Fire and Life in Tarangire

Effects of Burning and Herbivory on an East African Savanna System



Promotor: Dr. H.H.T. Prins

hoogleraar in het natuurbeheer in de tropen en de ecologie van vertebraten

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Proefschrift ter verkrijging van de graad van doctor op gezag van de rector magnificus van de Wageningen Universiteit, dr. C.M. Karssen in het openbaar te verdedigen op dinsdag 21 september 1999 des namiddags te vier uur in de Aula

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Stellingen

behorende bij het proefschrift: Fire and Life in Tarangire, Effects of Burning and Herbivory on an East African Savanna System.

- I. De interactie van vuur met het biotische en abiotische milieu bepaalt, meer dan vuur zelf, de effecten ervan op savanne systemen (*dit proefschrift*).
- **II**. Vuur wordt heden ten dage steeds minder doeltreffend als middel voor savanneweidebeheer (*dit proefschrift*).
- III. In Afrikaanse savannes kan vuur zowel een oorzaak van struikopslag zijn als een middel ter beheersing ervan.
- IV. Met het vuur in de hand begon de destructieve invloed van de mens op zijn omgeving.
- V. De economische malaise van veel Afrikaanse landen is in niet onbelangrijke mate mede een gevolg van het protectionisme van Westerse regeringen ten gunste van de eigen economie.
- VI. Het pad van de persoonlijke verantwoordelijkheid wordt licht verlaten voor de zijweg van het eigenbelang.
- VII. Door de preoccupatie met geld verdienen in de wereld van vandaag draagt de voortgang van de wetenschappen eerder bij tot de welvaart dan tot het welzijn van mensen.
- VIII. Er bestaat een positieve correlatie tussen de lengte van de naam van een onderzoekschool en de politieke complexiteit van zijn ontstaan en ontwikkeling.
- IX. Een stellingenoorlog is strategisch gezien nooit aantrekkelijk.
- X. Ondanks alle natuurschoon is het wandeltempo van een bioloog in een wildpark in Afrika significant hoger dan in de hortus botanicus.
- XI. Rokende savanne ecologen verhogen het brandgevaar in savannes niet.

Claudius van de Vijver Wageningen, augustus 1999

To my mother, from whom I learned so much about the important things in life

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Abstract

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This thesis investigates the effects of fire on quality and quantity of forage for grazers in the savannas of East Africa whereby the mechanisms that cause the effects, as well as the manner in which the effects are influenced by abiotic conditions, are also discussed. Generally fire enhances the quality of forage with higher concentrations of mineral nutrients, higher digestibility and improved structural vegetation characteristics that determine forage intake. Increased nutrient concentrations in post-fire regrowth can be ascribed to higher leaf:stem ratios, rejuvenation and reduced dilution of nutrients due to lower levels of standing biomass as compared to unburned vegetation. Forage available for grazing is not enhanced through fire. Rather, especially in growth seasons of below average rainfall, the availability of forage is reduced in the post-fire growth season. With water being the prime determinant of plant growth in these systems, reduced vegetation production after burning can be explained by the reduction of soil water content as result of vegetation litter removal, which increases loss of water through evaporation. This negative effect of fire on forage availability can have dire consequences for both domestic and wild herbivore populations when no areas are available with additional resources. With increased human activity in the East African savanna biome, causing a decline in natural/pastoral areas as well as an increase in grazing intensities and fire frequency, results suggest that the practice of burning should be reduced rather than advocated, especially because grazing itself improves forage quality. This thesis also shows that wildlife concentration in protected areas, particularly elephants, and high fire frequencies, also due to increased human activities, affect the tree structure but not the density. Restriction of wildlife habitat to protected areas which lie in the dry season range will however have large consequences for migratory herbivore population numbers due to insufficient quality and quantity of forage.

Key words: fire, savanna, forage quality and quantity, water, nutrients, wildlife compression, trees, East Africa.

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Chapter 1

General Introduction

Global fire, past and present

The history of our living planet earth is hardly intelligible without the history of fire (Pyne 1995). With oxygen and carbon fuel as essential elements for combustion and lighting, volcanic eruptions, sparks from falling rocks and spontaneous combustion as sources of ignition, terrestrial vegetation has been swept by fire since at least Mesozoic times (Pyne 1995). In the mid-Tertiary the frequency of fire increased significantly due to an increasing dominance of highly productive and easily flammable graminoid species (Whelan 1995, Bond and Van Wilgen 1996). The deleterious effects of fire on the herbaceous and woody vegetation component additionally contributed to the formation of graminoid dominated vegetation types (Vogl 1974). However, with the civilisation of mankind and the consequent increase in fire frequency, fire more and more became a determinant of many terrestrial ecosystems (Gill 1975, Pyne 1995, Whelan 1995, Bond and Van Wilgen 1996).

Fire can be seen as one of the largest anthropogenic influences on terrestrial ecosystems after urban and agricultural activities (Schüle 1990, Bond and Van Wilgen 1996). Particularly in the past century the extent of biomass burning has increased significantly and has resulted in 10 to 16 million km² of land burning annually in present times (Levine 1991). This world-wide biomass burning accordingly produces some 40% of the world's annual production of CO_2 (Table 1) and also significantly accounts for the production of other greenhouse gasses such as CO (32%), methane (10%), tropospheric ozone (38%) and over 86% of black soot (Crutzen and Andreae 1990, Levine 1991).

Table 1: Estimates of annual global biomass burning	; and resulting Carbon and CO ₂ release. (Total
area of the systems mentioned from Goudriaan and	I Ketner 1984, burned area and biomass and
emission data from Crutzen and Andreae 1990, Levine	1991, Bond and Van Wilgen 1996, Goldammer
1997).	

	Total area	Area burned	Biomass burned	C-release	CO ₂ -release
	(10 ⁶ ha)	(10 ⁶ ha)	(10 ⁶ tons)	(10 ⁶ tons)	(10 ⁶ tons)
Agricultural waste		-	2 020	910	-
Fuel wood	-	-	1 430	640	-
Charcoal	-	-	20	30	-
Boreal & temperate forests	1 650	10 - 15	280	130	-
Tropical rainforest	1 450	20 - 40	1 260	570	-
Savanna total	2 250	500 - 1 000	3 700	1 660	6 070
Savanna Africa	1 200	300 - 600	2 000	1 000	3 280
Total	-		8 710	3 940	13 500
All Anthropogenic sources		-'	-	-	33 700
(including fossil fuels)					

The extent and frequency of fire, however, are not evenly distributed among terrestrial ecosystems. Fire frequency can range from annual burning in grassland systems to once every 1000 years in the arctic tundra, while some systems never burn as for example the Antarctic (Whelan 1995). As can be seen in Table 1 most of annual global biomass burning occurs in the tropics. Although the amount of biomass burned per unit area in tropical forests is approximately 8 times higher than in savannas, the savanna biome accounts for most of the annually burned global biomass and the consequent CO_2 release. This is not only due to the fact that 15% of the world's land surface is savanna but also due to the high susceptibility of savanna vegetation to fire with the result that more than 40% of savanna areas burn annually (Bond and Van Wilgen 1996). This high fire susceptibility is related to the predominance of productive, easily flammable graminoid species, a distinct seasonality of rainfall with pronounced wet and dry seasons, and the presence of various natural and anthropogenic sources of fire in the savanna biome (Komarek 1972, Bond and Van Wilgen 1996).

Table 1 also shows that the African continent accounts for most of the area and biomass burned in the world's savannas (Komarek 1976, Levine 1991). Because more than 40 % of Africa belongs to the savanna biome and up to 50% of the African savanna burns every year (Hao and Liu 1994), Africa is recognised as the "fire continent" or "burn centre" of our planet (Komarek 1972). The magnitude of fire in Africa is certainly not limited to recent years. Early Portuguese explorers who rounded Africa in the 15th century already recorded large smoke columns coming from the interior and gave Africa the name "Terra dos fumos" (Phillips 1974, Scott 1972).

Fire in African savannas

For millennia fire has been a common, natural phenomenon in African savanna systems and can be seen as one of the determinants of savanna ecosystem structure and functioning (Walker 1981). Natural sources of fire are lightning, volcanic eruptions and sparks from falling rocks. Of these natural sources of fire lightning is by far the most important (Komarek 1972, Goldarnmer 1991, Clark and Robinson 1993). The combination of fusain (fossil charcoal) and fulgarite (fused inorganic material that is formed when lightning strikes the ground) that are found in coal beds of the Palaeozoic, Mesozoic and Tertiary periods, is evidence of large burning events in prehistoric times due to lightning (Harris 1958, Komarek 1972). Some savanna areas in Africa experience more than 100 lightning days per year (Komarek 1972). This high frequency of lightning on the African continent is related to the fact that Africa is the world's hottest continent where evapotranspiration rates generally exceed precipitation. The hot, moist air rises and is replaced by cold air. As a consequence large-scale atmospheric circulation patterns above Africa bring together the three ingredients for lightning: hot, cold and wet air (Komarek 1972).

Although natural fires affected savanna ecosystems, the role of fire became more prominent with the advent of anthropogenic fire (Bond and Van Wilgen 1996). It has been postulated that hominids in Africa first mastered fire over 1 million years ago (Brain and Sillen 1988, Schüle 1990, Hoffman 1997). Yet the earliest possible evidence of the use of fire by man in Africa, found at the old Kalambo site on the borders of Tanzania and Zambia, is from no more than 50,000 to 60,000 years ago (Brain and Sillen 1988). Here carbon dating of charcoal shows that fire was used in the Early Stone Age Industries which flourished more than 53,000 years ago (Clark 1959, Hoffman 1997). Even though the Early Stone Age societies may have been able to guard and transport fire, various lines of investigation support the belief that the actual making and control of fire are no more than 12,000 years old (Stewart 1956, Clark 1964). It is assumed that up to five thousand years ago man used fire for warmth, protection, cooking, honey gathering, tool-making, hunting purposes and to protect their own settlements from wildfire (Clark 1964, West 1972, Schüle 1990, Sutton 1990). Actual evidence regarding the use of fire, however, only exists for food processing (Sutton 1990). The extent of anthropogenic fire in these times must be presumed to be comparable to natural fires because of the small human population size and hence a low recurrence of fire (Komarek 1967, Pratt and Gwynne 1977, Gillon 1983).

However, with the advent of pastoralism and agriculture in African savanna systems some 5000 years ago, anthropogenic fires are likely to have increased significantly (Komarek 1967, West 1972, Pratt and Gwynne 1977). The practice of burning in pastoral and agricultural areas in historic times can be assumed to be similar to present day practices. Agriculturists use fire to clear land for cultivation or to remove old stubble while pastoralists use fire to remove old and moribund material, to create green regrowth, to reduce the cover of bush (Gillon 1983) and to reduce the infestation of pests such as ticks (Spickett et al. 1992). In many areas these burning practices even led to the formation of so called "derived" or "anthropogenic savannas" at the expense of more forested areas (Lind and Morrison 1974, Gillon 1983, Werger 1983, Tutin and White 1998). Together with the increase in human populations in the African savanna biome the extent of fire also increased, reaching present day levels where over 90% of all African savanna fires are of anthropogenic origin (Bond and Van Wilgen 1996). The extent of fire in the savanna biome of present day Africa is illustrated by Figure 1, the dark areas being the areas burned in 1993 as recorded through satellite imagery. It is additionally demonstrated by Kendall et al. (1997) who recorded more than 35,000 fires in Africa south of the equator in August 1989. All these fires in the African savanna biome contribute up to 27% of the Global CO_2 emission through biomass burning (Lacaux et al. 1993).



Figure 1: Distribution of fires in Africa in 1993. The image is composed of daily images derived from the NOAA-11 AVHRR satellite. Each image had a resolution of 1 km. (Data from http://shark1.esrin.esa.it/FIRE/fire.html).

At present the extent of fire in African savanna systems is not much different from that in savannas in other continents. A main distinction from other savanna systems is the concurrence of fire and herbivory in African savannas and the antiquity of this concurrence (Schüle 1990). Although large mammalian herbivore populations occurred in other continents, they strongly declined at the end of the Pleistocene. In Africa, however, they largely remained to exist (Eisenberg 1981, Prins 1998) and, to this day, large and diverse mammalian herbivore populations inhabit the African continent. This certainly applies to the savannas of East Africa that are characterized by the highest concentration and diversity of mammalian herbivores in the world (Prins and Olff 1998). Hence, in addition to the two abiotic determinants of African savannas, soil water and nutrient supply, herbivory and fire have also affected the structure and functioning of East African savanna systems for millennia (Vesey FitzGerald 1972, 1973, McNaughton 1985, Prins 1989).

Fire and herbivory in East African savannas

The high density and diversity of mammalian wildlife in East African savanna systems has been ascribed to the high concentration of mineral elements found in these soils of volcanic origin, phosphorus in particular (Medina 1987). Additionally, facilitation (Vesey-FitzGerald 1960, De Boer and Prins 1990) and resource partitioning between herbivores (Jarman and Sinclair 1979, Voeten and Prins 1999) may also be of significant importance. Although these systems can carry such large amounts of animal biomass, resource supply is both spatially and temporally heterogeneous due to spatial and temporal variability in rainfall, soil nutrients and fire. It is argued that this heterogeneity has led to the development of migratory systems which can be found in the East African savannas with large herds of grazing animals, wildebeest and zebra in particular, migrating from wet to dry season ranges annually (Sinclair and Arcese 1995).

Besides abundant wildlife populations, the nutrient rich and productive East African savannas also allowed for the establishment of numerous pastoral economies (Marshall 1994). These economies are presumed to have first entered East Africa some 4000 years ago, coming from the western foothills of the Ethiopian Plateau (Sutton 1990, Smith 1992, Marshall 1994, Prins 1999). These pastoralists were also confronted with resource heterogeneity and they too adopted a nomadic lifestyle related to resource availability (Homewood and Rodgers 1991).

For pastoral people to maintain their pastoral economies it was necessary to prevent vegetation to become too dense for grazing (Smith 1992). Thus, in the stages of establishing and maintaining a pastoral economy in an area of low cattle density, it was essential to burn vegetation in order to produce and preserve the very grazing lands themselves (Komarek 1965, 1967, Sutton 1990, Smith 1992). In the course of time these economies became

increasingly prominent (Smith 1992) and consequently the frequency of anthropogenic fires of pastoral origin also increased (Hamilton 1974). The long history of anthropogenic fire, pastoralism and other anthropogenic activities such as wood cutting has led to a situation in which 'natural' vegetation (i.e. unmodified by man) probably does not exist in East Africa below about 4000 m above sea level (Hamilton 1974, Prins 1989, Smith 1992).

The high density and diversity of mammalian fauna occurring in a relative state of naturalness has made the East African savannas the Eden for those ecologists interested in the effects of herbivores on savanna ecosystem dynamics. But, even though the importance of burning as an ecological factor in East Africa cannot be overemphasised (Hamilton 1974), it hardly has received the attention herbivores have. Hereby research on the effects of fire on East African savannas has primarily focussed on the effects on vegetation structure and composition. The effects on ecosystem processes such as water and nutrient cycling, and on the consequences for vegetation production and nutrient status, have received much less attention (Wein and Edroma 1986). This certainly applies for the knowledge on the effects of fire on herbivore forage quality and quantity in East Africa. This while the use of fire to improve grazing lands has been one of the main reasons for burning in East Africa. Pastoral use of fire and scientific observations that grazers congregate on post-fire regrowth (Moe et al. 1990, Wilsev 1996) would suggest improved forage quality and availability for grazers. Although a number of studies present data on the effect of fire on vegetation production in East Africa (Edroma 1979, 1984, 1986, McNaughton 1985), these do not elaborate on the actual consequences for herbivore forage supply. Even less is known about the effects of fire on forage quality, or on the mechanisms that cause these effects in East African savannas (Wein and Edroma 1986).

Research in other systems has shown that fire can improve herbivore forage quality and availability. However, these studies also show that generalisations on the effects of fire on herbivore forage quality and availability cannot easily be made since they depend on abiotic conditions such as rainfall, topographic position, soil type and nutrient status (Gill 1975). Given that soil water and nutrient supply are the two main abiotic determinants of African savanna systems, it can particularly be expected that the effects of fire will interact with these abiotic factors (Chapin and Van Cleve 1981, Walker 1981).

The high density and diversity of wildlife has also made the East African savannas one of the most popular game viewing centers of Africa. Thousands of tourists visit East Africa annually, supplying local economies with desperately needed hard currency. In the meantime high population growth, rising income and urbanisation in the past decades have led to a significant increase in livestock numbers and an increased demand for agricultural land (Happold 1995, Steinfeld et al. 1996). Consequently, wildlife is increasingly being restricted to areas with some form of protected status while nomadic pastoralists are being left with ever-decreasing grazing lands, many of which are of inferior quality since the more suitable areas are used for agriculture. One of the consequences is that in these remaining pastoral areas pastoralists increasingly use fire as a cheap management tool to obtain the lush, nutritious post-fire regrowth, as was done in the past. On the other hand, in the protected areas the compression of wildlife, elephants in particular, and increased fire frequency have caused concern for the sustainability of these savanna areas and the wildlife numbers. Here conservationists tend to adopt a policy of controlled burning to counter the wild fires that come from outside the park. These factors, amongst others, have led to a dramatic increase in the frequency of fire in many of the East African savannas.

The question however is whether burning to manage the pastoral areas at present still has the same beneficial effects as was the case in the past. Numerous studies have shown that high levels of biomass removal, though herbivory and fire, can lead to system degradation (Schlesinger et al. 1990, Van de Koppel et al. 1997). Furthermore, increased fire frequency and increased grazing intensities in East Africa have resulted in a reduction of fire intensity which, together with heavy grazing, is causing severe bush encroachment problems in many parts of East Africa (Pratt and Gwynne 1974, Gillon 1983).

Therefore: To burn or not to burn, that is the question. In many areas of present day Africa this burning question is posed by both managers of protected areas and by traditional pastoralists who are confronted with a changing savanna environment in which fire as a traditional tool for pasture management may not be appropriate anymore. The above mentioned questions about the effects of fire on herbivore forage quality and availability as well as the mechanisms through which these effects occur, are therefore not only interesting from and ecological point of view; they also increase the insight in the use of fire to manage these savanna systems in the present day situation.

Tarangire National Park

Research for this thesis was performed in Tarangire National Park (Figure 2) which is part of the Masai ecosystem in northern Tanzania as defined by Prins (1987, 1989). This system of approximately 35 000 km² is situated on the eastern boundary of the Great Rift Valley. It is



Figure 2: Tarangire National Park in northern Tanzania in relation to some important land features.

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defined by closed watershed boundaries, centred on Lake Manyara and Lake Burungi, and by boundaries between populations of migratory/nomadic large mammals, wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in particular (Prins 1987). These migratory herds congregate during the dry season in areas with permanent water supply and spread out over surrounding grazing areas during the wet season. Two national parks are situated in the Masai Ecosystem: Lake Manyara National Park and Tarangire National Park. Both these parks lie in the dry season range of the migratory herbivore populations. The encroachment of an ever-increasing human settlement and activities upon both parks is leading to restriction in migratory routes and to a decline in wet season grazing areas (Borner 1985, Prins 1987). A difference between the two parks is that Lake Manyara National Park has not burned since 1957, while in Tarangire National Park fire is a recurring event and particularly in the past decades the frequency has increased due to human activities (Lamprey 1964, Vesey-FitzGerald 1972, 1973). The frequent occurrence of fire in Tarangire was one of the main reasons why I chose this park as my research area.

Tarangire National Park was gazetted in 1969, but was already proclaimed as a game reserve as early as 1957 (Vesey FitzGerald 1972). It lies within the eastern part of the East African Rift Valley and is situated between latitude 3 $^{\circ}$ 40' and 5° 35' South and longitude 35° 45' and 37° East (Figure 2). Altitude ranges from 1000 m to 1350 m. The Park encompasses an area of approximately 2600 km² and is named after the Tarangire river, a perennial river that runs through the park from south to north ending in Lake Burungi. The river is one of the main characteristic features of the park and acts as one of the prime dry season water supplies for the migratory herds within the Masai Ecosystem (Prins 1987).

The park lies within the semi-arid climatic region (Pratt and Gwynne 1977) with an average rainfall of 620 mm which, however, is highly variable between location and years. A rainfall gradient can be seen from South-East (approx. 450 mm) to North-West (650 mm). Rain primarily falls between December and May. During the dry season (June-November) rainfall is very rare. Maximum day temperatures range from an average of 34 °C in December and January going down to 25 °C in July, August and September while minimum night temperatures are 21 °C in December and January and 15 °C in July and August.

The geology is based on three types of formations: the pre-Cambrian gneiss rock and the lacustrine and alluvial deposits of Miocene origin. During Miocene and Pleistocene volcanic eruptions vast areas were covered with volcanic ashes. The underlying gneiss and other pre-Cambrian crystalline rocks in much of the park give rise to different physical features. There are four major soil types. First there are the well drained red-loams along river valleys which, going upslope, become increasingly more sandy and stony, due to lack of depth. Below 1070 m, in areas of less undulation, soil types originating from lake deposits and sediments can be found; they vary from clays to sands and are normally alkaline. Finally, in low-lying flood plain areas the soils are made up of dark alluvial deposits that are predominantly vertisols, consisting of montmorilinitic clay components.

The park consists of various vegetation types which are related to elevation and soil type (Phillips 1959, Lamprey 1964). The vegetation mainly consists of grasslands and open savanna woodlands (Chuwa 1994). Apparent features of the park are the vast wooded grasslands which are dominated by Acacia tortilis, Balanites aegyptiaca, Adansonia digitata, Maerua triphylla and Grewia spp. tree species in the river valleys and plains and by Combretum spp. and Commiphora spp. tree species on the ridges. Furthermore, extensive grasslands (and floodplains) can be found in the park which are dominated by grass species such as Bothriochloa insculpta, Brachiaria spp., Cenchrus ciliaris, Dactyloctenium aegypticum, Digitaria spp., Panicum spp., Pennisetum mezianum, Sporobolus spp., and Urochloa spp.

Large migratory herds of wildebeest and zebra are present during the dry season but leave the Park during the wet season, moving to surrounding grazing areas, particularly to the Simanjiro Plains which lie east of the Park (Lamprey 1964, TWCM 1995). Other abundant but more sedentary herbivores in Tarangire N.P. are African elephant (*Loxodonta africana*) and African buffalo (*Syncerus caffer*) (TCP 1995), as well as impala (*Aepyceros melampus*), Coke's hartebeest (*Alcelaphus buselaphus cokii*), giraffe (*Giraffa camelopardalis*), Grant's gazelle (*Gazella granti*), oryx (*Oryx gazella*) and eland antelope (*Tragelaphus oryx*).

Outline of the thesis

The first aim of this thesis is to bridge an important gap in our knowledge of the effects of fire on herbivore forage quality and availability, which is discussed in Chapter 2. In this chapter the effect of fire on above-ground biomass as well as various chemical and structural plant characteristics that determine the intake of forage for grazers were investigated. Fires, that occurred on the four major soil types prior to a drought year in 1993/1994 and an excessive wet year in 1995/1996 in Tarangire National Park, allowed for the comparison of the effects of fire on grazer forage with varying rainfall and soil types.

· Chapter I

Accordingly this thesis addresses the mechanisms through which fire affects vegetation production and nutrient status. Studies describing herbivore congregation on post fire regrowth suggest that fire improves vegetation nutrient status (Frost and Robertson 1987) and ascribe the enhanced concentration of plant nutrients to alteration in plant nutrient supply, plant phenology and plant tissue composition (Savage 1980, Briggs and Knapp 1995, Bond and Van Wilgen 1996). However, very few data exist on the effect of fire on plant nutrient concentration in semi-arid savannas and no studies have actually addressed the various mechanisms through which fire may increase the nutrient content of post-fire regrowth. Although the mechanisms have been investigated in temperate systems (Christensen 1977, Boerner 1982, Briggs and Knapp 1995) and in humid grassland systems (Tainton and Mentis 1984), the mechanisms were not investigated simultaneously. For the relatively nutrient rich, semi-arid East African savanna systems the accounts about the effects of fire on plant nutrient status merely come from general, anecdotal statements with no presentations of empirical evidence (Wein and Edorma 1989). In Chapter 3 the effects of fire on grass nutrient concentrations in Tarangire, the duration of these effects and the mechanisms through which they occur are addressed.

In many ways the effects of fire on savanna ecosystem functioning are comparable with the effects of herbivory. Like herbivores, fire "consumes" large amounts of plant material and thus may profitably be viewed as a major generalistic herbivore (Bond and Van Wilgen 1996). Through removal of biomass the effects of fire on vegetation structure, plant water and nutrient status and consequently on plant growth, match those of herbivory (Crawley 1983). In East Africa soil water status is the main determinant for growth. Apart from rainfall and soil characteristics, the soil water status is determined by above-ground biomass (Whelan 1995). Chapter 4 specifically investigates the effects of biomass removal on the soil water status, the causes of these effects and their consequences for vegetation production and nutrient status.

Yet, the comparison of fire and herbivory on savannas does show some flaws which can have significant importance for the outcome of their effects on the ecosystems functioning. First of all, fire is not selective and removes all plant parts dry enough to burn while the majority of herbivores are selective feeders, removing specific species and plant parts, live grass leaves in particular. Secondly, fire and herbivory differ in the amount, frequency and season in which they remove above-ground biomass. Fire generally removes large amounts of biomass over a relatively short time span, during a period of the year in which vegetation is in a senescent phase of growth. Grazing on the other hand recurs year

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round whereby green, productive plant parts are selected. Chapter 5 was set up to investigate the effects of biomass removal, through repeated simulated grazing, on vegetation production and nutrient status. These data were accordingly used to investigate the consequences for the migratory populations when the migration routes to wet season ranges would be restricted and the migratory herds would have to reside year round in the dry season range.

A number of studies have been performed on the effects of fire and herbivory on East African savanna structure (Wein and Edroma 1986, Dublin 1995 and refs. within) whereby the focus particularly was directed on the effects of increased elephant density and fire frequency on the savanna woody component. However, many of these studies generally do not span periods longer than a decade and those that do were restricted to changes in the mature canopy. In 1996 we had the opportunity to repeat a study performed in 1971 by Dr. D. Vesey-FitzGerald on the density of trees in Tarangire National Park. The density of elephants in 1996 was nearly twice as high as compared to 1971 while fire frequency had also increased. The 1971 and 1996 data accordingly allowed for a study on the long-term changes in the structure of the savanna woody component in an area of high elephant density and recurring fires. This study and its conclusions are presented in Chapter 6.

Chapter 7 summarises the results of the previous chapters and considers the implications of these results for management. First the various purposes of fire in the past are reviewed. Accordingly the present situation is described and discussed, especially with regard to the different management objectives and options for using fire as a tool in the savannas of present-day Africa.

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Chapter 2

The effects of fire on herbivore forage quality and availability in relation to soil type and post-fire rainfall conditions

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Summary

The savannas of East Africa are characterised by large and diverse mammalian herbivore populations, pastoralism and frequent fires, many of which are lit by pastoralists. In Tarangire National Park, northern Tanzania, the effect of fire on herbivore forage quality and availability was investigated during two years that varied in rainfall (wet and drought year) and in four different soil types. Forage quantity (i.e. live and dead above-ground grass material) was determined at the beginning, middle and end of the post-fire growth. Forage quality was determined three months after the onset of the post-fire growth season (Middle Season). Live:dead and leaf:stem proportions as well as leaf volume of grass were used as structural forage quality parameters while N and P concentrations and digestibility of grass leaves were used as chemical forage quality parameters.

Both structural and chemical forage quality parameters were generally higher in post-fire regrowth as compared to unburned vegetation, with higher live:dead and leaf:stem proportions, grass leaf bulk densities, N concentrations and digestibility. The degree in which fire affected forage quality, however, depended on soil type and rainfall. Forage quantity, however, was adversely affected by fire. This effect was most prominent in the drought year where produce in the post-fire regrowth was even less than the already low produce in unburned vegetation. Although the forage quantity in the wet year was not enhanced through fire, the production in burned vegetation was such that at the end of the wet season green forage quantity was comparable to that of the unburned vegetation. As with forage quality, soil type significantly affected forage quantity and also the manner in which forage quantity was affected by fire. Results of this study are used to verify the traditional use of fire as a tool in pasture management for present day Africa.

Key words: fire, drought, grazing, forage quantity and quality, savanna

Introduction

In tropical savannas herbivory and fire are common phenomena and can be seen as two determinants of the structure and functioning of these systems (Walker 1981). This especially is the case in the semi-arid savannas of East Africa which have the highest diversity and density of wildlife herbivores in the world (Prins and Olff 1998) and where both natural and anthropogenic fires have occurred for millennia (Lind and Morrison 1974, Pratt and Gwynne 1977). The roles these two factors play, however, are not independent. While herbivores influence fire regime by altering quantity and quality of fuels available for combustion (Komarek 1965, Trollope 1982, Hobbs 1996), fire affects herbivore distribution because herbivores tend to concentrate on post-fire regrowth (Sinclair 1977, Moe et al. 1990, Stein et al. 1992, Pfeiffer and Hartnett 1995, Sparks and Masters 1996, Wilsey 1996). Phillips (1965 and refs. within) even mentions that a variety of herbivore species travel long distances to feed on post-burn vegetation. It has been suggested that therefore indigenous hunters have been using fire as a tool to attract wildlife (Daubenmire 1968, Komarek 1972, Vogl 1974, Pyne 1995). For grazers, grazing on post-fire regrowth leads to higher body mass gains than when they would graze on unburned vegetation (Miller and Watson 1974, Woolfolk et al. 1975, Anderson 1979, Svejcar 1989). Furthermore, fire can also increase grazing areas by reducing the cover of the savanna woody component (Vesey FitzGerald 1972, Gillon 1983, Werger 1983). Consequently, fire has become a common tool in the semi-arid pastoral systems of East Africa (Lemon 1968, Van Rensburg 1972, Smith 1992).

Although a significant body of literature describes the effects of fire on grass species composition, fuel reduction and tree:grass ratios in semi-arid African grazing lands (Gillon 1983, Trollope 1982, 1984, Frost and Robertson 1987, Frost 1992), knowledge on the effects of fire on forage quantity and vegetation characteristics that determine forage quality is poorly developed. Information from temperate and humid tropical grazing systems suggests that, compared to unburned vegetation, forage intake in post-fire regrowth is higher due to higher levels of digestible plant material (Hungate 1975, Hobbs and Spowart, 1984, Hobbs et al. 1991) and higher nutrient concentrations (Hill 1972, Daubenmire 1975, Smith and Kadlec 1985, Frost and Robertson 1987, Moe and Wegge 1997). Forage intake in post-burn vegetation can also be higher due to increased foraging efficiency as a result of improvement of structural properties of the vegetation which regulate herbivore forage selection time (Chacon and Stobbs 1976, McNaughton 1985, Prins 1996, Heitkönig and Owen-Smith 1998).

