ELEPHANTS - TREES - GRASS - GRAZERS

Relationships between climate, soils, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya)

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ABSTRACT

Wijngaarden, W van, 1985. Elephants - Trees - Grass - Grazers; relationships between climate, soil, vegetation and large herbivores in a semi-arid savanna ecosystem (Tsavo, Kenya). ITC Publication Number 4; 159 pages, 36 tables, 63 figures, 139 references, one appendix; English and Dutch summaries (also doctoral thesis, Wageningen).

Based on descriptions of the climate, soils, vegetation and large herbivore populations, relationships are described between the different components of the Tsavo ecosystem. It appears that there is a strong correlation between the floristic composition of the vegetation and the physical environment (climate and soil). The structure of the vegetation, however, is related more to the density of elephants and the activity of man (fire). The production of the vegetation is strongly related to rainfall and the percentage cover of the relevant vegetation component. Large herbivore distribution and density is related to human activity and the amount and type of forage that is available in a dry year. Static and dynamic models describing these relationships quantitatively are developed and, on the basis of simulations, some conclusions are drawn on the future management options for the national park and the nearby ranches.

Keywords: semi-arid ecosystems, primary production, vegetation dynamics, elephants, modelling, simulation, rangeland management

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poorly drained, alkaline/saline soils, *Acacia* spp and *Capparidaceae* are always the dominant woody species, while on the well-drained acid soils *Bursaceae* and *Lannea* spp always dominate.

The best known aspect of the Tsavo area, however, is the large herbivore population, dominated by elephants. With a density of approximately one elephant per km^2, Tsavo does not rank very high among areas with high elephant densities; considering the semi-arid climate, however, it represents a very high animal biomass. In addition to elephants, there is a variety of other large herbivores–including black rhinoceros, buffalo, giraffe, zebra, oryx, eland and several other antilopes.

It is not the large elephant population itself which has made Tsavo famous, but more the drastic impact they have had on the vegetation and abundance of other herbivores: "the Tsavo elephant problem".

In the 1960s, frequent heated discussions were held between the advocates of "cropping" and "laissez faire" policies on the management actions which should be taken. After a sample cropping for research purposes in 1966, the "laissez faire" policy was followed and no active measures were taken to control or reduce the elephant population.

Although the problem was "solved" in the late 1970s by a reduction of the elephant population by some 70 percent through poaching, it still presents a challenge to scientists and managers because this solution was not the result of careful scientific analysis of the problem followed by management recommendations and appropriate action.

1.2 RESEARCH BACKGROUND OF THE STUDY AREA

Most research in the Tsavo area was generated by and directed toward solving the "elephant problem". In the early 1960s, extensive damage to the woody vegetation by elephants was reported and, as a result of the 1961 drought, large numbers of black rhinoceroses died of starvation (Glover, 1963; Napier Bax and Sheldrick, 1964; Glover and Sheldrick, 1964). It was in that period that the discussion started on whether to control the elephant population in order to save some of the woody vegetation; it was thought that in this way the habitat and food supply of other herbivores could also be safeguarded.

Because of lack of data on the size of animal populations and of general knowledge on the functioning of such semi-arid ecosystems, no consensus emerged and the main outcome of those discussions was the establishment of the Tsavo Research Project in 1967. During the eight years of its existence, the main emphasis of the Tsavo Research Project was on the elephant and rhino population dynamics and ecology (Laws, 1969a, 1969b; Goddard, 1969, 1970a, 1970b; Schenkel and Schenkel- Hulliger, 1969; Corfield, 1973; Leuthold, 1977a). Later, important work on other herbivores was also done (Leuthold, 1970, 1971a, 1971b, 1972; Leuthold and Leuthold, 1972, 1975a, 1975b, 1976, 1978).

Studies of the vegetation and physical environment of the Tsavo ecosystem were limited (Agnew, 1968; Greenway, 1969; Glover, 1970), although some elephant exclosures, burning experiments and a network of storage rain gauges were set up in 1971.

In 1975, a study was published relating primary production to carrying capacity, based on simulated primary production data only. This study indicated that climatic variation in the Tsavo ecosystem was probably a severe limitation for the large herbivore population (Phillipson, 1975). The distribution of and utilization by animals of natural and artificial waterholes in the southern part of Tsavo National Park East was studied by Ayeni (1975).

Although Glover (1963) and Laws (1969b) published data on the size of the elephant population, it was only in 1976 that a complete picture was obtained of the distribution and abundance of all large herbivores (Cobb, 1976). In the meantime, some work was also done on the avifauna (Smeenk, 1974; Lack *et al*, 1980) and on some of the invertebrates, namely dung beetles (Kingston, 1977) and termites (Buxton, 1979).

On request of the Tsavo Research Project, a soil and vegetation survey was carried out from 1975 to 1978 in Tsavo National Part East and surroundings by the author, with support of the Kenya Soil Survey and the Netherlands Foundation for the Advancement of Tropical Research (WOTRO).[1] The technical soil and vegetation survey data and maps were published by the Kenya Soil Survey (Wijngaarden and Engelen, 1985). In the same period, data on primary production, vegetation dynamics and impact of herbivores on the vegetation were collected by the author.

During the analysis of the survey and other data, ideas were developed on the relationships between the major components of the Tsavo ecosystem. In the present text, extracts of the essential elements from the survey report are combined with data on primary production, large herbivore-vegetation interactions and the previously published data on the large herbivore population in an effort to present a holistic view of the Tsavo ecosystem.

[1] The history of this research project can be summarized as follows: In early 1974, Dr P E Glover, then chief biologist of the Tsavo Research Project, queried the Kenya Soil Survey about the possibility of conducting a soil survey of the Tsavo national parks to provide base- line information for on-going vegetation and animal behaviour studies in the area. Because the area was not included in the already-established list of their priority studies, Kenya Soil Survey's project manager, Dr Ir W G Sombroek, began looking for alternative sources of manpower and funds for such a survey. Initial contacts with Unesco's Division of Ecological Sciences and the Dutch government's Directorate for Technical Cooperation were not successful. In consultation with Professor Dr Ir Bennema of Wageningen Agricultural University and Professor Dr Baerends of Groningen University, Dr Sombroek then submitted a research proposal to WOTRO–which was already supporting similar studies in Serengeti National Park, Tanzania. In early 1975, WOTRO gave their support to the study (project number W77-52).

Chapter 2

THE TSAVO ECOSYSTEM

Most of the attributes of the Tsavo ecosystem have already been described in detail by various authors. In this chapter, a review of this information will be presented. Especially important references are:

- Climate: a study on the potential evapotranspiration by Woodhead (1968), and the analysis of the climate by Braun (1977, 1978)

- Geology and geomorphology: maps with descriptions of the geology and geomorphology of the Tsavo area were produced by Saggerson (1962), Sanders (1963) and Walsh (1963)

- Hydrology: no specific information on hydrology has been published, but papers on the geology and soils contain some information on the hydrology of the area. One special aspect, waterholes, was treated in a paper by Ayeni (1975)

- Soils: maps with descriptions of the soils of the whole of Kenya, including the Tsavo area, have been published at exploratory scale (1:1000000), (Sombroek *et al*, 1982), and of part of the Tsavo area at reconnaissance scale (1:250000), (Wijngaarden and Engelen, 1985)

- Vegetation: a checklist of species found in Tsavo National Part East and a short description of the physiognomic vegetation types were produced by Greenway (1969). A map and description of the vegetation of part of the area at reconnaissance scale (1:250000) with vegetation types described with floristic as well as structural characteristics were produced by Wijngaarden and Engelen (1985)

- Large herbivore population: a survey of the abundance and distribution of the large herbivore population of the entire Tsavo ecosystem was done by Cobb (1976). Information on the population dynamics, behaviour and habitat utilization can be found in an extensive list of publications. A summary of most of this work can be found in Laws (1969b) and Leuthold (1977a, 1977b)

- Data on other animals and the human activities in the Tsavo area are spread over a large number of publications and will be cited when relevant.

2.1 DEFINITION OF THE TSAVO ECOSYSTEM

An ecosystem is an assemblage of diverse animals and plants which form an interdependent living community, together with the set of physical and chemical features that make up the inanimate matrix in which they live (Pratt and Gwynne, 1977). It should be emphasized that both the living community and the inanimate matrix have dynamic characters. The dynamics of the inanimate matrix is partly autonome and partly influenced by the living community.

Based on the above definition, the Tsavo ecosystem is here defined as the area in which the major terrestrial animal populations find their home range on a yearly basis. Seasonal distribution patterns found by Cobb (1976) and home ranges of radio-tracked animals as found by Leuthold (1977a) indicate that most elephants–the dominant herbivore in the Tsavo ecosystem–find their home range in the area defined by Cobb (1966) as the Tsavo ecosystem (Figure 2.1). This area comprises approximately 43 000 km². The core of it is formed by Tsavo National Park East and West, together 21 000 km². The remaining area is occupied mostly by commercial ranches to which wildlife generally has free access.

The Tsavo ecosystem is bounded in the northwest by the densely populated parts of Ukambani, to the southwest by mountains such as Kilimandjaro, Pare and

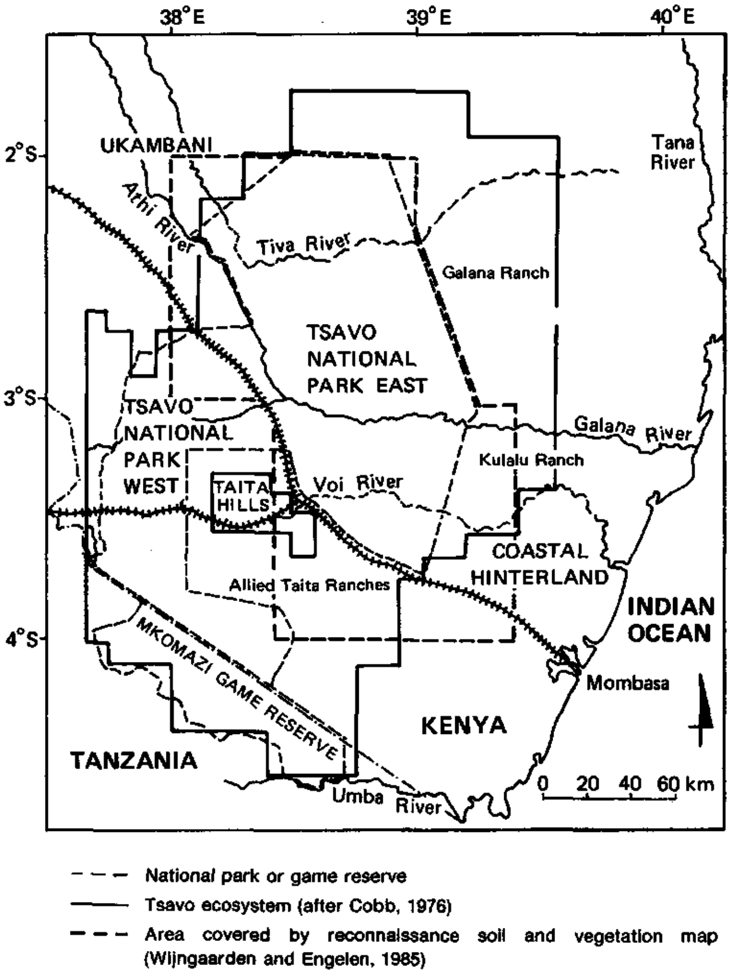


Figure 2.1 Location of the Tsavo ecosystem

Usambara, and to the southeast by the fairly densely populated coastal hinterland. These are all more or less natural boundaries which form a clear limit to the distribution of elephants and other wildlife. Only to the northeast is the boundary less clear. It was chosen rather arbitrarily, though it possibly constitutes the dividing line between the elephant populations retreating to the Tana and Tiva rivers in the dry season (see also Cobb, 1976).

The Mkomazi Game Reserve in Tanzania forms part of the Tsavo ecosystem, as there is free movement of animals across the boundary between the two countries. The gap in the centre is formed by the Taita hills. They rise approximately 1500 m above the general landscape and are densely populated because of the much higher rainfall.

2.2 PHYSICAL ENVIRONMENT

2.2.1 Climate

The Tsavo area is situated only a few degrees south of the equator and thus the distribution of the rainfall is roughly related to the movements of the tropical convergence zone. In general, this produces two rainy seasons around the time of the equinoxes (Brown and Cocheme, 1973). In the Tsavo area, this results in the following seasons:

- Short dry season: January - February
- Long rains: March - April/May
- Long dry season: May/June - October
- Short rains: November - December.

The average annual rainfall in the area varies from 200 to 700 mm per year (Figure 2.2) and these amounts are approximately equally divided over the two rainy seasons. Potential evapotranspiration is high, more than 2000 mm/year. Temperatures are fairly constant over the year; mean monthly maxima are around 30°C and the monthly minima around 20°C.

A practical tool to compress climatic data into one value for evaluation purposes is the concept of bio- climatic (ecologic) zones. This was originally based on the moisture index (Pratt *et al*, 1966), but later this concept was modified by the Kenya Soil Survey into a pure climatic variable: average annual rainfall divided by potential evapotranspiration (Sombroek *et al*, 1982). From the beginning, however, the strong correlation with the vegetation and agricultural potential was realized and, because of the lack of meteorologic data in many remote areas, vegetation is always used as an additional criterion to map the bioclimatic zones.

For the Tsavo area, a combination of (1) the analysis of data of approximately 100 meteorologic stations and (2) the correlation between vegetation and bioclimatic zones (Section 2.3.1.2) made possible rather detailed mapping of the bioclimatic zones, even in the remote parts of the ecosystem (Wijngaarden and Engelen, 1985). The spatial distribution of the bio-climatic zones occurring in the

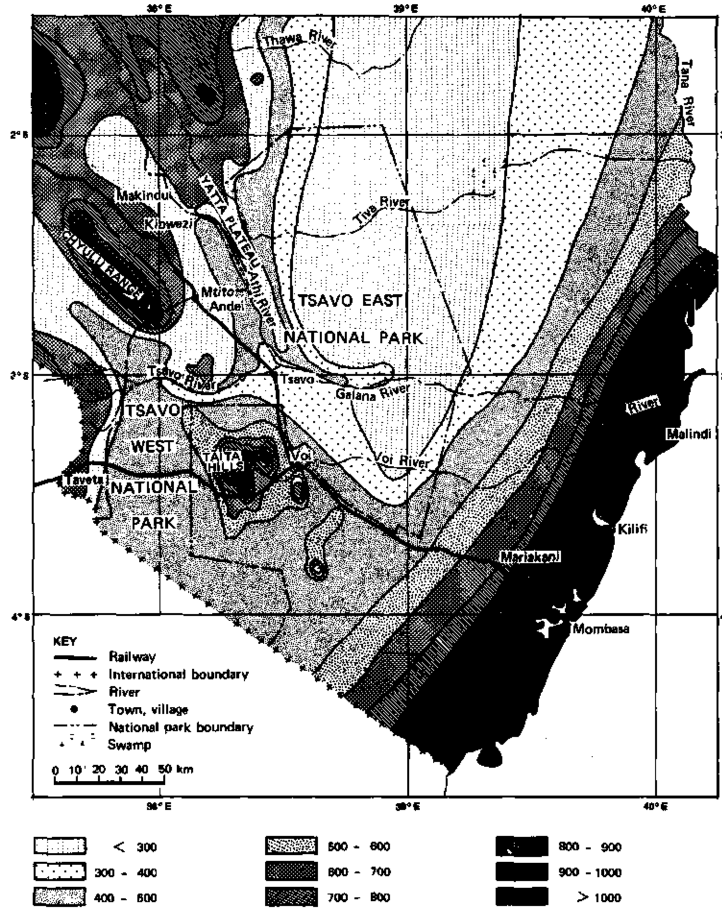


Figure 2.2 Average annual rainfall (in mm), (from Wijngaarden and Engelen, 1985)

Tsavo ecosystem is shown in Figure 2.3 and some of their characteristics are listed in Table 2.1.

It will be argued in Chapter 5 that the severity of the long dry season and the forage production in the long rains are crucial for the large herbivores, and that the level of the herbivore populations is strongly influenced by especially dry years. (A dry year is defined in this study as a year with an amount of rainfall less than the equivalent of the 90 percent probability of the rainfall.)

Because forage production is strongly related to rainfall (Section 2.3.1.4) and the severity of the dry season can be expressed in the duration and amount of rain that may be expected, it also seems useful to indicate those climatic variables for the bio-climatic zones (see Table 2.1). To obtain some insight into the possibilities for crop growth, the chance of obtaining one good crop of maize per year (Pr > 2/3 Eo, or the probability that the rainfall is less than two-thirds of the

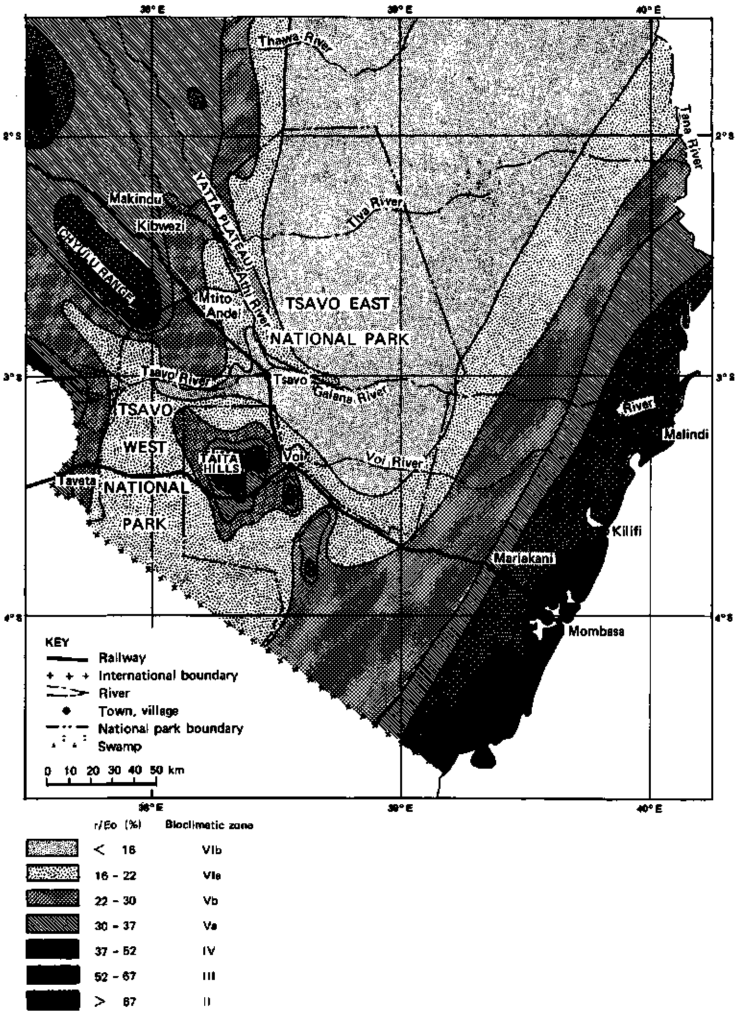


Figure 2.3 Bio-climatic zones (from Wijngaarden and Engelen, 1985)

potential evapotranspiration) and the chance of complete crop failure (Pr < 1/2 Eo, or the probability that the rainfall is less than one-half of the potential evapotranspiration) are also given (see also Braun, 1977; 1978).

Most of the Tsavo ecosystem is located in bio-climatic zone VI (Figure 2.3), which means dry years, as defined above, with rainfall of less than 50 mm during the long rains, a long dry season of 180 to 200 days and no possibility for rainfed agriculture (chances for a crop of maize less than 20 percent). It is only towards the edges of the ecosystem that the climate becomes more favourable. These areas are consequently also rather densely populated by agriculturists.

Table 2.1 Some characteristics of the bio-climatic zones

Bio-climatic zone	IV	Va	Vb	VIa	VIb
Average annual rainfall (R) (mm.)	700-1000	600-800	450-650	350-500	250-375
Average annual pot. evapotr (E) (mm.)	1800-2100	2000-2200	2000-2200	2100-2300	2200-2400
Ratio R/Eo x 100	53-37	37-30	30-22	22-16	16-12
RLR-90 (mm.)	100-200	75-100	50-75	25-50	10-25
RLD-90 (mm.)	10-50	0-10	0-10	0-10	0-10
LLD-90 (days)	140-160	160-180	180-200	180-200	180-200
Pr > 2/3 Eo (%)	60-80	40-60	20-40	10-20	< 10
Pr < 1/2 Eo (%)	< 20	20-40	40-60	60-80	> 80

RLR-90 = 90% probability of the rainfall during the long rainy season

RLD-90 = 90% probability of the rainfall in the long dry season

LLD-90 = 90% probability of the length of the long dry season

Pr > 2/3Eo = probability that the rainfall is more than 2/3 of the potential evapotranspiration in any period of 90 days

Pr < 1/2Eo = 100% probability that the rainfall is more than 1/2 of the potential evapotranspiration in any period of 90 days

2.2.2 Geology and geomorphology

The stratigraphy and lithology of the rock types occurring in the Tsavo area are listed in Table 2.2. The geomorphology is dominated by the occurrence of extensive planation levels of both erosional and sedimentary origin. A number of erosion surfaces can be distinguished, but only the latest, the Nyika level of end-Tertiary age, is present over large areas and not much dissected yet. Of the older surfaces, only remnants can be found (Figure 2.5), such as at the base of the Chyulu hills and the Yatta plateau (Oyani, 1976; Wijngaarden and Engelen, 1985). The Chyulu hills are relatively recent volcanic hills composed of basalts and in places covered by course pyroclastic deposits. The Yatta plateau consists of a protective cap of Miocene phonolites, only approximately 10 m thick, overlying gneisses of the basement system rocks (Figure 2.4). The erosional plains are developed on a variety of rock types, such as the basement system rocks and the Duruma sandstones.

Eastwards of approximately the 300 m contour line, accumulational processes have formed the landscape. These sedimentary plains are developed on Plio-

Table 2.2 Geology: stratigraphy and lithology

Stratigraphy		Lithology
	Unconsolidated deposits	
Quaternary	Fluviatile deposits	unconsolidated "sandy to clayey" sediments
Quaternary	Continental deposits	unconsolidated "sandy and loamy" sediments
Plio-Pleistocene	Bay deposits	unconsolidated "clayey" sediments
	Volcanic Rocks	
Quaternary	Chyulu volcanics	olivine basalt and pyroclasts
Miocene	Yatta lava	phonolite
Permo-Triassic	Duruma sandstones	
	Mariakani sandstones	fine grained micaceous sandstones
	Maji-ya-Chumvi beds	shales and siltstones
	Taru grits	arkoses, fine to coarse grained sandstones
Precambrian	Basement System Rocks	
	Psammitic group	quartzites, quartz-feldspar gneisses
	Pelitic group	hornblende and/or biotite gneisses
	Calcareous group	crystalline limestone

Figure 2.4 View of Yatta plateau and Galana river

Pleistocene "bay deposits" of an unconsolidated clayey and saline nature. In the transitional zone between the basement erosional plain and those sedimentary plains on the bay deposits, an area of continental deposits can often be found (Figure 2.5). The method of their deposition is not clear, but according to Sombroek *et al* (1976) they are probably of sheetwash origin.

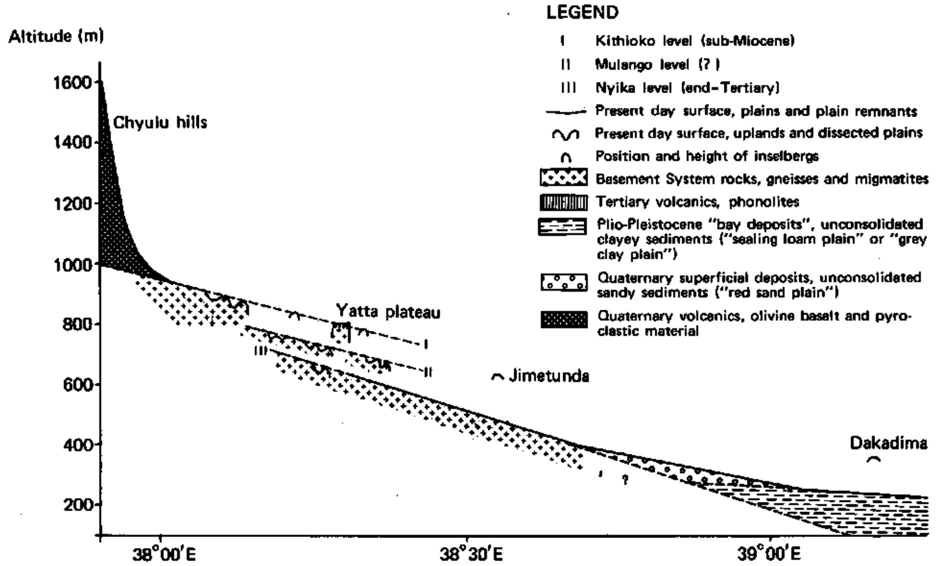


Figure 2.5 Simplified cross-section at approximately 2°30′ S (from Wijngaarden and Engelen, 1985)

When looking in detail at the basement erosional plain, important small differences appear (Figure 2.6). Towards the major rivers, the landscape has been dissected relatively recently, as shown by the gently sloping dissected topography towards the rivers and the V-shaped valleys. Also, minor depressions in the erosional surface have been filled with sheetwash sediments (sedimentary plains in Figure 2.6), making the general relief very flat, with slopes of–in general–less than 1 percent.

Within this extremely flat plain, a number of inselbergs occur, some more than 1000 m high. They consist mostly of a somewhat more quartzitic type of basement system rock, making them more resistant to weathering and erosion. Where the basement system rocks consist of crystalline limestone, they often form low elongated ridges. Most inselbergs have gently sloping areas at their bases, the footslopes. The footslopes are, in general, of accumulational origin, as they are covered by at least several meters of unconsolidated sediment (Figure 2.7).

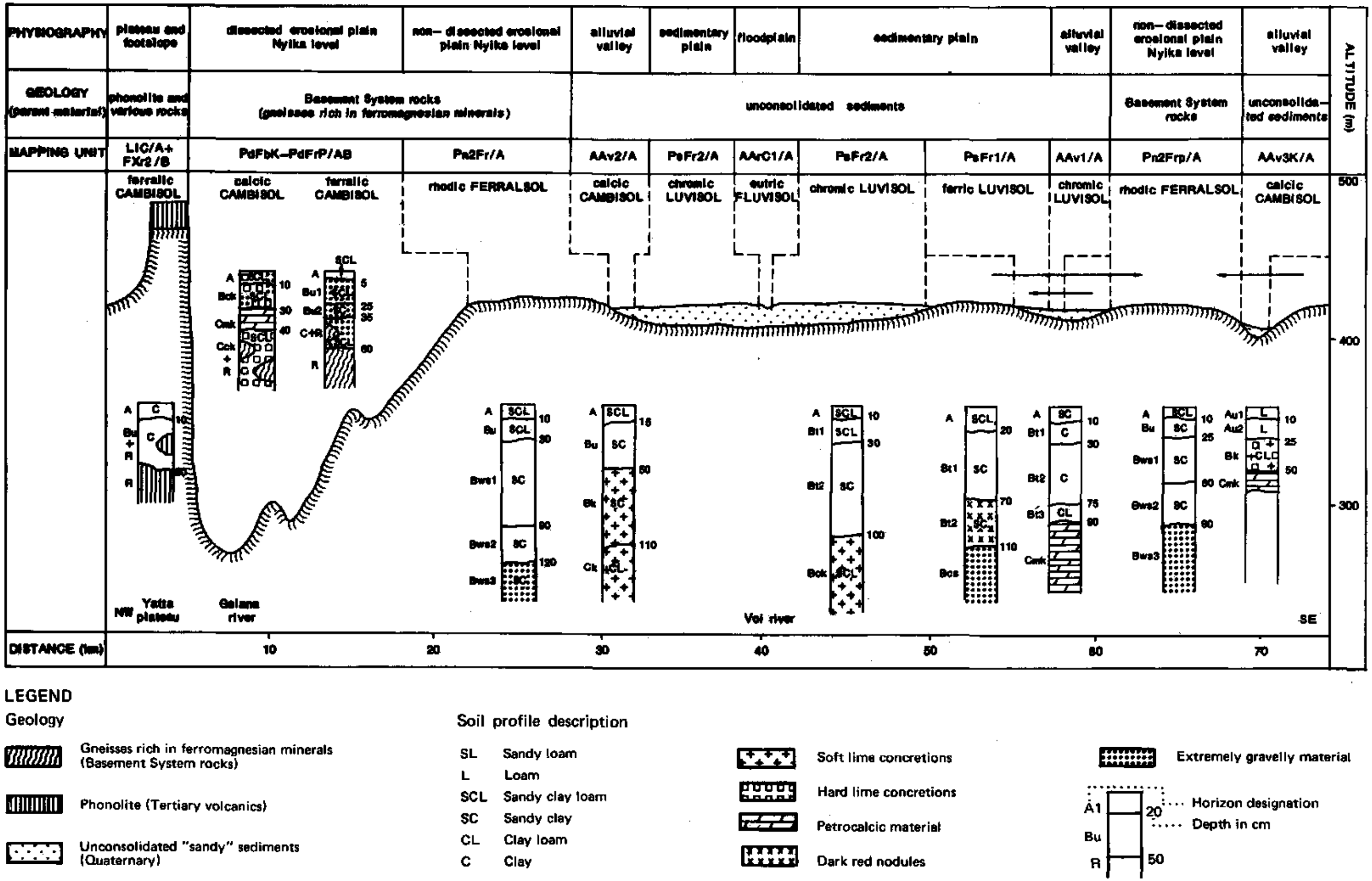


Figure 2.6 Cross-section Yatta-Buchuma (approximately NW - SE), (from Wijngaarden and Engelen, 1985)

Figure 2.7 *View of Irima hill, footslope and bottomland*

A floodplain of some importance is found only along the lower reaches of the Tiva river. Along the Athi-Tsavo-Galana river, it is virtually absent. The Voi river flows through a floodplain only a few hundred meters wide. Alluvial valleys are fairly regularly distributed over the ecosystem. They usually don't have an active stream channel and hardly any sedimentation takes place there at present. There are local areas with impeded drainage, the so-called "bottomlands".

2.2.3 Hydrology

The Tsavo ecosystem belongs to the drainage basins of the Tana (Tiva), Athi-Tsavo-Galana, Voi and Umba rivers, but these rivers originate in higher rainfall areas. In fact, large parts of the Tsavo area do not have functional external drainage. The amount of water generated by run-off in most years is apparently not sufficient to fill the broad alluvial valleys so that the water could flow all the way to the major rivers that cross the area.

The sources of permanent available surface water are very limited. Only the Athi-Tsavo-Galana and Umba rivers flow the entire year. The Tiva and Voi are seasonal. In the dry season they contain water only in the sandy riverbeds; water can be reached in many places in the sandy riverbeds by digging shallow holes, however–as is done by both man and wild animals.

Small springs are found along the Yatta plateau and in some places on the dissected plain. Their discharge is small, the water is often rather saline by the end of the dry season and, because of intensive use, they soon become highly contaminated.

The natural waterholes are an interesting source of water. These are shallow depressions in the landscape, which are filled in the rainy season by run- off water and may contain water for several months into the dry season. All larger and more important waterholes are found on the erosional plain at a density of approximately one per 10 km². Elephants and other wallowing animals have probably played an important role in their formation (Ayeni, 1975), (Figure 2.8).

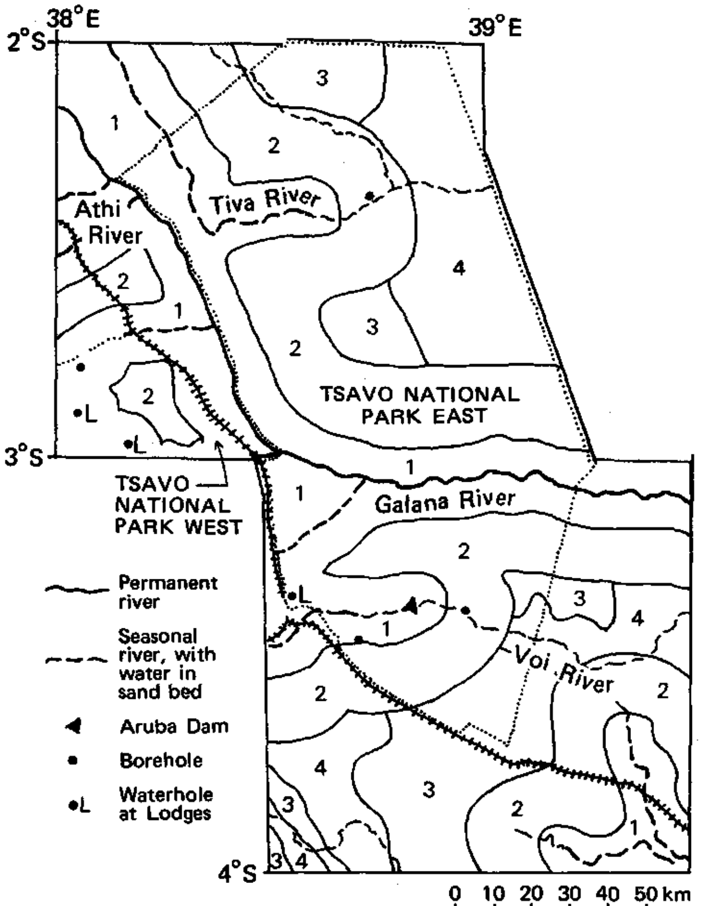
In the sedimentary plain, only very shallow and small waterholes are found. The swelling and shrinking upon wetting and drying of the clay minerals found there may be the reason that they dry up–through seepage–soon after the end of the rains. The only lake in the area is Lake Jipe in the far west.

Water development projects for both wildlife and cattle have increased the availability of drinking water in the Tsavo ecosystem. In Tsavo National Park East, a dam was built in the Voi river and the lake behind it is now a very important source of water for wildlife. Also, several boreholes were sunk. Most of them yield water of only marginal quality because of the high salt content.

Most ranches have their own water supply, either pumped from the Galana

Figure 2.8 Waterhole with elephants and buffalo

river (Galana and Kulalu ranch) or supplied from a branch of the pipeline running from Mzima springs to Mombasa. Some water tanks at the ranches are also accessible for wildlife. The artificial waterholes at the tourist hotels to attract game are a special case. The distribution of surface water in the area covered by the soil and vegetation survey (Wijngaarden and Engelen, 1985) is shown in Figure 2.9.



Permanent water supplies for wildlife

1 = Area within 10 km of permanent water supply

2 = Area between 10 and 25 km of permanent water supply

3 = Area more than 25 km from permanent water supply, but with large natural waterholes

4 = Area more than 25 km from permanent water supply, mainly without large natural waterholes

Figure 2.9 Surface water distribution (adapted from Wijngaarden and Engelen, 1985)

2.2.4 Soils

2.2.4.1 GENERAL PROPERTIES AND DISTRIBUTION OF THE SOIL TYPES

The soils of the Tsavo area show a wide range in depth, colour, drainage condition, structure, and chemical and physical properties. Extreme differences in texture, however, are uncommon. Most soils have a sandy-clay texture in the subsoil.

Sombroek *et al* (1982) and Wijngaarden and Engelen (1985) found that the distribution and properties of the soils were closely related to the geology and geomorphology of the area. In fact, they let the geology and geomorphology determine the hierarchy of the soil map legend. The following description of the distribution of the soils of the Tsavo area will therefore also follow this approach.

The morphologic characteristics of the soils of the main landscapes, the correlation with the legend symbols of Sombroek *et al* (1982) and Wijngaarden and Engelen (1985) and their classification according to FAO (1975) are given in Table 2.3. The correlation with the USDA Soil Taxonomy (1975) is given in the soil survey report by Wijngaarden and Engelen (1985). The distribution of the soils of the main landscapes within the Tsavo ecosystem is shown in Figure 2.10. A short description is given below.

Soils of the hills, low ridges and plateaus

These landforms are the most prominent landscape features, but occupy only a very small part of the Tsavo ecosystem. The soils are generally shallow, stony and rocky. The soils on top of the Yatta plateau vary from shallow to deep, are well-drained, dark red and have a clay texture. The low ridges on crystalline limestone also have stony soils, but they are relatively rich in organic matter.

Soils of the footslopes

The gently sloping areas at the bases of the hills and mountains have, in general, very deep, well-drained, dark red soils with a sandy-clay-loam to sandy-clay texture. The soils are strongly weathered and thus rather acid, and have a low mineral reserve.

Soils of the dissected plains

The relatively recently dissected landscape along the Athi-Tsavo-Galana river forms a band approximately 10 to 15 km wide. All soils are shallow, well-drained and gravelly. Because of the richness of the parent material and the present- day semi-arid climate, an accumulation of lime is often found in those soils.

Soils of the erosional plain and uplands on the basement system rocks

The soils of these landforms are formed directly from the underlying rocks. Most of the basement system rocks are ferro- magnesium rich gneisses (hornblende-biotite gneisses), so fairly rich soils can be expected. Because of the long stability of the land surfaces, however, the soils are rather strongly weath-

Table 2.3 Summary of the morphology and classification of the soil mapping units (legend of Figure 2.10)

Symbol	Landform	Slope	Parent material	Short description of the soil morphology	Classification (FAO 1975)	Mapping symbol (Sombroek et al.1982)	Mapping symbol (Wijngaarden and Engelen 1985)	Acreage (km2) (%)
H 1	Hills	> 16%	gneisses and sandstone	excessively drained , shallow, reddish brown to greyish brown, rocky and stony soils of varying texture	eutric REGOSOLS	H12; H13,22	HUC; HXC	420 km2 1.0 %
H 2	Low ridges	2-8%	crystalline limestone	well drained, shallow, black, calcareous gravelly loam	orthic RENDZINAS and calcic CAMBISOLS	H19	HLIK	420 km2 1.0 %
L	Plateau	< 2%	phonolite	well drained, shallow to very deep, dark red, friable, clay, in places bouldary or rocky	rhodic FERRALSOLS and ferralic CAMBISOLS	L4	LIC	390 km2 0.9 %
F	Footslopes	2-5%	various	well drained, very deep, dark red, friable to firm, sandy clay loam to sandy clay	chromic LUVISOLS and rhodic FERRALSOLS	F10,12,18,19; FY2; Y7	FU; FL; FX; YX	2840 km2 6.6 %
D 1	Dissected plain	2-5%	gneisses	well drained, shallow, yellowish brown to dark reddish brown, gravelly sandy clay loam	calcic CAMBISOLS and ferralic CAMBISOLS	Pd4	PdF	2500 km2 5.8 %
D 2	Dissected plain	2-5%	sandstones and shales	imperfectly to well drained, shallow to deep, strong brown, often stoney, firm sandy clay	orthic LUVISOLS and calcic CAMBISOLS	Pd6	PdStP; PdK; PdA	670 km2 1.6 %
U	Uplands	2-8%	gneisses	well drained, moderately deep to deep, dark red, friable to firm, sandy clay to clay	chromic LUVISOLS	UL10	U2Frp; PnIFr	500 km2 1.2 %
N 1	Erosional plain	< 2%	gneisses	well drained, deep to very deep, dark red to dusky red, very friable sandy clay	rhodic FERRALSOLS	Pn8,12	Pn2Fr; PnUb	14320 km2 33.3 %
N 2	Erosional plain	1-5%	siliceous sandstones	well drained, moderately deep to deep, dark brown, firm sandy clay	orthic ACRISOLS	Pn33	Pn2Stb	640 km2 1.5 %
N 3	Erosional plain	1-5%	gritty sand-stone	well drained, moderately deep to deep, red to dark red, friable sandy clay	chromic LUVISOLS	Pn32	Pn2Str	1060 km2 2.5 %
S 1	Sedimentary plain	< 2%	continental deposits	well drained, deep to very deep, dark reddish brown to dark red, firm sandy clay	ferric LUVISOLS	Ps3,4,8	PsAi1,14; PsF1	2980 km2 6.9 %
S 2	Sedimentary plain	< 2%	continental deposits	well drained, very deep, dark brown to red, friable sandy clay loam to sandy clay	orthic and chromic LUVISOLS	Ps6,7,14	PsAi2; PsFr2; PsStk; AAr1; AAf1	1140 km2 2.7 %
S 3	Sedimentary plain	< 2%	continental deposits	imperfectly drained, very deep, reddish brown, very firm sandy clay; underlying a loamy sand topsoil	solodic PLANOSOLS	Ps5, 20	Ps13	2310 km2 5.4 %
S 4	Sedimentary plain	< 2%	bay deposits	poorly drained, very deep, brown to dark greyish brown, very firm, calcareous, sodic and saline clay	orthic SOLONETZ	Ps15,16,17,19,23,24 Pf1,2,3; B8	PsA21,22; AAf2,3,4	8400 km2 19.5 %
B	Bottomlands	< 2%	alluvial and colluvial dep.	very poorly drained, very deep, dark greyish brown to black, calcareous, cracking clay	pellic VERTISOLS	Up4; B3,9	BXd; PnIFdk; PsA23; AAr2	305 km2 0.7 %
T	Terrace	< 2%	alluvial deposits	well drained, deep, reddish brown to dark reddish brown sandy clay loam to sandy clay	calcic LUVISOLS	Pt1	AAr3	970 km2 2.3 %
A 1	Infilled valleys	< 2%	alluvial and colluvial dep.	moderately well drained, shallow to deep, dark brown, calcareous sandy clay to clay	calcic CAMBISOLS	A10,12	AAv	1310 km2 3.0 %
A 2	Floodplains	< 2%	alluvial deposits	complex of very deep, brown to very dark brown, stratified soils of varying drainage and texture	eutric FLUVISOLS	A5,8	AAr4,5,6; AArC	640 km2 1.5 %
V	Volcanic plains	2-16%	basalt and pyroclasts	complex of well drained, shallow to deep, friable soils of varying texture, consistence and stonyness	mollic ANDOSOLS and haplic CHERNOZEMS	H5; Pv2,7; Y1	HPC; PvV	1200 km2 2.8 %

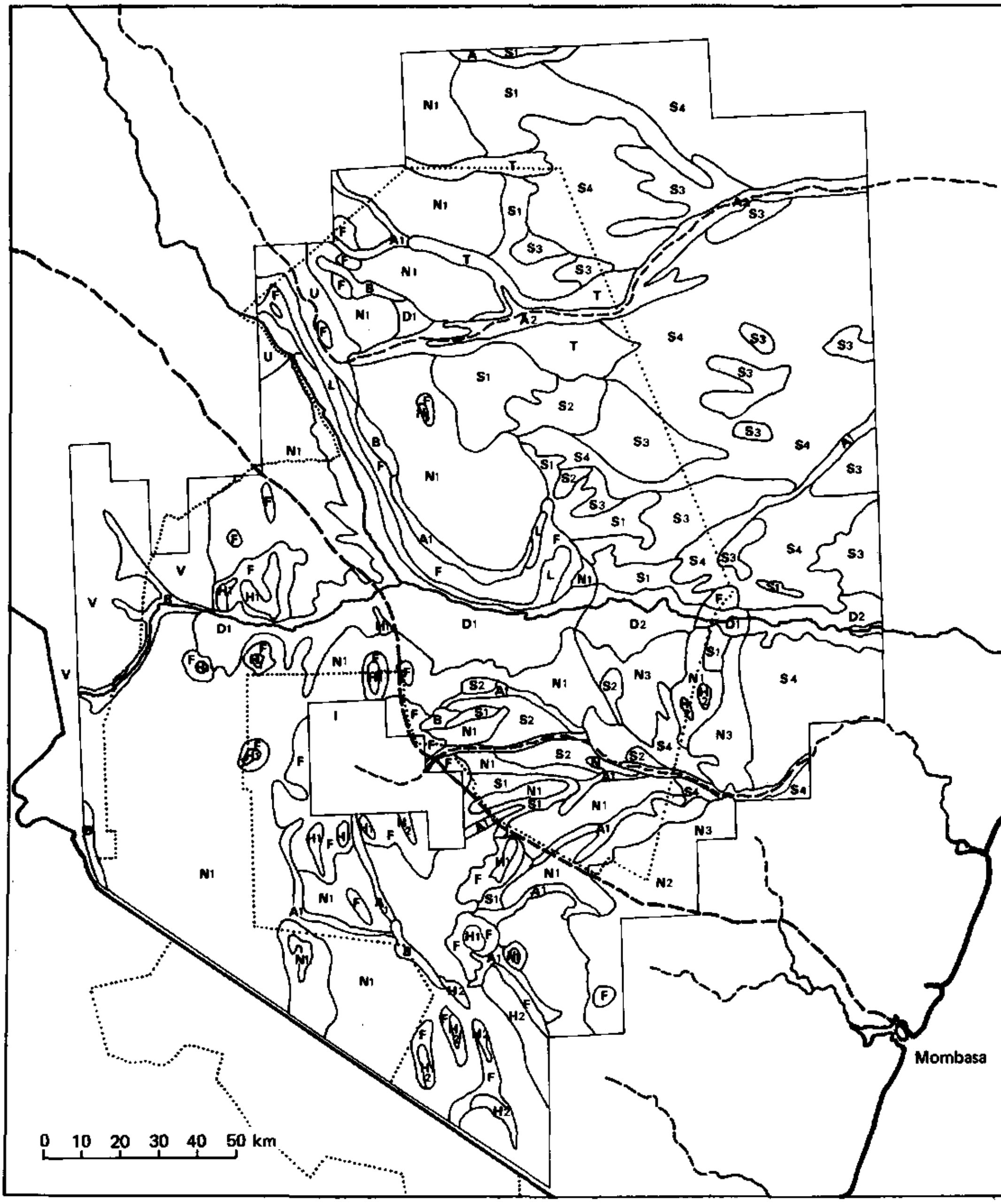


Figure 2.10 Generalized soil map of the Tsavo ecosystem (legend: Table 2.3), (simplified from Sombroek *et al*, 1982)

ered. Very deep, well-drained, dark red, rather acid sandy-clay soils are dominant. They are often referred to as the "red sandy soils" because of a sandy aspect caused by the strong cementation of the soil particles by iron compounds. In the gently undulating uplands, the soils are somewhat less weathered and so less acid.

Soils of the erosional plain on the Taru grits

The soils developed on the Taru grits vary from well-drained, moderately deep and dark red, with fair chemical and physical properties in the area north of the Nairobi-Mombasa road, to well-drained, shallow to moderately deep, reddish brown to dark brown soils with low chemical fertility in the area south of the main road.

Soils of the sedimentary plains on the continental deposits

There are two areas of these sedimentary plains. The first is found north and south of the Voi river in the Tsavo National Park East. The soils here are very deep, well-drained, red and have a sandy-clay texture. Chemical and physical properties are fair to good. Another large area is found along the infilled valleys and at the transition to the Tana river basin. The parent material is probably pre- weathered basement system rock. The soils are very deep, well-drained, dark red and of sandy-clay texture. The pH is rather low and they also show a rather poor topsoil structure (sealing).

Soils of the sedimentary plains on the bay deposits

As part of the Tana river basin, these soils are developed in unconsolidated marine or lacustrine deposits. The drainage is imperfect to poor, the colour dark brown to greyish brown and the texture sandy-clay to clay. These soils are nearly always alkaline and calcareous and often saline in the subsoil. The physical properties are poor, but they are fairly rich chemically.

Soils of the floodplains, valleys and bottomlands

Narrow stretches of recent or subrecent alluvium occur all over the Tsavo area. The soils vary strongly, depending on the mode of deposition. Well-drained, rather sandy soils are found, as well as poorly drained clayey soils. As a group, these soils have very favourable chemical and physical properties. The bottomlands always have very poorly drained, black, calcareous clay soils which are often salt- affected in the subsoil. Mappable stretches of terraces were found only along the lower reaches of the Tiva. The soils here are well-drained and relatively rich.

Soils of the volcanic hills, plains and lava flows

The Chyulu hills and surroundings are composed of various volcanic rocks. If there are any soils developed on the recent volcanic rocks, they are always well-drained, loamy and gravelly. Their chemical fertility is very high.

2.2.4.2 PHYSICAL AND CHEMICAL SOIL CHARACTERISTICS

Physical and chemical soil characteristics determine, to a large extent, how plants are able to perform under the prevailing climatic conditions. The amount of water available for plant growth is the result of the interaction of the climate and the physical soil characteristics. In semi-arid climates, it is important that all rainfall infiltrates properly into the soil and that the soil can store this infiltrated water to make it eventually available for the plants. Infiltration capacity and soil moisture retention characteristics are thus important variables.

To make optimal use of the available soil moisture, plants need an optimal supply of various minerals. Even in semi-arid climates, the nutrient supply is often a limiting factor in plant growth. Penning de Vries and Djiteye (1982) have shown that in the west African savanna soils, nutrients–especially nitrogen and phosphorus–normally limit the primary production at a rainfall of more than 300 mm per growing period. Some data about both physical and chemical soil characteristics will therefore be reviewed here.

Infiltration capacity

When the infiltration capacity of the soil is less than the rainfall intensity, run-off may occur and consequently less water is available for plant growth. Run-off can also initiate erosion processes. Rainfall intensity data for southeast Kenya are summarized by Lawes (1974) and Taylor and Lawes (1971). They indicate that rainfall intensities of more than 50 mm/hour are rare for long periods (Tables 2.4 and 2.5).

