from grazers who reduce the grass biomass, thus reducing competition for light with seedlings of woody species (Knoop and Walker 1985, Belsky 1992, Chapter 7). Indeed, *Acacia* rapidly invades grasslands after the grazing intensity is increased by the introduction of cattle (Van Vegten 1983). Selective browsing of seedlings, at the other hand, can prevent successful establishment of woody species (Smith and Goodman 1987, Myster and McCarthy 1989, Prins and Van der Jeugd 1993, Hoffmann 1996, Coppedge *et al.* 1998, Holl 1998). Prins and Van der Jeugd (1993) found that throughout northern Tanzania, *A. tortilis* trees belonged to certain age cohorts, which they associated with crashes in selective herbivore populations.

Knowledge of tree development with age is a prerequisite for reconstructing tree establishment in the past. In contrast to the fairly easy determination of tree age in temperate zones based on the periodicity of growth rings, such rings are absent or difficult to distinguish in tropical trees. On the other hand, Gourlay and Kanowski (1991), Gourlay and Barnes (1994), Gourlay (1995), Gourlay *et al.* (1996), and Martin and Moss (1997) have demonstrated for several *Acacia* spp. that periodicity in annual growth rings, formed by marginal parenchyma bands, is related to rainfall distribution.

Stem diameter is generally used to determine tree age after calibration with trees of known age. Stem growth is normally assumed to be isometric, but in closed canopy forests density dependent mortality results in self-thinning (Skarpe 1991): the growth rate of trees in such cases will depend on tree density. In the Rift Valley in northern Tanzania, *A. tortilis* forms closed canopy stands on abandoned arable fields. The *Acacia* woodlands of Lake Manyara National Park in Tanzania too have been described as closed-canopy woodlands, which later opened up by the action of elephants (Douglas-Hamilton 1972, Mwalyosi 1987). Self-thinning can therefore have played a role in these woodlands.

In this paper, the possibility to determine the age of *A. tortilis* trees was examined through the analysis of periodicity in parenchyma bands in relation to the potential maximum age of trees growing in old-fields, of which the year of abandonment was known. Secondly, the effect of tree density on stem growth rate is analysed. The results are compared with the outcome of other studies, and the ecological implications discussed.

Study area

The study took place in the valley of the Gregory Rift in northern Tanzania. Data were collected in Lake Manyara National Park, and in crop farms south of the Park (fig 1). Lake Manyara National Park in northern Tanzania (3°30'S, 35°45'E) is situated between the escarpment of the Great Rift Valley to the west, and the lake, Manyara, to the east (fig 1).

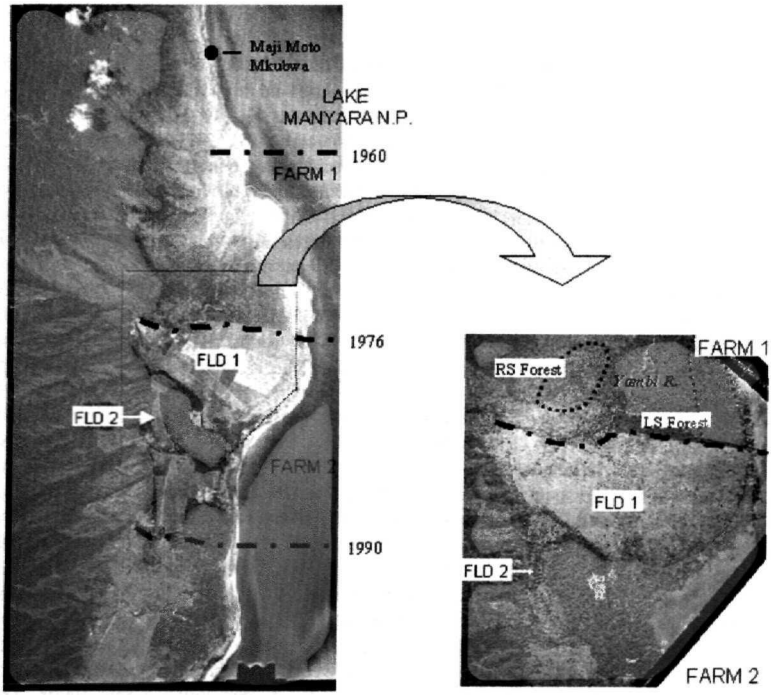

Figure 1. Southern part of Lake Manyara National Park, showing the escarpment of the Rift Valley at the left, and the lake at the right. The clouds at the top-left figure are above the Marang Forest. FARM 1 was added to the Park in 1976, but not used since 1963, and FARM 2 was added in 1990. FARM 2 was in use until the moment of hand-over. FLD1 and FLD 2 are different units within FARM 2, with FLD 1 as the only irrigated field. The light spots in FARM 2 is bare soil. In the inset: RS = Road Side forest, LS = Lake Side forest. Aerial photograph 1982, at appr. Scale 1:68,000. Inset: 1997 photograph, at appr. scale 1:20,000.

Before Lake Manyara N.P. was gazetted as a National Park in 1960, the area was declared a Game Reserve in 1958. Until that time the area had been used for sports hunting by white settlers since the 1920s; prior to that, human occupation was virtually absent for about two centuries, except for wandering hunter-gatherers (Prins 1996). During the 1950s the area south of the Reserve was allocated to white settlers. The last farm was leased out in 1958, and bordered the Game Reserve in the south. This farm (FARM 1) was incorporated into the Park in 1976, although it had been abandoned as early as 1963. Immediately after land clearing papaya (*Carica papaya*) was planted, followed after a few years by maize (*Zea mays*). Pepper (*Capsicum*) was planted as well. Between 1960 and 1963, maize was the main crop. The second farm (FARM 2)

was added to the park in 1990. This farm has a longer history of land use, with several changes of ownership. Also in this area papaya was planted immediately after clearing. An irrigation system, drawing water from Yambi River had been constructed in the unit (FLD 1) closest to this river (see fig 1). Coffee was planted in the irrigated fields and maize in the other fields. Along the lake shore, sisal was planted, but this crop was distroyed during high lake levels in 1962. After the farm changed ownership in 1984, all the coffee, except for a small area where it is still present, was replaced by sugar cane. Maize remained the main crop in the other fields. Additional data were obtained from a third farm (FARM 3) in the Rift Valley, 30 km to the south of the Park. This farm was leased out in the early 1950s, and is still in use, although a number of fields had been abandoned at various times (pers. comm. WaZee Mabeto, K. Mollel, R. Nachel, J. Peter, H. Musa, all former farm workers, and messrs M. Barengo and P. Strebel). The study area consists of the PARK with no human occupation for more than two centuries, 33 yr old-fields in FARM 1, 6 yr old-fields in FARM 2 and 2, 6, 18 and 20 yr old-fields in FARM 3.

A. tortilis had formed closed-canopy forests in the abandoned fields of FARM 1. In the forest near the Lake (LakeSide forest), occasionally *Balanites aegyptiaca* trees were found. These are shade trees that had been left in the field. The *Acacia* trees were straight-stemmed with the first furcation at 8-10 m height. In the forest closer to the escarpment (Road Side forest) *A. sieberiana* trees were occasionally found amidst the *A. tortilis* trees. Most of the *A. tortilis* trees had straight stems, but some trees had rather spreading branches from furcations below 5 m height. These trees, with thicker stems, were thought to be older than the rest Weyerhaeuser 1982). The growth characteristics of trees in the closed-canopy old-fields in FARM 1 were compared with those of free-standing trees in the PARK.

In one field in FARM 2 (FLD 2), *A. tortilis* regeneration was prolific. The trees in this field grow in distinct linear patterns, coinciding with old furrows that were still visible. This indicates that the trees had emerged from the seed bank. In another FARM 2 old-field (FLD 1), *A. tortilis* established from seeds imported mainly through elephant dung, as was suggested by the distribution of the species there, either single or in small clusters. In this field old furrows were much less pronounced.

Methods

To determine the age of *Acacia* trees based on the presence of marginal parenchyma bands, stem discs were cut from old-fields of which it was known since when the fields were abandoned. In the field, repeating patterns formed by the varying width of parenchyma bands were distinguished on the cut surfaces. The number of times that such patterns were found along a stem radius, agreed well with the age of the field. In the laboratory, the position of marginal parenchyma bands was measured. The width of parenchyma bands was also measured to determine whether the periodicity in parenchyma band width that was observed on untreated discs, could be confirmed by statistical analysis. Time series analysis was carried out to identify and describe the recurrent patterns in parenchyma band width. Spectral analysis is a form of time series

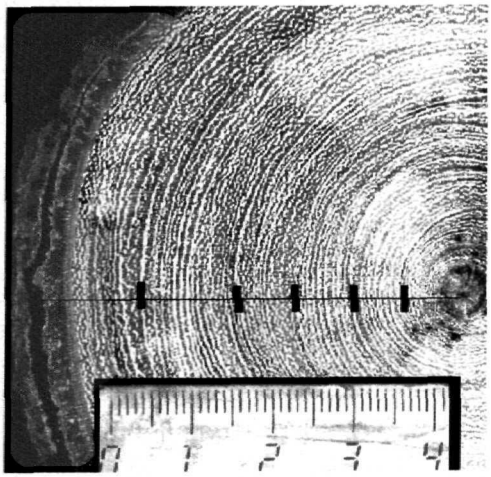

Figure 2. *Acacia tortilis* stem disc from a 6 yr old-field in Lake Manyara National Park. The light bands, tracheae with paratracheal parenchyma, are alternated by the dark parenchyma bands. Marginal parenchyma bands were not visible in this sample. The black bars mark the start of periods. Scale bar is in cm.

analysis that decomposes complex time series with underlying cyclic components into underlying sinusoidal functions of particular wavelengths (Statsoftinc 1999). The wavelength in this case is the number of parenchym bands required for one period. To estimate the maximum possible growth rate in the 6-year old-fields of FARM 2 where competition with other trees was assumed to be absent, the stem diameter at breast height (dbh) of 25 of the tallest trees in the site was measured. In the closed canopy forests in the 33 yr old-fields of FARM 1, growth rate, as annual stem diameter increment, was determined in relation to tree density. To determine whether density dependent growth occurred in the Park area, the height of the first furcation was considered to be a response to crowding, as a reaction upon the competition for light.

Age determination

Trees were cut at breast height (1.30 m) to obtain stem discs to analyse growth rings in the stems. Descriptive field data were collected in 1995 and 1996, trees were cut in 1996. Tree age was estimated in the field as the average number of repeating patterns along two radii, caused by varying parenchyma band thickness (fig. 2). Stem discs of 59 trees of different diameters were cut with a chain saw (number and field age with location given in parentheses): 1 (33; FARM 1, LS forest), 3 (20; FARM 3), 1 (18; FARM 3), 6 (6; FARM 3), 1 (6; FARM 2, FLD 2), 20 (6; FARM 2, FLD 1), 9 (2; FARM 3); 18 (unknown, PARK). In the Park only samples of trees with a dbh of about 10 cm were taken.