For the semi-arid grazing systems in African savannas little quantitative information is available regarding the effects of fire on forage quality parameters and most conclusions on this matter come from anecdotal information with very little empirical evidence (Pratt 1967, Mentis and Tainton 1984, Frost and Robertson 1987, Frost 1992). A recent book on the ecology and management of grazing systems (Hodgson and Illius 1996), for example, only mentions fire as an environmental factor in grazing systems, but does not address the manner in which fire affects forage quality nor the short or long-term effects on forage availability.

Besides affecting forage quality, fire can also significantly affect forage supply, another determinant of grazers' forage intake (Ungar 1996). Several studies have reported enhanced post-fire regrowth and consequently high availability of green nutritious forage for grazing in savanna systems (Sanford and Wangari 1985, Mentis and Tainton 1984, McNaughton 1985). Others found that fire caused a decline of forage yield (Edroma 1984, Tainton and Mentis 1984). This discrepancy may, amongst others, be related to post-fire growth conditions and the manner in which growth determining factors are affected by fire (Chapin and Van Cleve 1981, Boerner 1982, Mentis and Tainton 1984, Kauffman et al. 1994). In semi-arid African savannas the main determinant of plant growth is soil water supply which primarily is a function of rainfall and soil characteristics (Walker 1981). Hence it can be expected that in these systems vegetation response to fire will vary with soil type and post-fire rain conditions. For the East African savannas in particular, little information is available regarding these issues. This study was set up to investigate the effects of fire on herbivore forage quality and quantity and also how these effects differ with soil type and post-fire rainfall conditions.

Insight in the effects of fire on grazer forage is not only of interest from an ecological point of view but is also of importance for sustainable pasture management in the semi-arid savannas of present-day Africa. In the past decades livestock numbers in many of the African savannas have increased, while pastoral areas have decreased due to increased agriculture and urbanisation (Happold 1995, Steinfeld et al. 1996). In many of the remaining pastoral areas these changes have resulted in intensification of traditional burning practices, in order to cope with the loss of good grazing lands; as a consequence many areas even burn annually. Frequent burning of large pastoral areas may however lead to lack of forage for grazing animals since the standing hay acts as a reserve during the dry season and drought (Hill 1972, Prins and Beekman 1989). Rainfall in these systems in very variable (Pratt and Gwynne 1977,

Prins and Loth 1988) and therefore large scale burning of this standing hay may lead to forage shortage when it is not replaced by sufficient post-fire regrowth.

The effects of fire on forage biomass and forage quality parameters were investigated in a wet year and a drought year on 4 soil types in Tarangire National Park, northern Tanzania. To this end, during the post-fire rain season, standing biomass of grass in burned and unburned vegetation were compared while N and P concentrations, digestibility via NDF (Neutral Detergent Fibre), leaf:stem and live:dead proportions and grass bulk density were compared two months into the growth season after fire.

Material and Methods

Study area and site description

The research was performed in Tarangire National Park, situated on the eastern side of the Great Rift Valley in northern Tanzania (4 ° S, 37° E, 1200 m above sea level). The park is situated in the wooded, arid Acacia savanna belt and is dominated by *Acacia* and *Commiphora* species (Lind and Morrison 1974, Pratt and Gwynne 1977). It lies in the Masai Ecosystem as defined by Prins (1989) and is one of the main dry season ranges of this system. During the dry season large herds of migratory ungulates are found in the park but in the wet season very few animals remain since the majority of grazing animals migrate to surrounding grazing areas at the onset of the wet season.

The geology of the park is based on three types of soil formations: 1) Alluvial deposits that are predominantly vertisols with montmorolinitic clays, commonly known as Black-Cotton soils. These poorly drained soils generally are water logged in the wet season but dry up in the dry season which causes the soil to crack, 2) Coarse sandy loams of lacustrine origin which generally are saline, 3) Well-drained ferruginous red loams originating from pre-Cambrian gneiss rocks. These soils, which are found along the river valley slopes and on the ridges, increase in sandiness and rockiness going up slope. Because water availability decreases with increasing sandiness (Walker 1985), an additional distinction was made between red soils on the ridges and red soil on the slopes.

Average annual rainfall (from August through to next July), measured at Park Head Quarters in the northern part of the park, is 620 mm, but is very variable. The rainy season extends from December to May with a peak in March and April. Average maximum temperature is 27°C and average minimum is 16°C. In 1993/1994 the Park experienced a drought, only receiving 351 mm of rain which only started to fall in January and hardly any rain fell from May onwards. Rainfall in the 1995/1996 rainy season was well above average with 943 mm of rain, the first rain falling in December. During the July to November period in both 1993 and 1995, a significant area of the park was burned and fires occurred on all major soil types. This accordingly allowed us to compare the post-fire regrowth with unburned vegetation in a drought year (1993-1994) and a wet year (1995-1996) in the four defined soil types (Table 1). Grass species growing in research sites of the four soil types varied, as is shown in Table 1. The Black Cotton and Ridge Slope soils were dominated by perennial grass species.

Site name	Soil characteristics	Site location in landscape and slope	Dominant grass species e		
Black Cotton	Black, Montmorillonitic clay	Valley 0%	Sorgum versicolor Anderss. Pennisetum mezianum Leake Cenchrus ciliaris L. Brachiaria xantholeuca (Schinz) Stapf		
Lacustrine	Grey, Coarse sandy clay	Plain 0%	Urochloa mosambicensis (Hack.) Dandy Chloris virgata Sw. Dactylostenium aegyptium (L.) Willd. Bothriochloa insculpta (A. Rich) A. Camus		
Ridge Slope	Red, Fine sandy loam	Middle 3%	Themeda triandra Forssk. Heteropogon contortus (L.) Roem. & Schult. Sehima nervosum (Rottler) Stapf		
Ridge Top	Red, Course sandy loam	Тор 2%	Aristida adscensionis L. Eragrostis superba Peyr. Chloris virgata Sw. Dactyloctenium aegyptium (L.) Willd.		

 Table 1: Site description of the research areas in Tarangire National Park. Species names follow

 Flora of Tropical East Africa (Clayton 1970, Clayton et al. 1974, Clayton et al. 1982).

The effect of fire on vegetation production and nutrient status varies largely (Mentis and Tainton 1984) whereby the differences are related to various factors such as fire type (Trollope 1984), post-fire grazing (Pratt 1967, Van Rensburg 1972), soil type and rainfall (Bond 1997). Since all fires occurred in the dry season and since grazing during the post-fire growth season was negligible, differences in response to fire between sites and years can be ascribed to variation in rainfall and soil type.

Methods

In the post-fire rainy season of the drought year and the wet year, we randomly selected five plots in both burned and adjacent, unburned vegetation of the four soil types described above. Forage biomass in burned and unburned vegetation in the different soil types and wet and drought years was measured by sampling 1 m² quadrants at the onset of the rains (Begin Season), three months after the onset of the rains (Middle Season) and one month after the rains had stopped (End Season). "Middle Season" grass samples were sorted in leaf, stem and dead material while "Begin" and "End Season" samples were only sorted in live and dead material. Sorted material was dried at 70°C to a constant weight and weighed. During the sampling period grazing was negligible as grazing animals migrate outside the park during the wet season.

"Middle Season" grass samples were used to investigate herbivore forage quality. Parameters investigated were leaf:stem proportion (i.e. the proportion of green leaf biomass to the total live biomass), live:dead proportion (i.e. the proportion of live biomass to the total standing biomass) and grass leaf bulk density (leaf weight per unit volume). To determine grass sward bulk density, the height of the grass sward had to be measured. This was done by taking the mean of 4 leaf table height measurements in the 1 m² plots prior to harvesting. In the sites dominated by perennial grasses we additionally compared the percentage of dead grass clumps in burned and unburned plots to obtain insight in causes of variation of green biomass in relation to fire treatment and growth season rainfall conditions.

Chemical analysis

Grass leaf nitrogen (N) and phosphorus (P) concentrations and Neutral Detergent Fibre (NDF) of grass leaves were also analysed for the "Middle Season" samples. Prior to chemical analysis, samples were ground through a 1 mm sieve and digested using a modified Kjeldahl procedure with Se as a catalyst (Novozamsky et al. 1983). N and P concentrations were measured colorimetrically with a continuous flow analyser (Skalar SA-4000, The Netherlands). NDF samples were analysed according to Goering and Van Soest (1970).

Statistical analysis

Data were statistically analysed using SPSS 7.0 statistical package. Treatment, soil type and drought effects on biomass and on herbivore forage quality parameters were analysed using a full factorial ANOVA. For the analysis of live and total biomass, season of harvest was nested within one year (the wet and drought year respectively). Data were transformed to meet requirements of parametric analysis. Differences between means were tested using a Tukey-HSD test. Statistical significance was accepted for P<0.05.

Results

Forage quality

Middle Season vegetation data show that fire had a positive effect on the live:dead proportion whereby the degree in which live:dead proportion was enhanced depended on soil type and post-fire rainfall (Table 2, Figure 1a). Generally, the live:dead proportion was higher in the wet year with burned vegetation reaching values up to 100% live grass material, while the unburned had lower values. This effect was most apparent in those sites and treatments where fire had removed large quantities of dead material, which remained in the unburned vegetation (Figure 5). Depending on rainfall and soil type, Middle Season post-fire regrowth also had higher leaf:stem proportions than unburned vegetation or did not differ from it (Table 2, Figure 1b).

The grass leaf bulk density was calculated as the biomass of green leaves per unit volume (mg cm⁻³). We found large differences in grass leaf bulk density between treatments, the grass leaf bulk density values of burned vegetation tending to be higher than those of unburned vegetation (Figure 1c, Table 2). Here again, variation in the effect of burning was related to soil types and rainfall.

Table 2: The amount of variance explained by drought, soil type, burning and their interactions, given as a percentage of the total explained variance (r^2) , for live:dead proportion (LDR), leaf:stem proportion (LSR), grass leaf bulkdensity (GLBD), grass leaf nitrogen (N) and phosphorus (P) concentrations and grass leaf neutral detergent fibre (NDF). * P < 0.05, **P < 0.01 and ***P < 0.001, ** = not significant.

		Explained variance (%)					
Factor	df	LDP	LSP	GLBD	N	P	NDF
Model (r ²)	15	90.3***	82.3***	78.1***	92.9***	80.6***	77.0***
Drought (D)	1	60.3***	7.0***	4.3**	1.69**	5.5**	10.7**
Soil (S)	3	6.2***	13.2***	53.5***	45.2***	55.8***	27.0***
Burning (B)	1	1 5.3***	21.1***	19.1 ^{***}	12.4***	0.1 ^{ns}	13.7***
D*S	3	3.6**	39.4***	2.1 ^{ns}	30.1***	22.5***	36.6***
D*B	1	3.1***	2.2*	$0.7^{\rm ns}$	3.2***	9.0***	1.8 ^{ns}
S*B	3	8.1***	1.9 ^{ns}	12.3***	2.0^{*}	4.9*	3.6 ^{ns}
D*S*B	3	3.4**	15.3***	8.0**	5.3***	2.2 ^{ns}	6.6*



Figure 1: Live:dead proportions (LDP, %), leaf:stem proportions (LSP, %) and grass leaf bulk density (GLBD, mg cm⁻³) in burned and unburned vegetation three months after the onset of the post-fire rainy season in a year of above average rainfall (Wet) and a drought year (Dry) on 4 different soil types in Tarangire National Park. Bars are means \pm 95% confidence intervals (n=5).
Live grass nitrogen and phosphorus concentration and digestibility

Similar to the structural vegetation characteristics, the effect of fire on live grass nitrogen concentration, three months after the onset of rain, depended on soil type and rainfall (Figure 2a, Table 2). In the wet year differences were still present three months after the onset of the post-fire rainy season, except for the Black Cotton site. In the drought year these differences between burning treatments were less apparent, but the data do show that, except for the lacustrine soil, live grass leaf nitrogen concentration was higher in the drought year.



Figure 2: Grass leaf N and P concentration (%) in burned and unburned vegetation three months after the onset of the post-fire rainy season in a year of above average rainfall (Wet) and a drought year (Dry) on 4 different soil types in Tarangire National Park. Bars are means $\pm 95\%$ confidence intervals (n=5). \square = unburned \blacksquare = burned.

We found no clear differences in live grass leaf phosphorus concentration between burned and unburned vegetation (Figure 2b, Table 2). Analysis of the data does show that the effects of burning depended on rainfall (Table 2). Data from the drought year in the Black Cotton and Ridge Slope sites would suggest that burning has a negative effect while in the wet year it would appear to have a positive effect. (Figure 2b).



Figure 3: Neutral Detergent Fibre (NDF) of grass leaves in burned and unburned vegetation three months after the onset of the post-fire rainy season in a year of above average rainfall (Wet) and a drought year (Dry) on 4 different soil types in Tarangire National Park. Bars are means $\pm 95\%$ confidence intervals (n=5).

We measured the effect of burning on plant digestibility by analysing Neutral Detergent Fibre (NDF) of grass leaves (Table 2, Figure 3), NDF being an inverse measure of digestibility (Goering and Van Soest 1970). Three months after the onset of the post-fire growth season, post-fire regrowth still had a significantly higher digestibility than unburned vegetation (Figure 3). Here again the differences in NDF values between burned and unburned vegetation depended on soil type and rainfall with no significant differences in the dry year while burned vegetation had significantly lower NDF percentages in the wet year, except for the Black Cotton site. Furthermore the data show that the Lacustrine and Ridge Top sites, which were dominated by annuals, had lower NDF percentages as compared to the perennial dominated Black Cotton and Ridge Slope vegetation. No NDF data were available from the Ridge Slope site in the dry year.

Forage production

Does fire increase the availability of grass forage for herbivores? The present study shows that fire did not increase the amount of green grass biomass in the post-fire growth season (Figure 4, Table 3). Rather, the amount of available grass forage was adversely affected by fire.

Hereby the degree in which this occurred depended on post-fire rain conditions and soil type (Table 3). In the wet year green forage biomass increased rapidly and had reached values comparable to the unburned vegetation by the end of the post-fire growth season. In the drought year, however, the amount of grass biomass in the burned vegetation was still significantly lower than the unburned vegetation at the end of the post-fire growth season (Figure 4). The negative effects of fire on green forage biomass in the drought year were most pronounced in the more clayey soil (Black Cotton) and sandy soil (Ridge Top) where the amount of green forage during the post-fire growth season was negligible (Figure 4).



Figure 4: Green grass biomass $(g m^2)$ in burned and unburned vegetation at the onset of rains (Begin), three months after the onset of rains (Middle) and one month after the rains had stopped (End Season) in a year of above average rainfall (Wet) and a drought year (Dry) on 4 different soil types in Tarangire National Park. Bars are means $\pm 95\%$ confidence intervals (n=5). Note the differences in y-axes scaling. \boxtimes = unburned, \boxtimes = burned.

The data also show that harvest date and the amount of rainfall in the wet season gave rise to most of the variance in green forage biomass, with significantly lower quantities of green forage in the drought year (Table 3). The extent to which the amount of rainfall affected green biomass depended on soil type. This can clearly be seen when the effect of drought is compared for the different soil types (Figure 4).



Figure 5: Total grass biomass $(g m^2)$ in burned and unburned vegetation at the onset of rains (Begin), three months after the onset of rains (Middle) and one month after the rains had stopped (End Season) in a year of above average rainfall (Wet) and a drought year (Dry) on 4 different soil types in Tarangire National Park. Bars are means $\pm 95\%$ confidence intervals (n=5). Note the differences in y-axes scaling. \square = unburned, \square = burned.

Table 3: Results of an ANOVA analysis of the effects of Soil, Burning, Drought (wet year of 943 mm and dry year of 351 mm) and harvest date (begin, middle and end of season) on green grass biomass and total above-ground grass biomass (log transformed) in the wet season following fire whereby season of harvest was nested within drought. The amount of explained variance as a percentage of the total explained variance (r^2) is shown. * P < 0.05, ** P < 0.01 and *** P < 0.001, ** not significant.

<u></u>		Green grass biomass	Total grass biomass
Factor	df	Explained Variance (%)	Explained Variance (%)
Corrected Model (r ²)	45	95.3***	97.1***
Soil (S)	3	5.3***	8.8***
Drought (D)	1	27.71***	9.5***
Burning (B)	1	3.5***	32.95***
Harvest date (H) ^D	4	43.07***	24.4***
S * D	3	9.41***	1.84***
S * B	3	0.1 ^{ns}	1.6**
S * H ^D	12	6.46***	6.4***
D * B	1	0.1 ^{ns}	1.7***
B * H ^D	4	1.86***	9.2***
S * D * B	3	0.99***	2.2**
S*B*H ^D	10	1.56***	1.4***

The effect of fire was more apparent when total above-ground biomass was regarded (Table 3, Figure 5). This is due to a significant amount of dead material still present in the unburned plots but which was removed by fire in the burned plots, as compared to the green biomass which in both burned and unburned vegetation primarily was produced during that year's growth season. Similar to green forage biomass, the effect of fire on total above-ground biomass depended on soil type, rainfall during the growth season and date of harvest (Table 3, Figure 5).

Discussion

One of the main reasons for the use of fire in grazing systems is to provide herbivores, domestic and wild, with an abundant grass vegetation of high quality (West 1965, West 1972, Vogl 1974, Frost and Robertson 1987). So far, however, the actual effect of fire on vegetation characteristics that regulate forage intake by grazers in the relatively nutrient rich savannas of East Africa is poorly understood. Even less is known about the manner in which these effects vary with post-fire soil water supply, the main abiotic determinant of vegetation growth (Chapter 4). In this study we aim at getting more insight in these issues.

Forage quality

The amount of biomass taken with one bite is the fundamental unit of forage intake. It is the product of bite volume which is determined by specific animal characteristics and the bulk density of the herbage consumed (Stobbs 1973, Ludlow et al. 1982, Hodgson 1985, Ungar 1996). In tropical grasslands the sward bulk densities, leaf bulk density in particular, are considerably lower as compared to temperate grazing systems and is a major factor reducing intake rate (Ludlow et al. 1982, Prins and Beekman 1989). Our data show that, depending on soil type and post-fire rainfall, leaf bulk densities were higher in the post-fire regrowth than in the unburned vegetation and thus a higher amount of biomass can be taken per bite on the post-fire regrowth.

Another determinant of intake rate is the rate of biting which is primarily determined by the selection time for green grass material (Laca and Demment 1996, Ungar 1996). If an animal is grazing on a sward with a high proportion of grass leaves and a low proportion of

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dead material, selection time is reduced significantly (Ungar 1996). The increased leaf:stem proportion and the reduced amount of dead material in the post-fire regrowth, as found in this study, shows that selection time in burned vegetation may be reduced. Thus, the increased biting rate, together with an increased bite volume, brings about an increase in forage intake on burned vegetation.

Next to structural quality parameters, forage intake is also related to the chemical properties of forage which determine the passage rate of forage through the digestive system since these determine the amount that can be consumed (Arnold 1981, Van Wieren 1992, Van Soest 1994). Although the effect of fire on digestibility of forage varied with soil type and amount of post-fire rainfall, our data do suggest that, on average, post-fire regrowth is easier digestible than unburned vegetation since we found that the percentage of Neutral Detergent Fibre was lower in burned vegetation three months into the post-fire growth season.

Generally considered, the most critical limiting quality parameter for herbivores is nitrogen concentration in forage (Prins and Beekman 1989, Van Soest 1994). We found increased concentrations of N in the post-fire regrowth whereby this increase in two occasions resulted in concentrations above maintenance levels of 1.26% (Van Soest 1994). But, compared to other studies in semi-arid savannas (Mes 1958, Tainton and Mentis 1984, Singh 1993, Chapter 3), the increase in N concentration was not large. The effect of fire on the concentration of P in grass leaf material was even less apparent. This discrepancy with previous studies, in the first place, could be due to the fact that we compared nutrient concentrations three months after the start of the post-fire growth season, a period in which differences could have declined (Chapter 3). Secondly, soils in Tarangire are relatively nutrient rich, particularly P. It therefore appears that in these relatively nutrient rich soils the effects of fire on the nutritional status of forage for grazers may be less pronounced than in more nutrient poor savanna systems (Medina 1987, Mentis and Tainton 1984, Singh 1993).

We therefore suggest that in the relatively nutrient rich East African savannas, the positive effect of fire on the herbage quality parameters that affect grazer intake over the post-fire growth season, primarily is the result of improved structural sward characteristics and improved digestibility and to a lesser extent of increased nutrient concentration. Finally, daily intake is also determined by active grazing time. This also may be higher on post-fire regrowth because grazers are less bothered here by flies, ticks and other parasites (Sutherst 1987, Van de Vijver pers. obs.), which allows more time for grazing.

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Forage quantity

Besides forage quality, forage biomass is another important factor that determines herbivore forage intake (Ungar 1996). The present study shows a high variability in the quantity of available forage in Tarangire National Park and thus concurs with the conclusions of previous studies that forage supply in East African savannas is potentially rich but temporally and spatially unpredictable due to continual stochastic fluctuations of rainfall, soil type and also fire (Deshmukh 1984, McNaughton 1985).

Differences in response to drought and fire between the different sites investigated can be explained by soil characteristics. The largest differences in forage production between drought and wet years occurred in the Black Cotton site and the Ridge Top site. The large differences found between the wet and drought year in the Ridge Top site can be explained by the sandiness of the soil allowing infiltrated water to percolate to deeper soil layers where it is unavailable for grass growth (Kelly and Walker 1976). In the Black Cotton site the extreme large difference in forage production between wet and dry years, as well as the fast recovery of standing biomass in the burned area during the wet year, can be explained by the specific characteristics of the soil type in this site: montmorillonitic clay. This clay amplifies the effects of drought because it cracks when it is dry, thus creating a larger evaporation soil surface and also killing many plant roots. Moreover, because montmorillonite clays have the quality of reducing the osmotic potential of the soil (Lind and Morrison 1974), plants will sooner experience drought in this soil type. In wet years however, the large cracks at the start of the rainy season allow for high infiltration of water until the soils become saturated and hence plants do not experience any water shortage till the soil starts to dry up again in the next dry season.

Present data also show that fire does not increase the quantity of forage available for grazing. Rather, the effect of fire is detrimental, especially under drought conditions when, after fire, the already low amount of standing biomass is additionally suppressed. In the wet year, however, above-ground biomass production in the burned vegetation during the post-fire growth season can be so profuse that quantitative differences in available green forage with unburned vegetation become negligible by the end of the growth season. The additional reduction of the already low biomass produce in the drought year in burned vegetation suggests that soil water supply, the main determinant of plant growth, is reduced after fire with the reason that water evaporation from soil increases when vegetation is burned due to

the removal of insulating plant material which protects the soil from direct sunlight (Kelly and Walker 1974, Savage 1980, Ratzlaff and Anderson 1995, Chapter 4). Soils can accordingly dry up to such an extent that perennial grass tufts die off (O'Connor 1994). This was clearly visible in the perennial dominated Black Cotton and Ridge Slope sites where, in the drought year, respectively 85 and 50 % of the grass clumps had died in the burned areas while in the unburned areas this was only 27 and 5% (P<0.05, n=5). Our data therefore concur with previous observations that the response of vegetation production to burning is primarily related to soil water supply (Tainton and Mentis 1984, Briggs and Knapp 1995, Chapter 4) and that burning amplifies the negative effect of drought on vegetation production (West 1965).

The present study, however, contrasts with previous studies in East Africa (Pratt 1967, McNaughton 1985, Murray and Illius 1996) which found an increase of green forage quantity in post-burn vegetation, compared to unburned vegetation, when burning occurred at the end of the wet season. The discrepancy in findings can be explained by the difference in season of burning. At the end of the wet season the soil starts drying up and plants go into a senescent phase of growth. Burning in this period results in reduction of transpiring leaf surface and thus of plant water demand in relation to soil water supply. This accordingly leads to an improved plant water status and allows an increased production of green forage in burned vegetation, as compared to unburned vegetation (McNaughton 1985). In the present study, however, burning occurred in the dry season and soil water potentials in this period are too low to allow for a favourable response of the vegetation to burning.

Fire as a tool in semi-arid pasture management

In Africa, early explorers in the 18th and 19th century recorded that local people would burn the savanna (West 1965 and refs. within) and it has been recognised that, of old, pasture burning has been the main reason for anthropogenic fire in African savanna systems (West 1972, Pratt and Gwynne 1977, Gillon 1983). This particularly is true for the East African savannas where pastoral systems have flourished for some 4000 years (Sutton 1990, Homewood and Rodgers 1991, Smith 1992) and where livestock grazing and savanna burning have continuously increased (Pratt and Gwynne 1977, Prins 1989, 1992, Fratkin 1997).

Our study suggests that chemical and structural properties of forage, which regulate forage intake for grazers, are enhanced through burning but that the amount of forage can be reduced significantly by fire. We therefore conclude that the improved forage quality of postfire regrowth is the main cause of herbivore concentration on post-fire regrowth and the use of fire in pastoral areas, rather than forage supply. Particularly in drought years the negative effect of fire on the amount of available forage can lead to shortage of forage and thus will outbalance the positive effects of fire on forage quality. Since fire has been used in pasture management for so long, one would expect that the chances of a drought must be relatively small. This however does not appear to be the case.



Figure 6: Annual rainfall (mm), measured from August through to July the next year, over a period of 19 years (1976/1977 to 1995/1996) measured at the northern part of Tarangire National Park, northern Tanzania. Arrows indicate the 93/94 drought year and the 95/96 wet year in which research was performed.

Figure 6 shows the rainfall data of Tarangire National Park over a period of 19 years and demonstrates that annual rainfall is very erratic, as has been shown by others (Lind and Morrison 1974, Pratt and Gwynne 1977, Prins and Loth 1988). Furthermore Figure 6 shows that the chance of a year of below average rainfall is 53% while 6 of the 19 years had an amount of rain comparable to that of the 1993/1994 season. The question then arises why to use fire as a tool in pasture management when the risk of misfortune is high and the chances of drought are unpredictable?

In the past the ranges of pastoral systems were much larger and pastoralists would move to areas of higher resource when drought years occurred and thus they were able to avoid forage shortage which occurred in drought years after burning. At the present time, however, by expansion of human populations, settlements and agricultural activities, pastoralists are restricted to an ever declining pastoral area (Steinfeld et al. 1996). Thus the possibility to escape the effects of drought has diminished. Hence, the present study suggests that fire has become a risky tool in the semi-arid pastoral economies of East Africa. It therefore should be avoided or it should be performed just prior or after the first rains when soils are not exposed to direct sunlight for long periods of time (Chapter 4, 7) and soil water supply is sufficient to allow post-fire regrowth which makes the herbivores less dependant on standing hay as a resource.

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Chapter 3

Causes of increased nutrient concentrations in post-fire regrowth in an East African savanna

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Summary

The aim of the present study was to investigate the causes of increased macronutrient concentrations in above-ground post-fire regrowth in an East African savanna (Northern Tanzania). Experiments were set up to discriminate between the following possible causes: (1) increased soil nutrient supply after fire, (2) relocation of nutrients from the roots to the new shoots, (3) rejuvenation and related changes in plant tissue composition and (4) changes in nutrient uptake in relation to above-ground carbon gains.

N, P, K, Ca and Mg concentrations in post-burn graminoid vegetation were compared with clipped and with unburned vegetation during the post-burn growth season. One month after burning and clipping, nutrient concentrations in live grass shoots in the burned and clipped treatments were significantly higher than in the control. This effect, however, declined in the course of the season and, except for Ca, disappeared three months after onset of the treatments.

There were no significant differences in live grass shoot nutrient concentrations between burned and clipped plots which suggests that the increased nutrient concentration in post-fire regrowth is not due to increased soil nutrient supply via ash deposition. The relatively low input of nutrients through ash deposition, compared to the amount of nutrients released through mineralization during the first month after burning and to the total nutrient pools, supports this suggestion. There was no difference between burned and unburned vegetation in total root biomass and root nutrient concentrations. Relocation of nutrients from the roots to the new shoots did not, therefore, appear to be a cause of higher post-fire shoot nutrient concentrations.

The present study shows that in this relatively nutrient-rich savanna the increased nutrient concentration in above-ground post-fire regrowth is primarily due to increased leaf:stem ratios, rejuvenation of plant material, and the distribution of a similar amount of nutrients over less above-ground biomass.

Key words: East Africa, fire, plant nutrient concentration, savanna, soil

Introduction

In East African savanna systems fire is a common phenomenon that has a major impact on ecosystem structure and functioning (Hamilton 1974, Frost and Robertson 1987, Werger 1983). The most obvious effect of fire is the removal of old, dead vegetation, which is replaced by young regrowth, i.e. greenflush. Herbivores are attracted to this regrowth (McNaughton 1985, Moe et al. 1990, Sinclair 1977, Wilsey 1996), and feeding on post-fire regrowth leads to greater mass gains as compared to feeding on unburned vegetation (Anderson et al. 1970, Woolfolk et al. 1975).

The tendency of grazing herbivores to concentrate on post-fire regrowth is likely to be related to a greater foraging efficiency (McNaughton 1984), as well as a higher concentration of essential nutrients in the post-fire regrowth (Daubenmire 1968, McNaughton 1985). Numerous studies have shown that post-burn savanna vegetation has a higher nutrient concentration than unburned vegetation during the post-fire growth season (Batmanian and Haridasan 1985, Boerner 1982, Christensen 1977, Singh 1993). Causes for the increased above-ground nutrient concentrations of post-burn vegetation have been related to: (1) enhanced soil nutrient supply through ash (Boerner 1982, Christensen 1973, 1977) or increased mineralization (Dhillion and Anderson 1993, Hobbs and Schimel 1984, Hulbert 1988, Singh 1993), (2) rejuvenation and related changes in plant tissue composition (Christensen 1977, Frost and Robinson 1987, Gill 1974, Kauffman et al. 1994) and (3) relocation of nutrients from roots to shoot (Bowen and Pate 1993, Chapin and Van Cleve 1981, McNaughton et al. 1982).