The infiltration capacity of the soils in Tsavo appears to be related more to the cover of the soil surface than to the different soil types (Wijngaarden and Engelen, 1985). Especially the cover by herbaceous vegetation seems to be of crucial importance. The mechanism through which ground cover influences the infiltration capacity is probably the prevention or breaking up of surface sealing

Table 2.4 Rainfall intensity in mm/hour, likely to be exceeded once per 2 years (50 percent probability) and once per 50 years (2 percent probability) for various durations (from Taylor and Lawes, 1971)

Prob.	Station	Duration					
%		15 min	30 min	60 min	3 hours	6 hours	24 hours
50	Mombassa	80	58	39	18	12	5
50	Voi	84	62	42	20	11	3
50	Makindu	84	54	41	16	9	3
2	Mombassa	180	122	65	37	26	8
2	Voi	172	120	115	47	24	6
2	Makindu	120	102	82	28		

Table 2.5 Number of times per year that rainfall intensity of 25 mm/hour is exceeded for various durations (from Lawes, 1974)

Station	Duration		
	15 min	30 min	60 min
Mombassa	36	15	3
Voi	18	8	3
Makindu	16	7	2

and the funneling effect of the plants (Glover *et al*, 1962). The high activity of termites in places with a high vegetation cover probably also contributes to favourable infiltration rates (Wielemaker, 1984).

Surface sealing was observed on all soil types when the area was strongly overgrazed or otherwise denuded of vegetation, but strong surface sealing, combined with algae crusts, was observed only on the alkaline soils of the sedimentary plain on the bay deposits.

It is therefore not surprising that the results of some infiltration measurements by rainfall simulation on dry soils show a good relationship with the ground cover (Figure 2.11). The data presented in this figure are derived from various soil types. There were not sufficient data to present separate relationships for each, but the general trend in all soil types was the same.

Comparing these results with the rainfall intensity data in Tables 2.4 and 2.5 reveals that when ground cover percentage is high the infiltration capacity of most soils will be higher than the expected rainfall intensity. Substantial surface runoff can be expected only on nearly bare soils (Figure 2.12).

Soil moisture retention characteristics

The amount of soil moisture available for plants is the difference between water held at field capacity (0.3 bar) and wilting point percentage (15 bar). Braun and Kibe (1978) found a good relationship between the amount of available soil moisture and texture of the soil. They did not find significant differences between different soil types. This contrasts with Sanches (1976), who found that "Oxisols" (Ferralsols of Table 2.3) have approximately 10 percent available water regardless of their texture, and that Andepts (Andosols of Table 2.3) have much higher amounts of available water than other tropical soils, as a function of texture. Wijngaarden and Engelen (1985) also suspected lower amounts of available soil moisture in Ferralsols, compared with other soils, but their data were too few to calculate separate relationships.

Because the value for Ferralsols found by Sanchez (1976) is about the same as the value predicted by Braun and Kibe (1978) for soils with a sandy-clay texture, a reasonable approximation for the predominant soils in Tsavo is 10 mm of available soil moisture per 10 cm depth. The total amount of available

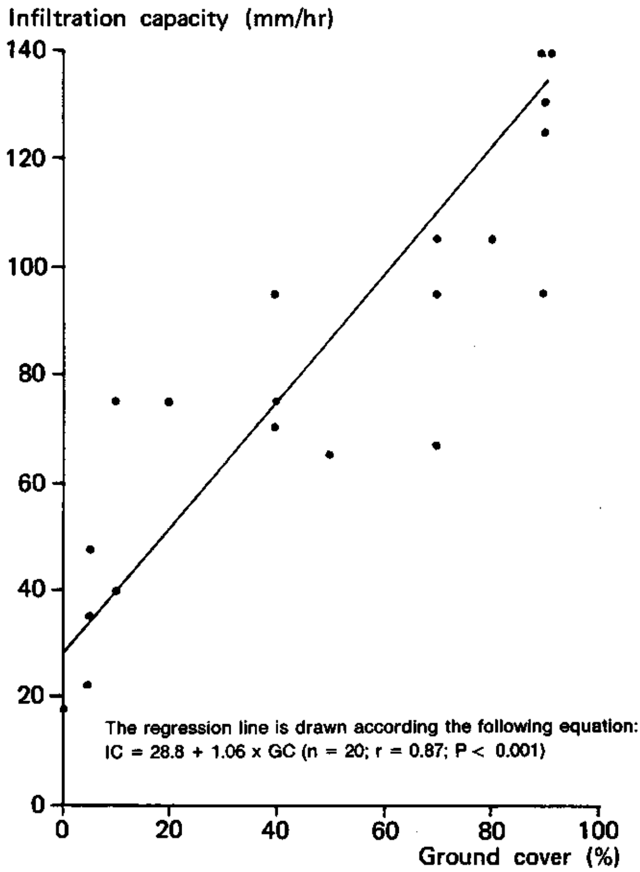


Figure 2.11 Relationship between infiltration capacity of the soil and ground cover of the vegetation

moisture which can be stored in the soil is then related mainly to the depth of the soil. Except for the hills and dissected plain, the soils in the Tsavo area are deeper than 100 cm, so in general at least 100 mm of available moisture can be stored.

Available soil nutrients

The availability of soil nutrients can have a major influence on ecosystem community structures (Bell, 1982) through its direct influence on primary production and indirectly also on the animal population. For the same soil types as listed in Table 2.3, the average values of some soil nutrients are summarized in Table 2.6.

Organic carbon and nitrogen are low, as can be expected under semi-arid conditions, but the C/N ratio is, in general, favourably low. The only exceptions are the soils on the crystalline limestone ridges and the volcanic plains (soil units H2 and V).

Phosphorus levels increase from low in the strongly weathered soils (soil units

Figure 2.12 Surface sealing and/or low vegetation cover causes a low infiltration capacity of the soil, ponding during heavy rainfall and run-off and sheet erosion on sloping terrain

F, U, N1, N2, N3 and S1) to moderately high values on the less weathered soils. High values are found only on the terraces, floodplains and volcanic plains (soil types T, A2 and V).

The content of calcium, magnesium, potassium and sodium also follows the soil development. Young calcareous soils have high Ca and Mg values (soil units H2, D1, D2 and S4). Old weathered soils are low in these elements (soil units L, F, U, N1 and N2). High Na values are found in salt-affected soils of parts of the sedimentary plain and the valleys and bottomlands (soil units S4, B and A1).

Copper and zinc values, as far as they are available, are above critical levels as indicated by Cox and Kamprath (1971, in Sanchez, 1976).

Absolute values, however, do not say very much. The important aspect is how available soil nutrients influence the production of vegetation and its quality as animal forage. No relationship was found between Ca, Mg, K and Na content of herbage samples and the content in the soil.

In Section 2.3.1.4, it will be shown that the primary production in Tsavo at normal rainfall is limited by the available soil moisture and that only in wet years (rainfall $>$ 400 mm per rainy season) do nutrients become a limiting factor, and then only in the "poor" soils (for example, soil units F, U, N1, N2 and S1).

The availability of soil nutrients thus plays a minor role in the primary production of the Tsavo ecosystem.

Soil unit	n	pH_{H2O}	C %	N %	C/N	P_{tot} ppm	P_{Ols} ppm	P_{av} ppm	Ca_{av} ppm	Mg_{av} ppm	K_{av} ppm	Na_{av} ppm	Cu_{tot} ppm	Zn_{tot} ppm
H1	3	6.8 6.4-7.5	0.59 0.4-0.9	0.13 0.1-0.2	5 3-8	-	-	25 17-30	2130 960-3200	640 520-830	130 72-200	35 7-55	-	-
H2	3	8.1 8.0-8.2	2.42 0.7-4.0	0.30 0.1-0.5	8 7-8	330 330	2.0 2.0	26 19-41	13460 9600-18000	840 630-1300	165 80-320	83 46-110	6 6	7 7
L	2	5.8 4.4-7.2	0.84 0.7-0.9	0.12 0.1-0.2	7 7	-	-	41 20-62	960 400-1520	640 400-880	610 520-700	55 28-82	-	-
F	7	6.5 5.7-6.9	0.68 0.3-1.0	0.11 0.1-0.2	6 3-12	130 130	1.3 1.3	21 12-75	620 360-1120	310 150-480	210 160-250	38 23-64	4 4	5 5
D1	5	7.3 6.3-8.0	0.55 0.3-0.7	0.07 0.05-0.1	8 6-10	330 290-360	4.0 2.0-6.0	67 10-184	5740 560-14000	450 250-880	220 110-260	52 35-120	7 6-8	12 8-17
D2	4	7.5 7.2-7.7	0.71 0.4-1.4	0.09 0.05-0.2	8 7-10	-	-	43 22-86	4200 1920-5200	750 620-1000	290 210-360	39 28-51	-	-
U	5	6.3 5.9-6.0	0.51 0.3-0.7	0.07 0.05-0.1	8 6-11	290 290	2.0 2.0	19 8-38	850 620-1360	490 400-720	260 230-320	22 tr-39	5 5	14 14
N1	15	5.8 5.1-6.8	0.76 0.3-0.9	0.09 0.05-0.2	9 4-10	150 80-220	1.3 1.0-2.0	13 7-33	630 240-1080	360 100-1040	250 110-400	23 7-55	6 3-12	8 5-11
N2	3	6.1 5.9-6.9	0.71 0.6-0.8	0.09 0.05-0.2	8 7-10	-	-	19 14-25	990 560-1520	360 200-600	210 180-240	34 8-55	-	-
N3	4	6.5 6.1-7.2	0.64 0.3-0.7	0.08 0.05-0.1	8 4-9	-	-	24 8-38	1160 880-1360	510 300-870	230 140-300	51 20-87	-	-
S1	9	6.2 5.6-7.0	0.43 0.2-0.8	0.07 0.05-0.1	6 3-7	110 100-120	1.3 1.0-1.5	26 15-37	850 240-1200	410 320-580	270 170-330	30 9-97	5 3-8	5 4-8
S2	7	6.8 5.9-7.5	0.60 0.2-1.2	0.10 0.05-0.2	6 3-12	260 140-370	4.2 4.0-5.0	63 42-118	1310 400-2080	700 470-1300	560 380-680	33 18-41	5 4-6	5 4-7
S3	2	6.5 6.1-6.9	0.28 0.2-0.4	0.04 0.00-0.1	7	-	-	21 20-22	680 640-720	1310 670-2000	400 330-470	55 55	-	-
S4	10	7.3 6.2-8.5	0.95 0.4-1.2	0.13 0.1-0.2	7 6-9	390 310-480	3.9 3.9	44 10-100	5260 880-12800	1360 400-2100	350 140-420	87 44-200	6 6	6 6
B	4	7.8 7.2-8.3	0.84 0.5-1.3	0.12 0.05-0.2	7 3-10	160 160	1.8 1.8	34 10-75	10970 6400-13300	2070 1800-2400	240 150-360	193 106-306	5 5	5 5
T	3	7.6 6.9-8.3	0.28 0.2-0.3	0.07 0.05-0.1	4 2-5	-	-	320 240-470	4690 2800-8000	910 720-1700	450 330-580	64 46-97	-	-
A1	10	7.3 6.3-8.0	0.64 0.3-1.2	0.10 0.05-0.2	6 3-10	120 120	1.4 1.4	26 11-40	5200 800-12000	1540 650-2300	410 140-760	110 35-280	4 4	9 9
A2	6	6.5 5.9-7.6	0.87 0.6-1.9	0.12 0.05-0.3	7 3-9	650 650	4.4 4.4	170 59-260	5600 3000-12000	1230 570-2100	390 200-670	91 35-120	17 17	19 19
V	3	6.6 5.9-7.1	2.01 1.1-3.0	0.10 0.1-0.2	11 9-12	-	-	177 120-204	6800 4900-7800	1700 1400-1900	930 430-1600	60 60	-	-

Table 2.6 Summary of average and range of available nutrients in topsoils (0 to 20 cm) of the soil mapping units

Soil unit = soil mapping unit as listed in Table 2.3
n = number of analyses; for $-_{tot}$ and P_{Ols} 1-3 analyses for some soil mapping units only
$-_{tot}$ = "total analyses": extraction with 25% HCl
$-_{av}$ = "Mehlig analyses": extraction with 0.1 N HCl/0.025 N H_2SO_4
P_{Ols} = "Olsen analyses": extraction with 0.5 M $NaHCO_3$ at pH 8.5

2.3 BIOTIC COMPONENTS

2.3.1 Vegetation

2.3.1.1 GENERAL PROPERTIES AND DISTRIBUTION OF THE VEGETATION TYPES

The available descriptions of the vegetation in east Africa are based mostly on the structure (physiognomy) of the vegetation, sometimes qualified by the dominant genera or species (Pratt and Gwynne, 1977). Continental European phyto-ecologists, however, use the floristic composition as the basis for their vegetation description and classification (see Mueller-Dombois and Ellenberg, 1975). In the description of the vegetation of the Tsavo area, these two lines of thought are combined, and both aspects are dealt with by Wijngaarden and Engelen (1985).

The floristic composition of the vegetation of the Tsavo ecosystem is described according to the Braun-Blanquet school of vegetation ecology (Mueller-Dombois and Ellenberg, 1974). This method consists of clustering lists of species (releves) into groups (plant communities) which show a similar composition of species, based mainly on their presence or absence. At the same time, groups of species appear that have a similar distribution over the various communities.

The idea behind this method is that groups of species give, in general, a more consistent indication of the environment than individual species (Zonneveld, 1982). Especially for dominant species, often used in other classifications, it holds that changes in abundance are not always correlated with clear differences in environmental factors (see, however, Section 2.3.1.2 and Chapter 4).

The structure or physiognomy of the vegetation is described here by the cover of the different strata. The strata considered are:

- tree layer; dominated by single-stemmed trees in general more than 6 m high
- high shrub layer; dominated by single or multi-stemmed trees or shrubs which have the larger part of the crown at a height of more than 2 m, but are in general less than 6 m high
- low shrub layer; dominated in general by multi-stemmed shrubs with most of their crowns less than 2 m high
- herb layer; dominated by annual and perennial herbs, including grasses.

All plant species potentially belong to one of these components. Grasses and herbs will always be found in the herb layer. Species which potentially grow into trees, however, can be found in either the high shrub layer or the low shrub layer–the latter only when they are in a juvenile stage, or when they are cut, browsed or burned down to a low level.

The structure classification adopted here follows the system used by the Kenya Soil Survey (Weg and Mbuvi, 1975), which is based on the classification of east African rangeland by Pratt *et al* (1966). This structure classification is based on the percentage cover by trees and shrubs only and can be presented in a two-dimensional graph (Figure 2.13). For practical reasons, the tree and high

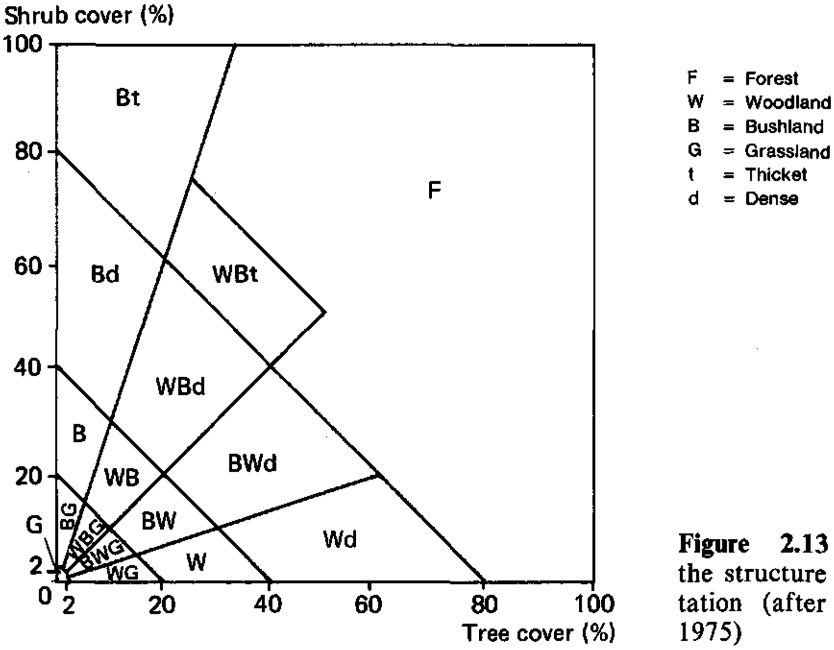


Figure 2.13 Classification of the structure of the woody vegetation (after Weg and Mbuvi, 1975)

shrub layers are taken together because their functions are comparable: providing shade and wind protection and food for only elephants and giraffes.

In this classification, no provision is made for the variation in cover of the herb layer. An additional classification was therefore made for the cover by perennial grasses (Table 2.7). The reason for taking only the perennial grasses into account follows from Section 2.3.1.4 and Chapters 4 and 5, namely their importance in determining the level and predictability of the production of the ground layer, their relative stability, their importance as forage for various animals and their value in increasing the infiltration capacity of the soils.

For practical reasons, the term "structure" will be used in the following only for the cover of the different strata of the woody vegetation and "grass cover" for the cover by perennial grasses. Both structure and grass cover were mapped for part of the Tsavo ecosystem (Wijngaarden and Engelen, 1985).

Based on the floristic composition (presence or absence of species), plant communities were formulated which show a close relationship with the physical enviroment (see Section 2.3.1.2). Most communities show a rather wide range of

Table 2.7 Classification of perennial grass cover

Class	Cover by Perennial Grasses
1	less than 20 %
2	20 to 50 %
3	more than 50 %

structure classes, which could be related to different actions of man and/or large herbivores (see Section 2.3.1.3 and Chapter 4).

Approximately 90 percent of the vegetation of the Tsavo ecosystem belong to plant communities which are often dominated by *Commiphora* spp and *Acacia* spp. Three groups of communities could be distinguished:

(1) *Commiphora-Lannea* group of communities, found in bio-climatic zones V and VI on well-drained often acid soils. Characteristic species, for example, are *Lannea elata* and *Grewia bicolor*. When the structure is wooded bushland or denser, the tree layer is nearly always dominated by *Commiphora* spp accompanied by some *Lannea* spp, *Boswellia hildebrandtii*, among others (Figure 2.14). When the tree layer has been destroyed by man, fire or large herbivores, these tree species are still present in the shrub or ground layer as saplings, but other shrubs–such as *Premna* spp, *Bauhinea taitensis*, *Sericocomopsis pallida*–then become the dominant woody species (Figure 2.15). The grass cover varies strongly because of differences in structure, climate and land use. When it is well developed, it is often dominated by short to medium-tall perennial grasses: *Chloris roxburghiana*, *Latipes senegalensis* and *Eragrostis caespitosa*. In the wetter parts of bio-climatic zone V, *Panicum maximum* and *Digitaria macroblephora* may become dominant.

Figure 2.14 Dense wooded bushland dominated by *Commiphora* spp (community CL1d). The ground cover is always very poor under such a dense woody cover, even in the absence of grazing and fire

Figure 2.15 Bushed grassland dominated by *Premna holstii* (community CL1c). This type of vegetation structure is common in areas where elephants have destroyed the tree layer. The lonely tree is a *Melia volkensii*. This area has an excellent grass cover; the dominant grass is *Panicum maximum*

(2) *Commiphora-Acacia* group of communities. These plant communities are found on the well to imperfectly drained non-acid, non-saline soils of bio-climatic zones V and VI. When the tree layer is not destroyed by man, fire or elephants, it is dominated by *Acacia* spp, locally accompanied by *Commiphora* spp. The more open-structured vegetation of this group of communities is dominated mostly by *Cordia gharaf, Boscia coriacea* and various *Capparidaceae.* The grass cover also varies strongly here; places with a high percentage cover are often dominated by the medium-tall perennial grasses *Tetrapogon bidentatus* and *Chrysopogon aucherii.*

(3) *Acacia-Schoenefeldia* group of communities, found only on the poorly drained, often alkaline and saline soils in bio- climatic zones V and VI. The structure is usually fairly open, bushed grassland or bushland with *Cadaba* spp, *Grewia tennax* and *Acacia* spp as dominant shrubs. Trees are absent (Figure 2.16). Locally dense bushland is found which is always dominated by *Acacia reficiens* (Figure 2.17). The ground cover percentage is usually high and dominated by the medium-tall perennial grasses *Schoenefeldia transciens* and *Sporobolus helvolus.*

The other 10 percent of the area is covered by a large variety of communi-

Figure 2.16 Bushed grassland dominated by *Sericocomopsis* spp (community AS1d). The tree/shrub layer here is also strongly influenced by elephants. The grass cover in this case is rather poor, and dominated by *Sporobolus helvolus*

ties. The *Combretum zeyheri* group of communities occurs only in the northwest of the ecosystem in zone IV on well-drained, rather acid soils. Dominant trees or shrubs here are always several broad-leaved *Combretum* spp. The ground cover percentage is usually very high and dominated by the medium to tall perennial grasses *Hyparrhenia* spp and *Themeda triandra.*

The *Diospyros-Manilkara* group of communities occurs only in the extreme southeast of the area in zones Va and IV in a wide range of soil conditions. Evergreen species such as *Diospyros* spp, *Manilkara mochisa* and *Euclea divinorum* are important components in this group of communities.

Very small areas are occupied by three remaining undifferentiated groups of communities, each with very specific soil and/or climatic conditions: (1) the undifferentiated vegetation of the hills and mountains, containing several large tree-like *Euphorbia* spp; (2) the undifferentiated vegetation of the lava flows and volcanic plains, in which the grass *Sehima nervosum* is often dominant, and (3) the undifferentiated floodplain vegetation, which contains a number of characteristic riverine tree species such as *Acacia elatior, Hyphaene coriacea* and *Newtonia hildebrandtii* (Figure 2.18).

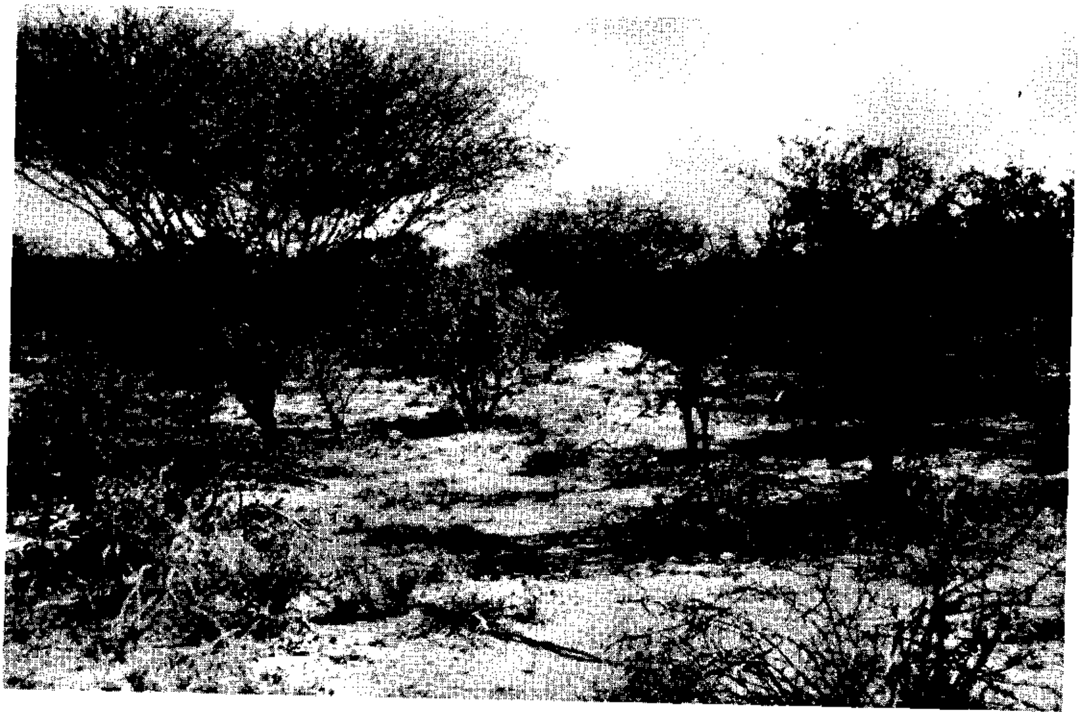


Figure 2.17 Bushland dominated by *Acacia reficiens, Balanites orbicularis* and various *Capparidaceae* (community AS1e). The perennial grass cover is rather poor due to the moderate woody cover and the extreme climatic conditions (bio-climatic zone VIb, annual rainfall approximately 250 mm)

2.3.1.2 FLORISTIC COMPOSITION

The classification of the vegetation of the Tsavo area–on the basis of the floristic composition–in nine communities, based on more than 400 releves, is summarized in Table 2.8. A list of the full names of the communities and variants is given in Table 2.9.

It can be seen that each community is characterized by a specific combination of species groups. In addition, it was found that a large group of species, which occurred in most communities, could be separated into several species groups (Table 2.8, species groups 16 to 22) which distinguished within each community a number of variants. These plant communities and variants were mapped at reconnaissance scale for part of the Tsavo area (Wijngaarden and Engelen, 1985).

By comparing the soil and vegetation map and the detailed environmental conditions (soil and climate) at each releve site, conclusions were drawn on the relationship between the plant communities and variants and the physical environment. The plant communities were very well correlated with the soil conditions,

Figure 2.18 A remnant of riverine woodland along the Galana river, dominated by *Hyphaene coriacea.* The riverine woodland is more threatened by river bank erosion than by elephants. The elephants in the background eat saline soil material from the river bank

as shown in Tables 2.10 and 2.11. In only a few instances is one soil unit correlated with more than one vegetation community. The latter soil units are known to be not completely homogeneous in physical and chemical characteristics. These differences, however, were not mappable at reconnaissance scale.

Table 2.11 clearly shows that communities CL4 and CA3 occur on shallow soils, and all others on deep soils, forming a gradient from well-drained and acid, to poorly drained, alkaline and often saline. The variants in each community are closely related to climatic conditions. Plotting the classification at variant level of releves made near a rainfall station to the rainfall/potential evapotranspiration ratio of that station revealed a good relationship (Figure 2.19). The boundaries of the bio-climatic zones as established earlier by the Kenya Soil Survey (Weg and Mbuvi, 1975) also fitted well.

Table 2.8 shows the presence (in percentage) of each of the species in the different plant communities and variants (+ = occurring only once); for the names of the plant communities and variants, see Table 2.9.

Abbreviations:

Te	= evergreen tree	Gp	= perennial grass
Td	= deciduous tree	Ga	= annual grass
Se	= evergreen shrub	Hp	= (short lived) perennial forb
Sd	= deciduous shrub	Ha	= annual forb

Spec. Group	Life Form	Group of Communities / Community / Variant	CL 1 b	CL 1 c	CL 1 d	CL 1 e	CL 2 b	CL 2 c	CL 2 d	CL 2 e	CL 3 b	CL 3 c	CL 3 d	CL 3 e	CL 4 d	CL 4 e	CA 1 d	CA 1 e	CA 2 c	CA 2 d	CA 2 e	CA 3 d	CA 3 e	AS 1 c	AS 1 d	AS 1 e	AS 2 b	AS 2 c	AS 2 d
		number of releves	12	32	27	21	12	9	14	14	8	16	27	36	3	23	5	25	9	15	29	3	8	5	13	25	3	7	7
		aver.% tree cover	23	16	4	4	16	5	4	8	25	17	8	7	1	2	4	3	2	3	2	0	2	3	0	0	0	1	0
		aver.% shrub cover	45	26	23	20	36	36	29	28	29	27	13	16	33	14	17	26	27	14	21	11	19	15	22	13	18	21	10
		aver.% total herbaceous cover	41	53	44	45	55	36	45	42	28	49	45	39	35	41	40	42	50	51	31	50	40	64	45	46	53	64	54
1	Sd	Premna holstii	75	56	74	38	83	89	93	86																			
	Sd	Ochna enerais	75	56	63	52	58	44	37	29						+													
	Se	Strychnos decussata	44	53	56	57	42	22	14	21						+													
	Sd	Hymenodiction parvifolium		22	22	+		+	+																				
	Hp	Astripomea hispidum		6	7		25	56	+	+		+																	
	Sd	Combretum mossambicense	25	6	7	+	+	22	14																				
	Sd	Tinnea europea	+	9	+	+			+	14				+															
2	Sd	Grewia bicolor	67	72	37	29	58	67	79	43	38	58	26	19		+		+											
	Td	Sterculea cf.rhynchocarpa	42	31	59	29	42	+	36	36	38	25	26	25		9	+			+					+				
	Td	Melia volkensii	+	9	19	14	58	56	64	36	25	+	11	+				+											
	Sd	Erythrococca atrovirens	25	16	26		58		43		+	19	19				+			+									
	Td	Adansonia digitata	42	9	+		58	44	50		25	+	11																
	Hp	Indigofera lupatana	17	9	11	14	17		21			+	7	11															
	Sd	Maerua edulis	17	9	+	14	33	+			+	+	+	8		+		+		+									
	Td	Entada leptostachya	58	9	7	18	17		+		+	19	7																
	Sd	Cassia longiracemosa	+	+	+		+			+	+	13	11			9													
3	Td	Lannea alata		47	26	19			+	43		25	11	39		22													
	Td	Boswellia hildebrandtii		50	+	18				36		25	7	22				+											
	Sd	Strophantus mirabilis		+	19	29				+		+		6		13		+											
	Sd	Momordica spinosa			11	10		+	14	+		13	15	8							+								
4	Td	Belonix elata	50	22	74	86	33	67	93	93	+	31	37	92	+	52	40	52	+	+	33	+	50						
	Gp	Latipes senegalensis	33	69	78	61	25	56	86	93	25	56	52	81	67	52	40	60		27	33	+	87			16			
	Sd	Xerophis kaniensis	50	31	78	62	17	33	50	71	+	38	44	75		9	80	60	+	40	33		25		+	8			+
	Td	Acacia tortilis	83	47	26	33	67	33	29	21	50	38	44	53		47	+	40	22	20	30		25						+
	Gp	Eragrostis caespitosa	42	62	74	81	17	22	21	64	+	19	22	56		26		16	+	+	7					+			
	Td	Platicelyphium voense		44	78	48	17	44	43	64	+	43	41	42	+	35	40	24	+	13	+	+	25						+
	Sd	Grewia tembensis	50	37	44	19	50	67	71	57	38		11	28	+	43	+	28	22	27	15		+						
	Td	Cassia abbreviata	50	50	37	48	42	22	36	50	38	13	11	39	+	39		+	+	20	7								
	Sd	Maerua endlichii	42	22	22	24	33	22	29	14	38	19	19	17	+	35	40	12	22	13	7	67	63		+	8			
	Sd	Grewia lilacina	33	6	22	24		44	36	21	+	25	30	55	+	26	+	16	+	13	19	+	25						
	Td	Commiphora holziana	33	9	11	24	42			50	+	13	+	61		17		20	+	13	33		+		+	+			
	Hp	Pupalia lappaceae	42	25	26	24	50	44	29	43	+	25	+	22		9		8	22		7	+	25						
	Sd	Vernonia cinerascens		19	11	+	17		14	+		43	33	14	+	22		12	22	27	26	+	25		+				
	Sd	Cordia ovalis	+	22	33	24	+	+	+	+	+	19	11	+	67	47	+	8	+	20	7	+	+			+			
	Td	Commiphora schimperi	+	19	7	10			+			13	31	11		9	+	+	+	33	7		+		15				
	Td	Commiphora boiviniana	17	9	11	10			+			13	30	11		9	+		+	+	15		+	+	+				+
	Sd	Sesamothamnus rivae	+	+	15	14	17	22	14	29		+	7	17		+		12			19		+			+			+
	Hp	Melhania ferruginea	33	19	11	10	17	+	14		+	19	15	6					+	+								+	
	Hp	Sida ovata	25	6	+		17	44	36		+	19	15	8		+		+		+	+				+				
	Hp	Blepharis fruticulosa	+		15	14	+		29	43			+	8		9		+		+	+		+						
	Hp	Pavonia patens	25	9	11		17	+	36				7	+			40	+					+			+			
	Ga	Sporobolus festivus	+	+							+		11				+	+	+										
5	Sd	Premna recinosa		13	48	77		33	64	57		43	48	81	99	86	40	60	+	33	48	67	38			+			
	Sd	Birichletia glaucescens		13	48	77		44	50	6		+	26	64	99	60		36		+	11	67	25						
	Sd	Euphorbia spinescens		40	44	40	+		21	36		31	33	14	+	22	+	+	+	33	11					+			
	Sd	Grewia nematopus		9	19	29			64	29		19	19	17	67	17		16		40	22		+						
	Gp	Cymbopogon pospischillii		34	19	14				+		19	44	8		30	+		22	20		+	+						
	Sd	Melinus integrifolius		9	11	24			21	43			15	17	99	13		28			7								
	Sd	Indigofera spinescens		9	+	29				21		+	+	14		52		16		+	11	+	25						
	Ha	Tribulus terrestris			+				+	14		13		17		17					+	+	25			+			
	Sd	Pyrenacantha malvifolia		+	19	19				+		+	+	8		+					+		+						

Spec. Group	Life Form	Group of Communities / Community / Variant	CL 1 b-e	CL 2 b-e	CL 3 b-e	CL 4 d-e	CA 1 d-e	CA 2 c-e	CA 3 d-e	AS 1 c-e	AS 2 b-d	CL-AS 1-4 b	CL-AS 1-4 c	CL-AS 1-4 d	CL-AS 1-4 e
		number of releves	92	49	87	26	38	51	11	43	17	35	78	114	179
		aver.% tree cover	11	8	11	2	3	3	1	0	0	19	11	4	4
		aver.% shrub cover	26	32	20	16	25	20	17	16	16	36	26	19	19
		aver.% total herbaceous cover	47	45	41	40	43	40	43	40	57	44	51	45	40
1	Sd	Premna holstii	60	88								54	33	29	11
	Sd	Ochna enerais	60	47		+						45	28	22	9
	Se	Strychnos decussata	52	24		+						26	24	15	9
	Sd	Hymenodiction parvifolium	15	4									10	6	+
	Hp	Astripomea hispidum	4	20	+							9	10	2	
	Sd	Combretum mossambicense	9	10								11	5	4	+
	Sd	Tinnea europea	7	6	+							+	4	2	2
2	Sd	Grewia bicolor	51	61	29	+	+					51	47	25	12
	Td	Sterculea cf.rhynchocarpa	48	33	26	8	+	6		+		37	19	29	12
	Td	Melia volkensii	13	53	8		+					29	12	15	6
	Sd	Erythrococca atrovirens	16	26	10		+	+				31	10	10	
	Td	Adansonia digitata	10	37	7							40	10	10	
	Hp	Indigofera lupatana	12	10	8			+				11	5	8	9
	Sd	Maerua edulis	10	10	7	+	+	+				28	6	3	4
	Td	Entada leptostachya	14	6	7							26	8	4	+
	Sd	Cassia longiracemosa	3	4	7	8						9	4	4	2
3	Td	Lannea alata	38	14	24	19							24	10	17
	Td	Boswellia hildebrandtii	21	10	16		+						25	3	9
	Sd	Strophantus mirabilis	13	+	3	12	+						3	5	7
	Sd	Momordica spinosa	5	8	10			+					4	8	4
4	Td	Belonix elata	55	73	56	50	50	22	45			31	24	42	57
	Gp	Latipes senegalensis	65	67	62	54	57	25	73	9		26	46	49	57
	Sd	Xerophis kaniensis	55	45	54	8	70	31	10	7	+	29	27	45	46
	Td	Acacia tortilis	42	37	47	42	37	25	10		+	63	35	24	34
	Gp	Eragrostis caespitosa	67	33	34	23	13	8		+		23	33	26	33
	Td	Platicelyphium voense	47	43	39	35	27	8	27		+	9	35	37	20
	Sd	Grewia tembensis	37	61	10	42	27	20	+			43	26	27	25
	Td	Cassia abbreviata	47	39	25	38	+	12				43	27	19	24
	Sd	Maerua endlichii	25	24	20	35	17	12	64	7		34	18	20	10
	Sd	Grewia lilacina	18	24	33	27	17	16	27			14	14	21	23
	Td	Commiphora holziana	16	24	30	15	23	24	+	5		29	8	6	31
	Hp	Pupalia lappaceae	27	41	16	8	7	8	27			34	23	11	15
	Sd	Vernonia cinerascens	11	10	27	23	10	25	27	+		6	17	18	13
	Sd	Cordia ovalis	24	8	9	50	10	12	10	+		9	15	18	13
	Td	Commiphora schimperi	12	+	16	8	7	16	+	5		+	12	17	7
	Td	Commiphora boiviniana	11	16	13	+	+	12	+	5	+	11	8	10	11
	Sd	Sesamothamnus rivae	10	20	10	+	10	10	+	+	+	9	5	8	13
	Hp	Melhania ferruginea	16	10	11			4			+	20	15	9	2
	Hp	Sida ovata	7	22	13	+	+	4		+		17	12	11	3
	Hp	Blepharis fruticulosa	9	22	5	8	+	4	+			6		4	9
	Hp	Pavonia patens	10	16	3		10		+	+		14	5	11	2
	Ga	Sporobolus festivus	2		8		7	+				6	6	4	+
5	Sd	Premna recinosa	36	41	56	80	63	57	45	+			19	44	60
	Sd	Birichletia glaucescens	36	47	36	65	30	8	36				10	29	44
	Sd	Euphorbia spinescens	38	10	33	15	7	10		+		+	22	29	20
	Sd	Grewia nematopus	15	27	16	23	13	24	+				7	24	17
	Gp	Cymbopogon pospischillii	21	+	21	27	+	10	10				21	19	8
	Sd	Melinus integrifolius	12	10	11	23	23	39					3	11	16
	Sd	Indigofera spinescens	11	5	8	46	13	8	27				4	4	20
	Ha	Tribulus terrestris	+	6	9	15		+	27	+			3	3	9
	Sd	Pyrenacantha malvifolia	11	+	5	+		+	+				3	5	6

Table 2.8 Summary vegetation table

Table 2.8 Summary vegetation (cont)

Spec. Group	Life Form	Group of Communities	CL														CA							AS						CL				CA			AS		CL-AS	CL-AS	CL-AS	CL-AS
		Community	1				2				3				4		1		2			3		1			2			1	2	3	4	1	2	3	1	2	1-4	1-4	1-4	1-4
		Variant	b	c	d	e	b	c	d	e	b	c	d	e	d	e	d	e	c	d	e	d	e	c	d	e	b	c	d	b-e	b-e	b-e	d-e	d-e	c-e	d-e	c-e	b-d	b	c	d	e
		number of releves	12	32	27	21	12	9	14	14	8	16	27	36	3	23	5	25	9	15	29	3	8	5	13	25	3	7	7	92	49	87	26	38	51	11	43	17	35	78	114	179
		aver.% tree cover	23	16	4	4	16	5	4	0	25	17	8	7	1	2	4	3	2	3	2	0	2	3	0	0	0	1	0	11	0	11	2	3	3	1	0	0	19	11	4	4
		aver.% shrub cover	45	26	23	20	36	36	29	20	29	27	13	16	33	14	17	26	27	14	21	11	19	15	22	13	10	21	10	26	32	20	16	25	20	17	16	16	36	26	19	19
		aver.% total herbaceous cover	41	53	44	45	55	36	45	42	28	49	45	39	35	41	40	42	50	51	31	50	40	64	45	46	53	64	54	47	45	41	40	43	40	43	40	57	44	51	45	40
6	Td	Commiphora campestris	42	65	19	19	17	22	29	29	75	56	19	50		22	40	+	+	13	26				23	16				38	24	44	19	10	10		16		37	42	18	24
	Ha	Tephrosia villosa	42	62	56	50	33	67	64	79	25	43	40	59	+	52	60	24	+	+	11			+	+	8				57	61	49	50	30	10		9		31	45	38	37
	Gp	Enteropogon macrostachys	99	47	56	30	83	67	71	43	30	19	15	42	+	22	40	20	33	+	15			+		12				54	65	31	23	23	16		9		74	36	29	26
	Ha	Tephrosia uniflora	+	16	10	24	+	44	43	21	25	13	37	19	+	35	+	12	+	13	15	+	25	+		12				36	31	24	35	13	14	27	9		11	17	31	20
	Se	Thylacium thomacii	25	9	15	10		22	14			25	11	+		+	+	12	22	+	15	+	+		23	8				13	6	9	+	13	14	18	12		9	14	13	8
	Ha	Digera mucronata	+	6	+	10	+	+	+	+			7	17	67	9		16			11			+	15	8				7	8	9	15	13	6		12		6	5	7	11
	Sd	Acacia thomacii	+	9							25	19	11	11	+	17		12	+	20			25	+		8				4		14	19	10	8	18	5		9	10	6	8
	Ga	Tragus berteronianus	17	+	7	10		+	+	14		+	+	11	+	17	+	+			7					8				8	8	7	12	6	4		5		6	4	5	9
	Td	Terminalia prunoides	+	+	+	10					38	19	+			+	+	+		+					23	8				5		8	+	6	+		12		11	5	6	9
	Hp	Sansevieria spp.	25	6	+	10				+									+		11				23	16				9	+				8		16		9	4	3	6
	Hp	Seddera hirsuta	+		+								+							+	11					12				2		+			8		7		+		3	3
7	Sd	Calypthrotica taitensis		6	22	24		+	14	21		+	19	14		9	40	16		20	15				15	20				14	12	13	8	20	14		21			5	18	17
	Ha	Cleome hirta		6	22	30		+	14	36		+	7	22		+		24			+		+			8				17	16	13	+	20	+	+	5			5	9	18
	Ga	Chloris virgata		9	11	24	+		29	+		25	11	6		17	+	8			+	+	+		15	16		+		12	12	10	15	10	+	18	14	+	+	10	12	11
	Ga	Aristida mutabilis		25	+	14						+	+	22		13		56			7	+	+			8				13		11	12	30	4	18	5			12	3	16
	Hp	Indigofera arrecta		19		10		+				13		6					33							+				9	+	5			6		+			15		3
	Ga	Eragrostis aethiopica		+		+				+		+		6		+			+	13	15			40	15	8				2	+	3	+		14		14			6	4	6
8	Sd	Disperma kilimandscharicum					99	67	21		38	25	37				40		+	27						+	67		29		43	20		7	10		+	24	49	14	19	
9	Sd	Baubinea taitensis						67	99	79		19	19	11	99	43	+	16		+	+		+								63	14	50	17	4	+				12	21	17
	Sd	Erythroclamys spectabilis						56	71	57		+	19	+	67	22	+	12		13	+		+								47	8	27	13	6	+				8	17	10
	Hp	Ecbolium revoltum						22					7	+	+	+	+	12	+	+	11	67	50			12					4	3	8	13	10	55	7			4	6	8
10	Sd	Acacia reficiens																20	33	20	26		+	40	31	36			+					23	25	+	36	+		6	7	13
	Te	Terminalia parvula										+						8	22	47	22		30	+		20			+			+		7	29	27	19	+		5	7	10
	Sd	Maerua subcordata						+									60	12	22	13	+				31	20			+		+			20	10		26	+		4	9	6
	Se	Anisotes parvifolius															40	24	+	27	19			+	8									27	20		5			3	6	6
11	Sd	Cadaba respolii												11		+	+	52	44	60	67	67	50	+	62	76		29	71			5	+	47	61	54	65	41		10	22	33
	Te	Dobera glabra										+	11			+	80	40	78	40	56	99	87	60	36	36		43	29			5	+	53	55	91	40	29		19	20	27
	Sd	Grewia tenax												6			40	32	33	60	59		25	40	77	60		29	43			2		33	55	18	63	29		9	21	20
	Se	Salvadora persica										13					40	16	22	27	37			+	54	40		27				2		20	31		42	12		10	12	13
	Se	Maerua denhardtiorum															60	36	33	13	30			40	31	24		+	+					40	25		20	12		8	9	13
	Sd	Acacia bussei									38	19	15	6			+	8	22	+	11			+	23	16		29	29			14		10	12		19	24	9	10	10	6
	Sd	Opilia celtidifolia					+					13	+				+	20	+	+	33		+			12			29		+	3		27	22	+	7	12	+	4	4	11
	Hp	Solanum dubium										+		+			+	8	+	27	7	+		60	15	+		29	+			2		10	14	+	14	8		10	7	4
	Hp	Ecbolium amplexicaule										+						+		20						12			29			+		+	8		7	12		1	4	2
12	Se	Cadaba glandulosa																	+	27	49	+	25	+	92	76		29	71						45	27	74	41		5	19	26
	Sd	Blepharispermum fruticosa																	33	33	37		30	+	46	44		+	+						35	27	42	12		6	11	13
	Gp	Sporobolus helvolus															+		22	13	19			40	60	64	67	57	86					+	18		63	71	6	10	16	12
	Sd	Sericocomopsis hildebrandtii																	22	13	44	67	30		+	40									31	43	26			3	4	4
	Td	Acacia zanzibarica																	55	40				60	31	8		57	99						22		21	65		15	15	1
	Se	Lycium europeum																	+	27	15				23	32									18		26			+	6	7
	Hp	Acalypha ciliata																	+		+		25			+			+						4	10	+	+		+	+	2
13	Gp	Schoenefeldia transiens																						80	39	30	67	86	71								44	74	6	3	9	6
	Se	Maerua sp.C.																	+		+				46	60			+						4		49	+		+	5	9
	Gp	Andropogon schinzii						+																	15		+	71			+						5	39	+	0	2	
	Ha	Aphelandra fusc.																						40	+		67	29									7	24	6	5	+	
	Ha	Tragia arabica											+											40			67	+				+					5	10	6	4	+	

Spec. Group	Life Form	Group of Communities	CL	CL	CL	CL	CL	CL	CL	CL	CL	CL	CL	CL	CL	CL	CA	CA	CA	CA	CA	CA	CA	AS	AS	AS	AS	AS	AS	CL	CL	CL	CL	CA	CA	CA	AS	AS	CL-AS	CL-AS	CL-AS	CL-AS
		Community	1	1	1	1	2	2	2	2	3	3	3	3	4	4	1	1	2	2	2	3	3	1	1	1	2	2	2	1	2	3	4	1	2	3	1	2	1-4	1-4	1-4	1-4
		Variant	b	c	d	e	b	c	d	e	b	c	d	e	d	e	d	e	c	d	e	d	e	c	d	e	b	c	d	b-e	b-e	b-e	d-e	d-e	c-e	d-e	c-e	b-d	b	c	d	e
		number of relevés	12	32	27	21	12	9	14	14	8	16	27	36	3	23	5	25	9	15	29	3	8	5	13	25	3	7	7	92	49	87	26	30	51	11	43	17	35	78	114	179
		aver.% tree cover	23	16	4	4	16	5	4	8	25	17	8	7	1	2	4	3	2	3	2	8	2	3	8	8	8	1	8	11	8	11	2	3	3	1	8	8	19	11	4	4
		aver.% shrub cover	45	26	23	28	36	36	29	28	29	27	13	16	33	14	17	26	27	14	21	11	19	15	22	13	18	21	19	26	32	28	16	25	28	17	16	16	36	26	19	19
		aver.% total herbaceous cover	41	53	44	45	35	36	45	42	28	49	45	39	35	41	48	42	58	51	31	58	48	64	45	46	53	64	54	47	45	41	48	43	48	43	48	57	44	51	45	48
14	Gp	Enteropogon somalensis																								+		71	71								+	59		6	5	
	Sd	Cephalocroton nudus																									67	43	71									59	6	4	4	
	Gp	Pennisetum massaicum																							+		+	29	71								+	47	+	4	4	
	Gp	Brachiaria sp.A																										57	29									35		5	2	
	Sd	Acacia stuhlmannii																										+	29									19		+	2	
	Sd	Acacia depranolobium																									67											12	6			
15	Sd	Caesalpinia trothae														35						67	63										31			64					2	7
	Gp	Schmidtia bulbosa				19		+	+	+			+	8	99	96	+	31	+		+	67	63			8		+		4	6	5	96	30	18	64	5	+		4	7	27
	Sd	Caucanthus albidus							+	29		+	+	31	99	61		24		13	19	+	75			+			+		10	15	65	20	14	64	+	+		+	8	26
	Sd	Combretum aculeatum		6			+	+		+		+	+	+	99	78	+	4		13	+	99	75	40	+	+	99	29	+	2	6	3	81	7	6	82	9	35	11	18	11	16
	Ha	Heliotropium albohispidum												+		26		8		13		+	38									+	23	7	4	36					3	7
	Hp	Commicarpus pinnosus														+							38										+			27					1	2
16	Td	Dalbergia melanoxylon	17	+			+																				99			3	+							18	17	+		
	Td	Combretum apiculatum	42				+			+	+	+																		5	4	2							28	+		
	Se	Cissus quadrangularis	25				+				25	+																		3	+	3							17	+		
	Se	Cissus rotundifolia	+	+							38																+			2		3							11	+		
	Td	Lonchocarpus bussei	+	+							25																			2		2						+	11	+		
	Td	Terminalia brownii	17				+				+																			2	+	+							11			
17	Sd	Acacia nilotica	42	34			+	+			63	31					+		+					+			67		+	15	4	11		+	+		+	18	37	22	2	
	Te	Boscia angustifolia	58	31			67	67			25	13			+															17	29	5	+						46	23	+	+
	Sd	Grewia fallax	58	34			+	33			25	25							+											19	8	7			+				29	24		
	Sd	Grewia forbesii	42	25			+				38	19							44					40				29		14	+	7			8		5	12	26	24		
	Te	Boscia mossambicensis	25	16			+	+			25	13							+	+				+			67	43	+	9	4	5			4		+	35	23	17	2	
	Sd	Acacia brevispica	33	16			25	+				13	+						22					+						10	8	3			4		+		28	14	+	
	Td	Albizzia anthelmintica	17	19				+			25	+							22					+						9	+	3			4		+		11	14		
	Sd	Cordia cf. quarensis	42	22				22			+								22											13	4	1			4				17	12		
	Td	Haplocoelum foliosum	33	16								19																		10		3							11	13		
	Se	Maerua kirkkii	33				58	22									+		+											4	16			+	+				29	5	+	
	Se	Maerua triphylla	25	13			25				+																			8	6	+						18	23	8		
	Sd	Dichrostachys cinerea	17	16			17	+			+																	29		8	6	+						12	14	18		
	Td	Lannea stuhlmannii	+	22							25	+															+			9		5						+	11	12		
	Gp	Themeda triandra		13			+				+								+								+	29		+	+	1			+			18	9	9		
	Gp	Cynodon dactylon		+			33				13								22									+		+	8	+			4			+	14	5		
18	Gp	Panicum maximum	58	59	37		67	44	43	+	63	56	19				+		44					+			+	29		38	39	22		+	8		+	18	57	50	19	+
	Gp	Digitaria macroblephora	17	59	67		+		21		+	38	52				60		33	40					23		+	+	+	42	8	24		10	18		7	18	14	37	42	
	Sd	Combretum exalatum	25	44	15		67	33	36	+	+	19	15		+					13				40	23			+	43	23	35	9	+		4		12	24	34	29	19	+
	Gp	Eragrostis superba	33	16	11		58	44	36		25	19	+				40		+		+	+								13	33	7		7	4	+			40	19	8	+
	Gp	Digitaria rivae		9	7			+	+			+	30		67		+			13		99			15			+	43	5	6	10	8	7	4	27	5	24		8	21	
	Sd	Acacia mellifera	58				25	+			+	31							+						23		+	29	+	8	8	7			4		7	24	34	13	4	
	Ha	Monechma debile	25	6			17	+	+		38	+		+								+		+	+		+			5	8	6				+	5	+	26	6	3	+
	Ga	Dactyloctenium aegypticum	+	6	7		+		21		25		+												+				43	5	8	3					+	18	11	3	9	
	Gp	Leptochloa obtusiflora	+	6	7		17	+				+					+		+						+			+	29	5	6	1		+	+		+	18	9	8	5	
	Hp	Hibiscus vitifolius	17	6	+		25		+				+	+			+										+			5	8	2		+				+	17	4	4	
	Gp	Eustachys paspaloides		13	+		+				25	+								+										5	+	3			+				9	6	2	
	Sd	Lantana verbenoides	8	9			+		+				7						+		+									4	4	2			4				6	5	3	+
	Sd	Croton dichogamus	17				+				+	+							+	13					31					2	+	2			6		9		11	3	4	