In the laboratory, 11 of these discs were sanded and analysed by measuring the width of the parenchyma band with a Positiometer under 20 or 45 x magnification. The position of marginal and other parenchyma bands along two radii were digitized to the nearest 0.01 mm using the Positio V 1.0 computer programme, developed by the Department of Environmental Sciences, Forestry Section, Wageningen University.

Allometric data in relation to competition

In 8 x 0.25 ha plots in the two 33 yr old Lake Side and Road Side forests, the stem diameter at breast height (dbh) of all trees was measured. With these data the correlation between tree density and stem diameter could be determined on stand level. In one 0.25 ha plot the distance to the four nearest neighbours in each of four quadrants around 47 trees in the plot was paced off to the nearest meter. The tree that was closest to the focus tree was positioned in the center of the first quadrant. Dead trees on the forest floor were registered, but not measured when close to a target tree.

Stem diameter and height of first furcation was measured in 46 mature trees between the rivers Ndala and Msasa (fig 1). Based on habitus, the trees were classified in two categories, 'not so old' and 'old'. The degree of competition was subjectively classed in four levels: *none* = trees free standing; *light* = tree canopies touching each other for less than 25% of the canopy circumference; *medium* = canopies of neighbouring trees touching 25 – 75% of canopy circumference; *severe* = closed canopy.

Stem diameter (dbh) was measured by two perpendicular caliper readings, or, when the stem diameter exceeded the caliper limits, by measuring the circumference with a measuring tape. In case the bolus forked at 1.30 m, the measurements were taken just below the point of furcation.

Self-thinning

The self-thinning rule, formulated by (Yoda *et al.* 1963), describes that plant mass is a power function of the number of plants per unit area, and in a log-log scale this relationship will give a straight line with a slope of –3/2. The –3/2 power rule is described by the equation:

$$w = k\, d^{-3/2} \qquad \text{[Eq 1]}$$

or:

$$B = k\, d^{-1/2} \qquad \text{[Eq 2]}$$

where w is the average mass per plant, B the plant mass per unit of area, d the plant density per area unit and k is a constant (Sackville Hamilton *et al.* 1995).

Self-thinning is usually calculated on the basis of biomass in relation to plant density, in particular in terms of leaf area (Sackville Hamilton *et al.* 1995), although stem diameter (Landsberg and Waring 1997, Fromard *et al.* 1998) has also been used as a predictive variable. Lonsdale (1990) suggested that the self-thinning rule applies to canopy volume, rather than biomass.

The typical flat-topped growth form of mature *A. tortilis* is shaped by sub-canopies, supported by spreading branches. The sub-canopies hardly overlap and are of equal height (pers. obs.), so that under these premises the –3/2 rule should apply for mature trees that form a closed canopy.

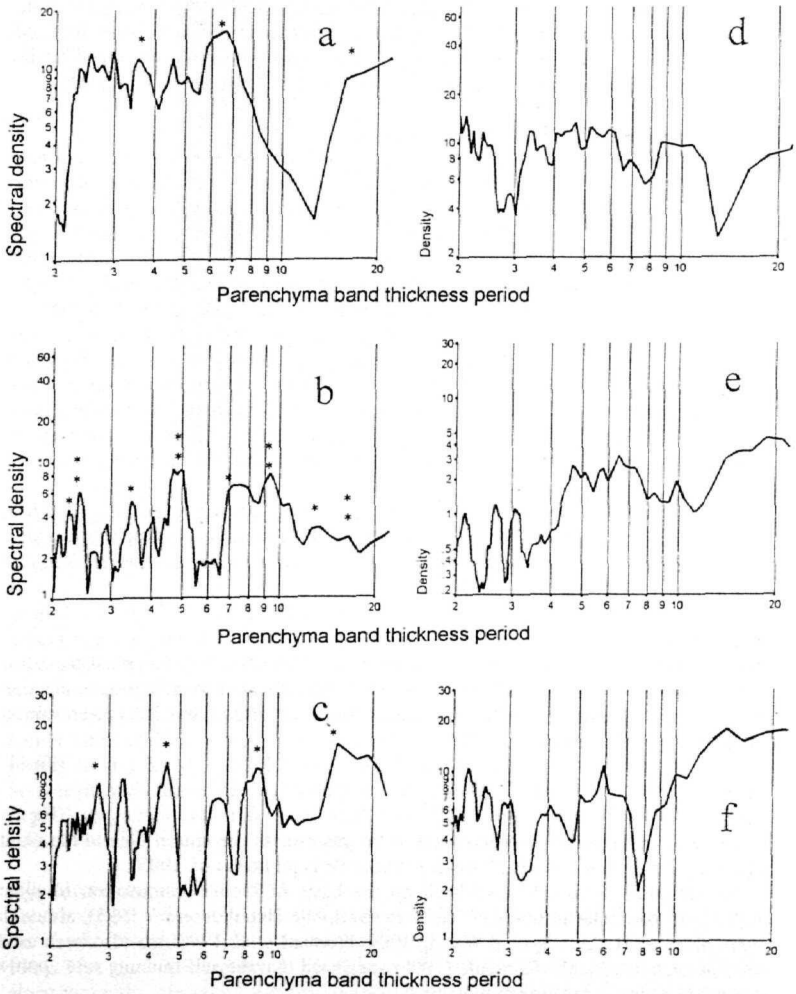

Figure 3. Spectral density plots of parenchyma band width in *A. tortilis* stems in the Rift Valley, northern Tanzania. (a-c) stems obtained from respectively 33, 20 and 18 yr old-fields, (d,e) 6 year old-fields, and (f) a Park tree. Asterixes indicate repetition of periods, suggesting that at those wavelengths a recurrent pattern in parenchyma band width is present.

Data analysis

For the spectral analysis the data were smoothed with a moving average filter (Tukey-Hamming window, with a width of 5; Statsoftinc 1999). Marginal parenchyma bands were encountered in a number of samples, but these growth rings were too infrequent for spectral analysis; in this statistical analysis no missing values are allowed.

To validate the field method of tree age estimation, linear regression analysis was carried out of estimated tree age on the number of periods in parenchyma band width established by spectral analysis.

Linear regression models were used to determine the relationship between stem diameter, height of first furcation and competition for mature trees in two age classes.

For the validation of the self-thinning rule the biomass w per tree was expressed as the tree basal area, and the density was calculated as the inverse of the mean distance to the four neighbouring trees [Eq 1]. The biomass B per plot was expressed as the total basal area, and density d was expressed as number of trees per m^2 [Eq 2]. In log-log plots, linear regression lines were fitted.

Results

Age estimation and allometric growth

In a number of samples marginal parenchyma bands were incidentically identified. Such bands were found towards the periphery of the stem, but were never found close to the stem core.

Spectral density plots show periodicity in parenchyma band width in *A. tortilis* stem discs (fig. 3). Periodicity in parenchyma band width is more distinctive in large trees than in small, young trees (fig. 3a and b, vs fig. 3c and d).

A period with a wavelength of 18 parenchyma bands (fig. 3a) is indicated in the corresponding figure of the thickness of consecutive parenchyma bands (fig. 4a). The sequence in this figure has been once adjusted by eye to align the pattern in the data set with the cycle length. In this way, 14 periods could be identified. The mean parenchyma band width was greater in the periods 7 – 9 (≈ 1.4 mm) than in the preceeding or the following periods (≈ 1.2 mm; fig. 4a). Note that parenchyma bands near the core of the wood are very thin, and that from the core of the wood parenchyma band thickness increases. Figure 4b is shows the parenchyma band thickness along a second radius, at 180° of the first radius (fig. 4a). The wavelength (number of parenchyma bands per period) along the second radius is the same, but the periodicity in parenchyma band width is less distinct. The thickness of the parenchyma bands remains constant over the period 5 - 10, but is considerably higher in the first three complete periods 2 - 4. The position of marginal parenchyma bands corresponds with dips in the thickness of parenchyma bands, approximately at a wavelength of 9 parenchyma bands. This tree was cut in a 18 yr old-field of FARM 3.

Periodicity in parenchyma band thickness is unclear as long as the parenchyma band thickness remains < 1 mm, close to the stem core. Periodicity in stems with diameters < 15 cm was therefore in general difficult to distinguish (fig. 3d-f). In 4 out

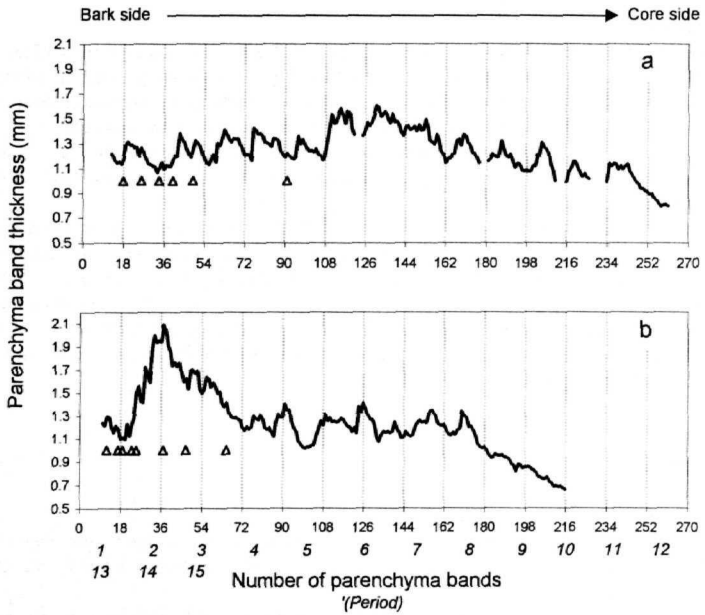

Figure 4. Parenchyma band thickness in a representative stem sample of an *A. tortilis* stem disc obtained from a 18 yr old-field (FARM 3) in the Rift Valley in northern Tanzania. An exponential average smooting function was applied, revealing a recurrent pattern of a wavelength of 18 parenchyma bands. The plots show parenchyma band width along two radii (a and b) at an angle of 180° of each other. Parenchyma bands are numbered from the edge of the wood towards the center of the disc. Triangles indicate location of marginal parenchyma bands. For ease of interpretation, the curves have been adjusted to coincides with periods. Figure 3c shows the spectral density plot corresponding with (a).

of 6 discs in this size category no distinct periodicity could be found in the spectral density plots.

Linear regression of the tree age estimated in the field showed a strong relationship between the number of periods determined by spectral analysis of parenchyma band width (fig 5a). The estimated tree age was also significantly and strongly related with the number of years that old-fields had been abandoned (fig 5b), but remained below the age of the old-fields. It is therefore reasonable to conclude that the number of repeating patterns caused by varying thickness in parenchyma bands, is a good estimator of *A. tortilis* age. Linear regression of stem diameter on tree age showed a strong, positive relationship (fig 5c), suggesting that the mean annual increase in stem diameter of *A. tortilis* trees, growing in old-fields in the Rift Valley, is about 2.3 cm yr^{-1}. Larger annual increments have been found in 6-year old-fields in FARM 2, where crowding effect was absent (4.6 cm yr^{-1}, SD = 4.95, N = 25; broken line in fig 5c).