The extent and duration in which the above-ground nutrient concentration of post-burn regrowth is enhanced varies with soil nutrient status (Boerner 1982, Christensen 1977), amount of plant material burned and hence ash produced (Van Reuler and Janssen 1993). It is also determined by the degree in which fire alters plant characteristics that influence plant nutrient concentrations, such as age and leaf:stem ratio (Chapin and Van Cleve 1981, Kauffman et al. 1994). For example, in nutrient-poor systems, where the greatest proportion of the system's nutrient pool is in above-ground biomass, the increased nutrient concentration in post-burn vegetation is due primarily to enhanced soil nutrient supply through ash (Boerner 1982, Cook 1994, Holt and Coventry 1990). In nutrient-rich systems, where the greatest proportion of the system's nutrient pool is below-ground, the increase in vegetation nutrient concentration is primarily expected to be through rejuvenatory effects, relocation of nutrients from roots to shoots and change in plant tissue composition (i.e. higher leaf to stem biomass ratios with leaves having higher nutrient concentrations) (Chapin and Van Cleve 1981, Frost and Robertson 1987). Finally, the extent to which fire increases concentration of specific nutrients in post-burn vegetation differs between the nutrients in question. This variation is related to the extent to which fire elevates the concentration of a specific nutrient and the extent to which nutrients are lost from the system through volatilisation and ash particles (Cook 1994, Pivello and Coutinho 1992, Raison et al. 1985). Although a large number of studies have investigated some of the above causes of increased macronutrient concentration in post-burn savanna vegetation (Christensen 1977, Frost 1992, Singh et al. 1991a,b), no studies have investigated all of the above factors simultaneously.

Compared to other savanna systems, East African savannas are relatively nutrient-rich (Medina 1987) and although general suggestions have been made (Frost and Robertson 1987, Lemon 1968), quantitative data describing the effects of fire on macronutrient dynamics for these systems are lacking. Therefore, the first aim of this study was to investigate the effects of fire on vegetation nutrient concentration and their underlying causes in an East African savanna.

We compared N, P, K, Ca and Mg concentrations of grass in burned, clipped and control plots during a growing season in a semi-arid savanna in Northern Tanzania. We determined to what extent the increased nutrient concentrations in above-ground biomass after fire were due to: (1) increased soil nutrient availability through ash deposition and increased mineralization, (2) relocation of nutrients from roots to the shoot, (3) rejuvenation and related changes in plant tissue composition, and (4) distribution of nutrients over less above-ground biomass due to a decreased biomass production in post-fire regrowth.

Although short-term effects of fire may be positive for vegetation nutrient concentrations, long-term effects may lead to a decline in vegetation nutrient concentration. In many of the East African savannas, fire frequencies have increased significantly during the past decades. Information from other savanna systems (Christensen 1977, Kauffman et al. 1998, Pivello and Coutinho 1992) suggest that high frequency of fire may result in significant losses of nutrients through volatilisation and erosion of ash, causing a decline in vegetation production (Cook 1994, Hayes and Seastedt 1989, Kauffman et al. 1993). To provide insight into the amount of nutrients lost through volatilisation and ash convection, we also measured the loss of nutrients after a single fire.

Material and methods

Study area

We conducted our study on the eastern border of Tarangire National Park, situated on the eastern side of the Great Rift Valley in northern Tanzania (4° S 37° E). The topography is gently undulating with slopes between 1 and 3 %. Soils consist of deep to very deep, well-drained, red sandy loams of Precambrian origin.



Figure 1: Monthly rainfall (mm) in the 1994/1995 wet season in the research area.

The rainy season extends from December to May with a peak in March and April (see Figure 1 for the rainfall data during the experimental period). Mean annual rainfall (August to July, after Prins and Loth 1988) is 452 mm, with high variability between years. Average maximum and minimum temperatures are 27 and 16°C, respectively. The vegetation is a wooded savanna with a tree cover of approximately 5%, primarily consisting of *Commiphora*, *Combretum* and *Acacia* species. Grass cover is well developed and is dominated by tufted perennial grasses. Dominant grasses are *Themeda triandra* Forssk, *Heteropogon contortus (L)* Roem and Schuldt and *Sehima nervosum* (Rottler) Stapf. Herb cover in the research area is negligible and was excluded from the analysis.

Vegetation in the research area is prone to regular burning due to high production of grass biomass and high occurrence of wild fires: on average the area burns once every three

years (P. Oliver pers. comm.). Herbivory occurs by large migratory herds of ungulates (Common wildebeest and Burchels zebra) which pass through at the beginning and end of the wet season and by residential African buffalo, African elephant and impala.

Experimental Design

Within the study area five blocks of 25 m x 25 m were selected via stratified random sampling, avoiding large trees and termite mounds. Within each block three plots of 5 m x 5 m were selected. Of these plots one was burned, one clipped to 5 cm height and one was used as untreated, control plot. Clipped treatment was imposed to investigate if variation in nutrient concentration due to burning was merely the result of factors related to biomass removal. Treatments were implemented in December at the end of the dry season (see Figure 1), the period in which traditional pastoralists burn (Homewood and Rodgers 1991). Pre-treatment above-ground dry mass was 412 ± 93 g m⁻² (SD). Temperature of experimental burns was measured with Tempil temperature pellets (Plainfield, New York) over the range of 150 to 700 °C with 50°C intervals. Burns were hot, ranging between 400 and 700 °C with an average temperature of 560 °C, and resulted in the removal of more than 95 % of plant material. Vegetation moisture content prior to burning was 19 ± 6.7% (SD) while average relative air humidity during fires was 35.2 ± 6.5% (SD). After the fire, ash samples were collected for chemical analysis.

Ash:Grass mass ratios were obtained by clipping all grass tufts from 1 m x 1 m plots (n=10) in the remaining area of the 25 m x 25 m experimental blocks. Five of these samples were dried and weighed to estimate grass dry weight while grass tufts of the other five samples were placed upright in a 1 m x 1 m metal frame in such a manner that the structure resembled the field situation. Accordingly the grass was burned after which ash was collected and weighed. Ash:Grass mass ratio and nutrient concentrations in grass and ash were used to calculate the loss of nutrients to the atmosphere. Loss was calculated as the difference between the mean nutrient content in the vegetation prior to burning (g m⁻²).

We obtained estimates of standing dry mass by harvesting $1 \text{ m}^2 (0.25 \text{ m x 4m})$ aboveground biomass in December before treatments were implemented and four times during the post-fire growing season (January, March, May and August). Harvested biomass was sorted into leaves, stem and dead material, air-dried to constant mass, weighed and analysed for N, P, K, Ca, and Mg. To exclude ontogenetic effects on plant nutrient concentration, similar nutrients were analysed in young, fully expanded grass leaves (young grass leaves from hereon) on the above-mentioned dates, except for August when young leaves were no longer present.

To investigate whether biomass removal through fire affected below-ground biomass and nutrient concentration, we sampled roots in January by taking duplo soil samples at 0-10 cm soil depth in each treatment plot with a metal pipe (n=5, $\emptyset = 4.2$ cm). Roots were separated from soil using a 2 mm sieve, dried to constant mass, weighed and analysed for nutrient content.

During the first month after implementation of treatments, we estimated soil nutrient availability and mineralization at 0-10 cm soil depth. We estimated soil nutrient availability by collecting soil samples with a metal pipe ($\emptyset = 4.2$ cm), prior to the implementation of treatments (December, T0) and one month after implementation of treatments (January, T1). Mineralization was estimated using stainless steel metal pipes ($\emptyset = 4.2$ cm) which were placed in the soil at T0 and removed at T1 (34 days incubation). All soil and mineralization samples were taken in duplicate in each treatment plot and mixed in the laboratory to reduce field variability and then sieved through a 2 mm mesh screen to remove small stones and root material (n=5). 10 g of the mixed sample was used to determine soil water content, which was analysed gravimetrically after drying at 100°C. The remaining sample was used to determine total soil nutrients concentrations as well as extractable soil nutrients. Net mineralization was estimated as the increment in extractable soil nutrients between T0 and T1.

Chemical Analyses

Prior to chemical analyses, ash, plant material and soil samples were digested using a modified Kjeldahl procedure with Se as a catalyst (Novozamsky et al. 1983). Soil organic matter was determined via combustion of soil samples at 550 °C for three hours. Plant-available N, K and Mg concentrations were extracted from soil using $0.01 M \text{ CaCl}_2$ solution (Houba et al. 1986) while P was extracted in a $0.1 M \text{ NaHCO}_3$ solution and Ca in an unbuffered $0.01 M \text{ BaCl}_2$ solution (Houba et al. 1995). Soil pH was measured in a $0.01 M \text{ CaCl}_2$ solution (Houba et al. 1986). N and P concentrations in destructed ash, plant and soil material, as well as extracted soil material, were analysed colorimetrically with a continuous flow analyser (Skalar SA-4000, The Netherlands) while K, Ca and Mg were analysed with an Atomic Absorption Spectrophotometer (Varian Spectra AA-600, Houten, The Netherlands).

Statistics

Data were statistically analysed using SPSS 7.0 statistical package. We analysed biomass and nutrient concentration of live biomass using a General Linear Model (GLM) with date of sampling and treatment as fixed factors and block as random factor. Analysis of variance was used to analyse treatment effects on root biomass as well as the nutrient concentrations of soil, roots, leaves, stems and young grass leaves in January. The nutrient concentration in young grass leaf mass was additionally analysed in an analysis of co-variance with treatment (burned, control) as factor and live standing biomass as co-variate. If necessary data were transformed to meet the requirements of parametric analysis. Differences between means were tested using a Tukey-HSD test with a level of significance of P<0.05.

Results

Effect of burning and clipping on above-ground nutrient concentrations and biomass

Figure 2 shows the development of the total above-ground biomass for the three treatments. Prior to the implementation of the treatments in December, the majority (90%) of the biomass consisted of dead material. After implementation, during the onset of the wet season, the plants quickly regained growth. Nine months later, three months after the start of the dry period (Figure 1), total above-ground biomass in burned and clipped treatments was similar again to that in the control (Figure 2). There was no significant difference between burned and clipped treatments in above-ground biomass, when compared over the full growing season (P>0.05).

The concentration of all macronutrients in living above-ground biomass declined during the experimental period (Figure 3, Table 1). For all macronutrients, except P, there was a clear treatment effect (Table 1). However, all nutrients including P showed a significant treatment x date interaction (Table 1). This was due to large treatment effects in January, which disappeared in the course of the season (Figure 3). In January, plants in the burned and clipped plots had higher nutrient concentrations than those in the control plots, but did not differ from each other (P>0.05). Three months after implementation (March) the concentration of macronutrients in living above-ground biomass was similar again with only small but significant differences (P<0.05) found for N and Ca, where the clipped treatment differed from the control in N concentration and the burned treatment differed from the clipped and control treatment in Ca concentration.



Figure 2: Total above-ground biomass \pm SE (g m⁻²) in burned, clipped and control treatments after implementation of treatments in December (N=5), + = burned, O = clipped, \blacktriangle = control.

Table 1: Analysis of the effect of treatment (n=3) and date (n=4) on total above-ground biomass, and on N, P, K, Ca and Mg concentrations in live above-ground biomass using a General Linear Model procedure. Treatment and date were entered as fixed factors and block (n=5) as random factor. F-values and degrees of freedom (df) are given with level of significance (* p < 0.05, **p < 0.01 and ***p < 0.001, ns not significant).

	Fixe	<u>ed</u>	Random			
7	Freatment (T)	Date (D)	Block (B)	<u></u> D	T*B	D*B
df	2	3	4	6	8	12
Biomass	126***	145***	2.27 ^{ns}	26.4***	1.50 ^{ns}	1.20 ^{ns}
N	31.3***	195***	2.46 ^{ns}	10. 6***	1.34 ^{ns}	1.63 ^{ns}
Р	0.27 ^{ns}	30.3***	1.91 ^{ns}	5.79**	4.76**	1.44 ^{ns}
К	9.36**	366***	8.54 ^{ns}	2.61*	0.82 ^{ns}	0.40 ^{ns}
Ca	24.4***	47.6***	0.57 ^{ns}	9.00***	0.43 ^{ns}	1.57 ^{ns}
Mg	17.1**	55.4***	2.93 ^{ns}	9.18***	0.61 ^{ns}	0.98 ^{ns}



Figure 3: Concentrations of N, P, K, Ca and Mg \pm SE (mg g⁻¹) in live standing biomass in burned, clipped and control treatments after implementation of treatments in December. + = burned, O = clipped, \blacktriangle = control.

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Possible causes for increased nutrient concentrations in post-fire regrowth:

Increased soil nutrient pools?

Loss of nutrients through volatilisation and ash convection after the fire varied between nutrients: there was only 12% loss of Mg while loss of N was 93% (Table 2a). However, in all cases the losses were negligible when expressed as a percentage of the total nutrient pool (Table 2a). The addition of nutrients via ash in the burned plots did not significantly increase availability of nutrients, since we found no significant differences between burned and clipped plots in the amount of extractable nutrients during the first month after implementation of treatments (Table 2b). Furthermore, biomass removal through burning and clipping did neither affect nutrient availability significantly, nor soil pH and organic matter.

Table 2 a) Averages of above- and below-ground (0-10 cm) nutrient pools $(g m^2)$ in a semi-arid savanna, northern Tanzania, before and after burning. The amount of nutrients lost through volatilisation and ash convection is expressed as a percentage of the above-ground as well as total nutrient pool before burning. b) Organic matter (OM, %) and pH in the top10 cm soil prior to implementation of treatments (T0) and one month later in burned, clipped and control plots as well as soil nutrient release (mg m⁻² day⁻¹) during the first month (December to January) after implementation of treatments, analysed through CaCl₂ extraction. Different superscript letters indicate significant differences between treatments for P<0.05.

a)			N	Р	K	Ca	Mg
Total soil nutrient pool			118	33	313	176	303
Above-ground nutrient pool prior to fire		2.02	0.31	1.32	1.77	0.33	
Nutrients in ash after fire			0.15	0.21	0.53	1.02	0.29
Nutrients lost from above-ground nutrient pool			93	32	60	42	12
Nutrients lost from total nutrient pool			1.6	0.30	0.25	0.42	0.01
				Soil nutrient release			
b)	OM	pН	Ν	P	K	Ca	Mg
T0	4.19 ^a	5.84ª		····			
Burned	4.09 ^a	5.98ª	58.3ª	5.44ª	140 [*]	441 ^ª	122"
Clipped	4.16ª	5.86ª	46.6ª	6.27 ^a	67.2ª	278 *	99ª
Control	4.08 ^ª	5.93ª	51.5°	6.51ª	115ª	413ª	133°

Redistribution of nutrients from roots?

Because general treatment effects on live biomass nutrient concentrations were only found in January, we will focus the next part of the results on the first harvesting interval (December to January). Also, we will only compare the burned and control treatments, because there were no differences between the burned and clipped treatments in live biomass nutrient concentrations and in soil nutrient pools (Figure 3, P>0.05, except Ca).

Burning did not affect the absolute amount of root biomass (Table 3). Roots of the burned treatment did however tend to have lower nutrient concentrations than those of the control, but this difference was only significant for Mg (Table 3).

Table 3: Average of root biomass $(g m^2)$ and N, P, K, Ca and Mg concentrations $(m g^{-1})$ in the 0-10 cm soil layer in December, and in the burned and control treatments in January, one month after implementation of treatments. Different letters in superscript indicate significant differences between means (Tukey P<0.05).

	December	January		
		Burned	Control	
Root Biomass	263.2ª	297.2	306.3 ^a	
N	6.8ª	4.5*	5.7ª	
Р	0.53 °	0.54 °	0.63 ^a	
Κ	2.7 °	2.6 °	3.4 ^a	
Ca	7.8 ^a	4.7°	5.1 ª	
Mg	1.9ª	2.1 ª	3.2 ^b	

Increased leaf:stem ratio?

The leaf:stem ratio in the post-fire regrowth was significantly higher than that in the control (Figure 4; $F_{1,32}$ = 33.1, P<0.001). However, this difference declined during the growing season ($F_{3,32}$ =14.75, P<0.001) with a large difference in January (, P<0.05), whereas no significant differences between the treatments occurred three months after burning (March) onwards (P>0.05) (Figure 4).



Figure 4: Leaf-stem ratios \pm SE in burned and control treatments after implementation of treatments in December (N=5). + = burned, \blacktriangle = control.





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Figure 5 shows the concentration of all nutrients analysed in the burned and control plots in January for young grass leaves as well as total live grass leaves and stems. Analysis of leaf and stem nutrient concentration in burned and control treatments revealed that, compared to stems, leaves had higher concentrations for N (+37% for both burned and control, P<0.05), K (+8% burned, P>0.05, +36% control, P<0.05), Ca (+50% burned, +74.5% control, P<0.05) and Mg (+27.6% burned, +42.9% control, P<0.05), but not for P (Table 4). By calculating above-ground biomass concentrations of N, K, Ca and Mg in the burned treatment using the leaf:stem ratio of the control plots, we quantified the effect of the increased leaf:stem ratio on nutrient concentrations. Increased leaf:stem ratios in post-burn vegetation significantly increased the concentration of live grass N by 9%, Ca by 12.7% and Mg by 6.5%, while for K and P this effect was not significant (p>0.05). Figure 5 also demonstrates that burning increased stem nutrient concentrations more than leaf nutrient concentrations (see also Table 4).

Table 4: Analysis of the effect of treatment (burned, control) and plant material (leaf, stem) on N, P, K, Ca and Mg concentration of material sampled in January. F-values and degrees of freedom (df) are given with level of significance ($^{*}P < 0.05$, $^{**}P < 0.01$ and $^{***}P < 0.001$, ns non-significant).

	Treatment (T)	Plant material (M)	T*M
di	1	1	1
1	v 53.6 ^{***}	197***	5.55*
]	2 17.7**	1.76 ^{ns}	2.12 ^{ns}
ŀ	10.6 ^{**}	15.1**	5.20*
C	a 83.8***	590***	30.6***
M	g55.3 ^{***}	56.0***	0.83 ^{ns}

<u>Rejuvenation?</u>

One month after implementation of the treatments above-ground biomass of the burned plots was, on average, younger than that of the control plots. To evaluate the effect of leaf age on nutrient concentrations, randomly sampled young grass leaves were compared with all grass leaves harvested per m². Young grass leaves had significantly higher concentrations of N ($F_{1,9}$ = 13.3, P<0.01), P ($F_{1,9}$ = 6.46, P<0.05) and Ca ($F_{1,9}$ =10.3, P< 0.01) as compared to all grass leaves (Figure 5). For K and Mg there were no clear differences between the younger and all grass leaves (Figure 5).

However, we also found that nutrient concentrations in the young leaves were generally higher for the burned plots (Figure 5). This was particularly the case for N (+15.4%, P<0.05) and K (+18.4%, P<0.05), while for the other nutrients the trend was not significant.

Distribution of nutrients over less biomass?

Because young grass leaves of the burned plots also had higher N and K concentrations, factors other than rejuvenation and changes in leaf:stem ratios must be involved in explaining the higher nutrient concentrations of the burned vegetation. Since biomass increment in the first month after burning on the burned plots was less than that on the control plots (62.3 gm^{-2} as opposed to 95.7 gm⁻², respectively, P<0.05), higher N and K concentrations in young leaves might simply be the result of the distribution of the nutrients over less biomass. To test this we analysed the nutrient concentrations of the young grass leaves in January in an analysis of co-variance, with treatment (burned, control) as factor and the amount of live standing biomass in January as co-variate (Table 5). This analysis demonstrates that the amount of live standing biomass accounted for a significant amount of variance in N and K concentration of young grass leaves while treatment did not.

Table 5: F-values and R² of an analysis of co-variance with concentration of nutrients in young grass leaves as dependent, treatment (burned, control) as factor and live standing biomass (g m⁻²) as co-variate (* P < 0.05, ** P < 0.01 and *** P < 0.001, ^{ns} not significant).

Nutrients in young grass leaves	Treatment (T)	Live biomass (B)	T*B	R ²
N	1.87 ^{ns}	37.1***	1.70 ^{ns}	70%
Р	0.00 ^{ns}	1.83 ^{ns}	0.02 ^{ns}	15%
К	0.75 ^{ns}	23.2***	1.31 ^{ns}	64%
Ca	0.87 ^{ns}	7.22*	0.07 ^{ns}	33%
Mg	1.24 ^{ns}	1.27 ^{ns}	1.96 ^{ns}	31%

Discussion

Our study demonstrates that post-fire above-ground regrowth had higher macronutrient concentrations than unburned vegetation, but that effect is short-lived. One month after burning post-fire regrowth had 53% higher N, 40% higher P, 23% higher K, 64% higher Ca, and 73% higher Mg concentrations, but after three months concentrations had declined to the levels of the control plots. These results concur with previous research reported elsewhere (Batmanian and Haridasan 1985, Boerner 1982, Christensen 1977, Frost and Robertson 1987, Mes 1958, Miller and Watson 1974, Singh 1993). Accordingly the question is to which factors these higher nutrient concentrations in the first month after burning can be attributed.

Increased soil nutrient pools?

To what extent were the increased nutrient concentrations in post-fire regrowth directly due to increased soil nutrient pools? Burning oxidises organically bound elements in the vegetation and litter (Frost and Robertson 1987). These nutrients are either released in forms available to plants through ash deposition or are lost through volatilisation and ash convection (Boerner 1982, Christensen 1973, Cook 1994, Frost and Robertson 1987). The extent to which addition of nutrients via ash contributes to enhanced soil nutrient supply, and consequently vegetation nutrient status, depends, however, on the total amount of available nutrients in the soil (Boerner 1982, Christensen 1977). The present data suggest that the amount of nutrients released via ash does not substantially increase the total amount of plant available nutrients. This is supported by the comparison of live biomass nutrient concentrations in January between burned plots and clipped plots, where no ash deposition occurred. Except for Ca, nutrient concentrations did not differ between these two treatments. We therefore conclude that ash does not significantly contribute to the increased post-fire vegetation nutrient concentration in these relatively nutrient-rich savanna systems.

Indirect effects of fire on plant-available soil nutrients can arise through enhanced mineralization rates after fire (Christensen 1973, Dhillion and Anderson 1993, Hobbs and Schimel 1984, Sharrow and Write1977, Singh et al. 1991a,b). This can be due to increased soil temperatures (Knapp and Seastedt 1986, Raison 1979, Savage 1980), reduced soil C:N ratios (Daubenmire 1975, Frost and Robertson 1987) or alterations in soil pH (Haynes et al. 1986). We did not find any effect of burning or clipping on soil pH or organic matter content, but the average maximum soil temperature in burned and clipped plots in the first month after burning was significantly higher as compared to that in control plots (37° C and 33° C, respectively, P<0.01). However, this did not lead to an increase in mineralization as was suggested by previous studies (Knapp and Seastedt 1986, Raison 1979, Savage 1980). Mineralization rates were highly variable but burning and clipping did not significantly contribute to the overall variation (Table 2b). This suggests that ash deposition did not affect soil nutrient release and that at these high soil temperatures mineralization rates are limited by factors other than soil temperature such as soil water (also see Haynes 1986). Taken together, the present data show that in this savanna system fire does not enhance plantavailable soil nutrients and that other factors have to be considered to explain the increased post-fire vegetation nutrient concentration.

Redistribution of nutrients from roots?

The increased nutrient concentrations in post-fire shoot regrowth could be due to a redistribution of nutrients from roots (Chapin and Van Cleve 1981). For example, biomass and nutrient concentrations of roots can decline following shoot defoliation, due to increased allocation of resources to the new shoots or because roots die due to carbon shortage (McNaughton 1979, Menaut and Cesar 1982, Ojima et al. 1994, Richards 1984). Our data suggest that above-ground biomass removal does not increase allocation of resources from the root to the shoot since, compared to the control plots, plants in the burned plots did not have significantly lower root biomass and macronutrient concentrations, except for Mg (Table 3). In the beginning of the wet season, soil water and nutrient supply are ample (McNaughton 1985 Menaut 1987). In situations where nutrient supply and carbon storage are sufficient to allow for fast regrowth of new leaves, biomass removal does not have to lead to decline in root biomass (Bowen and Pate 1993, Bond and Van Wilgen 1996, McNaughton and Chapin 1985). We therefore suggest that, in relatively nutrient-rich savannas, redistribution of nutrients from the roots is of less importance in explaining enhanced post-fire regrowth nutrient concentration than in nutrient-poorer savannas (Menaut and Cesar 1982).

Increased leaf:stem ratio and rejuvenatory effects?

Frost (1992) proposed that the primary causes of increased post-fire vegetation nutrient concentration may be the differences in age and leaf:stem composition of plant tissue. Indeed, we found that one month after burning leaf:stem ratios were twice as high as those in the control treatment. Similar to the above-ground biomass nutrient concentrations, this difference had declined significantly in March, three months after burning. Hence, depending on the degree to which concentrations between leaf and stem differed for the individual nutrients, the increased leaf:stem ratio contributed to the increased nutrient concentration of post-fire regrowth. However, leaves and stems of post-fire regrowth had higher nutrient concentrations than those in the control. Therefore, factors other than variation in leaf:stem ratios must also play a role. Various authors have related higher post-fire regrowth nutrient concentrations than old plant tissue (Christensen 1977, Jones and Wilson 1987). We found that rejuvenatory effects indeed contributed to the observed differences between post-fire regrowth and unburned vegetation for N, P and Ca.

The relative importance of morphological and ontogenetic factors for the explanation of differences in nutrient concentration between post-fire regrowth and unburned vegetation depends on the developmental stage of the vegetation prior to burning (Chapin and Van Cleve 1981). The large differences in stem nutrient concentrations between burned and control, as compared to those in the leaves, would support this. In the control plots all leaf material was produced from the start of the growing season onwards, whereas a significant amount of stem material (approximately 33%) originated from the previous year.

Distribution of nutrients over less biomass?

Because young grass leaves in burned vegetation also showed higher nutrient concentrations, especially for N and K, rejuvenatory effects and increased leaf-stem ratios alone cannot fully explain the enhanced nutrient concentration in post-fire regrowth. Chapin and Van Cleve (1981) reported that in post-fire vegetation reduced above-ground photosynthesising plant material leads to reduced production. Under conditions where soil nutrient supply and root biomass remain unaffected, reduced production in the post-fire regrowth will lead to the distribution of nutrients over less biomass and thus to higher nutrient concentrations (Chapin and Van Cleve 1981, Frost and Robertson 1987, Wilson and Keddy 1986). Our data concur with these findings since the N and K concentrations of young leaves were highly correlated with live standing biomass, whereas the effect of burning gave no additional explanation. The same appears when, during the first month after burning, the N uptake in the burned and control plots are compared with the production figures of that period. Average N uptake in burned and control treatments was 821 and 683 mg m⁻², respectively (P>0.05). Biomass increment in this period was 62.3 and 95.7 g m⁻² (P<0.05) and therefore the nitrogen in postfire regrowth was distributed over a smaller amount of carbon. Since burning did not affect the density of grass tufts per unit area, this conclusion also holds when data are reworked on a per plant basis, instead of the current analysis per square meter.

In contrast to N and K, we did not find any correlation between live standing biomass and the P concentration of young leaves. This might indicate that, as opposed to many other savanna systems (Penning de Vries et al. 1980), P is not a major limiting nutrient in our study area. The N:P ratios of grass material, which ranged between 6 and 7, also suggest that N rather than P is the major limiting nutrient (Penning de Vries et al. 1980)

Nutrient loss through volatilisation and ash convection: implications

When regarding the amount of nutrients lost through fire, the present data show that loss of nitrogen is most profound, with 96% of above-ground nitrogen being released to the

atmosphere (Table 2a). Relative losses of nutrients correspond with those found by Trabaud (1994) in Southern France and Villecourt et al. (1980) in Ivory Coast. The high loss of nitrogen as compared to that of the other macro-nutrients is due to the low volatilisation temperature of nitrogen which is around 200°C, while volatilisation of the other nutrients does not occur below 500 °C (Boerner 1982). Consequently, frequent burning may lead to such loss of nitrogen that the productivity of the system starts to decrease. This is especially so when the major part of the nitrogen pool is found above-ground and nitrogen return through N₂-fixation and -deposition are low (Turner et al. 1997). Although the amount of nitrogen lost from the above-ground nitrogen pool is significant, it is only 1.7 % of the total nitrogen pool in our study. Frost and Robertson (1987), reviewing the literature on nitrogen losses through fire, concluded that annual losses through fire in savanna systems do not exceed inputs through atmospheric deposition and fixation. N₂-fixation may even be enhanced since other studies have shown that N₂-fixing plants increase in cover after burning due to improved light conditions and increased soil temperature (Lemon 1967). Therefore, as opposed to nutrient poor systems (Cook 1994) or systems where large amounts of nutrients are found aboveground (Kauffman et al. 1993, 1998), burning in relatively nutrient-rich savanna systems does not lead to depletion of the nitrogen pool. This agrees with Trapnell et al. (1976) who found that soil nitrogen and organic matter levels were not significantly affected by annual burning over long periods of time in Zambia. However, when regarding long-term effects of fire on nutrient loss, fire itself is not the only factor that must be considered (Raison 1979). Grazing herbivores are attracted to burned vegetation. Since herbivores primarily select green, nutrient-rich plant material, the removal of nutrients by herbivores can be as much as five times the amount removed through fire (Hobbs et al. 1991). Therefore, especially in the East Africa savannas where high densities of grazing herbivores occur, predictions on long-term effects of fire on savanna nutrient pools should also consider the effect of grazing on nutrient pools (Hobbs et al. 1991).

In conclusion, the present study demonstrates that in a relatively nutrient-rich savanna system fire enhances the nutrient concentration of above-ground biomass but that these effects are short-lived and vary between nutrients. The enhanced nutrient concentrations in the first period after burning are not caused by increased soil nutrient supply, or by nutrient relocation from roots to shoot. They are due to increased leaf-stem ratios, reduced age of plant tissue and the distribution of nutrients over less biomass in post-burn vegetation. Furthermore, this study suggests that, in these nutrient-rich savannas, long term effects of repeated burning on vegetation nutrient status are not as extreme as compared to nutrient poor savannas.

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Chapter 4

Feedback relations between vegetation biomass and soil water content in a semi-arid savanna

C.A.D.M. van de Vijver, M. Rietkerk and H.H.T. Prins (submitted)

Summary

In African savanna systems above-ground biomass removal through herbivory and fire affects vegetation production and nutrient content. We investigated the effect of removal of above-ground biomass on soil water content and subsequent effects on grass tuft production and nutrient content in a factorial experiment in a semi-arid savanna in northern Tanzania.

We distinguished between removal of grass tufts and litter. We also investigated the mechanisms which accounted for the variation in soil water content when grass tufts and litter were removed. Removal of grass tufts did not significantly affect soil water content, but it did increase grass leaf N content of the remaining tufts. We attribute this effect to increased availability of soil N per individual grass tuft due to the reduction of the number of grass tufts per unit area. Removal of litter caused a significant decline in soil water content which we ascribe to an increased loss of water through evaporation. This effect outbalanced the reduced interception of rainfall after litter removal. Removal of litter additionally reduced grass leaf P content.

Removal of grass tufts did not affect production of the remaining tufts over the experimental period but removal of litter did. We conclude that this effect primarily was mediated by a reduced soil water content in the absence of litter, rather than by a reduced grass leaf P content, since soil P was not a main limiting factor during the experimental period. Fire removes both standing biomass and litter, while herbivores primarily select green standing biomass. We therefore suggest that the effect of above-ground biomass removal through fire on vegetation production and nutrient content, via changes in soil water content, is greater than the effect of above-ground biomass removal through herbivores.