Table 2.8 Summary vegetation (cont)

Table 2.8 Summary vegetation (cont)

Spec. Group	Life Form	Group of Communities	CL														CA							AS						CL				CA			AS		CL-AS	CL-AS	CL-AS	CL-AS
		Community	1				2				3				4		1		2			3		1			2			1	2	3	4	1	2	3	1	2	1-4	1-4	1-4	1-4
		Variant	b	c	d	e	b	c	d	e	b	c	d	e	d	e	d	e	c	d	e	d	e	c	d	e	b	c	d	b-e	b-e	b-e	d-e	d-e	c-e	d-e	c-e	b-d	b	c	d	e
		number of releves	12	32	27	21	12	9	14	14	8	16	27	36	3	23	5	25	9	15	29	3	8	5	13	25	3	7	7	92	49	87	26	30	51	11	43	17	35	78	114	179
		aver.% tree cover	23	16	4	4	16	5	4	8	25	17	8	7	1	2	4	3	2	3	2	0	2	3	0	0	0	1	0	11	8	11	2	3	3	1	0	0	19	11	4	4
		aver.% shrub cover	45	26	23	20	36	36	29	28	29	27	13	16	33	14	17	26	27	14	21	11	19	15	22	13	18	21	10	26	32	20	16	25	20	17	16	16	36	26	19	19
		aver.% total herbaceous cover	41	53	44	45	55	36	45	42	28	49	45	39	35	41	40	42	50	51	31	50	40	64	45	46	53	64	54	47	45	41	40	43	40	43	48	57	44	51	45	40
19	Td	Commiphora africana	75	75	44	29	33	44	71	79	50	36	41	39	+	24	40	+	44	13	7		25			12			43	54	59	52	27	10	16	10	7	10	46	53	36	29
	Gp	Chloris roxburghiana	83	81	81	62	83	78	93	86	99	75	74	56	67	52	99	84	78	87	63	+	25	+	39	48		43	+	77	86	69	54	87	73	27	42	24	80	71	72	61
	Ga	Aristida adscensionis	83	66	67	62	83	89	86	79	75	63	67	75	99	82	40	76	56	13	56	99	63	+	31	64	67	+	57	67	84	78	85	70	43	74	49	41	80	54	58	70
	Hp	Asparagus falcatus	42	31	59	43	33		14	+	+	75	52	31	+	17	60	24	44	53	19	67	38	+	69	48	67	43	57	43	18	44	14	30	33	45	51	53	34	30	52	30
	Ga	Tetrapogon tenellus	25	9	19	10	33	67	71	43	50	25	19	19	67	39	40	16		20	37		63	40	23	+	+		+	14	53	23	42	20	25	45	14	12	34	14	27	25
	Td	Lannea triphylla	25	25	44	48	+	+	14	14	25	19	48	42	+	22	+	+					38				67			35	12	38	23	7		27		12	23	15	25	20
	Ha	Ocimum americanum	42	6	15	10	33	22	36	36	75	13	7	22		9	40	+	+	+	19			+	23	16	67	29	+	14	33	21	8	10	14		19	30	49	13	16	16
	Ha	Solanum incanum	42	40	11	10	50	67	21	+	+	43	22	+			+	12	56	+	11			40		+	+		+	25	33	17		13	10		7	12	37	42	13	6
	Gp	Cenchrus ciliaris	25	31	15	10	25	+	14		38	19	32			9	+	8	33	27	7		+		+	+	+	29	29	21	12	17	8	10	10	+	5	29	29	24	20	6
	Sd	Combretum hereroense	17	25	11		+	+		36	38	+		25		+	40		22	20	7			60	23	12	99	57	+	14	14	15	+	7	14		21	47	26	24	11	11
	Gp	Botriochloa radicans		16	15	+			+	+	25	19	30	14			40	8	44	40	15		25		23	8		+	+	11	4	21		13	27	10	12	12	6	17	22	9
	Hp	Commelina benghalensis	17	25	19		33	22	21	14	+	25	26	6		+	40	+	22	13				40		8		+	+	16	22	15	+	10	8		9	12	20	24	9	4
	Ha	Svensonia laeta	17	6	+	10	17		+	14			11	+		13	+	+		20	37	+	25	40		20		+	43	8	10	5	12	7	25	27	16	24	11	6	10	16
	Hp	Abutilon fruticosum	+	13	11		50		29	+	+	13	19	11		13	40	8	22	+		67	+		+	+		+		9	22	14	22	13	6	27	5	+	23	12	16	7
	Hp	Neuracanthus spp.	+	+			17		14	+	+	13	+	+	+	9	+	+			22	+	63	+	+	36		43	43	2	10	6	12	7	12	55	26	35	11	9	9	14
	Hp	Indigofera schimperii		9	+		+		+			13	11	11		13		24	+	13	7			40	+	+	67	57	57	4	4	10	12	20	10		9	59	9	17	11	9
	Hp	Hibiscus micranthus	25	9	15		25	22	36	36	75	13	7	22		9	40	+	22	+	22		+	+	+	8	+			11	12	8	+	10	12	+	9	+	31	10	11	4
	Ha	Leucas spp.	25	9	7	10	+	+	+					+					+		15		+	+	15	20	67	+	43	11	6	+			10	+	23	35	17	9	7	8
	Te	Balanites orbicularis	+	+								13						36		+	22			40	23	12	67	+		2		2		30	14		19	10	9	8	3	10
	Hp	Heliotropium subulatum				19	17	33	+					17		9					7	+	25			12		29		4	12	7	8		4	27	7	12	6	6	2	11
	Td	Terminalia spinosa	42	25							+	+	+			9			22		+				+		+	+		14		3	8		6		+	12	20	15	2	2
	Sd	Acacia senegal	17	9			25					+		8		+		+	+		7							+		5	6	5	+	+	6			+	14	8		4
	Ha	Barleria diffusa		+	7	10	17					+	+	+		+		+		13	+	+	25					+		5	4	3	+	+	6	27		+	6	4	5	4
	Ha	Becium spp.		6	7	+			14				11	+				8			+				+	+	67	+		5	4	5		7	+		5	10	6	4	7	3
	Hp	Abutilon mauritianum		+		+							+	+										40	15	8	67	43	29	2	4	2					14	41	9	9	4	2
	Ha	Cassia mimosoides		9					22	29		+	+	+					22									+		3	12	3			4			+		12	4	+
	Gp	Cyperus obtusiflorus	+	6								13	11		+	9								40				+		3		6	12				5	+	+	9	4	1
19a	Te	Boscia coriacea	33	78	96	95	33	78	92	83	50	75	78	94	+	91	99	92	44	88	78	99	99	40	69	52	+	43	29	83	73	79	85	93	71	99	56	35	37	68	78	82
	Sd	Cordia gharaf	17	37	26	33	+	+	21	50	25	50	44	63		60	60	92	67	67	99	99	87	+	62	76	+	29	57	30	24	56	54	87	84	91	65	47	17	38	44	73
	Sd	Grewia villosa	42	66	41	29	33	89	79	71	75	87	52	56	67	30	60	40	78	27	33		25	40	31	8	+	+	29	47	67	62	35	43	39	16	19	24	46	68	41	37
	Se	Ehretia taitensis	42	25	30	29			29	14	+	50	44	22		56	40	24	33	40	19	67	75	+		20		+	+	29	12	33	50	27	27	73	14	12	17	20	31	20
	Gp	Chrysopogon aucheri	75	31	37	19					25	50	41	8		13		16	33	67	37	67	25	+	23	24		43	29	35		20	16	13	39	36	23	29	29	36	33	15
	Hp	Heliotropium steudneri	+	6	22	19	13	+	21		+	25	+	22		13	40	20	22	13	11	67	38			8		29	+	14	12	16	12	23	14	45	5	10	16	12	17	16
	Hp	Heliotropium strigosum	+	9	30	33			+	+	+	+	26	14		26	40	16				67	30			12	+		43	21	4	16	23	20		55	7	+	9	5	10	17
	Ga	Brachiaria leersioides		6	15	33	25	+	14	36	+		+			13	60	12	+	+	15		25		+	12		+	+	14	22	2	12	20	12	10	9	12	11	8	11	15
20	Sd	Sericocomopsis pallida	+	50	78	40		+	57	71		38	78	64	67	65	+	92	+	53	67	67	87		62	36			57	50	39	57	56	80	53	82	40	24	+	31	64	64
	Ga	Eragrostis cilianensis		9	11	10	+		21	14		13	22	11	67	17	+	16	56	+	11			40	39	16		+	86	9	12	14	23	17	10		26	41	+	17	24	13
	Ga	Brachiaria deflexa		6	19	14			36	+			19	4	67	22	40	+		+	11	+		+	39	20		43		11	12	11	27	10	8	+	26	10		8	23	13
	Hp	Barleria ramulosa							+				7	11	+	13		16	22	33	30	+			+	20			+		+	7	5	13	29	9	10	+		3	7	12
	Hp	Commelina erecta		9	19	14			21			+	15	+		9	+	12			7		+	40	+				43	12	6	7	8	13	4	9	7	10		8	6	7
	Ha	Phyllanthus maderaspatensis		6	11	14						+	11	11		+	+	8	+	13	+	+		+	15	8			43	9		9	+	10	8	9	12	10		6	13	7
	Hp	Talinum caffrum			+			+	14			+	11															29		1	6	5						12		5	5	
21	Gp	Tetrapogon bidentatus			+	+				+			19	17		22	+	76	+	13	30	67	38		15	40			+	2	+	13	19	67	22	45	33	+		+	12	31
	Ha	Blepharis linarifolia		+	15	19			36	50		+	15	56		30		24		20	26	67	50		15	20				10	24	29	27	20	20	55	16			3	10	34
	Te	Euphorbia robecchii			7	14							+	25		9		12		13	22		+			+				5		11	8	10	16	+	+				4	14
	Hp	Cucumis figarei			19	10							7	8						13	7									8		6			8						8	4
	Hp	Ipomoea mombassana			7	+			29				7			9														3	8	2	8								7	2
22	Td	Terminalia orbicularis								21				36		9		8		+			+			8		+			6	15	8	6	+	+	5	+		+	+	13
	Sd	Givotea gossai				29				+		+		17				+			+									7	+	8		+	+					+		8
	Sd	Hildebrandtia sepalosa												+				8			7					8						+		7	4		5					4

Table 2.9 *Major plant communities and variants*

CL	COMMIPHORA-LANNEA group of communities
CL 1	Commiphora spp.-Premna holstii-Strychnos decussata community
CL 1 b	Dahlbergia melanoxylon variant
CL 1 c	Grewia fallax variant
CL 1 d	Sericocomopsis pallida variant
CL 1 e	Givotia gosai variant
CL 2	Commiphora spp.-Premna holstii-Bauhinea taitensis community
CL 2 b	Boscia angustifolia variant
CL 2 c	Grewia fallax variant
CL 2 d	Sericocomopsis pallida variant
CL 2 e	Terminalia orbicularis variant
CL 3	Commiphora spp.-Boscia coriacea-Cordia gharaf community
CL 3 b	Cissus rotundifolia variant
CL 3 c	Acacia nilotica variant
CL 3 d	Sericocomopsis pallida variant
CL 3 e	Terminalia orbicularis variant
CL 4	Commiphora spp.-Caesalpinea trothae-Schmidtia bulbosa community
CL 4 c	Grewia forbesii variant
CL 4 d	Sericocomopsis pallida variant
CL 4 e	Tetrapogon bidentatus variant
CA	COMMIPHORA-ACACIA group of communities
CA 1	Commiphora spp.-Dobera glabra-Anisotis parvifolius community
CA 1 d	Digitaria macroblephora variant
CA 1 e	Tetrapogon bidentatus variant
CA 2	Commiphora spp.-Acacia reficiens-Cadaba glandulosa community
CA 2 c	Grewia forbesii variant
CA 2 d	Digitaria macroblephora variant
CA 2 e	Tetrapogon bidentatus variant
CA 3	Commiphora spp.-Caesalpinea trothae-Cadaba glandulosa community
CA 3 c	Grewia forbesii variant
CA 3 d	Digitaria rivae variant
CA 3 e	Tetrapogon bidentatus variant
AS	ACACIA-SCHOENEFELDIA group of communities
AS 1	Acacia spp.-Schoenefeldia tranciens-Maerua sp.C. community
AS 1 c	Grewia forbesii variant
AS 1 d	Digitaria macroblephora variant
AS 1 e	Tetrapogon bidentatus variant
AS 2	Acacia spp.-Schoenefeldia tranciens-Enteropogon somalensis community
AS 2 b	Dahlbergia melanoxylon variant
AS 2 c	Andropogon schinzii variant
AS 2 d	Digitaria rivae variant

Table 2.10 Correlation between plant communities, soil mapping units and soil classification units

Community	Soil mapping	and Soil classification units (table 2.3)
CL 1	F,N1,N2	rhodic FERRALSOLS, orthic ACRISOLS
CL 2	L,F,U,N1	chromic LUVISOLS, rhodic FERRALSOLS
CL 3	F,N3,S1	ferric and chromic LUVISOLS
CL 4	H2,D1	ferralic and calcic CAMBISOLS (shallow)
CA 1	S2	orthic and chromic LUVISOLS
CA 2	S3,A1,T	calcic LUVISOLS and CAMBISOLS, solodic PLANOSOLS
CA 3	D2	orthic LUVISOLS, calcic CAMBISOLS (shallow)
AS 1	S4	orthic SOLONETZ
AS 2	B	pellic VERTISOLS
H	H1	eutric REGOSOLS (shallow)
F	A2	eutric FLUVISOLS
L	V	mollic ANDOSOLS, haplic CHERNOZEMS

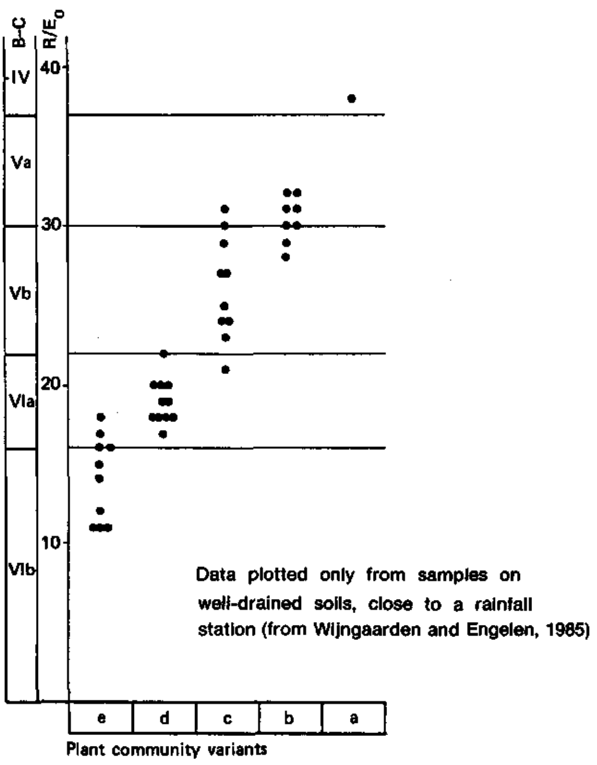


Figure 2.19 Relationship between bio-climatic zones and plant community variants

Table 2.11 Average and range of some soil properties recorded at releve sites, separated for each plant community

SOIL PROPERTIES	PLANT COMMUNITIES CL1	CL2	CL3	CL4	CA1	CA2	CA3	AS1	AS2
A-horizon									
carbon (%)	0.6	0.5	0.6	0.5	0.6	0.8	0.4	0.8	0.8
	0.5-0.8	0.4-0.7	0.3-0.9	0.2-0.7	0.5-0.7	0.4-1.3	0.3-0.5	0.4-0.9	0.4-1.2
pH_{H2O}	5.6	6.0	6.1	6.9	6.3	6.6	7.7	7.1	7.8
	5.1-6.1	5.5-6.7	5.5-6.7	5.6-7.7	5.8-6.8	6.3-7.5	7.4-7.9	6.3-7.7	7.3-8.4
base saturation (%)	77	84	90	87	87	98	100	95	96
	60-88	66-100	82-100	64-100	76-100	96-100	100	89-100	96-100
exch Ca+Mg+K (me%)	4.5	6.6	8.6	7.0	8.4	13.5	12.2	17.8	30.5
	2-5	6-9	7-12	4-10	4-9	7-14	10-14	9-25	25-32
available P (ppm)	13	20	30	26	93	103	64	80	25
	7-22	13-30	15-27	20-120	38-125	21-240	42-86	18-144	10-31
clay (%)	20	25	26	20	19	26	23	36	42
	16-22	10-42	20-30	19-21	16-21	17-33	20-25	20-46	33-48
B-horizon									
pH_{H2O}	5.0	5.8	6.0	6.9	6.7	7.4	7.7	8.0	8.7
	4.3-5.5	4.8-6.5	5.3-6.8	5.7-8.1	6.2-7.1	6.8-8.1	7.3-7.9	7.6-8.6	8.3-9.1
base saturation (%)	63	72	86	91	92	100	100	100	100
	50-82	55-84	81-100	72-100	88-100	100	100	100	100
exch Ca+Mg+K (me%)	4.4	7.2	10.5	9.9	14.0	15.9	16.5	18.9	30.2
	2-6	6-9	9-13	6-13	12-15	15-17	12-22	14-23	25-33
ESP (%)	tr	tr	1.4	1.8	3.1	7.1	3.5	23.6	11.5
	tr	tr	tr-2	tr-3	1-3	2-10	1-2	14-26	8-15
$EC_{2.5}$ (mmho/cm)	<0.2	<0.2	<0.2	<0.2	<0.2	0.6	0.4	2.2	1.3
	<0.2	<0.2	<0.2	<0.2	<0.2	0.3-2.3	0.3-0.6	0.8-5.0	0.6-2.5
clay (%)	35	40	39	28	34	42	32	47	46
	22-40	28-47	33-44	21-34	24-41	39-44	22-41	38-54	36-53
Whole profile									
drainage[1)]	1.0	1.0	1.0	1.0	1.1	1.8	1.3	3.3	3.8
	1	1	1	1	1-2	1-2	1-2	2-4	3-4
depth solum (cm)	>120	116	>120	35	>120	>120	38	>120	>120
	80->120	80->120	90->120	20-40	>120	90->120	20-45	>120	>120
depth at which free lime starts (cm)	>120	>120	>120	26	96	57	19	38	12
	>120	>120	90->120	0-40	90->120	30-100	0-45	10-50	0-10
no. of observations	17	11	21	7	7	18	3	23	6

exch = exchangeable
ESP = exchangeable sodium percentage
$EC_{2.5}$ = electrical conductivity of a 1:2.5 soil: water extract

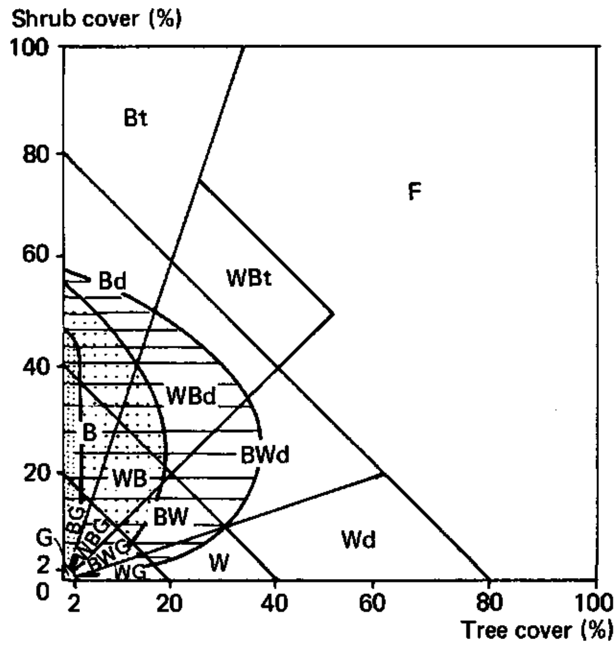
1)
1.0 = well drained
2.0 = mod well drained
3.0 = imperfectly drained
4.0 = poorly drained

2.3.1.3 STRUCTURE AND GRASS COVER

Structure

The structure of the vegetation in the Tsavo area varies from grasslands to dense wooded bushlands. The shrub cover varies from 0 to 60 percent and the tree cover from 0 to 40 percent. Only in the floodplains are very small patches of forest found with a much higher percentage tree cover. This variation in structure is only partly related to difference in physical environment and floristic composition of the vegetation (Figure 2.20). On the well-drained soils (*Commiphora-Lannea* group of communities), trees can be fairly common and may reach a cover of as much as 40 percent. On the less well- drained soils (*Commiphora-Acacia* and *Acacia- Schoenefeldia* groups of communities), trees never reach such high cover values.

Within each floristic community, a large variation in structure was found, related to the past and/or present activity of large herbivores, mainly elephants, sometimes in combination with fire. A quantification of those effects will be given in Chapter 4. These large differences in structure have only a minor



— *Commiphora-Lannea* group of communities, on well-drained, rather acid soils

:::: *Commiphora-Acacia* group of communities, on well to imperfectly drained, neutral to alkaline soils

• • • *Acacia-Schoenfeldia* group of communities, on poorly drained, alkaline and often saline soils

Figure 2.20 Variation in structure classes in three groups of plant communities influence on the floristic composition, however. Dividing all the releves into two groups, one with a high percentage cover of trees and shrubs and one with a low cover, and calculating the presence of all species in those two groups revealed only a very few (five from approximately 360) species which were confined to either a dense or an open structure (Table 2.12).

Grass cover

The cover by perennial grasses in the Tsavo area varies strongly, namely from 0 to 80 percent. When the woody cover percentage is high, the percentage cover by perennial grasses is always low; with a low percentage woody cover, the perennial grass cover varies considerably (Figure 2.21). Apparently the woody cover sets only a maximum limit to the cover by perennial grasses. This maximum limit increases in wetter climatic zones, which indicates that the

Table 2.12 Classification of the species in relation to vegetation structure

Woodland/Bushland facies		Grassland/Bushed Grassland facies	
Confined to: Pw > 10 Pg	Predominating in: 2 Pg < Pw < 10 Pg	Predominating in: 2 Pw < Pg < 10 Pw	Confined to: Pg > 10 Pw
Trees/Shrubs	Trees/Shrubs	Trees/Shrubs	
Acacia reficiens	Acacia brevispica	Anisotes parvifolius	none
Boswellia hildebrandtii	Acacia bussii	Caesalpinea trothae	
Entada leptostachya	Acacia mellifera	Cordia gharaf	
Opilia celtidifolia	Acacia nilotica	Ehretia taitensis	
Terminalia orbicularis	Acacia senegal	Grewia nematopus	
	Acacia tortilis	Lycium europeum	
	Balanites orbicularis	Platycelyphium voense	
	Combretum apiculatum	Sericocomopsis hildebrandtii	
	Combretum hereroense	Grasses	
	Commiphora africana	Chloris virgata	
	Commiphora boiviniana	Cymbopogon pospischillii	
	Commiphora campestris	Cynodon dactylon	
	Commiphora holziana	Digitaria rivae	
	Grewia bicolor	Schmidtia bulbosa	
	Grewia fallax	Forbs	
	Grewia forbesii	Cleome hirta	
	Grewia villosa	Commelina erecta	
	Haplocoelum foliosum	Cucumis figerei	
	Lannea alata	Heliotropium steudneri	
	Lannea stuhlmannii	Heliotropium strigosum	
	Maerua edulis	Phyllanthus maderaspatense	
	Sterculea spp.	Solanum dubium	
	Terminalia prunoides		
	Terminalia spinosa		
	Tinnea europea		
	Grasses		
	Aristida mutabilis		
	Enteropogon macrostachys		
	Panicum maximum		
	Forbs		
	Hibiscus micranthus		
	Melhannea ferrugina		
	Ocimum americanum		
	Pavonia patens		
	Sanseviera spp.		

Indifferent: more than 300 species (Pg < 2 Pw and Pw < 2 Pg)

Pw = presence (in %) in vegetation releves with a dense structure (on average 48% tree and shrub cover)
Pg = presence (in %) in vegetation releve with an open structure (on average 18 % tree and shrub cover)

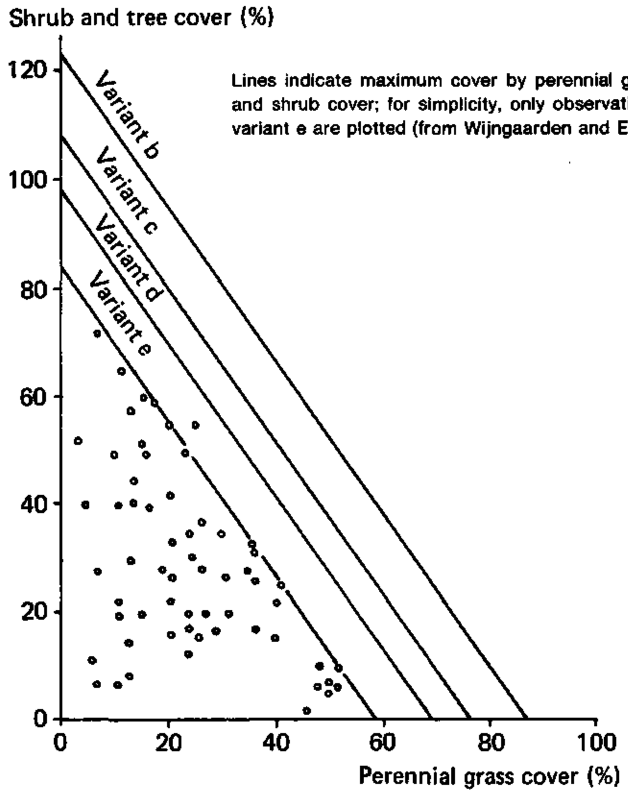


Figure 2.21 Relationship between cover of perennial grasses and cover by trees and shrubs in the different plant community variants

relationship between perennial grasses and the woody vegetation is governed by the competition for available moisture. The reasons why the maximum cover by perennial grasses is not always reached are given in Chapter 4.

2.3.1.4 VEGETATION PRODUCTION

Vegetation production in semi-arid environments is often controlled by the availability of water. Several authors found a good relationship between rainfall and vegetation production (Walter, 1971; Braun, 1973; Breman, 1975; Houerou and Hoste, 1977). Penning de Vries and Djiteye (1982), however, indicated that this is often an indirect relationship. In many cases, available nutrients (especially N and P) limit production, but the availability of these elements is also related to rainfall. They consider water as the limiting factor only when the rainfall per growing period is less than approximately 300 mm. In that case, properties of the vegetation (cover by the different strata, germination strategy of the annuals) can also play a role in primary production.

In this section, only those data necessary to calculate the amount of food available for the large herbivore population are described. Because the growing seasons in the Tsavo area are short and well-defined, the vegetation production of these periods must also supply the herbivores with forage in the ensuing dry seasons; thus the data on standing crop at the beginning of the dry season are very important. Because the "peak standing crop" (PSC = above ground biomass at the end of the growing period = beginning of the dry season) gives a reasonable approximation of vegetation production in areas with short growing seasons, these measurements are used as the basic data to describe vegetation production.

The PSC of the ground layer was harvested at the ends of several growing periods at approximately 20 sites. Each observation consisted of the dried and weighed standing crop of 10 randomly placed square meters. The standing crop was separated into old (from previous growing season) and newly-produced grasses, leguminous and other forbs. Sites which had obviously been heavily grazed in the growing season were avoided. Peak standing crop data are given only for newly produced material, in gr/m^2. The production of the woody vegetation was measured as current season's growth (CSG) per individual shrub (Thalen, 1979) for different species and at different sites in one season only. At each site, rainfall was recorded with storage rain gauges; soil properties were recorded and in most cases several soil samples were analyzed.

Production of the ground layer

The peak standing crop of the ground layer varied between 10 and 870 gr/m^2. The contributions of the different components were:

Component	*Range (%)*	*Average (%)*
Grasses	65 - 99	90.8
Leguminous forbs	0 - 12	2.7
Other forbs	0 - 35	6.5

There is some variation among the different vegetation communities. The vegetation of the dissected plain (communities CL4 and CA3) has, in general, a slightly higher proportion of leguminous forbs (approximately 6 percent).

The variation of PSC at individual sites is almost linearly related to the rainfall (r^2 = 0.82 - 0.99; n = 5). There are large differences in the slopes of the curves, however, and some curves are less linear than others (Figure 2.22). These differences in production relative to rainfall may be caused by differences in properties of the sites, *ie*, in physical and chemical soil properties, or in vegetation properties.

Extensive work on the relationship between production and the uptake of nutrients in the Sahel revealed an easy way to judge whether production was limited by N(itrogen) and P(hosphorus) or not. Penning de Vries and Djiteye (1982) found the following minimum values for N and P in grasses at different growing stages for growth not limited by nutrients:

	Before flowering *Minimum (%)*	*After flowering* *Minimum (%)*
Nitrogen	1.0	0.5
Phosphorus	0.09	0.09

The ratio P/N is always between 0.04 and 0.15.

The data found for the Tsavo area are presented in Figure 2.23. At flowering, most of the N values are above 1.5 percent, the P values between 0.09 and 0.20 percent and the P/N ratio between 0.04 and 0.10. At the end of the growing season (PSC data), some sites showed low P and low P/N values, especially when the biomass was high. This means that nitrogen is certainly not limiting the growth of grasses in Tsavo, but phosphorus may limit their growth towards the end of the growing period on certain sites in wet years.

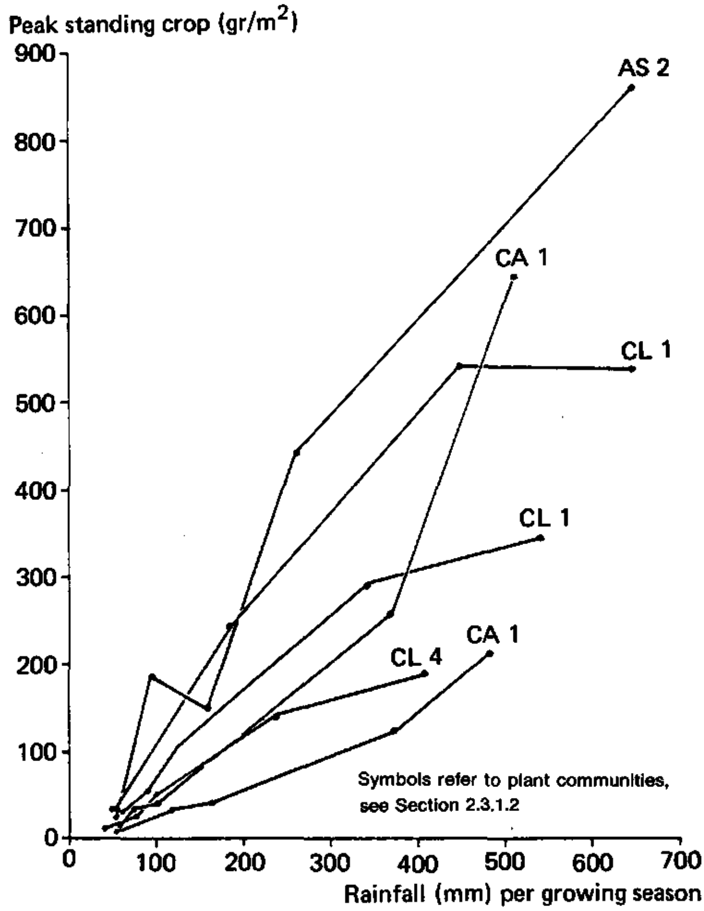


Figure 2.22 Peak standing crop at six different sites in five growing seasons in relation to rainfall during the growing season

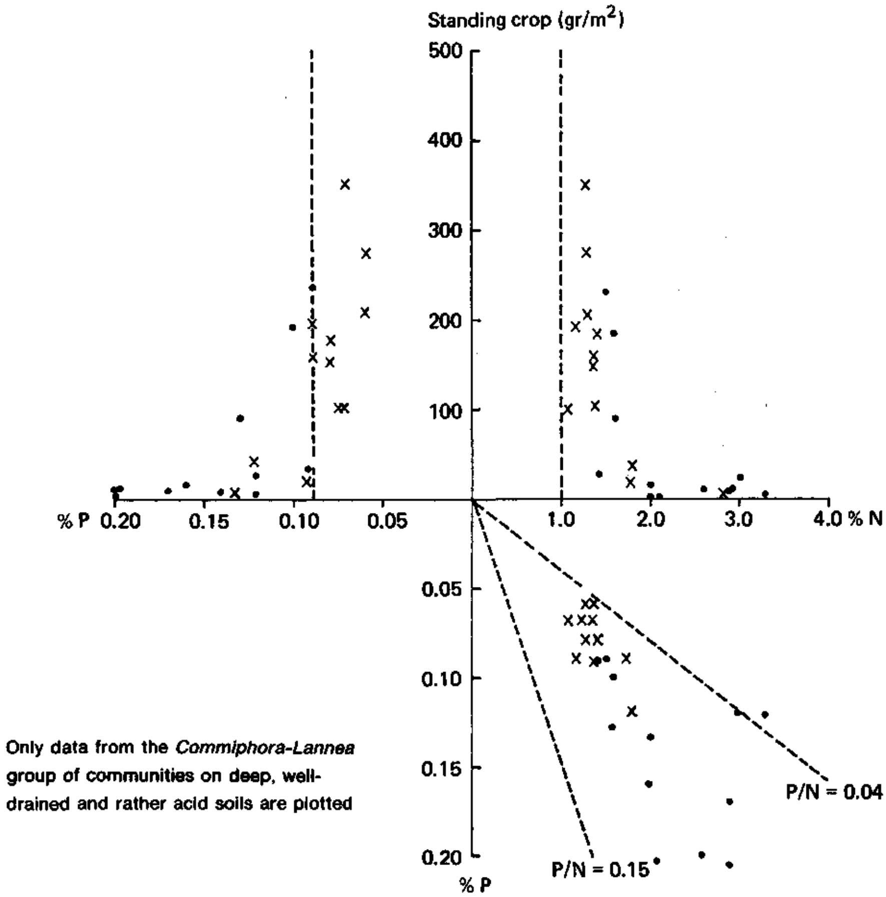


Figure 2.23 Relationship between standing crop, nitrogen content, phosphorus content, P/N ratio and growth stage in grasses

The levelling-off of some of the curves in Figure 2.22 at higher rainfall (more than 400 mm per growing season) could be related to a production limitation caused by the shortage of phosphorus, as all these cases refer to vegetation on soils with the lowest amounts of available P (soil unit N1, Table 2.3). The reason that the nutrients limit primary production at a higher rainfall level per growing season in Tsavo than in the Sahel is probably because the soils in the Sahel are "poorer", *ie*, have a lower available nutrient content. That nitrogen is certainly not limiting production in the Tsavo ecosystem may also be attributed to the fact that perennial grasses dominate the ground layer.

Because the average rainfall in the Tsavo area is approximately 150 to 300 mm per growing season, data representing rainy seasons with more than 400 mm are not very relevant and are excluded hereafter.

For the further analysis of the factors influencing production, all data were split into three groups, each representing sites with similar physical soil properties:

Group 1: all observations on deep, well-drained, sandy-clay soils; flat topography (slopes less than 2 percent, often less than 1 percent) where only some occasional run-off occurs; covered by vegetation communities CL1, 2, 3 and CA1.

Group 2: all observations on shallow, well-drained, gravelly soils; undulating topography (slopes 2 to 8 percent) where run-off is rather common; covered by vegetation community CL4.

Group 3: all observations on deep, imperfectly to poorly drained sandy-clay to clay soils; extremely flat to depressional topography where run-on occurs regularly; covered by vegetation communities CA2, AS1 and 2.

For the sake of discussion, it is now assumed that the PSC is not controlled by the availability of nutrients but by the availability of water and the condition of the vegetation. The availability of water within each of the three groups is directly related to the rainfall because the run-off, run-on and water-holding capacity of the soils within each group are about the same. Indeed, there is within each group a significant linear correlation between the PSC and rainfall ($r^2 = 0.40 - 0.78$; $P < 0.01$). A considerable part of the variation is not yet explained, however (see also Figure 2.22).

Braun (1973) attributed the differences in production with the same rainfall at different sites in the Serengeti National Park, Tanzania, to the differences in species composition of the herbaceous vegetation. He estimated that growth per mm of rainfall was 0.37, 0.87 and 0.45 to 1.05 gr/m^2 for the short, medium-tall and tall grassland types of the Serengeti, respectively.

Qualitative observations in the field in the Tsavo area gave the impression that sites dominated by perennial grasses instead of annual grasses and herbs were more productive and showed less variation in production, something that has also been observed in southern African savannas (Kelly and Walker, 1976).

Because we may expect zero production with zero rainfall and zero cover, regression equations without intercept were calculated. A multiple linear regression in steps between PSC divided by rainfall (PSC/R) and cover by perennial grass (PGC), annual grass and forb (AC) shows highly significant correlation coefficients (Table 2.13). The cover by perennial grasses alone explains a significant part of the variation. Including the annual grass and forb cover gives a slight but significant improvement of the correlation coefficient. The resulting regression equations are:

Group 1: $PSC/R(gr/m^2/mm) = 0.0120 \times PGC (\%) + 0.0069 \times AC (\%)$

Group 2: $PSC/R(gr/m^2/mm) = 0.0059 \times PGC (\%) + 0.0090 \times AC (\%)$

Group 3: $PSC/R (gr/m^2/mm) = 0.0137 \times PGC (\%) + 0.0065 \times AC (\%)$

The peak standing crop at the end of the growing season can thus be satisfactorily predicted for each of the three groups of data, representing different soil conditions, with the equations given above.

Table 2.13 Multiple linear regression in steps between peak standing crop divided by rainfall (PSC/R) and perennial grass cover, annual grass and forb cover

Group (Community)	Step	Variable included	Multiple R	Variation explained (%)	Partial F-test
1	1	Per.Grass Cover	0.82	68.3%	P < 0.001
(CL1,2,3)	2	Annual G/H Cover	0.94	87.5%	P < 0.001/0.002
(CA 1)					
2	1	Per.Grass Cover	0.89	80.1%	P < 0.005
(CL 4)	2	Annual G/H Cover	0.95	89.6%	P < 0.05/0.05
3	1	Per.Grass Cover	0.89	79.5%	P < 0.001
(CA 2)	2	Annual G/H Cover	0.92	85.4%	P < 0.001/0.02
(AS1,2)					

Woody vegetation production

Current season's growth shows a good relationship with certain shrub attributes (Thalen, 1978; Rittenhouse and Sneva, 1977). This was also found in the Tsavo area (Table 2.14). Because crown cover is a vegetation attribute that is rather easy to measure or estimate and can be directly related to total shrub and tree cover, it is used as the shrub attribute to estimate current season's growth.

The correlation coefficients in Table 2.14 are high and highly significant, but the regression equation parameters differ for the different species. The data for the different sites seem to overlap and the relationship is not clear. A clear picture was obtained only when the intensity of utilization by large herbivores was taken into account.

Three groups of species can be distinguished in this respect:

(1) Species generally not or only slightly browsed; for example, *Premna holstii* and *Premna recinosa*

Table 2.14 Simple correlation coefficients of the linear regression between current season's growth and height (H), largest diameter (D), crown cover (CC) and crown volume (CV) for some shrub species

Species	n	H	D	CC	CV
Sericocomopsis pallida	10	0.70	0.96	0.97	0.97
Xeromphis keniensis	11	0.52	0.84	0.87	0.92
Dirichletia glaucescens	5	0.35	0.95	0.94	0.83
Premna holstii	6	0.21	0.87	0.91	0.90
Bauhinea taitensis	5	0.61	0.86	0.91	0.91

(2) Species which are often browsed, but not very intensively; for example, *Sericocomopsis pallida, Ehretia taitensis* and *Cordia gharaf*

(3) Species which are very much favoured as food by herbivores and of which during the dry season a large part of the current season's growth is browsed; for example, *Caesalpinea trothae, Caucanthus albidus, Dirichletia glaucescens* and *Xeromphis keniensis.*

The relationship between current season's growth per m^2 crown cover and rainfall is given in Figure 2.24. Apparently each of the three groups of species has a different level of current season's growth divided by crown cover (CSG/CC) relative to rainfall. The calculated means for each of the three groups are 0.426, 1.965 and 1.028 $gr/m^2/mm$, respectively. In Figure 2.24 and the following chapters, rounded-off figures are used:

Browse intensity	*Production (in gr/m^2 crown cover per mm of rain)*
None to slight	0.5
Moderate	2.0
Strong	1.0

It seems that moderate utilization by herbivores favours the production of trees and shrubs. This has also been observed by other authors (Ferguson, 1973; McConnell and Smith, 1977; and others). This stimulating effect of browsing on shrub production is caused by the removal of the apical dominance of the terminal bud, which causes several lateral buds to sprout (Berg and Plumb; 1972).

For the data set presented here, the level of utilization is rather specific for each species because browsing pressure was about the same in the areas sampled. For other areas with a diverse browsing pressure, this relationship is expected not necessarily to be species specific.

Forage quality

Table 2.15 contains some data on the composition of bulk grass samples from the *Commiphora- Lannea* group of communities on well-drained, deep and rather acid soils. These data can be used to evaluate the quality of the primary production as forage for herbivores.

The highest concentrations of moisture, nitrogen and phosphorus are found at the beginning of the growing season. The values decrease as the season progresses. The opposite occurs with the crude fibre content. The Ca content varies less than the other components.

The variation in nutrient content within each growth stage is closely correlated with the standing crop (see also Figure 2.23). The species of the grass does not seem to have any influence. Each grass species shows the whole range of concentration of nutrients, depending on the growth stage and the standing crop. Grass samples from other plant communities with other soil conditions show a similar pattern.

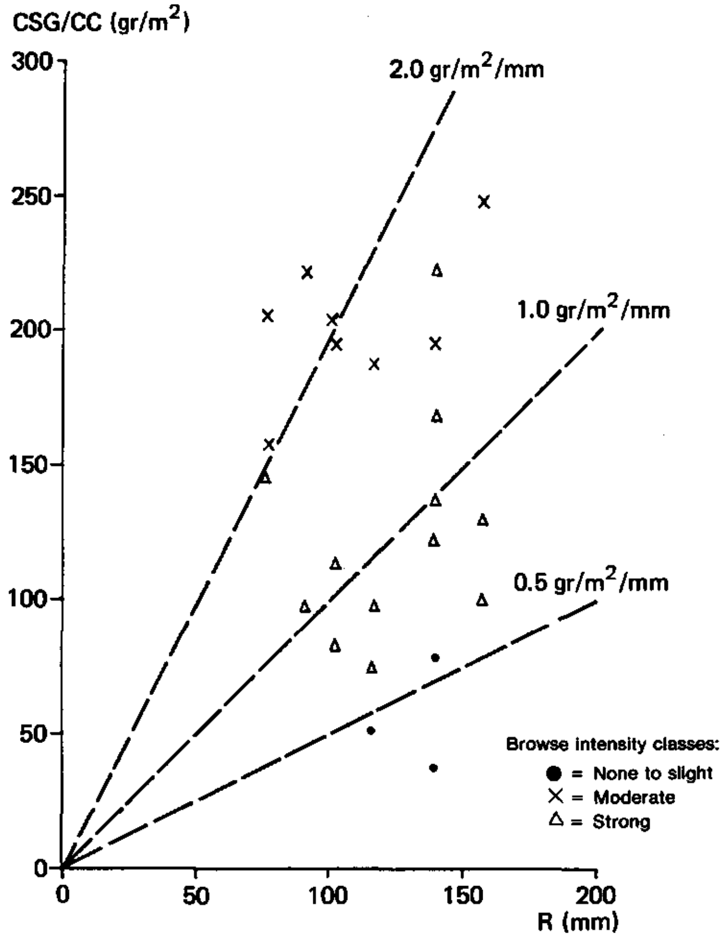


Figure 2.24 Relationship between current season's growth per m² crown cover, rainfall and browse intensity class

Forbs and browse (leaves and young twigs from shrubs) show a pattern in nutrient concentration similar to the grasses, but the values are in general higher (non-leguminous forbs and browse 1.5 to 3 percent N in the dry season, and leguminous forbs up to 4 percent N).

2.3.2 Large herbivore population

2.3.2.1 ABUNDANCE AND DISTRIBUTION

Considerable changes have taken place in the abundance of the large herbivores since Cobb's (1976) description, but his data are the only published ones for the whole ecosystem and for all larger herbivores. Moreover, those data also describe the situation in the years in which the data upon which this report is

Table 2.15 Nutrient content of bulk samples of grasses at different growth stages

Growth Stage	Dominant species	% M	SC	% N	% CF	% P	% Ca
Early growth	Brachiaria leersioides	73.2	7	3.2	25.0	0.14	0.41
Early growth	Brachiaria leersioides	82.1	97	2.9	32.2	0.23	0.43
	Average	77.7	52	3.1	28.6	0.19	0.42
Flowering	Aristida adscensionis	37.8	2	2.0	29.8	0.14	0.41
Flowering	Chloris roxburghiana	53.3	2	3.3	26.6	0.12	0.27
Flowering	Tetrapogon bidentatus	72.4	5	2.1	30.0	0.51	0.46
Flowering	Digitaria macroblephora	60.0	6	2.9	25.9	0.17	0.51
Flowering	Aristida adscensionis	71.7	11	2.6	27.2	0.20	0.39
Flowering	Aristida adscensionis	56.1	12	2.9	28.7	0.21	0.34
Flowering	Latipes senegalensis	64.8	13	2.0	34.9	0.16	0.29
Flowering	Latipes senegalensis	53.7	26	3.0	30.2	0.12	0.53
Flowering	Aristida adscensionis	41.0	29	1.4	35.0	0.09	0.39
Flowering	Aristida adscensionis	56.7	90	1.6	30.2	0.13	0.70
Flowering	Brachiaria leersioides	57.3	192	1.6	35.8	0.10	0.47
Flowering	Digitaria macroblephora	65.9	238	1.5	32.4	0.09	0.93
	Average	57.6	52	2.3	30.6	0.17	0.47
Peak SC	Chloris roxburghiana	49.2	7	2.9	28.2	0.13	0.30
Peak SC	Digitaria macroblephora	37.2	22	1.8	28.8	0.09	0.46
Peak SC	Aristida adscensionis	27.6	41	1.8	35.8	0.12	0.33
Peak SC	Aristida adscensionis	42.4	101	1.1	36.4	0.07	0.31
Peak SC	Eragrostis caespitosa	48.1	101	1.4	32.3	0.07	0.28
Peak SC	Digitaria macroblephora	29.3	154	1.4	35.4	0.08	0.66
Peak SC	Chrysopogon aucheri	59.7	156	1.3	34.7	0.09	0.46
Peak SC	Latipes senegalensis	47.7	187	1.4	34.1	0.08	0.85
Peak SC	Digitaria macroblephora	42.1	197	1.2	28.5	0.09	0.55
Peak SC	Digitaria macroblephora	39.7	207	1.3	37.1	0.06	0.55
Peak SC	Brachiaria leersioides	34.8	272	1.3	34.9	0.06	0.51
Peak SC	Aristida adscensionis	50.7	355	1.3	33.7	0.07	0.48
	Average	42.4	150	1.5	33.3	0.09	0.48
Beginning ds	Aristida adscensionis	5.9	31	1.6	28.4	0.16	0.50
Beginning ds	Digitaria macroblephora	11.5	153	1.1	39.5	0.07	0.49
	Average	8.7	92	1.4	34.0	0.11	0.50
End ds	Aristida adscensionis	10.4	7	1.3	34.7	0.09	0.46
End ds	Latipes senegalensis	9.0	21	1.4	36.7	0.07	0.20
End ds	Latipes senegalensis	14.7	27	1.2	37.3	0.09	0.53
End ds	Digitaria macroblephora	10.7	92	1.1	37.4	0.07	0.26
	Average	11.2	37	1.3	36.5	0.08	0.36

M = moisture (%)
SC = standing crop (g/m2)
N = nitrogen (%)
CF = crude fibre (%)
P = phosphorus (%)
Ca = calcium (%)
ds = dry season

based were collected. Cobb's description will therefore be used. More information on the changing herbivore population will be given in Chapter 5.

