Wildlife resources of the West African Savanna

Promotoren: dr. C.W. Stortenbeker, emeritus hoogleraar in het natuurbehoud
en -beheer
dr. R.H. Drent, hoogleraar in de dieroecologie, Rijksuniversiteit
Groningen

S. de Bie

Wildlife resources of the West African Savanna

Proefschrift
ter verkrijging van de graad van
doctor in de landbouw- en milieuwetenschappen
op gezag van de rector magnificus,
dr. H.C. van der Plas,
in het openbaar te verdedigen
op vrijdag 11 oktober 1991
des namiddags te vier uur in de aula
van de Landbouwuniversiteit te Wageningen

These thesis also published as number 91-2 (1991) of the
WAGENINGEN AGRICULTURAL UNIVERSITY PAPERS

STELLINGEN

1\.

De hoefdiergemeenschap van de Westafrikaanse savanne moet gekarakteriseerd worden als een vuur-climax-gemeenschap en daarom is het verstandig gebruik van vuur als een instrument in het beheer van deze levensgemeenschap onontkoombaar.

Dit proefschrift.

2\.

Het ontbreken van 'medium-sized grazers', zoals het wildebeest en de zebra, in de Westafrikaanse savanne moet worden toegeschreven aan de landschappelijke eenvormigheid en specifieke floristische samenstelling van deze savanne waardoor de droge tijd een onoverbrugbare barrière voor deze diersoorten vormt.

Dit proefschrift.

3\.

Alhoewel de moeilijkheden zoals samengevat in de uitspraak van Bell (1984): '...the estimation of carrying capacity is the graveyard of ecological reputations; it is easy to be wrong; it is easy to be shown to be wrong and being wrong can be expensive...' blijven gelden, moeten zij geen belemmering vormen voor de bepaling van de draagkracht; met de huidige kennis en wetenschappelijke methodieken is een verfijning van de voorspelling mogelijk.

R. H. V. Bell, 1984. Carrying capacity and off-take quotas. In: R. H. V. Bell & E. McShane-Caluzi (eds.) Conservation and management in Africa. Proc. Workshop US Peace Corps.

Dit proefschrift.

4\.

De veehouderij en het behoud van wilde hoefdieren zijn onverenigbaar als vormen van landgebruik in de Westafrikaanse savanne, wat wordt ondersteund door resultaten van onderzoek elders.

Dit proefschrift.

D. C. P. Thalen, 1979. Ecology and utilization of desert shrub rangelands in Iraq. Junk Publ., The Hague.

5\.

De beperkingen aan het gebruik van de natuurlijke bestaansbronnen op onze aarde verplichten economen en politici bij de uitwerking van het concept van duurzame groei rekening te houden met het concept oecologische draagkracht van deze bestaansbronnen.

6.

Vanwege het positieve verband tussen de presentie van herbivoren en de verspreiding en hoeveelheid van hun mest kan het terreingebruik van herbivoren goed aan de hand van alleen de mest worden vastgesteld.

M. Rawes & D. Welch, 1969. Upland productivity of vegetation and sheep at Moor House National Nature Reserve. Oikos Suppl. 11: 9–72.

J. P. Bakker, S. de Bie, J. H. Dallinga, P. Tjaden & Y. de Vries, 1983. Sheep-grazing as a management tool for heathland conservation and regeneration in the Netherlands. J. Applied Ecology, 20: 541–560.

7.

De kolonisatie van eilanden door het rendier en latere heruitzettingen van deze diersoort door de mens in beide poolgebieden hebben steun gegeven aan de opvatting dat predatoren geen sleutelrol spelen bij de aantalsregulatie van hoefdieren.

H. Kruuk, 1972. The Spotted Hyena, a study of predation and social behavior. Univ. of Chicago Press, Chicago.

S. de Bie & S. E. van Wieren, 1980. Mortality patterns in wild reindeer on Edgeøya (Svalbard). In: E. Reimers, E. Gaare & S. Skjenneberg (eds.) Proc. 2nd Int. Reindeer/Caribou Symp., Røros, Norway, 1979. p. 605–610.

N. Leader-Williams, 1988. Reindeer on South Georgia. Cambridge Univ. Press, Cambridge.

8.

Het mislukken van veel ontwikkelingsprojecten en -programma's hangt samen met het niet onderkennen van het gegeven dat ook de mens zich in zijn overlevingsstrategieën aanpast aan veranderende milieuomstandigheden.

9.

De omvang der middelen als percentage van het Bruto Nationaal Produkt die in Nederland worden uitgetrokken voor het behoud en beheer van natuur steekt beschamend af tegen wat wij vragen van ontwikkelingslanden voor het behoud van de olifant, het tropisch regenwoud en andere ons aansprekende natuur in die landen.

10.

Het ontbreken van een duidelijk beeld in het beleid van de overheid van wat in Nederland 'natuur' zou moeten zijn, geeft geen hoge verwachtingen met betrekking tot de uitkomst van haar natuurontwikkelingsbeleid.

11.

Onderzoek in de tropen zou onmogelijk zijn zonder het werk van taxonomen en dus is een positieve herwaardering van de taxonomie van planten en dieren in het universitair onderwijs en onderzoek dringend gewenst.

12.

Het is verheugend te constateren dat binnen de vakgroep Natuurbeheer van de Landbouwuniversiteit Wageningen nu expliciet aandacht kan worden gegeven aan onderwijs en onderzoek in de tropen. Het valt daarom te hopen dat de Landbouwuniversiteit de mogelijkheden zal bieden dit gestalte te geven in de tropen zelf.

Stellingen behorende bij het proefschrift van S. de Bie: Wildlife resources of the West African savanna.

Wageningen, 11 oktober 1991.

'...nothing can be more improving to a young naturalist, than a journey in distant countries.' Charles Darwin – The Voyage of the Beagle

'...and the path that leads there is not a path to a strange place, but the path home.' Peter Matthiessen – The Snow Leopard

Abstract

Bie, S. de, 1991. Wildlife resources of the West African savanna. Doctoral thesis, Agricultural University, Wageningen, The Netherlands, 267 pp., English and Dutch summaries.

The wild fauna in Africa is a renewable resource and its overexploitation has led to the depletion of animal populations. This thesis focusses on the ecological characterization of the ungulate community of the West African savanna, with special reference to the Biosphere Reserve 'Boucle du Baoulé' in Mali, and makes a contribution to the ecological knowledge required for the conservation and management of West African savanna ecosystems.

Part I contains background information on the environment of the West African savanna and its use by man, and it gives a description of the study area.

Part II describes phenological patterns, production and quality for different groups of herbaceous plants, shrubs and trees and analyses the vegetation of the West African savanna as a source of food for the different ungulate species. Choice of habitat, diet composition, energy and protein requirements in relation to the metabolic weight of animal species are investigated as they are necessary for the analysis of the mechanisms of ecological separation of ungulates.