Key words: African savannas, production, fire, herbivory, litter, standing biomass, soil water, nitrogen, phosphorus

Introduction

It has long been recognized that fire and herbivory affect vegetation production and nutrient content in savanna systems through a variety of direct and indirect effects (McNaughton 1985, Ruess 1985, Frost and Robertson 1987). This especially is the case for African savanna systems where high levels of wildlife and livestock herbivory and reoccurring, mainly anthropogenic, fires have affected savanna ecosystems for millennia (Walker 1981).

One of the effects of fire and herbivory on vegetation production and nutrient content operates through the removal of above-ground biomass. This results in changes in the plant's physiology, due to rejuvenation of plant material, and reallocation of carbon and nutrients as result of changes in shoot:root ratios. Furthermore, removed biomass by fire and herbivores is deposited back to the system in the form of ash and dung, respectively, and can thus result in an increase in nutrient availability (McNaughton 1985, see also Chapter 3). Besides these factors mentioned, biomass removal also affects vegetation production and nutrient content by altering soil water content, which is the main factor determining annual production in semiarid savanna systems (Walker 1981, Goldstein and Sarmiento 1985, Chapter 2).

In this study we focus on the effects of above-ground biomass removal on soil water content and the consequences for production and nutrient content of the vegetation in a semiarid savanna. Soil water content is determined by the amount of water that infiltrates into the soil (I) and the amount of infiltrated water that is subsequently lost through evapotranspiration (E) and drainage (D). Thus, the change in soil water content in the rooting zone (ΔS) is

$$\Delta S = I - (E + D) \tag{1}$$

where

$$I = P - (E_i + R) \tag{2}$$

P being the amount of rainfall, and E_i and *R* the loss of rain water through interception and run-off respectively. These determinants of soil water content are not only affected by amount and intensity of rain, slope and soil physical properties but also by above-ground biomass (Kelly and Walker 1976, Fischer and Turner 1978, Van Wijngaarden 1985, Dunin 1987).

Above-ground biomass can have positive as well as negative effects on soil water content. Positive effects are through reduced run-off, increased infiltration rates and lower evaporation rates, and negative effects are through increased interception and transpiration, due to increased area transpiring surface (Savage 1980, Eldridge 1993). Thus, the net effect of

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above-ground biomass removal on soil water content depends on the balance between these processes. Hereby the degree in which biomass removal affects these processes depends on its extent and frequency. In situations of intensive biomass removal over several decades a decline in soil water occurs which primarily is attributable to increased levels of run-off (Redmann 1978, Knapp 1984). In situations of moderate biomass removal, however, run-off is of less importance in the soil water balance and here enhanced soil water content can occur due to lower levels of interception (Cass et al 1984, Dunin 1987). This especially is the case when rain falls in a large amount of small rain showers because in this situation the amount intercepted, relative to the total amount fallen, increases (Scholes and Walker 1993) and therefore removal of biomass will lead to a stronger reduction of interception than when the same amount of rain would fall in one single event.

Finally, the effect of biomass removal on the soil water content also depends on whether the removed biomass consists of live or dead material, such as litter. Litter is amorphous and primarily has a positive effect on the soil water content by reducing evaporation rates, due to reduced soil temperature and wind speed at soil surface (Kelly and Walker 1976, Savage 1980). Moreover, since litter is compacted to the ground, it tends to have a stronger positive effect on infiltration than standing biomass which may even negatively affect the soil water content since it largely consists of live, transpiring material, which results in loss of soil water.

Although fire and herbivores both remove above-ground biomass, they differ in the selectivity in which this occurs. Fire is non-selective, removing the bulk of biomass and litter whereas herbivores are selective, primarily consuming green, palatable plant material (Prins and Beekman 1989). On the basis of the aforementioned it can be expected that there will be variation in the effects of biomass removal by herbivory or fire on soil water content and subsequently on vegetation production and nutrient content.

In this study we investigated how different levels of above-ground biomass removal, as well as the composition of biomass removed (i.e. standing biomass or litter) affect soil water content and subsequently vegetation production and nutrient content. To this end, we measured soil water content, production and nutrient content of grass tufts in a semi-arid savanna during a rainy season in untreated plots and plots from which litter and various amounts of standing biomass were removed. Additionally, we investigated the mechanisms through which above-ground biomass affects soil water content (i.e. the effect on the different soil water balance parameters, see Equations 1 and 2) by performing rain simulation experiments in which the water content of soil and vegetation was monitored for several days.

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Methods

Study area

The study was carried out on the eastern boundary of Tarangire National Park, situated on the eastern side of the Great Rift Valley in Northern Tanzania (4 ° S 37° E). The topography is gently undulating with slopes between 1 and 3 %. Soils consist of deep to very deep, well drained, red sandy loarns of Precambrian origin. Mean annual rainfall is 452 mm but is very variable within and between seasons. The rainy season extends from December to May with a peak in March and April. Average maximum temperature is 27°C and average minimum is 16°C. The vegetation is a wooded savanna with a tree cover of approximately 5%, primarily consisting of *Commiphora, Combretum* and *Acacia* species. Grass cover is well developed and is dominated by tufted perennial grasses. Dominant grasses are *Themeda triandra* Forssk, *Heteropogon contortus (L)* Roem and Schuldt and *Sehima nervosum* (Rottler) Stapf. Herb cover in the research area is negligible.

The vegetation is prone to regular burning due to high production of grass biomass and high occurrence of fires; on average the area burns once every three years (Van de Vijver, unpubl.). Herbivory occurs by large migratory herds of ungulates (common wildebeest and Burchels zebra) which pass through at the beginning and end of the wet season and by residential African buffalo, African elephant and impala (Lamprey 1964, Kahurananga and Silkiluwasha 1997).

Rainfall data

A self-registering rain gauge with data logger (Eijkelkamp Agrisearch Equipment b.v., The Netherlands) was used to measure the amount, distribution and intensity of rain showers over the season. Data were collected from August 1993 to August 1996. Recording interval of the logger was 30 minutes. A rainfall event was recorded as one separate shower when the time interval between rainfall events was more than 1 hour. Yearly rainfall averages were obtained by summing the amounts of individual showers between August and July (after Prins and Loth, 1988).

Experimental design

The research consisted of three separate experiments. The first experiment was set up to investigate the effect of biomass removal on soil water content and consequently grass production and nutrient content (*Experiment 1*). The second was a rain simulation experiment to investigate which parameters of the soil water balance (Equations 1 and 2) cause the changes in soil water content due to biomass removal. (*Experiment 2*). The third experiment was performed to investigate how the amount of rain water intercepted is affected by biomass (live and dead) and rainfall amount (*Experiment 3*), since we expected interception to have an important effect on soil water content (Cass et al. 1984, Scholes and Walker 1993).

Experiment 1

We selected a total of 30 experimental plots of 5 m x 5 m via stratified random sampling in an area of one hectare whereby trees, shrubs and termite mounds were avoided. We imposed treatments by manually removing predetermined amounts of biomass whereby we distinguished between removal of whole grass tufts (tuft treatment) and removal of litter (litter treatment). Tuft treatment consisted of three levels: '75' which was the field situation (control) of approximately 75% tuft cover, '50' in which tuft cover was reduced to 50% and '25' in which tuft cover was reduced to 25%. We reduced tuft cover by cutting away randomly selected grass tufts below the apical meristem, to prevent resprouting during the experiment. Removal of tufts led to the following tuft density: 3.2 tufts per m² for the '75' tuft treatment, 2.0 for the '50' tuft treatment and 1.6 for the '25' tuft treatment. Litter treatment consisted of two levels: total removal of litter (-) and no removal (+). Thus there were six treatments (75+, 75-, 50+, 50-, 25+ and 25-), each being replicated five times. The experimental trial ran from March to August 1996.

To determine soil water content we collected soil samples five times during the research period (March, April, May, June and July) with a metal pipe ($\emptyset = 4.2$ cm) at four different soil depths (0-10, 10-20, 20-30 and 30-40 cm). Per plot and depth we took two subsamples which we bulked to reduce variability. Soil water content was measured gravimetrically after drying at 100 °C.

To determine the effect of above-ground biomass removal on grass water content we measured the grass water content in the different treatments on the same dates that the soil samples were taken. We used the relative water content of young, fully expanded grass leaves as a measure of variation in grass water content in the different treatments (Schmidt and Kaiser 1987, Lo Gullo and Salleo 1988). Samples were taken at 09.00 am, 01.00 pm and 05.00 pm (East African Standard Time). Approximately five grams of fully expanded young grass leaves were collected per plot and weighed (W_{field}). Samples were then placed in water for 24 hours and weighed again after removal of hanging water (W_{H2O}). Finally, samples were dried (60 °C, 48 hours) to obtain dry weight (W_{dry}). Relative grass leaf water content was subsequently calculated as: ($W_{field} - W_{dry}$) / ($W_{H2O} - W_{dry}$). Grass leaf samples used for determining relative water content were also used to analyse nitrogen (N) and phosphorus (P) content of grass leaf material. Hereby, we bulked the samples that were taken at three different times in the day. Prior to chemical analysis samples were ground through a 1 mm sieve and digested using a modified Kjeldahl procedure with Se as a catalyst (Chapman 1976). Grass leaf N and P concentrations were determined colorimetrically with a continuous flow analyser (Skalar SA-4000).

We estimated production by comparing biomass of grass tufts at the beginning of the research period (March) with the biomass at the end (August), whereby a correction was made for decomposition (Cox and Waithaka 1989). All grass samples were dried to a constant weight prior to weighing. We used five randomly selected tufts that were removed for the '50' and '25' tuft treatments at the beginning of the experiment to estimate average tuft biomass in March. At the end of the experiment we harvested all tufts and litter from the plots. Here also five randomly selected tufts were used to estimate average tuft biomass per treatment in August. Difference in biomass allocation between treatments was measured by weighing sorted leaf, stem and dead biomass.

We used a full factorial ANOVA to analyse treatment effects on soil water content and the production, nutrient content and water content of grass tufts. If necessary data were transformed to meet with the conditions for ANOVA (log transformation for biomass data and arcsine for ratios) (Sokal and Rolff 1981). Differences between means were analysed with a Tukey-HSD test.

Experiment 2

We investigated the effect of biomass removal on the various parameters affecting soil water content by measuring the soil and grass water content for three days, after 7 mm of rain was applied over a period of 10 minutes to 2 m x 1 m plots which varied in tuft cover and presence of litter. The 7 mm rain shower was used since this represents a typical rain shower (based on 4 years of rainfall data collected at Park Head Quarters situated 40 km north-west of the research area). Tuft and litter treatments were obtained in the same manner as in the previous

experiment, but the 50+ and 50- treatments were left out. Thus, there were four treatments (75+, 75-, 25+ and 25-). Each treatment was replicated five times and the experiment was carried out twice, once in the wet season (April 1996) and once in the post-rain period (July 1996). We simulated rain showers with a watering can with a one metre wide nozzle which distributed water over the plots evenly.

We measured soil water content in the same way as in the previous experiment, but the 30-40 cm soil depth was not sampled. Variation in infiltration was estimated by comparing the soil water content in the different treatments 30 minutes after applying 7 mm of rain (T1). We estimated water loss through evapotranspiration and percolation to deeper layers of the rooting zone by comparing T1 with the soil water content 1 day after (T2) and two days after (T3) rain simulation. Treatment effects on relative grass water content were analysed by comparing the relative water content of young, fully expanded grass leaves on the T2 and T3 soil sampling dates at 09.00 am, 01.00 pm and 05.00 pm. Procedures were the same as in *Experiment 1*. Since the majority of grass water data collected during the wet season trial (April 1996) were lost, analysis of grass water data was restricted to the post-rain period trial (July 1996). Data analysis occurred as explained for the previous experiment.

Experiment 3

Firstly, we investigated the effect of amount of rainfall and above-ground biomass (including and excluding litter) on the amount of rain intercepted by simulating three different rain showers (7, 3 and 1.5 mm respectively) over a period of 10 minutes on 2 m x 1 m plots which varied in tuft biomass and presence or absence of litter. Within 30 minutes after rain simulation, all biomass from the plots was harvested and weighed, whereafter it was dried and weighed again. After subtraction of the vegetation water content, which we obtained from unrained control plots, we compared the amount of water that was intercepted for the different treatments. Replication per treatment was five.

Secondly, we investigated the effect of the weight percentage of dead grass material on interception by applying 7 mm of rain over a period of 10 minutes on 2 m x 1 m plots for which the percentage of dead grass material was estimated. Plots were categorized in four different groups: 100%, 75%, 50% and 25% dead grass material, using four replicates.

Finally, we measured the total amount of water that potentially could be intercepted by the vegetation by harvesting all biomass from 1 m^2 plots, weighing it, soaking it with water in a drum and weighing it again. Here, we compared two treatments: with and without litter, using five replicates.

Since biomass was a continuous variable in the first mentioned interception experiment, we analysed the data with an ANCOVA with litter and rain as main effects and biomass as co-variate. The effect of weight percentage of dead grass material on interception was analysed with a one-way ANOVA. Finally, the total amount of water that was intercepted by biomass, expressed in gram water per gram biomass, was compared with that of the 1.5, 3 and 7 mm of rain in an ANOVA with rain and litter as main factors.

Results

Rainfall data

Total rainfall in the 1995-1996 rain season was 513 mm, of which the largest proportion fell in February, March and April (30, 20 and 30 % of total respectively), and which was higher than the average of 452 mm. Although the average rainfall for the study area was only based on three years of rainfall, higher than average rainfall was also recorded in rainfall stations around Tarangire National Park (TCP 1998).





Figure 1: The cumulative amount of annual rainfall produced by rain showers of X mm (= — -- —) and the probability distribution of a rain shower exceeding X mm (P(x>X), = —). Three year daily rainfall records were used for rainfall averages and to calculate the probability distribution (August 1993 - July 1996). Average total number of showers per year is 70, average annual rainfall = 452 mm.

Based on the rain data from the 1993-1996 period, mean annual rainfall was produced by an average of 70 rain showers per season. Rain showers up to 10 mm accounted for approximately 80% of the rain events (Figure 1). These showers, however, only produced about 30 % of the mean annual rainfall, while intensive rain showers of more than 65 mm were rare but produced about 25 % of the mean annual rainfall.



Figure. 2: Soil water content (weight %, \pm SE, n = 5) of the 0-10 cm soil depth in plots varying in tuft cover ('75', '50' and '25'), with litter (dark bars) and without litter (hatched bars) on five different dates in the growing season.

Experiment 1

Soil water content

Tuft treatment did not significantly affect soil water content while removal of litter significantly reduced soil water content (Table 1, Figure 2). Analysis of variance, with soil depth included as factor (Table 1), revealed that the effect of litter was affected by soil depth but this effect was primarily restricted to the top 10 cm soil layer. However, the effect of litter on the soil water content depended on sampling date because the effect was reduced as soil water content declined after the rains had stopped and soils started to dry up.

Table 1. F-values and levels of significance (*: $p \le 0.05$, **: $p \le 0.01$, ***: $p \le 0.001$, ns = not significant, n = 5) as a result of ANOVA with soil water content of inividual sampled depths (H₂O per layer, soil water content of the total profile (H₂O profile), water content, N and P content and N:P ratios of grass leaves as well as production of grass tufts and leaf weight ratios (LWR) as dependent variables, and litter (L), tuft cover (T), date of sampling (S), depth of sampling (D) and hour of sampling (H) as factors. - indicates that the factor or interaction concerned was not in the design. If not significant, higher order interactions are not shown.

Factor	Dependent									
	Soil			Grass						
	H ₂ O per layer (%)	H ₂ O profile (%)	Leaf H ₂ O (%)	Leaf N (%)	Leaf P (%)	Leaf N:P-ratio	Tuft production (g day ⁻¹)	LWR		
L	124***	58.0***	7.84**	3.09 ^{ns}	4.03 [*]	12.8**	19.4***	1.15 ^{ns}		
Т	2.59 ^{ns}	0.60 ^{ns}	5.01**	27.9***	0.09 ^{ns}	8.73***	0.51 ^{ns}	8.01**		
S	1083***	563***	100***	120***	33.0***	10.8***	-	-		
D	279***	-	-	-	-	-	-	-		
Н	-	-	25.4***	-	-	-	-	-		
LxT	1.46 ^{ns}	1.25 ^{ns}	3.1*	0.12 ^{ns}	0.67 ^{ns}	2.31 ^{ns}	2.14 ^{ns}	0.49 ^{ns}		
LxS	5.18***	2.52^{*}	1.39 ^{ns}	1.36 ^{⊪s}	1.44 ^{ns}	1.11 ^{ns}	-	-		
LxD	20.8***	-	-	-	-	-	-	-		
LxH	-	-	0.11 ^{ns}	-	-	-	-	-		
TxS	2.33*	1.58 ^{ns}	3.61***	0.23 ^{ns}	1.27 ^{ns}	1.80 ^{ns}	-	-		
TxD	1.65 ^{ns}	-	-	-	-	-	-	-		
ТхH	-	-	0.58 ^{ns}	-	-	-	-	-		
SxD	76.4***	-	-	-	-	-	-	-		
SxH	-	-	5.21***	-	-	-	-	-		
LxSxD	2.75**	-	-	-	-	-	-	-		

Grass leaf water content

Both removal of litter and grass tufts affected grass water content significantly (Table 1, Figure 3). Litter removal generally led to a reduction in grass leaf water content, while removal of grass tufts generally led to an increase in grass water content. These effects, however, were only apparent in the post-rain period (July, August) while the reduction of grass water content, due to the removal of litter, was primarily restricted to the '25' tuft treatment (Figure 3).



Figure 3: Relative grass leaf water content (weight %, \pm SE, n = 5) measured in the morning, midday and afternoon in plots varying in tuft cover ('75', '50' and '25'), with litter (dark bars) and without litter (hatched bars), in April and July.

Grass tuft production

Individual grass tuft production (g day⁻¹) in plots with litter was higher than in those without litter (Table 1, Figure 4a). Figure 4a suggests that the response of grass tuft production to litter was dependent on tuft cover, but this interaction was not significant. Although tuft cover did not affect production it did affect the live leaf weight ratio (LWR, live leaf weight per total tuft weight), which increased with decreasing tuft cover (Table 1, Figure 4b).



Figure 4: (a) Grass tuft production (g day⁻¹) and (b) ratio of leaf weight to total weight (LWR) (\pm SE, n = 5) in plots varying in tuft cover ('75', '50' and '25') with litter (dark bars) and without litter (hatched bars).

N and P content

The N and P content of young grass leaves decreased significantly during the season (Table 1, Figure 5). The P content of young grass leaves in plots with litter was higher than in plots without. Plots with litter tended to have a lower grass leaf N content than plots without litter, but this effect was not significant. N content increased significantly with decreasing tuft cover, while P content did not.

We analysed N:P ratios of grass leaves during the season for different tuft and litter treatments to determine which of the two nutrients was most limiting for growth (Verhoeven et al. 1996, Koerselman and Meuleman 1996). N is most limiting if N:P ratios are below 6.67, whereas P is most limiting if the ratios are above 25 (Penning de Vries and Djitèye 1991).

During our experiments, N was more limiting than P, because the N:P ratios fluctuated around 6.67 for all data and treatments sampled. ANOVA also revealed that litter significantly reduced the N:P ratio, which was a result of increased P content in grass leaves in treatments with litter. The N:P ratios also decreased significantly with increasing tuft cover, which was due to a decline in N content (Table 1, Figure 5).



Figure 5: Grass leaf N and P content (%) in plots varying in tuft cover ('75', '50' and '25' resp.) and litter (+ = with litter, - = without litter) in April ($\textcircled{\bullet}$), June ($\textcircled{\bullet}$) and July (\blacksquare). — : N:P ratio = 25, -----: N:P ratio = 6.7.

Experiment 2

Soil water content

Tuft removal did not significantly affect soil water content while significant sampling time and litter effects were primarily restricted to the 0-10 cm soil layer. At T1, plots with litter had a dryer 0-10 cm soil layer than plots without litter, while at T2 and T3 the reverse was true (Table 2, Figure 6). No significant effect of tuft removal on soil water content was found.



Figure 6: Soil water content (weight %, \pm SE, n = 5) in April and July in different soil layers (0-10, 10-20, 20-30 cm) in plots varying in tuft cover (75 and 25 %) and litter (+ = with litter, - = without litter) ½ an hour after (T1, dark bars), 1 day (T2, hatched bars) and 2 days (T3, open bars) after administering 7 mm of water.

Table 2: F-values and levels of significance (* $p \le 0.05$, ** $p \le 0.01$, *** $p \le 0.001$, ns = not significant, - = factor or interaction not in the design, n = 5) as a result of ANOVA with soil water content and relative grass leaf water content after 7 mm rain simulation as dependent variables, and litter (L), tuft cover (T), interval after rain simulation (I), depth of sampling (D) and hour of sampling (H) as factors.. If not significant, higher order interactions are not shown.

Factor	Soil water content (%)	Soil water content (%)	Relative grass leaf water content (%)
	(April)	(July)	(July)
L	13.1***	0.28 ^{ns}	1.57 ^{ns}
Т	0.21 ^{ns}	2.51 ^{ns}	1.41 ^{ns}
I	10.52***	2.88 ^{ns}	19.27***
D	38.84***	43.52***	-
н	-	-	0.67^{ns}
LxT	0.29 ^{ns}	0.40^{ns}	0.94 ^{ns}
LxI	6.08**	2.33 ^{ns}	1.18 ^{ns}
LxD	2.69*	3.12*	-
LxH	-	-	0.36 ^{ns}
TxI	0.78 ^{ns}	0.151 ^{ns}	8.74**
TxD	2.81"	1.19 ^{ns}	-
ТхН	-	-	0.13 ^{ns}
IxD	8.33***	5.39***	-
IxH	-	-	1.74 ^{ns}
LxIxD	3.09*	2.49*	-

Grass leaf water content

Relative grass leaf water content varied significantly during the day (9.00, 13.00, 17.00 hours resp.) (Table 2). Furthermore, a significant decline was found in relative grass water content between the day after rain simulation and the following day (T2 and T3 respectively) (Table 2, Figure 7) The decline, however, depended on tuft treatment since the '75' tuft treatment showed no significant decline while the '25' tuft treatment did ($p \le 0.01$). No significant effects were found for litter.



Figure 7: Relative grass leaf water content (%, \pm SE, n = 5) of young grass leaves at midday in plots varying in tuft cover (75 and 25 %) and litter (+ = with litter, - = without litter) 1 day (T2, dark bars) and 2 days (T3, hatched bars) after applying 7 mm of water in the July rain simulation experiment.

Experiment 3

Since we observed no run-off during rain simulation, variance in the amount of water infiltrating into the soil could be attributed to interception (see Equation 2). The amount of water intercepted (g_{water} m⁻²) significantly increased with above-ground biomass (Table 3). After we excluded the effect of biomass, we found a significantly higher interception in plots with litter than in plots without litter and interception also significantly increased with rainfall. Similar results were found when interception was expressed in mm of rain

intercepted (Tables 3, 4). Expressed as a percentage of the amount of rain applied, interception significantly declined with increasing rainfall. Hereby, an interaction with litter was found, the litter plots having a higher percentage intercepted for the 1.5 and 3 mm rain treatments while litter did not significantly affect the percentage intercepted for the 7 mm rain treatment. The percentage of rain water intercepted reached up to 58% in plots with litter if rain showers of 1.5 mm were applied (Tables 3, 4).

Table 3: F-values and levels of significance (*: $p \le 0.05$, **: $p \le 0.01$, ***: $p \le 0.001$, ns = not significant, n = 5) as a result of ANCOVA with interception of rainwater by above-ground herbaceous biomass as dependent variable, litter and rain amount applied as factors, and biomass as co-variate. Interception is expressed in: gram water m⁻², mm and percentage of rainfall intercepted.

Dependent		Factor		Co-variate
Interception	Litter	Rain (mm)	Litter x Rain	Biomass
g _{water} m ⁻²	8.83**	4.97*	0.67 ^{ns}	6.0*
mm	20.3***	3.93*	0.33 ^{ns}	38.7***
%	15.1**	55.9***	16.4***	26.5***

Table 4: Interception by above-ground biomass (expressed in mm of rainfall intercepted and % of the amount of rainfall applied) in plots with litter (+) and without litter (-) and for different amounts of rainfall applied. Average biomass of plots with and without litter was 698 and 479 g m⁻² respectively.

			Rain	(mm)		
	1	.5	-	3	,	7
	Li	tter	Li	tter	Li	tter
Interception	+	-	+		+	-
mm	0.87	0.50	0.99	0.50	1.11	0.69
%	58	33	33	17	16	10

The maximum amount of water intercepted by grass vegetation was 1.74 $g_{water} g_{biomass}^{-1}$ and 1.48 $g_{water} g_{biomass}^{-1}$ for litter and non-litter plots, respectively. These values were not significantly different from the interception during the experimentally applied 7 mm rain shower which were 1.59 $g_{water} g_{biomass}^{-1}$ and 1.44 $g_{water} g_{biomass}^{-1}$ for litter and non-litter plots, respectively. Finally, grass tufts with a high proportion of dead material intercepted significantly more rainfall than tufts with a low proportion of dead material (Figure 8).



Figure 8: Amount of water intercepted $(g_{water} g_{biomass}^{-1})$ for biomass varying in the weight percentage of dead material. Letters denote significant differences between means ($p \le 0.05$).

Discussion

Herbivory and fire affect production and nutrient content of vegetation by removing aboveground biomass (McNaughton 1985, Ruess 1985, Frost and Robertson 1987). We investigated how above-ground biomass removal affects soil water content and the consequences of this effect on production and nutrient content of grass tufts. Tuft removal did not affect soil water content over the season while removal of litter clearly reduced the soil water content over the season (Table 1, Figure 2). This effect, however, declined as soils became drier in the postrain period (June, July) and also was primarily restricted to the 0-10 cm soil layer. Accordingly the question arises which parameters of the soil water balance (Equations 1 and 2) were affected by biomass removal that consequently resulted in the observed effects?

At the onset of rain, the first effect that above-ground biomass has on the soil water balance is through interception of rain water which evaporates from the vegetation without even reaching the soil (Daubenmire 1968, Scholes and Walker 1993). We found that interception, expressed in g_{water} m⁻² and in mm, increased with increasing biomass, rainfall and with the presence of litter (Tables 3, 4). Higher interception for biomass with litter can be ascribed to the lack of a wax layer and broken cell wall structure in dead plant material which accordingly allows a higher absorption of water. The maximum amount of water that grass

vegetation can intercept ($g_{water} g_{biomass}^{-1}$) did not differ from the interception during a 7 mm rain shower. This suggests that above 7 mm of rainfall no additional rainfall is intercepted by the vegetation. Hence, with an annual rainfall of 452 mm, distributed over 70 showers, and an average grass biomass including litter of 698 g m⁻², annual interception in the research area would probably range somewhere between 61 mm and 78 mm, which is 13 to 17 % of annual rainfall. This is in line with Dunin (1987) and Scholes and Walker (1993), who found values of 11 and 18.5 % respectively. As heavy showers are infrequent, the light showers are of greater importance for keeping up the soil water content during the growing season (Fischer and Turner 1978). Since it is especially during these light showers that interception is relatively high (Table 4), our data therefore suggest that, especially when vegetation contains much dead material, total annual interception can have a significant effect on the soil water content over the growing season and hence affect vegetation production.

However, removal of litter reduced the soil water content during the experimental period (Figure 2). This indicates that positive effects of litter on soil water content somehow outbalanced the negative effect of litter through interception. Litter can have a positive effect on soil water content by reducing run-off and loss of infiltrated water through evaporation (Kelly and Walker 1976, Fischer and Turner 1978, Cass et al. 1983). The 7 mm of rain applied in a period of 10 minutes in the rain simulation of *Experiment 2* did not cause run-off. Soil water content even tended to be higher in plots without litter immediately after rain simulation (T1) (Figure 6) which can only be explained by lower levels of interception. That we found no run-off can be ascribed to the high infiltration rate of the soil in the research area, which was a sandy loam, and that rain primarily occurred in light showers of several millimetres. Furthermore, as biomass removal only occurred at the start of the experiment, changes in soil physical properties which reduce infiltration rates could not yet have taken place. Present data therefore suggest that under high infiltration conditions run-off is a less prominent factor in the soil water balance and will therefore be less affected by removal of above-ground biomass (see also Snyman and Fouché 1991, Veenendaal 1991, Eldridge 1993, Scholes and Walker 1993). Consequently, the positive effect of litter on the soil water content must be ascribed to reduced loss of infiltrated water (Equations 1 and 2). This is supported by data from the rain simulation experiment (Experiment 2) as decline in soil water content in the days after rain simulation was significant in plots where litter was removed while no significant decline was found in plots with litter.

Loss of infiltrated water can be the result of evapotranspiration and percolation of water into deeper layers. Data from the rain simulation experiment show that loss through percolation cannot explain the decline of soil water in the 0-10 cm soil layer, since we found no increase in soil water content in the deeper soil layers (Figs 6a, b). This finding is in line with Fischer and Turner (1978), Scholes and Walker (1993) and Snyman (1993), who found that percolation of water into deeper soil layers only plays an important role during exceptionally wet years. Therefore, loss of soil water must be attributed to evapotranspiration.

The rain simulation of *Experiment 2* showed that the tuft treatment did not significantly affect loss of soil water, while the effect of litter primarily was restricted to the 0-10 cm soil layer (Figure 6). Since litter is amorphous, primarily affecting evaporation, and since loss of soil water through evaporation only occurs from the top soil, data suggest that variation in loss due to litter removal primarily is attributed to changes in evaporation rates. This effect is due to the insulatory effect of litter which decreases convective vapour loss to the air and keeps soil temperature lower than bare soil (Kelly and Walker 1976, Chase and Boudouresque 1987). For example, midday temperatures of top soil where litter is removed can be 12 ° C higher than of top soil where litter is present (pers. obs., Savage 1980). However, after the rains stopped and the soil started drying up, the positive insulatory effect of litter declined.

Thus, we conclude that the higher soil water content in plots with litter during the season (Figure 2) is the result of reduced evaporation, whereby this positive effect on soil water content more than compensated for the negative effect of interception.

Removal of litter led to decline in grass tuft production during the growing season while removal of tufts did not. This reduced production could not only be the result of a decline in soil water content, but can also be due to reduced soil nutrients since these are the second limiting factor for plant growth in semi-arid savanna systems, N and P in particular (Walker 1981, Medina 1987). Besides their individual content, also the ratio of these two nutrients in plant material is important in determining which one is most limiting for growth (Verhoeven et al. 1996). Removal of litter caused a decline in grass leaf P content but did not significantly affect grass leaf N content. Hence, reduced grass tuft production in plots without litter may also be the result of reduced P content in grass material. However, since N:P ratios indicate that P was not a main limiting factor (Medina 1987, Penning de Vries and Djitèye 1991, Lüttge 1997), and grass leaf N content was not affected by litter removal, we ascribe the observed decline in tuft production after litter removal to a decline in soil water content rather than to a decline in grass leaf P content.