Based on six systematic reconnaissance flights, Cobb (1976) described the abundance and distribution of the large herbivores of the Tsavo ecosystem. The main findings are listed in Table 2.16. Only data for hippopotamus were added, based on data from Mwenge International (1982). The species mentioned in Table 2.16 are not the only herbivores in the Tsavo ecosystem. Several other species occur, but they were too small or too rare to be observed from low-flying aircraft and form only a small proportion of the total vertebrate herbivore population.

Although the elephant was not the most numerous species, it played a dominant role in the Tsavo ecosystem because it made up approximately half of the total large herbivore biomass (Table 2.17). Black rhinoceros did not occur in very high densities, but the total population of approximately 6000 represented one of the largest populations in the world.

Notably absent in the Tsavo area were antelopes, which dominate other ecosystems in east Africa, such as the wildebeest, topi and Thomson's gazelle. On the other hand, several species of the arid regions were particularly numerous in Tsavo: oryx, gerenuk and lesser kudu.

The herbivores were not homogeneously distributed over the ecosystem. For each of the major species, some remarks on their distribution will be made, based mainly on the work of Cobb (1976).

Elephants (Figure 2.25) can be found throughout the ecosystem, although the densities near the boundaries and outside the park are often lower.

Rhinoceros are found mainly inside the park near the Athi-Tsavo-Galana rivers.

Buffalo (Figure 2.26) *and waterbuck* are confined to the areas with permanent water supplies.

Zebra, eland, oryx (Figure 2.27), *Grant's gazelle, ostrich and warthog* occur all over the area, although at somewhat lower densities in the more wooded central north.

Giraffe, lesser kudu and gerenuk (Figure 2.28) are also widespread but with concentration areas of kudu near the Athi river and of the gerenuk in the northeast.

Cattle and shoat (sheep and goat) occur only outside the park and shoat only to the west and south of it.

2.3.2.2 HABITAT UTILIZATION

The very rough description of the distribution of the large herbivores in Section 2.3.2.1 may give the impression that several animal species use the same area. Several studies have shown that different species may occupy the same general area at the same time, but that each often selects–at a detailed level–a different position on the topographic catena or different parts of the vegetation

Table 2.16 Population estimate and density of the large herbivores in the Tsavo ecosystem (from Cobb, 1976)

Species	Population Estimate			Density		
	Total	Inside Park	Outside Park	Total n/km^2	Inside Park n/km^2	Outside Park n/km^2
Elephant	34700	24600	10100	0.80	1.17	0.50
Buffalo	17200	14100	3100	0.39	0.67	0.22
Giraffe	7100	3100	4000	0.16	0.14	0.17
Zebra	25600	16400	9200	0.59	0.77	0.44
Rhino	5800	4800	1000	0.13	0.22	0.02
Oryx	23100	8900	14200	0.53	0.42	0.66
Eland	7300	3200	4100	0.16	0.15	0.19
Kongoni	19500	10700	8800	0.45	0.50	0.39
Grant's gazelle	39200	18100	21100	0.90	0.86	0.99
Lesser kudu	20700	7800	12900	0.47	0.37	0.53
Gerenuk	28800	9500	19300	0.66	0.45	0.85
Impala	26100	11100	15000	0.60	0.52	0.66
Waterbuck	3500	1900	1600	0.08	0.09	0.06
Hippopotamus	700	600	100	0.02	0.03	0.00
Warthog	4300	2100	2200	0.09	0.09	0.11
Ostrich	2900	1700	1200	0.06	0.08	0.05
Cattle	165800	0	165800	3.83	0.00	7.47
Shoat	51900	0	51900	1.19	0.00	2.33
Sum all	484200	138600	345600	11.19	6.59	15.71
Sum wildlife	266500	138600	127900	6.16	6.59	5.90

(Bell, 1970; Duncan, 1975; Stanley Price, 1974). As described in Sections 2.2 and 2.3.1, the environment in the Tsavo region is rather heterogeneous. The various wildlife species employ different strategies to cope with this variation of the environment.

Climatic hardship (heat stress) determines at a large scale that some species, such as kongoni and impala, are not found in the low- lying, hot and arid northeast of the ecosystem. In contrast, the gerenuk seem to prefer the arid parts (Cobb, 1976). Even the absence of wildebeest, Thomson's gazelle and topi in the whole ecosystem can very well be related to this climatic factor.

The availability of permanent drinking water determines at a somewhat smaller scale the distribution of the various animals in the dry season (Western, 1975; Ayeni, 1975; Cobb, 1976). Several species are apparently independent of drinking water in the dry season (Table 2.18). An important strategy to exploit this arid environment in the dry season–without drinking–is feeding at night when the vegetation absorbs moisture from dew, selecting plant parts with relatively

Table 2.17 Biomass and contribution to the biomass of the large herbivores of the Tsavo ecosystem (from Cobb, 1976)

Species	Unit Mass kg	Biomass Total kg/km²	Biomass Inside Park kg/km²	Biomass Outside Park kg/km²	Contribution Biomass Total %	Contribution Biomass Inside Park %	Contribution Biomass Outside Park %
Elephant	1725	1383	2018	864	46.7	65.4	31.7
Buffalo	450	179	302	100	6.0	9.7	3.6
Giraffe	750	123	110	128	4.1	3.5	4.7
Zebra	200	118	156	88	3.9	5.0	3.2
Rhino	816	109	186	20	3.6	6.0	0.7
Oryx	150	80	63	99	2.7	2.0	3.6
Eland	340	57	52	67	1.9	1.6	2.4
Kongoni	125	56	64	50	1.8	2.0	1.8
Grants gazelle	40	36	35	40	1.2	1.1	1.4
Lesser kudu	70	33	26	37	1.1	0.8	1.3
Impala	40	24	21	27	0.8	0.6	0.9
Gerenuk	25	17	11	21	0.5	0.3	0.7
Waterbuck	160	13	15	11	0.4	0.4	0.4
Hippopotamus	522	8	12	2	0.2	0.4	0.1
Ostrich	114	8	9	6	0.2	0.2	0.2
Warthog	45	4	4	5	0.1	0.1	0.1
Cattle	180	690	0	1121	23.3	0.0	41.1
Shoat	18	22	0	35	0.7	0.0	1.2
Sum all		2960	3084	2721	100.0	100.0	100.0
Sum wildlife		2248	3084	1565	75.9	100.0	57.5

high moisture content and/or resting in the shade during the daytime (King *et al*, 1975).

At an even smaller scale, animals make use of different parts of the vegetation by employing different feeding habits. Various classifications of the way herbivores select their diet have been published (Jarman, 1974; Hofmann, 1973). They are based on the proportion of browse or grass in the diet and on the relationship of the ruminant digestive tract with the type of diet eaten. In Table 2.19, herbivores are classified by feeding behaviour based on Hofmann's (1973) classifications with modifications by Soest (1982), McDowell *et al* (1983) and inclusion of all large herbivores of the Tsavo ecosystem.

Even animals classified in Table 2.19 in the same or closely related categories show different patterns in utilization of certain species of food plants or parts of food plants. Differences in preference for certain food plants in Tsavo were recorded for three species classified as "less selective browsers", namely rhino (Goddard, 1970), lesser kudu (Leuthold, 1971a) and giraffe (Leuthold and Leut-

Figure 2.25 Group of foraging elephants; even when browse is available, they also eat grass in large quantities

Figure 2.26 Buffalo; a water-dependent, not very selective grazer (bulk and roughage feeder)

Figure 2.27 Oryx; a water-independent selective grazer

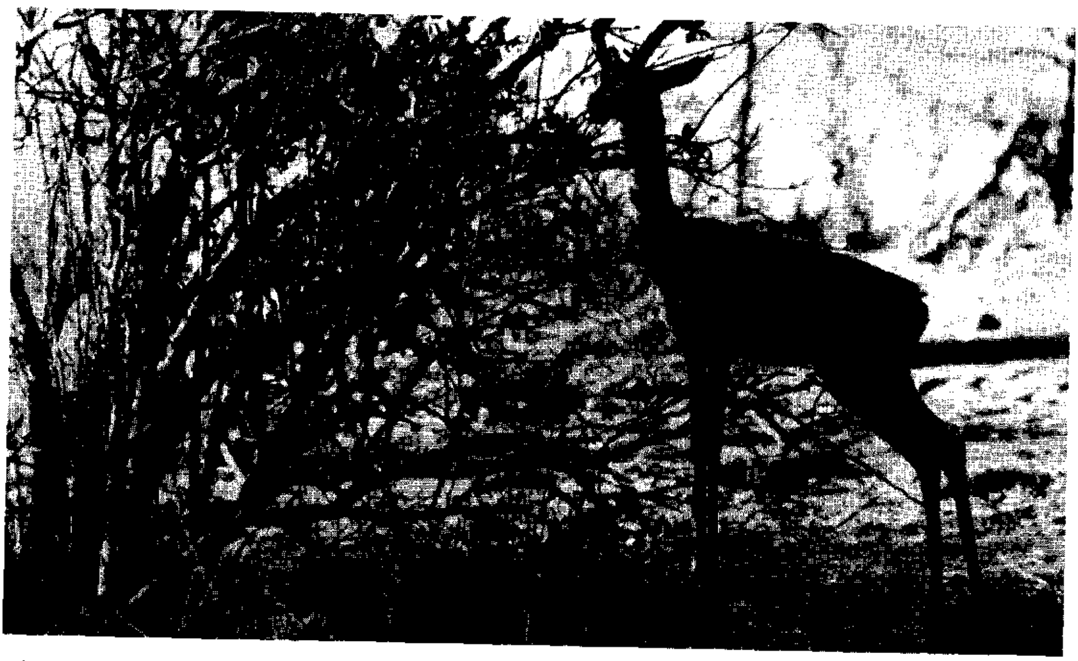


Figure 2.28 Gerenuk; a water-independent selective browser; feeds predominantly on young leaves, twigs and buds

Table 2.18 Water relationships and feeding behaviour of the large herbivores

Species	Drinking water dependency	Feeding habit
Elephant	dependent	mixed feeder
Buffalo	dependent	grazer
Giraffe	indep /dependent	browser
Zebra	dependent	grazer
Rhino	dependent	browser
Oryx	independent	grazer
Eland	independent	mixed feeder
Kongoni	indep./dependent	grazer
Grant's gazelle	independent	mixed feeder
Lesser kudu	independent	browser
Impala	independent	mixed feeder
Gerenuk	independent	browser
Waterbuck	dependent	grazer
Hippopotamus	dependent	grazer
Ostrich	independent	grazer
Warthog	indep /dependent	mixed feeder
Cattle	dependent	grazer
Shoat	dependent	mixed feeder

Independent/dependent indicates that under certain conditions or in certain regions this animal can behave differently

hold, 1972). All three are again different in food plant selection from the "selective browser", the gerenuk (Leuthold, 1970).

The elephant is classified here as an "intermediate feeder, preferring grass, but not very selective". Laws *et al* (1975) argue that elephants eat a large proportion of grass only when no browse is available. Olivier (1982), however, postulates that–based on body size, dental features and characteristics of the digestive tract–elephants are highly adapted to a staple diet of abundant, non-toxic, fibrous food of low quality (*eg*, grass) but to correct for dietary imbalances have to supplement it with a wide variety of different food plants of higher nutrient value (*eg*, browse). Observed diets of both African and Indian elephants fulfill those criteria (Olivier, 1982).

Because data on the quantity of food available for free-ranging herbivores are seldom available at a great level of detail, the crude division into grazers, browsers and mixed feeders is also given in Table 2.18.

Given all these differences in utilization of the habitat by the different animals, it is not surprising to find several species using the same general area. The general harsh conditions, the low reliability of the rainfall and thus the vegetation production, however, favour animals which are not very selective in their diet and are very mobile. For the Tsavo area, this is the elephant.

Table 2.19 Classification by feeding behaviour of ruminant and non-ruminant herbivores (modified from McDowell *et al*, 1983), (species occurring in the Tsavo area are underlined)

CLASSIFICATION	RUMINANTS	NON-RUMINANTS
1 Browsers		
1.1 Selective	duikers dik-dik <u>gerenuk</u>	rabbits
1.2 Less selective	deer <u>giraffe</u> <u>lesser kudu</u>	<u>rhinoceros</u>
2 Intermediate Feeders		
2.1 Preferring browse		
2.1.1 Selective	<u>grant's gazelle</u> goat	
2.1.2 Less selective	<u>eland</u> moose camel	
2.2 Preferring grass		
2.2.1 Selective	<u>impala</u> thomson's gazelle	<u>warthog</u>
2.2.2 Less selective	sheep	<u>elephant</u>
3 Grazers		
3.1 Selective	<u>kongoni</u> <u>waterbuck</u> wildebeest <u>oryx</u> topi	<u>ostrich</u>
3.2 Less selective	cattle <u>buffalo</u> <u>hippopotamus</u>	<u>zebra</u> horse

2.3.3 Other animals

Apart from the large herbivores mentioned above, quite a variety of other vertebrate animals occurs in the Tsavo region. Williams (1967) produced a checklist of the mammals and birds in Tsavo National Park. A much more complete and detailed checklist of the birds of Tsavo National Park East was prepared by Lack *et al* (1980). The ecology of some birds of prey was described by Smeenk (1974). All larger predators, such as lions, leopards, cheetahs, hyenas and wild dogs, occur all over the ecosystem, but no data are available about their numbers.

Phillipson (1975) indicated that the biomass of invertebrates is probably at least 10 times that of the large herbivores. No real estimates on the composition, size and biomass of the invertebrate population are available for the group as a whole, but some groups and some aspects have been studied in detail.

Dung beatles and their effect on removal of herbivore dung were studied by Anderson and Coe (1974), Kingston (1977) and Kingston and Coe (1977). Dung beatles play a very important role in the incorporation of herbivore dung into the soil, especially in the wet season (Figure 2.29). In the dry season, most of the dung remains on the soil surface and is consumed or transported into the soil by termites during the next rainy season. The systematics of one group of dung beatles (Onitini) was treated by Krikken (1977).

The contribution of termites in the removal of dead wood was studied by Buxton (1979). During the period of his study (1976-1977), more than 90 percent of the yearly dead wood litter-fall was consumed by termites. He also indicated that the quantity of dead wood consumed by termites was similar to the quantity of grass and browse consumed by the large herbivores. When the termites' consumption of other materials is also considered, they probably remove considerably more than the large herbivores do. In doing so, termites also play an important role in increasing the infiltration capacity, permeability and structural stability of the soil (Wielemaker, 1984). The density of mounds built by *Macrotermis* sp, the main wood-consuming species in the Tsavo ecosystem (Figure 2.30), was found to be positively related to rainfall and elephant damage to the woody vegetation (Buxton, 1979). Buxton also listed another 27 termite species occurring in the Tsavo ecosystem, each with specific nest-building and feeding habits.

2.3.4 Human population

Archeological evidence indicates that, from 8000 BP onwards, the area was inhabited by hunter-gatherers at a density probably higher than found in the last few centuries (Thorbahn, 1984). The first written records date from the middle of the last century (Krapf, 1860). At that time, the area was thinly populated and used mainly by the Waliangulu tribe who specialized in elephant hunting. Other pastoral tribes made occasional use of the area, probably only in the wet season: the Orma in the east, the Kamba in the north and the Masai in the west. Only the climatically more favourable Taita hills were occupied by settled agriculturalists, the Taita.

With the establishment of the British colonial administration, district boundaries were delineated and, in 1933, "native reserves" were established for the settled agricultural tribes and the Masai, and the rest was designated as "crown land". Some parts of the crown land were set apart as "grazing reserves" for the pastoral tribes. No provision was made for the hunting tribes, however; the

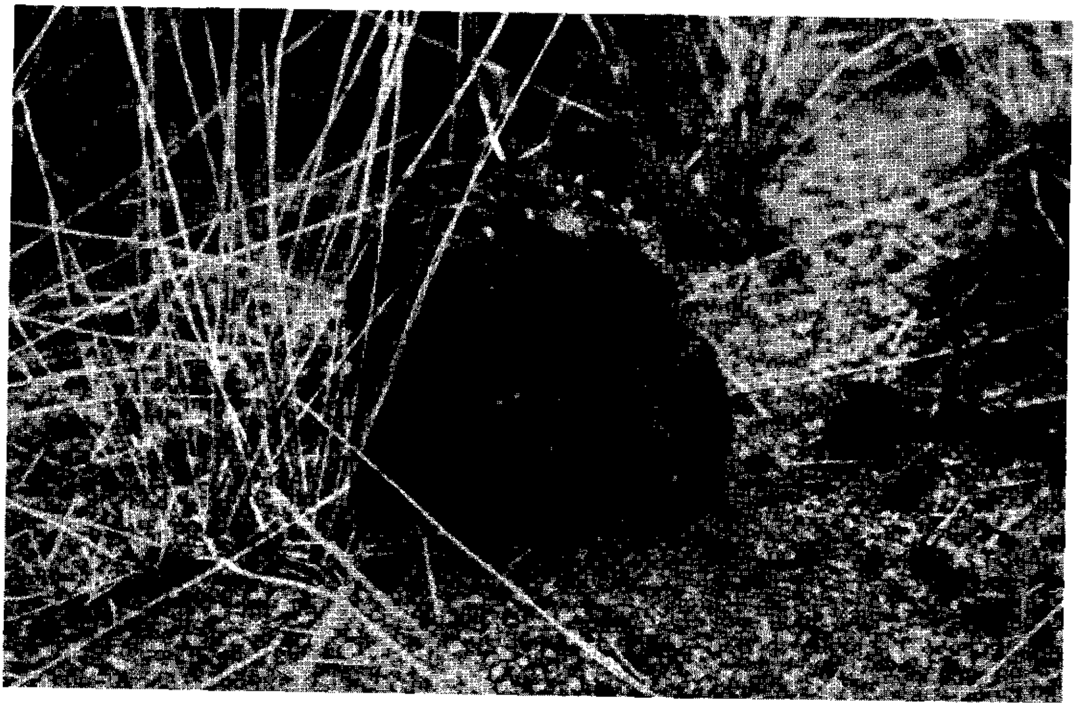


Figure 2.29 Dung beatles; in the rainy season they play an important role in the quick recycling of animal dung

Figure 2.30 Termite mound; the termites *(Macrotermis* sp) which build these play an important role in the decomposition of dead vegetative material, especially wood

failure of the administration to identify hunting as a lawful way of life made the Waliangulu "outlaws" (Ecosystems, 1982).

In 1948, Tsavo National Park East and West was proclaimed in the area gazetted as crown land east and west of the Mombasa- Nairobi main road. The hunting and pastoral tribes were evicted and settled just outside the park boundaries.

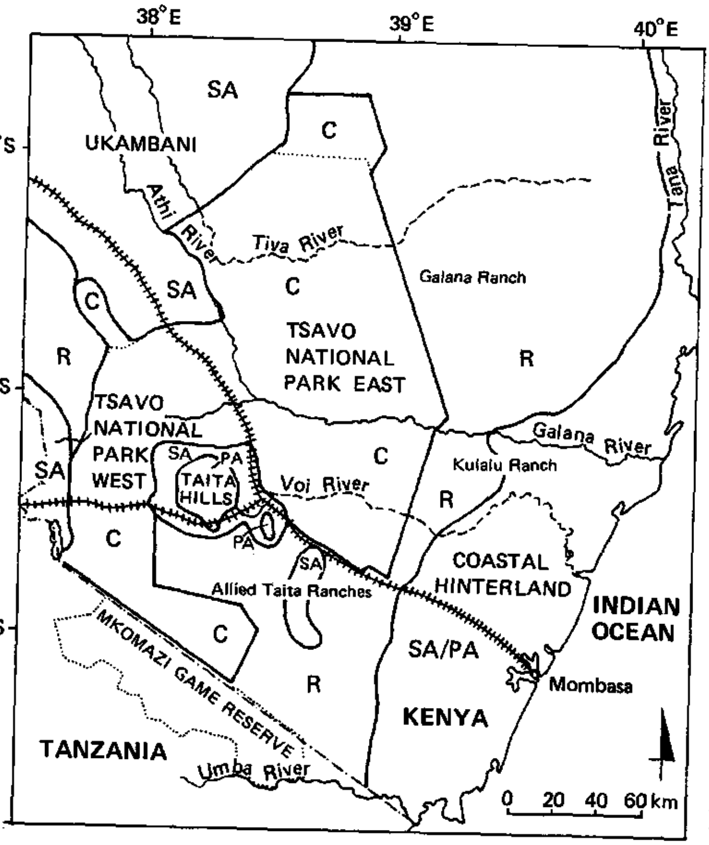
Ranches were established in the late 1960s on those parts of the crown land not included in the national park (Figure 2.31). Until recently, wildlife had free

Figure 2.31 Rukinga ranch. Cattle coming out of the dip

access to those ranches, and the ranches thus did not form a serious threat to the wildlife. The tremendous increase in area and intensity of cultivation northwest of the parks in the Kitui and Machakos districts does pose a threat, however (Figure 2.32). This is also true, though not so serious yet, for the area towards the southeast (the coastal hinterland).

The present land use of the Tsavo area is presented in Figure 2.33.

Figure 2.32 Cultivation close to the park boundary in Ukambani



C = Conservation
R = Ranching
SA = Semi-permanent agriculture and pastoralism
PA = Permanent agriculture

Figure 2.33 Major land uses in the Tsavo region

Chapter 3

SOIL DYNAMICS

The present soils in the Tsavo area are the result of a long period of soil formation, during which their properties have changed gradually. Some idea of these changes can be obtained when soils developed from the same parent material but in different landforms, indicating different periods of stability and soil formation, are compared (Table 3.1). The longer the period of stability, the deeper the soil and the lower the chemical fertility because of weathering of the bedrock and subsequent leaching of the soil material. This lower chemical fertility is shown by the lower cation exchange capacity (CEC) and lower base saturation (Table 3.1). The more strongly weathered soils also have a lower content of silt and weatherable primary minerals. These weathering and leaching processes take many thousand–and probably many hundred thousand–years to show up clearly in the physical and chemical properties of the soils.

Some soil properties, however, can change in a relatively short time. Destruction of the vegetation cover can be followed by erosion, which affects the characteristics of the topsoil in particular. A change of the woody or grass cover–by large herbivores, fire or interference by man–can also have minor effects on some soil properties without directly causing erosion.

The effect of shifting cultivation is a well-documented example of changes in the physical and chemical properties of the soil after clearing the "natural vegetation" by cutting and burning. Decrease of the infiltration rate, porosity and organic matter content are reported, and continued cultivation after clearing not only further lowers the organic matter content but also the amount of available nutrients and pH (Sanchez, 1976).

Protection from burning over a period of 25 years of a humid savanna vegetation in Malawi increased enormously the cover of the woody vegetation. The organic matter and nitrogen content did not change, but the amount of exchangeable bases in the soil decreased. This effect was attributed to the accumulation of vegetative material by termites and concentration of it in their mounds, rather than in the soil (Trapnell *et al*, 1976).

The direct effect on the soil of grazing is less well documented. Dunn (1978) reports that heavy trampling caused a decrease in infiltration rate of the soil. Glover and Wateridge (1968), Wit (1978) and Jager (1982) all report on the effect of large herbivores in the formation of low erosion terraces in the Loita plains (Kenya) and Serengeti areas (northwestern Tanzania). Penning de Vries and Nditeye (1982) present evidence of a redistribution of minerals in the soil

Table 3.1 Some characteristics of soils developed on ferro- magnesian rich gneisses on different erosion levels and landforms (from Wijngaarden and Engelen, 1985)

	Physiography	Non-dissected flat	Erosional Plain very gently undulating	Dissected Plain (Upland) gently undulating
	Slope	< 2 %	1 - 3 %	2 - 8 %
Kithioko/Mulango level	mapping unit*	Pn1Fb	Pn1Fr	U2Frp
	classification	xanthic FERRALSOL	Ferral-chromic LUVISOL	chromic LUVISOL
	depth solum (cm.)	> 120	> 120	50 -120
	B-horizon:			
(Miocene-	clay (%)	54 - 64	42 - 66	38 - 47
-Late Tertiary)	silt/clay ratio	0.13-0.17	0.20-0.24	0.31-0.42
	CECclay (me%)	10 - 14	16 - 20	30 - 40
	base sat. (%)	40 - 70	60 - 100	50 - 90
	weath prim min	2	10	19
	nr observ	2	2	2
Nyika level	mapping unit*	Pn2Fr	PdFrp	PdFrP/PdFbK
	classification	rhodic FERRALSOL	chromic LUVISOL	ferralic/calcic CAMBISOL
(Late Tertiary)	depth solum (cm.)	> 70	40 - 80	15 - 45
	B-horizon:			
	clay (%)	32 - 41	38 - 42	24 - 41
	silt/clay ratio	0.15-0.28	0.15-0.31	0.38-0.55
	CECclay (me%)	12 - 16	16 - 28	13 - 38
	base sat (%)	40 - 70	60 - 80	80 - 100
	weath prim min	10	22	n.d.
	nr observ	9	2	4

through grazing in the Sahel region in Mali: areas which are lightly grazed are depleted of minerals; areas which are heavily grazed, or where animals concentrate during the night, show an accumulation of the same minerals. Hatton and Smart (1984) report a dramatic increase in extractable minerals in the soil after 24 years exclusion of grazing by large herbivores of a sub-humid savanna area in Uganda. Because their results are derived from side-by-side comparison of two plots, and not by successive sampling of the same plot, the results are probably strongly influenced by initial differences in soil fertility (different soil types at the two plots). Trials with different grazing intensities in South Africa showed a lowering of the infiltration rate of the soil at higher stocking densities, but no change in the organic matter content of the topsoil (Gillard, 1975). Similar results were obtained by Kelly and Walker (1976) in semi-arid savannas in Zimbabwe.

3.1 SHORT-TERM DYNAMICS IN RELATION TO LARGE HERBIVORE GRAZING AND CULTIVATION

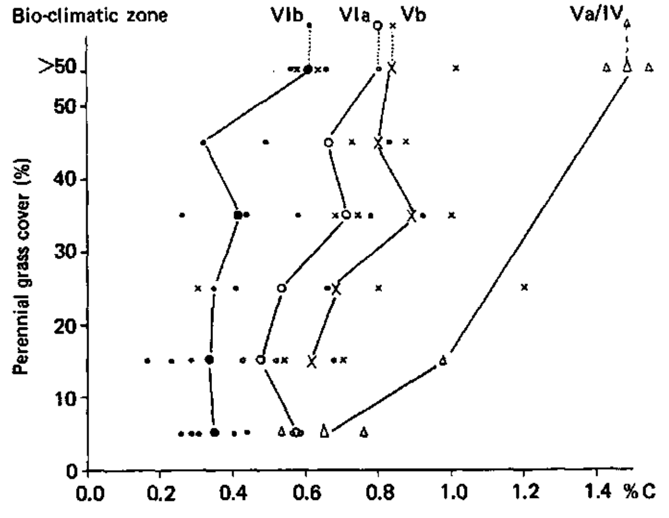
3.1.1 Physical and chemical soil properties

The destruction of the woody vegetation by elephants has in general resulted in an increase of the cover by grasses (Section 2.3.1.3 and Chapter 4). The infiltration rate of the soils is strongly related to the cover of the ground layer (Section 2.2.4.2). The change from a vegetation dominated by trees and shrubs to a more open vegetation has thus generally resulted in a better infiltration rate of the soils. Only in areas where the grass cover is low because of strong overgrazing will the soils have a low infiltration rate, whatever the cover by trees and shrubs is.

Examination of soil data from the same soil type and the same vegetation community, but with a different vegetation structure, did not reveal any relationship between mineral content of the soil and vegetation structure and grass cover. A positive relationship was found only between rainfall (bio-climatic zone) and organic matter content of the topsoil and also a weak but not significant ($P > 0.1$) positive relationship between organic matter content of the topsoil and grass cover (Figure 3.1).

When the mineral content in the vegetation is compared with the amount available in the soil, it is not surprising that no differences in mineral content were found in soils covered with different vegetation structures. The decomposition of dead herbaceous material is very rapid. The standing crop of herbaceous material left over from the previous growing season disappears more quickly in the rainy season than new material grows (Figure 3.2). Animal dung decomposes by different means in the dry and wet seasons (Section 2.3.3), but both are very rapid (Anderson and Coe, 1974; Kingston, 1977). The consumption of dead wood by termites is about equal to the annual dead wood litter-fall (Buxton, 1979). Thus accumulation of dead vegetative material (litter) on the soil surface scarcely occurs in Tsavo. Accumulation of nutrients thus takes place mainly in the woody vegetation.

No total woody biomass data are available for the Tsavo area but we may assume a maximum of 10000 kg/ha above ground biomass and the same amount



Only observations from deep well-drained soils; small symbols indicate individual observations; large symbols, connected by a line, indicate average for 10 percent grass cover classes

Figure 3.1 Relationship between carbon content of topsoils (0 to 20 cm), bio-climatic zones and perennial grass cover

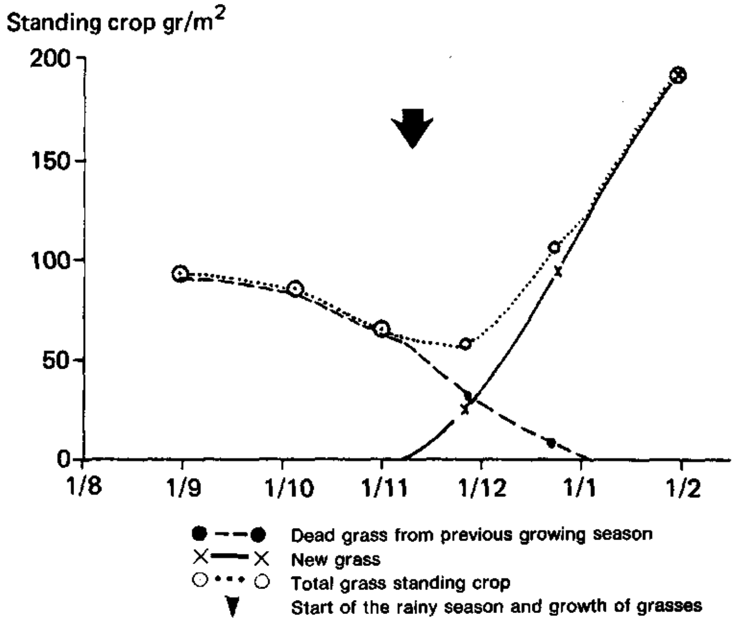


Figure 3.2 Changes in the standing crop of old and new grass within one growing season

below ground (Rutherford 1978, Vegten 1983). When the average phosphorus content is 0.05 percent (Tsavo Research Project, unpublished data), it gives a maximum of only 10 kg phosphorus stored in the woody vegetation. With only 10 ppm of available phosphorus in the "poorest soils", one meter of soil contains approximately 150 kg of available phosphorus per ha.

These data show that a maximum of approximately 7 percent of the amount of phosphorus available in the soil is accumulated in the woody biomass. In less "poor" soils and for other minerals, this percentage is far less. In contrast, accumulation of phosphorus in the forest vegetation in humid tropical climates on "poor" soils may be as much as 90 percent of the total amount in the ecosystem (soil plus vegetation), (Sanchez, 1976). This indicates again that the soils–although most in the Tsavo area are acid and are known in Kenya as "poor"–contain enough minerals to give an ample supply to the vegetation under these semi-arid conditions–a conclusion also reached in Section 2.3.1.4.

Some effect of redistribution of minerals by large herbivores was also observed. Analyses of topsoil samples at various distances from Aruba dam (an important dry season watering point since its construction in 1951) indicates that at least phosphorus shows a tendency of higher values close to the dam (Table 3.2). The soils of the dissected plain near the Galana river, another dry season concentration area, also show rather high phosphorus values in the area up to 3 km from the river (Table 3.3).

Table 3.2 Some characteristics of the topsoil (0 to 20 cm) at increasing distance from Aruba dam (soil unit S2 of Table 2.3)

Dist km	pH	Na me%	K me%	Ca me%	Mg me%	Mn me%	P ppm	N %	C %	C/N	sand %	silt %	clay %	si/c
0.05	7.2	0.02	1.26	4.8	2.6	0.62	112	0.07	0.70	11.1	82	10	8	1.3
0.10	6.9	0.16	1.96	4.2	5.2	0.82	140	0.13	0.76	5.8	76	12	12	1.0
0.20	7.0	0.02	1.19	5.2	2.8	0.78	92	0.09	0.83	9.2	68	17	15	1.1
0.30	7.1	0.10	1.70	4.0	3.1	1.12	91	0.13	0.92	7.1	67	16	17	0.9
0.50	6.6	0.02	1.44	4.8	3.7	0.68	56	0.08	0.80	10.0	58	14	28	0.5
1.00	7.4	0.04	1.50	7.2	3.2	0.58	50	0.10	0.63	6.3	68	8	24	0.3
1.50	6.3	0.08	1.70	1.6	2.0	1.06	82	0.08	0.51	6.4	68	12	20	0.6
2.00	7.4	0.07	1.85	5.2	5.0	0.92	70	0.10	0.80	8.0	60	10	30	0.3
4.00	7.6	0.01	1.19	3.4	3.2	0.74	56	0.07	0.55	7.9	66	6	28	0.2
8.00	7.4	0.13	1.42	5.2	2.6	0.64	38	0.10	0.69	6.9	56	16	28	0.6
10.00	6.6	0.04	0.72	3.2	2.0	0.52	52	0.11	0.92	8.4	66	9	25	0.4
10.70	7.5	0.16	1.14	4.0	1.9	0.54	56	0.11	0.97	8.8	62	10	28	0.4

3.1.2 Erosion

All usually distinguished forms of erosion –such as sheet, rill, gully, wind and streambed remodelling–occur in the Tsavo area and each has its specific influence on the soils.

Sheet and rill erosion are widespread in the area but at a very low intensity because of the flat topography and mostly relatively high infiltration rates of the soils, at least partially attributed to the good grass cover. This form of erosion is thought to have very little influence on the soils, as no indication was found of recent deposition of eroded material in the shallow, broad alluvial valleys. Only some redistribution of topsoil material over very small distances takes place. In the dissected plain with its undulating relief, sheet and rill erosion probably occur, but not very much. The soils show in general a well developed A- horizon, with amounts of organic matter comparable to soils in areas with a flat relief.

Only the undulating uplands in the northwest and southeast are often strongly affected by sheet and rill erosion. The main reason is the over-grazing by cattle, often after a period of cultivation. This results in low ground cover, surface

Table 3.3 Some characteristics of the topsoil (0 to 20 cm) at increasing distance from the Galana river (soil unit D1 of Table 2.3)

Dist km	pH	Na me%	K me%	Ca me%	Mg me%	Mn me%	P ppm	N %	C %	C/N	gravel %	sand %	silt %	clay %	si/c
1.75	7.2	0.15	0.62	4.4	2.1	0.55	122	0.04	0.30	7.5	10	72	8	20	0.4
2.25	7.0	0.04	0.64	4.0	2.1	0.73	53	0.06	0.60	10.0					
2.75	8.0	0.30	0.64	27.0	2.2	0.48	184	0.08	0.76	9.5	23	71	8	21	0.4
3.00	6.3	0.20	0.50	1.4	1.0	0.50	28	0.06	0.41	6.8	3	71	8	21	0.4
3.50	7.9	0.44	0.38	35.0	1.7	0.07	18	0.09	0.67	7.4	11	72	10	18	0.6
8.25	8.2	0.48	0.80	24.0	2.6	0.02	41	0.11	0.73	6.6	20	72	8	20	0.4
10.50	6.7	0.17	0.70	2.4	1.6	0.60	18	0.04	0.43	10.8					
13.00	6.0	0.12	0.80	0.4	1.8	0.60	8	0.06	0.33	5.5	4	72	6	22	0.3

sealing and thus poor infiltration rate and–consequently–run-off. The topsoils here are sometimes less deep and often have a lower organic matter content than in comparable areas inside the park.

Gully erosion is found only on some of the footslopes. Comparison of aerial photographs from 1948 and 1974 showed that patches badly affected by gully erosion already existed in 1948. In the park, these patches are apparently stable, but this form of erosion has often increased in acreage and/or intensity outside the park. According to local information, all affected areas, including those inside the park, were formerly cultivated (Figure 3.3) The effect on the soils of gully erosion is rather dramatic. This process usually stops only when hard, coherent, non-erodible material is reached by the gullies.

Streambed remodelling occurs in the floodplains of the Voi and Tiva rivers; both floodplains play an important role in the ecology of the Tsavo ecosystem. They contain stretches of backswamp grasslands which are flooded several times per year and as a result are highly productive. A change from a meandering to a braiding sedimentation system in the last 20 years has resulted in deposition of thick layers of sand and silt in the floodplains and the formation of gullies in some of the backswamps. Many of the backswamp grasslands have thus disappeared or at least become far less productive. The changes in soil characteristics associated with this change in sedimentation patterns are coarse textured

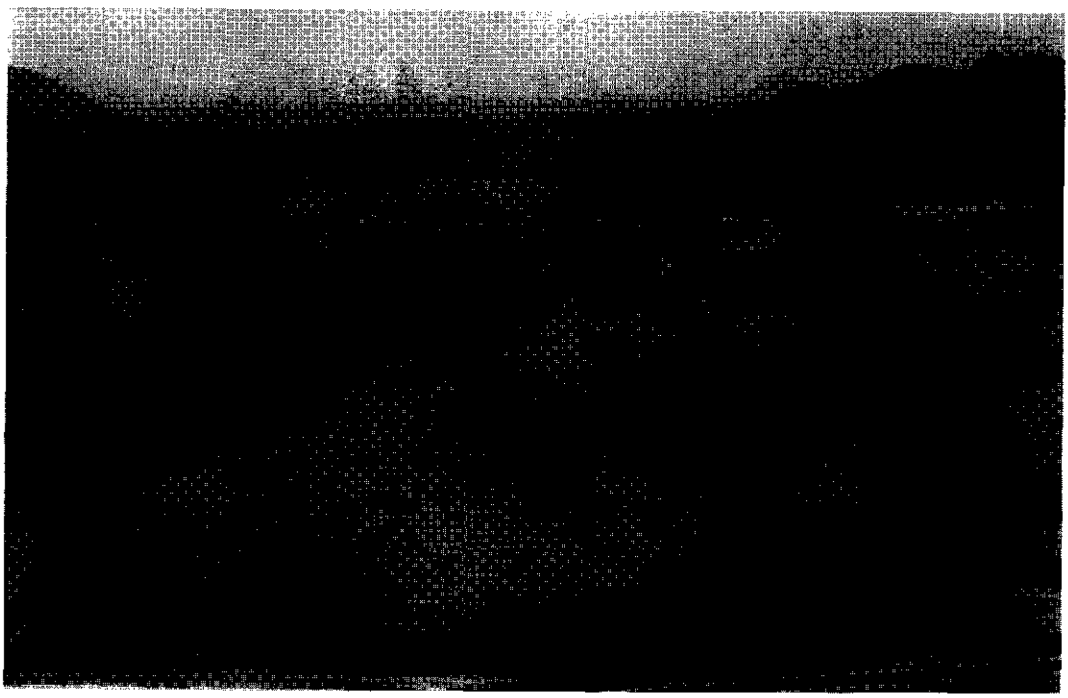


Figure 3.3 Gully erosion in formerly cultivated footslope; in the background a sisal plantation

soils with a low moisture-holding capacity on the newly laid down deposits and a change in soil moisture regime of the heavy textured former backswamp soils because of less frequent and shorter flooding.

The reason for this change in sedimentation pattern is probably a change in the flow regime. Because of the increase in cultivation and overgrazing in the upper catchment areas outside the park area (Taita hills and Kitui highlands), peak discharges have increased considerably. For the same reason, stream bank erosion occurs on the narrow stretches of alluvium along the Athi-Galana river, gradually also destroying the narrow stretch of riverine woodland. Although this form of erosion occurs inside the ecosystem, the reason for it must be sought in the upper catchment areas of the major rivers, all situated outside the ecosystem.

Wind erosion. At the end of the dry season, dust storms occasionally occur in the Tsavo area. One of the worst affected places is the area around Aruba dam. The trampling of the large concentration of animals in this area in the dry season apparently causes a loosening of the topsoil, which is then easily blown by the strong winds. Analyses of topsoil samples show an effect in the area only up to a maximum 500 m from the dam (Table 3.2). The clay content of the topsoil is lower, the sand fraction higher and the silt/clay ratio much higher. Apparently it is mainly the clay fraction that is blown away. The input of phosphorus from animal dung in this area, however, is more than the amount lost by wind erosion.

3.2 Conclusion

The destruction of the woody vegetation in the Tsavo area does not seem to significantly effect the soils. Usually, the only effect is an increased infiltration rate and a slightly higher organic carbon content of the topsoil, related to the better grass cover. Reversion to a tree and shrub dominated vegetation is not thought to give the same decrease of available nutrients as reported by Trapnell *et al* (1976) because the soils of the Tsavo area are much richer and also because the build-up of woody biomass will be much smaller in the much more arid climate of the Tsavo area than in the sub- humid savannas of Malawi.

Erosion in the Tsavo area seems to be related mainly to human activities. Agriculture alone, or in combination with grazing, is responsible for most of the present erosion. Even wind erosion around Aruba dam is related to human activities, since this permanent water supply is man-made.

The data for the Galana river area suggest that large concentrations of wild herbivores do not seem to have any negative effects on the soils. The landscape and soils in this area have probably evolved under this condition and are in equilibrium with it. This equilibrium has not been reached yet at Aruba dam, but it is unlikely that serious soil erosion will degrade a large area in the future.

A beneficial side effect of the concentration of herbivores near the dry season water supplies is the local enrichment of phosphorus in the soil. Although higher phosphorus content was not found in vegetation samples, there are some indications that leguminous herbs are more common in this area and that the regeneration of perennial grasses and *Acacia* spp is very good in years with good rainfall. An increase of mineral accumulation in the area can be expected in the very long term. The radius of the affected area around Aruba dam after 25 years is only approximately 500 m, while there is a band approximately 3 km wide along the Galana river, a natural concentration site of long standing.

Chapter 4

VEGETATION DYNAMICS

As shown in Section 2.3.1, there is a strong correlation between the occurrence of plant species, organized in plant communities, and the physical environment. The presence or absence of a certain species in a certain stand is determined by the soil and climatic conditions. Because soil and climate are relatively stable, very little variation in the distribution of plant species can be expected in the short term.

The abundance of individual species, expressed in this study by the areal cover, however, shows a great deal of variation. This can be clearly seen on the vegetation map of part of the Tsavo area (Wijngaarden and Engelen, 1985), where in most plant communities different structure types (cover of trees and shrubs) and grass cover types (cover of perennial grasses) were mapped. This was also shown in Figure 2.20.

This spatial variation in structure and grass cover is not static: until 1950, most of the area had a fairly dense cover of trees and shrubs. In the 1960s, elephants began to destroy the woody vegetation. This destruction was concentrated initially in the vicinity of the permanent water sources, the areas with the highest concentrations of elephants in the dry season. This often gave the impression of the existence of a "destruction front". Even in the late 1970s, this could still be observed in the northern part of Tsavo National Park East.

Fires certainly helped in that period to further thin out the woody vegetation. At the same time, an increase in the cover of the grasses was observed. This process is described qualitatively by, for example, Napier Bax and Sheldrick (1963). Some quantitative observations were published by Agnew (1968), Watson (1968) and Laws (1969b).

Some aspects of the dynamics of the woody vegetation, such as the destruction of trees by elephants and/or fire and bush encroachment through overgrazing, have been studied in various areas in eastern and southern Africa. In modelling the dynamics of the *Acacia tortilis* woodlands in the Serengeti (Tanzania), Pellew (1983a) found that, to maintain a high canopy cover, measures to promote regeneration were more effective in the long term than measures to reduce mature tree mortality. High giraffe densities (1.2 per km^2, compared with 0.3 in Tsavo) or a high frequency of fires were capable of preventing regeneration of *Acacia tortilis*. Elephants at a density of 0.3 per km^2 played an important role in the destruction of the mature trees, but were by themselves not capable of preventing regeneration. Barnes (1983) found that in Ruaha National Park (Tanzania), with a very high density of 2.5 to 4 elephants per km^2, elephants were destroying mature trees and also preventing regeneration.

As stated by Pratt and Gwynne (1977), bush encroachment is the rule rather than the exception in east Africa. That means that without fire, large browsing herbivores or man's intervention, there will be a natural succession towards a high percentage cover by woody species. Over-grazing by cattle even seems to promote this succession. For example, Vegten (1983) calculated a yearly increase in woody biomass of approximately 100 kg/ha caused by over-grazing by cattle in Botswana.

It seems that elephants at "low" densities act as a destroyer of mature trees–an activity which is common in many areas and for which there is no good explanation (Eltringham, 1982). At higher densities, elephants both destroy mature trees and prevent regeneration through browsing of the saplings and young trees. Giraffe–and probably other browsers–are capable of controlling only the regeneration and so can ultimately also create tree- and shrubless habitats. This capacity is not confined to wild herbivores. The domestic goat has the same capabilities.

Fire influences mainly the regeneration capacity of the shrubs and trees; it attacks them, but seldom kills mature trees in savanna vegetations. In contrast, over-grazing can result in opening the grass sward and may lead to an increase of the woody biomass.

Walter (1971) proposed a hypothesis on the tree/grass relationship in savanna vegetations. The relative abundance of grass and trees depends on the competition for soil moisture. The trees have the capability of using sub-soil moisture, and grasses out-compete the trees in the upper soil layers.

Walker and Noy-Meir (1982) developed a model based on this hypothesis. They show that there exists, in principle, an equilibrium between the tree and grass cover, the nature of which depends on the physical soil conditions and rainfall. Thinning the woody stratum by either elephants or fire means that more soil moisture is available for the grasses and they become more abundant. This increase of grass abundance and production as a result of a partial or complete clearing of woody vegetation is well-documented (Barnes, 1979).

The effect of fire on the herbaceous vegetation is well-documented for the more humid savannas, where it is widely used to open up the woody vegetation, remove the old unpalatable grass standing crop and induce new growth of the grasses. It can be harmful when it is followed by heavy grazing (Barnes, 1979, Pratt, 1967).

The effect of burning in more arid savannas is much less documented. There are some indications that fire alone can have a detrimental effect on the grasses (Riney, 1963). Heavy grazing in semi- arid savannas not only reduces the total ground cover, but also causes a change in composition. Annual grasses increase in importance under increasing grazing pressure (Kelly and Walker, 1976).

The influence of all these factors on the woody vegetation of the Tsavo area will be described in Section 4.1 The dynamics of the herbaceous vegetation will be treated in Section 4.2.

4.1 DYNAMICS OF THE WOODY VEGETATION

4.1.1 Effect of elephants and other large herbivores

Incidental observations in the late 1960s indicate that elephants were destroying 2 to 6 percent of the trees per year in certain parts of Tsavo National Park East (Agnew, 1968; Watson, 1968; Laws, 1969b). Long-term monitoring of changes in the woody vegetation in the Tsavo area started only in 1971 with the establishment of the "elephant exclosures" and the adjacent "control points" (Glover, 1974), (Figure 4.1). In these plots of approximately two ha each, regular counts of the woody vegetation were done at approximately two-year intervals. From these counts, data on the shrub cover (woody plants less than 4 m high), tree cover (woody plants more than 4 m high) and total woody cover (tree plus shrub cover) were extracted (Tsavo Research Project, unpublished data).

Complete data are available only for the period 1971 to 1978 from three exclosures and their control plots in the southern section of Tsavo National Park East, and the so-called "HQ block" (Figure 4.2). The climatic, soil and vegetation data for the different plots are given in Table 4.1.