In Part III the ecological carrying capacity of the West African savanna in the Baoulé is estimated by calculating dry-season stocking rates on the basis of the availability of quality forage. Results are compared with other approaches for the assessment of the ecological carrying capacity in the West African savanna zone and in other savanna ecosystems, elsewhere in Africa and in Australia.

Using information on the ungulate community and the ecological carrying capacity of the West African savanna, in Part IV management options for the conservation and management of wild ungulate populations are suggested.

Acknowledgements

I wish to thank the Government of the Republic of Mali for allowing me and my colleagues on the project 'Recherche sur l'Utilisation Rationnelle du Gibier au Sahel' (R.U.R.G.S.) to work in the Biosphere Reserve 'Boucle du Baoulé', and the Forestry Service of Mali for their cooperation.

The fieldwork in Mali was carried out while working as an ecologist for the Directorate-General for International Cooperation of the Netherlands' Ministry of Foreign Affairs.

I am very much indebted to Chris Geerling, not only for introducing me to the beauty of tropical countries but also for showing me that tropical ungulates are as fascinating as their relatives in the high Arctic. In all the years that we worked together in finalizing and publishing the various R.U.R.G.S.-project reports, often in difficult circumstances, he always emphasized the importance of this thesis to me. I also want to thank him for allowing me to include his photographs of ungulates, taken in West African national parks and game reserves.

I very much appreciate the support and encouragement I received from the late Harm van de Veen. The study benefited greatly from his enthusiasm for ungulate research and his experience in it. I feel therefore very sad that he will not see the result.

I wish to express my gratitude to all my colleagues on the R.U.R.G.S.-project. Their cooperation was of vital importance both scientifically and socially. Especially I want to mention Mr. M. Diakité, director of the project, who continuously gave me support and helped to obtain ministerial permission for carrying out parts of this research, and I also thank Mr. N. Traoré, my Malian counterpart.

The administrative and technical staff of the Department of Nature Conservation, Agricultural University of Wageningen, helped me in numerous ways for which I am very grateful. I thank my colleagues at the Department for the valuable discussions about this research. During the research period many students helped me. I am very grateful to them and especially want to mention I. Heitkönig, C. Smits, J. van der Steege and W. Legemaat.

I wish to thank Prof.Dr. R.A. Prins for his introduction to the digestive physiology of ruminants and Dr. B. Deinum whose practical advice made the numerous chemical analyses much easier.

Dr. R.M. Watson introduced me to the art of aerial surveys and showed me that ecological research in tropical areas can benefit enormously from aerial reconnaissance for which I thank him very much. Various chapters were improved by the comments of Prof.Dr.Ir. L. 't Mannetje (Chapters 2, 9 and 10), Prof.Dr.Ir. S. Tamminga (Chapter 7), Dr. C. Geerling (all chapters), Dr.

R. Putman (Chapters 1 to 9) and Dr. H. Breman (Chapters 9 and 10).
Many thanks to Ms. H. Dokter, Ms. A. Smitt and Mr. M. Zieren who typed parts of the preliminary chapters when I had not yet crossed the barrier between typewriter and word processor. Mrs. C. Hengeveld devoted much time in turning the text into real English and showed me where the text did not fit my ideas, for which I am very grateful. Mr. C. Rijpma and Mr. D. Visser skilfully prepared the figures.

Especially I wish to thank Prof.Dr. C.W. Stortenbeker and Prof.Dr. R.H. Drent for their involvement in all stages of the research. Prof. Stortenbeker gave me the opportunity to work in Mali and later invited me to join the staff of his department for which I am very gratefull as for his trust and guidance during the progress of this research. When I was a student at the University of Groningen, Prof. Drent taught me how to carry out ecological research and I realize how valuable this training has been for my research. I am much indebted for his positive criticism during the preparation of the manuscript.
They invested much time in tutoring me and in discussing scientific problems which improved the thesis. Their encouragement helped me to continue when the work still to be done seemed endless.
My parents deserve a special word. Their continuous support during my university years and afterwards their encouragement to continue on the path of ungulate research, even when prospects were dim, mean a lot to me.
Finally I am very much indebted to my wife Mechteld. Her stimulating force as a partner and biologist was essential in all stages of this research. Her sacrifices made it possible for me to complete this thesis. This book which bears my name is also hers!

Curriculum vitae

Steven de Bie werd geboren op 9 december 1950 te Gorinchem. Na te Zwolle het Gymnasium Celeanum te hebben bezocht werd aan het Stedelijk Gymnasium te Arnhem in 1969 het Gymnasium-B diploma behaald. Van 1969 tot 1977 studeerde hij Biologie aan de Rijksuniversiteit Groningen met als hoofdvak Dieroecologie. In 1977 nam hij deel aan een expeditie naar Spitsbergen ter bestudering van rendieren in een arctisch oecosysteem. Verbonden als gastmedewerker aan het zoologisch laboratorium van de Rijksuniversiteit Groningen werden na terugkeer de expeditie-waarnemingen uitgewerkt.

In de periode 1980-1983 was hij in dienst van het Ministerie van Buitenlandse Zaken en van de Landbouwuniversiteit Wageningen; hij werkte als dieroecoloog in het R.U.R.G.S.-project (Recherche pour l'Utilisation Rationnelle du Gibier au Sahel) in Mali.

Tussen 1984 en 1986 was hij als zelfstandig consultant werkzaam in Nederland en daarbuiten.

Van 1986 tot 1989 was hij als wetenschappelijk ambtenaar met verschillende taakopdrachten verbonden aan de vakgroep Natuurbeheer van de Landbouwuniversiteit Wageningen. Vanaf 1989 is hij als universitair docent werkzaam bij de vakgroep Natuurbeheer, sectie tropen.

Contents

Part I: General background

Part II: Ecological characterization of wild ungulates in the West African savanna

Part III: Ecological carrying capacity

Part IV: Conservation and management

1. Introduction

1.1. Scope of the study

All over the world man exploits the land cultivating his crops, herding his animals, hunting the wild fauna, gathering the natural vegetation for food, felling timber and building houses and factories. Obviously the more people present or the higher their demands, the greater the effects of man's activities on the land around him, effects, that are much more drastic in the so-called developed world of Europe, America and Australia than in developing countries such as those in Africa.

Traditionally, land-use in Africa depended on the renewable natural resources: soil, water, vegetation and fauna. This sort of exploitation is based on the regenerative capacity of the resource and has a low input technology: inputs other than labour are scarce. In West Africa *traditional* land-use is characterized by (De Bie & Geerling, 1988):

- a relatively high production in relation to the available resources; a low level of technology results in an optimum, that is non-exhaustive, exploitation (Fig. 1.1, phase a);
- relatively stable land-use, dependent on the demographic situation.