However, Figure 4a suggests that, although not significant, the negative effect of litter removal on production increased with decreasing tuft cover, an effect that was not observed for the soil water content. Besides affecting the soil water balance, removal of above-ground biomass also affects microclimatic conditions by increasing surface wind speed, air temperature, radiant flux density and by reducing relative air humidity, which accordingly affect vegetation water content (Knapp 1984, Savage 1980). This can result in reduced relative grass water content when transpired water is not replenished, and can thus explain the lower relative grass water content in the '25' tuft plots without litter at the end of the rainy season in July when soil started to dry up (Figure 3). The same mechanism may also explain why we only found a significant decline in grass water content from T2 to T3 in the rain simulation experiment for the '25' tuft treatment and not for the '75' tuft treatment, while this was not found for the soil water content (Figs 6, 7). Therefore, the increased relative grass leaf water content with decreasing tuft cover in the post rain period, which again does not correspond with the soil water content data, is a surprising observation since the reverse would be expected (Figure 3). The higher grass leaf water content could however be explained by a greater availability of water per individual grass tuft, as there were less tufts present per unit area in the lower tuft cover treatments. Likewise the higher grass leaf N content in the lower tuft cover treatments could be explained.

The increased relative grass water content during the post-rain period, however, did not result in an increased production in plots with low tuft cover. The data therefore suggest that the greatest proportion of production occurred in the wet months. However, a significant higher LWR, found at the end of the season in plots with low tuft cover (Figure 4b), does suggest that plots with lower tuft cover can prolong their growth period into the dry season due to higher biomass of photosynthetically active leaf material in this period.

Our study clearly demonstrates that removal of above-ground biomass affects soil water content and consequently vegetation production and nutrient content. The effect of removal of litter was more pronounced than that of tuft cover. Since fire removes both standing biomass and litter, while herbivores primarily remove standing biomass, our data suggest that the effect of fire on soil water content and subsequently vegetation production is more pronounced than the effect of herbivory.

Recent theoretical work has shown that when biomass reduction exceeds a certain threshold, production may collapse as a consequence of reduced water infiltration (Rietkerk and Van de Koppel 1997, Rietkerk et al. 1997). In our study, reduction in production indeed occurred when a significant amount of above-ground biomass was removed. However, we found that this effect was mainly due to enhanced loss of soil water through evaporation when litter was removed, and not the consequence of reduced water infiltration.

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Chapter 5

Effects of grazing on forage quality and forage quantity for migratory ungulates in the Masai Ecosystem, northern Tanzania.

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Summary

Several observations in Africa indicate that restriction of seasonal movement of migratory ungulates can cause a significant decline in numbers of the populations involved. Causes for this decline have, however, hardly been addressed. We investigated if the dry season range of migratory wildebeest and zebra in the Masai Ecosystem, northern Tanzania, can sustain current populations when access to the wet season range would be restricted and migratory herds would reside in the dry season range year-round. Both forage quality and quantity were considered.

Grazing itself can affect herbivore forage quality and quantity. Presently, however, the dry season range is not grazed during the wet season by migratory ungulates. This will be the case when access to the wet season range is restricted. We therefore performed clipping experiments to investigate how grazing affects forage quality and quantity in the dry season range.

Clipping had a positive effect on the quality of forage whereby the clipped vegetation had higher proportions of live and leaf material as compared to unclipped vegetation. Moreover, clipping increased the concentration of nutrients in leaf material, N and P in particular. Although clipping improved the mineral nutrient concentration of forage, the concentrations were not sufficient to meet herbivore nutrient requirements, especially P. Furthermore, the present study suggests that through grazing the annual production of forage in the dry season range would be reduced and that also forage quantity would be insufficient for the current herbivore numbers.

We therefore conclude that, if the animals were forced to stay year-round in their dry season range, current population numbers of migratory herds would decline. Consequently this study shows the necessity of protecting current wet season ranges from the expanding human activities to safeguard this migratory system.

Key words: East Africa, migratory system, forage quantity and quality, simulated grazing, forage requirements, savanna

Introduction

East African savannas are (still) renown for the large-scale seasonal migration of large grazing ungulates (Lamprey 1964, Pennycuick 1975, Prins 1987, Fryxell and Sinclair 1988, Williamson et al. 1988). Generally, the annual cycle of migration involves a concentration in areas with permanent water availability during the dry season, followed by a movement and dispersion into surrounding grazing areas at the onset of the wet season. This movement into the wet season range has been explained by the higher nutritious quality of the grasslands in the wet season range as compared to the dry season range (Kreulen 1975, Bell 1982, McNaughton 1990, Murray 1995, Voeten 1999). During the dry season, most grasses are in a senescent phase and forage quality and quantity are limited in both the wet season range and dry season range. The animals however concentrate in their dry season range lack water in the dry season. Table 1 shows the annual cycle of migratory herbivores in East Africa with the main factors involved: forage quantity, forage quality and drinking water.

Table	1: Migra	tory pop	pulations	move	between	a wet	season	range	in (the w	et se	eason	and	a dry
seasor	n range in.	the dry	season. I	he sug	gested m	ain fac	tors inv	volved	are	indica	ated.	++ =	suffi	cient,
= in	sufficient	and ? =	unknown	n when	grazed.									

		Ar	rea
		Wet season range	Dry season range
	-	Forage quality : ++	Forage quality : ?
	Wet	Forage quantity : ++	Forage quantity : ?
a		Water : ++	Water : ++
Season		Forage quality :	Forage quality :
	Dry	Forage quantity :	Forage quantity :
	-	Water :	Water : ++

The once free roaming wildlife of East Africa has been greatly affected by increasing human populations and by expanding agricultural activities (Lamprey 1983, Prins 1992, Happold 1995, Newmark 1996). Nowadays most wildlife is confined to National Parks and the consequences of this confinement for migratory wildlife are becoming an important management issue. In some areas, like in the Serengeti-Mara migratory system in Tanzania and Kenya, large tracks of the wet season range lie within the protected area of the National Park. In many other migratory systems, however, the wet season range is situated in unprotected areas and these areas becoming less accessible for migratory ungulates.

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A migratory system where this is occurring is the Masai-ecosystem, northern Tanzania (Prins 1987). Most migratory wildebeest (*Connochaetes taurinus*) and zebra (*Equus burchelli*) in the Masai-ecosystem congregate in Tarangire National Park during the dry season. The Tarangire River, which runs through this park, is one of the few permanent dry season water sources in the 35.000 km² Masai-ecosystem. During the wet season most of the wildebeest and zebra move to the Simanjiro plains. Due to human settlement and agricultural activities the accessibility of these unprotected plains is increasingly becoming restricted (Borner 1985, TWCM 1995a). Consequently the question is if the dry season range, Tarangire National Park, would be able to sustain current migratory populations when the wet season range becomes inaccessible and migratory herds would be restricted to the dry season range year-round.

Research in the migratory systems of the Serengeti (McNaughton 1990, Murray 1995) and Masai ecosystems (Voeten 1999) shows that during the wet season, the forage quality in the wet season ranges meets herbivore nutritional requirements, while in the dry season range it does not during this period. However, most comparisons between wet and dry season range forage quantity and quality were done during the wet season on grazed wet season range herbage and ungrazed dry season range herbage. Regarding this comparison, the absence of herbivory in the dry season range during the wet season can be of importance since vegetation production and mineral concentration in the vegetation in African savannas are not only determined by rainfall and soil nutrients (Bell 1982, Le Houerou et al. 1988), but also by herbivory itself. Indeed, much research has shown that grazing can keep the vegetation in an open, young, productive stage of growth and can improve plant available soil nutrients and water status, thus contributing to the maintenance of a high above ground production of good quality (McNaughton 1979, 1984, Hilbert et al. 1981, Coppock 1983, Georgiadis et al. 1989, Georgiadis and McNaughton 1990, Oesterheld and McNaughton 1991, Milchunas et al. 1995, Hobbs 1996, but see, Belsky 1987, Verkaar 1988, Belsky et al. 1993). When the migratory herbivores would be forced to stay in the dry season range year-round, the animals will also graze there during the wet season which is the growing season. Therefore, this study also investigated the effects of grazing on vegetation production and nutrient status during the wet season in the dry season range and if these effects would improve dry season range forage to levels that meet herbivore requirements. This information subsequently was used to predict if current migratory populations could be sustained in the park when migratory routes were to be cut off and the animals would reside in the park year- round.

We investigated the effects of clipping on biomass production, composition of above ground standing crop and mineral concentrations. We simulated medium and heavy grazing pressure by frequently clipping the vegetation down to two different heights. The experiment was conducted on mixed grasslands on the three main soil types of the dry season range to incorporate possible differences between soil types in grass production, in mineral contents and in their response to clipping. Finally we placed the outcome of the clipping experiment in the context of forage requirements of the migratory herds and discussed if, through grazing, forage quantity and quality in the dry season range is sufficiently enhanced to sustain current migratory populations if their range would be restricted to Tarangire National Park.

Methods

Study area

Data were collected in Tarangire National Park (4° S, 36° E, and 1200 m above sea level), the dry season range of migratory herds of wildebeest and zebra. The Park is located in northern Tanzania on the eastern side of the Great Rift Valley and encompasses an area of approximately 2600 km². The Tarangire River runs through the Park and is the main permanent dry season water supply within the entire 35 000 km² Masai Ecosystem (Prins 1987) in which the Park lies. The vegetation mainly consists of grasslands and open savanna woodlands (Chuwa 1996). Dominant grass species of the grasslands and floodplains are *Bothriochloa insculpta, Brachiaria spp., Cenchrus ciliaris, Dactyloctenium aegypticum, Digitaria spp., Pennisetum mezianum, Sporobolus spp., and Urochloa spp.* Dominant tree species of the woodlands in the riverine area are *Acacia tortilis, Balanites aegyptiaca, Adansonia digitata, Maerua triphylla* and *Grewia spp.*. Soils are of lacustrine and alluvial origin underlain by pre-Cambrian gneiss rock.

Average annual rainfall is 620 mm with high temporal and spatial variability. Most rain falls between December and May. During the dry season (June-November) rainfall is very rare. Large migratory herds of wildebeest and plains zebra are present during the dry season but leave the Park at the onset of the wet season. Other abundant herbivores in Tarangire N.P. are African elephant (*Loxodonta africana*), African buffalo (*Syncerus caffer*), impala

(Aepyceros melampus), Coke's hartebeest (Alcelaphus buselaphus cokii), giraffe (Giraffa camelopardalis), Grant's gazelle (Gazella granti), oryx (Oryx gazella) and eland antelope (Tragelaphus oryx). These species, although more sedentary also disperse over a larger area during the wet season and very few animals remain in the Park in this period.

Data collection

In Tarangire National Park we selected 3 study sites: one on the open plains, one on a ridge slope and one in the river valley area, close to Tarangire river. These sites were selected because the soil types on which these sites were located represent the main soil types on which the migratory ungulates congregate during the dry season (TWCM 1995a). The Plains site was situated on a brownish loarn soil with medium fertility and medium drainage capacity. This site consisted of open grassland, dominated by *Chloris virgata, Dactyloctenium aegyptium, Urochloa mosambicensis and Sporobolus ioclados.* The Ridge site was located halfway up the ridge on red loarny sand soil with medium fertility and high drainage capacity in open woodland dominated the tree species *Combretum apiculatum, Balanites aegyptiaca, Adansonia digitata* and *Maerua triphylla.* The grass layer was dominated by: *Dactyloctenium aegyptium, Urochloa mosambicensis, Cynodon nlemfuensis,* and *Cenchrus ciliaris.* The River site was located on a light clay soil with high fertility and low drainage capacity on a floodplain next to the Tarangire river, and the vegetation was dominated by the grasses *Pogonarthria squarrosa, Brachiaria decumbens and Urochloa mosambicensis.*

Clipping experiment

The experiment was started in January 1996 in the beginning of the wet season and lasted until September 1996, which is halfway the dry season. The 1995-1996 rainy season was wetter than average and annual rainfall was 943 mm. First rains came in the second half of December 1995 and last showers occurred at the end of May 1996. The Plains and Ridge sites were set up at the 15th of January and sampled 9 times. The River site was set up two weeks later and sampled 8 times. In each site, five chain-link fence exclosures of 2.4 m by 1.2 m were put up. Each exclosure was divided in three equal parts, each of them receiving a different clipping treatment: the heavy treatment was clipped to 3 cm, the medium treatment was clipped to 15 cm and the control treatment was left unclipped. The clipping height of the medium treatment was based on average grass height found in the Simanjiro plains, the area that the Tarangire ungulates use during the wet season (Voeten 1999).

The heavy and medium treatments were clipped every 3 to 4 weeks and the clipped biomass was collected. At each clipping date we also measured the above ground biomass of the control treatment. The control sample was harvested to ground level in a 0.5 m x 1.0 m frame in matched plots outside the experimental exclosures, because the exclosures were not big enough to harvest the control treatment inside the exclosure throughout the growing season. Since most large ungulates are outside the Park during most of the growing season, vegetation outside the exclosures could be considered as ungrazed. Only at the end of the growing season, when the animals had returned to the Park, the control was clipped inside the exclosures.

At the end of the experiment, when grasses had stopped growing, the medium treatment was also harvested to ground level to determine the above ground annual production. For the heavy treatment the biomass below 3 cm was negligible and not included in further analysis. All plant material was hand-sorted into green leaf, green stem and dead material, dried to a constant weight and weighed.

To describe the soil properties of the different sites, we collected soil samples from each site in May 1996. Samples were collected with a metal pipe ($\emptyset = 4.2$ cm) from 0-10 cm soil depth. All soil samples were taken in duplicate and mixed to account for spatial variability. Bulked samples were sieved through a 2-mm mesh screen to remove small stones and root material. Samples were dried to a constant weight and stored for chemical analyses.

Chemical analysis

Prior to chemical analyses, plant material and soil samples were digested using a modified Kjeldahl procedure with Selenium as a catalyst (Novozamsky et al. 1983). Total nitrogen (N) and phosphorus (P) concentrations in plant and soil material were analyzed colorimetrically using a continuous-flow analyser (Skalar SA-4000, The Netherlands). Total calcium (Ca) and sodium (Na) concentrations were analyzed with an Atomic Absorption Spectrophotometer (Varian Spectra AA-600, The Netherlands). Soil organic matter content was determined via combustion of soil samples at 550 °C for 3 hours. Soil pH was determined in the extraction residue from soil, using a 0.01 M CaCl₂ solution (Houba et al. 1986).
Data analysis

Seasonal changes in total above ground biomass, proportion of leaves and proportion of live biomass were compared between clipping treatments and sites. The above ground biomass of the medium clipping treatment was calculated as the regrowth from each period plus an estimated value of the biomass between ground level and 15 cm. The latter was calculated by interpolating the biomass harvested at the end of the experiment for the medium treatment to the biomass at the beginning of the experiment. The proportion of leaves was calculated as leaf biomass divided by the sum of the leaf and stem biomass. The proportion of live material was calculated as live biomass divided by the sum of live and dead biomass.

Annual above ground production was calculated for both total biomass and live biomass. For the control treatment, annual above ground production was calculated as the sum of the positive biomass increments between harvests (McNaughton 1979). For the heavy and medium clipping treatments, annual production was calculated as the sum of the removed regrowth plus, for the medium treatment, the biomass harvested at the end of the experiment. Differences in annual live and total production between treatments and sites were tested with a two-way analysis of variance followed by Tukey HSD contrasts.

Seasonal changes in the proportion of leaves, proportion of live biomass and nutrient concentrations (N, P, Ca and Na) in green leaf were analysed per site, using an analysis of covariance with clipping treatment as the independent factor and harvest time as a the covariate. To analyse differences between treatments, we subsequently tested the treatments pair wise (medium-control, heavy-control and medium-heavy) per site, using an analysis of covariance with clipping treatment as the independent factor and harvest time as a covariate.

Prior to statistical analyses, data were either log-transformed (biomass-data) or arcsine-transformed (proportions and mineral nutrient concentrations) to adjust for deviations of normality and to improve homogeneity of variance. All statistical calculations were performed with SPSS 7.0 for Windows.

Forage production and requirements

To calculate the total forage availability for herbivores, we first determined the total surface area of the soil types that we investigated in Tarangire NP (unpublished data C.A.D.M. Van de Vijver). Other soil types were excluded since the vegetation in these areas, such as forest, dense woodlands and swamps, do not form important habitat types for the migratory herbivores (TWCM 1995a). Subsequently, we estimated the total annual production of the graminoid vegetation for the selected part of the Park by multiplying the measured annual production in each of the three study sites with the total area of the soil type of the study site and accordingly adding up the three figures. Total forage requirements of all large herbivore species were estimated by multiplying the individual intake requirements by the herbivore population numbers (TWCM 1995a,b). The intake requirements were estimated assuming an average daily intake of dry matter of 2.5 % of a herbivore's bodyweight (Van Wijngaarden 1985, p.102). Grass intake of the intermediate feeders (Hofmann 1989) such as elephant and Grant's gazelle were taken from Hofmann (1973), Drent and Prins (1987) and Estes (1991). Mineral requirements for P, Ca, and Na during lactation and pregnancy were taken from Murray (1995) who adjusted AFRC (1991) cattle requirements for wildebeest. The minimum nitrogen requirement for maintenance was set at 1.3 % (Van Soest 1994).

Results

Soils

The soil of the River site was more fertile than the Plains and Ridge sites with significantly higher concentrations of total nitrogen, phosphorus, calcium and sodium as well as a higher organic matter content (Table 2). Only total soil nitrogen and soil pH did not differ significantly between the River site and the Plains site.

Table 2: Mean values of total soil nutrients, soil organic matter and pH. Different letters denote significant differences (one-way ANOVA, P < 0.001 and Tukey-HSD contrasts).

Site	N (%)	P (%)	Ca (%)	Na (%)	Soil Organic matter (%)	pН
Ridge	0.06 *	0.04 ª	0.35 ª	0.05 *	3.04 °	5.86 *
Plains	0.10 ^{ab}	0.02 ª	0.35 ª	0.03 ^b	4.96 ^b	6.24 ^b
River	0.16 ^b	0.11 ^b	0.63 ^b	0.10°	10.61 °	6.16 ^b

Above ground biomass and production

In the beginning of the wet season, the vegetation recovered well from the clipping treatments (Fig.1). This recovery especially occurred in the Ridge and River site (Fig 1b and 1c). At the end of the wet season however, the growth response of the clipped treatments in all sites declined.



Figure 1: Average total above ground biomass (g m⁻², \pm SE) for the control, unclipped (+ — +) and medium clipped (∇ — ∇) treatment as well as regrowth of the medium clipped (\odot - \odot) and heavy clipped (O-O) treatments. Total above ground biomass for the medium clipped treatment is the sum of the regrowth plus the interpolated biomass under 15 cm. Day of harvest: day 0 = 1-01-1996 and day 235 = 22-08-1996.

Compared to the results of the unclipped control, clipping resulted in a significantly lower annual production of live above ground biomass (Fig 2a) and total above ground biomass (Fig 2b) in all three sites. For both live and total biomass production, the response to clipping did however differ between sites (site x treatment interaction: $F_{4, 36} = 3.09$, P < 0.05; $F_{4, 36} = 3.45$, P < 0.05 respectively). In the River site, which had the highest annual production,

the clipped treatments recovered relatively less, as compared to the control, than in the Plains and Ridge sites. This was especially so for the annual live production of the medium clipped treatment which produced only 36 % of the control treatment on the River site as compared to 64 % on the Plains site and 46 % on the Ridge site. The medium and heavy clipped plots did not show many significant differences. Only in the Plains and Ridge sites, the annual total production differed significantly between heavy and medium clipped plots.



Figure 2: Mean annual live (a) and total (b) production $(g \text{ m}^2 \text{ yr.}^1, \pm \text{SE})$ for the control unclipped, $(=\Box)$, medium $(=\Box)$ and heavy $(=\Box)$ clipped in the Plains, Ridge and River site in Tarangire National Park. Different letters denote significant differences (Tukey HSD, p<0.05). (see also data analyses in the material and methods section).

Composition of biomass

In general, clipping maintained the proportion of live material rather constant (Fig 3a,b,c). The proportion of live material was primarily affected by date of harvest, thus by the time in the growing season (Table 3). Pairwise comparisons between treatments per site showed that, in the course of the experiment, the unclipped plots decreased significantly more in the proportion of live material than both the clipped plots (date x treatment interaction for medium-control in the Plains site: $F_{1,76} = 94.76$, P<0.001, in the Ridge site: $F_{1, 59} = 61.80$, P<0.001 and in the River site: $F_{1, 58} = 16.97$, P<0.001; date x treatment interaction for heavy-control in the Plains site: $F_{1, 74} = 81.28$, P<0.001 and in the Ridge site: $F_{1, 61} = 93.56$, P<0.001). Only in the River site (Fig.3c), the decrease in proportion of live biomass for the heavy treatment and the control did not differ significantly. Also no significant differences were found between the medium and heavy clipping treatments.



Figure 3: Mean proportions of live material (a,b,c) and leaves (d,e,f) for the control, unclipped (+ - +), medium clipped $(\oplus - \oplus)$ and heavy clipped (O-O) treatments in the vegetation in the Plains, Ridge and River site respectively. The proportion live material was calculated as live biomass divided by live plus dead biomass. Medium and heavy proportions of live material refer to the regrowth. For the Ridge and River site, the proportion live in the clipped treatments at the end of the season could not be calculated because either no dead or live biomass was present. Day of harvest: as in Figure 1.

Clipping significantly increased the proportion of leaves (Fig.3a,b,c). For all three sites the proportion of leaves was primarily affected by the clipping treatments (Table 3) and less by date of harvest and date x treatment interaction. Pairwise comparisons between treatments showed that, in all the sites, the difference between clipped plots and unclipped plots significantly increased during the season, whereby the unclipped plots showed a decline in proportion of leaves while the clipped plots tended to show an increase in the proportion of leaves (date x treatment interaction for medium-control in the Plains site: $F_{1, 74} = 30.95$, P<0.001, in the Ridge site: $F_{1, 66} = 87.85$, P<0.001 and in the River site: $F_{1, 79} = 28.02$, P<0.001; date x treatment interaction for heavy-control in the Plains site: $F_{1, 79} = 28.02$, P<0.001, in the Ridge site: $F_{1, 71} = 46.13$, P<0.001 and in the River site: $F_{1, 71} = 52.13.13$, P<0.001). The proportion of leaves did not differ significantly between the heavy and medium clipped treatments in either of the sites. Table 3: Results of analyses of co-variance in which the effect of clipping treatment (medium, heavy or unclipped) was tested on live/dead ratio, leaf/stem ratio and mineral concentrations (nitrogen (N), phosphorus (P), calcium (Ca) and sodium (Na)) in green leaves during the course of the season. Date of harvest was used as co-variable. Values indicate the percentage of variance explained per factor, summing up to the variance explained by the model (r^2). The explained variance per factor was calculated as the SS per factor divided by the SS of the corrected total. The significance levels refer to the F-test of the ANCOVA procedure. * $P \le 0.05$, ** $P \le 0.001$.

Site	Factor	df	Proportion		Proportion Grass leaf nutrient concentr		ration		
			live	leaves		Ν	Р	Ca	Na
Plains	Date (D)	1	0.35***	0.04***	_	0.32***	0.00 ^{ns}	0.37***	0.00 ^{ns}
	Treat (T)	2	0.19***	0.60***		0.29***	0.19***	0.00 ^{ns}	0.03 ^{ns}
	DxT	2	0.26***	0.10***		0.06***	0.02 ^{ns}	0.01 ^{ns}	0.06 ^{ns}
	r ²	5	0.79***	0.73***		0.67***	0.21***	0.39***	0.09 ^{ns}
Ridge	Date (D)	1	0.49***	0.00 ^{ns}		0.51***	0.06**	0.00 ^{ns}	0.00 ^{ns}
	Treat (T)	2	0.13***	0.38***		0.17***	0.30***	0.12**	0.07 ^{ns}
	DxT	2	0.25***	0.29***		0.01 ^{ns}	0.04	0.02 ^{ns}	0.04 ^{ns}
	r ²	5	0.87***	0.67***		0.68***	0.40***	0.14**	0.11 ^{ns}
River	Date (D)	1	0.47***	0.02**		0.52***	0.15***	0.50***	0.31***
	Treat (T)	2	0.05**	0.51***		0.18***	0.06*	0.18***	0.12***
	DxT	2	0.06***	0.22***		0.04**	0.00 ^{ns}	0.10***	0.01 ^{ns}
	r ²	5	0.58***	0.74***		0.74***	0.21***	0.78***	0.44***

Plant mineral concentrations

Clipping resulted in higher nitrogen (N) concentrations in grass leaves (Fig 4a,b,c) but N concentrations were mainly affected by date of harvest (Table 3). In all three sites, plant N concentrations decreased in the course of the wet and dry season. Pair wise comparisons between most clipped and unclipped treatments showed that over time, the clipped plots decreased less in N concentration than the control treatment (date x treatment interaction for medium-control in the Plains site: $F_{1, 78} = 8.53$, P < 0.01 and in the River site: $F_{1, 71} = 8.23$, P < 0.01; date x treatment interaction for heavy-control in the Plains site: $F_{1, 79} = 20.45$, P < 0.001 and in the River site: $F_{1, 71} = 13.22$, P < 0.01). In other cases, only main treatment effects were significant (medium- control in the Ridge site: $F_{1, 68} = 20.68$, P < 0.001 and heavy-control in the Ridge site: $F_{1, 71} = 47.90$, P < 0.001). The differences between medium and heavy clipped plots were significant except in the River site (medium- heavy in the Plains site: $F_{1, 81} = 9.14$, P < 0.01 and in the Ridge site: $F_{1, 63} = 6.65$, P < 0.05).



Figure 4: Concentration of Nitrogen (a,b,c), Phosphorus (d,e,f), Calcium (g,h,i) and Sodium (j,k,l) in green leaves in the Plains, Ridge and River site respectively for unclipped (+ - +), medium (-) and heavy clipped (O-O) treatments. Medium and heavy concentrations refer to the regrowth. No data are available for clipped treatments in the Ridge and River site at the end of the season due to lack of material. Minimum N requirement for maintenance (- - -) as well as minimum requirements of P, Ca and Na during pregnancy (- - -) and lactation (- - -) is indicated. Day of harvest as in Figure 1.

Clipping also had a positive effect on grass leaf phosphorus (P) concentration (Fig.4d,e,f). The response however differed between sites and was not similarly affected by date of harvest or treatment (Table 3). In the Plains site grass leaf P concentration did not change significantly during the year while in the Ridge and River site they increased towards the dry season. Grass leaf P concentrations in the Plains site were considerably lower than in the Ridge and River site. Pairwise comparisons showed that in the Plains and River sites,

plant P concentrations in clipped plots showed the same trend in time as the unclipped plots since only significant main effects were found (medium-control in the Plains site: $F_{1, 78} = 23.12$, P < 0.001 and in the River site: $F_{1, 71} = 4.97$, P < 0.05. Heavy-control in the Plains site: $F_{1, 79} = 21.68$, P < 0.001 and in the River site: $F_{1, 71} = 6.78$, P < 0.05). Only in the Ridge site, P levels increased more in the clipped plots than in the unclipped plots (date x treatment interaction for medium- control in the Ridge site: $F_{1, 68} = 4.98$, P < 0.05 and for heavy-control in the Ridge site: $F_{1, 71} = 5.11$, P < 0.05). No significant differences between medium and heavy clipped plots in any of the sites were found.

Clipping negatively affected calcium (Ca) concentrations (Fig. 4g,h,i). Just as for P, the response differed between sites and concentrations were not similarly affected by date of harvest or treatment (Table 3). In the Plains site, Ca levels increased during the seasons but clipping had no effect at all. In the River site, Ca levels also increased in the course of the season, but clipping resulted in a less steep increase (Table 3). In the Ridge site, Ca levels were lower as a result of clipping but stayed constant over the year. Pairwise comparisons between treatments showed that medium and heavy clipped plots on the River site increased less in Ca levels than the unclipped plots (date x treatment interaction for medium-control in the River site: $F_{1, 71} = 23.26$, P < 0.001 and for heavy-control in the River site: $F_{1, 71} = 35.02$, P < 0.001). In the Ridge site, the heavy and medium clipped plots showed the same trends in time as the unclipped plots, since only the main effects of treatment were significant (for medium-control in the Ridge site: $F_{1, 71} = 11.28$, P < 0.01). As with P, the medium and heavy clipped plots did not differ significantly in the concentration of Ca for all three sites investigated.

Clipping did not have a clear effect on the sodium (Na) concentrations in most sites and also no clear seasonal trends were found (Fig. 4j,k,l and Table 3). However, between sites large differences in grass leaf Na concentrations were observed. The River site had a \pm 15 time's higher Na concentration as the Plains and Ridge site and also showed most differences between clipped and unclipped treatments. Pairwise comparisons showed that, only in the River site, clipped plots had higher Na concentrations and that Na concentrations decreased in the course of the season. This decrease was similar in all treatments since only the main effects were significant. (for heavy-control: $F_{1, 71} = 24.50$, P < 0.001, for medium-control $F_{1, 71} = 5.15$, P < 0.05 and for medium-heavy: $F_{1, 71} = 4.77$, P < 0.05). None of the other comparisons did differ significantly.

Consequences for herbivore forage availability and quality

Table 4 and Table 5 show that, when the animals do not graze in Tarangire National Park during the growing season (as is the present situation), they find upon their return to the park ample total standing biomass to satisfy their required consumption. However, under heavy grazing pressure during the growing season (as would be the case when the animals would stay year-round in Tarangire NP), and assuming that the herbivores only consume the green (live) biomass, the annual production of 211,000 ton/year is close to the total estimated consumption of 199,000 ton/yr.

Table 4: Estimates of the annual live and total above ground primary production on different soil types for Tarangire NP. Production was estimated for an ungrazed situation (based on the control plots) and for a medium and heavy grazed situation (based on the clipped plots, see also Fig. 2).