From the data in Table 4.1, we may conclude that the different plots are representative for a large part of the Tsavo ecosystem (approximately 50 percent),

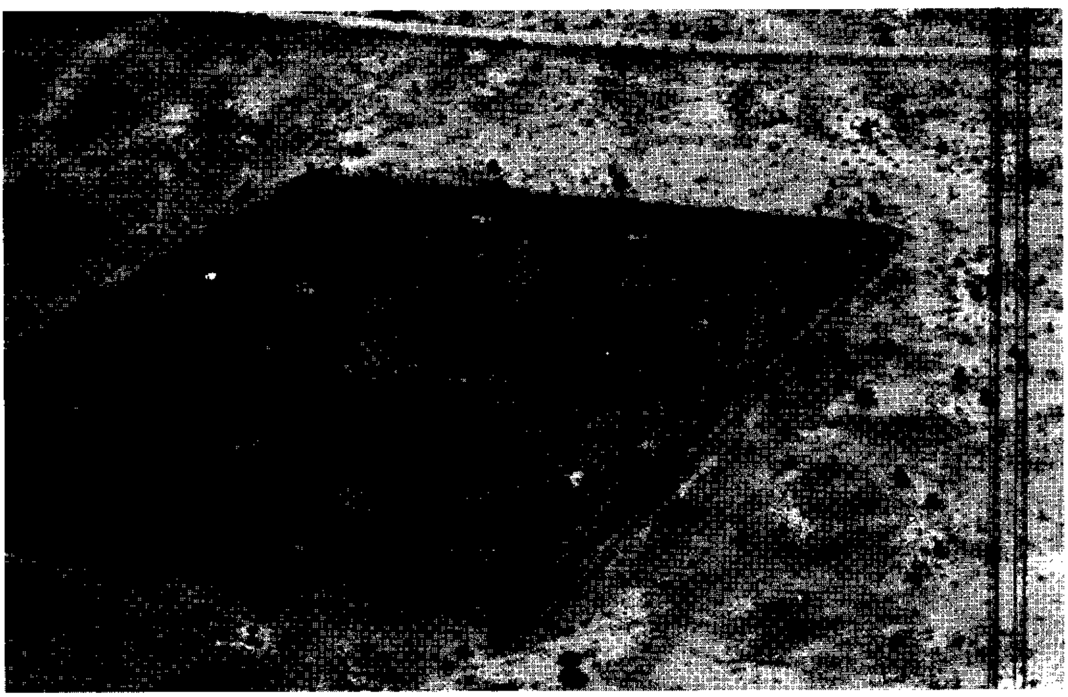


Figure 4.1 Elephant exclosure; an area of approximately 2 ha, surrounded by an elephant-proof ditch about one meter wide and two meters deep. Because the photo was taken at the end of the dry season, the deciduous woody plants do not show up very well

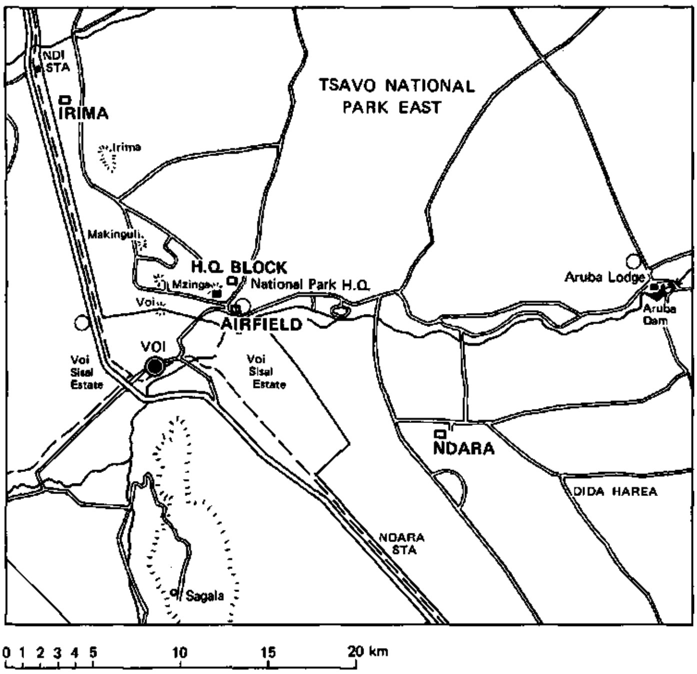


Figure 4.2 Location of the exclosure and control plots in the southern section of Tsavo National Park East

namely the part with well-drained, deep soils in bioclimatic zone VIa and probably also Vb and VIb, and covered with a vegetation of the *Commiphora-Lannea* group of communities (CL1, 2 and 3). The range of possible vegetation structure types is also well covered by the different plots (bushed grassland to dense wooded bushland).

From observations on the kind of damage to trees and shrubs in the control plots (broken branches, bark damaged, uprooted), it seems obvious that elephants are the major cause of the decline in tree and shrub cover (Figures 4.3 and 4.4). The fact that elephants made up approximately 65 percent of the total animal biomass and the other browsers such as giraffes, rhinos, gerenuks and lesser kudus only approximately 10 percent (Table 2.17), makes it likely that elephants had the largest impact on the woody vegetation in the Tsavo area as a whole.

The elephant density in the southern section of Tsavo National Park East between 1971 and 1975 varied from 0.9 to 2.1 per km^2 (Leuthold, 1973 and Cobb, 1976). An average of 1.5 per km^2 is assumed for this period. The elephant density is assumed to be only 1.0 per km^2 in that period for only the airfield control plot very near park headquarters, the entrance gate and airstrip. Mainly because of poaching, the elephant density decreased significantly in 1976 and 1977. Based on the data presented by Ottichilo (1981), an elephant density of 0.5 per km^2 is taken for the years 1976 to 1978. During the period 1971 to 1978,

Table 4.1 Climate, soil and vegetation conditions at the exclosure and control plots

Plot	Climate		Soil		Vegetation		
	B-C zone	Rainfall mm/yr	Description and classification	unit	Community and variant	Structure (1971==>1978) exclosure	control plot
Irima	Vb-VIa	470	well drained, very deep, reddish-brown, clay (Ferral-chromic LUVISOL)	F/S1	CL3c	BG ==> B	WBG ==> BG
Airfield	VIa	430	well drained, very deep, dusky red, sandy clay (rhodic FERRALSOL)	N1	CL2d	WBd ==> WBd	WB ==> B
HQ-Block	VIa	420	well drained, very deep, dark red, sandy clay (Ferral-chromic LUVISOL)	F	CL1d	-------	WBd ==> BG
Ndara	VIa-VIb	400	well drained, very deep, dusky red, sandy clay (rhodic FERRALSOL)	N1	CL1e	BG ==> B	BG ==> BG

- climate: compare Table 2.1
- soil: compare Tables 2.3 and 2.6
- vegetation composition: compare Table 2.8
- vegetation structure: compare Figure 2.13

no fires occurred in either the elephant exclosures or control plots.

The data on the shrub and tree cover in different years in the exclosures and control plots and for the different elephant densities make it possible to draw some conclusions on the effect of elephants on the dynamics of the woody vegetation. The relationship between the change in shrub cover, the initial shrub cover and the elephant density is shown in Figure 4.5. The highly significant relationship is shown by the following multiple linear regression equation:

$$dS/dt = 3.6 - 0.1 \times S - 2.6 \times ED \quad (n = 28, r = 0.86. P = 0.000)$$

Figure 4.3 *Commiphora* trees uprooted by elephants

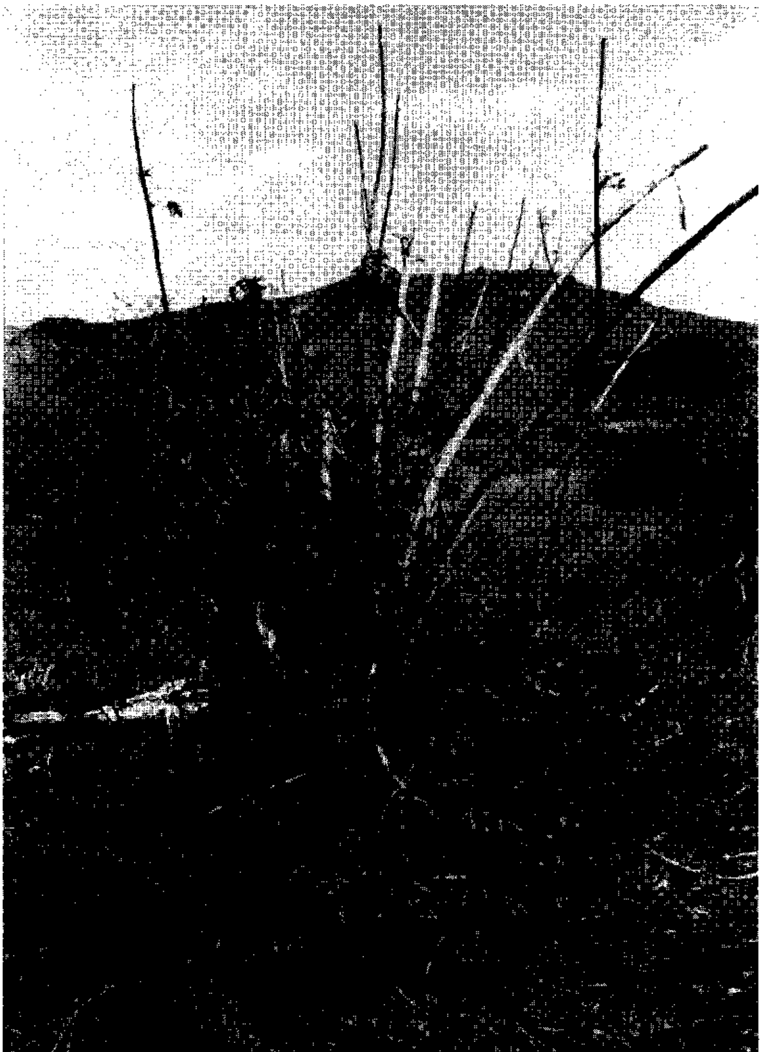


Figure 4.4 Young *Melia volkensii* tree heavily browsed by elephants

in which dS/dt = the change in shrub cover (percent/year), S = the initial shrub cover (percent) and ED = the elephant density (n/km^2).

This means that in the absence of elephants, a low shrub cover percentage increases by approximately 3.6 percent/year. This change diminishes to 0 percent/year when the shrub cover approaches the maximum value of 36 percent.

In the presence of elephants, the change in shrub cover declines in relation to the elephant density. The consequence is that there is a shrub cover equilibrium for each elephant density, at which no change in cover takes place. At initial shrub covers above this equilibrium value, destruction by elephants will be greater

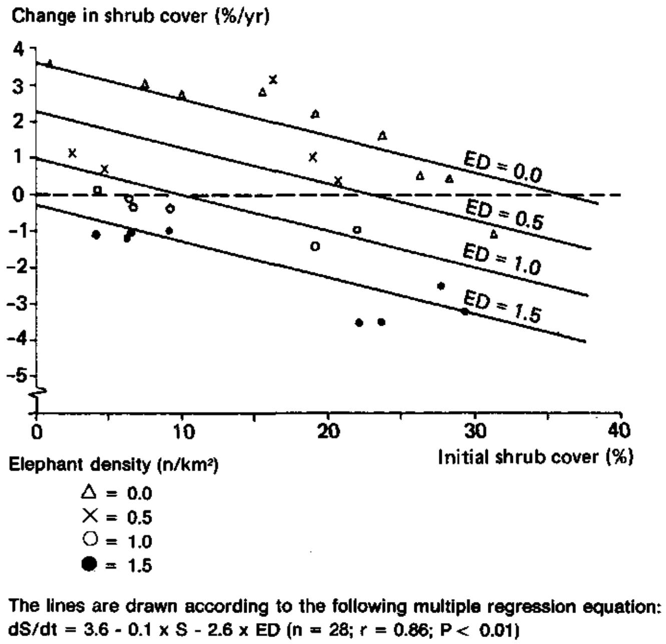


Figure 4.5 Relationship between change in shrub cover, initial shrub cover and elephant density

than the natural growth rate; *eg*, at an initial (maximum) shrub cover of 36 percent and an elephant density of 1.5 per km², the shrub cover will decline by approximately 4 percent per year.

The relationship between the change in total woody cover (tree plus shrub cover), initial woody cover and elephant density is fairly similar to that of the shrub cover and is shown in Figure 4.6. The highly significant multiple linear regression equation for this relationship is:

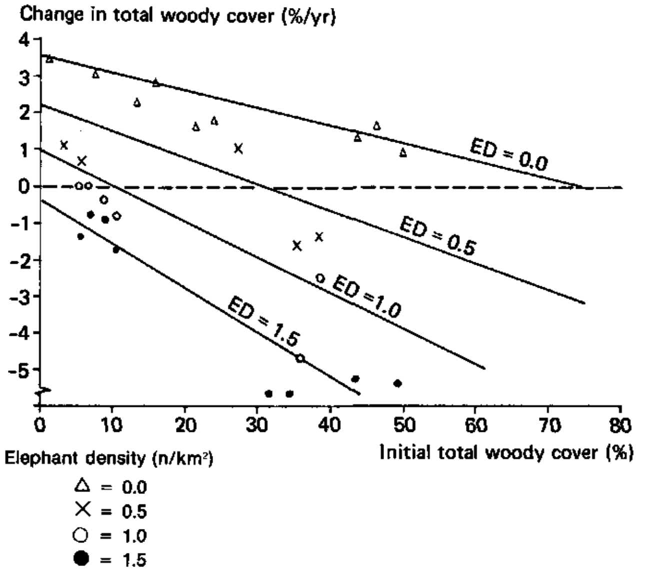
$$dW/dt = 3.6 - 0.048 \times W - 2.6 \times ED - 0.05 \times W \times ED \quad (n=28, r= 0.93, P=0.000)$$

in which dW/dt = change in total woody cover (percent/year), W = initial total woody cover (percent) and ED = elephant density /km²).

The additional term -0.05 x W x ED indicates that the rate of decline of the total woody cover becomes higher with increasing elephant densities and initial total woody cover. For example, the lines indicating the change in total woody cover in relation to the initial total woody cover at a certain elephant density diverge (Figure 4.6), while for shrub cover they are parallel (Figure 4.5).

The change in tree cover can be found by subtracting the change in shrub cover from the change in total woody cover. This yields the following highly significant multiple linear regression equation:

$$dT/dt = 0.1 \times S - 0.048 \times W - 0.05 \times W \times ED \quad (n=28, r=0.65. P=0.000)$$



The lines are drawn according to the following multiple regression equation: dW/dt = 3.6 - 0.048 x W - 2.6 x ED - 0.05 x ED x W (n = 28; r = 0.93; P < 0.01)

Figure 4.6 Relationship between change in total woody cover, initial total woody cover and elephant density

or because W = T + S

$$dT/dt = 0.052 \times S - 0.048 \times T - 0.05 \times ED \times (T+S)$$

in which dT/dt = change in tree cover (percent/year), S = initial shrub cover (percent), T = initial tree cover (percent), W = initial total woody cover (percent) and ED = elephant density (n/km^2).

The change in tree cover is thus positively related to the shrub cover. This is fairly obvious, since woody plants which can grow into trees must first go through the shrub stage (up to 4 m high) before they reach the tree stratum (more than 4 m high). The equation also shows that the tree cover increases only when the initial tree cover is less than the initial shrub cover. The tree cover declines sharply when the total woody cover and/or the elephant densities reach high values.

Although the tree cover is very strongly affected by elephants, species which can grow into trees are not endangered at high elephant densities. Large numbers of potential trees of various species were found inside and outside the exclosures in the "regeneration class" (< 1 m), (Table 4.2 and Figure 4.7).

This observation was also made by Leuthold (1977c). His count of belt-transects along the park road system indicated that although mature trees declined between 1970 and 1974, specimens in the regeneration class increased considerably in number.

Table 4.2 Number per ha and distribution over height classes of potential tree species in the exclosures and control plots

Plot	Height classes in meters					Total
	< 0.5	0.5-1	1-2	2-4	>4	
Irima exclosure	45	179	444	112	2	782
Irima control	47	78	20	-	1	146
Airfield exclosure	3	8	22	33	30	96
Airfield control	3	5	5	5	10	28
HQ-Block control	81	33	25	17	9	165
Ndara exclosure	129	269	420	5	1	824
Ndara control	225	84	7	1	-	317

- all species included which can grow into trees (> 4 m)
- data from 1978 after seven years duration of the experiment, only HQ- Block 1976 data

Figure 4.7 Regeneration of *Commiphora* in an elephant exclosure (age ± 6 years)

Under the climatic and soil conditions of the Tsavo area, woody species seem to be able to out-compete the grasses and forbs in the absence of large browsing herbivores. Without the competition with grasses and forbs, regeneration of the woody species is probably even faster than the rates indicated above. This is confirmed only by some qualitative observations on badly overgrazed areas on some of the ranches.

With a stable elephant population, an equilibrium will develop between the cover of the vegetation strata and the elephant density. These equilibrium values are presented in Figure 4.8. The result compares fairly well with the actual situation in the Tsavo area in 1976/1977. The average elephant density in the whole park was approximately 1.2 per km² (Table 2.1). Those parts of the park with higher than average elephant densities already had a very open vegetation structure in 1976/1977 (bushed grasslands on the vegetation maps; Wijngaarden and Engelen, 1985). Those areas of the park still having a dense vegetation structure are in general those with a lower than average elephant density (Cobb, 1976), because of either the absence of drinking water (northeastern part of Tsavo National Park East) or the poaching pressure (near park boundaries in the northwest and southeast). Outside the park, the elephant density was much lower, at approximately 0.5 per km² (Table 2.16) and the vegetation structure much denser. Wooded bushlands and dense wooded bushlands are commom here (vegetation map; Wijngaarden and Engelen, 1985), (Figure 4.9).

The exclosure experiments also give some data on the effect of elephant browsing on individual species. *Boswellia hildebrandtii*, a species listed in Table 2.12 as being confined to the denser vegetation, disappeared from the Irima

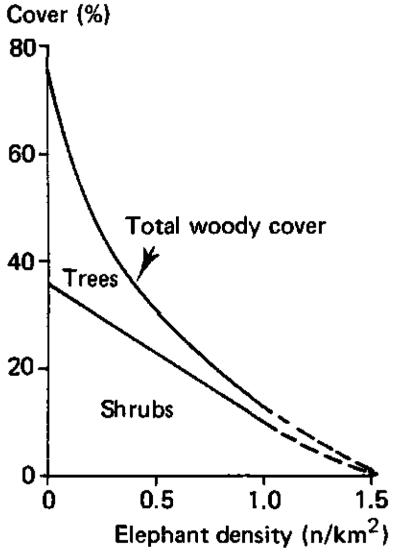


Figure 4.8 Equilibrium cover of the tree and shrub stratum in relation to the elephant density

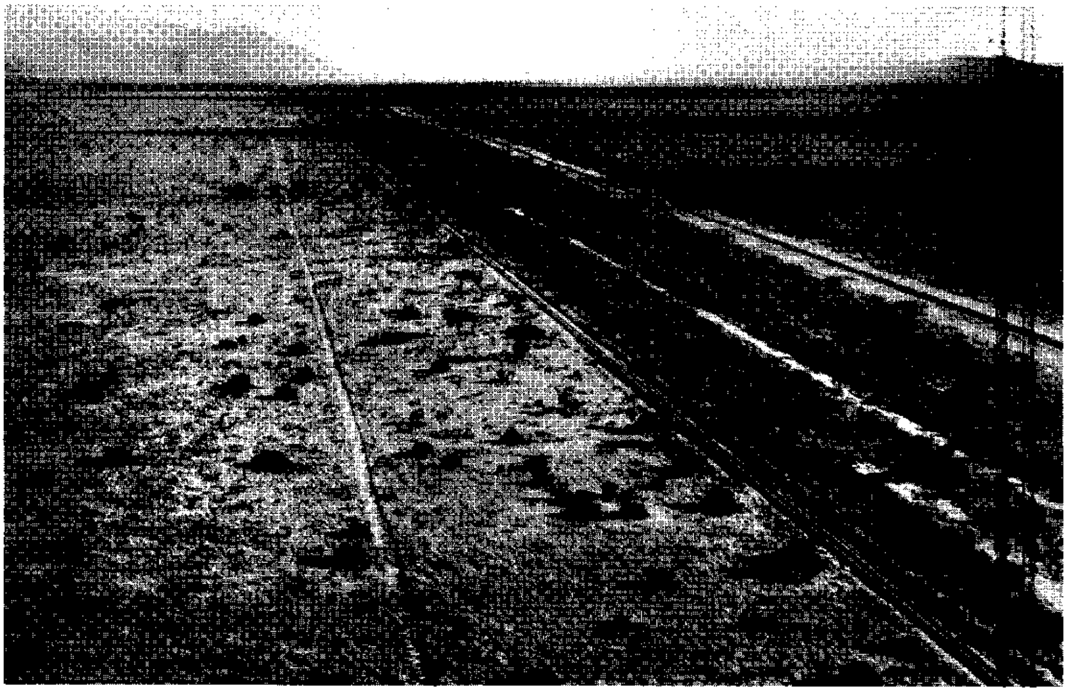


Figure 4.9 Park boundary showing the contrast in vegetation structure inside and outside the park. In the park, predominantly bushed grassland due to the impact of elephants and occasional fires; outside dense wooded bushlands because of the absence of elephants and fire

control plot (Table 4.3). This species is not of essential importance for the large herbivores, however, and the equilibrium vegetation structure will not be affected by its absence because enough other species can take its place in the tree stratum. The species listed as predominating in the more dense vegetation (Table 2.12), such as *Commiphora* spp, are indeed disappearing slowly from the control plots but regenerate prolifically as soon as elephants are excluded. This even applies to the Ndara exclosure which has had a very open vegetation for more than 25 years (Sheldrick, personal communication), (Table 4.2). This group of species constitutes the majority of the dominant woody species in the original "*Commiphora* bushlands". The regeneration of those species does not necessarily take place through seedlings. They also often form new shoots from the bases of the stems of pushed over trees, or even from the larger roots.

4.1.2 Effects of fire

Fires are not a common phenomenon in the Tsavo ecosystem. In most years, production of the ground layer is so sparse that not enough combustible material is available to cause a widespread and hot fire. Also, the parks are for a large part surrounded by well-maintained fire breaks. In the past, however, fires have

Table 4.3 Number per ha of all woody species in the exclosures and control plots in 1971 and 1978

Plot	Irima				Airfield				HQ-Block		Ndara			
	Exclosure		Control		Exclosure		Control		Control		Exclosure		Control	
Species / Year	1971	1978	1971	1978	1971	1978	1971	1978	1971	1976	1971	1978	1971	1978
Commiphora spp.	282	662	117	113	42	33	32	7	51	20	208	451	592	175
Lannea spp.	2	72	3	10	3	12	1	-	-	5	358	304	20	88
Acacia spp.	15	20	8	11	10	11	3	2	34	20	13	10	11	11
Boscia coriacea	11	12	20	5	22	16	24	11	128	111	83	25	24	14
Sterculea spp.	2	12	6	6	19	20	14	2	9	3	15	21	19	19
Platycelyphium voense	-	-	-	-	1	1	-	2	2	2	16	11	12	10
Cassia abbreviata	6	3	7	1	-	-	1	1	1	-	2	2	2	-
Melia volkensii	-	-	-	-	3	2	6	2	3	2	-	-	-	-
Boswellia hildebrandtii	1	1	2	-	1	1	1	-	-	-	-	-	-	-
other tree species	-	-	-	-	-	-	-	1	4	2	-	-	-	-
Total (potential) trees	319	782	163	146	101	96	82	28	232	165	695	824	680	317
Grewia spp.	323	230	405	292	206	92	88	13	337	204	42	32	53	24
Sericocomopsis pallida	37	41	52	51	1	1	-	-	55	40	1040	669	627	365
Cordia spp.	33	27	33	39	4	2	4	2	34	33	4	3	17	35
Euphorbia spp.	11	80	14	29	60	3	48	33	19	6	49	122	43	39
Combretum spp.	3	8	1	2	177	63	291	1	95	33	2	-	-	-
Dirichletia glaucescens	-	-	1	1	56	48	72	38	148	94	18	13	3	2
Premna spp.	1	1	1	2	236	162	247	186	137	176	1	-	3	1
Xeromphis keniensis	3	-	-	-	30	15	7	2	57	52	172	75	38	19
Bauhinea taitensis	14	10	-	-	180	124	129	62	469	148	1	-	-	-
Ochna enermis	-	-	-	-	60	16	45	13	7	4	-	1	-	-
Maerua spp.	5	18	1	1	10	4	10	2	13	10	30	6	22	3
Ehretia taitensis	2	4	1	12	1	1	-	1	7	7	-	-	-	-
Erythrococca atrovirens	-	-	1	-	11	3	10	1	1	-	-	-	-	-
Sesamothamnus rivae	-	1	-	1	1	1	8	2	11	10	1	-	-	-
Thylacium thomacii	-	1	-	1	3	2	-	-	3	3	-	-	-	1
Hymenodiction parvifolium	-	-	-	-	2	2	19	1	6	1	5	2	3	3
Calypthrotica taitensis	-	-	-	-	1	1	8	3	1	1	10	3	1	1
Erythroclamis spectabilis	-	-	-	-	-	-	2	2	14	12	2	-	-	-
other shrub species	-	-	4	-	7	5	5	3	6	4	6	4	6	-
Total shrubs	432	421	514	431	1046	545	1001	365	1420	838	1391	930	816	493
Total woody plants	751	1203	677	577	1147	641	1083	393	1652	1003	2085	1754	1496	810

played a role in the park (Napier Bax and Sheldrick, 1963) and fires still occur occasionally outside the park on some of the ranches.

No quantitative data are available on the effect of fire alone on the woody vegetation. Casual observations give the impression that fire seldom occurs when the woody vegetation is dense (more than 40 percent cover). This is probably related to the fact that in such cases the ground cover and grass production is so low that not enough combustible material is available. This is confirmed by the observation of Napier Bax and Sheldrick (1963) that fire was particularly effective in those areas where elephants had already destroyed the woody vegetation and where the grass cover had increased.

Occasional fires on the ranches south of the Taita hills do a lot of damage to the shrubs up to approximately 3 m high, but seldom damage or kill mature trees (Mayers, personal communication). As a result, shrub cover is fairly low there, but most of the time a well developed tree cover is found. On the other hand, fires never occur in overgrazed areas on the ranches, and shrubs are plentiful as a result.

4.2 DYNAMICS OF THE HERBACEOUS VEGETATION

4.2.1 Perennial grasses versus annual grasses and forbs

The data from the 400 releves (Section 2.4.1.2) show that the areal cover in any of the plant communities varied from 5 to 70 percent for the perennial and annual grasses and from 0 to 35 percent for the forbs. The contribution of both perennial and annual grasses to the total herbaceous cover varied from 10 to 90 percent. The contribution of the forbs varied from 0 to 60 percent. In addition, large differences were observed in the abundance of the annual species. Some indications were found of the causes of this variation.

As shown in Section 2.3.1.3 and Figure 2.21, perennial grass cover is limited to a maximum value, depending on the total woody cover and the bio-climatic zone. Several observations show that this maximum cover is not always reached. The reasons for this will be given in Sections 4.2.2 and 4.2.3.

The relationships between the perennial grass cover and the annual grass cover, the forb cover and the total annual herb cover are negative and significant (Table 4.4), but there is no significant relationship between the annual grass cover and the forb cover. The annuals as a group thus seem to complement the perennials. Annuals probably have a chance only when water resources are not fully utilized by perennials.

Which annual species benefit from this situation is not clear from the available data. Work on the germination biology of annual grasses and forbs in the Sahel has indicated that there are consistent differences in the speed and homogeneity of germination between different species. Moreover, many annual species respond to day length and show a different length period of vegetative growth, independent of the availability of water and nutrients. Knowledge of these properties of the species and the distribution of the rains at the beginning of

Table 4.4 Relationship between perennial grass cover and total annual herb cover, annual grass cover and forb cover

Independent variable	Dependent variable	Equation	n	r	P
Perennial grass cover	Total annual cover	TAC=24.4-0.30*PGC	37	0.37	<0.05
Perennial grass cover	Annual grass cover	AGC=12.7-0.20*PGC	37	0.29	<0.1
Perennial grass cover	Forb cover	FC=11.8-0.10*PGC	37	0.20	NS
Annual grass cover	Forb cover	FC=10.0-0.06*AGC	37	0.08	NS

Based on one community variant only (CL3e)

the growing season would permit explanations for the large differences in species composition at different sites, or at the same site in different years (Penning de Vries and Djiteye, 1982). East African annual herbs probably have similar properties, but no data are available to date.

4.2.2 Influence of fire on the herbaceous cover

Some quantitative data are available from experimental burning in Tsavo National Park West in the period 1972 to 1978. Annual observations are available for two burning frequencies, three different seasons and a control plot (Tsavo Research Project, unpublished data). Some conclusions on the effect of fire on the herbaceous cover can be drawn from Table 4.5.

Table 4.5 Influence of different frequencies and seasons of fire on the herbaceous vegetation cover

Burning program	Control	Every two years			Every year		
Frequency	Control	Every two years			Every year		
Season	--	E.R.	E.D.	L.D.	E.R.	E.D.	L.D.
Cover in %							
Perennial grasses	80	76	81	45	55	57	56
Annual grasses	5	12	11	23	21	12	18
Leguminous forbs	+	+	+	0	3	1	0
Other forbs	0	7	4	16	7	12	7
Some important species							
Latipes senegalensis	26	16	16	11	17	6	9
Chloris roxburghiana	20	14	26	20	14	22	14
Digitaria macroblephora	18	23	18	7	12	11	12
Cynodon dactylon	9	21	15	5	8	14	12
Aristida adcencionis	5	11	11	21	15	12	17

Data collected in 1978, seven years after the Murka fire plots in Tsavo National Park West were started.

E R = early in the long rains
E D = early in the long dry season
L D = late in the long dry season
+ = cover less than 1%, but present

Yearly burning, independent of the season, results in a reduction of the perennial grass cover and an increase of the percentage cover of annual grasses and forbs and the percentage bare soil. The season of burning seems to be important only when burning takes place once every two years. Burning late in the dry season seems to have an effect similar to yearly burning, except possibly for the leguminous forbs. Burning early in the rainy season or early in the dry season does not have a large effect on the cover of the different components of the ground layer, except possibly for the non- leguminous forbs.

4.2.3 Herbivory and the cover by perennial grasses

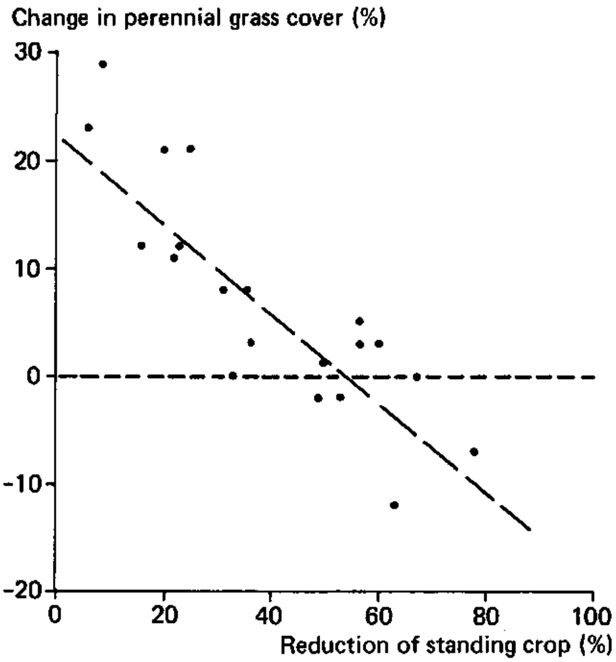
The data collected on herbaceous vegetation standing crop (Section 2.3.1.3) revealed that at sites strongly dominated by annuals, grass and forb standing crop (SC) at the end of the long dry season was still between 85 and 95 percent of the standing crop at the beginning of the dry season. On sites dominated by perennial grasses, this varied from 20 to 90 percent.

Observations on feeding behaviour of grazing herbivores in Tsavo indicate that perennial grasses are strongly preferred to annual grasses and forbs (see, for example, Leuthold, 1972). As indicated by Anderson and Coe (1974) and Buxton (1979), activity of invertebrates is strongly reduced in the dry season, so the change in standing crop during the dry season can be largely attributed to consumption by large herbivores.

The difference in standing crop between the beginning and the end of the dry season is plotted in Figure 4.10 against the change in cover by perennial grasses, measured before and after the particular dry season. A zero change in cover is observed at 54 percent decrease in standing crop. Allowing for some 10 percent loss of standing crop by invertebrates and other losses (wind erosion, natural decay, etc), this means that large herbivores can apparently consume approximately 45 percent of the standing crop in the dry season without doing any damage to the perennial grasses.

Maximum cover by perennial grasses can therefore be maintained only when the large herbivore consumption in the dry season is less than approximately 45 percent of the standing crop at the beginning of the dry season. This result compares well to the guesses of a "proper use factor" of 50 percent often given in textbooks on range ecology (for example, Heady and Heady, 1982). Figure 4.10 shows that the cover by perennial grasses is reduced by approximately 15 percent per year at 90 percent consumption. Because the cover by perennial grasses seldom exceeds 50 percent, this means that perennial grasses can disappear after only three years of very intensive grazing in the dry season (Figure 4.11).

Consumption by large herbivores in the rainy season is thought to be of very small influence in the Tsavo region. Cobb (1976) indicates that herbivores tend to disperse over the entire ecosystem in the rainy season, so there is at least no systematic concentration of large herbivores in any region of the Tsavo ecosystem in the rainy season.



The perennial grass cover was measured during the rainy season before and after the dry season for which the standing crop data were available; the regression line is based on:
Change PGC = 22.1 - 0.413 x Red St Cr (n = 20; r = 0.83; $P < 0.01$)

Figure 4.10 Relationship between the reduction of the standing crop during the dry season and the change in cover by perennial grasses

Because the long dry season is at least five times as long as either of the growing seasons, large herbivore consumption will also differ by roughly a factor of five. Because no production takes place in the dry season, consumption in the wet season can thus be a maximum one- sixth, or approximately 15 percent, of the production. This assumes complete consumption of the herbaceous production by large herbivores. This is very unlikely to occur, so the consumption in the rainy season is probably far less than 10 percent of the production in that period. This is thought to have only a very minor influence on the production itself.

4.2.4 Effect of variation of rainfall on perennial grass cover

The effect of rainfall alone on the cover by perennial grasses can be judged only when the effects of herbivore consumption and fire are excluded; in dry years, production will be low and the fraction consumed by herbivores will consequently be high. This high consumption has–by itself–an important effect on the cover by perennial grasses, especially when it reaches the 45 percent of the standing crop limit (Section 4.2.3). The often observed effect of a reduction in cover by perennial grasses in dry years can therefore very well be an indirect effect.

Figure 4.11 Over-grazing in *Commiphora* woodland; a much higher percentage cover of perennial grasses is possible under this open woody cover

Data from the control plots on experimental burning in Tsavo National Park West (Tsavo Research Project, unpublished data) allow study of the effect of variation in rainfall only. These plots are situated rather far from dry season watering places and show relatively low animal densities in the dry season. The effect of herbivory in the dry season on the cover by perennial grasses is therefore probably very small here. No fires occurred in the observation period.

Table 4.6 lists the cover by perennial grasses and rainfall during various periods before the cover measurement. The highest correlation coefficients are found for the relationship between the cover by perennial grasses and the average rainfall over the previous two or three years. Rainfall during the previous rainy season shows a very low correlation with the perennial grass cover.

When not effected by herbivory, perennial grass cover thus seems relatively stable, and is not affected by short-term (less than two-year) variations in rainfall.

4.3 CONCLUSION

The dynamics of the vegetation of the Tsavo area is confined mainly to that of structure (cover by the different strata). There is fluctuation in species abundance, but not so much in presence. Only a small group of species, confined to the vegetation with a dense woody cover, does not regenerate easily. They do

Table 4.6 Relationship between perennial grass cover and rainfall

Year	1972	1973	1974	1975	1976	1977	1978	Regression coefficient r
Perennial grass cover	72	80	86	NR	46	67	80	
Rainfall in mm								
previous long rains	159	80	207	152	145	32	255	0.29
previous year	349	401	264	264	242	351	704	0.41
average prev 2 years	301	375	332	264	253	297	527	0.59
average prev 3 years	297	334	337	310	257	286	432	0.70
average prev 4 years	314	318	316	320	293	280	390	0.50

NR = not recorded

not form an essential part of the woody stratum, however.

Quantitative data on the dynamics of the vegetation are available for only one particular part of the ecosystem, namely the vegetation on well-drained deep soils in bio- climatic zones Vb, VIa, VIb *(Commiphora-Lannea* group of communities, variants c, d and e). This covers a large part of the ecosystem (approximately 50 percent), however, and there are no good reasons why relationships should, in principle, be very different in other plant communities. Some of the values or rates will probably differ only slightly.

The dominant impact on the vegetation is the destruction of the woody vegetation by elephants. Mature trees are nearly eliminated when elephant densities are higher than approximately 1 per km^2, but shrubs and the recruitment/replacement of trees are somewhat less effected. The ultimate cover by both trees and shrubs will be only approximately 1 percent at a continuous elephant density of 1.5 per km^2, however.

Regeneration of the woody vegetation upon reduction of the elephant density is remarkable. Nearly all important woody species apparently have the capability to overcome easily a drastic reduction in their biomass. Trees such as *Commiphora* spp regenerate prolifically from the base of the stem when they are pushed over, or even from the larger roots. They maintain this capacity for a period of at least 25 years after continually being destroyed down to ground level. The presence of those species in the vegetation is thus not threatened by intensive elephant browsing.

As a result of the destruction of the woody vegetation by elephants, the cover by the herbaceous vegetation increases. The maximum cover by perennial grasses is limited by the total woody cover. This maximum cover, however, is not always reached. The main reasons for this are the effects of herbivory and fire. Wet season consumption by large herbivores probably has very little influence when grazing is not concentrated in one particular area. As soon as consumption in the dry season exceeds 45 percent, there will be a decrease in cover by perennial grasses.

Annual fires also have a detrimental effect on the cover by perennial grasses. When perennial grass cover is not at the maximum, the open spaces are taken over by annual grasses and forbs. Which annual grasses and forbs take up the space probably depends on their germination biology, for which no data are available. Short-term variation of rainfall does not have an effect on the cover by perennial grasses. The often observed decrease of perennial grasses in dry years has to be attributed to herbivory (over-grazing).

Chapter 5

DYNAMICS OF THE LARGE HERBIVORE POPULATION

For a detailed description of the dynamics of animal populations, data on the rates of birth, death, immigration and emigration are needed. Together, these demographic variables determine the increase, decrease or stability of an animal population.

Even for relatively well-studied animal populations, such data are scarce. Attempts to simulate the dynamics of large herbivore populations in east Africa can be found, for example, in Sinclair (1979) for buffalos, in Hilborn and Sinclair (1979) for wildebeest, and for elephants in Laws *et al* (1975). It is interesting to note that in all these studies food availability was seen as the single most influential factor determining the equilibrium size of the populations (grazing capacity). For example, for wildebeest in the Serengeti, it was shown that forage availability in the dry season strongly influenced calf survival and below certain values also adult mortality (Hilborn and Sinclair, 1979). Only with buffalo and wildebeest does a serious disease such as rinderpest–in combination with predators, or in the case of elephants human predation–seem to be able to maintain the population at a level far below the "grazing capacity".

The speed at which populations change, however, can be strongly influenced by other factors, such as immigration, predation, or behaviour of the animals. Especially the last was proved for the migrating behaviour of the wildebeest in the Serengeti, which prevented the non- migrating predators having a substantial influence on the wildebeest population dynamics (Hilborn and Sinclair, 1979).

Immigration is generally seen as a very important factor in the growth of the elephant population in protected areas. The maximum natural rate of increase of an elephant population is between 4.5 and 7 percent per year (Hanks and McIntosh, 1973, Hall-Martin, 1980). In Ruaha National Park (Tanzania), for example, Barnes (1983) found that immigration contributed to the growth of the elephant population at least as much as the natural increase. This often observed immigration into national parks or other conservation areas is caused by the increased settlement of the surrounding areas. It is commonly called the "compression theory" (Eltringham, 1982), which also contains an explanation of why elephants are not capable of adjusting their numbers to "overcrowding" caused by immigration. The long life of the elephants prevents quick regulation of their numbers, even though they show lower birth rates under such conditions through longer calving intervals and delayed sexual maturity (Laws, 1969b).

Data on the herbivore population dynamics in Tsavo are available to some extent. Most refer to changes in population size, but some data on population structure and other demographic variables are also available for some species. They will be summarized in Section 5.1. The direct and indirect impact of man on the large herbivore population in Tsavo will be discussed in Section 5.2. The hypothesis that the ultimate size of the large herbivore population in the Tsavo ecosystem is regulated by forage availability will be tested in Section 5.3.

5.1 POPULATION PARAMETERS

Data collection on large herbivore populations in a large ecosystem such as Tsavo (40000 km^2) is difficult. Although total numbers of herbivores are impressive, densities are still relatively low. Only repeated sample counts have proved to give population estimates with a statistical significance, even though coefficients of variation remain rather high (8 to 40 percent, Cobb, 1976).

Most data on population dynamics in Tsavo were collected for elephants. They include estimates on population size, population age structure, age-specific mortality and reproduction, over the period 1962 to 1980. For other animals, far fewer data are available, *ie*, from only one year, or one locality or only casual observations. The available data will be discussed per animal or group of animals.

Elephant

Estimates of the size of the elephant population in the Tsavo ecosystem are available from 1962 onwards, and are summarized in Figure 5.1. Early total counts revealed that in the period 1962 to 1967, the elephant population within

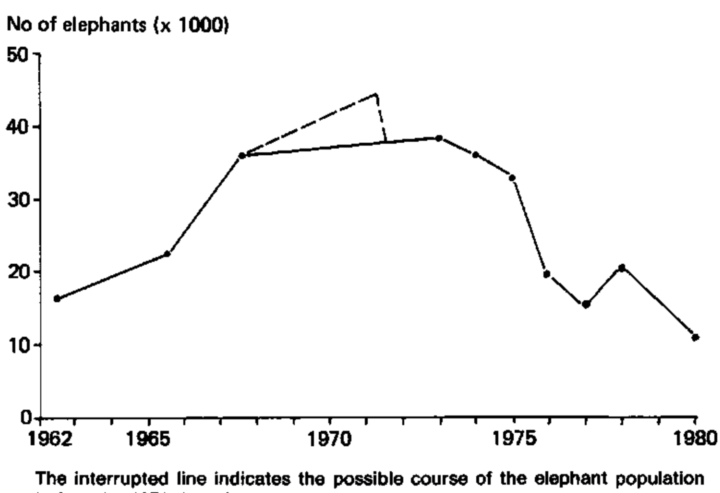


Figure 5.1 Elephant population estimates for the Tsavo ecosystem in the period 1962 to 1980 (from Ottichilo, 1981)

the park varied from 7000 to 17000 and outside the park from at least 3000 to 5000. Laws (1969b) indicates that these were probably gross under- estimates and he concludes on the basis of sample counts that the total elephant population was 35000 ($\pm$ 7000) in 1967/1968. On the basis of collected lower jaws and a cropping programme, Laws (1969b) estimated mortality in that period at approximately 5 percent per year and also contended that natural population regulation by increased calving interval and postponed sexual maturity was just starting to operate.

During the drought years 1970/1971, some 6000 elephants died in Tsavo National Park East. This extreme mortality was confined to the drier parts of the ecosystem and affected particularly juvenile and adult female elephants (Corfield, 1973). The main reason was probably starvation, as no evidence was found for increased poaching activities and disease.

On the basis of the population age structure in 1974, Leuthold (1976) concluded that the Tsavo elephant population was probably in decline. Younger age classes were severely under-represented. Cobb (1976) presents data which indicate that the elephant population was still at a level of 36000 in the period 1973-1975. On the basis of carcass counts, he estimated a mortality rate of approximately 10 percent per year, largely attributed to poaching, and a population decline of approximately 4 percent per year.

From the data available, it seems that the population was more or less stable between 1967 and 1975. The mortality of some 6000 elephants in 1970/1971 was apparently more than compensated by the natural growth of the population and certainly also by immigration from areas surrounding the Tsavo ecosystem which were being settled in that period.

Between 1976 and 1980, increased poaching brought about a spectacular decline in the elephant population–from 36000 in 1976, to 20000 in 1978 to approximately 11000 in 1980 (Ottichilo, 1981), (Figure 5.2). The population structure in 1980 was such that, even in the absence of poaching, a short-term increase of the population was not to be expected because the population consisted mainly of juveniles and sub-adults (Ottichilo, 1981).

Some important points can be derived from the available data. The data from Laws (1969b) on reduced natality and the high mortality reported by Corfield (1973) both indicate that the elephant population was under "stress" in the early 1970s, most likely because of the limited availability of food, certainly in dry years. This effect was probably most pronounced in the central, most arid part of the Tsavo ecosystem. The total population remained stable in that period, probably because of immigration–an effect which must have gradually diminished in that period as most areas surrounding the ecosystem, apart from the ranches, became densely populated.

As early as 1976, Cobb (1976) reported significant poaching. This later became the major factor in controlling the elephant numbers, even to such an extent that the population decreased by approximately 70 percent in only four years (Figure 5.2).

Figure 5.2 Elephant killed by poachers. Elephants are killed with poisoned arrows or guns, after which the face is cut to remove the tusks. The rest of the body is left to be eaten by predators or scavengers, as in this case, vultures

Rhinoceros

The first semi-quantitative data on rhinoceros are from 1961. In that dry year, some 300 rhinos died–apparently of starvation (Forster, 1961). It was argued that this was caused mainly by the disappearance of the major food source of the rhino–browse from shrubs–through elephant damage. The first estimate of the population is given by Goddard (1969). On the basis of sample counts, he estimated the total population in 1967/1968 between 6100 and 9200. On the basis of found skulls and population structure, Goddard (1970a) suggested that the population was stable with mortality and recruitment rates of approximately 11 percent per year.

In contrast to the elephants, no large scale mortality was reported for rhinos in the 1970/1971 drought. Cobb (1976) estimated the total population in 1973-1975 at 5800, but concluded that his estimate was not significantly different from Goddard's estimate in 1967/1968.

The next data on rhino are from an unpublished total count in 1978 and unpublished estimates from KREMU in 1978 and 1980. They show a tremendous decrease of the total number of rhinoceros to only a few hundred in 1978, an effect which has to be attributed entirely to poaching. The data presented seem to indicate, as with the elephant, that the rhino population was more or less stable from 1967 to 1975.

From these data alone, no conclusion can be reached whether the rhino population was strongly influenced by elephants. Although Goddard (1970b) reported more than 100 food plants in their diet, it still comprises a rather select group of species which are not always common. The abundance of those plant species is not always related to the elephant distribution: the area near the Athi and Tsavo river junction had a fairly high elephant density and still had a good cover of low shrubs, several of which are preferred by rhino. One thing is very clear: poaching can have a disastrous effect on the rhino population. A reduction of more than 90 percent of the population took place in only four years.

Other large herbivores

The only population estimates for the other large herbivores in the whole ecosystem are from 1973-1975 (Cobb, 1976), and unpublished KREMU data from 1978 and 1980. The estimates from the period 1973 to 1975 are given in Table 2.13. Because of the fairly large confidence limits, no conclusions can be drawn on the changes between 1973 and 1980.

For part of Tsavo National Park East, south of the Galana river, data from 1969/1970 are available (Leuthold and Leuthold, 1973). Comparison with the estimates from Cobb (1976) revealed significant changes only for the population of Grants gazelle and gerenuk. This, however, may be entirely attributed to the difference in counting methods (ground versus aerial count). Observations on population structure and individual animals of giraffe led Leuthold and Leuthold (1978) to the conclusion that the giraffe population was probably declining in Tsavo East in the period 1969 to 1975. This is attributed by them to the lack of food because of the destruction of the woody vegetation by elephants, but their study also coincided with a number of years with below-normal rainfall. Also, in this group of herbivores large-scale starvation was not observed in the 1970/1971 drought.

Quantitative data on other large herbivores are lacking. Although it is sometimes speculated that the number of grazing ungulates has increased in the Tsavo area because of the increased availability of grass, no data are available to prove this speculation. For one particular area in Tsavo West, Cobb (1976) contended that the number of grazing herbivores was reduced; they were replaced by elephants. Data from Leuthold and Leuthold (1975b) and Cobb (1976) indicate that recruitment of most ungulates was at a healthy level, but no conclusions can be drawn on the effect on their populations because no data are available on the mortality rates.

5.2 IMPACT OF MAN

There is certainly sufficient evidence that man, through poaching, can have a tremendous influence on large herbivore populations, especially those of elephant and rhino. This effect became very clear in the late 1970s. Before that period, poaching was more or less under control and did not seem to strongly influence large herbivore populations.

Apart from poaching, man can also have an indirect effect on the wildlife populations through his domestic stock. In the Tsavo ecosystem, as defined in Section 2.1, the total area outside the national park is used for either ranching or grazing by (semi-)nomadic pastoralists (see also Figure 2.33). The composition of the large herbivore population in- and outside the park shows differences which can be attributed to this difference in human activity.