The height at which the first furcation of mature *A. tortilis* trees occurs, depends on the degree of competition only (Table 1), whereby the furcation height above the ground increased with increasing competition (Table 2).

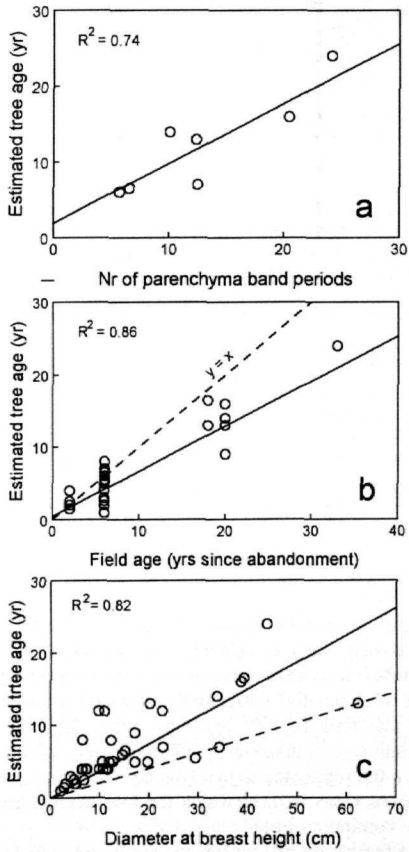

Figure 5. *A. tortilis* stem allometry in the Rift Valley in northern Tanzania. Estimated tree age in the field was positively related with the number of parenchyma band cycles found by spectral analysis *(a)*, and the number of years that had passed since old-fields had been abandoned *(b)*. Tree age was related to stem diameter, showing maximum annual stem increase of 5.1 cm yr^{-1} under competition-free conditions (broken line in *(c)*). Regression equations:

(a) $y = 1.6 + 0.82 * x$, $F_{1,5} = 17.2$, $P < 0.05$;
(b) $y = 0.45 + 0.62 * x$, $F_{1,34} = 154.1$, $P < 0.001$;
(c) $y = 2.2 + 2.26 * x$; $F_{1,46} = 103.6$, $P < 0.01$.

Table 1. Linear model describing mean height of the first furcation in mature *A. tortilis* trees in Lake Manyara National Park, Tanzania, with stem diameter as covariate, and age (2 categories), and competition (4 levels) as factors. N= 46, $R^2 = 0.66$. F = F-ratio, *P* = significance value.

Factor	d.f.	F	*P*
Dbh	1	0.377	NS
Age	1	0.456	NS
Competition	3	16.474	<0.001
Age*Competition	3	1.459	NS

Table 2. Mean height (± S.E.) of first furcation in mature *A. tortilis* trees in Lake Manyara National Park, Tanzania, under 4 levels of competition: *none* = trees free standing; *light* = canopies trees of similar age, or older, touching less than 25% of the canopy circumference; *medium* = canopies of neighbouring trees touching 25 – 75% of canopy circumference; *severe* = closed canopy, or tree leaning over. Letters denote significant differences ($P < 0.05$) between the means (one-way ANOVA followed by Tukey's multiple comparisons test)

Competition	N	mean height (m)
None	17	1.8 (± 0.12)^{a}
Light	12	2.4 (± 0.23)^{ab}
Medium	13	3.2 (± 0.23)^{b}
Severe	4	5.2 (± 0.34)^{c}

Self-thinning

In the mono-specific *A. tortilis* forests of the 33-yr FARM 1 old-fields, the mean diameter (dbh) was negatively correlated with tree density (fig. 6a). For individual trees in the Lake Side forest, no correlation was found between dbh and the distance to the nearest tree. A weak positive correlation was found when the mean distance to the four nearest trees was used (fig. 6b), and thus to the neighbourhood area available to the tree. The maximum stem diameter in 33 yr old trees would be about 57 cm when all trees are used in the regression model (fig. 6a and fig. 6b: broken line), and 72 cm when only those trees were used, of which the four nearest trees did not include any dead trees (fig 6b.: continuous line).

The slope of the regression line for tree mass per unit area, expressed as the average basal area per m^2 [Eq 2] was –0.49 (fig. 6c). The regression line based on the basal area per tree per m^2 [Eq 1] had a slope of –1.13 when all trees were included, and a slope of –1.47 when only trees were used, of which the four nearest trees did not include any dead trees (fig. 6d).

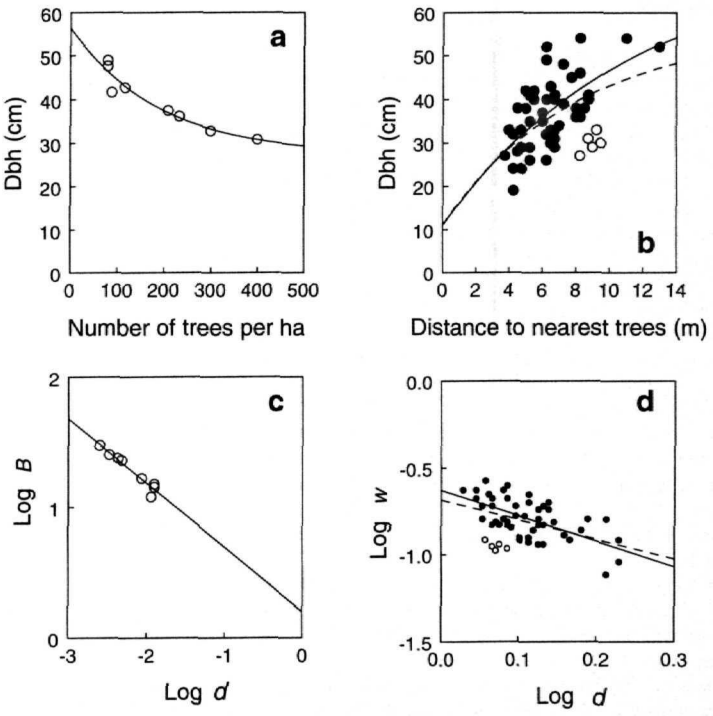

Figure 6. *Acacia tortilis* stem allometry and self-thinning lines in relation to tree density in closed canopy forests in two 33-year old-fields of Baker's Forest, Lake Manyara National Park, Tanzania. *(a)* Mean stem diameter (dbh) against tree density in 33 yr old-fields; *(b)* stem diameter (dbh) against the mean distance to the 4 nearest trees. Continuous line, filled dots: trees with living nearest neighbours only, broken line for all trees (including trees with fallen neighbours = open dots; see text for explanantion). *(c)* Tree biomass B expressed as mean basal area on tree density d in log-log scale. The slope of the linear regression line of log B on log d is close to the expected slope of $-1/2$: *(d)* Tree biomass per tree w against tree density d calculated as the inverse of the mean distance to the four nearest trees. The regression line of log w on log d has a slope close to the expected slope of $-3/2$ when only trees with living nearest neighbours are used. Fitted curves:

(a) $y = 27.9 + 29.2 * \exp(-x/176.2)$; $F_{2,5}=29.5$, $P<0.01$, $R^2=0.89$;

(b) $y = 72.3 - 61.3*\exp(-x/11.5)$; $F_{2,46}=15.1$, $P<0.001$, $R^2=0.40$ (—●—)

$y = 56.1 - 44.9*\exp(-x/8.1)$; $F_{2,45}=9.4$, $P<0.001$, $R^2=0.26$ (all trees: ● and O, -----)

(c) $y = 0.199 - 0.49 * x$, $F_{1,6} = 89.1$, $P < 0.001$, $R^2 = 0.93$;

(d) $y = -0.63 - 1.47 * x$, $F_{1,47} = 30.8$, $P<0.001$, $R^2 = 0.38$ (—●—)

Discussion

Annual growth rings have been identified in *A. tortilis* (Gourlay and Kanowski 1991, Martin and Moss 1997), but such marginal parenchyma bands are difficult to detect. In this study, some marginal parenchyma bands had been identified, but could not be found consistently throughout the sampled discs. Gourlay and Kanowski (1991) found one band per year in *Acacia spp* that grew in areas with unimodal rainfall distribution, and two in those from areas with bimodal rainfall. In one tree examined in this study, two marginal parenchyma bands appeared to be present within one period of parenchyma band thickness, which corresponds with one year. Since Lake Manyara National Park has a bimodal rainfall distribution (Loth and Prins 1986), this agrees with Gourlay and Kanowski (1991),

Much easier to distinguish as indicators of tree age is periodicity in parenchyma band width. The number of periods distinguished in the field corresponded well with the number of periods found in spectral analysis, and the estimated age of trees taken from old-fields agreed with the number of years that the fields had been abandoned. It should be noted, however, that spectral analysis did not reveal clear periodicity in most stems smaller than 15 cm, because the parenchyma bands are too thin. Furthermore, only few discs were obtained from trees which were larger than 15 cm, and finally, the samples bigger than 15 cm all came from old-fields. It is therefore necessary to study samples of trees which have grown in undisturbed soils, before it is concluded that this method is also valid for the age assessment of trees growing in undisturbed, natural habitats.

In the Park, the height above the ground at which trees have their first furcation depends on the degree at which they experience competition from neighbouring trees. The growth rate of trees in the closed-canopy *Acacia* woodlands thus can be expected to have varied with varying tree density.

Density dependent mortality by self-thinning in closed-canopy forests is characterised by dead trees on the forest floor (Osawa and Allen 1993). These were also found in the 33-year old-fields of FARM 1. Smaller trees in crowded situations have less canopy area available to them, and this will have consequences for stem allometry. The self-thinning rule describes a constant relationship between plant mass and plant density to the power –3/2 in closed canopy stands where density dependent mortality occurs (Yoda *et al.* 1963, Matthew *et al.* 1995), but others have suggested that deviation are possible, because of allometric canopy growth (Weller 1987, Lonsdale 1990). The slope of the regression line of log-log transformed tree biomass and density data is –3/2, suggesting that *A. tortilis* canopies, at least of flat-topped trees, are invariable of shape. The self-thinning line can thus be used as the dynamic thinning curve of a given population.

The maximum stem diameter of 33 year old *Acacia* trees was found to be between 57 to 72 cm when competition takes place, which amounts to an isometric growth rate of about 2 cm yr^{-1}. Although this is already 2 to 4 times higher than has been reported in the litterature (see table 1 in Martin and Moss 1997, and Table 4 in Prins and Van Der Jeugd 1993), it is still only half of that of 6 year old trees growing in old-fields under competition-free circumstances. In 1981, 18 years after abandonment, the mean

growth rate in the Maji Moto Unit 1 fields was 1.6 cm yr^{-1} (calculated from Weyerhaeuser 1982), which is lower than the maximum growth rate calculated for the same stand in 1996. Evidently, stem growth was already affected by the high density in 1981, so that the calculated potential growth rate for 33 year old trees will be higher than the maximum growth rate calculated for the entire stand.