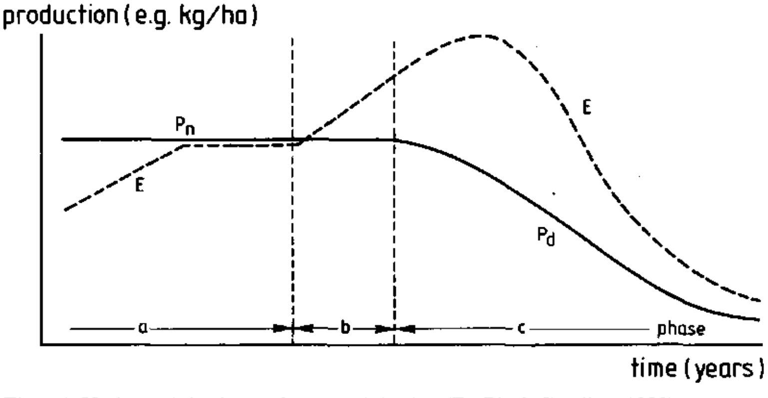


Fig. 1.1. Underexploitation and overexploitation (De Bie & Geerling, 1988)

P_n = potential exploitation level in a non-degraded system
P_d = potential exploitation level in a degrading system
E = actual level of exploitation
a = optimum and sustainable exploitation
b = exploitation exhausting the reserves of the resource
c = exhausting exploitation and degradation of the land

Types of land-use such as crop farming, animal husbandry, hunting and forest exploitation are traditionally complementary and interact. However this system of land-use does not work any more because it could not stand up to the manifold social, economic and political changes, brought about by the rise of the modern state, population growth, the concentration of economic and political activities in the urban zones, and investments that are insufficient or wrongly placed. Natural resources have come under pressure through the increase in exploitation, aggravated by ecological variation such as that in rainfall. Although at first production remained high, as the reserves of the natural resources were exhausted, stability of the ecosystems decreased (Fig. 1.1, phase b).
A further increasing pressure on the land led to a decreasing regenerative capacity of the resources, aggravated by the cumulated effects of the different types of land-use, resulting in a decrease in production (Fig. 1.1, phase c), and finally in a degradation of the land. This has resulted in serious problems in large parts of West Africa today:

* insufficient food for the local population;
* overexploitation of pastures and an increased livestock mortality;
* degradation and reduction of the natural vegetation leading to decreasing wildlife populations;
* breakdown of the agricultural system;
* insufficient money through diminishing revenues to cover investments necessary for maintaining productivity of various types of land-use.

In West Africa wildlife is hunted for economic reasons. Furthermore wildlife tourism is of, albeit minor, economic importance (De Bie et al., 1987).

The model in Fig. 1.1 can be used to describe the decline of the utilization of this renewable natural resource. The original subsistence hunting has developed into a more intensive, uncontrolled exploitation because of a higher demand for meat with the growing human population, a decline of traditional social structures and thus a disregard of hunting regulations, and an increasing commercial interest in wildlife exploitation. All this has led to overexploitation of the resource and the depletion of animal populations.

The present situation for the wildlife of West Africa, especially larger mammals, is alarming. Several species such as the black rhinoceros *Diceros bicornis* in Cameroon and the Central African Republic, and the giant eland *Tragelaphus derbianus* in Cameroon, Senegal and Mali, are on the edge of extinction. Other species are threatened over most of their distribution area within West Africa such as the elephant *Loxodonta africana* (Douglas-Hamilton, 1987), topi (*Damaliscus lunatus korrigum*) (Poché, 1974a; Esser & Van Lavieren, 1979; Sayer, 1982), reedbuck *Redunca redunca* (Esser & Van Lavieren, 1979) and several carnivores (Poché, 1974b). Populations of nearly all mammal species have become much smaller and so fragmented and localized that their long-term viability is in danger. Relatively larger populations are mostly found in national parks or in game reserves but even here they are not entirely safe as despite official laws

Plate 1. Black rhinoceros: on the edge of extinction

and rules, man comes into these areas for land as a means for subsistence.

The degradation of the savanna ecosystem in West Africa has become a matter of great concern (e.g. Geerling & De Bie, 1986) and there is a consensus that we must preserve what is left and try to restore what has been destroyed. Conservation and management of the savanna ecosystem with their characteristic fauna means more than managing wildlife as a natural resource. As animals have been driven back to unfavourable areas by the expansion of agriculture, their conservation also requires a thorough understanding of the savanna ecosystem, especially how the savanna ecosystem functions under the impact of man. In parts of East and southern Africa a long history of ecological research has led to the development of guidelines for nature conservation and management (Sinclair & Norton-Griffiths, 1979; Owen-Smith, 1983), some of which may be applicable to West Africa. However, in West Africa the necessary information is scarce and fragmentary, if available at all, most workers having concentrated on animal numbers and distribution.

Wildlife conservation is not only a question of preservation of a natural heritage. Hunting, both subsistence and commercial, is an essential part of the West African rural economy (De Bie et al., 1987): subsistence hunting provides food for the hunter, his family and village, whereas commercial hunting supplies the regional and national markets. Therefore, wildlife conservation should also form the framework within which wildlife is used for the sustenance of the present human population. The present numbers of wildlife populations are low and hence cropping figures, estimated by trial and error, are well below the potential secondary productivity of an area (Van Lavieren, 1979; De Bie et al., 1987).

Thus for a sound management of wildlife utilization the potential stocking rate of animal species under natural circumstances, that is the ecological carrying capacity, and the effect of various levels of exploitation and other human activities on animal populations must first be known.

It is generally assumed that in Africa rainfall, primary production and herbivore biomass are strongly correlated (Coe et al., 1976; Bell, 1984; East, 1984). However, further studies (e.g. Bell, 1984; East, 1984) have revealed a considerable variation between the herbivore biomass of different regions in Africa with comparable annual rainfall. Densities of wildlife in the best protected areas in the West African savanna are well below the values predicted by Bell's (1984) herbivore biomass/rainfall relationship. Animal densities in the West African savanna are supposedly limited by the availability and quality of forage, which are in turn limited by the availability of soil nutrients, especially nitrogen and phosphorus (Penning de Vries & Djitèye, 1982). However, observed densities are sometimes above those expected from the assumed limit set by forage.

There are, so far, no satisfactory data on the relationship between vegetation and herbivore biomass in the savanna ecosystem of West Africa to explain these density differences and hence there is no reliable way of predicting potential stocking rates and assessing harvesting levels for viable wildlife populations.

Before the ecosystem of the West African savanna can be understood and conservation and sustainable utilization of its wildlife realised, basic information on the ecology and population dynamics of the animal species is essential. In my research I have analysed the West African savanna ecosystem and the ecology of its larger herbivores. This thesis focuses on:

1 the ecology of the larger herbivores with respect to their food availability and selection, habitat utilization and some aspects of their social behaviour, in the Biosphere Reserve 'Boucle du Baoulé' in Mali;
2 the ecological characterization of the ungulate community in this area;
3 the estimate of the ecological carrying capacity of the West African savanna ecosystem compared to other savanna ecosystems;
4 the implications for the management of the ungulate community.