		Ungrazed	Ungrazed	Medium grazed	Medium grazed	Heavy grazed	Heavy grazed
Soil description	Soil type area (km ²)	Live prod. (ton/yr.)	Total prod. (ton/yr.)	Live prod (ton/yr.)	Total prod. (ton/yr.)	Live prod (ton/yr.)	Total prod. (ton/yr.)
Brownish loam soil (Plains)	632	277,000	396,000	176,000	248,000	136,000	146,000
Red loamy sand (Ridge-slope)	236	126,000	172,000	58,000	78,000	44,00 0	45,000
Light clay (Riverine)	96	88,000	98,000	32,000	37,000	31,000	32,000
Total	964	491,000	666,000	266,000	363,000	211,000	223,000

The mineral requirements (see Fig.4), show that the mineral concentrations in the plant material are not sufficient at all times to meet the animals requirements (based on wildebeest requirements). In the wet season the females are lactating and have high mineral requirements, especially for phosphorus and calcium. The lactation period is approximately 3-6 months and in the beginning of the dry season the calves are weaned and mineral requirements drop to maintenance and pregnancy levels.

Clipping increased the nitrogen concentrations so that these were above maintenance levels for a longer period of time (Fig. 4a,b,c). Phosphorus levels were, however, continuously too low in the wet season when females are lactating (Fig.4d,e,f). Calcium concentrations were well above or around lactation and pregnancy requirements throughout the wet and dry season (Fig.4g,h,i). Sodium levels in the grasses in Plains and Ridge-slope soil types are too low for lactating and pregnant females but high enough in the Riverine soil types (Fig.4j,k,l). For reasons of clarity, we did not include zebra requirements in Fig. 4. However, a zebra's nitrogen, phosphorus and sodium requirements are comparable to wildebeest's (Duncan et al. 1990) while calcium requirements are slightly higher.

Table 5: Estimate of yearly dry matter intake by all large herbivores in Tarangire NP if they would be forced to stay in the Park. Population estimates for large herbivores were taken from aerial surveys of Tarangire NP (TWCM 1995ab). Body weight was taken for average adult animals from Estes (1991). % grass in diet of intermediate feeders was taken from Drent and Prins (1987), Estes (1991) and Hofmann (1973). Total dry matter intake per year was calculated as (0.025 (in kg)* body-weight * 365 (days) * population # * proportion of grass in diet)/1000.

species	Population	Body weight	% of grass	Total intake of grass for
	numbers	(kg)	in diet	whole population (ton/yr.)
Grazers:	•			
Wildebeest	23,923	230	100	50,208
Zebra	29,835	240	100	65,339
Buffalo	5,321	630	100	30,589
Hartebeest	1,462	135	100	1,801
				sub total = 147,937
Intermediate feeders:				
Impala	2,973	55	95	1,417
Elephant	2,077	3,500	70	46,434
Grant's gazelle	1,311	40	40	191
Oryx	1,263	200	70	1,613
Eland antelope	438	475	65	1,234
-				sub total = 50,890
				Total = 198,827

Discussion

East African savanna systems are well known for the large migratory herbivore populations. These populations, however, are increasingly being threatened by expansion of human activities in their migratory ranges, the wet season range in particular. Restricted access to the wet season range could have severe consequences for migratory population numbers since quality of ungrazed vegetation in the dry season range does not meet herbivore requirements (Voeten 1999). However, it has long been recognized that through grazing herbivore forage quality and quantity can be enhanced (Vesey-FitzGerald 1960, McNaughton 1979, 1984, Georgiadis et al.1989, Georgiadis and McNaughton 1990, Oesterheld and McNaughton 1991,

Belsky 1987, Verkaar 1988, Belsky et al.1993). Therefore, in this study, we questioned if grazing during the wet season in the dry season range of migratory herbivores in the Masai ecosystem, Tarangire National Park, will improve herbage quality and quantity to levels that would be sustainable for current migratory herbivore numbers when migration routes to the wet season ranges were to be cut off.

Indeed, we found that grazing improved forage quality whereby the concentration of nitrogen and phosphorus in particular was enhanced. This positive effect of clipping on grass leaf nitrogen and phosphorus concentrations can be partly explained by a reduced dilution, due to a lower biomass of standing plant material in the clipped treatments (Chapin and Van Cleve 1981, Wilson 1984, Rittenhouse and Roath 1987, Milchunas et al. 1995, Chapter 3). The younger age of leaves in the clipped treatments may also explain the higher tissue nutrient concentrations since nutrient concentrations decrease during ageing (McNaughton 1979, Georgiadis and McNaughton 1990, Chapter 3).

Nitrogen concentrations remained above maintenance requirements for a longer period of time through clipping but eventually also fell below the critical levels in the course of the dry season. In most semi-arid savanna systems, nitrogen concentration in the vegetation is well below maintenance levels during at least part of the dry season (Boutton et al. 1988, Prins 1996) and most animal species will use their reserves built up during the wet season. So, the positive effect of grazing on nitrogen levels will delay the use of reserves and hence can be advantageous if the dry season is prolonged.

Although phosphorus concentrations were enhanced through clipping, they did not reach levels required by lactating females during the wet season. Short periods of limitation may be overcome by release of phosphorus that was previously stored in bones (Wallis de Vries 1996), but quantitative information on this is not yet available. Also Sodium concentrations, which were not consistently enhanced by clipping, remained below requirement levels, except for the River site where concentrations in all treatments were exceptionally high. Also for calcium concentrations no consistent clipping effects were found; here, however, concentrations were well above lactation requirements in all treatments and sites. Additional supplies of minerals by drinking (river)water (Voeten 1999), soil consumption (Kreulen and Jager 1984) and licking on recently burned areas (Komarek 1969, Van de Vijver C.A.D.M. pers.obs.) may be important when nutrient concentrations in the vegetation are too low. Quantitative insight into the importance of these sources is however lacking. Since plant concentrations of phosphorus and sodium in Tarangire in the clipped

treatments are, on average, still insufficient for lactating females, exclusive foraging on these grasses in the dry season range during the lactation period, the wet season, may result in repercussions for herbivore reproduction and survival of their young.

Quality parameters related to composition of vegetation material, such as the proportion of leaves and live material in the vegetation, were also higher in clipped treatments as compared to the unclipped treatment (see also Coppock 1983, Hik and Jefferies 1990, Hamilton et al. 1998). This effect primarily was due to a larger build up of stem and dead material in the unclipped treatment while regrowth after clipping primarily consisted of leaf material. Because of the increased proportion of leaves and live material, the most nutritious parts will be more readily available for herbivores. But, as discussed before, the mineral concentrations of leaf material, although higher than stem and dead material, were still not sufficient to meet the animals' requirements. Moreover, since our previous interpretation of forage quality was based on green leaf material and a herbivores diet also contains stem and dead material, the mineral intake will be even less and requirements will be even more difficult to meet than previously suggested.

Results of this study show that, for all three soil types investigated, clipping adversely affected forage quantity, with significantly lower annual production in both clipped treatments as compared to the unclipped control. Other studies have however shown that in semi-arid grazing systems grazed vegetation can compensate for the amount of material grazed and in some situations can even produce more than ungrazed vegetation (McNaughton 1979, Oesterheld and McNaughton 1991, Wegener and Odasz 1997). However, in this study no evidence of such (over)compensation was found.

Considering production of biomass in relation to herbivore consumption, Drent and Prins (1987) reported that 80 % of the above ground net primary production was being consumed by large herbivores in Manyara National Park in Tanzania. This figure seems exceptionally high (Prins 1989) and average consumption is more likely to be around 50 % (Lamprey 1983) or even lower (25 %), as was calculated for the Serengeti National Park (Prins 1989). Our own estimates show that, when the Park would not be grazed during the wet season, the estimated consumption by all large herbivores would be 20 % of the live annual production or 15 % of the total annual production (estimated consumption is hereby supposed to be half of that calculated in Table 5 since the animals would only graze for half of the year). Clearly, this is enough to satisfy the requirements as indeed the present-day situation shows. However, under a year-round medium grazing pressure, while consuming only the green

biomass, the estimated consumption by large herbivores would already be 75 % of the estimated production. Moreover, since rainfall is a prime determinant of annual production and this research was performed in an exceptionally wet year (50 % above average), it may well be expected that the annual production in a year of average rainfall will be lower and consequently herbivore forage availability will be even more limited.

This brings us to the central question posed in this study: Can herbivore forage supply and quality in the dry season range of migratory herbivores be sufficiently enhanced through grazing to allow the current herbivore populations to reside year-round in the dry season range when access to the wet season range is cut off? Our data show that, although grazing in the dry season range during the wet season improved forage quality, both forage quantity and quality, phosphorus in particular, would not meet the herbivore's requirements. Here we should however consider the fact that no nutrient returns via dung or urine occurred in our experiment. This would be the case when the animals would graze year-round. Enhanced soil nutrient supply through dung and urine after grazing can contribute to increased nutrient concentrations and vegetation growth after grazing (McNaughton 1979, Georgiadis et al. 1989, Day and Detling 1990). It thus can be questioned if year-round nutrient input would have resulted in different conclusions regarding the effect of grazing on forage quality and quantity and the consequences for the migratory herbivores.

Since our experimental plots were situated on sites where large herds of ungulates congregate during the dry season, the deposition of nutrients through urine and accumulated faeces was high already. Moreover, Van de Vijver et al. (1999) found that in these relatively nutrient rich savannas, where the majority of nutrients are below-ground, nutrient returns after biomass removal do not significantly contribute to enhanced nutrient status of regrowth. We therefore expect that additional nutrient returns via dung and urine will not lead to an additional increase in plant nutrient concentrations. If additional nutrient returns would have resulted in more regrowth after grazing can also be questioned since we found that the most nutrient rich site, the River site, showed least compensation after clipping as compared to the other sites investigated. We therefore postulate that increased input of nutrients through faeces and urine will not lead to higher vegetation production as compared to what we found in our experiment. Our production data are more likely to be higher than average due to the exceptionally wet year in which the experiment was performed, as was mentioned previously.

We conclude that if the current migratory populations of the Masai ecosystem were to be confined to their dry season range year-round, their numbers would be negatively affected. Our conclusions are based on the short-term effects of simulated grazing on forage quantity and quality and do not include the possible long-term changes, plant species composition amongst others. The latter deserves further attention. The present study does however clearly demonstrate that protection of migration routes and wet season grazing areas is essential to safeguard current migratory ungulate populations.

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Chapter 6

Changes in the woody component of an East African savanna during 25 years

C.A.D.M. van de Vijver, C.A. Foley and H. Olff (Journal of Tropical Ecology, in press)

Summary

The aim of the present study was to investigate the changes in density, structure and species composition of the woody component of the two predominant savanna types in Tarangire National Park, northern Tanzania, during a period of 25 years. The Park is known for its large and still increasing elephant numbers and high frequency of fires. In 1971 a study was performed on the woody species density, composition and age structure in the park. In 1996 this study was repeated, using the same transects and method. Access to the original data of 1971 allowed for a full comparison of the changes and for an investigation whether these could be related to changes in elephant numbers and fire frequency.

The total tree density declined during the 25 years, but the decline was not evenly distributed over the different tree height classes. Although the density of trees taller than 5 m declined significantly, the greatest decline occurred in the density of trees shorter than 1 m. The density of trees in the intermediate height class of 1-5 m did not decline. Although damage to trees by elephants increased during the 25-year period, c. 25% showed no browse damage and elephant damage was not found to reduce tree vigour, except for some severely damaged trees. Elephants affected the size distribution of the savanna woody component much more than the density. We found no clear evidence that fire contributed to the observed changes. The large decline in density of small trees was attributed to a severe drought in 1993.

Based on the large number of elephants that have occurred in the park during the past decades and on relatively low elephant impact on the total tree density, the present study suggests that the current elephant number of 2300 can be sustained in the Park without causing detrimental effects, provided that their current range is maintained.

Key words: deciduous and microphyll savanna, elephants, savanna structure, Tanzania, tree density, tree species, woodland dynamics

Introduction

The vegetation structure of African savannas is in a continuous state of transition, leading to shifting mosaics of woodland and open grasslands (Caughley 1976, Dublin 1995, Sinclair and Arcese 1995). The role that elephants can play in affecting these local transitions has been described by various authors (Buechner and Dawkins 1961, Laws 1970, Caughley 1976, Croze et al. 1981, Van Wijngaarden 1985, Buss 1990, Ben-Shahar 1993, Sinclair 1995); many associating high elephant densities with a decline in large trees (Laws 1970, Caughley 1976, Lamprey et al. 1980, Barnes 1983a b, Abel and Blaikie 1986, Lewis 1986). Despite the decline in total elephant numbers in sub-Saharan Africa, due to poaching and habitat loss (Douglas-Hamilton 1987, Prins et al. 1994), elephant densities have increased in parks and reserves that offer them protection (Barnes 1983b, Douglas-Hamilton 1987). The concurrent loss of large trees caused concern to the managers of these protected areas (Douglas-Hamilton 1972), as large trees provide food and shelter for a variety of animals and are of high aesthetic value (Barnes 1983b, Belsky 1989, Herremans 1995). This concern has become known as 'the elephant problem' (Caughley 1976), and has led to controversial management policies such as culling (Buechner and Dawkins 1961, Laws 1970, Barnes 1983b).

Although many studies emphasized the effect of high densities of elephants on large trees, the question is: can these studies be used to predict long-term changes in the savanna woody component? A decline in large trees does not necessarily lead to a decline in total tree density because large trees are not always killed, but merely reduced in height after which they are classified in a smaller height class. In addition, a decline in the density of large trees, for example Acacia tortilis, may even enhance the establishment of seedlings which do not grow under the mature canopy (Weyerhaeuser 1982). Consequently the effect of elephants on the savanna woody component may merely result in changes in the age/size distribution of trees rather than a decline in total tree density (Weyerhaeuser 1982). The understanding of the effects of elephants on savanna woodland dynamics is additionally complicated by the fact that the extent to which elephants affect the savanna woody component depends on factors such as tree density and age structure (Barnes 1985), soil type (Van Wijngaarden 1985), other herbivore species (Belsky 1984, Pellew 1983, Prins and Van der Jeugd 1993, Dublin 1995) and fire (Trollope 1996). Both altered herbivore assemblages and increased fire frequency, due to increased human settlement and poaching around protected areas, may also have contributed to savanna woodland change in the past decades.

Therefore, in order to understand the effect of elephants on savanna woodland dynamics, studies on the whole savanna woody component should be performed (Weyerhaeuser 1982). Furthermore, sufficiently long time spans must be considered because these are less sensitive to the short-term oscillations that can provide erroneous indications of long-term trends (Prins and Van der Jeugd 1993). However, data on the long-term effects of elephants on the dynamics of the savanna woody component are incomplete (Dublin 1995) because no published studies exceeding 20 years describe long-term changes across all cohorts and tree species.

The aim of this study was to investigate the change in density, structure and species composition of the woody component of the two predominant savanna types in Tarangire National Park, northern Tanzania, during a 25-year period. Tarangire National Park is known for its large herds of elephants and recurrent fires. Many people have stated that the vegetation has become considerably more open in the past decades (Ecosystems Ltd. 1980) and have attributed this to increasing elephant numbers and fire frequency. In 1971, Vesey-FitzGerald (1973b) investigated tree density, structure and composition in two predominant savanna types. The present study repeated this study in 1996, using the same sampling sites and methods. As we had access to the original data from 1971, we were able to analyse changes in the woody component during a 25-year period. The variation in change of tree distribution over different height classes during the 25-year period and spatial variation in elephant density and fire occurrence, allowed for identification of possible causes of the changes observed.

Study area

Tarangire National Park (N.P.) is situated between latitude 3 ° 40' and 5° 35' S and longitude $35^{\circ} 45'$ and 37° E and covers an area of <u>c</u>. 2600 km². The Tarangire River runs through the park and is one of the main permanent dry season water supplies within the entire $35\ 000\ \text{km}^2$ Masai Ecosystem (Prins 1987) in which Tarangire N.P. lies. Average rainfall in the Park, based on 21 years of data, is 620 mm, which falls primarily from December to May. Two wooded savanna types dominate the Park: (1) the microphyll savanna which can be found in the riverine area with dark alluvial, lacustrine soils has *Acacia tortilis* (Forsk.) Hayne ssp., *Maerua triphylla* A. Rich. var.(Vahl and Gilg), *Grewia* spp. as the dominant tree species; (2) the deciduous savanna which is situated on the ridges and upper slopes has well-drained red

loams of Pre-Cambrian origin and has *Combretum* spp. and *Commiphora* spp. as the dominant tree species.

During the past 40 years, elephant numbers in the park have fluctuated markedly. Prior to being gazetted as a protected area in 1958, the Tarangire area was used for wildlife hunting and elephants numbered c. 440 in 1960 (Lamprey 1964). After the park obtained protected status, the elephant population number increased markedly and in 1980 c. 2900 were counted in Tarangire and its direct surroundings (Ecosystems Ltd. 1980). This high increase was not only due to high birth rates but also due to immigration from surrounding areas where heavy poaching started to occur in the 1970s (Ecosystems Ltd. 1980). By the end of the 1970s poaching pressure also became high in Tarangire and large numbers of dead elephants were recorded in and around the park (Ecosystems Ltd. 1980). The population of c. 2900 in Tarangire plummeted accordingly. After the mid 1980s, poaching pressure was reduced and the number of elephants started to increase again, reaching 2300 by 1996 (TCP 1995). In this period, elephant numbers also increased owing to movement of elephants into the park from other, non-protected, areas where human settlement and commercial farming have increased drastically in the past 20-year period (Borner 1985, TWCM 1994). No data are available on the density of elephants in Tarangire in 1971. But, with the population estimates of 1960 and 1980, annual increase in elephant numbers would be 9% and elephant density in 1971 would accordingly be estimated at 1200.

The majority of the elephants using the park disperse during the wet season into surrounding areas to forage. In the dry season they return to the park because the Tarangire River is their major water source in the dry season. During the dry months, elephants switch from predominantly grazing to predominantly browsing (Western and Lindsay 1984, Beekman and Prins 1989, Buss 1990, Sinclair 1995), and it is during this period that the impact on woody vegetation is likely to be highest (Laws 1970, Barnes 1982).

The frequency of fires also increased in the past decades in Tarangire N.P. The Park experiences regular dry season fires, most of which are of anthropogenic origin from outside the Park, even though park managers adopted an early dry season burning policy between 1984 and 1994 to counter these fires.

Methods

This study replicated the transects and methods used by Vesey-FitzGerald in 1971 (Vesey-FitzGerald 1973b: Figure 1). He drew the original transect locations on a park map (1:100 000) and on the original data sheets he provided detailed information on the starting point of the transects through various roads and landmarks and compass bearing of transect directions. This allowed us to relocate and repeat the transects accurately and we estimate that the error of the transect starting point is no more than \pm 200 m. Twenty transects were located in the microphyll savanna and 12 in the deciduous savanna. These two vegetation types were originally chosen because they were the most dominant vegetation types and provided the bulk of browse material (Vesey-FitzGerald 1973b).



Figure 1: Map of Tarangire National Park showing transect locations in the microphyll and deciduous savannas.

The point-centred quarter method (PCQ, Cottam and Curtis 1956) was used to determine tree density. This method was selected by Vesey-FitzGerald (1973b) because it is suitable for determining the density of sparsely spaced trees (Mueller-Dombois and Ellenberg 1974), such as that in savanna systems. PCQ is a plotless sampling technique in which a number of sampling points are selected along a transect of fixed direction. A total of 50 points were sampled per transect with 25-m intervals between consecutive points. Thus each transect covered a distance of 1250 m. At each sampling point, the perpendicular to the transect direction was used to obtain four quadrants. In each quadrant, the distance (d) from the centre point to the nearest woody plant, taller than 50 cm, was measured in m. We did not record trees shorter than 50 cm because this was not done during the original study, most likely because they are too easily overlooked in the grass. A total of 200 trees were sampled per transect and no individual tree was measured twice. A total of 6400 trees were recorded along the 32 transects. The number of trees per hectare (D) was calculated for each transect as:

$$D = \frac{10000}{\left(\overline{d}\right)^2}$$

where d = the mean d of a transect (m).

Species, diameter at base, height and crown radius were also recorded for each tree. Crown area was calculated using the estimated average radius of the tree canopy. Multiplication of crown area with density estimates was used to determine woody cover. Tree height was classified according to vegetation stratum as done by Vesey-FitzGerald (1973b). Trees between 0.5 and 1 m ($0.5 \le x \le 1$ m) were distinguished as a separate group because these are still within the herbaceous layer, where they have to compete for light with the herbaceous vegetation and are extremely susceptible to fire damage (Trollope 1996). Trees between 1 and 5 m tall ($1 < x \le 5$ m) were classed separately because they include the majority of shrubs. Trees between 5 m and the canopy height of 10 m ($5 < x \le 10$ m) were classed separately from those in the canopy level (> 10 m) which were distinguished as fully-grown. For the 9 most frequently occurring species in the two savanna types, data were also analysed at the species level.

Trees were further classified by browser damage and condition scales, each having four levels. The four damage levels, based on the criteria used by Vesey-FitzGerald, were: (1) No damage: no damage or slight evidence of browsing on leaves. (2) Light damage: twigs and small branches lightly damaged. (3) Heavy damage: damage to trunk, branches or stem; branches broken and bark ripped off with the structure of the tree significantly altered. (4) Extensive damage: tree trunk severely damaged, multiple branches broken, leaves denuded. Condition scores were as follows: (A) Good: perfect condition and vigorous growth. (B) Average: tree healthy but leaf cover not complete and not all leaves in good condition. (C) Poor: leaf growth uneven and leaves in poor shape; dead branches clearly present. (D) Very poor: tree dying; leaves, if present, in bad condition; majority of branches dead.

Within the two savanna types the occurrence of elephants and fires were not evenly distributed. Hence we were able to group transects into 'high' and 'low' elephant occurrence transects, and into 'high' and 'low' fire frequency transects. Distinction of 'high' and 'low' elephant presence was based on 4 years of observation (1993-1996) by the second author. The 'high' and 'low' elephant occurrence concurred with the occurrence of other herbivores. Therefore the transects were categorised as 'high' and 'low' herbivore occurrence areas whereby we assume that these relative densities did not change in the Park during the 25-year period. Distinctions between 'high' and 'low' fire frequencies areas were based on fire mapping during the period 1990-1996. Transects in areas that had burned in this period were categorised as having a 'high' fire occurrence, while those that had not burned were categorised as having a 'low' fire occurrence. No transect with a 'high' fire occurrence burned more than once during the 6-year period.

Statistical analysis

Because we had access to the original data of Vesey-FitzGerald (1973b), we were able to do a full comparison of the data collected in 1996 with those of 1971. Prior to statistical analysis, all density estimates were log-transformed to meet the requirements of parametric analysis.

Changes in tree density during the 25-year period were assessed using general linear model analysis (GLM) with the two years and four height classes as fixed effects and transect as a random effect. The analysis was run separately for each savanna type because the two savanna types had unequal numbers of transects and therefore savanna type could not be put into the model. To test whether possible changes in density varied between savanna types, differences in density between 1971 and 1996 were tested in a Student's <u>t</u>-test. Student's <u>t</u>-test was also used to analyse the differences in density between the two savanna types. Change in density of individual height classes and species over the 25-year period was tested 'a

posteriori', using a paired <u>t</u>-test with tree density as dependent and individual transects in 1971 and 1996 as pairs. Changes in the relative frequency, damage levels and canopy area between 1971 and 1996 for individual height classes and species were tested with Wilcoxon's matched-pairs test because distributions could not be normalised, due to too many zeros.

Additionally, linear regression analysis was used to investigate if variation in density change during the 25-year period could be explained by fire occurrence, herbivore occurrence or savanna type. Difference in density between 1971 and 1996 was entered as the dependent variable while fire occurrence, relative herbivore density and savanna type, with all possible interactions, were entered as factors using a stepwise procedure.

Results

In 1972 and 1996, tree density was significantly higher in the deciduous savanna than in the microphyll savanna (t=167, df = 19, P<0.001 and t=15.56, df = 11, P<0.001 for 1971 and 1996 respectively) and tree density declined with increasing height class (Tables 1 and 2a). During the 25-year period, tree density declined in both savanna types, but the extent of decline did not differ between the two savanna types (t = 0.133, df = 30, P> 0.05).

Table 1: Average tree density (ha⁻¹) of individual height classes and all trees (total) in the microphylland deciduous savanna in Tarangire National Park in 1971 and 1996. Change (%) gives the difference in density between years as a percentage of the 1971 density. Negative percentage indicates a decline. Asterisk indicates a significant change in density as measured by a paired <u>t</u>-test, $* = P \le 0.05$, $** = P \le 0.01$, $*** = P \le 0.001$.

	Microphyll savanna			Deciduous savanna		
Height class (m)	1971	1996	Change (%)	1971	1996	Change (%)
0.5 - ≤1	473	262	-45***	978	513	-48**
1< - ≤ 5	139	142	2	252	426	69
5< - ≤ 10	6	4	-33	47	12	-74***
>10	12	3	-75**	2	1	-50
Total	630	411	-35**	1279	952	-26*

The decline in density did however differ between height classes, the major part of the decline being accounted for by the 0.5-1 m height class in both savanna types (Tables 1 and 2a). Exclusion of this height class from the analysis resulted in no significant changes in total tree density between 1971 and 1996 ($\underline{t} = 0.83$, df = 20, P>0.05 and $\underline{t} = 0.507$, df = 10, P>0.05

for the microphyll and deciduous savanna resp.). In the microphyll savanna the density of large trees (>10 m) declined by 75%, while no significant decline was found for the 1-5 and 5-10 m height classes (Table 1). In the deciduous savanna, the density of the 5-10 m height class declined by 74 % while the density of large trees (> 10 m) declined, but not significantly, from 2 to 1 tree per hectare (Table 1). In contrast, the density of trees in the 1-5 m height class increased by 69%, although this was not significant.

In both the microphyll and deciduous savanna the height frequency distribution changes during the 25-year period, with an apparent decline in the frequency of trees between 0.5 and 1 m and an increase of trees between 1 and 5 m.(Table 3). Additionally, the already low frequency of trees above 10 m in the microphyll savanna dropped significantly, while in the deciduous savanna the frequency of trees in the 5-10 m height class declined (Table 3).

Table 2: Variance ratios from an ANOVA (repeated measurements; GLM) of tree density with (a): Year (1971, 1996) and height class (0.5-1, 1-5, 5-10 and >10 m) as fixed factors and transect as random factor and (b): Year (1971, 1996) and the nine most common species as fixed factors and transect as random factor. $= P \le 0.05$, $** = P \le 0.01$ and $*** = P \le 0.001$.

	Source	Microphyll savanna	Deciduous savanna
(a)	Year (Y)	10.62**	26.59***
	Height Class (HC)	270.1***	202.6***
	Transect (T)	1.42	3.97*
	Y x HC	2.07*	6.61***
	ΥxΤ	1.04	0.61
	HC x T	1.12	2.07*
(b)	Year (Y)	4.55*	3.42
	Species (S)	15.00***	32.87***
	Transect (T)	1.04	1.36
	Y x S	6.07***	7.46***
	ΥxΤ	0.97	0.93
	S x T	3.14***	2.29***

Table 3: Frequency of height-classes in the microphyll and deciduous savanna in 1971 an 1996. Asterisk in the 1996 column indicates a significant change in frequency between 1971 and 1996 as measured by a Wilcoxon's matched pairs test $* = P \le 0.05$, $** = P \le 0.01$ and $*** = P \le 0.001$.

	Microphy	'll savanna	Deciduor	us savanna
Height Class	1971	1996	1971	1996
(m)	(%)	(%)	(%)	(%)
0.5 - ≤1	75.0	63.7*	76.4	53.8**
1< - ≤ 5	22.0	34.5*	19.7	44.7**
5< - ≤ 10	1.0	1.0	3.7	1.3**
>10	1.9	0.7**	0.2	0.2

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Table 4: Average tree density (ha ⁻¹) for different height classes and totals of the nine most common
genera in the microphyll and deciduous savanna. Asterix indicate a significant change in density as
measured by a paired <u>t</u> -test = $P > 0.05$, * = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$

		Microphyll savanna			Deciduous savanna		
Species	Height class (m)	1971	1996	Р	1971	1996	Р
Acacia tortilis	0.5 - ≤1	67.5	71.7	-	1.4	9.9	**
	1<-≤5	9.7	21.1	**	0.4	2.3	-
	5< - ≤ 10	0.6	1.1	-	0	0	-
	>10	8.5	2.7	*	0	0	-
	Total	86.3	96.6	-	1.8	12.2	**
Balanites aegyptiaca	0.5 - ≤1	17.9	4.1	***	1.6	0.9	-
	l<-≤5	3.2	2.0	-	5.7	0	-
	5< - ≤ 10	0.9	1.2	•	0.6	0	-
	>10	2.7	0.1	**	0	0_	
	Total	24.7	7.4	***	7.9	0.9	-
Maerua triphylla	0.5 - ≤1	56.7	23.5	**	0.7	1.3	-
	1<-≤5	29.1	31.7	-	0	0.5	-
	5< - ≤ 10	0	0	-	0.7	0	-
	>10	0_	_0		0	0	
	Total	85.8	55.2	**	1.4	1.8	-
Dalbergia melanoxylon	0.5 - ≤1	21.5	12.8	-	82.8	77.5	-
	1<-≤5	12.1	6.1	-	24.6	35.5	*
	5< - ≤ 10	0.7	0.3	-	0.6	1.4	-
	>10	0	0	-	0	0	
	Total	34.3	19.2	-	108.0	114.4	-
Commiphora spp.	0.5 - ≤1	51.2	8.6	***	241.6	61.8	***
	1<-≤5	5.0	7.9	-	22.5	16.3	*
	5< - ≤ 10	0.4	0	-	1.8	0	-
	>10	0.1	0	-	0	0	
	Total	56.7	16.6	***	265.9	78.1	***
Combretum spp.	0.5 - ≤1	9.0	0.7	**	278.2	138.0	-
	1< - ≤ 5	3.8	0.6	-	101.0	226.7	**
	5< - ≤ 10	0.1	0	-	35.0	9.4	***
	>10	0	0	-	0.2	0	-
	Total	12.9	1.3	*	414.4	374.1	-
Grewia spp.	0.5 - ≤1	107.9	73.8	-	52.6	60.6	-
	1< - ≤ 5	34.8	15.9	-	39.4	44.8	-
	5< - ≤ 10	0	0.1	-	0.4	0.2	-
	>10	0	0	-	0	0	
	Total	142.7	89.8	-	92.4	105.6	-
Markhamia spp.	0.5 - ≤1	36.4	18.6	-	24.3	7.1	-
	1< - ≤ 5	10.3	17.7	-	7.4	18.5	-
	5< - ≤ 10	0	0	-	0	0.7	-
	>10	0	0	-	0	0	-
	Total	46.7	36.3	-	31.7	26.3	-
Cordia spp.	0.5 - ≤1	6.2	10.1	-	1.0	7.2	**
	1< - ≤ 5	9.7	17.1	**	2.3	11.1	**
	5< - ≤ 10	0.3	0.1	-	0	0.1	-
	>10	0	0	-	0	0	-
	Total	16.2	27.3	**	3.3	18.4	**

Change in density during the 25-year period varied significantly between species, with a decline in *Balanites aegyptiaca* (L.) Del., *Maerua triphylla, Commiphora* spp. and *Combretum* spp. species and an increase in *Cordia* spp. and *Acacia tortilis* (Table 2b, Table 4). For the other species listed (Table 4), no significant changes were found. Decline in density of specific species was primarily the result of a decline in the 0.5-1 m height class while increase in density was the result of an increase in the 1-5 m height class (Table 4). Finally, of all trees listed, only *Acacia tortilis* and *Balanites aegyptiaca* still had trees in the large phase, although their density had declined significantly since 1971 (Table 4).