In Table 5.1, biomass per species is listed in- and outside the national park; Table 5.2 indicates the difference in biomass per feeding habit and water dependency. Ecologic conditions outside the park are somewhat more favourable (less arid). It is therefore surprising that the total animal biomass here is somewhat less. Large differences occur per individual species, however. Apart

Table 5.1 Biomass of large herbivores in the Tsavo ecosystem, per species inside and outside Tsavo National Park (calculated from Cobb, 1976)

Species	Biomass Inside kg/km²	Biomass Outside kg/km²	Difference Out-In kg/km²	Difference Out-In %	Water dependency	Feeding habit
Elephant	2018	864	-1154	-57	dep	mixed
Buffalo	302	100	-202	-66	dep	grazer
Rhino	186	20	-166	-89	dep	browser
Zebra	156	88	-68	-43	dep	grazer
Kongoni	64	50	-14	-21	ind-dep	grazer
Hippopotamus	12	2	-10	-80	dep	grazer
Waterbuck	15	11	-4	-26	dep	grazer
Ostrich	9	6	-3	-33	indep	grazer
Warthog	4	5	1	25	ind-dep	mixed
Grants gazelle	35	40	5	14	indep	mixed
Impala	21	27	6	28	indep	mixed
Gerenuk	11	21	10	90	indep	browser
L.kudu	26	37	11	42	indep	browser
Eland	52	67	15	28	indep	mixed
Giraffe	110	128	18	16	ind-dep	browser
Oryx	63	99	36	57	indep	grazer
Shoat	0	35	35	nc	dep	mixed
Cattle	0	1121	1121	nc	dep	grazer
Sum all	3084	2721	-363	-11		
Sum wildlife	3084	1565	-1519	-49		

Table 5.2 Difference in biomass of large herbivores inside and outside the national park per feeding habit and water dependency (calculated from Cobb, 1976)

Difference in Biomass (Out-In)		Wildlife sp	Domestic sp
Water-dependent	grazing	-291	1121
	mixed feeding	-1154	35
	browsing	-157	-
Total water-dependent		-1602	1156
Water-independent	grazing	26	-
	mixed feeding	27	-
	browsing	30	-
Total water-independent		83	-
Total grazing		-265	1126
Total mixed feeding		-1127	35
Total browsing		-127	0

from the obvious difference in domestic biomass, the wild herbivores react in different ways, as follows:

- in general, all water-dependent wildlife species show a lower biomass outside the park. Most of the water-independent species, however, are more numerous outside the park

- all grazing wildlife species have lower densities outside the park, except for the water-independent oryx. Except the rhino, all other browsers are slightly more numerous outside the park

- independent of feeding habit, wildlife has an approximately 50 percent lower biomass per unit area outside the park.

The picture which evolves from these data is that man with his domestic stock has occupied the areas close to dry season water supplies and so has pushed away the water- dependent wildlife. Water-independent wildlife occurs in slightly higher densities outside the park, which may be attributed to the more favourable ecologic conditions. The lower total herbivore biomass outside the park can be caused by less effective utilization of the natural resources by domestic herbivores, but also by higher levels of poaching of elephants and rhinos. The fact that the disappearance of wild, mixed feeding and browsing herbivores is only partially compensated by mixed feeding domestic stock (shoat) may indicate that poaching outside the park was indeed at a higher level.

5.3 LARGE HERBIVORE POPULATIONS AND FOOD AVAILABILITY

In Section 5.2, several cases were noted in which it was implied that the amount of food was limiting the size of the herbivore population–situations where large scale mortality occurred in years with low rainfall. Phillipson (1975) also concluded that elephant deaths in 1971 occurred only in the area with a calculated annual primary production of less than 200 $gr/m^2/year$. To date, however, no data have been available on the actual production of vegetation in the Tsavo area; all conclusions on the availability of forage were based on casual observations or on relationships between rainfall and primary production established in other ecosystems.

The data presented in Section 2.3.1.4, however, permit calculation of vegetation production in any area and for any amount of rainfall in the Tsavo ecosystem. Only a certain fraction of this is available as forage for the large herbivores. The conversion of vegetation production into amount of available forage will be discussed in Section 5.3.1.

Data on forage requirements of livestock are widely published. Forage requirements of wild herbivores should be comparable for related animals (*eg*, buffalo and cattle), but they may be different for other wildlife species. The forage requirements of the different species will be discussed in Section 5.3.2.

Given the data on forage availability and forage requirements, comparisons can be made between the calculated size of the large herbivore population that can be supported by the amount of available forage and the number of large herbivores actually present. Two cases seem suitable for this comparison:

(1) the level of the large herbivore population in the dry central part of the ecosystem after the dry years of 1970/1971. In this area and those years, high elephant mortality was attributed to starvation (Corfield, 1973). The post-drought population should then have had a food requirement that was approximately equal to the amount available in the drought years (Section 5.3.3).

(2) the number of domestic livestock that the ranch managers found the ranches in the area south of the Taita hills could support after experiencing some dry years. Large scale mortality also occurred here in the dry years 1970/1971 and 1975, mainly because of insufficient available forage. Here also a comparison can be made between the forage requirements of the livestock at the presumed safe stocking densities and the amount of available forage (Section 5.3.4).

5.3.1 Forage availability

Forage is produced in Tsavo only during in the two rainy seasons. This production thus also has to provide the animals with food in the ensuing dry season. The long dry season (May-October) is approximately four times as long as the short dry season (January-February) and the rainfall in the two rainy seasons is about the same. The long dry season is therefore a critical period for the large herbivores.

Available grass forage

Grazers in Tsavo predominantly consume perennial grasses. Especially the dominant annual grass, genus *Aristida*, is rejected (Leuthold, 1972). Within the group of perennial grasses, there are differences in preference, but no species is rejected and, certainly when food becomes scarce, they are all consumed.

The peak standing crop of perennial grasses can be predicted using the equations in Section 2.3.1.4. These values are then the potential amount of food available during the dry season. To convert this to actual amounts available for the large herbivores, these values must be reduced by 10 percent for invertebrate consumption and natural decay in the dry season. To ensure long-term stability of the perennial grass cover and thus of forage availability, another 45 percent must be subtracted (see Section 4.2.3). This results in the following simple equations, relating available grass forage to rainfall and perennial grass cover:

for the vegetation on well-drained, deep and acid to neutral soils:

$$GA = 5.4 \times R \times PGC$$

for the vegetation on well-drained, shallow and neutral to alkaline soils:

$$GA = 2.7 \times R \times PGC$$

for the vegetation on imperfectly to poorly drained, deep, alkaline and often saline soils:

$$GA = 6.2 \times R \times PGC$$

in which GA = available grass forage in kg/km^2, R = rainfall in mm, PGC = perennial grass cover in percentage.

Available browse forage

Browsing animals consume a large variety of species of shrubs and trees. Each animal species has its own set of preferred and rejected vegetation species. There is considerable overlap in preferred species, but it is also observed that species rejected by one kind of animal are an important food source for others (Leuthold, 1970, 1971a; Leuthold and Leuthold, 1972; Goddard 1970b; Napier Bax and Sheldrick, 1963).

The plant species belonging to the family of the *Bursaceae*, such as *Boswellia* spp and *Commiphora* spp, are a notable exception. They are browsed upon occasionally by various animal species, but never form an important part of the diet, although these plant species are the dominant shrubs/trees in the denser bushlands/woodlands.

The current season's growth of woody species can be predicted with the equations as presented in Section 2.3.1.4. This can be regarded as the potential amount of available browse for the ensuing dry season. To convert this to actual amounts of available browse, we must take into account the cover of the more or less preferred species (browse intensity classes), the productivity of the browse intensity classes, the fraction that is utilizable and the accessibility. The current season's growth and the fraction that is utilizable by browsing herbivores for each of the browse intensity classes is given in Table 5.3.

With the data from the releves (Section 2.3.1.2) and published information on animal preference (see above), an estimate was made of the contribution of the different species, belonging to the different browse intensity classes, to the tree and shrub cover. The contribution of the moderately and strongly browsed species to the total cover decreases with increased total cover. For the slightly browsed and less preferred species, it is the other way around. No tree species were found to belong to the browse intensity class "strong". The (vertical) accessibility of the browse from trees was judged to be only 20 percent because large parts of the tree crowns are outside the reach of most browsing animals, even giraffe and elephant. With low percentage cover of shrubs, all browse is accessible; with high percentage shrub cover only part of the produced browse is accessible for the browsing herbivores.

The effect of all these aspects on the availability of browse forage for different tree and shrub covers is given in Tables 5.4 and 5.5, respectively. With the help of these tables, availability of browse during the dry season can be calculated for any structural vegetation type and any amount of rainfall. No differentiation is made for the different plant communities and soil conditions because enough data were not available (see also Section 2.3.1.4). With the data from Tables 5.4 and 5.5, the availability of browse forage can be expressed in the following equations:

$$BAT = R \times (0.015 + 1.099 \times TC - 0.00899 \times TC^2)$$

$$BAS = R \times (-4.535 + 8.751 \times SC + 0.0179 \times SC^2 - 0.0056 \times SC^3 + 0.000055 \times SC^4)$$

in which BAT = available browse from trees in kg/km^2, BAS = available browse from shrubs in kg/km^2, R = rainfall in mm, TC = tree cover in percentage, SC = shrub cover in percentage.

Table 5.3 Production and utilization of the browse intensity classes

Browse intensity class	none/slight	moderate	strong
Current season's growth ($gr/m^2/mm$)	0.5	2.0	1.0
Utilizable fraction (%)	20	50	80
Available browse ($gr/m^2/mm$)	0.1	1.0	0.8

Table 5.4 Forage availability for browsing herbivores from the tree stratum

Tree cover (%)	2	10	20	30	40	50	60
Contribution of the browse intensity classes to the tree cover (%)							
BIC slight	50	55	60	65	70	75	80
BIC moderate	50	45	40	35	30	25	20
Accessibility (%)	20	20	20	20	20	20	20
Available browse from trees ($kg/km^2/mm$)							
BIC slight	0.2	1.1	2.4	3.9	5.6	7.5	9.6
BIC moderate	2.0	9.0	16.0	21.0	24.0	25.0	24.0
Total ($kg/km^2/mm$)	2.2	10.1	18.4	24.9	29.6	32.5	33.6

Table 5.5 Forage availability for browsing herbivores from the shrub stratum

Shrub cover (%)	2	10	20	30	40	50	60
Contribution of the browse intensity classes to the shrub cover (%)							
BIC slight	50	20	20	40	55	70	85
BIC moderate	0	40	50	40	30	20	10
BIC strong	50	40	30	20	15	10	5
Accessibility (%)	100	100	100	90	80	70	60
Available browse from shrubs ($kg/km^2/mm$)							
BIC slight	1.0	2.0	4.0	10.8	17.6	24.5	30.6
BIC moderate	0.0	40.0	100.0	108.0	96.0	70.0	36.0
BIC strong	8.0	32.0	48.0	43.2	38.4	28.0	14.4
Total ($kg/km^2/mm$)	9.0	74.0	152.0	162.0	152.0	122.5	81.0

BIC = browse intensity class

5.3.2 Forage requirements of the large herbivores

As noted in preceding sections, forage requirements are relatively well studied for domestic herbivores. Various publications give indications of the quantity and quality of food required by specific animals at specified performances. To adjust for differences in bodyweight, requirements are often given for the metabolic bodyweight (bodyweight $kg^{0.75}$). It is generally agreed that the basal metabolism of an animal at complete rest is linearly related to the metabolic bodyweight according to the following: basal metabolism = 70 x $W^{0.75}$ (kcal per day), (Kleiber, 1975). For a variety of domestic animals, however, it has been established that minimal activity and stable feeding require approximately 40 percent more energy than the strict resting metabolism, so that under these conditions the energy expenditure of animals is approximately 100 kcal per kg $W^{0.75}$ per day (NRC, 1975, 1976, 1978a, 1978b, 1979, 1981a and 1981b).

The total digestible nutrient content of the forage in Tsavo varies between 55 and 65 percent (Wijngaarden and Engelen, 1985) and one kg of total digestible nutrients contain 3615 kcal (NRC, 1975). This means that the average dry matter consumption of domestic herbivores will be at least 0.046 kg dry matter per kg $W^{0.75}$ per day.

Data on forage requirements of wild herbivores are not widely available, but energy requirements are probably very similar to those of comparable domestic animals. Digestibility of various components in the diet seems to be somewhat higher in some large grazing species and somewhat lower for smaller browsing wild animals, when compared with cattle or sheep. Differences are very small, however–virtually always less then 10 percent and often only 1 or 2 percent (Soest, 1984). We may thus assume that wild herbivores of similar size and similar digestive systems have about the same requirements as domestic herbivores. The only wild herbivores which are then not directly comparable to domestic species are the giraffe, rhino and elephant.

Pellew (1983b) studied the feeding behaviour, intake and requirements of giraffe in the Serengeti National Park, Tanzania. He concluded that a daily intake of 1.6 to 2.6 percent of bodyweight, or 0.085 to 0.124 kg dry matter per kg $W^{0.75}$ of highly digestible and protein-rich material in the Serengeti, probably exceeds the minimum maintenance requirement. In Tsavo, however, it is very unlikely that the diet is of the same high nutritive value as in the Serengeti because the dominant food source in the Serengeti (*Acacia* spp) forms a much lower proportion of the diet in Tsavo (Leuthold and Leuthold, 1972). Pellew's estimate may thus be even on the low side for the conditions found in the Tsavo ecosystem.

Intake estimates for elephants based on stomach content (Laws *et al*, 1975), dung production (Coe, 1972) and feeding rate, combined with estimates of weight of trunksful (Guy, 1975) give values varying from 105 kg per day for females to 300 kg per day (fresh weight) for adult males. Converted to dry weight, this is between 1.8 and 3.0 percent of the bodyweight, or 0.11 to 0.21 kg dry matter per kg $W^{0.75}$.

Several of these observations are from elephant populations under conditions of limited food availability, and thus probably approach food intake under conditions close to maintenance level. No data are available for rhino.

The requirements of domestic animals given above are based on conditions comparable to stable feeding and minimum activity. Thus growth, pregnancy, lactation and work are not taken into account.

According to NRC (1981a), energy requirements and thus intake of goats, when the food quality is the same, has to be increased by 25 percent for light activity under grazing conditions of intensive management, by 50 percent for grazing in semi-arid rangelands and by at least 75 percent for grazing in sparsely vegetated land and/or long- distance travel. For other animal species, no data are available, but we may assume that they are of the same order of magnitude.

In the dry season of dry years, the vegetation is sparse and water sources are rather sparely distributed over the Tsavo ecosystem. Energy requirements (and dry matter intake) for domestic herbivores under dry season conditions in the Tsavo ecosystem will therefore be at least 50 to 75 percent more than the quantities indicated above.

The same is probably valid for the wild herbivores; especially the water-dependent wildlife species will also spend a considerable amount of energy in travelling from food to water sources in the dry season. The water-dependent species comprise most of the larger wild herbivores, such as elephant, rhino and buffalo. For example, elephants in Tsavo rest only approximately 15 percent of the day. The rest of the day is spent walking from place to place and feeding–during which they also move around (Ndumo, 1978). In addition, they spend energy in wallowing, ear-flapping and drinking, and they sometimes even dig their own waterholes in the riverbeds.

An indication of the movements of elephants can be obtained from the observations of radio-tracked animals (Leuthold, 1977a). The average home range recorded for 21 elephants over observation periods varying from two to 37 months was 1235 km^2, with a maximum of 3700 km^2. The mean daily movements were as much as 5 km, but individual movements of 80 km (as the crow flies) in eight days were also recorded (Leuthold and Sale, 1973).

In contrast, most of the water-independent animals are relatively small, such as the gerenuk, impala, lesser kudu and oryx. In general, they spend much less time moving around. For example, the home ranges of the gerenuk are very small (2.4 to approximately 6 km^2) and although no data were given, we may assume that daily movements are also very small (Leuthold, 1971b).

From the above observations, it is estimated that–under the conditions in Tsavo–energy requirements in the dry season of the smaller water-independent herbivores is approximately 50 percent and for the larger water-dependent herbivores approximately 100 percent above maintenance levels of domestic herbivores. Using this assumption and the average data for elephant and giraffe as given above, calculated food requirements for animals of different weight are listed in Table 5.6. From this table, it may be concluded that the food

Table 5.6 Dry matter requirements for maintenance of domestic and wild herbivores under dry season conditions in the Tsavo ecosystem

Daily dry matter requirement in kg and as percentage of body weight		Small water-indep (domestic) herbiv (0.069 kg/ $W^{0.75}$)		Larger water-dep (domestic) herbiv (0.092 kg/ $W^{0.75}$)		Giraffe (0.105 kg/ $W^{0.75}$)		Elephant (0.160 kg/ $W^{0.75}$)		Average
		kg	%BW	kg	%BW	kg	%BW	kg	%BW	%BW
Live weight	Metabolic weight									
10	5.6	0.4	3.9							3.9
50	18.8	1.3	2.5							2.5
100	31.6	2.1	2.1	2.9	2.9					2.5
250	62.9	4.2	1.7	5.8	2.3	6.6	2.6			2.2
500	105.7			9.7	1.9	10.3	2.3	6.9	3.4	2.5
1000	177.8					18.6	1.9	28.4	2.8	2.5
1500	241.0					25.3	1.7	38.6	2.6	2.2
2000	299.1							47.9	2.4	2.4
3000	405.4							64.9	2.2	2.2

requirements of the entire herbivore population at maintenance level in an ecosystem like Tsavo can be taken as 2.5 percent of the bodyweight in dry matter per day.

Another important aspect of the nutrition of herbivores is the quality of the food, of which a dominant aspect is often the crude protein content. The minimum requirement for a variety of domestic herbivores is 7 to 8 percent crude protein (NRC, 1975, 1976, 1978a, 1978b, 1979 and 1981a). Because the crude protein content of even bulk grass samples in the dry season in Tsavo seldom falls below 8 percent (Table 2.15), no problems are expected in fulfilling this requirement. The protein content of browse is usually even higher.

5.3.3 Post-drought wildlife population

Approximately 6000 elephants, or about 15 percent of the total population, died in the 1970/1971 drought. Some deaths occurred in the end of the long dry season of 1970, but most of the elephants died in the second part of the long dry season in 1971 (Corfield, 1973). Starvation was confined to the central part of the Tsavo National Park East, fairly close to the permanent water sources, *ie*, the Tiva and Galana rivers and Aruba dam. This area coincides with the area as defined by Cobb (1976): the eastern part of the Tsavo ecosystem, inside the park and within 25 km of permanent water sources. For this area, he gives an effective herbivore biomass of 3277 kg/km^2 for the period 1973 to 1975.

The area considered falls entirely in bio-climatic zones VIa and VIb (see Section 2.2.1). This means that the average annual rainfall is between 250 and 500 mm, of which approximately half falls during the long rains (March to May). Rainfall in 1970 in the long rains was between 110 and 160 mm, and from early April to early December no substantial rain was recorded. Rainfall in 1971 in the central part was only 25 to 50 mm in the long rains, and the dry season lasted from early May to November. In the area away from the central part, rainfall was between 80 and 150 mm in the same period (Tsavo Research Project, unpublished records).

From the vegetation maps (Wijngaarden and Engelen, 1985), the acreage occupied by each vegetation type can be estimated. With the help of the relationship between plant community, structure, grass cover, rainfall and amount of available forage (as given in Section 5.3.1), the amount of forage which was available for the large herbivores in the central part of Tsavo National Park East in the long dry season of 1971 can be calculated.

The average rainfall during the long rains (March-May) 1971 in bio-climatic zone VIb (vegetation variant e) was taken as 35 mm, and in bio-climatic zone VIa (vegetation variant d) as 80 mm. The result of this calculation is given in Table 5.7.

If it is assumed that the large herbivore population at the beginning of the long dry season in 1971 was the same as it was in the period 1973 to 1975, plus the number of elephants that died, then the average biomass of the large

Table 5.7 Forage availability in the long dry season of 1971 in the central part of Tsavo National Park East

PER MAPPING UNIT							WHOLE AREA		
Plant Community	Var	Struct class	Grass cover class	Avail browse kg/km²	Avail grass kg/km²	Total av forage kg/km²	Acreage km²	%	Av forage per km² (kg)
CL4,CA3	e	BG	2	2240	6493	8733	950	19	1659
CL1,2,3,CA1	e	BW	2	3220	13230	16450	450	9	1480
idem	e	B	2	5670	13230	18900	550	11	2079
idem	e	BG	2	2240	13230	15470	800	16	2475
idem	e	B	1	5670	3780	9450	350	7	661
idem	e	BG	1	2240	3780	6020	350	7	421
idem	d	Bd	1	10640	8640	19280	150	3	578
idem	d	B	2	12960	30240	43200	200	4	1728
idem	d	B	1	12960	8640	21600	100	2	432
idem	d	BG	2	5120	30240	35360	200	4	1414
idem	d	G	3	560	51840	52400	50	1	524
CA2,AS1,2	e	B	2	5670	15068	20738	150	3	622
idem	e	B	1	5670	9840	15510	50	1	155
CA2,AS1,2	e	BG	2	2240	15068	17308	500	10	1730
idem	d	BG	2	5120	34440	39560	100	2	791
idem	d	G	3	560	59040	59600	50	1	596
						TOTAL	5000	100	17348

herbivores during the long dry season of 1971 was approximately 4300 kg/km². The forage requirement at a maintenance level of this population was then 2.5 percent of 4300 kg, *ie*, 107.5 kg dry matter per km² per day. This means that the forage requirements could be met during only 161 days (17348/107.5).

The dry season lasted from early May to November, *ie*, approximately 180 days. Thus there was not enough forage for the whole large herbivore population at a maintenance level throughout the dry season. Animals can survive for some time on considerably less than their maintenance requirements; as food becomes more scarce, however, more energy must be spent in feeding and for the water-dependent species probably also in travelling between food and water sources. The animals must have consumed far less than their maintenance requirements over quite a long period, and this might explain the death towards the end of the dry season of 1971 of approximately 6000 elephants as reported by Corfield (1973). Forage availability in the long dry season of a dry year thus sets the maximum size of the large herbivore population in the Tsavo ecosystem.

5.3.4 Domestic herbivore populations at the ranches

Development of ranches south of the Taita hills, in the area between Tsavo National Park East and West, started in the 1960s. Initial stocking densities were approximately 10 ha per livestock unit (LU). The late 1960s had above average rainfall, followed by several dry years (1970/1971 and 1975). In those dry years, thousands of cattle died of starvation (Mayers, pers comm). The stocking rates in 1977 were at a level that was assumed by the ranch managers, to be "safe", *ie* that number of livestock could survive dry years.

Using the same approach as described in Section 5.3.3, the "grazing capacity" for each ranch covered by the vegetation map of Wijngaarden and Engelen (1984) was calculated. The following assumptions were used:

- forage availability in the long dry season in a dry year limits the maximum number of cattle that can be kept;

- the rainfall during the long rains of a dry year is taken here as the 90 percent probability of the rainfall (Table 2.1);

- peak standing crop at the end of the long rainy season represents the potential amount of forage for the long dry season; only 45 percent of this is actually available as forage for large grazing herbivores (Sections 4.2.3 and 5.3.1);

- forage requirement for maintenance is 2.5 percent of the bodyweight in kg dry matter per day (Section 5.3.2);

- cattle are exclusive grazers;

- a livestock unit (LU) is taken as a 450 kg steer;

- forage quality is not considered a problem (always > 8 percent crude protein);

- water is available throughout the dry season on the ranches;

- wildlife on the ranches represents approximately 40 percent of the large herbivore biomass; because a large part of this wildlife population consists of mixed feeding and browsing herbivores, it is estimated that they consume only approximately 20 percent of the available grass forage.

Using these assumptions, the amount of available grass forage and grazing capacity for cattle were calculated. These data and the actual livestock stocking rates in 1977 (Mwova, 1977) are presented in Table 5.8 and Figure 5.3.

On most ranches, there is good agreement between the stocking density considered "safe" by the managers (data 1977) and the calculated grazing capacity. This means that in most cases the managers had learned their lessons well in the dry years and were not overstocking except on the Maungu and Ndara ranches. Especially from the last ranch, it is known that the cattle make use of a large area outside the actual ranch. The fact that no or little overstocking takes place at the moment does not mean that all parts of the ranches have always been properly managed. Severe damage has already been done to the grass cover on several ranches by over-grazing. As a result, problems with bush encroachment are starting at several sites.

5.4 CONCLUSIONS

Data on the dynamics of the large herbivore population in the Tsavo ecosystem are available for only some aspects and some species. Still, some important conclusions can be drawn.

Comparison of the composition of the large herbivore populations inside and

Table 5.8 Grazing capacity and livestock stocking density of some ranches south of the Taita hills

Ranch	Acreage (ha)	Available grass (kg/km^2)	Length dry season (days)	Grazing Capacity (kg/km^2)	Grazing Capacity (ha/LU)	Stocking density 1977 (ha/LU)
Kasigau	20920	5920	160	1482	30	36
Maungu	21232	3040	180	676	67	38
Mgeno	21323	10776	180	2395	19	19
Ndara	2060	1376	180	306	147	7
Rukinga	34425	6496	160	1624	28	23
Sagalla	18515	5120	180	1138	40	45
Taita	41000	8520	140	2434	18	16

outside the park revealed large differences. Outside the park, domestic animals have taken the place of the water-dependent wildlife species. Other wild herbivores, not water-dependent, however, showed a slightly higher biomass per unit area outside the park. This human encroachment along the edges of the Tsavo ecosystem dates from only the last 20 to 30 years. As a result, large numbers of wild herbivores have probably immigrated into the park area during that period, although this is not recorded by accurate data on animal numbers.

The replacement of wild herbivores outside the park by domestic animals is not only a question of competition for food or water. A large number of these wild herbivores are browsers and mixed feeders, and they are replaced mainly by predominantly grazing domestic animals.

The disappearance of the browsing and mixed feeding wild herbivores can be explained only by poaching. This poaching has to be seen as the factor with the largest impact, in the short term, on the large herbivore populations in the Tsavo

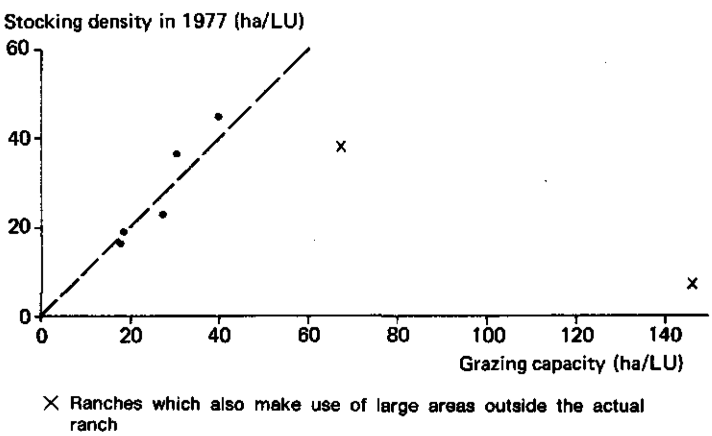


Figure 5.3 Relationship between stocking density in 1977 and the "grazing capacity" at some ranches south of the Taita hills

ecosystem. In the period 1976 to 1980, approximately 70 percent of the elephant population and more than 90 percent of the rhinoceros population were killed by poachers.

In the absence of poaching, forage availability sets the maximum size of the large herbivore populations that can be supported by the Tsavo ecosystem. Especially the quantity of forage is important because the quality, in terms of protein content, is never a limiting factor. Comparison of the herbivore requirements with the quantity of available forage revealed that in the dry year of 1971, not enough food was available for the whole large herbivore population on a maintenance level in the central part of Tsavo National Park East. It is very unlikely that all wild herbivores could meet their maintenance requirements under these circumstances; it explains the death of some 6000 elephants in this area during this drought period.

The stocking density considered safe by ranch managers correlated very well with the grazing capacity calculated on the basis of forage availability in a dry year.

The only solid conclusion that can be drawn so far on the dynamics of the large herbivore populations is that, in the absence of poaching, the maximum size of the large herbivore population is determined by forage availability in a dry year. As a consequence, there is an excessive supply of forage in normal or wet years when rainfall is at least three times as much as in dry years. In those years, large herbivores can be very productive.

There are too few data on birth and death rates to infer rates of change of the size of the large herbivore populations in the Tsavo ecosystem. Even so, it is clear that poaching has been a major factor controlling numbers of certain species in the last decade.

Chapter 6

THE "ELEPHANTS - TREES - GRASS - GRAZERS" MODEL

Models are simplified representations of systems, describing only a limited part of the reality, with well-defined boundaries. Models can be constructed if the structure of the system under consideration is sufficiently well-known so that the various processes which play a role in the system can be described in detail.

The models developed here are empirical because the interrelationships between the model components are derived from field observations, not theoretical considerations. These models therefore describe only the interrelationships between the components of the Tsavo ecosystem and do not "explain" how the ecosystem functions.

The objectives of modelling the Tsavo ecosystem are:

- to demonstrate the interrelationships between the components of the ecosystem described separately in the preceding chapters
- to show the possible long-term consequences for the ecosystem of a number of conclusions drawn from observations made in a relatively short period (three to eight years).

In the preceding chapters, sufficient accumulated knowledge was demonstrated to justify constructing a model that describes the interrelationships of the different components of the Tsavo ecosystem. Sufficient values for the crucial variables are also available to quantify those interrelationships.

The observations in the Tsavo ecosystem confirm in general the "minimum savanna model" of Walker and Noy-Meir (1982), *ie*, there is always an equilibrium between the herbaceous and woody components of the vegetation. The nature of this equilibrium depends on the physical conditions of the soil and the rainfall (Section 2.3.1 and Chapter 4). The level of the equilibrium is strongly influenced by the action of herbivores and man (fire). In Chapter 4, it was shown that fire is of very minor importance in the Tsavo ecosystem, but that elephants strongly influence the cover of the woody vegetation.

The maximum grass cover is limited by the woody cover (Section 2.3.1.3) and can be (temporarily) reduced to lower values through heavy utilization (overgrazing) by herbivores (Section 4.2.3). In Chapter 5, it was concluded that the maximum populations of the large herbivores were governed by forage availability in the long dry season of a dry year, which was assumed to be the peak standing crop produced during the preceding long rains. Forage production was found to be a function of the cover by the relevant vegetation component and the rainfall in the rainy season (Section 2.3.1.4).

In the short term, soil characteristics play a role in determining soil moisture storage capacity and the amount of water available for plant growth, but in Chapter 3 it was shown that, in the long term, soils in the Tsavo area are relatively stable unless man interferes strongly with the ecosystem. Thus in modelling the ecosystem for periods longer than one growing season, and by neglecting strong human influence, it is not necessary to include the soil explicitly in the model. Such a model is then valid only for the particular soil conditions given.

Because the quantitative data on the dynamics of the vegetation are available from only one particular part of the Tsavo ecosystem (the vegetation on deep, well-drained soils in bio-climatic zone VIa, *Commiphora-Lannea* group of communities, variant d), the models are developed for only this part of the ecosystem. These climate, soil and vegetation conditions, however, cover approximately 50 percent of the ecosystem.

The ecosystem components included in the model are shown in Figure 6.1. A static model is developed in Section 6.1, which describes the equilibrium relationship between the different components of the vegetation and the large herbivore population.

When the dynamic behaviour of the system is also known, dynamic models can be built: a technique known as "simulation". Also in this respect, some of the accumulated data make it possible to quantify the dynamics of the system.

The rate of change in cover of the woody vegetation as a function of the elephant density was given in Section 4.1. In that section, some data were also presented on the rate of change in the perennial grass cover. Much less complete and precise data are available on the dynamics of the large herbivore popula-

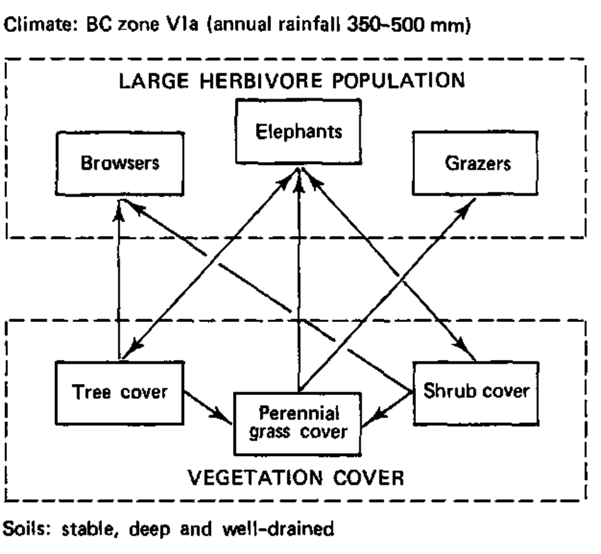


Figure 6.1 Component model of the Tsavo ecosystem

tions. Only the dramatic effects of poaching are quantified in detail (Chapter 5).

To develop a dynamic model of the Tsavo ecosystem and to simulate changes in the different components of the vegetation and the large herbivore population over time, several assumptions had to be made concerning the dynamics of the large herbivore populations (Section 6.2.).

For the execution of the simulation runs, a small program was written for a personal computer with dot matrix printer output (Appendix A).

6.1 STATIC MODEL

The basis for the static model is shown in Figure 6.1. The interrelationships between the various components were described in the preceding chapters. To be able to evaluate the results of the modelling process, some limitations and restrictions of the model were defined in a number of assumptions.

(1) The model is valid only for the part of the Tsavo ecosystem on deep well-drained soils (Ferrisols, Acrisols, ferric/chromic Luvisols) in bio- climatic zone VIa, *ie*, the typical "Nyika *Commiphora- Acacia* bushlands and derived bushed grasslands", with an average annual precipitation of 350 to 500 mm. (It can also possibly be used for bio-climatic zones Vb and VIb.)

(2) It is assumed that the entire "home range" of the large herbivores falls within a region with these characteristics, that drinking water supply for the animals is unlimited and that the animals have unlimited access to all parts of the above defined part of the ecosystem.

(3) The large herbivores considered can be domestic herbivores as well as wild ones, as long as the management of the domestic ones falls within the assumptions given here.

(4) In this model, three groups of large herbivores are distinguished: elephants, grazers and browsers.

(5) The grazers exclusively consume grass forage, the browsers exclusively browse. The elephants consume grass and browse in proportion to their availability, but the elephant diet never contains less than 10 percent browse or 30 percent grass (Section 2.3.2).

(6) The dry matter consumption at maintenance level for all large herbivores is set at 2.5 percent of bodyweight, in kg dry matter per day (Section 5.3.2).

(7) Only the elephants influence the tree and/or shrub cover. The effect of browsing animals or other factors (fire, disease, etc) is assumed to be very small and therefore neglected. The relationship between the elephant density and the equilibrium tree and shrub cover is given in Figure 4.8. The empirical equations derived from that figure and the equations in Section 4.1.1 are:

$$WC = (75 - 54.17 \times ED)/(1 + 1.042 \times ED)$$

$$SC = 36 - 26 \times ED$$

$$TC = WC - SC$$

in which TC = tree cover in percentage, SC = shrub cover in percentage, WC = total woody (tree + shrub) cover in percentage, ED = elephant density in number/km^2

(8) In the long term, herbivory is assumed to have little influence on the cover by perennial grasses. A reduction in perennial grass cover in one year through over-grazing causes a subsequent reduction in forage availability and so a reduced herbivore population in following years. The perennial grass cover is thus in the long term related only to the total woody cover (Figure 2.21). For bio-climatic zone VIa, this relationship is expressed in the equation:

$$PGC = 60 - 0.667 \times WC$$

in which PGC = perennial grass cover in percentage.

(9) The maximum size of the herbivore population is determined by the availability of forage in the long dry season of a dry year (Section 5.4). The availability of browse depends on the rainfall in the long rains preceding the long dry season and on the cover by trees and shrubs. The availability of grass forage depends on the rainfall in the long rains and on the cover by perennial grasses (Section 5.3.1). These relationships can be expressed in the following set of equations:

$$BAT = (0.015 + 1.099 \times TC - 0.00899 \times TC^2) \times R$$

$$BAS = (-4.535 + 8.751 \times SC + 0.0179 \times SC^2 - 0.0056 \times SC^3 + 0.000055 \times SC^4) \times R$$

$$BA = BAT + BAS$$

$$GA = 5.4 \times PGC \times R$$

in which BAT = available browse from trees in kg/km^2, BAS = available browse from shrubs in kg/km^2, BA = total available browse in kg/km^2, GA = total available grass in kg/km^2, R = rainfall in mm.

(10) A dry year is taken here as a year with rainfall equivalent to the 90 percent probability of the rainfall. For bio-climatic zone VIa, this means a rainfall of 35 mm in the long rains. The length of the long dry season of a dry year is 180 days (Table 2.1).

(11) Fire does not occur in the area and so does not influence the structure of the vegetation.

On the basis of the above assumptions and the component model (Figure 6.1), it is implicitly incorporated in the model that the elephants are the driving force in the Tsavo ecosystem. The elephant density determines entirely, within one set of environmental conditions and within certain limits, the structure of the vegetation and the size and composition of the populations of the other large herbivores. The calculated equilibrium values of the components of the Tsavo ecosystem, as a function of the elephant density, are depicted in Figure 6.2. The practical implications of the results will be discussed in Chapter 7, but some remarks can be made here.

A high percentage cover by trees and shrubs is, in the long run, possible only with a very low elephant density. Especially trees become rare when elephant density is more than 0.8 per km^2. For the perennial grasses, the reverse is true (Figure 6.3). With the soil and climatic conditions defined in assumption 1, the elephant population will, in the long run, never exceed a density of 1.26 per km^2 because of limited available appropriate forage.

Browsers attain high densities only at low elephant densities and practically disappear from the system when elephants reach a density of approximately one per km^2 (Figure 6.4). Grazers apparently attain their maximum density at moderate elephant densities (0.3 to 0.9 elephants per km^2), although the grass cover and hence the amount of available grass forage reaches its maximum at the maximum elephant densities. In that situation, however, most of the grass forage is consumed by elephants and less is available for grazers, as compared with lower elephant densities and lower total amounts of available grass.

6.2 DYNAMIC MODEL

The preceding static model predicts only the equilibrium value of the various components of the ecosystem in relation to a certain constant elephant density. It does not say anything about the relative rate of change in certain components in response to changes in other components.

By defining the rates of change in the static model, this model becomes a dynamic one. The rates of change are expressed as differential equations which, through integration, give the state of the variable under consideration at any given time. Thus we can see how the values of the model components change in time.

The dynamic model was developed under the same assumptions that underlie the static model. The only additional assumption was that there may be some variation in rainfall in the area but that the simulation is influenced only by the climatic conditions in a dry year as defined in Section 6.1 (see also Section 6.3). The integration interval in the dynamic model is one year.

In Section 4.1.1, a detailed account was given of the changes in the tree and shrub cover in relation to elephant density. The rate of change of the tree and shrub cover was related to both elephant density and the initial tree or shrub cover. The rates of change of the tree and shrub cover can be expressed in the following empirical differential equations:

$$dT/dt = 0.052 \times S - 0.048 \times T - 0.05 \times ED \times (T + S)$$

$$dS/dt = 3.6 - 0.1 \times S - 2.6 \times ED$$

in which dT/dt, dS/dt = the rates of change of the tree and shrub cover in percent/year, respectively; ED = elephant density in number/km^2; T = tree cover in percentage and S = shrub cover in percentage

The rate of change of the perennial grass cover is shown in Figure 4.10. That figure is based on data from years with average rainfall conditions. The large herbivore population, as determined by the forage availability in dry years, consumes only approximately 15 percent of the dry season standing crop

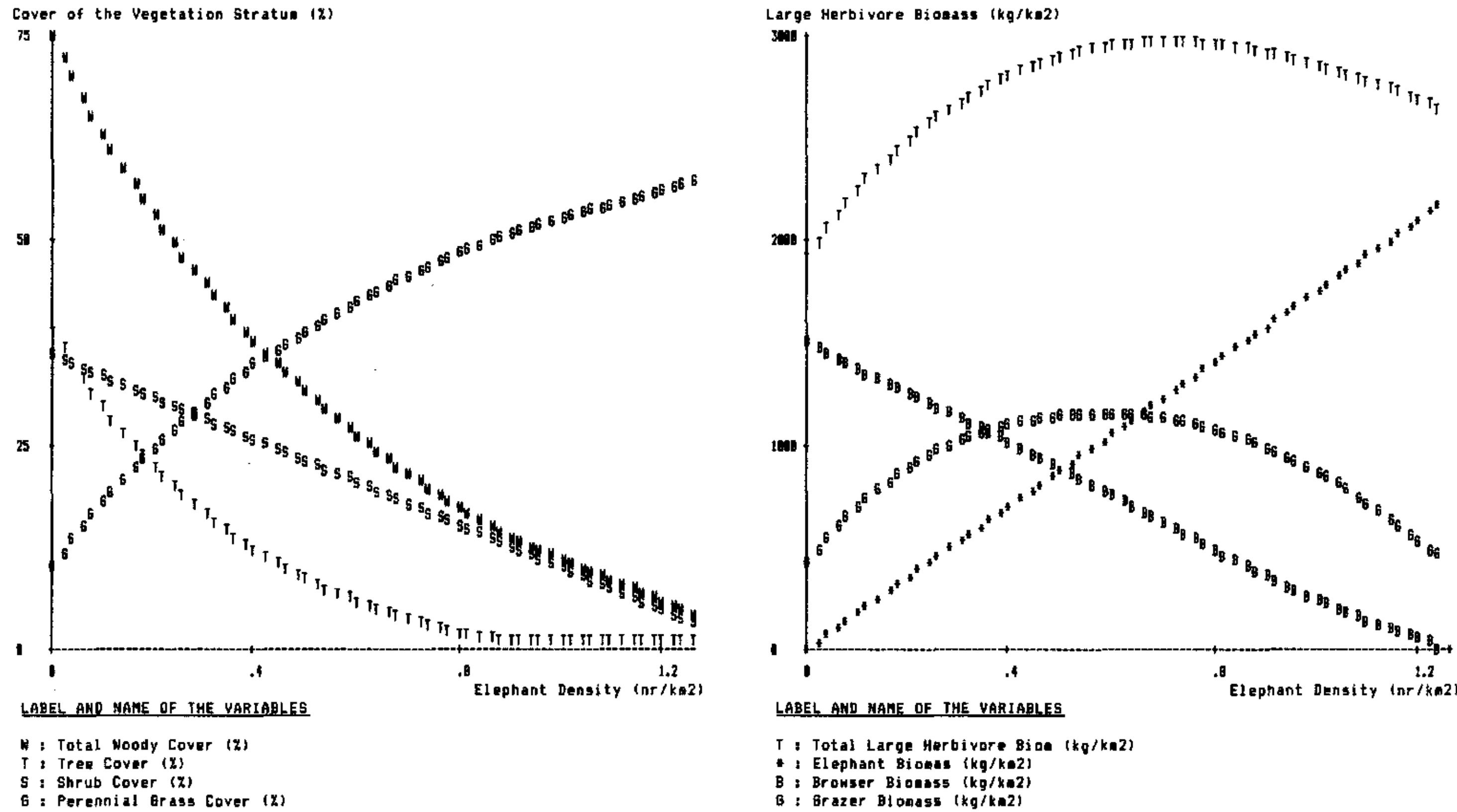


Figure 6.2 Equilibrium values of the cover of the different vegetation strata (left) and the biomass of different groups of large herbivores (right) in relation to elephant density

Figure 6.3 After the destruction of most of the woody vegetation, there is an ample supply of forage for grazing and also for mixed feeding herbivores

Figure 6.4 Little browse is left for exclusive browsers at high elephant densities

in average years. Together with the 10 percent allowance for invertebrate consumption and natural decay (Section 4.2.3), this should give an average annual increase of the perennial grass cover of approximately 10 percent. This increase probably occurs only when there is a large difference between the potential perennial grass cover and the actual one. This is taken into account in the following equation:

$$dG/dt = 10 \times (PGM - PGC)/PGM$$

in which dG/dt = the rate of change of the perennial grass cover in percent/year, PGM = the potential perennial grass cover under the current total woody cover in percentage, and PGC = the actual perennial grass cover in percentage.

As mentioned above, few quantitative data exist on the dynamics of the large herbivore populations in Tsavo. In the absence of field data, it is assumed that the large herbivore populations follow the logistic growth model (Klomp, 1975):

$$dN/dt = r \times N \times (K - N)/K$$

in which dN/dt = the rate of population growth, r = the relative population growth rate, N = the population size, K = the maximum possible population (*ie*, grazing capacity)

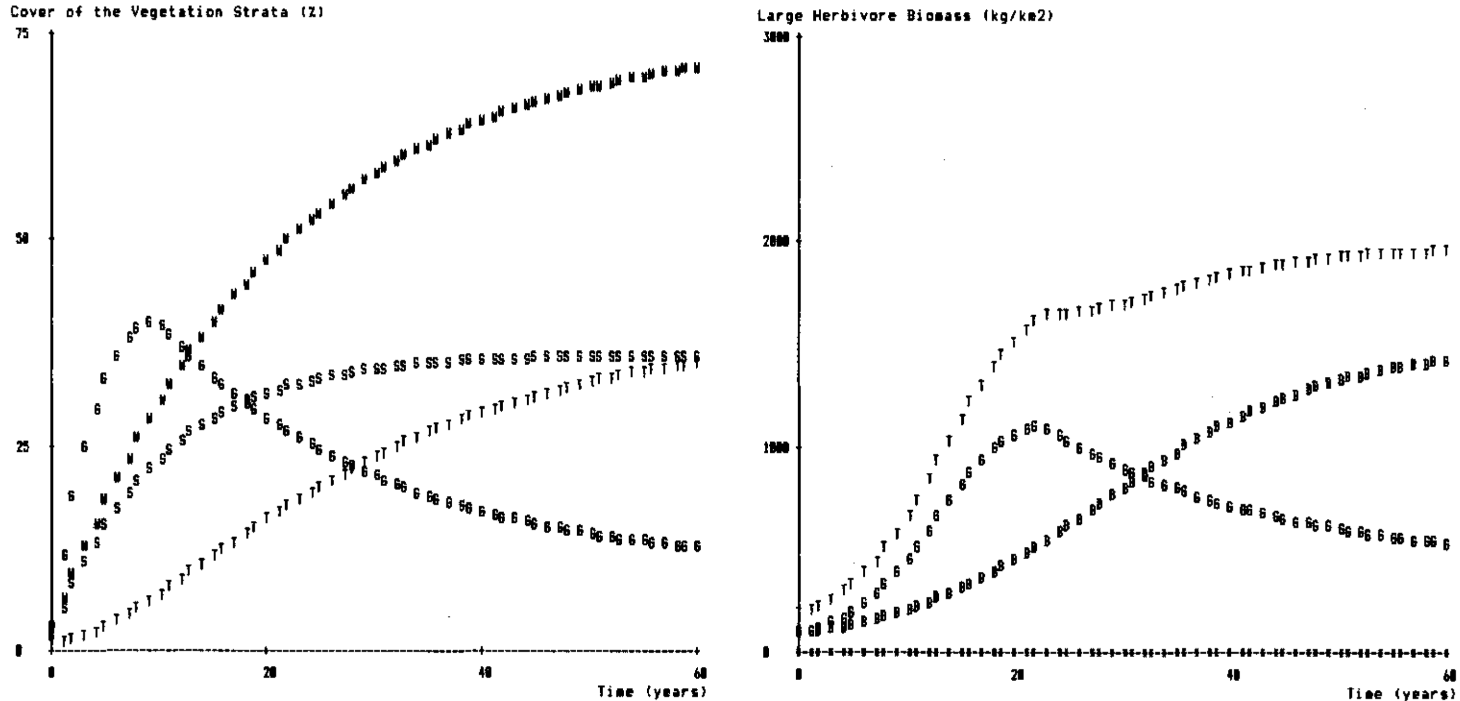
N, the population size, must be given a starting value in the simulation; K (grazing capacity) can be calculated when the available forage is known, as shown in Chapter 5. The only unknown in this equation is then "r", or the relative growth rate of the population. Various values for the relative growth rate of large herbivores can be found in the literature. They vary from 5 to 30 percent and increase in general with decreasing body size (Sinclair and Norton-Griffiths, 1979; Western, 1979; Crawley, 1983). For the three components of the large herbivore population distinguished in this model, the following values are used:

Elephants: r = 5 percent/year
Browsers: r = 10 percent/year
Grazers: r = 20 percent/year

Only when the grazer population consists predominantly of domestic herbivores was a value of 30 percent/year used. Varying those values by ± 50 percent, however, did not strongly influence the results of the simulation. The size of the large herbivore populations approached the grazing capacity only somewhat sooner after a disturbance.

To show the behaviour of the dynamic model, two runs covering a period of 60 years were executed. The first run started with a hypothetically strongly degraded system in which both the herbivore and vegetation components were set at very low values. Elephants were assumed to be absent. The starting values and the results of the simulation are depicted in Figure 6.5.