How can these differences in stem growth rates between this study and other studies be explained? In this study the growth rates of trees growing on abandoned fields was determined. Growth rates of 1 to 2 cm yr^{-1} had been found for *planted* trees (Gourlay 1995, Martin and Moss 1997), while growth rates < 1 cm yr^{-1} have mainly been reported for trees in natural settings (Herlocker 1976, Weyerhaeuser 1982, Mwalyosi 1977, Prins and Van Der Jeugd 1993, quoted in Prins and Van der Jeugd 1993, Table 4). This indicates that growth rates in disturbed soils are greater than in undisturbed soils, because in disturbed soils water availability and mineralization rates are likely to be higher than in undisturbed soils. However, Weyerhaeuser's data for trees in the park area show that the annual growth rate of trees with a dbh of more than 60 cm, varies between < 0.2 cm yr^{-1} to > 1 cm yr^{-1}, with a mean of 0.55 cm yr^{-1}. Tree growth is variable, and also depends on tree vitality and tree density. Without detailed analysis of large *Acacia* trees from undisturbed habitats, it is not possible to conclude the age of such trees from their stem size only.

Browsers may be able to arrest tree growth as long as the trees are within reach of browsers. In Hluhluwe-Umfelozi National Park in South Africa, *Acacia* trees are maintained at a level of around 1 m height by a large browser community, consisting of Nyala and impala. The trees were found in an otherwise short grazed, dense grass sward of *Cynodon dactylon* L. (H. Olff, pers. comm.). Branching occurs as a reaction to top meristeme removal, and I suggest therefore that the typical spreading *Acacia* trees reflect browsing impact at a young age. Possibly branching trees have different growth rates compared to single stemmed trees.

Prins and Van der Jeugd (1993) concluded that *A. tortilis* age cohorts resulted from gaps in browser pressure, allowing seedlings to escape. Also Sinclair (1979) mentioned that the Serengeti grasslands turned into woodlands after the rinderpest, although (Dublin 1995) was less specific and described that woodland formation took place over a time span of 30 to 50 years after the turn of the century. Indeed, browsers are likely to have played a role in the formation of size cohorts (Chapter 5), but by limiting growth rates at a certain stage by continuous browsing, rather than by direct removal of tree seedlings. It is unlikely that massive *Acacia* seedling establishment took place after the 1893 rinderpest in northern Tanzania, because the taller grasses became an even more competitive environment for *Acacia* seedlings (see chapter 5). Therefore, if the age of tree cohorts coincides with the first rinderpest outbreak, *Acacia* seedlings must have already been present so that they could profit from the deminished browsing pressure, following the rinderpest epidemic. Alternatively, the increase in standing hay may have resulted in increased fire frequency and intensity, and since fires stimulate *Acacia* establishment (Sabiiti and Wein 1987, Auld and O'Connell 1989, Bradstock and Auld 1995, Mucunguzi and Oryem-Origa 1996), the disappearance of the grazers indirectly may have resulted in increased *Acacia* establishment.

In conclusion, the number of repetitive partterns formed by variation in parenchyma band thickness in *A. tortilis* tree stem discs taken from old-fields, corresponds with the number years that those old-fields had been abandoned, and can be used to estimate the age of the trees. In stems with a diameter < 15 cm, and towards the center of larger discs, periodicity in parenchyma band thickness is less distinct, because near the center of the wood the parenchyma bands are too thin. *A. tortilis* is a successful colonizer of abandoned fields, growing in even-aged stands. Self-thinning occurs in closed-canopy 33-yr old *A. tortilis* forests according to the –3/2 rule. The growth rate is highly variable; trees in disturbed soils grow much faster than growing in undisturbed situation. Stem diameter may therefore not be a good estimator for tree age. Crashes in herbivore populations may cause the formation of *A. tortilis* age cohorts, either because small trees can escape continuous browsing, or because fire frequency and intensity increase, so that competition by grasses is temporarily excluded.

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Chapter 7

A decade of change in the herbivore assemblage of Lake Manyara National Park

Summary

Herbivores may influence vegetation dynamics either directly, by the selective removal of plant species, or indirectly, by altering the abiotic environment in which plants grow. Depending on body size, herbivores use the vegetation at different scales. Changes in the herbivore assemblage may therefore lead to changes in vegetation. This hypothesis was tested in Lake Manyara National Park, an area with one of the highest herbivore densities in Africa. Elephant numbers had fallen by 75% between 1985 and 1991, as a result of illegal hunting during this period. Since elephant and buffalo are competitive grazers, an increase in buffalo numbers was expected. Contrary to expectations the buffalo population decreased as well when the number of elephants decreased. The 'gap' in grazing pressure was instead filled by wildebeest. It is suggested that the decline in dry-season high density bulk forage in *Cyperus* grass marshes is the main reason for the decline in buffalo.

In conclusion, the composition of the herbivore assemblage appears to depend on vegetation characteristics, rather than that the herbivores shape the vegetation.

Introduction

Herbivores may influence plant communities directly, by selective consumption of preferred plant species (Furbish and Albano 1994), and indirectly, by altering nutrient cycling (Ruess and McNaughton 1988, Berendse *et al.* 1992, McNaughton 1992, Turner *et al.* 1993), or when nutrient availability is not limited, by altering access to light (Crawley 1997, Huisman *et al.* 1999). When grazers differ in body weight, they use the vegetation at different scales (Prins and Olff 1998, Van de Koppel and Prins 1998). A change in the composition of the herbivore guild therefore may lead to a change in vegetation. In African savannas, tree destruction by elephant *Loxodonta africana* results in the transition from woodlands to grasslands (Norton-Griffiths 1979, Pellew 1983, Van Wijngaarden 1985, Mwalyosi 1987, Buss 1990, Dublin 1991). Other herbivores, especially grazers, may benefit from such transitions where before browsers had an advantage.

Lake Manyara National Park has one of the highest herbivore densities in Africa (Drent and Prins 1987). During the dry season, a large proportion of the Park's grazers is supported by the alkaline grasslands, which then provide sufficient bulk of relative good quality forage (Prins and Beekman 1989). The lake has no outlet, so that in periods of above average rainfall the lake fills up, while during periods of drought the lake dries out. Consequently, the extent of the grass swards varies over the years, and competition between grazers utilising the alkaline grasslands in particular may vary with changing lake levels. Although the composition of the herbivore assembly has been changing over time, the total herbivore biomass has remained fairly constant. Elephant and buffalo make up the majority of the herbivores, and were found to be competitors (Prins and Douglas-Hamilton 1990). The *Acacia* woodlands of Lake Manyara National Park has been opened up progressively by the feeding behaviour of the Park's elephants (Douglas-Hamilton 1972, Mwalyosi 1990). Between 1987 and 1991 poaching caused a 75% reduction in the elephant population (Prins *et al.* 1994). The decrease in elephant numbers due to poaching provides the opportunity to determine to what extent the population sizes of other herbivores change as a result of a drastic change in the herbivore assembly. Since elephants and buffalo are competitive grazers, a drop in elephant numbers is expected to result in an increase in the numbers of other grazers, especially buffalo. This hypothesis is tested by comparing historical animal population census data with recent census data.

Methods

The study took place in Lake Manyara National Park in northern Tanzania. In 1990 the Park area had been extended with 5 km^2 by the inclusion of an arable farm. The alkaline grasslands were fully extended after a drought in 1993/1994, so that the area available to the herbivores was 105 km^2.

The Park's animal populations below the escarpment were censused over the period November 1994 – July 1996. For census purposes, the Park area was divided into a

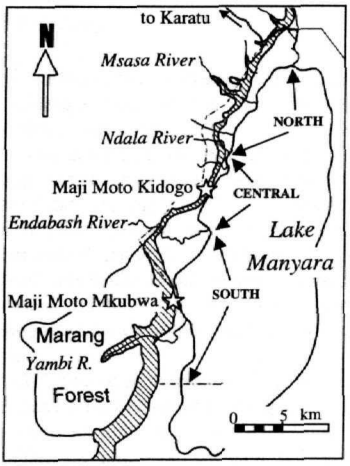

Figure 1. The division of Lake Manyara National Park in a northern, central and , southern region. Maji Moto Kidogo is the small Hot Spring, and Maji Moto Mkubwa the large Hot Spring).

northern, central and a southern region, separated by, respectively, Ndala River and Endabash River (fig 1).

Large herbivores were censused from a vehicle at least twice a month during my movements in the Park. The road system was divided into transects, defined by road junctions and river crossings. The length of each transect was measured to the nearest 50 m on the vehicle odometer. A distinction was made for animals occurring within a strip of 15 m at both sides of the road, and those further away. By counting the animals within a strip, animal densities could be calculated (Prins and Van der Jeugd 1993). Species that preferred the alkaline grasslands (wildebeest and zebra, but also buffalo, elephant and giraffe), were regularly counted from vantage-points overseeing the alkaline grasslands from August 1995 onward. The size of each area that could be counted from the vantage-points was estimated from the vegetation map (Loth and Prins 1986).

In addition to the above-mentioned methods, elephants were censused during a 24-hour count on 6 and 7 November 1995 at full moon. Elephant movements on the preceding days indicated that many elephants would be moving between Endabash area and Bagayo River. From a vantage point on the escarpment near the small Hot Springs (fig. 1) overseeing the total width of the Park (400 m), only the elephants were counted which moved in one (northern) direction. One distant group, which had been encountered on the days before, and immediately after the 24-hour count, had been added to the total.

The number of baboons were estimated by counting the number of groups in the park multiplied by the mean number of baboons. Thirteen baboon groups had been identified (five in the ground water forest, one in the delta area of Msasa River, one in Ndala River gorge, three in the Endabash area and three in Yambi area).

Data analysis

The population size of herbivores with restricted home ranges (impala, waterbuck, bushbuck, and warthog) was estimated on the basis of the maximum counts of known herds or groups. For herbivores, which could be counted on the alkaline grasslands, the highest counts were used as population estimates. These counts were obtained during one or two consecutive days, when double counts of groups or herds could be ruled out. The Park's baboon population was estimated by multiplying the number of baboon groups in the Park with the mean group size.

Wildebeest migrating into the Park from the north was observed, and also zebra moved in and out of the Park. Monthly counts of these two herbivores were compared to determine to what degree these populations fluctuated throughout the year.

The growth rate of the elephant population between 1991 and 1995 was compared with the maximum potential growth rate. The potential growth rate, λ, of the elephant population was calculated according to Van Langevelde (1999):

$$\lambda = P_a + P_j\beta \qquad (1)$$

where P_a is the annual survival probability of adults, P_j is the survival probability of offspring, and β is the average number of offspring per adult. For the calculation of the maximum growth rate for elephants the following assumptions were made. The mean life expectancy of adult elephants was assumed to be 65 years. Adult survival probability P_a thus equals (1-1/65). Although mortality rates is likely to be higher for calves and juveniles, the survival probability for young animals was assumed to be the same as that for adult elephants. Equation (1) thus becomes:

$$\lambda = P(1+\beta) \qquad (2)$$

The mean age at which the first ovulation occurs is 11 years, and the mean calving interval is 4 years (Eltringham 1982). Female fecundity after the age of 55 rapidly declines to zero (Armbruster and Lande 1993), so that a female produces during her reproductive life on average [(55-11)/4=] 11 calves. For a population with equal sex ratio, the yearly production probability per adult, β, equals (5.5/55=) 0.1. Substitution of the values for P and β in equation (2) yields a mean intrinsic growth rate λ for elephants of 1.083. The maximum growth rate of elephant populations therefore is about 8%.