Stepwise regression procedure revealed that variance in the decline of total tree density could be explained only by the relative herbivore occurrence ($r^2 = 0.26$, F=-3.23, P<0.01), with a greater decline in the high occurrence areas. The same analysis, with the individual height classes investigated as dependent, revealed that only for the 1-5 m height class the herbivore occurrence significantly contributed to the variance in decline ($r^2 = 0.34$, F=-4.09, P<0.001). For total density and the separate height classes, the other two factors, fire occurrence and savanna type, as well as the various interactions, did not contribute significantly to the model. However, the low r^2 value does show that most of the variance was not explained by the model.



Figure 2: Cover of woody vegetation as a percentage of total area in the microphyll and the deciduous savanna in 1971 (71) and 1996 (96) for the different height classes. $= 0.5 \text{ m} - \le 1 \text{ m}, \qquad = 1 \text{ m} < -\le 5 \text{ m}, \qquad = 5 \text{ m} < -\le 10, \qquad = >10 \text{ m}.$

Tree cover declined during the 25-year period, but the decline depended on savanna type and height class. Figure 2 demonstrates that in the microphyll savanna the decline in cover from 24.7 % in 1971 to 10.3 % in 1996 (z=-3.35, P<0.001) was caused by the >10 m height class which declined from 18 to 4% (z=-3.46, P<0.001) while no significant changes occurred in the lower height classes. In the deciduous savanna decline in tree cover was only 5% (z=-2.05, P<0.05). This less acute decline was due to a significant increase in the cover of the 1-5 m height class (z=-2.05, P<0.05), even though the cover of the 0.5-1 m and 5-10 m height classes declined (z=-2.85, P<0.01 and z=-2.93, P<0.01 respectively).



Figure 3: Relative frequency of damage classes for the different height classes as well as all trees (Total) in the microphyll savanna (top) and deciduous savanna (bottom) in 1971 (71) and 1996 (96). \blacksquare = no damage, \blacksquare = light damage, \blacksquare = heavy damage and \blacksquare = extensive damage)



Figure 4: Relative frequency of damage classes for the predominant tree species in the microphyll savanna (top) and deciduous savanna (bottom) in 1971 (71) and 1996 (96). A.t.= Acacia tortilis, B.a. = Balanites aegyptiaca, M.t. = Maerua triphylla, D.m. = Dalbergia Melanoxylon, Cm.= Commiphora spp., Cb. = Combretum spp., Gr. = Grewia spp., M.k. = Markhamia spp. = no damage, \mathbb{ZZ} = light damage, \mathbb{ZZ} = heavy damage and \mathbb{ZZ} = extensive damage).

Damage level to trees increased during the 25-year period in both savanna types, but the increase differed between height class and species (Figures 3 and 4; Table 5). The major shift was from trees with 'no damage' to trees with 'light damage' (Figure 3). The frequency of trees with 'extensive damage' also increased, especially in the 0.5-1 m height class. But, despite the increase, the frequency of 'extensively damaged' trees remained low. The frequency of trees with 'heavy damage' in the deciduous savanna also increased. Except for the 5-10 m height class, we also found significant correlations (Spearman's coefficient of rank correlation test) between the damage levels to trees and the diameter at base for the 0.5-1 m, 1-5 m and >10 m height classes. The average diameter at base ranged from 1.6 cm for trees with 'no damage' to 5.9 cm for trees with 'extensive damage' for the 0.5-1 m height class ($r_s = 0.376$, P ≤ 0.01), from 4.9 to 11.7 cm for the 1-5 m height class ($r_s = 0.313$, P ≤ 0.01) and from 53.6 to 79.2 cm for trees taller than 10 m ($r_s = 0.431$, P ≤ 0.01). The most obvious difference in the damage level between individual species was the relatively large increase in damage for *Dalbergia melanoxylon* Guill. and Per. in contrast to the relatively small one for *Commiphora* spp. (Figure 4, Table 5).

Table 5: Z-values of a Wilcoxon paired comparison (with transects in 1971 and 1996 as pairs) of damage levels in the microphyll and deciduous savanna for different height classes and all trees (Total) and for the predominant woody species. -= P > 0.05, *= $P \le 0.05$, **= $P \le 0.01$, **** = $P \le 0.001$.

	Microphyll savanna							
Height class (m)	None	Light	Heavy	Extensive				
0.5 - ≤1	-3.54***	-3.22**	-1.81	-3.17**				
1< - ≤ 5	-2.41*	-3.06**	-2.42	-1.76				
5< - ≤ 10	-2.52*	-2.67**	-0.40	-1.00				
>10	-2.80**	-2.67**	-2.02*	-				
Total	-3.58***	-3.42***	-1.73	-2.60**				
Species	None	Light	Heavy	Extensive				
Acacia tortilis	-3.57***	-3.29***	-0.36	-0.26				
Balanites aegyptiaca.	-2.78**	-2.04	-0.59	-1.34				
Maerua triphylla	-3.14**	-2.54**	-1.30	-1.82				
Dalbergia melanoxylon	-2.02*	-2.2*	-1.01	-1.21				
Commiphora spp.	-0.80	-0.86	-2.13*	-1.00				
Grewia spp.	-3.07**	-3.07**	-1.32	-1.33				
		Deciduou	s savanna					
Height class (m)	None	Light	Heavy	Extensive				
0.5 - ≤1	-2.81	-2.80	-2.20	-2.29				
1<-≤5	-2.80	-1.99	-0.97	-1.84				
5< - ≤ 10	-2.20	-0.81	-0.94	-1.07 ⁻				
>10				-				
Total	-2.80**	-2.80**	-2.29*	-2.19*				
		- · · ·						
Species	None	Light	Heavy	Extensive				
Dalbergia melanoxylon	-2.24	-1.26	-1.82	-0.94				
Commiphora spp.	-2.70	-0.96	-0.41	-1.00				
Combretum spp.	-2.80	-2.59	-0.51	-2.20				
Grewia spp.	-2.07	-1.54	-0.53	-2.02*				
Markhamia spp.	-1.09	-0.37	0.	-1.00				

No data on tree condition in 1971 were available. Tree condition in 1996 was better in the microphyll than the deciduous savanna (χ^2 =17.49, df = 3, P< 0.001) (Figure 5 a, b). The main cause of this difference was a higher frequency of trees in the average condition class in the microphyll savanna (χ^2 = 23.71, df = 1, P< 0.001). The majority of trees were in good to average condition with little difference between height classes, although the condition of tall trees tended to be slightly better. Very few trees were in a very poor condition and dying, 1% and 0.6% for the microphyll and deciduous savanna respectively. Larger differences were found in condition between tree species (Microphyll: χ^2 = 361.34, df = 6, P< 0.001, Deciduous: χ^2 = 144.92, df = 6, P< 0.001). Acacia tortilis and Commiphora spp. were in better than average condition while Grewia spp. and Markhamia spp. were in poor condition (Figure 5c, d).



Figure 5: Relative frequency of tree condition in 1996 in the microphyll and deciduous savanna in different height classes (A,B) and species (C,D). \blacksquare = Perfect condition and vigorous growth, \blacksquare = Average condition, tree healthy but leaf cover not complete and not all leaves in good condition, \blacksquare = Poor condition, leaf growth uneven and leaves in poor shape, dead branches clearly present, \blacksquare = Very poor condition, tree dying - leaves, if present, in bad condition, majority of branches dead. A.t.= Acacia tortilis, M.t. = Maerua triphylla, D.m. = Dalbergia Melanoxylon, Cm.= Commiphora spp., Cb. = Combretum spp., Gr. = Grewia spp., M.k. = Markhamia spp.

Discussion

Various reports mention that increasing elephant numbers and re-occurring fires were having a major impact on the woody component of Tarangire N.P. (Ecosystems Ltd. 1980). H. Lamprey (pers. comm. 1991) and I. Douglas-Hamilton (pers. comm. 1993) estimated that more than 50% of the large trees in the Tarangire valley had disappeared since the 1960s. This period was one during which the number of elephants reached 2900 in 1980, then plummeted, but then increased to 2300 in 1996, a number double the previously estimated 1200 of 1971. These reports on woodland change in Tarangire were, however, all based on circumstantial evidence. Since we replicated the research performed by Vesey-FitzGerald (1973b), using the same transects and including all trees above 0.5 m, the changes in the whole savanna woody component during a period of 25 years could be investigated.

Present data show that during the 25-year period the tree density declined and changes occurred in the structure and species dominance in both savanna types investigated in Tarangire N. P. The total tree density in the microphyll and deciduous savannas declined by 35% and 26% respectively, a situation which could be expected to reflect the increase in elephant density and fire occurrence. However, the decline was not evenly distributed over the different height classes identified. The most apparent decline occurred in the 0.5-1 m height class. If this height class is excluded from the analysis, no significant decline in tree density during the 25-year period is found. Conversely, the density of trees in the intermediate height class of 1-5 m did not decline and even tended to show an increase in the deciduous savanna while the already low density of large trees taller than 5 m in 1971, declined even further.

Changes in tree density and structure did not differ between savanna types, but the cover of woody species did decline more in the microphyll than the deciduous savanna. This difference in decline can be attributed to a strong decline in the cover of large trees in the microphyll savanna, while the cover of trees in the 1-5 m height class in the deciduous savanna increased. The presented difference in change between tree density and cover demonstrates that savanna woodland dynamics are not accurately reflected by the woody cover alone and indicates that erroneous conclusions can be drawn when aerial observations of tree canopy are used to determine the effect of elephants on the savanna woody component.

Because the effects of elephants and fire on the savanna woody component vary with tree size, and because elephant density and fire occurrence varied between transects, the present study allows for a discussion on the possible causes for the observed changes.

Large trees

The large decline in trees taller than 5 m concurs with the estimates of H. Lamprey (pers. comm., 1991) and I. Douglas-Hamilton (pers. comm. 1993). This decline, as well as the observed increase in damage levels to large trees, probably reflects the increase in elephant impact on large trees during the 25-year period.

However, it can be questioned whether this decline is due to mortality of large trees and whether elephants are the prime cause of this mortality. Although the increased damage levels, as compared to 1971, reflect high elephant usage of large trees, we only found a small percentage of large trees with extensive elephant damage and none of these trees appeared to be dying as a result of current elephant usage. We did, however, find stands of large *Acacia tortilis*, the predominant large tree in the Park, that had died but showed no signs of elephant damage. This suggests that increased mortality of large trees may be partly due to causes other than elephants, such as change in ground water tables (Weyerhaeuser 1982) and life stage dependent processes. Many of the large *Acacia tortilis* in East African savannas are from a single cohort because these trees became established at the turn of the century when rinderpest first struck Sub-Saharan Africa (Prins and Van der Jeugd 1993). The consequent decline in herbivore density and fire frequency led to bush encroachment in many parts of East Africa (Dublin 1995). This cohort of trees may now be reaching maximum age, and hence have started to die (Western and Van Praet 1973, Young and Lindsay 1988).

It can also be questioned whether the decline in large trees is due to mortality or whether elephants merely browsed large trees down to smaller size classes. Much elephant usage of big trees is through the breaking of branches, which does not necessarily kill trees but converts them to smaller height classes (Pellew 1983, Buss 1990).

Intermediate sized trees

Our data show that, in contrast to the other height classes, the 1-5 m height class did not decline in the microphyll savanna and even tended to increase in the deciduous savanna. Increased damage levels in the 1-5 m height class during the 25-year period reflect the high use by elephants of trees in this height class. Damaged trees in this height class had greater base diameters than undamaged trees. This indicates that they were either formerly taller trees that have been knocked down to a lower height class by elephants, or have been prevented
from growing into the next height class by repeated elephant feeding or browsing by other browsers. The significant relationship between change in tree density and relative herbivore occurrence would additionally suggest high elephant browsing on this height class. All these findings correspond well with other studies that have shown that the preferred feeding height for elephants is within the 1-5 m range (Croze 1974, Barnes 1983a, Jachmann and Bell 1985, Buss 1990).

Despite the increase in damage to trees in the 1-5 m height class, most of them were in average to good condition and many damaged trees had responded by coppicing. This has also been noted in other studies (Lawton and Gough 1970, Caughley 1976, Guy 1981, Jachmann and Bell 1985, Lewis 1991). In Tarangire several woody species, notably *Combretum* spp., *Dalbergia melanoxylon* (Guillemin and Perrottet), *Maerua* spp., *Grewia* spp., and *Acacia tortilis*, responded to elephant damage by coppicing. Although these species showed higher damage levels than in 1971, their condition was average to good, and their densities either remained stable or increased, as was the case for *Acacia tortilis* in the microphyll savanna and *Dalbergia melanoxylon* and *Combretum* spp. in the deciduous savanna (Table 4). This indicates that a change in species abundance due to elephant browsing may not only be the result of preferential selection by elephants (Field 1971, Vesey-FitzGerald 1973a, Guy 1981, Jachmann and Croes 1991, Lewis 1991), but also the result of the differing ability of tree species to respond to damage by coppicing (see also Barnes 1983a).

Small trees

At first glance the strong decline in density and the increased damage levels of trees in the 0.5-1 m height class would suggest a significant impact of elephants on this height class. However, there is conflicting evidence as to whether elephants have much impact on trees less than 1 m tall. Some studies found that elephants omit this size category by disproportionately feeding on woody species taller than 1 m (Vesey-FitzGerald 1973a, Croze 1974, Norton-Griffiths 1979, Pellew 1983, Jachmann and Bell 1985). However, when this browse becomes less abundant, elephants divert browsing to small trees and hence can become a major causal factor in the mortality of trees smaller than 1 m (Dublin 1995).

Pellew (1980) found a high positive relation between tree cover and available browse. Hence, the high cover percentage of trees in height classes above 1 m in Tarangire N.P. would suggest that most of the browse present was above 1 m. This again would suggest that elephant feeding would not have concentrated on the 0.5–1 m height class. However, we also found an increase in damage to small trees. At the same time we found a correlation of damage level and diameter at base with some extensively damaged trees having base diameters of 18 cm. This suggests that increased damage level to trees in this height class is not so much the result of increased elephant damage to the small trees but rather is the result of elephants browsing larger trees down to this height class. Moreover, ample evidence exists that, besides elephants, other browsing animals affect density of small trees (Croze 1974, Belsky 1984, Dublin et al. 1990, Prins and Van der Jeugd 1993). We however found that the decline in density of trees in the 0.5-1 m height class was not greater in areas where the occurrence of herbivores is high.

Fire is another factor that is known to have a large impact on small trees (Trollope 1984), but it appears that only under severe, annual burning the density of small trees will be reduced (Dublin 1995). This may explain why we found no significant difference in tree density decline between the 'high' and 'low' fire frequency areas. No transects in the 'high' fire frequency areas experienced two consecutive severe fires in the 1990-1996 period, the period that fire occurrence was monitored.

Finally, density of small trees can be very much dependent on rainfall because soil water has a strong impact on germination rates and seedling establishment (Gerhardt 1993). In 1993 a severe drought afflicted Tarangire with a rainfall of only 50% of the average. It might therefore well be that the significant lower density of the 0.5-1 m height class in 1996, as compared to 1971, is due to the drought in 1993.

Final suggestions

Why did the increased elephant numbers in Tarangire National Park not result in a large decline in tree density as has been described in other studies (Laws 1970, Caughley 1976, Lamprey et al. 1980, Barnes 1983a b, Abel and Blaikie 1986 Lewis 1986)? We suggest that this could be explained as follows.

The annual increase of elephant numbers in the park of 9% between 1960 and 1980, due to birth and immigration, is high since it reaches maximum elephant population growth rates (Calef 1988, H.H.T. Prins and C. Moss pers. comm.). This indicates that elephants were not limited by forage supply during this period. Furthermore, elephants congregate in the Park during the dry season, when their diet is predominantly browse (Western and Lindsay 1984, Beekman and Prins 1989, Buss 1990, Dublin 1995). These observations would suggest that the supply of dry season forage in Tarangire N.P. does not seem to be limiting for elephants when their numbers are below c. 3000, as is currently the case.

We did not investigate the annual production of browse in Tarangire. However, in other studies highly significant correlations were found (r > 0.95) between browse production and tree diameter (Rutherford 1978, Cissé 1980, Pellew 1980). Using these browse production estimates browse production in Tarangire would range between 350 to 1000 kg ha⁻¹ y⁻¹. Given the current elephant numbers of c. 2300, average elephant mass of 1800 kg and elephant daily forage intake (dry weight) of 2% live body mass, maximum annual browse would be c.116 kg $ha^{-1}v^{-1}$. This shows that annual browse production more than compensates for annual elephant browse, even if the conservative estimate of 350 kg ha⁻¹ y⁻¹ were to be considered. The average of 25% trees that had no browse damage does indeed suggest that browse production exceeds the annual browse consumption in the Park. Furthermore, elephants move to foraging areas outside the Park during the wet season, allowing trees to recover from dry season browsing through coppicing. If access to foraging areas outside the park were to be blocked and the elephant population growth were to remain high, elephant browse may reach levels at which response by coppicing of trees would decline. Consequently, this might result in the more dramatic decline in tree density as experienced in other parks where elephant densities were as high as 6 km⁻² (Prins and Douglas-Hamilton 1989).

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Chapter 7

"Fire and Life" in a changing savanna environment

Overview

For aeons, diverse and abundant wild herbivore populations and re-occurring fires have affected the structure and functioning of East African savanna systems (Vesey-FitzGerald 1972, Pratt and Gwynne 1977, Prins 1989). Next to wild herbivores, these relatively nutrient-rich and productive systems also allowed for the establishment of numerous pastoral economies (Smith 1992, Marshall 1994, Fratkin 1997). These pastoral economies did not only affect the role of herbivory in these savanna systems through livestock grazing, but also the role of fire since they adopted the use of fire to manage their pastoral areas (Langlands 1967, Homewood and Rodgers 1991, Prins 1992). Consequently man's influence on these systems was primarily expressed through herbivory and fire, particularly in the more arid areas of the East African savannas, which were not suited for agriculture.

Over time man's influence on these systems increased and especially in the past century human activities have had profound effects on wildlife populations and their habitat. Large scale trophy hunting, which started in the Western colonial period, and the introduction of exotic animal diseases were a direct cause of widespread decline in wildlife populations. Furthermore, a large demand for cash-crops and food, to meet the ever growing human population requirements, led to the annexation of vast areas of the savanna biome, the more fertile and productive in particular, for agricultural activities. Consequently wildlife populations increasingly were restricted to the protected areas which very often lie in the less productive, more arid savanna areas. In the past decades even these areas are more and more being encroached upon by human activities. This has led to a further compression of wildlife populations in an ever diminishing natural habitat (Prins 1992) and accordingly has affected the structure (Chapter 6) and dynamics (Chapter 5) of these systems.

Not only wildlife but also the traditional pastoral economies are confronted with loss of pastoral land to agriculture (Fratkin 1997). At the same time livestock numbers have increased significantly (Happold 1995). As a consequence pastoral societies are pushed back into the more arid, less productive grazing lands with no refugia to move to whenever their resources become limited (Prins 1992, Waller and Sobania 1994, Fratkin 1997). The higher densities of livestock in a smaller grazing range also pose an additional threat on wildlife population numbers due to resource competition (Prins 1992, Voeten 1999).

Apart from causing large changes in the herbivore component, intensification of man's activities in the East African savanna biome has also resulted in a significant change in the

spatial and temporal distribution of fire (Bond and Van Wilgen 1996). Ecologists and managers have been noting that many savanna areas are being "overburned" (Vesey-FitzGerald 1972, 1973, Pratt and Gwynne 1977). Although in numerous studies the consequences of increased livestock grazing and compression of wildlife on savanna ecosystem functioning have been discussed (Walker 1985, Dublin 1995, Prins 1987, 1989, 1992, Rietkerk 1996, Van de Koppel et al. 1997), the changing role of fire has earned much less attention.

In this chapter several aspects of "fire and life" in the changing East African savanna environment are brought together. First the objectives for using fire in pastoral systems are discussed. Hereby the effects of fire, as well as the mechanisms through which the effects occur, are elaborated on. Next the focus is on the causes and consequences of the changing fire regime in pastoral and protected areas. Finally I address the core question: " Is fire at present still an appropriate tool in East African savannas to help sustain the unmatched wildlife populations as well as the rural/pastoral economies?"

Fire and savanna pasture management: goals, mechanisms and effects

Since the establishment of pastoral economies in East African savannas some 4000 years ago, pastoralists have been the main instigators of fire in these systems (Langlands 1967, Pratt and Gwynne 1977). Several reasons can be mentioned why pastoralists adopted fire as a tool in the management of their grazing areas.

First of all, because the early pastoralists had relatively few cattle, vegetation production may have exceeded consumption and consequently the pastoral areas tended to become encroached by bush and large amounts of senescent plant material (Pratt and Gwynne 1977, Smith 1992). Therefore, in order to develop and maintain the grazing lands, it was a necessity to burn (Langlands 1967, Smith 1992). High fuel loads allowed for intense fires which thus made burning of the vegetation an effective means to reduce bush cover and keep the vegetation open (Van Wilgen et al. 1990). Additionally, burning of the vegetation also reduces the dominance of coarse and unpalatable species such as *Cymbopogon excavatus* and *Digitaria abyssinica* and favours the growth of palatable forage species such as *Themeda triandra* (Langlands 1967).

A second reason for burning in pastoral areas is that the removal of coarse and senescent plant material allows for the growth of new grass (Chapter 2, 3). For various reasons this post-fire regrowth has a higher forage quality than unburned vegetation. Firstly, post-fire regrowth has higher concentrations of mineral nutrients (Chapter 2, 3), although the elevation does decline sharply in the course of the post-fire growth season (Chapter 3). Secondly, structural vegetation characteristics that determine forage intake are improved: Higher forage bulk densities of post-fire regrowth allow for higher intake per bite, while higher ratios of leaf material in forage for grazers result in higher intake of high quality forage (Chapter 2). Finally, the forage consumed is easier to digest, which consequently allows a higher rate of intake (Chapter 2).

In a number of systems the effects of fire on vegetation dynamics have been attributed to fire-specific effects, such as the addition of ash and temperature effects (Bond and Van Wilgen 1996). In the nutrient-rich East African savannas, however, these effects primarily relate to above-ground biomass removal and consequent rejuvenation of the vegetation (Chapter 2, 3, 4). For instance, the increased nutrient concentrations in post-fire regrowth can be explained by higher ratios of young leaf material and by reduced dilution of nutrients due to lower standing biomass production (Chapter 3). We, however, found no indications that ash deposition increased soil nutrient supply after fire and therefore it did not contribute to the enhanced vegetation nutrient concentration in post-fire regrowth, as was suggested elsewhere (Gillon 1983, Frost and Robertson 1987, Singh 1993). The initial higher forage quality of post-fire regrowth, as compared to that of unburned vegetation, declined to levels comparable to unburned vegetation with the increase in standing biomass in the course of the post-fire growth season (Chapter 3).

Although burning pastoral savanna areas keeps the vegetation open and of high forage quality, pastoralists are confronted with a very variable effect of fire on forage supply. The manner in which fire affects herbivore forage supply primarily depends on rainfall (Chapter 2). Especially in drought years the effect of fire on available forage is clearly negative. This can be explained by the fact that soil water supply, which is the prime determinants of plant growth in these relatively nutrient-rich savannas (Chapter 2, Deshmukh 1984). does not only depend on rainfall and soil characteristics but also on above-ground biomass itself (Chapter 4), which is removed by fire. We found that removal of above-ground biomass reduces the soil water status. The main mechanism through which this occurs is an increase in evaporation when above-ground biomass, litter in particular, is removed (Chapter 4).

Because rainfall is very variable (Pratt and Gwynne 1977, Prins and Loth 1988) pastoralists are confronted with a significant risk that burning of vegetation may result in lack of forage supply (Chapter 2). To reduce this risk specific burning regimes were adopted. Traditionally fires would be lit at the end of the dry season or even shortly after the first rains (Langlands 1967, Homewood and Rodgers 1991). This timing has several good reasons. Firstly, in this period, the woody component of the savanna is most sensitive to fire since trees sprout earlier than grasses which are still dormant and which thus escape harm through fire (Gillon 1983, Prins 1988, De Bie et al. 1999). Secondly, in contrast to early dry season burning, burning late in the dry season reduces the period in which bare soil is exposed to direct sunlight and so the drying up of soils, which negatively affects grass growth and survival (Chapter 2, 4). Finally, by burning at the end of the dry season or shortly after the first rains (Jacobs 1975, Homewood and Rodgers 1991, Smith 1992) the negative effects of drought after burning are more likely to be avoided.

If, despite traditional burning regulations, fire would result in shortage of forage, due to delay of additional rains, the nomadic lifestyle of these pastoral societies allowed them to evade the forage shortage by moving to areas with better resources (Smith 1992, Waller and Sobania 1994, Fratkin 1997). At present, however, the possibility to evade forage shortages is increasingly becoming restricted due to the increase in other human acitvities in the savanna biome.

Temporal and spatial changes in fire and herbivory

In the past century increased human activities have changed the role that herbivory plays in East African savanna dynamics. While the role of wild herbivores is becoming more and more restricted to the protected areas (Prins 1992), livestock grazing has intensified due to increased livestock numbers and loss of pastoral land (Waller and Sobania 1994, Steinfeld et al. 1996, Fratkin 1997). Additionally, increased human activities, and more in particular the intensified livestock grazing, have also altered the spatial and temporal distribution of fire in East African savannas (Pratt and Gwynne 1977, Van Wilgen et al. 1990).

For example, high grazing intensities in the restricted wet season ranges of both wild and domestic grazing animals cause a decline of the combustible fuel load. Fire intensity is strongly related to fuel load and therefore fires have become less intense in these areas. Because intense fires are required to counter bush-encroachment, these less intense fires have little use in controlling bush-encroachment (Trollope 1982, 1984). The loss of grass cover also enhances the soil water reserve in deeper soil layers, due to increased percolation and reduced competition (Knoop and Walker 1985). Since woody species primarily root in these layers the growth conditions for woody species are improved. Both factors described above cause bush encroachment in many areas (Skovlin 1972, Pratt and Gwynne 1977, Van Vegten 1983, Archer 1996). The occurrence of bush encroachment in areas where fire impact has declined, demonstrates that historically fire was an effective tool to keep pastures open and that it led to the formation of so called anthropogenic or derived savannas (Hill 1971, Gillon 1983, Prins 1992). The current decline of intense fires in areas with high grazing intensity is also allowing an invasion of undesired, unpalatable plants which is causing an additional loss of secondary production (Pratt and Gwynne 1977, Tainton and Mentis 1984).

It is worth noting here that not only fire but also grazing itself affects subsequent forage production and quality (Vesey-FitzGerald 1960, Chapter 5). Alike those of fire, many of the effects of herbivory on vegetation production and nutrient status occur through the removal of above-ground biomass which leads to increased quality of regrowth for grazing, with higher nutrient concentrations and improved structural qualities of grass forage (Chapter 2, 3, 4, 5). Therefore, with the present high grazing intensities and the subsequent lower impact of fire in reducing bush-cover, the use of fire in the wet season ranges to improve forage quality for herbivores would seem superfluous. Furthermore, this study suggests that since grazers generally feed selectively avoiding litter material, while fire is less discriminative removing all biomass, the effects of grazing on vegetation production, particularly under drought conditions, would be less detrimental than the effects of fire (Chapter 4).

Through expanded human activities not only the intensity of savanna fires has changed, but also the frequency and season of burning. Loss of nutrient-rich productive grazing areas to agriculture have resulted in a decline in quality of forage available for livestock, particularly during the dry season when vegetation is of much lower quality than during the wet season (Chapter 2,3,5). In the dry season ranges low grazing intensities during the wet season (Lamprey 1964, Voeten 1999) allow a large build-up of grass material. This has resulted in frequent burning of current dry season ranges to obtain lush, post-fire regrowth. Generally these fires are lit, not in the traditional period of burning at the end of the dry season, but in the beginning of the dry season (Van de Vijver, pers. obs.). In this period normal vegetation growth is retarded and the above-ground vegetation dies off due to lack of

available water. After burning, however, reduced evaporating leaf surface improves the vegetation's water status and causes a temporary growth stimulation of highly nutritious forage (McNaughton 1985). But, since carbon and nutrients for storage may be lost to grazers, the vegetation has no advantage of this burning practice (Edroma 1984, Edwards 1984a,b). Additionally, the loss of vegetation cover through fire and subsequent grazing at the beginning of the dry season leads to loss of soil water which is crucial for plant survival during the dry season (Chapter 4). The practice of early dry season burning therefore leads to a decline in vegetation production in the subsequent growth season and can have deleterious effect on perennial species which are deprived from stored nutrients and carbon (Edroma 1984, Edwards 1984a,b, Bond and Van Wilgen 1996). Apart from the large effects that these fires can have on the grass vegetation of the dry season range, they also have a large negative impact on the woody vegetation because the high fuel loads, which are present in the dry season range during this time of the year, cause fires to be hot and intense and consequently have a large impact on trees (Trollope 1982, 1984). Another reason why it seems unwise to practice early dry season burning is that, with the present loss of refugia to overcome periods of shortage, the available biomass in dry season ranges is becoming increasingly important as a resource for wild and domestic herbivores to survive the dry season.

From the above, and given a significant chance of a drought year in which vegetation regrowth after fire is negligible (Chapter 2), one would hope for a decline in the use of fire in the East African savannas. However, if one thing, intensification of man's activities in these savannas has resulted in increased burning. The tantalising question accordingly is what causes have led to the unfavourable changes in fire regime for these savanna systems.

Reasons why fire regime has changed

Although legislators and village elders might advocate restriction of burning (Homewood and Rodgers 1991, Van de Vijver unpubl. interview), currently fires are widespread and occur throughout the dry season whereby burning practices appear to be haphazard. Historically, however, burning was not haphazard. On the contrary, local people had various rules, laws or taboos on conducting fires (Pyne 1995) whereby every man had the right to burn on the provision he set fire under the correct weather conditions, in the correct season and only when the vegetation had specific characteristics (Komarek 1972, 1976). These rules must have been

brought about to reduce the risk of negative effects and to maximize the positive effects of burning as discussed previously.