The vegetation components react with a rather small time constant. After only 10 years, the perennial grass cover reaches a maximum value of 35 percent, after which it starts decreasing because of the increased cover by shrubs and trees. The shrubs increase faster in cover than the trees and approach their



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

W :	Total Woody Cover (%)	=	3.0	===>	71.1
T :	Tree Cover (%)	=	1.0	===>	35.2
S :	Shrub Cover (%)	=	2.0	===>	35.9
G :	Perennial Grass Cover (%)	=	3.0	===>	12.5

LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

* :	Elephant Biomass (kg/km2)	=	0	===>	0
B :	Browser Biomass (kg/km2)	=	100	===>	1428
G :	Grazer Biomass (kg/km2)	=	100	===>	527
T :	Total Large Herbivore Biom (kg/km2)	=	200	===>	1955
:	Rel Growth rate Elephant Pop (%/yr)	=	0	===>	0
:	Rel Growth rate Browser Pop (%/yr)	=	10	===>	10
:	Rel Growth rate Grazer Pop (%/yr)	=	20	===>	20

Figure 6.5 Development of cover of the different vegetation strata (left) and the biomass of different groups of large herbivores (right) over a period of 60 years, starting with a strongly degraded system and in the absence of elephants

theoretical maximum cover of 36 percent after approximately 30 years. The tree cover approaches its theoretical maximum cover of 39 percent after 60 years, and reaches only half of this maximum value after 25 years. The grazers and browsers react strongly to the increased cover of the different vegetation components, which implies an increase in the availability of forage. The biomass of the grazers increases faster than that of the browsers because of a higher relative growth rate. The maximum biomass of the total large herbivore population is approached after 20 years, after which only a gradual replacement of the grazers by browsers takes place due to the reduced availability of grass and the increased availability of browse.

In the second run, it was assumed that through a sudden immigration, a fairly densely wooded area is faced with a high elephant density. The result of this run is shown in Figure 6.6. The first 10 years show a low and stable elephant population with the accompanying high cover by trees and shrubs and relatively high biomass of browsers (Figure 6.6: A). In the next 10 years, the elephant population is assumed to increase by approximately 50 percent per year because of immigration (Figure 6.6: B). For the remainder of the period, normal relative growth rates of the herbivore populations are assumed (Figure 6.6: C).

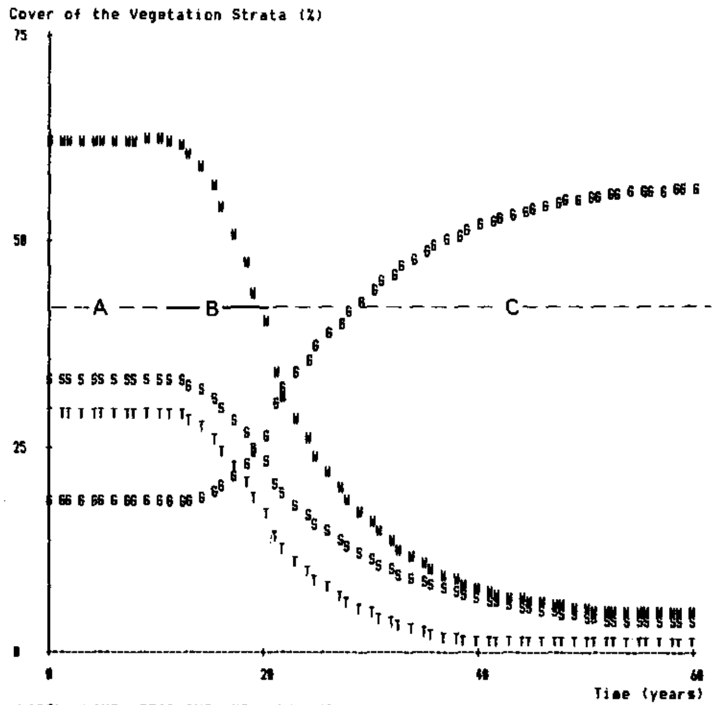
As could be expected, the strong increase in the elephant population initiates a strong decrease in the tree and shrub cover. The total woody cover is reduced to nearly half of its initial value during 10 years of elephant invasion and it stabilizes another 20 years later at less than one-tenth of its initial value. The cover by perennial grasses increases at about the same rate as the tree and shrub decreases. The elephant biomass remains relatively stable after the end of the invasion period; only after 20 years is there a small, abrupt decrease of the elephant biomass. The reason for this is that the growing elephant population "overshoots" the equilibrium grazing capacity.

The available forage for both grazers and browsers declines quickly with the invasion of elephants. This is due more to the strong competition with the elephants for food than to the system's lower production of forage. As a result, the biomass of both the browsers and the grazers drops significantly. The browsers nearly disappear from the system when the tree and shrub cover reaches very low values. The grazers recover somewhat after the end of the elephant invasion because of the increasing grass cover and the associated increase in amount of grass forage.

These two runs of the dynamic model clearly demonstrate the dramatic changes that can take place in the components of ecosystems like Tsavo. They also quantitatively confirm existing ideas on the functioning of the Tsavo ecosystem (Laws, 1969b; Sheldrick, 1973).

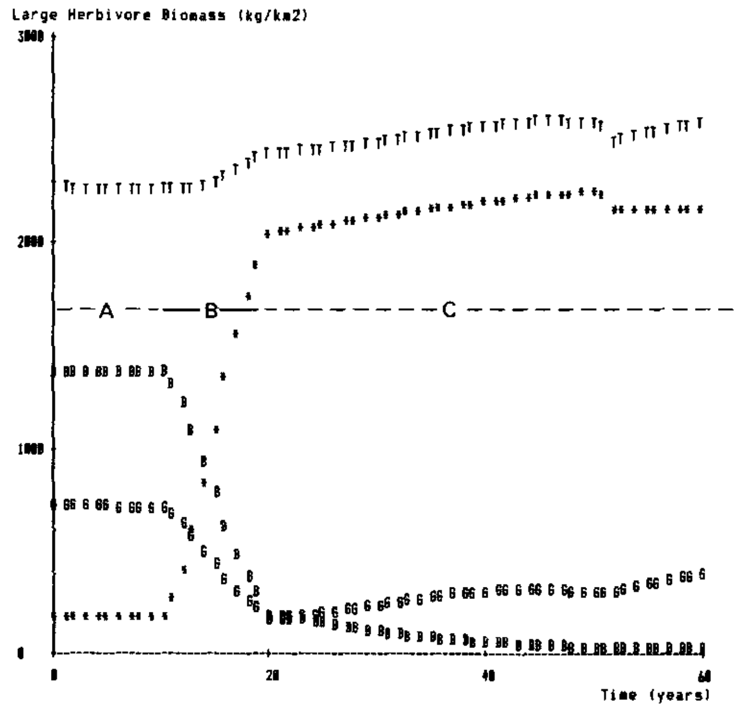
6.3 LIMITATIONS OF THE MODEL

Because of the limited available data, this elephants - trees - grass - grazers model describes only a part of the Tsavo ecosystem. Moreover, the necessary



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

	YEAR	0		10		20		60
W : Total Woody Cover (%)	=	62.0	=>	62.4	=>	36.7	=>	4.9
T : Tree Cover (%)	=	29.0	=>	29.2	=>	15.1	=>	1.0
S : Shrub Cover (%)	=	33.0	=>	33.3	=>	21.6	=>	3.9
G : Perennial Grass Cover (%)	=	18.6	=>	18.3	=>	28.1	=>	56.5



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

	YEAR	0		10		20		60
* : Elephant Biomass (kg/km2)	=	175	=>	175	=>	2057	=>	2159
B : Browser Biomass (kg/km2)	=	1374	=>	1373	=>	202	=>	24
G : Grazer Biomass (kg/km2)	=	723	=>	711	=>	188	=>	396
T : Total Large Herbivore Biom (kg/km2)	=	2272	=>	2259	=>	2447	=>	2578
: Rel Growth rate Elephant Pop (%/yr)	=	0	=>	0	=>	50	=>	5
: Rel Growth rate Browser Pop (%/yr)	=	10	=>	10	=>	10	=>	10
: Rel Growth rate Grazer Pop (%/yr)	=	20	=>	20	=>	20	=>	20

Figure 6.6 Development of cover of the different vegetation strata (left) and the biomass of different groups of large herbivores (right) over a period of 60 years, after an invasion of elephants into a wooded area

data were not always available in detail for all included components. This resulted in the following important limitations of the model:

Rainfall is kept at a constant dry year level

It is thought that the dynamics of the vegetation components are not influenced because their rates of change are derived from observations under "average" conditions–including dry, normal and wet years. The large herbivore components are somewhat influenced; in normal or wet years, they will grow somewhat faster than in the present simulation because of the higher grazing capacity. The equilibrium values do not change, however, because the large herbivore biomass will be limited by the available forage in the irregularly occurring dry years. Because of the faster growth in years with normal or above normal rainfall, large herbivore populations can further exceed the grazing capacity of dry years and can therefore show more frequent and larger dramatic declines (population crashes) than, for example, is indicated in Figure 6.2.

The constant relative growth rates of the large herbivore populations

Increasing the relative population growth rates of the large herbivores results in reaching the grazing capacity more quickly. It also results in overshooting the grazing capacity of dry years more frequently and by a greater margin, and therefore may also result in more frequent and larger crashes in the large herbivore populations. When density population control mechanisms are operating, those effects will be much smaller. Laws (1969b) indicated that those mechanisms–such as delayed sexual maturity and increased calving interval–existed in the elephant population of the Tsavo ecosystem in the late 1960s. He doubted, however, whether these mechanisms were capable of effectively controlling the growth of the elephant population.

The non-spatial character of the model

All large herbivores show restricted or extensive movements over the seasons, during which they come encounter various climate/soil/vegetation conditions. This is not taken into account in the model. That limitation can be overcome only when:

(1) This dynamic model is linked to a "geographic information system" containing information about the spatial distribution of the environmental variables.

(2) The movements of the large herbivore populations are known exactly in time and place.

(3) A dynamic model as described in Section 6.2 is also developed for the other environmental conditions of the Tsavo ecosystem.

(4) A "super-model" is developed which incorporates aspects 1, 2 and 3.

This, however, is, beyond the scope of this study. Nevertheless, the environmental conditions for which the model is valid occur in approximately 50 percent of the area of the Tsavo ecosystem, and it may thus be assumed that the present non-spatial model gives a reasonable approximation of the real situation.

Some of the possible developments in Tsavo National Park and some of the ranches south of the Taita hills will be presented in Chapter 7. On the basis of the results of these simulations, conclusions will be drawn on the implications for the management of the park and ranches.

Chapter 7

MANAGEMENT IMPLICATIONS

The manner in which semi-arid ecosystems are managed is determined largely by the objectives for the area. In commercial livestock ranching, the objective is to maximize yield and income, mainly through the production of beef cattle. One of the main problems is to regulate animal numbers in such a way that maximum production is obtained in years with normal or above normal rainfall, and that in drought years animals will have enough to eat to survive.

Managers are very often tempted to overstock. In unfavourable years (droughts), losses can then be overcome by sale of livestock or, in economically strong systems, by the purchase of extra forage. In many traditional systems, however, droughts normally result in the death through starvation of often a considerable part of the herds.

In the ranches south of the Taita hills, beef cattle are the main herbivores, and thus managers will be interested in a maximum supply of grass forage. This means that trees and shrubs must be kept to a minimum and that the grass cover must be protected from overgrazing to maintain a maximum cover and thus maximum productivity.

Until 1980, there were no clear indications that the ranch managers were actively involved in the management of the vegetation. Elephants and occasional uncontrolled fires kept the woody vegetation more or less under control, and the grazing capacity was respected at most ranches only after the experience of some very dry years (Section 5.3.4).

The effect of the reduced elephant impact, in the absence of other management actions to control the woody vegetation, is described in Section 7.2. Some alternatives for the management of the vegetation at those ranches will also be discussed.

The objectives for the management of national parks can be diverse and sometimes even conflicting: preservation of one or more animal species or a soil/plant/animal ecosystem, biologic and aesthetic diversity, ecologic stability, minimal interference with nature, animal welfare, maximum tourist satisfaction, etc. The management of Tsavo National Park in the last decade was geared towards minimal interference with nature (laissez-faire policy). The large-scale poaching in the years 1976 to 1980 conflicted with this management objective. If the policy of minimal interference in Tsavo National Park is maintained in the near future, the outcome for the ecosystem will depend largely on the capability of the management to control this poaching. Different scenarios will be shown in Section 7.1.

7.1 IMPLICATIONS FOR TSAVO NATIONAL PARK

It is assumed that the management objective for Tsavo National Park for the near future will be carried out in the "laissez-faire" policy. The major management actions in that case will be directed at control of poaching. To simulate the success of this policy, three scenarios are presented:

(1) complete control of poaching so that the elephant population grows by approximately 5 percent per year

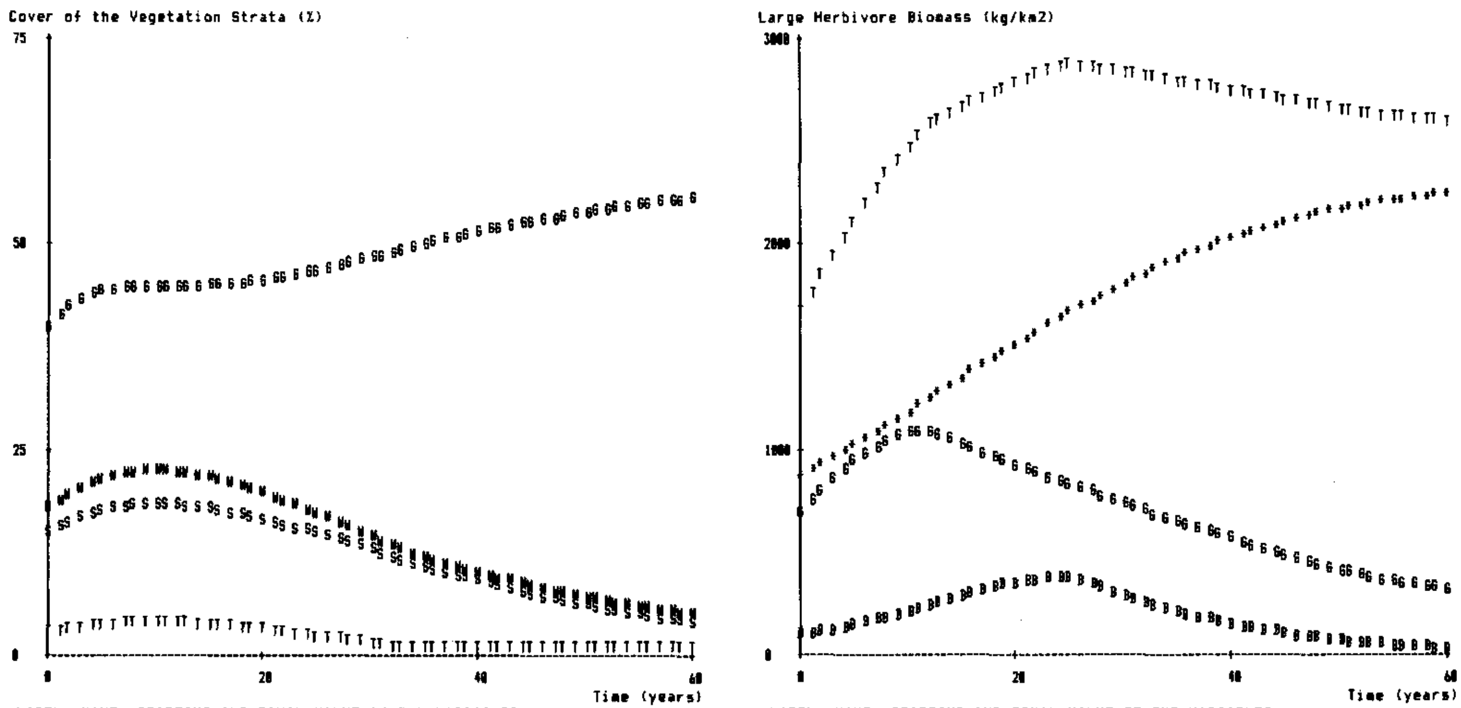
(2) partial control of poaching so that the elephant population remains about stable

(3) a continuous poaching problem so that the elephant population decreases by approximately 5 percent per year.

Because the southern section of Tsavo National Park East is more or less representative for the conditions for which the model–as developed in Chapter 6–is valid, the scenarios consider this area only. The state of the vegetation and the large herbivore population for this area in 1980 are therefore taken as a starting point. This means a vegetation with a rather open woody cover (3 percent tree cover and 10 percent shrub cover) and a relatively high grass cover (perennial grass cover 40 percent, see vegetation map in Wijngaarden and Engelen, 1985). The elephant density is taken as approximately 0.5 elephants per km^2 (Ottichilo, 1981) and the other herbivore densities are estimated as browsers 100 kg/km^2 and grazers 700 kg/km^2. The effect on the vegetation and the total large herbivore population is shown for each scenario in Figures 7.1, 7.2 and 7.3, respectively.

Case 1: Complete control of poaching (Figure 7.1)

In the beginning, there is an increase in the woody and grass cover, still attributable to the sharp reduction of the elephant population in the preceding years. At the same time, however, the elephant population grows and, after 10 years, elephants begin controlling the woody vegetation again; after 30 years, the vegetation is in the same state as in 1980. Because of the increased grass cover and initially reduced competition from elephants, the grazer population grows quickly. After only 10 years, however, the competition for food with the elephants is so strong that the grazer population declines again. The browser population also increases initially (but at a lower rate than the grazers) until in approximately 30 years the reduction of the woody vegetation by elephants–and thus the available browse–is so great that the browser population starts declining. An elephant density of approximately one per km^2 is reached again after 30 years. A situation similar to the mid-1970s is reached–as existed before the severe poaching. At that stage, similar events can be expected, such as starvation of elephants in drought years, outcries about the "desert- like" appearance of the Tsavo Park, etc. If human settlement around the park increases, and as a result appreciable numbers of elephants immigrate into the park, this situation may be reached even earlier.



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

W : Total Woody Cover (%)	=	19.0	===>	5.1
T : Tree Cover (%)	=	3.0	===>	1.0
S : Shrub Cover (%)	=	15.0	===>	4.1
G : Perennial Grass Cover (%)	=	40.0	===>	55.8

LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

* : Elephant Biomass (kg/km2)	=	875	===>	2237
B : Browser Biomass (kg/km2)	=	100	===>	25
G : Grazer Biomass (kg/km2)	=	700	===>	318
T : Total Large Herbivore Biom (kg/km2)	=	1675	===>	2580
: Rel Growth rate Elephant Pop (%/yr)	=	5	===>	5
: Rel Growth rate Browser Pop (%/yr)	=	10	===>	10
: Rel Growth rate Grazer Pop (%/yr)	=	20	===>	20

Figure 7.1 Development of vegetation (left) and large herbivores (right) after 1980 in the southern section of the Tsavo National Park East when poaching is completely controlled (growth of elephant population 5 percent/year)

Case 2: Slight poaching; stable elephant population (Figure 7.2)

In this scenario, there is an initial increase of cover of all vegetation components, but after some years the grass cover is controlled by the increased woody cover, the shrub cover reaches its equilibrium value of approximately 20 percent after 20 years and the trees a cover of slightly less than 10 percent after about 30 years. The elephant population remains stable at 0.5 per km^2, but the grazer density quickly increases to approximately 1100 kg/km^2 in 10 years. The browser population grows more slowly, reaching approximately 800 kg/km^2 after 50 years.

Case 3: Continuous poaching; decreasing elephant population (Figure 7.3)

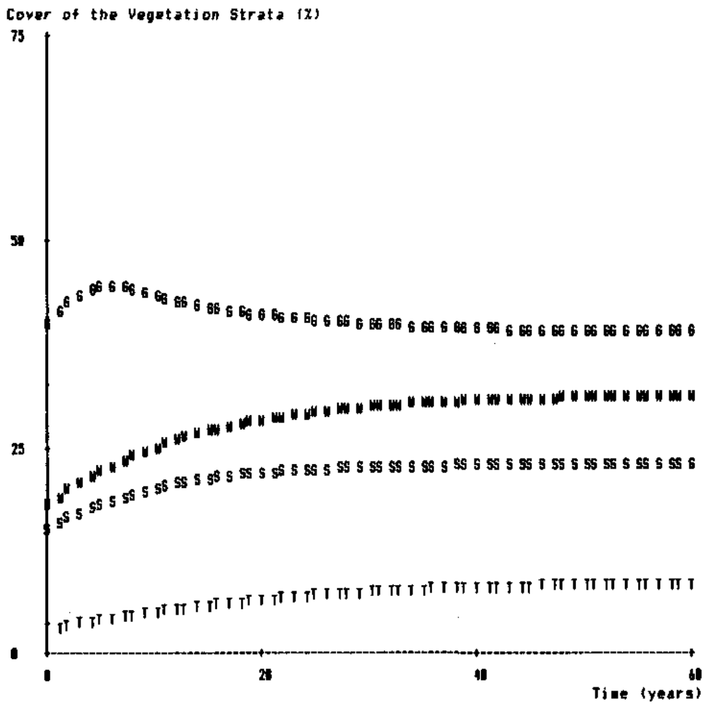
Because of the continuous decrease in the elephant population, tree and shrub cover increase, reaching fairly high values of approximately 30 and 35 percent, respectively. After a short initial increase, the grass cover declines steadily as a result of the increased woody cover. Because of the reduced competition for food with elephants, the grazer population increases initially, but starts decreasing after 20 years because of the reduced amount of grass forage available. The browser population increases slowly but continuously.

Discussion

The degree of elephant poaching–and thus the level of growth or decline of the elephant population–determines completely the future structure of the vegetation and the size and composition of the large herbivore population. Whatever management actions will be in the near future, Tsavo will look different in 10 or 20 years. Even in Case 1 (complete control of poaching, Figure 7.1), it is unlikely that severe permanent damage will be done to either soil or vegetation (Chapters 3 and 4), and all processes are reversible. This can therefore never serve as an ecological argument to decide on the control of the number of a certain species (see also Jewell and Holt, 1981).

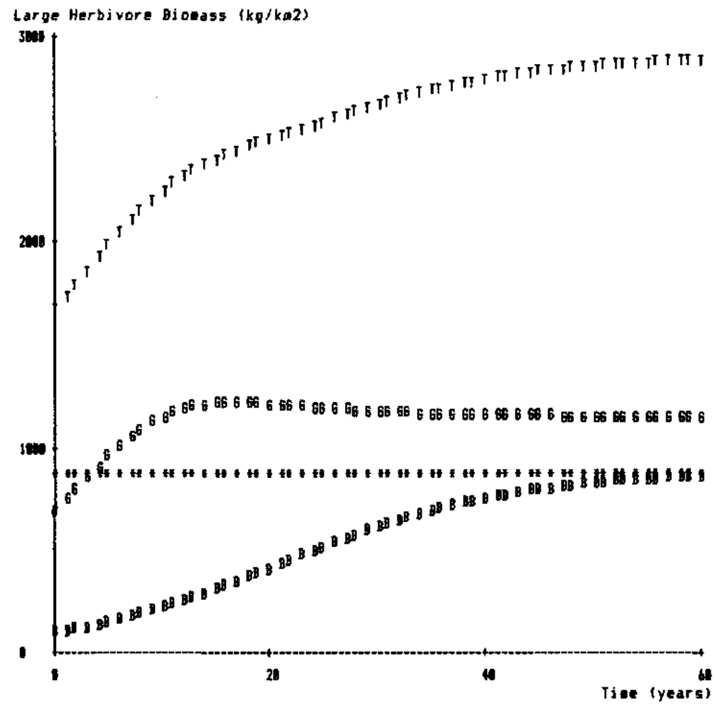
To keep the area interesting for most tourists, poaching should be controlled–at least to some extent. If the elephant population continues decreasing, the woody vegetation will very quickly become thicker, which makes the animals less visible. That situation also has the lowest total density of large herbivores (Figure 7.3). In that event, an adapted "laissez faire" policy for the national park might be considered, and introduction of range management practices such as burning, to ensure the continuous interest of the tourist industry.

All three alternatives describe a situation with a uniform distribution of elephants and their uniform effect on the vegetation and other large herbivores. In practice, this will not be the case. Density of elephants in the dry season will be inversely related to distance to drinking water supplies. In all cases, there will thus be some variation over the ecosystem, with slight fluctuations of the data presented in Figures 7.1, 7.2 and 7.3.



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

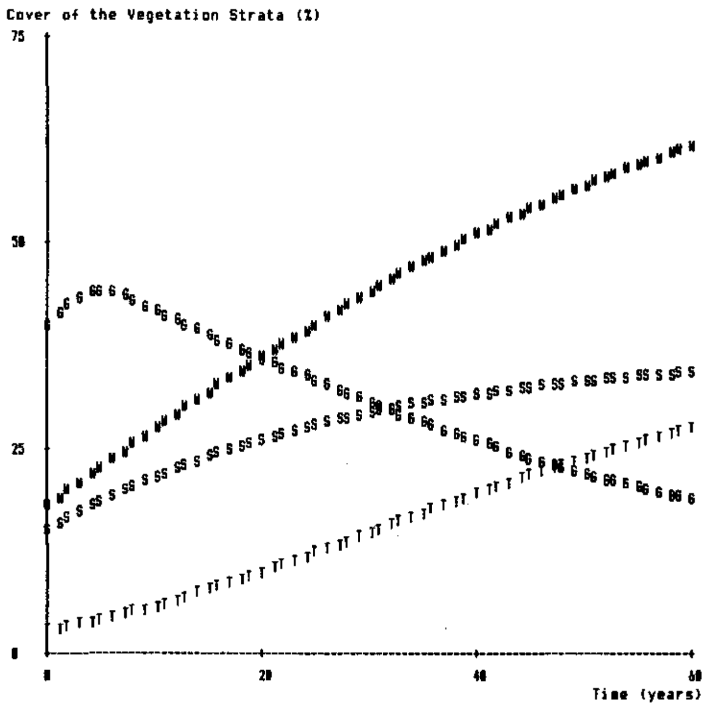
W	: Total Woody Cover (%)	=	18.0	===>	31.3
T	: Tree Cover (%)	=	3.0	===>	8.4
S	: Shrub Cover (%)	=	15.0	===>	23.0
G	: Perennial Grass Cover (%)	=	40.0	===>	39.1



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

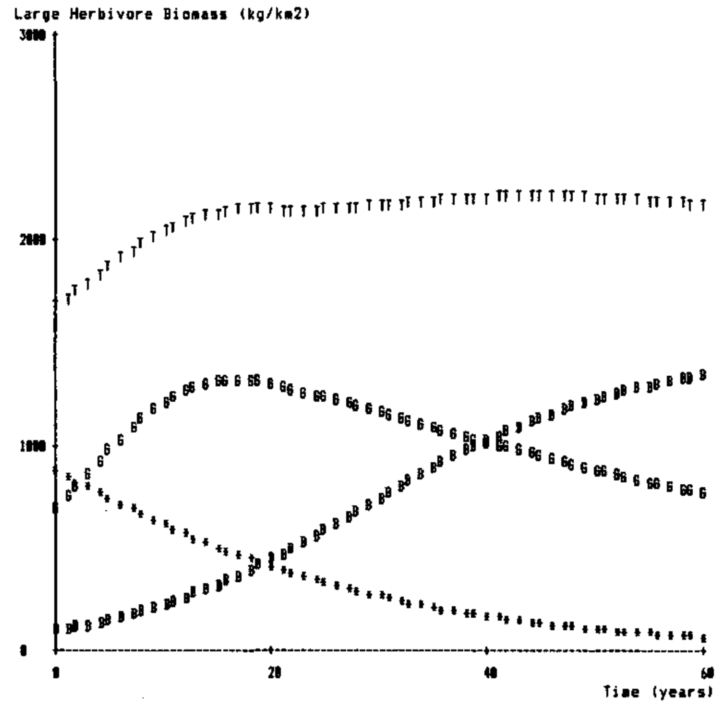
#	: Elephant Biomass (kg/km2)	=	875	===>	875
B	: Browser Biomass (kg/km2)	=	100	===>	861
G	: Grazer Biomass (kg/km2)	=	700	===>	1147
T	: Total Large Herbivore Biom (kg/km2)	=	1675	===>	2883
	: Rel Growth rate Elephant Pop (%/yr)	=	0	===>	0
	: Rel Growth rate Browser Pop (%/yr)	=	10	===>	10
	: Rel Growth rate Grazer Pop (%/yr)	=	20	===>	20

Figure 7.2 Development of vegetation (left) and large herbivores (right) after 1980 in the southern section of Tsavo National Park East when poaching is only partially controlled (stable elephant population)



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

W :	Total Woody Cover (%)	=	18.0	===>	62.2
T :	Tree Cover (%)	=	3.0	===>	27.9
S :	Shrub Cover (%)	=	15.0	===>	34.3
G :	Perennial Grass Cover (%)	=	40.0	===>	18.5



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

* :	Elephant Biomass (kg/km2)	=	875	===>	62
B :	Browser Biomass (kg/km2)	=	100	===>	1347
G :	Grazer Biomass (kg/km2)	=	700	===>	756
T :	Total Large Herbivore Biom (kg/km2)	=	1675	===>	2165
:	Rel Growth rate Elephant Pop (%/yr)	=	-5	===>	-5
:	Rel Growth rate Browser Pop (%/yr)	=	10	===>	10
:	Rel Growth rate Grazer Pop (%/yr)	=	20	===>	20

Figure 7.3 Development of vegetation (left) and large herbivores (right) after 1980 in the southern section of Tsavo National Park East when poaching continues (decrease of elephant population 5 percent/year)

7.2 IMPLICATION FOR RANCHES

Whatever the management of the animals will be, all ranchers in the area south of the Taita hills will be interested in maximum production of the grass layer because the main herbivores on those ranches are beef cattle and forage quality problems do not play a serious role in this ecosystem (Section 2.3.1.4). The reduction of the elephant population in the Tsavo ecosystem in the 1970s will also have an effect on the ranches, because elephants generally had free access to the ranches–which were indeed a part of their home range (Cobb, 1976; Leuthold, 1977a; Mayers, pers comm).

A simulation was done for two kinds of ranches, showing the development of the vegetation and large herbivore population in a 30 year period, starting with 1980.

Well managed ranch

Fairly good "range condition", *ie*, a good cover by perennial grasses and a stocking density in accordance with the grazing capacity; the elephant density is low and is thought not to increase; other wildlife (both grazers and browsers) are tolerated; burning is avoided as much as possible (examples: Mgeno, Rukinga and Taita ranches).

The result of this simulation is shown in Figure 7.4. With a constant low elephant density and in the absence of fire, there is a quick increase in cover of the woody vegetation. This means a reduction of the grass cover and thus a reduction in the grazing capacity for grazing herbivores. Even in respecting the grazing capacity and eliminating all wildlife grazers, the number of beef cattle that can be kept on these ranches will decrease constantly in the future.

Poorly managed ranch

"Over-grazed", *ie*, a lower grass cover than is possible with the woody cover present; elephants are absent; other wildlife is more or less tolerated; burning is normally not a problem because of insufficient fuel present (examples: Maungu and Ndara ranches).

The result of this simulation is shown in Figure 7.5. As with the well managed ranches, bush encroachment (increase in cover of the woody vegetation) limits the number of beef cattle that can be kept on the ranch in the near future. Only during the first few years, when it is assumed that the ranch is no longer over-grazed, is there a slight increase in the grazing capacity for grazing animals.

Thus–whatever the management practices–in the absence (or very low density) of elephants and without fire, all ranches south of the Taita hills will face a severe bush encroachment problem and a reduction of the grazing capacity for grazing animals within 10 years (after 1980).

If beef cattle production remains the primary interest of the ranches, methods have to be found to combat this bush encroachment. The alternative is that the ranches change their production objective. Either they make wildlife utilization (consumptive or non-consumptive) part of the management or change to another domestic herbivore which is more a browser (for example, goat).

The first alternative is not likely to be of interest in the short term because of the ban on hunting and trade in trophies in Kenya and the competition from a network of national parks. Moreover, McDowell *et al* (1983) expressed severe doubts whether game ranching is economically feasible in Kenya. The second alternative might be viable, but there is little experience to date with large-scale commercial goat production.

In the short term, it is thus imperative that ways are found to combat bush encroachment. A number of options are available:

- Elephants: at higher densities, elephants are very effective in controlling the woody vegetation.

- Fire: hot fires at the end of the dry season not only burn the dry grass but also control the woody vegetation to a certain extent.

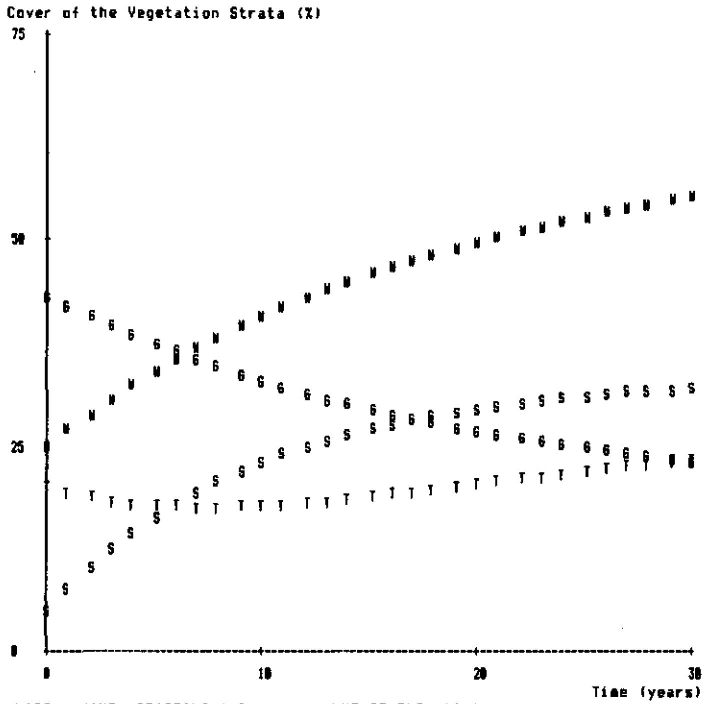
- Mechanical control: cutting by hand or with heavy machinery can be used to remove trees and/or shrubs. A useful by-product can be firewood or charcoal. Cutting usually has to be repeated or followed by the application of herbicides.

- Herbicides: herbicides can kill whole plants, and there is in general less risk of regrowth compared with mechanical clearing. The herbicides used should be appropriate for the plant species to be controlled.

Because of the high costs involved in mechanical control and the use of herbicides, it is unlikely that those methods can be economically applied in the conditions found on the ranches south of the Taita hills (Pratt and Gwynne, 1977). Therefore only the use of elephants and fire will be examined in more detail.

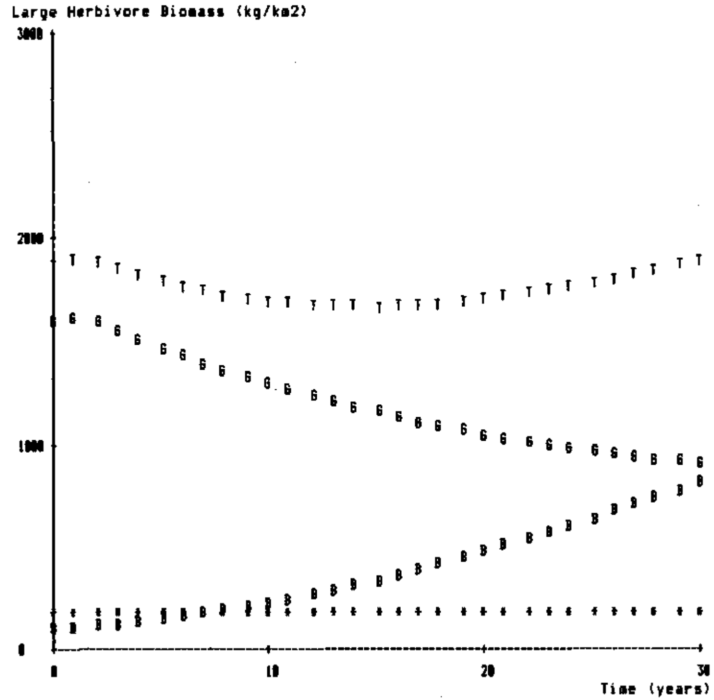
The effect of strict protection of elephants on the ranches can be simulated easily with the data available. In Figure 7.6, the same starting values as in Figure 7.4 are used. The relative population increase rate of elephants is set at 10 percent instead of 0 percent, however, because the strict protection envisaged not only enhances the natural reproductive performance of the elephants but probably also attracts elephants from surrounding areas.

The result is shown in Figure 7.6. The elephant population grows slowly and begins controlling the woody vegetation only after approximately 15 years. After 30 years, the grasses and woody vegetation have about the same cover as in 1980. The grazing capacity for grazing animals, however, is reduced to only approximately 40 percent of the starting value. This is because–although the total amount of grass forage available is the same–elephants also consume a large amount of grass and thus less is available for strictly grazing herbivores. To obtain the maximum grazing capacity for grazing herbivores in the long term, elephants should be controlled at a level of approximately 0.3 to 0.7 per km^2 (Figure 6.2). Elephants thus offer a solution to the bush encroachment problem,



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

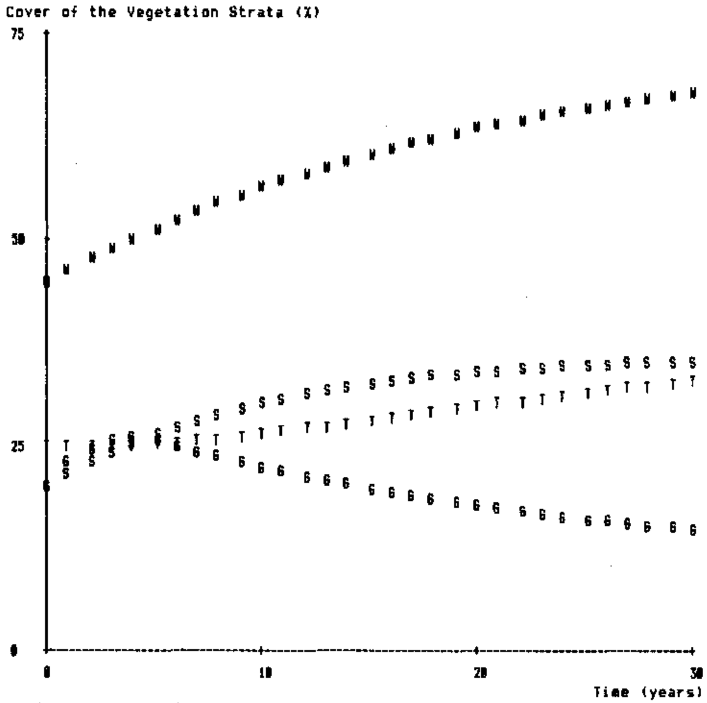
W : Total Woody Cover (%)	=	25.0	===>	55.7
T : Tree Cover (%)	=	20.0	===>	23.5
S : Shrub Cover (%)	=	5.0	===>	32.1
G : Perennial Grass Cover (%)	=	43.0	===>	22.9
: Interval between fires (years)	=	0.0	===>	0.0



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

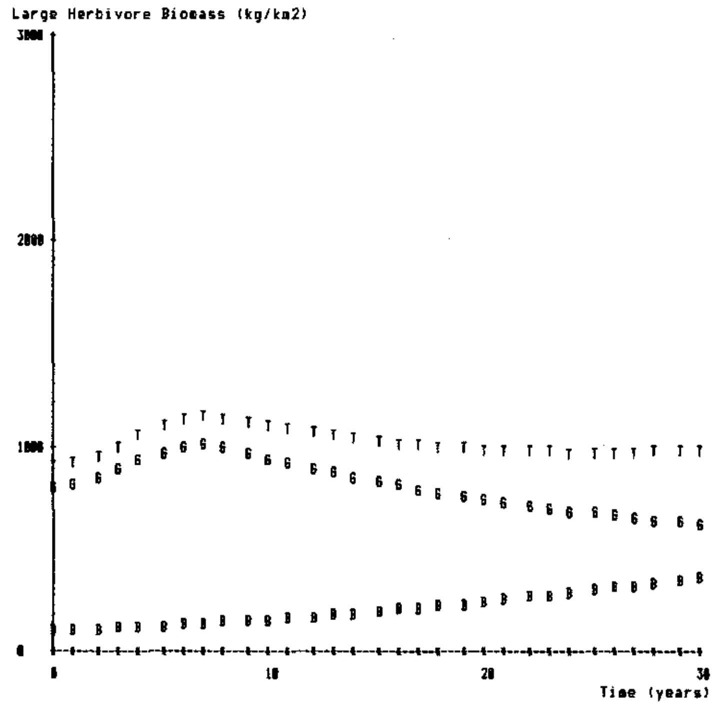
* : Elephant Biomass (kg/km2)	=	175	===>	175
B : Browser Biomass (kg/km2)	=	100	===>	839
G : Grazer Biomass (kg/km2)	=	1600	===>	891
T : Total Large Herbivore Biom (kg/km2)	=	1875	===>	1906
: Rel Growth rate Elephant Pop (%/yr)	=	0	===>	0
: Rel Growth rate Browser Pop (%/yr)	=	10	===>	10
: Rel Growth rate Grazer Pop (%/yr)	=	30	===>	30

Figure 7.4 Development of vegetation (left) and large herbivores (right) after 1980 on a well-managed ranch with a low and stable elephant population and in the absence of fire



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

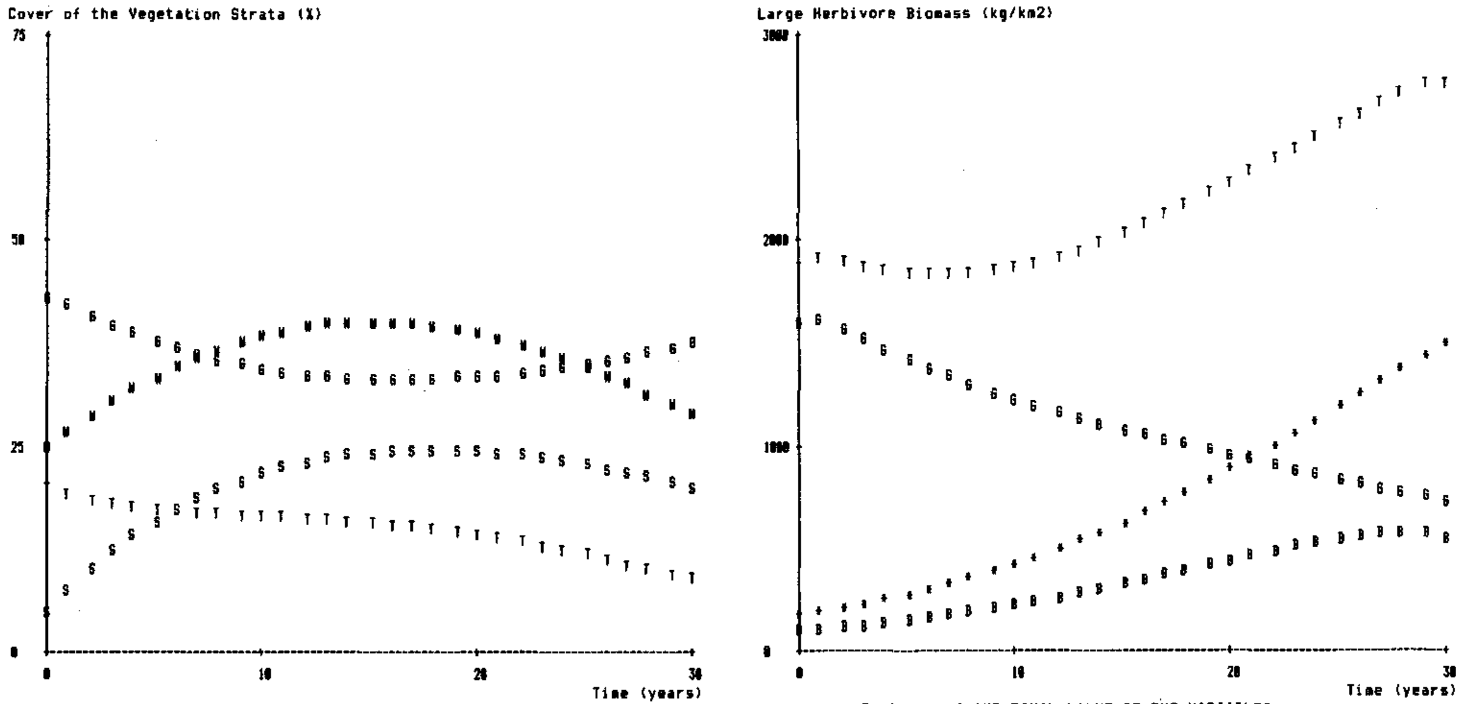
W :	Total Woody Cover (%)	=	45.0	===>	68.2
T :	Tree Cover (%)	=	25.0	===>	32.9
S :	Shrub Cover (%)	=	20.0	===>	35.3
G :	Perennial Grass Cover (%)	=	20.0	===>	14.5
:	Interval between fires (years)	=	0.0	===>	0.0



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

* :	Elephant Biomass (kg/km2)	=	0	===>	0
B :	Browser Biomass (kg/km2)	=	100	===>	376
G :	Grazer Biomass (kg/km2)	=	800	===>	609
T :	Total Large Herbivore Biom (kg/km2)	=	900	===>	985
:	Rel Growth rate Elephant Pop (%/yr)	=	0	===>	0
:	Rel Growth rate Browser Pop (%/yr)	=	5	===>	5
:	Rel Growth rate Grazer Pop (%/yr)	=	30	===>	30

Figure 7.5 Development of vegetation (left) and large herbivores (right) after 1980 on a previously poorly managed ranch in the absence of elephants and fire



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

Label	Name	Starting value		Final value
W	Total Woody Cover (%)	= 25.0	===>	27.8
T	Tree Cover (%)	= 20.0	===>	8.3
S	Shrub Cover (%)	= 5.0	===>	19.5
G	Perennial Grass Cover (%)	= 43.0	===>	38.3
	Interval between fires (years)	= 0.0	===>	0.0

LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

Label	Name	Starting value		Final value
*	Elephant Biomass (kg/km2)	= 175	===>	1549
B	Browser Biomass (kg/km2)	= 100	===>	503
G	Grazer Biomass (kg/km2)	= 1600	===>	704
T	Total Large Herbivore Biom (kg/km2)	= 1875	===>	2757
	Rel Growth rate Elephant Pop (%/yr)	= 10	===>	10
	Rel Growth rate Browser Pop (%/yr)	= 10	===>	10
	Rel Growth rate Grazer Pop (%/yr)	= 30	===>	30

Figure 7.6 Development of vegetation (left) and large herbivores (right) after 1980 on a well-managed ranch with strict protection of elephants and in the absence of fire

but the ranches will still face reduced grazing capacity for their domestic stock.

The other alternative to control bush encroachment is the use of fire. Figure 7.7 indicates the simulated effect of a fire, once every five years, on the vegetation structure and the large herbivore population. Because very few quantitative data are available on the effect of fire on the cover by the different strata, several assumptions were made.

- The intensity of fire is related to the amount of combustible material (Pratt and Gwynne, 1977). This is related to the production of the ground layer, and thus mainly to the cover by perennial grasses.
- Trees are little affected by fire (Section 4.1.2).
- Shrubs are fairly strongly affected (Section 4.1.2).
- Perennial grasses are affected also (Section 4.2.2).

The quantitative effect is estimated as follows: at the maximum perennial grass cover of 60 percent, the relative reduction in tree cover is 5 percent, in shrub cover 60 percent and in grass cover 10 percent of the present cover. The cover of the different strata after a fire can then be expressed in the following equations:

$$TC = (1 - PGC/1200 \times TC$$

$$SC = (1 - PGC/100) \times SC$$

$$PGC = (1 - PGC/600) \times PGC$$

in which TC = tree cover (percentage), SC = shrub cover (percentage), PGC = perennial grass cover (percentage).

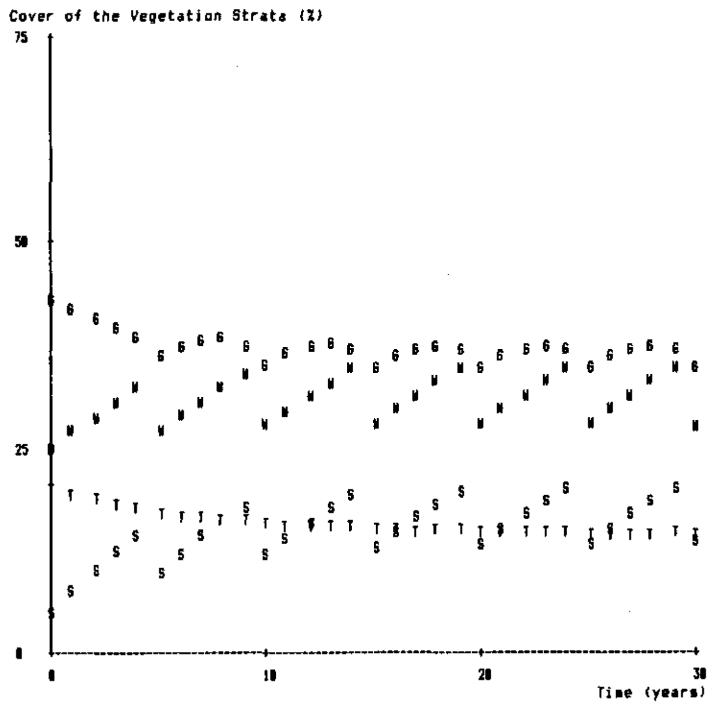
Figure 7.7 shows that with fires at five year intervals, a rather stable situation develops. With the quantitative effect of fire assumed here, the vegetation and the large herbivore population stabilize after 10 to 15 years. The shrub cover is somewhat higher than before; the grass cover–and the grazing capacity for grazing herbivores–is at a slightly lower level. The exact level of this equilibrium depends on the quantitative effect of fire, especially on the shrub cover.