Herbivore consumption requirements (dry matter consumption) on a daily basis were compared with earlier data provided by Prins and Douglas-Hamilton (1990). Conform these authors, the daily dry matter intake for free-ranging herbivores has been assumed to be 2.5% of live weight. This general figure has been proposed for ruminants (Van Soest 1982, Prins 1996) and elephants (Van Wijngaarden 1985), but this figure can be expected to be lower for browsers, because the quality of their forage is higher. Because the biomass of browsers in Lake Manyara National Park was one fifth of that of the grazers, the same figure was applied to the browsers as well.

Results

The results of the animal censuses are presented in Table 1. Based on strip counts, the elephant population in the Park was 262 ± 65 (95% C.L.; n=1513), and the maximum number of elephant counted on a single day (6-7 November 1995) was 193. The elephant population in 1996 was estimated to be about 200 animals, including 6 elephants that had moved from the Ngorongoro Conservation Area in March 1996. In 1996 the buffalo and elephant populations were about half the size of those in 1984. The populations of the other grazers had increased, or remained at the same level, except for reed buck, a species that had become extinct in the Park (Table 1).

Elephant numbers sharply decreased after 1985 to reach a low of 63 in 1991, and increased again to around 200 in 1996 (Table 1, fig 2). This increase represents a growth rate of 28% per annum.

The mean number of wildebeest throughout the year was 975. About 2000 animals had been counted during the dry season. Initially, most wildebeest had been predominantly found in the northern part of the Park, but wildebeest were increasingly encountered in the south. Most wildebeest left the Park again at the first rains in December, and a resident population of about 300 remained throughout the rainy season. Wildebeest numbers started to increase again during the following dry season (fig 3).

Zebra numbers fluctuated throughout the year, but these were independent of the time of the year. There was a positive and significant relationship between the monthly number of zebra, and the size of the area that had been counted (fig 4). A population of 335 zebra resided in the Park.

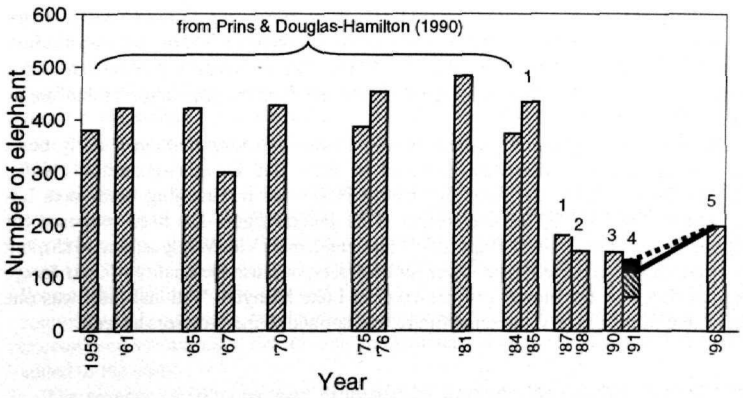

Figure 2. Elephant numbers in Lake Manyara National Park, Tanzania, between 1959 and 1996. 1: Douglas-Hamilton (unpubl.), 2: Campbell (1988); 3: Tanzania Wildlife Conservation an Monitoring (unpubl.), 4: Prins *et al.* (1994), 5: this study. Solid line: minimum population size required in 1901 to obtain population size of 200 in 1996 at growth rate of 8%, broken line at 12%. For details, see text.

Table 1. Number of large herbivores (grazers and browsers) , mean daily food intake requirements (kg d.m.) in Lake Manyara National Park in 1984 and 1996, and Park size. Daily dry matter (d.m.) requirements are assumed to equal 2.5% of live weight (see Prins and Douglas-Hamilton 1990, Tables 2 and 3).

	Numbers of large grazers		Daily d.m. requirements			
			1984		1996	
	1984	1996	(kg)	(%)	(kg)	(%)
Grazers						
Buffalo	2,097	1,062	17,038	*44.6*	8,628	*31.0*
Elephant	373	199	11,097	*29.0*	5,920	*21.3*
Wildebeest	675	975	3,797	*9.9*	5,484	*19.7*
Hippopotamus	179	182	4,475	*11.7*	4,550	*16.4*
Zebra	225	335	1,406	*3.7*	2,094	*7.5*
Impala	150	500	178		594	
Baboon	500	2,000	50		200	
Waterbuck	17	49	68	*1.1*	196	*4.1*
Warthog	95	130	107		146	
Bushbuck	50	50	7		7	
Reedbuck	10	0	10		0	
Total Grazers			**38,233**		**27,818**	
			-27.2%			
Browsers						
Elephant	373	199	4,755	*68.7*	2,537	*52.9*
Giraffe	66	73	1,262	*18.2*	1,396	*29.1*
Baboon	500	2,000	175	*2.5*	700	*14.6*
Bushbuck	50	50	68		68	
Waterbuck	17	49	17		49	
Impala	150	500	9	*1.5*	31	*3.4*
Warthog	95	130	12		16	
Reedbuck	10	0	1		0	
Black rhinoceros	25	0	625	*9.0*	0	
Total Browsers			**6,924**		**4,797**	
			- 30.7%			
Total forage requirement			**45157**		**32615**	
			- 27.8%			

Among the browsers, black rhinoceros and reedbuck had become extinct in the Park. The baboon population had increased four times compared to 1984 and baboon had become, after elephant and giraffe, the third most numerous browser. The impala population had increased more than 3 times, despite the occurrence of an anthrax (pers. obs.).

The total daily forage requirement in 1996 was reduced by 30 percent compared to 1984. The proportional reduction in forage requirements was equally high for both grazers and browsers (Table 1).

In 1984 elephant and buffalo made up about 75% of the total grass forage requirements, in 1996 these grazers accounted for only half of the forage requirements

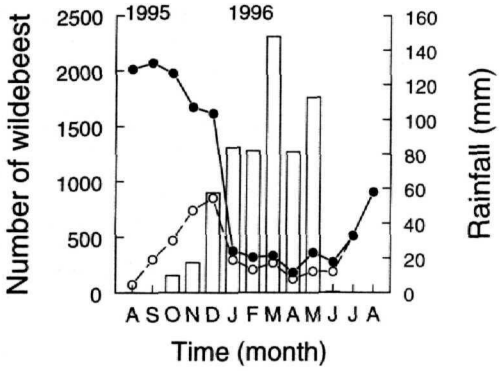

Figure 3. Monthly wildebeest numbers and rainfall in Lake Manyara National Park, Tanzania, between August 1995 and August 1996. Thick line: total population, broken line: southern population. Note, that in July and August 1996 the northern part of the Park had not been censused.

of all grazers. This decrease in daily food requirements of the combined buffalo and elephant populations by far outweighed the increase of the other grazers (Table 1).

The daily forage requirement for the wildebeest population varied between 11,250 kg d.m. in the dry season, to 1,690 kg d.m. in the wet season. The total daily requirement for all grazers in the Park was 25,755 kg d.m. in the wet season, and 35,315 kg d.m. in the dry season, when the wildebeest population reached it's peak.

Discussion

The estimates of the herbivore populations presented in this paper are minimum estimates, because the numbers are based on total counts. For the estimation of animal populations from transect censuses, random distribution of the animals within each habitat type is presumed (Prins and Weyerhaeuser 1987). Each patch of a particular vegetation type must therefore be used in the same degree, independent of its position in the landscape, and of its size. This is unlikely in Lake Manyara National Park, where surface water is not evenly distributed, relative to the home-range size of at least some of the smaller herbivore species. A second condition which has to be fulfilled when transect censuses are used is, that the presence of the animals in any habitat type should be independent of the time of the day. Buffalo ruminate during the day on the alkaline grasslands, and graze during the night (Prins 1996). Zebra was encountered in the woodlands more often during the dark than during the day, and a number of impala groups took shelter on the escarpment during the night, and descended again to the lowland at dawn (pers. obs.). Total counts, visibility permitting, are therefore good alternatives in a small, but varied area as Lake Manyara National Park.

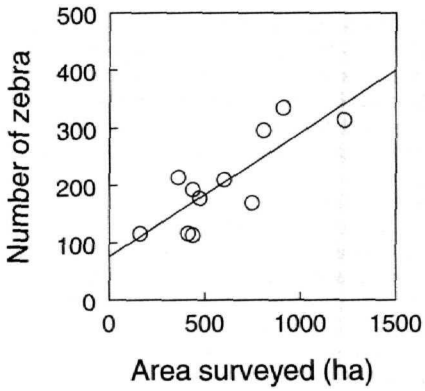

Figure 4. Monthly numbers of zebra counted in Lake Manyara National Park, in relation to the size of the counted area.

The estimate of the elephant population based on the highest count achieved on one day, augmented with animals that had immigrated after the count, was within the 95% confidence limits of the strip counts. The outcome of the two independent methods suggests that a population estimate of around 200 elephants has not been an over-estimate. The potential growth rate of 8 % p.a. agrees well with the calculation of the intrinsic growth rate of 10.2% according to the formula $1.2*W^{-0.33}$ (recalculated from Table 1 in Western (1979), and with reported growth rates of up to 9% in Uganda (Laws *et al.* 1975, Buss 1990). Under ideal (low-density) situations, however, the first ovulation may occur at the age of 8 years and the calving interval could be 3 years (Calef 1988). This yields 15.7 calves per female, which works out to a (1-1/65)(1+(7.85/55) ≈) 12% growth rate. Such a growth rate was also reported by Kerr (1978, quoted in Calef 1988) at Mana Pools National Park in Zimbabwe, after 3 years of culling operations. The 28% p.a. growth rate of the elephant population in Lake Manyara National Park between 1991 and 1996 by far exceeded the maximum possible growth rate of 12%. After the elephant population in Queen Elisabeth National Park in Uganda had been decimated during the civil war between Obote and Museveni, the elephant population recovered rapidly thanks to the birth of twins (Cynthia Moss, pers. comm). Twins have, however, not been observed in Lake Manyara National Park. The increase in numbers could have been caused by immigration into the Park. Except for the one instance in March 1996 the Park's rangers had, however, not mentioned elephant movements between the neighbouring conservation areas Tarangire National Park or the Ngorongoro Conservation Area and Lake Manyara National Park. Such movements through the densely populated areas around the Park do not go unnoticed. Alternatively, part of the Park's population could have remained out of sight during the 1991 census. Prins *et al.* (1994) censused the elephants north of Endabash River between May and November 1991. In August 1990 an arable farm was incorporated in the Park, which now forms the southern end of the Park. On the farm sugar cane was grown, a crop, which had attracted the Park's

elephants in the past. Possibly part of the elephant population had remained in this area during the 1991 census period. If immigration from distant populations is ruled out, the minimum population size in 1991 must have been about 110 elephants to arrive at a population of 200 elephants in 1996 at 12% growth rate. Unless a second bout of severe poaching had occurred between 1990 and 1991, the population estimates mentioned in other reports suggest that the elephant population in 1991 had been undercounted (figure 2).