As all mathematical approaches for assessing the carrying capacity can be narrowed down to the comparison of the availability of resources and the species-specific resource requirements, the first two aspects have to be considered before an estimate can be made.

Habitat selection, food choice, social organization and distribution can be considered as adaptations to the prevailing environmental conditions, that is

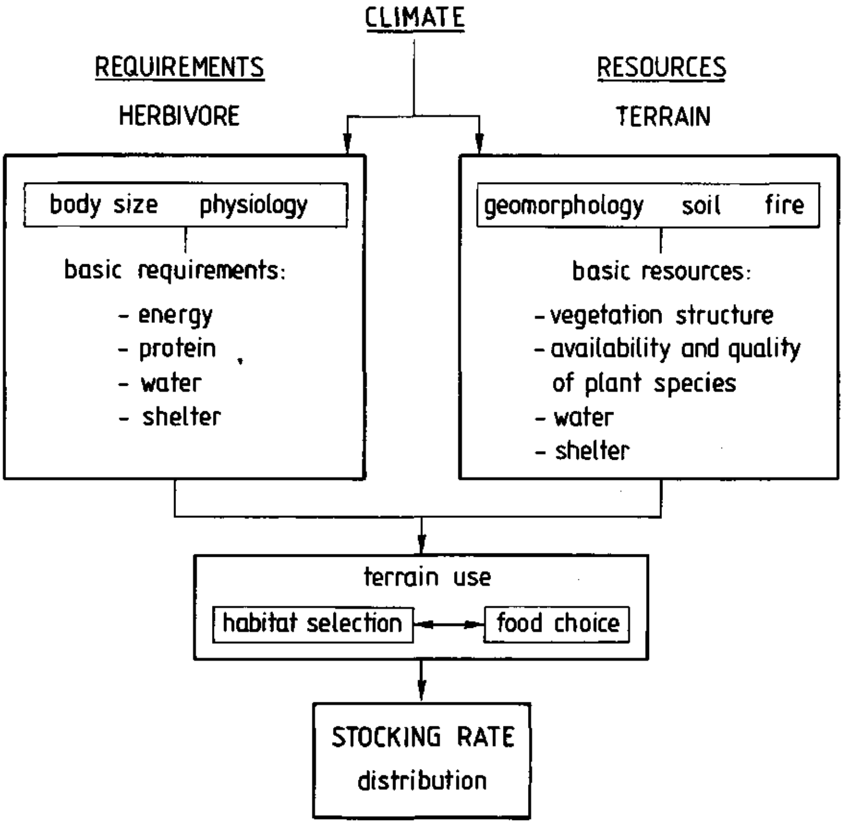


Fig. 1.2: Interrelationships between intrinsic factors of the herbivore and environmental characteristics.

to extrinsic factors, within the limits set by intrinsic factors found in the basic physiology of the herbivore. Fig. 1.2 shows a schematic outline of these interrelationships which give a framework for the analysis of the ungulate community and for the calculation of the ecological carrying capacity.

1.2. Organization of the research

In the Sahel and the northern Sudan zone the severe drought in 1969-1973 had drastic consequences for the local rural population and the environment. The research programme 'Recherche pour l'Utilisation Rationnelle du Gibier au Sahel' (R.U.R.G.S.) was one of the results of numerous discussions and moves in the developed countries to help the governments of the countries affected.

This programme aimed at the sustainable utilization of renewable natural resources, with the emphasis on wildlife (Geerling & Diakité, 1988). The National Forestry Service of Mali and the Department for Nature Conservation of the Agricultural University of Wageningen in the Netherlands cooperated in carrying out the programme which started in 1977. I joined the project in March 1980, when the second phase (1979-1981) was underway. The objectives of this phase were:

1 to indicate the possibilities for sustainable wildlife utilization in the Sudan zone of Mali and other countries;
2 to present a management plan for the National Park 'Boucle du Baoulé', with emphasis on wildlife utilization as a type of sustainable land-use.

Special attention was given to the ecology of the larger mammals, as there was no information on them in this national park or elsewhere in Mali. Furthermore information from comparable climatic regions elsewhere in West Africa was scarce. Therefore, the 18 months available were entirely devoted to collecting field data. Laboratory analyses and data processing took another three years. Results on the conservation and sustainable utilization of wildlife, are published in the final report of the R.U.R.G.S.-project (De Bie et al., 1987; Heringa et al., 1987). This thesis presents the underlying analysis of the ecology of the ungulate community of West African savanna. The relatively short period available for field work meant that it was sometimes necessary to complete data by including information from other regions in West Africa savanna and additional information from more recent work in Burkina Faso.

This thesis is divided into three parts. Part I gives the general background of the West African savanna, and describes the study area 'Boucle du Baoulé', and the methods used for the ecological characterization of larger herbivores and for the analysis of the ungulate community in the West African savanna, the subjects of Part II. The ecological carrying capacity of the West African savanna is discussed in Part III and compared with that of other savanna ecosystems. Finally in Part IV the findings of Parts II and III are related to wildlife conservation and management.

2. The concept of carrying capacity

Carrying capacity is one of the terms in the management of rangelands leading to a lot of confusion (in company with terms such as overpopulation, overgrazing and overharvesting) (MacNab, 1985). Not the least because this term is also used by many workers in other scientific fields: in anthropology, geography, fisheries and business management (Fearnside, 1986). The various definitions have in common the aspect of the number of individuals that can be supported by a certain area (Fearnside, 1986) but also '...the amount of goods and services that a specific site can support and sustain without deterioration...' (Sinclair et al., 1973).

For a long time carrying capacity has been related to the growth pattern of an animal population entering a previously unoccupied environment with limited resources. When a logistic equation is used to describe the theoretical sigmoid curve of population growth, carrying capacity is defined as the upper limit the population approaches asymptotically in time (logistic carrying capacity, '*ceiling model*', Pollard, 1981) (Fig. 2.1a). However, when population growth is described in terms of a dynamic, stochastic process, carrying capacity is the equilibrium between resource consumption and resource supply ('*equilibrium model*', Pollard, 1981). Whereas logistic carrying capacity is static, setting the upper limit for population growth which can never be surpassed, the 'sustainable' carrying capacity (Fearnside, 1986) is dynamic. The population fluctuates around its equilibrium density, always tending to return to the latter through density-dependent growth or decline (Dempster & Pollard, 1981) (Fig. 2.1b).