With Western colonization of the sub-Sahara African many issues regarding the use of fire in savanna areas changed. In those times many of the pastoral and wildlife areas were administered by managers from the Forest Department (Komarek 1972, 1976). These administrators, who often had their roots in forestry, believed fire to be nothing more than a "human artefact" and considered it an alien, destructive factor to natural systems (Raison 1979, Whelan 1995). Their ignorance of the natural history of fire in savanna systems stems partly from their prejudiced forester's view developed in the European forest environment where wild fires would destroy vast areas of pristine forest, putting back the system into early stages of succession (Whelan 1995). Consequently, they looked with disdain upon the knowledge and use of fire by local communities in savanna areas and brought out various anti-fire legislations (Komarek 1972, 1976). In the colonial period, however, the Western perception of traditional knowledge and use of fire was very often coloured by incendiarism which was the reaction of the local communities to the colonial anti-fire legislation (Komarek 1965, 1967). Hereby they developed incendiary devices, such as burning dung or coals in a nutshell, which would set fire to the grassland long after the "arsonist" was gone (Komarek 1976 and refs within).

In the course of this century fire increasingly became recognized as an integral component and determinant of many ecosystems and it was realized that many of the traditional ideas and uses of fire for savanna/pasture management were based on sound principles (Gillon 1983, Bond and Van Wilgen 1996). Ironically, now that scientific evidence shows the value of fire in savanna/grassland management, much of the traditional knowledge has disappeared under the rural savanna inhabitants themselves due to the anti-fire policy during the colonial time (Batchelder 1967, Komarek 1976). In some pastoral groups, like the Masai around the Ngorongoro Crater in Northern Tanzania, the traditional fire ecology still exists and the methods and techniques they use show a profound knowledge of fire ecology (Trollope 1995). But, in general, these knowledgeable groups are outnumbered by those who have lost this knowledge or by agricultural/pastoral immigrants who are oblivious of any sustainable savanna management through fire.

In addition to the loss of knowledge of savanna management through fire, increased incendiarism only adds up to the "fire problem" in East Africa. These fires are lit by poachers and cattle hustlers to clear their tracks (Smith 1992). Also a large number of these fires are caused by cattle boys who have easy access to matches and who, because they are afraid of

danger (predators and snakes), burn the vegetation to obtain a better view and thus get rid of their fears (P. Oliver pers. comm.). These factors combined have not only altered the extent to which fire occurs in these savanna systems, but have also increased the damage caused by fire because many fires occur during periods in which their effects are deleterious to the pastoral savanna areas.

Fire and Wildlife

As mentioned previously in this chapter, the continuous encroachment of human activities in the savanna biome of East Africa is resulting in restriction of wildlife populations to protected areas such as national parks (Prins 1992). These National Parks in East Africa do not only have an immaterial, ecological value for the conservation of wildlife, but certainly also an economic one since these wildlife areas have become a major source of income for local governments through tourism and trophy hunting (Prins 1987).



Figure 1: Distribution of areas burned (marked grey) in Tarangire National Park during the period 1991 to 1998.

At present, the protected areas too are under increasing human pressure (Prins 1992, Happold 1995). Loss of the natural habitat to agriculture and urbanisation around the protected areas is continuous and poses a threat for migratory ungulate populations (Chapter 5). Increased competition with livestock for resources as well as excessive hunting around the protected areas are also causing a decline in wildlife numbers (Happold 1995, Prins 1999, Voeten 1999). Finally, the increased human activities around the protected areas have resulted in an increased occurrence of fire, thus adding another threat to the natural habitat and wildlife of these protected areas.

A good example of the situation described above is Tarangire National Park in northern Tanzania which, apart from the migratory herds of wildebeest and zebra, is known for its large number of elephants (Chapter 6). Large-scale human settlements and activities around the park are cutting off migratory routes and are reducing the wet season range for many of the migratory animals of the park (Borner 1985, TWCM 1994, TCP 1998), while their fires cause large areas of the park to burn annually (Figure 1).

Already in the 1970s (Vesey-FitzGerald 1972, 1973) and 1980s (Lamprey pers. comm.) concern was raised about the consequences of high fire frequency and of large elephant numbers in the park for the woody component. In many protected areas savanna woodland decline has been primarily attributed to the combination of large elephant numbers and fire (Dublin 1995). We, however, found that the woody component of the savanna in Tarangire is quite resilient to the increased elephant pressure and fire frequency (Chapter 6). Although the tree density did indeed decline during the last 25 years (1971-1996), this decline was primarily caused by a decline of 0.5-1m tall trees but there was no clear evidence that elephants or fire were a major contributory cause (Chapter 6). The elephants did however cause a change in woodland structure over the 25-year period. That we found no clear effects of fire on the tree density in Tarangire may partly be due to the lesser intensity of actual fires fires because of low standing biomass due to high grazing intensities of the migratory herds that return to the park at the beginning of the dry season i.e. when fires start to occur. These less intense fires are less damaging to trees (Trollope 1982, 1984, Starfield et al. 1993). Yet, the recurring haphazard dry season fires do form a threat for the migratory and residential wildlife herbivores which reside in the park during the dry season (TWCM 1994, TCP 1998) since they depend on the available forage to survive the dry season.

Recently, efforts for the conservation and management of these areas have been put, to a large extent, into fire prevention. Hereby, ironically, fire itself is one of the frequently used tools. Park managers burn early in the dry season to create wide fire breaks along the park boundaries to prevent dry season fires from entering the park. Furthermore, burning is also used to rid animals that have died of anthrax or to clear thick vegetation in order to attract game and to facilitate wildlife viewing which promotes tourism. Using fire to improve forage quality in Tarangire, however, has little value since the majority of the grazing animals are outside the park when the positive effects of fire are apparent and these effects are gone when the animals return (Chapter 2,3).

The future

Savannas can provide an ideal habitat for both domestic and wild ungulates (Gillon 1983). Consequently, grazing by domestic herbivores is a primary form of income for local communities (Steinfeld et al. 1996) while wildlife tourism significantly contributes to the national income of foreign currency. In the past fire appears to have been an appropriate tool in the management of savanna pastoral systems. Currently widespread fires in the African savanna biome are annually consuming more than 2000×10^6 tons of above-ground biomass (Levine 1991), a large proportion of which can be potential forage for herbivores. These extensive fires, in combination with other human activities, appear to have resulted in the negative effects of fire outbalancing the positive effects desired by pastoralists and managers of wildlife areas. Furthermore, the positive effects of fire on forage quality for herbivores are short-lived and can be substituted by grazing itself, while the risk for the negative effects of fire is large and these effects are more lasting than the positive effects (Chapter 2). One would consequently argue that the use of fire has become inappropriate in the management of present day savannas and should be restricted.

Indeed, in many areas the use of fire is regulated by law and sometimes even banned completely (Homewood and Rodgers 1991, Frost 1992, Van Wilgen and Scholes 1997). However, past experience has shown that, since there are seldom means to enforce fire laws outlawing fire is meaningless and only leads to increased incendiarism (Komarek 1965, 1967, Frost 1992). Moreover, a complete ban on fire may be counter-productive since in areas where this has happened the consequent invasion of bush and of unpalatable plant species and a build-up of senescent plant material resulted in a numerical decline of wild and domestic animals (Brynard 1972, Homewood and Rodgers 1991). In fact, although the extent of burning in African savannas should indeed be reduced, the question should not concern the use of fire per se, but rather the fire regime. Variation in the effects of fire is not only related to variation in the abiotic and biotic environment (Chapter 2, Bond and Van Wilgen 1996), but also to the fire regime which is specified by the season of burning, type and frequency of fire (Bond and Van Wilgen 1996, Bond 1997). Therefore fire cannot be regarded as a unifunctional tool. Rather, variability in the effects of fire through the application of different fire regimes allows for the use of fire for various management objectives (Gill et al. 1990, Bond and Van Wilgen 1996). For example, to counter bush encroachment one needs a hot, intense fire. This is obtained by creating a head fire (i.e. burning with the wind) during the dry season when wind speed is high, air humidity is low and when the fuel load is high enough to sustain a hot fire. On the other hand back fires (burning against the wind) on cool, windless days at the end of the wet season when, vegetation is just dry enough to burn, do not cause large damage to trees and should be used in order to create fire breaks to counter wild fires. Hereby the area burned must be large enough to prevent wildfires from jumping the firebreak but also to prevent high grazing concentrations on small tracks of post-fire green flush.

The array of different effects that fire can have on savanna ecosystems makes it difficult to generalize about its use in savanna management. Furthermore, although we increasingly learn to understand the short-term effects of fire, more insight is needed about the long-term consequences of various fire regimes on savanna ecosystem processes, particularly the consequences for wild and domestic grazers. Insight in these issues will contribute to a better concept for the useful application of fire for the sustainable management of savanna ecosystems.

In conclusion I quote Phillips (Phillips 1936) who, already in 1936, made the statement: "Fire is a bad master but a good servant". Currently, "Fire, the master", representing the more destructive fires caused by arsonists and people with no knowledge of fire management, has gained too much importance and overrules "fire the servant", respresenting the fires based on proper fire knowledge and fire management and which lead to the accomplishment of well defined management goals. This thesis shows that at present in East African savannas the "servant" can still be employed to help sustain the unmatched wildlife populations as well as a greater proportion of the rural/pastoral economies, but that particularly it is the "master" who should be opposed in order to accomplish this goal.

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Summary

In tropical savanna ecosystems fire can be seen as a natural phenomenon. Next to grazing it is also one of the largest human impacts on tropical savanna ecosystems. This especially is the case in the relatively nutrient rich savanna systems of East Africa, an area of high ecological value due to the large numbers of highly diverse mammal populations. Here pastoralists have used fire for centuries to improve the availability and quality of forage for their livestock. The first part of this thesis investigates in which manner fire affects forage quality and quantity as well as the mechanisms that cause these effects.

We found that fire improves various vegetation characteristics that determine the quality of forage for grazers. Firstly, fire improves the composition of forage for grazers since the amount of nutritious leaf material, in relation to less nutritious stem and dead material, is enhanced in post-fire regrowth. Secondly, structural vegetation characteristics that determine forage intake, such as the amount of biomass per unit volume, are also enhanced. Furthermore we found that digestibility of post-fire regrowth was higher than that of unburned vegetation. These alterations accordingly allow for a higher rate of forage intake in post-fire regrowth. Moreover, we found that fire increases the nutrient content of forage with higher concentrations of N, P, K, Ca and Mg in post-fire regrowth as compared to unburned vegetation. In contrast to what was so far suggested, this increase in nutrient concentration is not the result of enhanced nutrient availability through ash or higher mineralisation rates. Rather, the present study shows that in the relatively nutrient-rich savannas of East Africa the increased nutrient concentration in post-fire regrowth is primarily due to increased leaf:stem ratios, rejuvenation of plant material, and the distribution of a similar amount of nutrients, compared to unburned vegetation, over less above-ground biomass. The positive effects of fire on forage for grazers are however short-lived and have disappeared by the end of the post-fire growth season.

Although fire may improve the quality of forage for grazers, we found that the amount of forage generally is reduced. Particularly in a year of drought the effect is clearly negative, since we found that the production of post-fire regrowth was even less than the already low produce in unburned vegetation. This can be explained by the fact that soil water supply, the prime determinant of plant growth in these systems, does not only depend on rainfall and soil characteristics but also on above-ground biomass itself. By removing above-ground biomass, litter in particular, fire reduces the soil water status since this removal results in higher evaporation rates. Because rainfall is very variable in the East African savanna systems, there is a significant risk that burning of vegetation may result in lack of forage supply. The nomadic lifestyle of pastoral economies, however, allowed for the evasion of forage limitation when these would occur.

Over time, and particularly in the past decades, expansion of human activities in the East African savannas has resulted in a decline of both pastoral and wildlife areas. This increasingly has resulted in restriction of wildlife to protected areas with migratory routes being cut off, while at the same time increased livestock numbers have to be sustained on smaller areas of pastoral land resulting in high grazing intensities. Furthermore, increased human activities have also led to changes in the spatial and temporal occurrence of fire. The second part of this thesis discusses the consequences of wildlife compression and altered fire regime for the East African savannas.

Restriction of wild herbivores to protected areas, elephants in particular, and high fire frequencies can have severe consequences for the woody component of savannas. We found the increased elephant density in Tarangire National Park had resulted in a change of the structure of the woody component over a period of 25 years whereby especially large trees taller than 5 m were reverted to trees of 1 to 5 m tall. A decline in density of trees over the 25 year period also occurred, but this decline, which primarily occurred in the 0-1 m height class, was most probably the result of drought rather than increased fire frequency or herbivory. That we found no effect of increased fire frequency on the tree density may be attributed to lower fuel loads due to high grazing intensities at the onset of the dry season which result in less intense and therefore less destructive fires.

Restriction of migratory herbivores to protected areas can also have severe consequences on population numbers when forage quality and quantity in the protected areas does not meet herbivore requirements. Since forage quantity and quality is not only determined by abiotic factors and fire but also by grazing itself, we investigated if grazing could enhance forage quality and quantity to meet herbivore requirements when their movements would be restricted to their dry season range. We found that, similar to the effects of fire, the effects of repeated biomass removal through simulated grazing resulted in a significant increase in forage quality with higher nutrient concentrations and improved structural qualities of grass forage. As with fire, biomass removal through grazing did not result in enhanced forage production and, although grazing did enhance forage quality, this enhancement was not sufficient to allow grazers to reside year round in the protected area.

Finally this thesis addresses the question if fire is still an appropriate tool in the management of savannas in present-day Africa. With the present high grazing intensities and the positive effects of grazing on forage quality, as well as the subsequent lower impact of fire

in reducing bush-cover, this study suggests that use of fire to improve forage quality for herbivores would seem superfluous. Furthermore, this study suggests that since grazers generally feed selectively avoiding litter material, while fire is less discriminative removing all biomass, the effects of grazing on vegetation production, particularly under drought conditions, would be less detrimental than the effects of fire. Nevertheless it is concluded that, under the correct biotic and abiotic conditions and using the correct regime, fire can still be an appropriate tool to help sustain the unmatched wildlife populations, as well as a greater proportion of the rural/pastoral economies.

Samenvatting

In de semi-aride savannesystemen van Afrika kan vuur worden beschouwd als een natuurlijk verschijnsel, dat al duizenden jaren invloed op deze systemen heeft gehad. Daarnaast is vuur ook een instrument met behulp waarvan de mens reeds gedurende eeuwen grote invloed op deze systemen uitoefent. Dit geldt zeker voor de savannes van Oost Afrika. In deze relatief nutriëntrijke systemen, bekend om hun hoge dichtheid en diversiteit aan wilde zoogdieren, hebben herdersvolkeren al eeuwen lang vuur gebruikt om hun weidegronden te beheren, dankzij bepaalde effecten van vuur die kunnen leiden tot een verbetering van deze gronden; zo kan vuur de dichtheid van de begroeiing door bomen verminderen en ook de voor het vee niet eetbare plantensoorten verwijderen. Tevens blijken grazende dieren, na afbranden van de oude vegetatie, zich te verzamelen op de jonge vegetatie. Onderzoek in gematigde streken en in nattere tropische gebieden hebben aangetoond, dat de nieuwgroei na branden een hogere voedingswaarde heeft dan niet gebrande vegetatie. Hoewel in de semi-aride savannes van Oost Afrika steeds meer van vuur gebruik wordt gemaakt, blijkt er zeer weinig bekend te zijn over de gevolgen ervan voor de beschikbaarheid en kwaliteit van het voedsel voor herbivoren.

Op welke wijze vuur de kwaliteit en de hoeveelheid van voedsel voor grazende dieren beïnvloedt, wordt in het eerste gedeelte van dit proefschrift besproken alsook hoe deze effecten tot stand komen, hoe lang ze voortduren en hoe ze worden beïnvloed door sturende abiotische factoren, zoals beschikbaarheid van water en bodemgesteldheid. Het onderzoek toonde aan, dat vuur een positief effect heeft op verschillende eigenschappen van de vegetatie die de kwaliteit van het voedsel voor grazers bepalen. Ten eerste heeft nieuwgroei na branden een hogere verhouding aan levend plantmateriaal en tevens bestaat een groter gedeelte hiervan uit blad, terwijl de niet gebrande vegetatie hoofdzakelijk uit stengel en dood materiaal bestaat. Ten tweede heeft nieuwgroei na branden, door z'n lagere structuur, een hogere biomassa per volume eenheid dan niet gebrande vegetatie, waardoor een grotere opname van voedsel per hap mogelijk is. Ook vindt een verbetering plaats in de chemische samenstelling van de vegetatie als voedsel voor grazers. Zo wordt het voedsel beter verteerbaar en heeft het hogere concentraties aan stikstof, fosfaat, kalium, calcium en magnesium. Door combinatie van al deze factoren kan meer voedsel van hogere kwaliteit worden opgenomen dan uit niet gebrande vegetatie. De grotere dichtheid van grazende dieren op gebrande savannevegetatie zou hiervan een gevolg kunnen zijn. De verbetering van de kwaliteit van het voedsel is echter van korte duur en is grotendeels verdwenen aan het einde van het groeiseizoen dat volgt op het branden.

Een andere vraag, waarop in dit proefschrift wordt ingegaan, betreft de oorzaak van de verhoogde concentratie aan nutriënten in een gebrande vegetatie en van de tijdsduur waarin zij blijft bestaan. Wij tonen hier aan dat, in tegenstelling tot wat eerder door anderen is gesuggereerd, de toename van de nutriëntenconcentratie in nieuwgroei na branden niet het gevolg is van een, door middel van asdepositie en verhoogde mineralisatie, toegenomen beschikbaarheid van nutriënten in de bodem. Het blijkt immers dat, in deze relatief nutriëntrijke savannes waar de meeste nutriënten zich ondergronds bevinden, de toename het gevolg is van een verhoogde blad:stengel verhouding, van verjonging en van een geringere verdunning van nutriënten als gevolg van een mindere hoeveelheid bovengrondse biomassa.

Terwijl vuur de kwaliteit van voedsel voor grazers verbeterde, toonde het onderzoek echter aan dat vuur op de hoeveelheid voedsel geen positief effect heeft. Dit is met name het geval in drogere jaren waarin de reeds lagere productie van gras, door gebrek aan water, nog eens verder door vuur wordt gereduceerd. Dit negatieve effect van vuur op de productie van gras, met name in drogere jaren, kan verklaard worden door het feit dat waterbeschikbaarheid, de meest beperkende factor voor groei in deze systemen, niet alleen door neerslag en bodemeigenschappen wordt bepaald maar ook door de bovengrondse biomassa zelf. Verwijdering van bovengrondse biomassa, met name in droge jaren kan dit leiden tot afsterven van perenne grassoorten, die juist een primaire voedselbron voor grazende dieren vormen.

In de Oostafrikaanse savannes is neerslag zeer variabel en de kans op droge jaren is groot. Gelet op het bovenstaande is er een groot risico dat de nomadische herders geconfronteerd worden met voedselgebrek voor hun vee wanneer hun brandpraktijken worden gevolgd door een droog jaar. Wanneer dit zich in vroegere tijden voordeed, konden deze herdersvolken, dankzij hun nomadische levenswijze, uitwijken naar gebieden waar nog wel voedsel aanwezig was.

Menselijke activiteiten zijn mettertijd in de savannes van Oost Afrika steeds meer toegenomen. Met name in de afgelopen decennia hebben een sterke bevolkingstoename en een toename in landbouwactiviteiten onder andere geleid tot een afname in zowel de traditionele weidegebieden alsook de gebieden waar het wild voorkomt. Voor het wild heeft dit tot gevolg dat het steeds meer wordt teruggedrongen in de beschermde natuurgebieden en de seizoensgebonden bewegingen van kuddes migrerende grazers steeds beperkter worden. Voor de herdersvolken betekent afname in weidegebieden dat zij zich moeten handhaven in een steeds kleiner wordend gebied, zodat hun nomadische levensstijl steeds meer wordt bemoeilijkt en zij noodgedwongen een meer sedentaire levensstijl aannemen terwijl hun veestapel juist is toegenomen. De toename van menselijke activiteiten in de savannes van Oost Afrika heeft bovendien ook in de orde van ruimte en tijd het vóórkomen van vuur beïnvloed; zo is bijvoorbeeld de frequentie van branden in veel gebieden sterk toegenomen. In het tweede gedeelte van dit proefschrift worden verschillende aspecten van de gevolgen van deze veranderingen op de Oostafrikaanse savannes besproken.

In het verleden is bij menig onderzoek gesuggereerd dat er een sterke afname van de dichtheid en bedekking van bomen en een verandering in hun structuur optreedt in gebieden waar populatieverdichting voorkomt van wilde herbivoren, met name van olifanten, alsook daar waar de vuurfrequentie is toegenomen. Veel van deze studies beslaan echter periodes van slechts enkele jaren of kijken alleen naar bepaalde cohorten van de boompopulatie. Wij waren in staat om een studie over de dichtheid, structuur en samenstelling van bomen in Tarangire National Park, die in 1971 was uitgevoerd, te herhalen. Sinds die tijd zijn zowel de dichtheid aan olifanten als de brandfrequentie sterk toegenomen. Wij vonden dat de getalsmatige toename van olifanten inderdaad een duidelijk effect heeft gehad op de structuur van bomen in Tarangire over een periode van 25 jaar; o.a. zijn er nu minder grote bomen van hoger dan 5 m en meer kleinere bomen van 1 tot 5 m. Ook was over deze periode de dichtheid van bomen teruggelopen, vooral door een sterke afname van de 0.5 tot 1 m hoge bomen. Onze gegevens suggereren echter dat deze afname het gevolg is van een droogte in 1993 en niet, in tegenstelling tot wat eerder beweerd is, het gevolg van toegenomen olifantendichtheid en vuurfrequentie. Dat wij geen noemenswaardige effecten van een hoge vuurfrequentie op de boomdichtheid vonden, kan verklaard worden door de lage intensiteit van de branden die daardoor minder schade aan bomen toebrengen. Deze lage intensiteit, en de bijgevolg geringere destructiekracht van het vuur, komt door de relatief lage hoeveelheid brandbaar grasmateriaal als gevolg van intensieve begrazing door migrerende wildebeest- en zebrapopulaties die vlak voordat het brandseizoen begint het park intrekken.

Beperking van wilde herbivoren tot beschermde gebieden heeft niet alleen invloed op de vegetatie van deze gebieden maar ook op de aantallen herbivoren, met name wanneer de kwaliteit en kwantiteit van het voedsel niet voldoende zijn om de populaties van herbivoren te handhaven. Wij onderzochten of Tarangire National Park, waar de migrerende wildebeesten en zebra's in het droge seizoen verblijven, in staat zou zijn deze populaties het hele jaar door te kunnen onderhouden wanneer de migratieroutes van de dieren naar de buiten het park

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liggende graasgebieden in de natte tijd, zouden worden afgesloten. Momenteel wordt Tarangire National Park in de natte tijd grotendeels niet begraasd. Daar de kwaliteit en kwantiteit van voedsel voor grazende dieren niet alleen door neerslag, bodem en vuur worden beïnvloed maar ook door begrazing zelf, hebben we in dit onderzoek de gevolgen van begrazing op het voedsel bestudeerd door knipexperimenten uit te voeren in gebieden met verschillende bodems, daar waar migrerende kuddes zich in de droge tijd het meest ophouden. Herhaaldelijk knippen verhoogde, evenals branden, de kwaliteit van het voedsel, gemeten in hogere proporties aan levend materiaal, en met name blad, alsook in hogere nutriëntgehaltes van het blad in vergelijking met de niet geknipte vegetatie. Ondanks deze toename was de concentratie van nutriënten in het voedsel, met name van fosfaat, niet afdoende om aan de behoeften van de grazende dieren te voldoen. Tevens vonden wij dat ook door deze wijze van biomassaverwijdering het totale voedselaanbod verminderd werd en in het algemeen niet afdoende zou zijn om de huidige populatie-aantallen te handhaven. Hieruit valt af te leiden dat beperking van de migratieroutes negatieve gevolgen zal hebben voor de migrerende kuddes.

Als laatste wordt in dit proefschrift de vraag behandeld of vuur nog steeds een bruikbaar middel is om savannes heden ten dage te beheren. Op basis van de gegevens van dit proefschrift moet het gebruik van vuur in veel gevallen worden afgeraden. Ten eerste maakt de hoge begrazingsdruk door de positieve effecten van begrazing op de kwaliteit van het voedsel, in deze vergelijkbaar met die van vuur, het branden van savannes overbodig. Bovendien is door de hoge begrazingsdruk in de droge tijd minder brandbaar materiaal beschikbaar, wat tot gevolg heeft dat de branden minder intens zijn en daardoor als middel tegen verstruiking minder geschikt zijn geworden. Terwijl grazers selectief biomassa verwijderen en derhalve dood en strooisel materiaal vermijden, is vuur daarentegen niet selectief en verwijdert zonder onderscheid het merendeel van de grasachtige vegetatie. Omdat we hebben gevonden dat strooisel de verdamping van bodemwater vermindert, kan uit dit onderzoek bovendien worden afgeleid dat, met name in periodes van droogte, begrazing minder negatieve gevolgen zal hebben voor vegetatieproductie dan vuur.

Desalniettemin wordt hiermede niet betoogd dat gebruik van vuur in het geheel geen nut meer zou hebben. Mits savannevegetatie onder de juiste biotische en abiotische omstandigheden wordt gebrand en daarbij de juiste brandmethode gebruikt wordt, kan vuur nog steeds een geschikt middel zijn om, voor de ongeëvenaarde wildpopulaties alsook voor het merendeel van de lokale/pastorale bevolkingsgroepen, de voor hun levensbelangrijke Oostafrikaanse savannes in stand te houden.

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Now that I have completed this thesis, the moment has come to look back on the 6 years during which I performed the work that has resulted in this thesis. It started in 1993 when I took off to Tanzania together with Margje, accompanied by 800 kg of luggage and a similar amount of weight in expectation about what we were going to encounter along the PhD road we had turned on to. From the start I new this road was not an easy one and that it could get bad with pot-holes and ruts, and that at times I would get stuck completely. Indeed, sometimes it felt like driving through stretches of "black cotton soil" in the wet season in Tarangire; you get bogged down continuously in this soil and the moment you think you are out you get stuck again. Nevertheless, building and running Chatu Research Camp, as well as the daily activities that come with living in the bush, gave me a learning experience which I could not have obtained elsewhere. By sampling 1000 kg of grass, 500 m in total length of soil cores and 7000 trees in Tarangire, I literally and metaphorically harvested an enormous amount of experience and knowledge of savannas. And this was only the cake. The icing on top was living and working in a park full of wildlife and undisturbed nature whereby the unexpected visits of African wildlife, particularly elephants, to our camp gave an additional thrill to our life in Tarangire which cannot be matched. I never had anticipated that, after having lived in Tarangire for three years, I would return with such a multitude of the mass that I had with me on arrival in knowledge, experience and memories. The toughest stretch of black cotton soil I encountered along the PhD road must have been during the period after my return from Tanzania. But, as in Tanzania, one learns to drive in this soil and slowly but surely I learned to manage the wheel, gears and accelerator in such a way that I now have come to the end of the road. Conclusion of this all, I would not have wanted to miss the past 6 years in a lifetime! However, this period could never have been so magnificent and immensely valuable if I had not had the help and support from so many people.

In the propositions of a previous thesis it was stated that the acknowledgements should not be used to thank one's partner. I would disagree with this, particularly when the partner has also been the closest colleague. Therefore I hereby address some words to Margje. Together we started this trip and together we have come to the end of it successfully. Because of you, I was able to get much more out of this period than I would ever have been able to do alone. You made the valleys I went through less deep and the mountaintops I stood on higher. I treasure many great and beautiful moments with you in Tanzania. Someone who certainly deserves a word of thanks is my promoter, Professor Herbert Prins. I could never have imagined that when I was talking to you about fire ecology on the veranda of Ndala Research Camp in Manyara in 1991, I would get a PhD on this topic 8 years later. Thank you for creating this opportunity for me and for having confidence in me when I lacked it. As a teacher you are one who does not let his pupils rest in the shade of his tree of knowledge for long. Rather, you are one who sends his pupils off to grow their own tree, teaching them how to cherish this tree so that they may prosper from the shade it develops and showing them the many ways and shapes in which a tree can be grown. By teaching me in this manner, I did not only learn much about savanna ecology and science in general, but also about how to function as an independent and objective scientist. Likewise, I want to thank my previous mentors at Utrecht University: Hans Lambers Hendrik Poorter, René Boot, Marinus Werger, Roland Bobbink, Wim Dijkman and Rien Aerts.

Using the growth of a seedling to a tree as a metaphor of acquiring knowledge and scientific insight, my gratitude also goes to the ones that helped me select the seed and plant it. One person in particular helped me enormously in this process, showing me how to prepare the seedbed and the conditions for appropriate sowing. It is the same person in whose shade of knowledge and wisdom I did allow myself to rest and who also helped me tremendously in fine-tuning the text of this thesis in the past months. How lucky I am to say that he is my father.

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Curriculum vitae

Claudius van de Vijver was born on the 25'th of September 1965 in Heerlen (The Netherlands). In 1985 he obtained his high school degree from the Koningin Wilhelmina College, Culemborg (The Netherlands). In that same year he started the study Biology at Utrecht University. During his graduate studies he did two major research projects. The first was on phenotypic plasticity of inherently slow and fast growing grass species in response to nitrate supply which was done at the Ecophysiology Group of Prof. H. Lambers (Department Plant Ecology and Evolutionary Biology, Utrecht University). The second project was performed in the Serengeti National Park (Tanzania) where he studied the effects of fire on savanna grassland in the post-fire growth season. This project was supervised by Prof. M.J.A. Werger of the Department Plant Ecology and Evolutionary Biology and Evolutionary Biology (Utrecht University), Prof. S.J. McNaughton of the Biological Research Laboratories (Syracuse University) and Prof. F. F. Banyikwa the Department of Botany (University of Dar es Salaam). He obtained his "doctorandus" degree in 1992.

In that same year he became a guest-research fellow at the Department Plant Ecology and Evolutionary Biology (Utrecht University) where he worked together with Dr. R. Aerts on the potential for heathland restoration on formerly arable land at a site in Drenthe (The Netherlands).

In June 1993 he got a position as a PhD at the Tropical Nature Conservation and Vertebrate Ecology Group, Department of Environmental Sciences, Wageningen University. From 1993 to 1996 he lived in Tanzania where he performed the fieldwork of which the results are included in this thesis. From 1993 to 1998 he taught in various courses in Tanzania and Wageningen on the ecology and management of savanna ecosystems. From 1998 onwards he has been educational coordinator of the C.T. de Wit Graduate School for Production Ecology, Wageningen University.