Discussion

When deliberate manipulation of the vegetation is not part of the management of the ranches south of the Taita hills, all ranches will be faced with a strong increase of the woody vegetation and consequently a reduction of the grass cover–and thus a reduction of the grazing capacity for grazing herbivores.

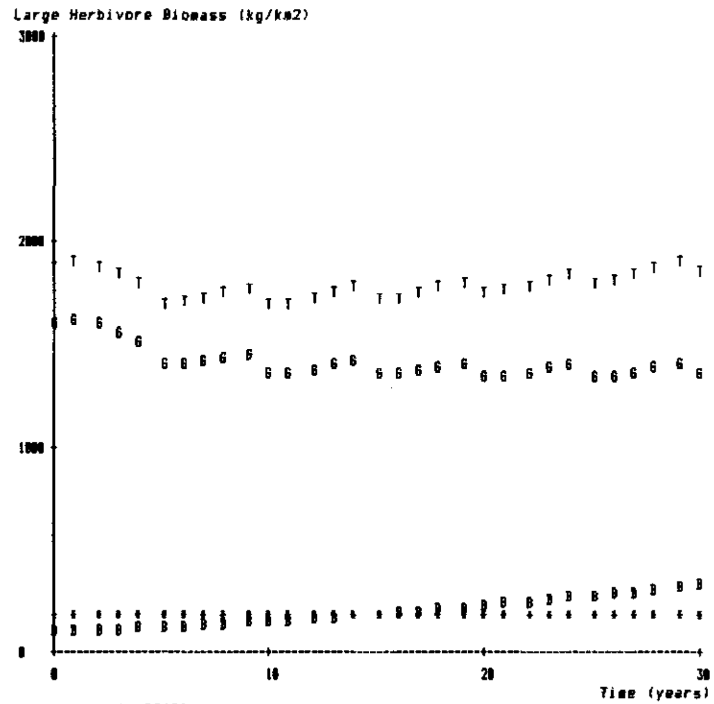
In the short term, it is unlikely that a change in the production objectives can help the ranches. Wildlife utilization or another type of domestic herbivore does not seem feasible at the moment. The only alternative is to maintain a maximal grazing capacity for grazing herbivores by controlling the bush encroachment.

Mechanical and chemical methods do not seem to be economically feasible. Thus the only options left are biologic and fire control of the woody vegetation. Elephants at higher density are capable of controlling the woody vegetation, but grazing herbivores benefit only partially from the increased availability of grass forage because a large part is consumed by elephants. The



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

W	: Total Woody Cover (%)	=	25.0	===>	29.5
T	: Tree Cover (%)	=	20.0	===>	14.2
S	: Shrub Cover (%)	=	5.0	===>	15.3
G	: Perennial Grass Cover (%)	=	43.0	===>	36.2
	: Interval between fires (years)	=	5.0	===>	5.0



LABEL, NAME, STARTING AND FINAL VALUE OF THE VARIABLES

*	: Elephant Biomass (kg/km2)	=	175	===>	175
B	: Browser Biomass (kg/km2)	=	100	===>	337
G	: Grazer Biomass (kg/km2)	=	1600	===>	1350
T	: Total Large Herbivore Biom (kg/km2)	=	1875	===>	1861
	: Rel Growth rate Elephant Pop (%/yr)	=	0	===>	0
	: Rel Growth rate Browser Pop (%/yr)	=	5	===>	5
	: Rel Growth rate Grazer Pop (%/yr)	=	30	===>	30

Figure 7.7 Development of vegetation (left) and large herbivores (right) after 1980 on a well-managed ranch with a low, stable elephant population and with the use of fire once every five years

conclusion is thus that fire has to be used on these ranches to control the woody vegetation and to maintain a high grazing capacity for grazing herbivores.

Although the quantitative data are very limited, there are some indications that fire can retard and may be even arrest bush encroachment in the absence of elephants. An important condition is that the area is not over-grazed so that the grass cover is high enough to produce enough combustible material to give a hot fire. Research in the application of fire–perhaps in combination with other methods–to control the woody vegetation would appear to be of utmost importance for the survival of the beef-producing ranches in the Tsavo ecosystem.

Chapter 8

FINAL REMARKS

The Tsavo ecosystem is a typical example of the very large area, so-called *"Commiphora-Acacia"* deciduous bushlands, or Nyika (see, for example, White, 1983) in east Africa: *ie*, semi- arid savanna ecosystems at low altitude, with a bi-modal rainfall regime and soils developed mainly from basement system rocks, with the associated large herbivore fauna. This can serve as a valid argument for conservation of the Tsavo ecosystem.

Approximately half of the ecosystem is conserved in Tsavo National Park East and West. Although the park covers a large area of approximately 21 000 km^2, this does not mean that the continued existence of the ecosystem is secure. The functioning of the ecosystem inside the park depends–in various ways–on what happens outside. Two examples have been described.

(1) Changes in land cover/land use outside the park cause changes in the flow regime of the rivers inside the park with associated floodplain remodelling and loss of valuable floodplain grasslands (Section 3.1.2).

(2) The increase in human population density outside the park causes an immigration of large herbivores into the park area, resulting in excessive growth rates of the large herbivore populations and "over- shooting" of the grazing capacity. The large scale starvation of elephants in the early 1970s has to be attributed, at least partially, to this effect (Section 2.3.2 and Chapter 5). Thus to ensure the healthy functioning of the national park, conservation measures should also include the area outside the park belonging to the same ecosystem. Combining the park and the ranches into one management unit, ultimately comprising the entire Tsavo ecosystem, could be a good starting point. By allowing free access of wildlife and giving it proper protection, ranches benefit somewhat through the impact of elephants on the woody vegetation. The ranches could also then more successfully participate in the tourist industry, which yields another benefit and could partially compensate for the reduction of grazing for their domestic stock.

The Tsavo ecosystem includes a wide variety in cover by trees, shrubs and grasses under the same climatic and soil conditions, because of the influence of elephants and–in some parts–also fire. The open woody cover and associated high grass cover inside the park may be judged by range-ecologists as a rangeland in good condition, very suitable for ranching. This is a very unstable situation, however, depending entirely on the effects of elephants on the woody vegetation as shown in Chapter 4. As demonstrated for the surrounding ranches, with elephants, domestic herbivores cannot benefit; without elephants, bush encroachment very quickly becomes a problem, with a resulting loss of grazing capacity for grazing herbivores (Section 7.2). Thus the perception of the area as a seemingly unused grazing resource, as is sometimes suggested, is certainly not accurate–especially in the long term.

In this study, we have tried to cover all major aspects of the ecosystem in their mutual relationships. This is thought to be indispensable for reaching a clear understanding of an ecosystem. Only on the basis of good knowledge of the functioning of an ecosystem can objective decisions be made on the management of the ecosystem as a whole–or of parts of it.

The use of models and simulation techniques made it necessary to select and define the relevant components of the ecosystem and their relationships, and to quantify them. The insight into future developments was greatly enhanced by these techniques. The models presented here can be expanded and improved when more data become available; especially more detailed data on the dynamics of the large herbivore populations, climate variation and the effect of fire on the woody vegetation are needed.

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TABLES AND FIGURES

TABLES

FIGURES

APPENDIX A:

Simulation Program

For the execution of the simulation runs, a small program was written in Microsoft BASIC, to run on a "8 bit, 64K RAM computer", with a dot matrix printer as output.

The listed program shows only the input and calculation of the variables. The output was printed with the help of a plotting sub-routine published by:

Burwell,A.D.M. and Topley,C.G. (1983)
Polyplot - an interactive modular program in basic for plotting graphs.
Computers and Geosciences Vol.9, No.2, pp. 157-209.

The variables used for the output are:

1. information for the bottom of the graph:
```
    N1     = number of variables
    L$(J)  = lable of variable
    S$(J)  = name of variable
    I(J)   = initial value
    V(J)   = final value
    X$     = lable x-axis
    Y$     = lable y-axis
```
2. information for plotting the graph:
```
    X(I)   = value of time unit
    Y(I)   = value of variable at time X(I)
    V$(I)  = lable of variable
```

Due to the small memory of the computer used, the program has been split in two parts, one to calculate and print the output of the changes of the vegetation strata, the other for the changes in the large herbivore population. Only the first program is given here. In the second part only the stored variables and labels are different; the calculations are the same.

Listing Program DYNETSG.BAS

```
10000 'FILE: DYNETSG.BAS
10010 PRINT CHR$(26)
10020 PRINT "*************** ELEPHANTS-FIRE-TREES-SHRUBS-GRASS **************"
10030 PRINT
10040 PRINT "A DYNAMIC MODEL, THAT DESCRIBES THE EFFECT OF ELEPHANTS AND FIRE"
10050 PRINT "     ON THE VEGETATION, AND THROUGH THE FORAGE AVAILABILITY"
10060 PRINT "              ALSO ON THE OTHER LARGE HERBIVORES.
10070 PRINT "         Part 1: Vegetation (part 2: Large Herbivores)
10080 PRINT "                Version 6, d.d. 9-4-1985
10090 PRINT "               WRITTEN BY: Willem VAN WIJNGAARDEN"
10100 PRINT "******************************************************************"
10105 'INPUT OF VARIABLES AND STARTING VALUES
10110 INPUT "   Duration of the run (years)                          = ";FT
10120 INPUT "   Relative Growth Rate of the Elephant population in %/yr= ";GE
```

```
10130 INPUT "   Relative Growth Rate of the Browser population in %/yr = ";GB
10140 INPUT "   Relative Growth Rate of the Grazer population in %/yr  = ";GG
10150 INPUT "   Rainfall during the 'long rains' (mm)                  = ";RL
10160 INPUT "   Interval between fires (years)                         = ";FI
10170 PRINT
10180 INPUT "        Initial Elephant Density (nr/km2)       = ";ED
10190 INPUT "        Initial Browser Population (kg/km2)     = ";G(2)
10200 INPUT "        Initial Grazer Population (kg/km2)      = ";G(3)
10210 INPUT "        Initial Tree Cover  (1 - 39 %)          = ";G(4)
10220 INPUT "        Initial Shrub Cover (1 - 36 %)          = ";G(5)
10230 INPUT "        Initial Perennial Grass Cover (1-60 %)  = ";G(6)
10235 'CHECK VALUE INPUTS
10240 G(1)=1750*ED
10250 WC=G(4)+G(5)
10260 PGM=60-.667*WC
10270 IF G(6)>PGM THEN G(6)=PGM
10280 GOSUB 13000
10290 IF G(1)>GCE THEN G(1)=GCE
10300 GOSUB 13090
10310 IF G(2)>GCB THEN G(2)=GCB
10320 IF G(3)>GCG THEN G(3)=GCG
10330 'STORAGE OF LABEL, NAME, STARTING AND FINAL VALUE OF VARIABLES
11000 N1=13
11010 L$(1)=" ":S$(1)="Elephant Biomass (kg/km2)":I(1)=G(1)
11020 L$(2)=" ":S$(2)="Browser Biomass (kg/km2)":I(2)=G(2)
11030 L$(3)=" ":S$(3)="Grazer Biomass (kg/km2)":I(3)=G(3)
11040 L$(4)=" ":S$(4)="Total Large Herbivore Biom.(kg/km2)":I(4)=G(1)+G(2)+G(3)
11050 L$(5)="W":S$(5)="Total Woody Cover (%)":I(5)=WC
11060 L$(6)="T":S$(6)="Tree Cover (%)":I(6)=G(4)
11070 L$(7)="S":S$(7)="Shrub Cover (%)":I(7)=G(5)
11080 L$(8)="G":S$(8)="Perennial Grass Cover (%)":I(8)=G(6)
11090 L$(9)=" ":S$(9)="Rel.Growth rate Elephant Pop.(%/yr)":I(9)=GE:V(9)=GE
11100 L$(10)=" ":S$(10)="Rel.Growth rate Browser Pop.(%/yr)":I(10)=GB:V(10)=GB
11110 L$(11)=" ":S$(11)="Rel.Growth rate Grazer Pop.(%/yr)":I(11)=GG:V(11)=GG
11120 L$(12)=" ":S$(12)="Rainfall during the'long rains'(mm)":I(12)=RL:V(12)=RL
11130 L$(13)=" ":S$(13)="Interval between fires (years)":I(13)=FI:V(13)=FI
11140 X$="Time (years)"
11150 Y$="Cover of the Vegetation Strata (%)"
11160 'CALCULATION AND STORAGE OF VARIABLES IN SIMULATION
12000 TT=0
12010 U=6
12020 I=1
12030 IF TT>FT THEN RETURN
12040 X(I)=TT
12050 Y(I)=WC
12060 V$(I)="W"
12070 I=I+1
12080 X(I)=TT
12090 Y(I)=G(4)
12100 V$(I)="T"
12110 I=I+1
12120 X(I)=TT
12130 Y(I)=G(5)
12140 V$(I)="S"
12150 I=I+1
12160 X(I)=TT
12170 Y(I)=G(6)
```

```
12180 V$(I)="G"
12190 I=I+1
12200 N=I-1
12205 'SIMPLIFIED RUNGE-KUTTA SUBROUTINE TO SOLVE SET OF DIFFERENTIAL EQUA.
12210 GOSUB 12440
12220 FOR J=1 TO U
12230 XP(J)=G(J)
12240 G(J)=G(J)+F(J)
12250 K1(J)=F(J)
12260 G(J)=XP(J)+K1(J)/2
12270 NEXT J
12280 GOSUB 12440
12290 FOR J=1 TO U
12300 K2(J)=F(J)
12310 G(J)=XP(J)+K2(J)/2
12320 NEXT J
12330 GOSUB 12440
12340 FOR J=1 TO U
12350 K3(J)=F(J)
12360 G(J)=XP(J)+K3(J)
12370 NEXT J
12380 GOSUB 12440
12390 FOR J=1 TO U
12400 K4(J)=F(J)
12410 G(J)=XP(J)+(K1(J)+2*K2(J)+2*K3(J)+K4(J))/6
12420 NEXT J
12430 TT=TT+1:GOTO 12510
12440 F(1)=GE/100*G(1)*(GCE-G(1))/GCE
12450 F(2)=GB/100*G(2)*(GCB-G(2))/GCB
12460 F(3)=GG/100*G(3)*(GCG-G(3))/GCG
12470 F(4)=.052*G(5)-.048*G(4)-2.857E-05*(G(4)+G(5))*G(1)
12480 F(5)=3.6-.1*G(5)-.001486*G(1)
12490 F(6)=10*(PGM-G(6))/PGM
12500 RETURN
12505 'CHECK VALUE VARIABLES AND OCCURRENCE OF FIRE
12510 IF FI=0 THEN GOTO 12530
12520 IF (N MOD 4*FI)=0 THEN GOSUB 14000
12530 IF G(4)>39 THEN G(4)=39
12540 IF G(4)<1 THEN G(4)=1
12550 IF G(5)>36 THEN G(5)=36
12560 IF G(5)<1 THEN G(5)=1
12570 WC=G(4)+G(5)
12580 PGM=60-.667*WC
12590 IF G(6)>PGM THEN G(6)=PGM
12600 IF G(6)<1 THEN G(6)=1
12610 GOSUB 13000
12620 IF G(1)>GCE THEN G(1)=GCE
12630 IF G(1)<0 THEN G(1)=0
12640 GOSUB 13090
12650 IF G(2)>GCB THEN G(2)=GCB
12660 IF G(2)<0 THEN G(2)=0
12670 IF G(3)>GCG THEN G(3)=GCG
12680 IF G(3)<0 THEN G(3)=0
12685 'TEMPORAY STORAGE OF FINAL VALUE VARIABLE
12690 V(1)=G(1)
12700 V(2)=G(2)
12710 V(3)=G(3)
```

```
12720 V(4)=G(1)+G(2)+G(3)
12730 V(5)=WC
12740 V(6)=G(4)
12750 V(7)=G(5)
12760 V(8)=G(6)
12770 GOTO 12030
12780 'CALCULATION FORAGE AVAILABILITY AND GRAZING CAPACITY
13000 GA=RL*5.4*G(6)
13010 BAT=RL*(.014920+1.0992*G(4)-8.9902E-03*G(4)^2)
13020 BAS=RL*(-4.5356+8.7510*G(5)+.017894*G(5)^2-5.6060E-03*G(5)^3+5.4634E-05*
      G(5)^4)
13030 BA=BAT+BAS
13040 GCE=(BA+GA)*.2
13050 IF GCE>BA*2 THEN GCE=BA*2
13060 IF GCE>GA*.667 THEN GCE=GA*.667
13070 IF GCE<0 THEN GCE=0
13080 RETURN
13090 ECT=G(1)*4.5
13100 ECB=BA/(GA+BA)*ECT
13110 IF ECB<.1*ECT THEN ECB=.1*ECT
13120 ECG=ECT-ECB
13130 IF ECG<.3*ECT THEN ECG=.3*ECT
13140 ECB=ECT-ECG
13150 RB=BA-ECB
13160 RG=GA-ECG
13170 GCB=RB/4.5
13180 IF GCB<0 THEN GCB=0
13190 GCG=RG/4.5
13200 IF GCG<0 THEN GCG=0
13210 RETURN
13220 'CALCULATION EFFECT FIRE ON VEGETATION
14000 G(4)=(1!-G(6)/1200)*G(4)
14010 G(5)=(1!-G(6)/100)*G(5)
14020 G(6)=(1!-G(6)/600)*G(6)
14030 RETURN
```

SUMMARY

The objective of this publication was to quantify the climate - soil - vegetation - large herbivore interactions in the Tsavo ecosystem and to develop a model describing those relationships quantitatively. The various components of the Tsavo ecosystem and their dynamics are described, followed by the development of a mathematical model and various simulations of the management options for the park and nearby ranches in the near future.

The Tsavo area is located in southeastern Kenya between 2° and 4°S and 37°30′ and 39°30′E. It lies 70 to 250 km from the coast and comprises approximately 40000 km² of arid bushland at an altitude of 200 to 1000 m. In 1948, 21000 km² were set aside as a national park. Large parts of the remaining area were developed in the 1960s into large-scale commercial cattle ranches.

The climate of the Tsavo area is typical equatorial semi- arid, with an average annual rainfall of 200 to 700 mm, falling in two short rainy seasons. The area is crossed by only one permanent river system, the Tsavo-Athi-Galana, and two major seasonal rivers, the Voi and Tiva. All have their major water supply outside the study area in higher rainfall areas. Natural waterholes, which often contain water for as long as four months into the dry season, are an important source of water for the wildlife.

The landscape is not very spectacular. Most of the area consists of flat, featureless plains developed on various kinds of parent material. The soils are generally deep, well-drained and rather acid, except near the major rivers where the landscape has been rejuvenated; here the soils are shallow, stony and fairly rich. In the eastern part, subrecent marine sediments are found in which poorly drained, alkaline and often saline soils have developed. An important soil characteristic, the infiltration capacity, seems to be related more to the vegetation cover than to the differences in soil type.

The vegetation generally reflects the semi-arid climate; the open woody canopy is dominated by deciduous species which are in leaf only during the short rainy seasons. The ground layer is dominated by short to medium-tall perennial grasses.

The floristic composition reflects the physical environment. Nine major plant communities are recognized on the basis of the presence or absence of groups of species. Each community indicates a particular soil condition (depth, drainage and fertility). Within each community, several variants are established which were used to define and map the bio-climatic zones. The structure (percentage cover by trees and shrubs) is independent of the floristic composition. Variations in structure within each community are related to density of elephants and/or the occurrence of fire.

Vegetation production in Tsavo is not limited by the availability of nutrients. Especially nitrogen seems to be in ample supply, judging from the high concentrations of nitrogen in plant tissue throughout the year. On some soil types, phosphorus may limit primary production only in wet years.

Vegetation production can be very well explained by the rainfall and the cover of the relevant stratum. The production of the ground layer is closely related to the cover by perennial grasses. Annual grasses and forbs contribute less in quantity and also less in predictability. Browse production can be sufficiently predicted by rainfall and the percentage cover of the woody species when their respective browse intensities are taken into account. Moderately browsed shrubs and trees are most productive, followed by the strongly browsed woody species. An absence of browsing results in the lowest browse production per amount of rainfall.

The Tsavo ecosystem harbours a wide variety of wildlife, dominated by elephants. With a density of approximately one elephant per km², Tsavo does not rank very high among areas with high elephant densities but, considering the semi-arid climate, it represents a very high animal biomass. In addition to elephants, there is a variety of other large herbivores, such as black rhinoceros, buffalo, giraffe, zebra, oryx, eland and several other antilopes.

Soil dynamics

The destruction of the woody vegetation in the Tsavo area has little effect on the soils. Most of the time, the only effect is an increased infiltration rate of the soil and a slightly higher organic carbon content of the topsoil, related to the better grass cover.

Erosion in the Tsavo area is related mainly to human activities. Agriculture alone, or in combination with grazing, is responsible for most of the present erosion.

The presence of large concentrations of wild herbivores does not seem to have any negative effect on the soils. In the area surrounding the Galana river, for example, the landscape and the soils have probably evolved under this large herbivore pressure and are in equilibrium with it. This equilibrium has not been reached yet at Aruba dam, but it is unlikely that serious soil erosion will degrade a large area in the future.

A beneficial side-effect of the concentration of herbivores near the dry season water supplies is the local enrichment by phosphorus in the soil. Although higher phosphorus content was not found in vegetation samples, there are some indications that leguminous forbs are more common in this area and that the regeneration of perennial grasses and *Acacia* spp is very good. An enlargement of the area of mineral accumulation can be expected in the very long term in the area around Aruba dam; the radius of the affected area after 25 years is only approximately 500 m, while along the Galana river, a natural concentration site of long standing, there is a band approximately 3 km wide.

Vegetation dynamics

The vegetation dynamics of the Tsavo area is confined mainly to that of the structure (cover by different strata). Species fluctuate in abundance, but not much in presence. Only a very small group of species, confined to the vegetation with a dense woody cover, does not regenerate easily. They do not, however, form a very essential part of the woody stratum.

Quantitative data on vegetation dynamics are available from only one particular part of the ecosystem, namely that of the well-drained deep soils in bio-climatic zones Vb, VIa and VIb. This covers a large part of the ecosystem (approximately 50 percent), however, and there are no good reasons why relationships should, in principle, be very different in other soil and climate conditions.

The dominant impact on the vegetation is the destruction of the woody vegetation by elephants. Mature trees are nearly eliminated when elephant density is higher than approximately one per km²; shrubs and the recruitment/replacement of trees are effected somewhat less. The ultimate cover by both trees and shrubs will be only approximately 1 percent at a continuous elephant density of 1.5 per km², however.

Regeneration of the woody vegetation upon reduction of the elephant pressure is remarkable. Nearly all important woody species apparently have the capability to overcome easily a drastic reduction in biomass. Trees such as *Commiphora* spp regenerate prolifically from the base of the stem when they are pushed over–or even from the larger roots. They maintain this capacity over a period of at least 25 years after continuously being destroyed down to ground level. The presence of those species in the vegetation is thus not threatened by intensive elephant browsing.

As a result of the destruction of the woody vegetation by elephants, the cover of the herbaceous vegetation increases. The maximum cover by perennial grasses is limited by the total woody cover. This maximum cover, however, is not always reached. The main reasons for this are the effects of herbivory and fire. Wet season consumption by large herbivores has very little influence when grazing is not concentrated in one particular area. As soon as consumption in the dry season exceeds 45 percent, there is a decrease in cover by perennial grass. Annual fires also have a detrimental effect on the cover by perennial grasses.

When the perennial grass cover is not maximal, the open space is taken up by annual grasses and forbs. Which annual grasses and forbs take up the space probably depends on their germination biology, for which no data are available. Short-term variation of rainfall does not have an effect on the cover by perennial grasses; their often observed decrease in dry years has to be attributed to herbivory (over-grazing).

Large herbivore population dynamics

Data on the dynamics of the large herbivore populations in the Tsavo ecosystem are available for only some aspects and some species. Still, some important conclusions can be drawn.

Comparison of the composition of the large herbivore populations inside and outside the park revealed large differences. Outside the park, domestic animals have taken the place of the water-dependent species. Other wild herbivores, not water-dependent, however, showed a slightly higher biomass per unit area outside the park.

The human encroachment along the edges of the Tsavo ecosystem began in the last 20 to 30 years. As a result, probably large numbers of wild herbivores have immigrated in that period into the park area, although this is not recorded with accurate data on animal numbers. The replacement of wild herbivores outside the park by domestic animals is not only a question of competition for food or water. A large number of these wild herbivores were browsers and mixed feeders, and they are replaced mainly by predominantly grazing domestic animals.

The disappearance of the browsing and mixed feeding wild herbivores can be explained only by poaching, which has to be seen as the factor having the largest short-term impact on the large herbivore populations in the Tsavo ecosystem. In the period 1976 to 1980, approximately 70 percent of the elephant population and more than 90 percent of the rhinoceros population were killed by poachers.

In the absence of poaching, forage availability limits the maximum size of the large herbivore populations. Especially the quantity of forage is important because the quality–in terms of protein content–is never a limiting factor. Calculation of the herbivore requirements and the quantity of available forage revealed that in the dry year of 1971 not enough food was available in the central part of Tsavo National Park East for the whole large herbivore population on a maintenance level, which explains the death of approximately 6000 elephants in this area during the drought period.

The stocking density considered as "safe" by ranch managers also correlated very well with the "grazing capacity" calculated on the basis of forage availability in a dry year.

The only solid conclusion that can be drawn to date on the dynamics of the large herbivore populations is that, in the absence of poaching, the maximum populations are determined by forage availability in a dry year. There is an excessive supply of forage in normal or wet years when rainfall is at least three times as high as in dry years. In those years, large herbivores can be very productive. The populations then exceed the grazing capacity of subsequent dry years, which results in large numbers of animals starving to death. Data on birth and death rates are too few to permit presentation of rates of change of the sizes of the large herbivore populations in the Tsavo ecosystem. Despite climatic hardships, however, it is shown that poaching has been the major factor controlling numbers of certain species in the last decade.

The elephant - trees - grass - grazers model

The models developed here are empirical because the interrelationships upon which they are based are derived from (field) observations and not from theoretical considerations. Both a static and a dynamic model were developed. The static model describes the equilibrium values of the percentage cover of the different strata of the vegetation and the biomass of the different groups of large herbivores in relation to the elephant density.

The most important conclusions are:

- A high percentage cover of trees and/or shrubs is possible only with a very low elephant density (less than 0.2 per km^2).
- In the long term, the elephant density will never exceed approximately 1.3 elephants per km^2 because of limitations in the available forage of the right type and quantity.
- Browsers can attain high densities only at low elephant densities.
- Grazers attain their maximum densities at moderate elephant densities, although at high elephant densities more grass forage is available–but much of this is consumed by the elephants themselves.

By defining the rate of change of the components in the static model, this model is transformed into a dynamic one. The major problem encountered was the lack of data on the dynamics of the large herbivore populations. It was assumed that they followed a "logistic growth model".

With the dynamic model, the development in time of the percentage cover of the different vegetation strata and the biomass of the different groups of large herbivores can be simulated, starting at a specified level. The dynamic model can thus be used to show quantitatively the long-term consequences of a number of conclusions drawn from observations made in a relatively short period. The dynamic model was tested in a few sample simulations. They confirmed, quantitatively, previous ideas about the functioning of the Tsavo ecosystem.

Management implications for Tsavo National Park

On the assumption that the management objective for Tsavo National Park in the near future will remain the "laissez faire" policy, three scenarios are presented:

(1) Complete control of elephant poaching. The effect in 20 to 30 years will be a situation similar to that of the early 1970s, with a risk of large-scale mortality of elephants in a dry year and a low percentage cover of the woody vegetation.

(2) Partial control of poaching; a stable elephant population. Shrub and tree cover will increase fairly quickly, but will still permit a reasonable grass cover and thus a moderate grazer population.

(3) Continued poaching problem. The continuous decrease in the elephant population will permit a quick and strong increase of the shrub and tree cover, but perennial grasses, and thus grazers, will become rare. Only browsers, if well protected, will benefit from this situation.

If Tsavo is to remain interesting for tourists (attracted mainly by large numbers of a variety of easily visible large herbivores), then poaching should be controlled to at least some extent. Whether complete control of poaching and the consequent situation are desirable depends entirely on subjective views on conservation.

Management implications for the ranches

Several scenarios were also simulated for the ranches. The results indicate that, in the absence of fire, all ranches will be faced with a reduction of the grazing capacity for domestic herbivores in the near future (within 10 years). If sufficient elephants are not present to control the woody vegetation, bush encroachment will reduce grazing capacity. At high elephant densities, however, they will themselves consume a large part of the available grass forage. The only option seems to be to control the woody vegetation by fire because other methods do not seem to be economically feasible at present. Knowledge of the quantitative effect of fire on woody vegetation in this environment is very limited, however, so detailed recommendations cannot be given.

OLIFANTEN - BOMEN - GRAS - GRAZERS; interacties tussen klimaat, bodem, vegetatie en grote herbivoren in een semi-aride savanna-ecosysteem (Tsavo-Kenya).

SAMENVATTING

Het doel van deze publicatie is om de interacties tussen klimaat, bodem, vegetatie en grote herbivoren in het Tsavo-ecosysteem te beschrijven, om deze relaties te kwantificeren en een rekenkundig model te ontwikkelen waarin deze relaties ook kwantitatief worden aangeduid. Met dit model worden verschillende beheersmogelijkheden voor het park en de omliggende "ranches", extensieve veeteeltbedrijven, gesimuleerd.

Beschrijving van het gebied

Het Tsavo ecosysteem ligt in Zuidoost-Kenya. Het omvat ongeveer 40000 km² semi-aride savannes op een hoogte van 200 tot 1000 meter. In 1948 is 21 000 km² hiervan gereserveerd als nationaal park en in de jaren zestig ontstonden in de rest ranches. Het klimaat wordt gekarakteriseerd door twee droge en twee natte seizoenen per jaar. De gemiddelde regenval varieert van 200 tot 700 mm per jaar.

De geologische formaties in het Tsavo gebied behoren merendeels tot de "Basement System Rocks", die bestaan uit diverse soorten gneisses. Het landschap bestaat voornamelijk uit grote vlakten, waar alleen een paar kleine "Inselbergs" en het Yatta-plateau bovenuit steken. Het gebied wordt slechts door één permanente rivier en twee belangrijke semi-permanente rivieren doorkruist, die echter alle drie buiten het ecosysteem ontspringen in gebieden met een hogere neerslag. Natuurlijke "waterholes" vormen in de eerste paar maanden van de droge tijd een belangrijke bron van water voor de wilde dieren.

De bodem is over het algemeen diep, goed gedraineerd en nogal zuur, behalve in de buurt van de grote rivieren, waar de bodem ondiep, stenig en tamelijk rijk is. In het oostelijke deel bevinden zich sub-recente mariene afzettingen waarin zich slecht gedraineerde, basische, en vaak zoute gronden hebben ontwikkeld. Een belangrijke bodemeigenschap, de infiltratie-capaciteit, lijkt meer gerelateerd te zijn aan de bedekking van de bodem door de vegetatie dan aan verschillen in bodemtype. De vegetatie weerspiegelt het semi-aride klimaat: de boom- en struiklaag vormt slechts een open bedekking en de bomen en struiken behoren voornamelijk tot de bladverliezende soorten. De kruidlaag wordt gedomineerd door lage tot middelmatig hoge overjarige grassen.

De floristische samenstelling van de vegetatie vertoont een nauw verband met de fysische milieu- omstandigheden. Op basis van het al dan niet voorkomen van bepaalde groepen plantensoorten zijn negen belangrijke plantengemeenschappen te onderscheiden. Elk van deze gemeenschappen indiceert een bepaalde bodemgesteldheid wat betreft diepte, drainage en vruchtbaarheid. Binnen elke gemeenschap konden een aantal varianten worden onderscheiden, die werden gebruikt om de bioklimatologische zones te definiëren en te kaarteren. De structuur van de vegetatie (bedekkingsgraad van bomen en struiken) blijkt onafhankelijk te zijn van de soortensamenstelling. De variatie in structuur binnen elke plantengemeenschap is gerelateerd aan de dichtheid van olifanten en/of het voorkomen van branden.

De productie van de vegetatie in het Tsavo ecosysteem wordt niet gelimiteerd door de beschikbaarheid van mineralen, die in voldoende mate beschikbaar zijn in de grond. Vooral stikstof blijkt voldoende aanwezig te zijn, gezien het relatief hoge gehalte in de planten gedurende het gehele groeiseizoen. Alleen op enkele arme gronden kan fosfaat een limiterende factor zijn voor de primaire produktie, en dat alleen in natte jaren.

De productie van de vegetatie kan zeer goed worden verklaard met de regenval en de bedekkingsgraad van de relevante vegetatie component. Zo is de productie van de kruidlaag nauw gerelateerd aan de bedekkingsgraad van overjarige grassen en de regenval; éénjarige grassen en kruiden dragen minder bij, zowel in kwantiteit als in voorspelbaarheid. De grootte van de productie aan "browse", kan goed worden verklaard met de regenval en de bedekkingsgraad van de bomen en struiken, waarbij rekening gehouden moet worden met de mate waarin browse gegeten wordt. (Het begrip "browse" heeft geen equivalent nederlands woord; het omvat knoppen, jonge twijgen, scheuten, bladeren en vruchten waarmee bepaalde dieren (browsers) zich voeden. Het woord, evenals afgeleide woorden zoals browsers, browsing etc, zal hier verder onvertaald blijven). Bomen en struiken die matig gegeten worden zijn het meest productief, gevolgd door die waarvan de bladeren en twijgen veel gegeten worden, terwijl bomen en struiken die niet gegeten worden het minst productief zijn.

Het Tsavo gebied herbergt een grote verscheidenheid aan wilde dieren, gedomineerd door de olifant met een dichtheid van ongeveer 1 olifant per km^2. Ofschoon dit in absolute zin niet erg hoog is, is er, gezien het semi-aride klimaat, toch sprake van een hoge dierlijke biomassa. Afgezien van olifanten is er nog een flink aantal grote herbivoren, zoals zwarte neushoorns, buffels, giraffes, zebras, oryx, elanden en verschillende andere antilopen.

Dynamiek van de bodem

De bodem in het Tsavo ecosysteem is op korte termijn relatief stabiel. De destructie van de boom- en struikvegetatie heeft meestal alleen een verhoging van de infiltratiecapaciteit van de bodem en een enigszins verhoogd organische stof gehalte tot gevolg, hetgeen verband houdt met een betere grasbedekking. Erosie komt voornamelijk voor als gevolg van menselijke activiteiten. Akkerbouw, al dan niet gecombineerd met begrazing, is momenteel de belangrijkste oorzaak van erosie.

Grote concentraties van wilde dieren blijken geen negatieve invloed op de bodem te hebben. Een duidelijk voorbeeld hiervan is het gebied langs de Galana rivier, waar in de droge tijd grote aantallen dieren voorkomen. Waarschijnlijk is het landschap met zijn bodem hier geëvolueerd onder deze grote druk van de herbivoren en is er daardoor mee in evenwicht. In het geval van de Aruba dam is dit evenwicht nog niet bereikt, maar het is onwaarschijnlijk dat een groot gebied in de toekomst zal worden aangetast door erosie.

Een positief effect van de concentratie van herbivoren bij drinkwaterplaatsen is de lokale verrijking van de grond met vooral fosfor. Ofschoon er geen hoger fosfaat gehalte werd gevonden in de vegetatie monsters, zijn er aanwijzingen dat vlinderbloemige kruiden hier talrijker zijn en dat de regeneratie van overjarige grassen en *Acacia* spp buitengewoon goed is. Op lange termijn mag een vergroting van het gebied met een accumulatie aan mineralen rondom de Aruba dam verwacht worden, aangezien na 25 jaar de invloed pas tot ongeveer 500 m van de dam rijkt, terwijl langs de Galana rivier,van oudsher een natuurlijk concentratiegebied van wild, zich een verrijkte strook van 3 km breedte bevindt.

Dynamiek van de vegetatie

De dynamiek van de vegetatie in het Tsavo gebied beperkt zich voornamelijk tot de structuur van de vegetatie. De individuele soorten fluctueren in kwantiteit, maar veel minder in voorkomen (presentie of absentie). Slechts een zeer kleine groep soorten, alleen voorkomend in de vegetatie met een hoge bedekkingsgraad van bomen en struiken, regenereert slecht. Deze groep vormt echter geen essentieel deel van de bos- en struikvegetatie. Alleen van de vegetatie op goed gedraineerde, diepe gronden in de bioklimatologische zones Vb, VIa en VIb (jaarlijkse regenval 250 tot 650 mm), zijn kwantitatieve gegevens beschikbaar over de dynamiek van de vegetatie. Deze zones vormen echter ongeveer de helft van het ecosysteem en er zijn bovendien geen goede redenen om aan te nemen dat de relaties in het overige deel van het ecosysteem principieel anders zijn.

De dominerende invloedsfactor op de vegetatie is de destructie van bomen en struiken door olifanten. Bij een olifantendichtheid van meer dan één per km^2 worden volwassen bomen bijna geheel geëlimineerd; struiken en opslag van bomen wat minder snel. Uiteindelijk blijft er slechts een bedekking van 1 procent bomen en struiken over bij een constante olifantendichtheid van 1.5 per km^2. De regeneratie van de bomen en struiken bij een vermindering van de olifantendichtheid is opmerkelijk. Bijna alle belangrijke boom- en struiksoorten blijken de capaciteit te hebben om een drastische reductie in hun biomassa gemakkelijk te boven te komen. Bomen zoals *Commiphora* spp, regenereren rijkelijk vanuit de stamvoet als ze omvergeduwd zijn, of zelfs vanuit de grotere wortels. Ze behouden dit vermogen gedurende een periode van tenminste 25 jaar, na steeds weer tot op de grond te zijn vernietigd. De aanwezigheid van deze soorten komt dus blijkbaar niet in gevaar door de intensieve browsing activiteiten van de olifanten.

Als gevolg van de reductie van de bedekkingsgraad van bomen en struiken krijgen de grassen de kans om zich uit te breiden. De bedekkingsgraad van overjarige grassen is gelimiteerd door die van bomen en struiken. Deze maximale bedekking met overjarige grassen wordt echter niet altijd gehaald als gevolg van branden en begrazing door herbivoren. Begrazing door grote herbivoren in de natte tijd heeft weinig effect op de overjarige grassen, als ze tenminste niet al te geconcentreerd plaatsvindt. Maar zodra in de droge tijd meer dan 45 procent van de biomassa aan overjarige grassen gegeten wordt, zal de bedekkingsgraad van deze grassen verminderen. Jaarlijkse branden hebben eveneens een negatief effect op de bedekking met overjarige grassen. In het geval dat de overjarige grassen niet hun maximale bedekkingsgraad halen, wordt de open plaats ingenomen door een verscheidenheid aan éénjarige grassen en kruiden. Welke soorten dat precies zijn hangt waarschijnlijk af van het kiemgedrag van de éénjarigen; hierover zijn voor dit gebied geen gegevens bekend.

Variaties in regenval over kortere periodes (minder dan drie jaar) hebben geen effect op de bedekkingsgraad van overjarige grassen. De vermindering daarvan in droge jaren moet toegeschreven worden aan overbegrazing.

Dynamiek van de populatie der grote herbivoren

Er zijn slechts een beperkt aantal gegevens beschikbaar over de dynamiek van de populatie van grote herbivoren in het Tsavo-ecosysteem. Toch konden er een paar belangrijke conclusies worden getrokken.

De populatiedichtheid van de grote herbivoren binnen en buiten het park vertoont enkele belangrijke verschillen. Koeien, geiten en schapen hebben buiten het park de plaats ingenomen van vooral die wilde herbivoren die van water afhankelijk zijn. De andere wilde herbivoren vertonen daar zelfs een iets hogere dichtheid. Het opdringen van de menselijke bevolking langs de randen van het Tsavo-ecosysteem begon zo'n 20 tot 30 jaar geleden. Als gevolg hiervan hebben waarschijnlijk vele wilde herbivoren hun toevlucht gezocht binnen de grenzen van het park. Betrouwbare gegevens in de vorm van tellingen zijn hierover echter niet beschikbaar.

Het verdringen van de van water afhankelijke wilde herbivoren door gedomesticeerde dieren buiten het park is niet alleen een kwestie van concurrentie wat betreft voedsel of water. Een groot deel van de wilde herbivoren waren "browsers" en dieren met een gevarieerde voedselkeuze, en ze zijn vervangen door voornamelijk grasetende gedomesticeerde herbivoren. Het verdringen van deze groep wilde herbivoren kan alleen verklaard worden doordat er buiten het park meer gestroopt wordt. Op korte termijn is het stropen de factor die de grootste invloed heeft op de populatie van grote herbivoren in het Tsavo-ecosysteem. In de periode van 1976 tot 1980 is ongeveer 70 procent van de olifanten en meer dan 90 procent van de zwarte neushoorns door stropers omgebracht. Als er niet gestroopt wordt, wordt de maximale grootte van de populatie van grote herbivoren bepaald door de mate waarin voer beschikbaar is in een droog jaar. Speciaal de hoeveelheid voer is van belang, daar de kwaliteit, uitgedrukt in het ruw eiwitgehalte, altijd voldoende is.

Een becijfering van de hoeveelheid beschikbaar voer in het droge jaar 1971 en de behoefte van de grote herbivoren maakte duidelijk dat er in deze droogte niet genoeg voer beschikbaar was voor de gehele dierenpopulatie; dit verklaart de dood van ongeveer 6000 olifanten in dit gebied in die periode. De begrazingsdichtheid met koeien die door de managers van de ranches als veilig wordt beschouwd komt ook goed overeen met het aantal koeien dat kan overleven op grond van de hoeveelheid beschikbaar voer, zoals berekend voor een droog jaar.

De enige goed gefundeerde conclusie over de dynamiek van de populatie van grote herbivoren die dus tot nu toe kan worden getrokken is dat, als er tenminste niet gestroopt wordt, de maximale grootte van de populatie van grote herbivoren wordt bepaald door de beschikbaarheid van voer in een droog jaar. In jaren met een normale of overvloedige neerslag is er een overvloed aan voer. In zulke jaren kunnen de populaties van grote herbivoren flink groeien. De onvoorspelbare, maar steeds terugkerende droge jaren zullen dan tot gevolg hebben dat grote aantallen dieren omkomen vanwege gebrek aan voedsel. Het is evenwel aangetoond dat ondanks deze klimatologisch bepaalde ontberingen het stropen de belangrijkste oorzaak is van de lage aantallen van bepaalde diersoorten in de laatste 10 jaar.

Het Olifanten - Bomen - Gras - Grazers model

Een tweetal modellen zijn ontwikkeld, gebaseerd op de onderlinge relaties van de verschillende componenten van het Tsavo- ecosysteem. Het zijn empirische modellen, omdat ze gebaseerd zijn op (veld)waarnemingen en niet op theoretische overwegingen. Zowel een statisch als een dynamisch model zijn ontwikkeld. Het statische model beschrijft de evenwichtswaarden van de bedekkingsgraad van de verschillende vegetatielagen en de biomassa van verschillende groepen grote herbivoren in relatie tot de olifantendichtheid.

De belangrijkste conclusies zijn:

- een hoge bedekkingsgraad van struiken en vooral bomen is alleen mogelijk bij een zeer lage olifantendichtheid (minder dan 0.2 per km^2);
- de olifanten dichtheid zal nooit meer dan ongeveer 1.3 per km^2 zijn, vanwege de beschikbaarheid van voer;
- "browsers" kunnen alleen in aanzienlijke aantallen voorkomen bij een lage olifantendichtheid;
- graseters zijn het grootst in aantal bij een matig hoge olifantendichtheid, ofschoon de hoeveelheid beschikbaar gras het grootst is bij hoge aantallen olifanten. In het laatste geval wordt een groot deel van het gras echter reeds door de olifanten zelf opgegeten.

Door het tempo van verandering van de componenten in het systeem erbij te betrekken, verandert het statische model in een dynamisch model. Het grootste probleem hierbij was om de dynamiek van de populatie van grote herbivoren te kwantificeren. Aangenomen werd dat zij het zogenaamde "logistieke groeimodel" volgden. Met het dynamische model kunnen simulaties worden uitgevoerd hoe, vanuit een bepaalde beginsituatie, de bedekkingsgraad van de verschillende lagen in de vegetatie en de biomassa van de verschillende groepen grote herbivoren zich in een bepaald tijdsbestek ontwikkelen. Het dynamische model kan derhalve worden gebruikt om kwantitatieve voorspellingen te doen voor een relatief lange periode (enkele tientallen jaren), op grond van gegevens verzameld in een relatief korte periode (3 tot 8 jaar).

Gevolgtrekkingen voor het beheer van het Tsavo Nationaal Park

Drie verschillende scenario's zijn gesimuleerd, die er elk vanuit gaan dat het beheersbeleid in de naaste toekomst hetzelfde blijft zoals dat tot nu toe was, nl: een "laissez faire" beleid, dat wil zeggen, een minimum aan ingrepen en stricte bescherming. Of de (stricte) bescherming gerealiseerd kan worden, hangt af van de capaciteit van de beheerders om het stropen te beteugelen. De volgende scenario's worden onderscheiden:

- Het stropen wordt met succes ten volle bestreden. Het resultaat zal zijn dat in 20 tot 30 jaar tijd een situatie zal zijn bereikt die vergelijkbaar is met die in de beginjaren zestig: een sterk gegroeide populatie van grote herbivoren en een lage bedekkingsgraad met bomen en struiken met het risico van een op grote schaal afsterven van olifanten in een extreem droog jaar. Er zal echter geen permanente schade aan bodem of vegetatie plaatsvinden. Alle processen zijn omkeerbaar.
- De omvang van het stropen wordt beperkt. De beperking is zodanig, dat de olifantenpopulatie ongeveer stabiel blijft. In dat geval zal de bedekkingsgraad van bomen en struiken vrij snel iets toenemen, maar zal nog steeds een redelijk goede grasbedekking toestaan en dus een matig grote populatie van grasetende herbivoren.
- Het stropen gaat onbeperkt door. De olifantenpopulatie zal in dit scenario blijven afnemen. De bedekkingsgraad van bomen en struiken zal daarom sterk toenemen tot hoge waarden. Daarmee verdwijnen de overjarige grassen en dus de grazers. Alleen de "browsers" zullen van deze situatie kunnen profiteren, als zij tenminste wel goed worden beschermd.

Om het Tsavo gebied interessant te houden voor toeristen (vooral aangetrokken door een verscheidenheid van flinke aantallen grote, gemakkelijk zichtbare herbivoren), zal het stropen op zijn minst behoorlijk beperkt moeten worden, anders zal het aantal dieren te laag worden en dit geringe aantal zal bovendien door de dichte begroeiing nagenoeg onzichtbaar zijn.

Gevolgtrekkingen voor het beheer van de "ranches"

Op een zelfde manier als voor het park zijn hier ook een aantal scenarios gesimuleerd. De conclusie is dat men op alle ranches met een vermindering van de koeienpopulatie rekening zal moeten houden, als men de boom- en struikvegetatie niet bestrijdt met vuur of op een andere manier. Zouden in deze gebieden voldoende olifanten voorkomen, dan zou de bedekkingsgraad van bomen en struiken beperkt blijven, maar de grote hoeveelheid gras die dan beschikbaar komt, wordt voor een groot deel al door de olifanten zelf geconsumeerd. Zonder olifanten zal de toeneming van bomen en struiken zo sterk zijn dat er weinig gras meer beschikbaar zal zijn.

Omdat andere methoden (kappen, herbiciden) economisch niet toepasbaar zijn, blijft er voor de ranches slechts de mogelijkheid over om het opdringen van de bomen en struiken te bestrijden met vuur. De kwantitatieve kennis omtrent het effect van vuur op de boom- en struikvegetatie in dit ecosysteem is echter te gering om gedetailleerde aanbevelingen te doen.

CURRICULUM VITAE

The author was born in 1946 in Hagestein, The Netherlands. After completing secondary school, he started his studies in 1963 at the Higher Horticultural College in Utrecht. He received his diploma in 1967, after which he fulfilled his compulsory military service.

In 1969, he started his studies at the Agricultural University in Wageningen, The Netherlands. In 1975, he obtained his Ingenieur's degree with distinction, with a specialization in soil science and the additional subjects of vegetation ecology, aerial photo interpretation and nature conservation.

From 1975 to 1978, he was employed as a soil scientist by the Netherlands Foundation for the Advancement of Research in the Tropics (WOTRO) and seconded to the Tsavo Research Station of the Kenyan national parks organization. During 1979, he was a guest research scientist at ISM (now ISRIC, the International Soil Reference and Information Centre) in Wageningen, The Netherlands.

In 1980 and 1981, he was employed as an ecologist with the RURGS project (Research pour l'Utilisation Rationnelle du Gibier au Sahel) in Mali. Since 1982, he has been a member of the scientific staff of the land ecology group of the Department of Natural Resources Surveys and Rural Development of the International Institute for Aerospace Survey and Earth Sciences (ITC), in Enschede, The Netherlands.