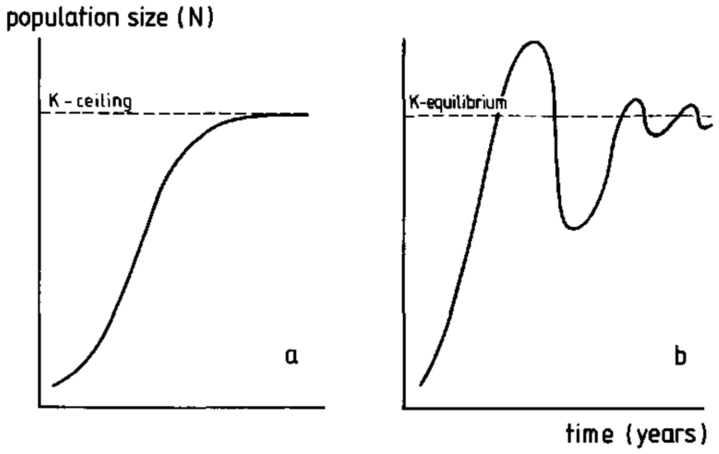


Fig. 2.1. Population growth in (a) the ceiling model in which N < K and (b) the equilibrium model in which N oscillates around K (modified after Pollard, 1981)

Most authors studying grazing systems, whether with wild or domestic herbivores, usually mean sustainable carrying capacity whereas their calculations often use the concept of logistic carrying capacity as a practical but necessary simplification.

Traditionally in range management, carrying capacity referred (and often still does) to the density of cattle or grazing animals, that in general provides (maximum) production for an indefinite period of time (e.g. Stoddart et al., 1975; Butterworth & De Ridder, 1984) or as stated by Heady (1975): '...the number of animals that produces the greatest return without damage to the physical resources and in contact with other values received from the land...'. A difficulty arises when the concept of carrying capacity is used for grazing systems where the aim is the conservation of animal species or total ecosystems rather than production. Carrying capacity is then used to indicate the natural equilibrium between the herbivores and their food supply in the absence of human interference, defined as '*ecological carrying capacity*' by Caughley (1979). Such an equilibrium referring to the maximum number of animals, is characterized by a zero rate of increase of both plants and animals. This concept closely resembles Pollard's (1981) equilibrium model.

According to the general theories of population growth, harvesting a population temporarily reduces its density; to produce a sustained yield, the stocking rate should be kept below the ecological carrying capacity. The result is a controlled equilibrium, called the economic carrying capacity by Caughley (1979), but here called '*exploitation carrying capacity*' because different intensities of exploitation may result in different equilibria. With a lower biomass of animals and a higher biomass of vegetation, such equilibria can only be maintained by human intervention (Fig. 2.2); without it, the animal population grows until it reaches the ecological carrying capacity (Caughley, 1979; MacNab, 1985).

This distinction between ecological carrying capacity and exploitation carrying capacity, the latter being defined as a level of population size appropriate

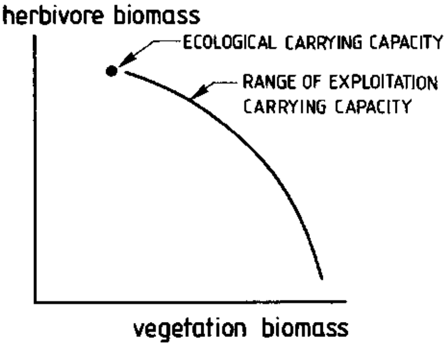


Fig. 2.2. Relation between ecological carrying capacity and exploitation carrying capacity

for a certain intensity of exploitation, is the main source of confusion between the traditional range managers and those who manage wild herbivore populations. Bell (1984) lists some complications to the concept of carrying capacity as given by Caughley (1979). Animal population growth does not, for example, immediately respond to a decreasing forage production; there is a time-lag during which the population size overshoots the equilibrium level. This is followed at first by a decline of animal numbers to below equilibrium level, and finally by an adjustment to the production of forage. By how much and for how long the animal populations overshoot the equilibrium level, and to which extent the population is reduced thereafter, depends on their innate reproduction rate and the degree to which it is affected by food shortage. Caughley (1979) suggested that ultimately the population stabilizes at the same level whether or not an overshoot and crash took place. According to Bell (1984) this is not so if the environment degrades during 'overpopulation'; in that case this will result in a lower carrying capacity. Other complications are environmental fluctuations, emigration and immigration, predation, and interactions with other herbivores. However, in my opinion all Bell's complications will only affect the quantification of carrying capacity in a particular situation rather than affect the concept itself. They play as essential a role to carrying capacity as forage availability but act over a longer period than a year. Therefore carrying capacity should be assessed for a time unit of several years. Moreover it strengthens my opinion that carrying capacity cannot be indexed by an exact number but rather by a range of values between which the population size fluctuates.

Once one recognises that the carrying capacity reached is a level of equilibrium between herbivores and their food supply, independent of the management objective, this term can be defined more precisely. Caughley (1979) defines it as the equilibrium between the rate of food consumption and the rate of food production. Carrying capacity strongly depends on soil fertility. Land in the African savanna is often not only used for grazing but also its trees are exploited for fuel. Felling trees and grazing both mean a loss of soil nutrients. The carrying capacity of the grazing system is therefore also strongly related to the exploitation level of the woody component of the area. Both trees and grasses use the same pool of available soil nutrients, thus both types of land-use are dependent on the same limiting factor. Therefore the use of a general but more applicable definition is proposed: carrying capacity is a level of equilibrium in an ecosystem between the availability and degree of exploitation of that element, which limits a given type of ecosystem use (cf. Geerling & De Bie, 1986). This definition can be explained as follows:

* *a* level of equilibrium: as more than one equilibrium is possible (see Fig. 2.2) 'a level of equilibrium' is preferred to carrying capacity being 'the' equilibrium.

* the level is indexed either by the species composition, biomass and growth stages of the range plants or by the number or biomass of the herbivores (see Fig. 2.2).

- the element concerns that element (or combination of elements) that sets the limit to the exploitability of the ecosystem, such as grass or water for cattle or soil nutrients for shrubs and trees. Its availability depends on more or less variable factors such as rainfall, and soil nutrients, that can sometimes be manipulated; the degree of its exploitation depends on the type of ecosystem use. Those elements which could fluctuate relatively quickly in time are key-elements with respect to the carrying capacity.
- ecosystem use covers any type of land-use, e.g. beef production, forest exploitation, conservation, that is determined by economical, political or social factors and includes the aims of land-use such as food, maximum number of animals, as well as the means of production available such as the level of technology.

Once the limiting element(s) and the type(s) of ecosystem use are known, the definition could be rewritten in a more specific way.

Whereas in the assessment of carrying capacity all factors that are potentially limiting are considered, the calculation of the *grazing capacity* is based upon the amount of forage of a specified standard quality, available to herbivores in a certain area for a given period of time (cf. Zonneveld, 1984).

In this study our interest is primarily the conservation of 'settled' animal population as a type of land-use, preserving the natural equilibrium between wild herbivores and their environment, that is the ecological carrying capacity. Using this index we can assess whether it is possible to utilize wildlife. Present numbers of ungulate populations are far below the ecological carrying capacity, and hence if areas are to be set aside for the survival of viable populations as well as for their sustainable utilization, knowledge of the ecological carrying capacity is essential. Thereafter optimum utilization of ungulates can also be assessed but as data on population dynamics are needed for this calculation, it is beyond the scope of this thesis.