The mean daily food intake of five grazer species: buffalo, elephant, wildebeest, hippopotamus and zebra, made up more than 95% of the total requirements of all the park's grazers. Compared to the last count of the entire herbivore population in 1984, elephant and buffalo numbers were lower, and all other grazers had increased, except for the locally extinct reedbuck. In terms of forage requirements, the other grazers did not compensate the decrease in elephant and buffalo numbers. The total grazer forage requirement was reduced by about 30%.

Despite the decline in elephant numbers, buffalo had not profited as could be expected (Prins and Douglas-Hamilton 1990). In terms of forage requirements, the decrease in elephant numbers between 1984 and 1996 could sustain about 1000 buffalo, so that, if buffalo had been able to fill up the gap left by the elephants, the size of the present buffalo population should have been close to 3000 buffalo. In stead, the buffalo population in 1996 was half the size of that in 1984.

The daily forage requirement of wildebeest during the dry season was equivalent to that of 1730 buffalo. Wildebeest exclusively graze the alkaline grasslands (pers. obs.), and during the dry season, buffalo are confined to these grasslands because other grasses are not available (Prins and Beekman 1989). When the dry season wildebeest numbers are used to calculate the daily forage requirements for the grazer assembly, the total requirement for 1996 was only 15% below that of 1984. Note that the 1984 data reflect dry season wildebeest populations, because the data had been collected during the dry season.

Competition between wildebeest and buffalo on the alkaline grasslands during the dry season could explain the lower than expected number of buffalo. Habitat overlap of buffalo and wildebeest was greatest of all pair wise comparisons between buffalo and the other main grazers. Direct competition between grazers involving buffalo as one of the grazing species could, however, not be proven because negative associations did not occur (De Boer and Prins 1990). Is it possible to explain the number of wildebeest and buffalo of earlier censuses in this context? Wildebeest were absent when the alkaline grasslands were submerged by high lake levels, and the lowest buffalo numbers occurred during high lake levels, when the data for 1961, which had been extrapolated from 1965, are omitted from table 1 in Prins and Douglas-Hamilton (1990). It is therefore conceivable that also in the past wildebeest has been a competitor of buffalo.

Prins (1987) found most buffaloes in the northern and central parts of the Park, and only a small herd in Yambi area in the south. This study shows that buffalo numbers had decreased throughout the Park, except in the southern-most part. Judging by the extreme cautious behaviour of the Yambi buffalo, these buffalo had been poached. This was in sharp contrast with the buffaloes in the northern part of the park that appeared not to be intimidated at all by the presence of vehicles. In the dry season the

northern buffalo use the *Typha* swamp at the mouth of Simba River, where *Cyperus laevigatus* abounds, and graze the *Cynodon dactylon* swards of the forest glades in the ground water forest. Wildebeest had never been observed in these habitat types. The absence of wildebeest in the southern part of the Park suggests that the current distribution of buffalo in the Park is a result of the displacement of the buffalo by wildebeest, possibly in combination with poaching.

The alkaline grasslands thus form the arena where buffalo and wildebeest contest each other during the dry season. The accessibility of these grasslands depends on the lake level. Between 1984 and 1996 all the *C. laevigatus* swards (A1 plant community) north of Endabash River had been replaced by *Sporobolus spicatus* grasslands (A2 plant community; see Chapter 3). The replacement of 97 ha of the A1 plant community by the A2 plant community resulted in a 15% loss of green standing crop of the alkaline grasslands in the northern part of the park during the dry season (calculated from table 2.2, page 40 in (Prins 1996). The available green standing crop may be even further reduced when the loss of grasslands due to bush encroachment on A3 and G2 plant communities has been taken into account (Chapter 3).

At present, the grazing pressure exerted by the herbivore biomass in Lake Manyara National Park at its peak during the dry season corresponds with the level exerted by the herbivore assembly in previous years, when migrating populations were smaller (Drent and Prins 1987, Prins and Douglas-Hamilton 1990). Wildebeest use the Park in increasing numbers as a dry season refuge (M. Voeten, pers. comm.), and make up the loss in elephant and buffalo biomass. If this is a continuing trend, then it can be expected that buffalo numbers will not increase again. Consequently, changes in the vegetation caused by altered abiotic factors ultimately determine the outcome of the competition among herbivores.

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Chapter 8

Synthesis: Scale-dependent states and transitions in the African Rift Valley

Introduction

Savannas are dynamic ecosystems, where the balance between woody species and grasses is continuously shifting to one side or the other. Changes in the state and transition model (Westoby *et al.* 1989) may occur under the influence of herbivores and fire (Frost and Robertson 1987, McNaughton 1992, Dublin 1995, Van de Vijver 1999). Geology (nutrient availability) and climate (rainfall) anchor the pivoting point.

Herbivores may influence plant communities directly by the selective removal of plant species (Furbish and Albano 1994), and indirectly, by causing reductions in top soil moisture content (Goldstein and Sarmiento 1985, Van de Vijver and Rietkerk 1998), altered nutrient cycling (Ruess and McNaughton 1988, Berendse *et al.* 1992, McNaughton 1992, Turner *et al.* 1993), or, when these resources are not limiting, by causing altered access to light (Crawley 1997), all as a result of biomass removal. Fire also removes standing biomass, altering soil moisture content (Van de Vijver 1999) and accessibility for light as a resource. Heat produced by fires stimulates seed germination of hard-seeded Leguminosae (Dell 1980, Chapter 4).

The time scale and magnitude at which the above mentioned processes operate, can vary considerably. The destruction of stands of trees by elephant, *Loxodonta africana*, in combination with fire, has been considered a key process in the conversion of *Acacia tortilis* woodlands to grasslands (Norton-Griffiths 1979, Pellew 1983, Van Wijngaarden 1985, Mwalyosi 1987, Buss 1990, Dublin 1991). On the other hand, catastrophic crashes in herbivore populations have been considered to cause sudden changes in the ecosystem. Large-scale changes in the vegetation have been interpreted as a consequence of such events, while some authors even note that without catastrophes among herbivore populations such changes would not be possible (Sinclair 1979, Prins and Van der Jeugd 1993, Dublin 1995). In this study the changes in the vegetation of Lake Manyara National Park as representative for other Rift Valley lake systems, have been regarded against the background of herbivore impact and changes in abiotic factors working at different spatial and temporal scales.

Reconstructing the past

Looking back in the past requires methods that place events in the appropriate time frame. Trees are generally the longest living components in the landscape, and consequently, trees are often used to reconstruct historical events that have occurred in the landscape. In temperate zones, the alternation of growing and non-growing seasons is reflected in the formation of annual growth rings. The characteristics of the growing season can be deducted from the thickness of these growth rings (Fritts 1976, Hughes *et al.* 1982, Woodward *et al.* 1994). In the tropics, seasonality occurs generally in water availability, rather than in temperature. Differences in growing seasons are not as evident as in the temperate zones –at least not for deep-rooting plants. In tropical rain fed agriculture, growing seasons and rainy seasons are often synonyms, because annual crops with shallow rooting systems use water from the topsoil only, replenished by rainfall. Tree roots reach much deeper, and because trees and grasses use different soil layers for their water resources, trees and grasses can coexist (Walter 1971). Although trees may compete with grasses for water in the upper soil layers (Belsky 1994), fluctuations in soil water availability are dampened with increasing depth, until

soil water is permanently available. In all likelihood *A. tortilis* trees have permanent access to water in deeper soil layers, considering the fact that, after the trees have shed their leaves during the dry season, the new leaves are formed *before* the onset of the rains (pers. obs.). Despite the year-round water availability, growth rings in *A. tortilis* are formed according to rainfall distribution; one marginal parenchyma band is formed in areas with unimodal rainfall distribution, and two in areas with a bimodal rainfall distribution. These marginal parenchyma bands are, however, not readily seen, and often not found in stem discs (Chapter 6). In this study a different method was therefore used to determine tree age. I assessed the age of a tree immediately after a tree was cut by counting the number of bands that are formed by the repetitive pattern in parenchyma band thickness. The method was calibrated by comparing the number of periods counted with the age of old- fields, but needs additional verification with big trees from undisturbed soils. The presence of clear banding in cut branches of two trees in the Park in this respect is promising.

Lake Manyara National Park

In this thesis the changes in the vegetation of Lake Manyara National Park in northern Tanzania are viewed against the background of herbivore impact and changes in abiotic factors. Lake Manyara National Park is, however, not representative for all East African savannas, but is a model for the Rift Valley lake systems, such as Lake Eyasi, Lake Natron, Lake Nakuru, and others. Due to its position between the steep escarpment of the rift valley and the soda lake (Chapter 2) the area experiences exceptional circumstances. Up to 800 to 1000 mm annual rainfall, primary production in grasslands is primarily determined by rainfall (Coe *et al.* 1976, Lauenroth 1979, Deshmukh 1984), especially in eutrophic soils (East 1984). At higher rainfall amounts, other site-specific factors –nutrients- become more important (Scholes 1991). Lake Manyara with its 640 mm of rainfall has the highest herbivore biomass of Africa, and this is much larger than can be expected on the basis of annual rainfall (Coe *et al.* 1976). The high primary production in the park with high forage quality (Prins 1996) is sustained by year-round water availability, fed by seepage and underground water flows. Surface water for the park's animals is widely available due to the numerous rivers draining in the lake, and the presence of plentiful springs. Water infiltrating the forested slopes of the Ngorongoro Crater emerges via numerous springs at the foot of the escarpment in the northern part of the park. Water from these springs supports the groundwater forest in the northern part of the park, where the groundwater remained within 6 m depth (pers. obs.). Hot springs, emerging at the foot of the escarpment about halfway the park, support extended marshes of *Cyperus* grass. Elsewhere between the escarpment and the lakeshore groundwater is relatively close to the surface, and is thought not to exceed 20 m (Chapter 3).

The lake has no outlet and salts leached from volcanic material that was formed during, and after the formation of the Rift, have accumulated in the basin area. The shallow and saline Lake Manyara may dry out almost completely after a period of low rainfall, although the perennial rivers in the north and the south ends of the lake maintain swamps where they enter the lake. Salt tolerant grass species can grow on the lakebeds, but because the grasses do not tolerate flooding, the expanse of the grass

swards fluctuates with the lake level. Extreme high lake levels occasionally occur, submerging higher elevated areas.

Fluctuations in lake levels, groundwater levels, and associated salinization and de-salinization processes appear to be of key importance in understanding vegetation changes in these Rift Valley systems (Chapter 3). My study shows that not only grasses react to these fluctuations, but the tree *A. tortilis* too.