Part I: General background

This part presents background information on the study. In Chapter 3, the West African savanna is defined and the environment and its use by man described. Chapter 4 gives an outline of the study area and Chapter 5 deals with the methods used to collect and analyse field data.

3. The West African savanna: an introduction

3.1. Definitions

West Africa can be defined as the area extending from the Atlantic Ocean in the south to the Sahara desert in the north (c. 15°N) and from Senegal in the west to the highlands of Cameroon in the east (Fig. 3.1).

According to Geerling (1982) and White (1983) five phytogeographical zones can be distinguished in this area. Fig. 3.1 shows these zones which are:

* the Sahara, a desert
* the Sahel, a semi-arid steppe vegetation
* the Sudan zone, a subhumid savanna
* the Guinea zone, a transition from the Sudan savanna to tropical rainforest
* the tropical rainforest

The Sahel and Sudan zones are narrow bands across Africa, from Senegal to the Ethiopian Highlands. They are 500-700 km wide, narrower in the west and

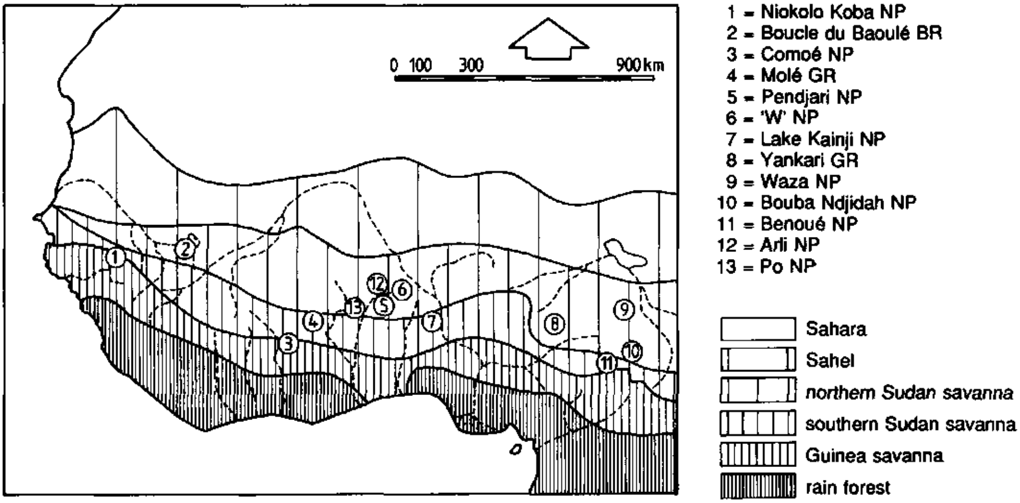


Fig. 3.1. Phytogeographical zones of West Africa (adapted from Geerling, 1982 and White, 1983); the location of major conservation areas in the West African Sudan savanna is indicated
NP = national park, GR = game reserve, BR = biosphere reserve

wider in the east (Hopkins, 1974; White, 1983). The Sahel zone continues across the Arabian peninsula into the Indian subcontinent; it is absent in southern Africa. The Sudan savanna is a characteristic African phytogeographical zone and shades into the Zambesian zone in East and southern Africa (White, 1983). In this study I have limited myself to the Sudan savanna.

The complexity of the savanna ecosystem due to the variability of determining factors such as rainfall, prevents a precise definition of the savanna; usage of the term 'savanna' has been subject to extensive discussions and reviews (e.g. Schnell, 1970-1977; Bourlière & Hadley, 1970; UNESCO, 1979; Johnson & Tothill, 1985). In this study Bourlière & Hadley's (1970) definition of savanna as 'a tropical formation where the grass stratum is continuous and important, but occasionally interrupted by trees and shrubs; the stratum is burnt from time to time and the main growth patterns are closely associated with alternatively wet and dry seasons' is used.

As the woody layer is variable, savannas are differentiated according to their vegetation structure: from grassland savanna, where no woody layer is present, to savanna woodland.

There is a difference of opinion about the origin of savannas: whether they are natural or caused by man. Most authors consider savannas as the unnatural end of succession, maintained by fires (mainly man-made) since prehistoric times (Schnell, 1970-1977; UNESCO, 1979). The Sudan savanna is considered to be partly a degraded form of extinct dry ecosystems such as 'dry woodland' or 'dry forest' (White, 1983), and partly the result of its own evolution with 'zone-specific' species giving it a characteristic vegetation (Geerling, 1982) (see Aubreville (1949) for an extensive treatment of the history of the vegetation of West Africa). Kortlandt (1972) emphasizes the role of larger mammals in the natural vegetation and supports the hypothesis that the broken forest and forest-savanna mosaic were also formed by large herbivores, acting like bulldozers in the Mid-Miocene and Late Miocene. Although there is no evidence for such a large-scale 'savannization', this explanation may be added to the more accepted one of the savanna being a fire-climax.

3.2. Characterization of the West African savanna

3.2.1. General

The Sudan savanna (and its southern equivalent) is the 'typical' African savanna with an annual precipitation between 600 and 1200 mm and a dry season of 2 to 8 months. Soil water conditions and fires control the balance between trees and grasses (Menaut et al., 1985). The growth of grass is very seasonal and the amount produced limited by the availability of water and soil nutrients and affected by annual fires. There are large herbivores and the soil fauna is characterized by the earthworm/termite balance (Menaut et al., 1985). Traditional, intensive shifting cultivation is dominant (De Bie & Geerling, 1988). Although the ecosystem functions according to how much rain falls during the growing season, the length and severity of the dry season are the most limiting factors (Menaut et al., 1985).

3.2.2. *Abiotic diversity*

The Sudan savanna is characterized by its climate and falls within the tropical summer rainfall zone, defined by Walter (1979). The main variable is rainfall, the annual rains limited to the single wet season, a relatively humid period lasting from May-June to September-October (Table 3.1 and Fig. 3.2). From south

Table 3.1. Climatological characteristics of the Sudan savanna[1])

	northern Sudan savanna	southern Sudan savanna
Average annual rainfall (mm)	600-900	900-1200
Rainfall variability (%)	30- 20	20- 15
Rainfall in dry years (mm/y)	425-725	725-1025
Average length of wet season (days)	100-140	140- 190
Average daily temperature (°C) wet season	27	26
dry season	32	31

[1]) sources: De Bie & Geerling (1988) and Heringa (1988)