Acacia tortilis

Apart from its importance as a bio-indicator for processes in the past, *A. tortilis* is of significance because of its prominence in the Rift Valley ecosystems, and as a major food source for wildlife and livestock. *A. tortilis* establishment depends on the presence (or better: absence) of vegetation. Underneath tree canopies, *Acacia* establishment does not occur (Chapter 5), even though seeds may germinate there (Chapter 4). Germination and establishment in grass swards is less successful than in bare soil patches (Chapter 4 and 5). Seeds of *Acacia* spp with indehiscent pods end up underneath the parent trees, unless they are dispersed by herbivores (Coe and Coe 1987, Miller and Coe 1993, Miller 1994). Pod ingestion by herbivores enhances the viability of the ingested seeds, because during the passage of the seeds through the gastro-intestinal tract bruchid larvae in the seeds are killed (Lamprey *et al.* 1974, Halevy 1974).

A. tortilis seedlings growing in shade and seedlings that are clipped have reduced growth, both above and below ground (Chapter 5). I suggest that root growth is the key factor determining successful *Acacia* establishment, because the plants must have reached freely accessible soil water before the end of the dry season, to make it possible that plants shed their leaves and form new leaves before the onset of the new rains.

The opening up of the Acacia woodlands since the 1960s by the debarking behaviour of the elephants (Douglas-Hamilton 1972, Mwalyosi 1987), appears to speed up the cyclic rejuvenation of the woodlands. *Acacia* regeneration will not occur in closed-canopy woodlands, but only after gap formation, as long as the herbivore density in the Park remains high enough to prevent the formation of perennial grass swards in the gaps. In bare patches, *Acacia* regeneration is possible, because the situation is favourable for germination (Chapter 4) and seedling establishment (Chapter 5) and seed is present in the seed bank. I estimate that it takes an *A. tortilis* tree about eight to ten years to develop into an adult tree (producing pods), although the canopy of trees of that age may not have developed into the typical flat-topped shape yet.

The study shows that in these Rift Valley systems edaphic factors and their fluctuations in time and space are at least as important as fluctuations in herbivore pressure to understand the dynamics of these ecosystems. Indeed, the occurrence of bare patches is not only caused by elephants and other herbivores, but also by the fluctuations in water levels and salinity. Abiotic and biotic fluctuations in the African Rift Valley systems may have different cycle duration and affect different expanses of land (Chapter 2, 3 and 7).

Scale-dependent changes

Fluctuations in the lake level submerge the grasslands with a frequency of approximately once every two years there where *Psilolemma jaegeri* grows, and approximately five years in the *Cynodon dactylon* zone (Chapter 2). These fluctuations thus cause changes in the exact location of the species within these grasslands on the spatial level with the finest grain (figure 1). Patches of *Cyperus laevigatus* marsh disappeared between 1982 and 1995 as a result of lowering groundwater tables, which process started about half a century ago by the removal of the natural vegetation on the Mbulu Plateau, west of the Park. If the hydrology of the Park has changed permanently, it must be feared that the *Cyperus* marshes have permanently vanished too.

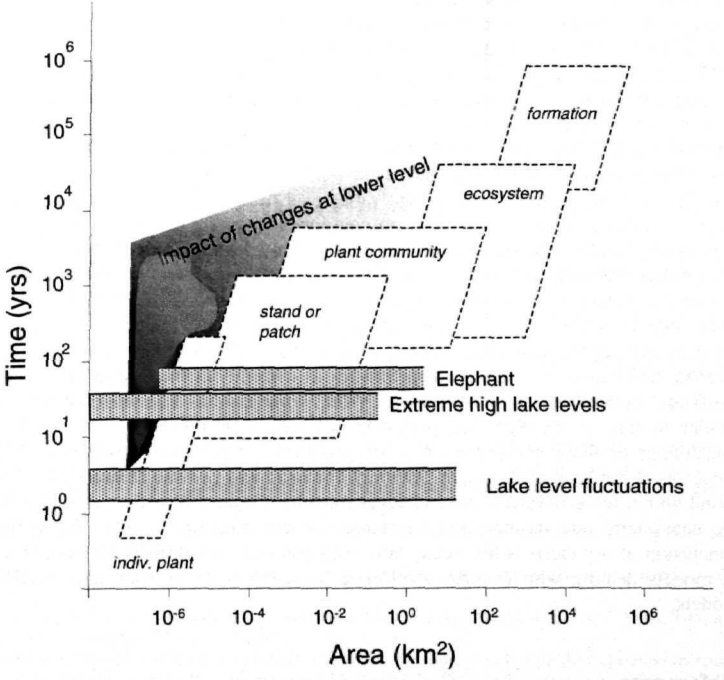

Figure 1. Changes at different spatial and temporal scales of vegetation patterns. High-frequency disturbances cause changes at the finest spatial scales, disturbances with lower freqencies affect larger areas. The effect of changes occurring at fine-grained scales decreases with increasing scale. Changes at the highest level (formations, e.g. savanna), may take hundreds of thousands of years.

The replacement of the high bulk density *C. laevigatus* marshes by saline tolerant grass species with lower bulk density as a result of the lowering groundwater table, has contributed to the decline of buffalo numbers in the park (Chapter 7). Until the late 1980s, buffalo and elephant were the most important grazers in the park, and the two species were competitors. The decline in grazing pressure by one species was compensated by the other (Prins and Douglas-Hamilton 1990). Elephant numbers in the 1980s declined rapidly, due to poaching. Contrary to expectations, however, the buffalo population did not fill the gap. In stead, wildebeest appears to have stepped in as the major competitor of buffalo. Despite the fact that also poaching of buffalo has taken place, it appears that the dynamics of the buffalo and the wildebeest interaction has to be understood as a consequence of patch-level dynamics, namely, the dynamics of the *C. laevigatus* patches. Dynamics at the patch level is thus carried over onto the level of the ecosystem (figure 1). Indeed, the herbivore assemblage of Lake Manyara National Park seems to be changing as a result of the loss of a large area of an important dry-season forage plant community (Chapter 7).

Woodland gap dynamics is due to processes of tree mortality (Chapter 6 and 7) and seedling establishment (Chapter 4 and 5). Recolonization by *Acacia* trees is at a time scale of 20 to 50 years (Chapter 5 and 6), and at a spatial scale of one to ten hectares (Chapter 2 and 3). This study clearly indicates that within the Manyara landscape, and thus at the level of the ecosystem, patches or stands of *A. tortilis* always occur, but the exact location and stage of development varies over time. Thus the opening up of the *Acacia* woodlands by elephants is of no consequence for the existence of the plant community, let alone for the integrity of the ecosystem. Also in Tsavo National Park in Kenya, Van Wijngaarden (1985) found that the plant community remained intact, despite the change from woodland to grassland caused by elephants. At the ecosystem level, with its very long time scale of tens of thousands of years, the dynamics of patches may appear to be insignificant. Indeed, the Olduvai Gorge, now an empty lakebed, had similar vegetation characteristics as currently is found at Manyara, and the faunal assemblage as demonstrated by the world famous Laetoli footprints was similar to that of the Rift Valley systems of today. However, to understand the functioning of these ecosystems it is of paramount importance to understand the processes at the level of the patch. Although faunistic and floristic changes have been found within the ecosystem, these changes must be considered as fluctuations within the ecosystem, and do not lead to change of the ecosystem itself. The general conclusion of my thesis is that scale, both temporal and spatial, must be incorporated in models dealing with changes (with)in ecosystems, such as state and transition models.

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Summary

Changes in vegetation can be either directional or successional, that is, away from an initial stage, or changes are reversible fluctuations. Currently, many empirical studies and models emphasize the impact of herbivory on vegetation. A lot of studies are showing interest in changes and their causation. An important school of thought deals with a family of models focussed on 'states' and 'transitions'. The character of changes in vegetation depends, however, on the scale, both temporal and spatial. Changes at the level of the individual plant occur in a short time span. At increasing spatial scale, from patch or stand level, via the level of plant communities, the ecosystem level, and finally, to the level of formations, it takes longer for systems to change. In this study, the temporal and spatial scale dependency of changes in vegetation was investigated in Lake Manyara National Park, in the Rift Valley of northern Tanzania. Lake Manyara National Park is taken as a model for many other alkaline lakes in the Rift Valley, such as Lake Nakuru in Kenya, and the Lakes Natron and Eyasi in Tanzania. In addition, long-term data on vegetation and herbivore populations are available of this Park. The thesis starts at the landscape level, continues at the individual level, and via stand level returns to the landscape level. The study concentrated on the dynamics of the *Acacia tortilis* woodlands because this tree is characteristic of East African savannas and because of its important role in plant-animal interactions (Chapter 1).

In Chapter 2 the spatial patterns of the vegetation are described and presented in a vegetation map at a scale 1:50,000. The results are based on a landscape ecological survey, in which both terrain aspects and the vegetation are used to define the units in the landscape. The species composition and the vegetation structure are separately indicated, because these aspects of the vegetation may change at different time scales.

Due to the position of the Park between the steep wall of the Rift Valley and the shallow alkaline Lake Manyara, a dynamic abiotic environment exists, as is further examined in Chapter 3. The fluctuating lake level perpetuates the extreme physiological environment near the lakeshore, where only few grass species can grow. Higher up the shore sporadic high lake levels can cause cyclic changes in the vegetation. Woodlands emerge at places with sandy soils where salts have sufficiently been leached out after flooding, but these woodlands are destroyed again by the next period of high lake levels. Reduced groundwater flows have resulted in the loss of a forage species that is especially important during the dry season for buffalo. Because these changes in groundwater level are related to altered vegetation cover elsewhere, caused by human activities, these changes are unlikely to be reversed in the near future.

In the recent past elephants opened up the *Acacia tortilis* dominated woodlands at such a rate that a permanent loss of these woodlands was feared. The number of trees in the regeneration class has, however, since the time of worry increased. As is shown in Chapters 4 and 5, the impact of elephants on the woodland dynamics accelerates the woodland cycle. At the level of individual plants, *Acacia* trees can establish most successfully at bare patches. In patches of bare soil conditions for the temperature and moisture regulated germination are better than in vegetated patches. On these patches

seedlings survived longest, due to the absence of light competition and competition for soil moisture in the upper soil layer. Root growth rate is the key factor for successful establishment, because the roots must have reached permanent available soil water before the dry season is at its worst and the top layers of the soil have dried out.

Continuing at the stand level (Chapters 5 and 6), elephants opened up the *Acacia* woodlands, creating opportunities for the establishment of new trees. Although on the stand level elephants are able to change the structure of the vegetation in a relatively short period of time, on the long-term the woodland plant communities will remain unchanged.

The occurrence of *Acacia tortilis* trees in age cohorts on old-fields (Chapter 6) was used to determine growth rates. Tree growth is density dependent. Consequently, the existence of *A. tortilis* age cohorts throughout East African savannas, that is, at the ecosystem level, cannot be reliably related to crashes in herbivore populations. At the ecosystem level (Chapter 7), changes in the herbivore assemblage do not result in any changes in the vegetation. On the contrary, the composition of the herbivore assemblage appears to be determined by the vegetation.

In Chapter 8 it is argued that changes in vegetation are scale dependent, both in time and space, whereby changes within an ecosystem do no lead to changes in the ecosystem itself. It is proposed that scale, both temporal and spatial, is to be incorporated in state and transition models.