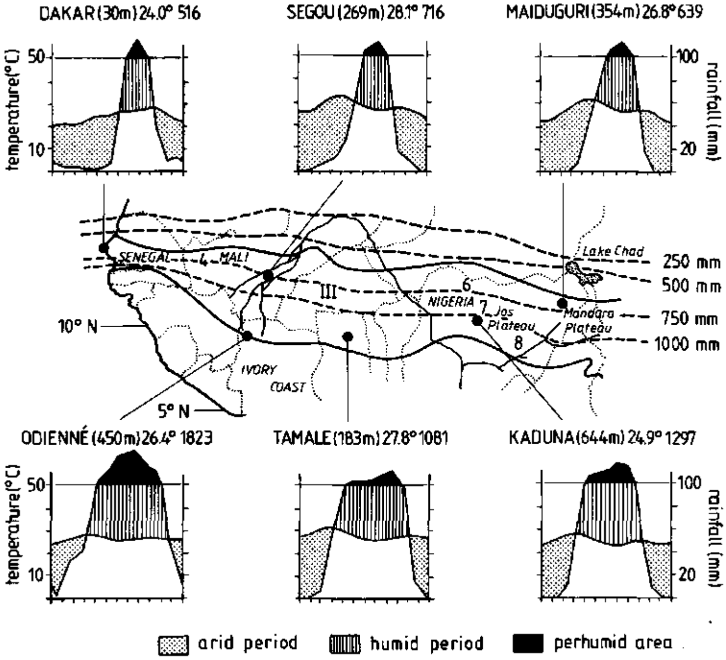


Fig. 3.2. Climatic diagrams for several stations in the Sudan savanna (after Nix, 1983 and White, 1983)

to north, climatic conditions become more unpredictable, with relatively greater annual variation in rainfall and a more irregular rainfall distribution within the wet season.

Series of relatively wet and dry years alternate. Since the end of the sixties the yearly rainfall has drastically decreased to 200 mm below the long-term average (Fig. 3.3 and Heringa, 1988). Temperatures are high throughout the year (Table 3.1 and Fig. 3.2), in the dry season daily temperatures sometimes exceeding 40 °C.

Especially regarding rainfall, the climate of the Sudan savanna is broadly similar to that of the Zambesian region, its equivalent in southeast and southern Africa

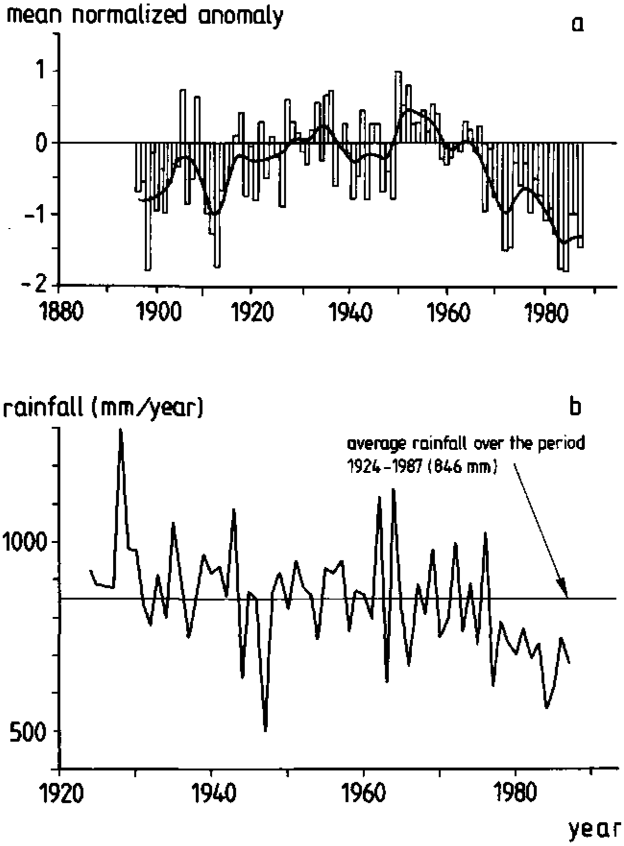


Fig. 3.3. Rainfall trends

a: Trends in rainfall in the Sahel and northern Sudan savanna (10-15 °N, 20 °W-10 °E) over the period 1897-1986; expressed as the mean normalised anomaly of the period 1941-1970 (IUCN, 1989).

b: Rainfall trend in Ouagadougou, Burkina Faso (Sudan savanna) over the period 1924-1987 (source: Bureau Météorologique de Burkina Faso)

(White, 1983). However the climate of the Sudan savanna has much higher temperatures and is much more severe due to very dry, northern winds, the Harmattan, in the dry season.

Geologically the Sudan zone is uniform with Precambrian and Cambrian rocks predominating in the occurrence of ancient granitic shields and sandstone. Ancient erosion has resulted in an undulating or almost flat landscape. However in some areas, such as in Mali, extensive eroded sandstone outcrops with steep escarpments, and partly weathered into laterite stone caps, give the landscape a quite different appearance.

The altitude is usually lower than 700 m, with the exception of the Jos Plateau in Nigeria, the Mandara Mountain in Cameroon and Fouta Djalon in Guinee.

Terraces are found along rivers, sometimes in combination with flood plains and backswamps (= flood basins behind natural levées (Thornbury, 1969)). Recent volcanic activity is rare.

Although large areas are covered with deposits from Pleistocene age, for example the consolidated dunes in the north of the zone, soils are mainly the product of physical and chemical erosion of the Precambrian and Cambrian rocks. Most soils are acrisols and luvisols (Menaut et al., 1985), the clay consists mainly of kaolin with iron and aluminium oxides (Hopkins, 1974). As these soils have a remarkable chemical stability, the cation exchange capacity is low, resulting in a low fertility; the content of organic matter is also low (Menaut

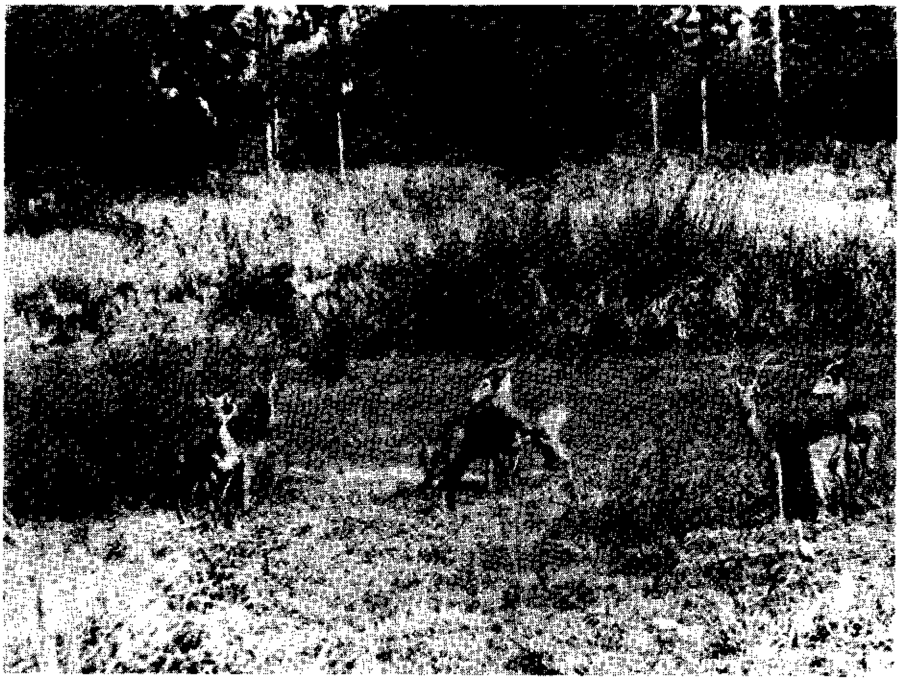


Plate 2. The flood plain attracts various species of grazing ungulates such as the kob

et al., 1985). Ironstone concretions are common and where erosion by wind and water has removed the topsoil they come to the surface as laterite stone caps.