Samenvatting

Veranderingen in de vegatatie zijn hetzij gericht of successief, dat wil zeggen, een ontwikkeling vanuit een beginstadium, hetzij omkeerbare schommelingen. Tegenwoordig zijn er nogal wat empirische studies die de invloed van herbivoren op de vegetatie benadrukken. Veel studies gaan in op de oorzaken van veranderingen binnen de vegetatie. Een belangrijke gedachtenschool houdt zich bezig met een groep van modellen die gebaseerd zijn op toestanden (*'states'*) en veranderingen (*'transitions'*). De aard van veranderingen binnen de vegetatie hangt echter af van de schaal, zowel ruimtelijk als in tijd, waarom men de vegetatie beschouwd. Veranderingen op het niveau van de individuele plant gebeuren binnen een korte tijd. Naarmate de ruimtelijke schaal toeneemt, vanaf een veld of bossage, via het niveau van de plantengemeenschappen, het niveau van het oecosysteem naar, tenslotte, het niveau van formaties, duurt het langer voordat deze eenheden veranderen. In dit onderzoek is de temporele en ruimtelijke schaalafhankelijkheid van de veranderingen in de vegetatie onderzocht in het Nationale Park Lake Manyara, gelegen in de de Grote Afrikaanse Slenk in het noorden van Tanzania. Het Nationale Park Lake Manyara staat model voor de vele andere soda-meren in de Grote Slenk, zoals het Nakuru Meer in Kenia en de meren Natron en Eyasi in Tanzania. De keuze van dit Nationale Park als studiegebied is mede ingegeven door het feit dat al veel informatie over vegetatie en de herbivoor-populaties beschikbaar is. In dit proefschrift worden de resultaten van het onderzoek eerst op landschappelijk niveau gepresenteerd. Daarna worden processen die een rol spelen op het niveau van de individuele plant beschreven, vervolgens die op het niveau van een veld of bossage om uiteindelijk weer uit te komen op het niveau van het landschap. Het onderzoek richtte zich met name op de dynamiek van het *Acacia tortilis* bos, niet alleen omdat deze karakteristiek boom een belangrijke plaats inneemt in de Oost Afrikaanse savannes, maar ook vanwege de belangrijke rol die deze boomsoort inneemt in plant-dier interacties (Hoofdstuk 1).

In Hoofdstuk 2 worden de ruimtelijke vegetatiepatronen van het Nationale Park Lake Manyara beschreven, en gepresenteerd als een vegetatiekaart met een schaal 1:50.000. De resultaten zijn gebaseerd op een landschapsoecologische kartering, waarbij zowel terreinaspecten als aspecten van de vegetatie gebruikt zijn om de landschapseenheden te definieren. De soortensamenstelling en de structuur van de vegetatie zijn afzonderlijk aangegeven, omdat deze vegetatie-aspecten op verschillende tijdsschalen kunnen veranderen.

Vanwege de ligging van het Park tussen de steile wand van de Grote Slenk en het ondiepe soda meer Manyara bestaat er een dynamisch milieu, wat verder uiteen gezet wordt in Hoofdstuk 3. Dankzij de voortdurend wisselende waterstanden van het meer wordt het extreem fysiologische milieu in stand gehouden, zodat er slechts enkele grassoorten kunnen groeien. Op de hoogst gelegen delen van de meeroevers kunnen sporadisch voorkomende, extreem hoge waterstanden cyclische veranderingen in de vegetatie veroorzaken. Bossen ontstaan op plekken met zandige bodems waar zouten uit de bodem gespoeld zijn sinds de laatste overstroming, maar die zullen weer verdwijnen zodra het basische meerwater, wat een hoog zoutgehalte heeft, tijdens de volgende extreem hoge waterstand deze plekken weer overspoelt. Voortdurende

afname van grondwaterstromingen hebben geresulteerd in het verdwijnen van een grassoort, welke vooral tijdens het droge seizoen een belangrijke voedselbron voor buffels is. Deze veranderingen in groundwaterstromingen kunnen in verband gebracht worden met de verwijdering van de natuurlijke vegetatie ten behoeve van de landbouw buiten het Park. Het is niet waarschijnlijk dat in de nabije toekomst hierin verandering zal komen

Nog niet eens zo lang geleden verwoestten olifanten *Acacia tortilis* bomen met zo'n snelheid, dat gevreesd werd dat de *Acacia* bossen in het Park geheel zouden verdwijnen. Het aantal bomen dat de gesneuvelde bomen vervangt is sindsdien aanzienlijk toegenomen. In Hoofdstuk 4 en 5 is aangetoond dat het enige effect dat olifanten hebben op de dynamiek van deze bossen een versnelling is van het vervangen van oude bomen door nieuwe. Op het niveau van de individuele boom blijkt dat Acacia's zich vooral op kale plekken kunnen vestigen. Kieming van Acacia zaad wordt vooral bepaald door temperatuur en vochtigheid. Op kale plekken zijn deze condities voor zaadontkieming gunstiger in vergelijking met met plaatsen waar vegetatie aanwezig is. Hier overleven zaailingen ook het langst, omdat er geen concurrentie om licht is en ook concurrentie om het beschikbare vocht in de bovenste laag van de bodem ontbreekt. De snelheid waarmee wortels kunnen groeien is de belangrijkste factor die bepaalt of een boom zich uiteindelijk kan vestigen. Immers, omdat de wortels van het kiemplantje moeten al voordat het natte seizoen is afgelopen toegang gevonden hebben tot permanent beschikbaar bodemvocht.

Voortgaand op het niveau van het bossage (Hoofdstukken 5 en 6) blijkt, dat olifanten door de Acacia bossen te openen juist de omstandigheden hebben geschapen voor de vestiging van nieuwe bomen. Hoewel olifanten weldegelijk in staat zijn om in een mum van tijd individuele toefjes bomen volledig op te ruimen, heeft dit op de lange termijn geen effect op het bestaan van de plantengemeenschappen van deze bossen.

Het voorkomen van *Acacia tortilis* bomen in diverse leeftijdsklassen op verlaten landbouwgronden was gebruikt om de groeisnelheid van deze bomen te bepalen (Hoofdstuk 6). De groeisnelheid is afhankelijk van de dichtheid van het bos. Daardoor kan het bestaan van Acacias in leeftijdsklassen in de Oost Afrikaanse savannes, dus, op het niveau van het oecosysteem, minder vanzelfsprekend in verband gebracht worden met ineensortingen van herbivoren populaties, dan eerder wel is verondersteld. Immers, deze beweringen zijn gebaseerd op de aanname dat alle Acacias met dezelfde snelheid groeien. Verder blijkt (Hoofdstuk 7), dat veranderingen in de samenstelling van de herbivorenpopulaties geen enkele blijvende invloed hebben op de vegetatie. Integendeel, veranderingen in de vegetatie blijken eerder de herbivoren-populaties te beinvloeden.

In het laatste hoofdstuk (Hoofdtstuk 8) wordt beargumenteerd dat veranderingen in de vegetatie schaalafhankelijk zijn, terwijl veranderingen binnen een oecosysteem niet leiden tot veranderingen van het oecosysteem zelf. Ik stel voor dat schaal, zowel ruimtelijk als temporeel, in de zogenaamde 'state and transition' modellen wordt opgenomen.

Curriculum Vitae

Paul Loth was born on 17 September 1954 in Pijnacker, the Netherlands. He holds a BSc ('Kandidaats Diploma') in Biology of Wageningen University (1973 –1977), and a MSc ('Doctoraal Diploma') in Biology of the University of Groningen (1977 – 1983), with ecology as the main subject. He obtained a post graduate diploma 'Rural Survey' at the International Institute for Aerospace Survey and Earth Sciences (ITC) in Enschede, the Netherlands (1983. During his study he spent one year in Surinam, where he participated in a primate research project. His first experience in Africa was in Tanzania in 1982, when he made a vegetation map of Lake Manyara National Park.

Between 1985 and 1988 he worked in Kenya for the United Nations Environment Programme (UNEP) in a project liased with the National Geographical Society. In this project he carried out a vegetation survey of Kora Game Reserve. Furthermore he was responsible for the preparation of guidelines to carry out vegetation surveys, and of the training of personnel. While in Kenya he did consultancies for the African Wildlife Foundation (AWF) and the Primate Research Institute of the National Museums of Kenya. In 1988 he went to Zimbabwe in employment of the Food and Agricultural Organization of the United Nations. There he worked as a remote sensing expert in an early warning for food security project covering the southern African countries until 1994.

In 1994 he started his PhD study, financed by WOTRO, in Lake Manyara National Park, where he spent two and a half years for field work.

Paul is married and has two daughters.

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This map is available in colour at the website:
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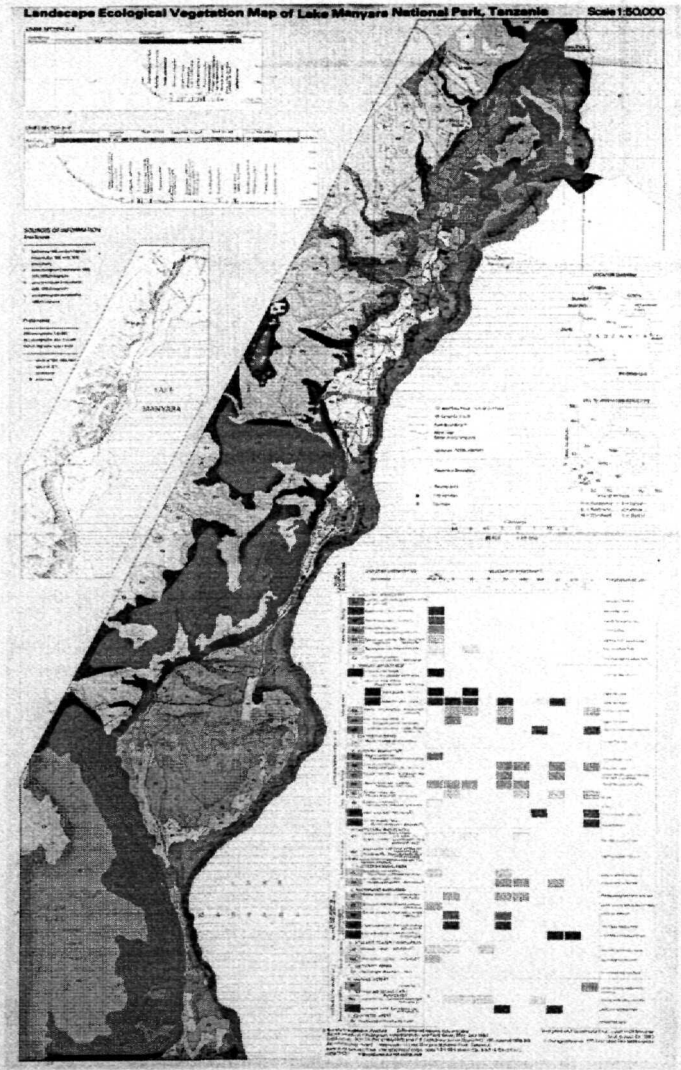

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