Local geomorphology, soil characteristics and natural drainage patterns are very important for the vegetation structure and composition.

Referring to annual rainfall and low soil fertility, the Sudan savanna is classified as a **moist/dystrophic savanna** (Bell, 1984; East, 1984).

3.2.3. Vegetation

It is generally agreed that climate and/or fire account for the origin of the savanna but the determinants of the maintenance and evolution of different vegetation types are still debated (Menaut et al., 1985). The soil moisture regime (a combination of climate, soil type and physiographic position) emerges as the determinant of the savanna structure. Soil nutrients are assumed to play a major role with respect to the species composition of the herbaceous layer, and fire to maintain the prevailing situation (Menaut et al., 1985). Generally the geological parent material strongly influences the arboreal vegetation (Geerling, 1976). Not enough is known to assess the effect of herbivory on vegetation structure (Cumming, 1982). Exploitation however could affect vegetation composition and structure severely.

The Sudan savanna is dominated by woodland savanna. Tall grasses, both perennial species, including *Andropogon spp.* and *Hyparrhenia spp.*, and annuals such as *Andropogon pseudapricus*, *Ctenium spp.* and *Loudetia spp.*, characterize

Plate 3. Woodland savanna is the dominant vegetation system of the West African savanna

the herbaceous layer. In general trees and shrubs form an open woodland with 40% or more canopy cover but never closed. Vegetation structure is primarily determined by competition between woody plants and grasses for available light and soil moisture.

Floristic composition of the woody layer changes gradually from south to north: *Isoberlinia doka*, *Terminalia spp.*, *Afzelia africana* and a high percentage of broad leafed legumes dominate the tree layer in the south, where the active growing period lasts 5-7 months, whereas in the north, where the active growing period is only 3-5 months, the Combretaceae characterize the Sudan woodland. The *Isoberlinia* savanna can be considered as an impoverished variant of the 'miombo' in south and southeast Africa (White, 1983).

White (1983) points to the strong influence of past and present-day cultivation on the vegetation, especially in the northern part of the Sudan savanna. Most of the woodland savanna here is secondary (modified by previous cultivation activities). For this reason the original floristic diversity, i.e. a mosaic of dense and open patches with a characteristic species composition due to for example termitaries and drainage patterns, is now masked or has disappeared. The original woodland has been degraded to various stages, ranging from bush fallow (= woodland in various stages of regeneration after a period of cultivation) to wooded farmland (= woodland under nearly permanent cultivation). Shrublands have developed where cattle grazing and wood cutting are dominant. Extensive secondary grasslands and shrublands are found where cultivation and cattle grazing inhibit the regeneration of the woodland, an effect reinforced by bush fires.

Plate 4. Swamps and riparian forest cover only a small part of the West African savanna

Undisturbed vegetation is only found where there is less human activity such as on rocky hills and where water is not easily accessible to man.

Permanent swamps and riparian forests cover only a small part of the area. The flora of riparian and swamp forests is poor. These forests are semi-evergreen in the south and semi-deciduous in the north where the riparian forests are mostly degraded to riparian woodlands due to human activity. Non-wooded savannas are rare in the Sudan savanna. The flood plains support seasonally inundated grasslands where species like *Oryza*, *Echinochloa*, *Vetiveria nigritana* and *Hyparrhenia rufa* grow. Grass also grows on the laterite stone caps covered with a shallow soil (locally known as 'bowal'). White (1983) characterizes this vegetation as an open seasonal marsh.

Bush fires occur nearly everywhere in the Sudan savanna; areas such as swamps and riverine forests, or rocky and arid areas, lacking a continuous layer of combustible material, escape (Geerling, 1982). Fire destroys litter and also kills young woody plants. In this way fire reduces the amount of shade and favours the grasses in the competition for light (Geerling, 1982, 1985). In the past lightning caused bush fires but today natural bush fires hardly occur, since 90% of the susceptible areas are burnt by man by the start of the dry season. The vegetation is set alight by man for various reasons: to prevent bush encroachment, to induce and improve the (re)growth of perennial savanna grasses, to improve the visibility for hunting and to clear fields for arable use. Afolayan (1978), Rodgers (1979), Brookman-Amissah et al. (1980) and Geerling (1982) have summarized the following effects of bush fires:

* early fires (i.e. early in the dry season and of relatively low temperature): woody species hold their own position, and both fire-sensitive and fire-climax grass species (*Hyparrhenia*, *Andropogon*) flourish, so the status quo is maintained;
* late fires (i.e. late in the dry season and of very high temperature): affect the woody species and the fire-sensitive grasses negatively but benefit the fire-climax grasses resulting in a very open savanna with a dense stand of these coarse grasses;
* no fires: favour the growth of trees whereas grasses and herbaceous plants gradually decline after an initial invasion of fire-sensitive species, leading finally to a closed dry forest or thicket, supposedly the original climax vegetation (see White, 1983).

Fire has adverse effects on wildlife populations, destroying their habitats and exposing them to predators. However, it benefits them too by stimulating the nutritious dry-season growth of perennial grasses: complete defoliation allows plants to use the limited store of soil water for the growth of new leaves (Fisher, 1978).

Heavy, uncontrolled burning, especially combined with other excessive uses of the ecosystem, e.g. overgrazing, is harmful to the vegetation and soil. The precise regime for controlled burning is difficult to delimit (White, 1983), depends on objectives (De Bie et al., 1987) and is difficult to carry out anyway.

The floristic composition of the herbaceous layer is the result of the competition between species for the limited resources of nutrients, light and water. Probably because of environmental heterogeneity and vegetation dynamics, the more vigorous species do not eliminate the 'weaker' ones (Breman et al., 1982). Vegetation dynamics is determined by plant characteristics such as germination strategy, rate of growth and length of the growing period, and environmental characteristics such as water availability (in turn influenced by precipitation, soil texture, topography), nutrient availability, amount of light and disturbances such as grazing, fire, felling trees. Breman et al. (1982) have described and analysed the distribution and dynamics of the herbaceous vegetation along a north-south transect through the Sahel steppe and Sudan savanna in Mali; their generalized findings are shown in Fig. 3.4. and can be briefly summarized as follows. Perennial grasses dominate the Sudan savanna, when relatively undisturbed. In favourable periods, a series of wet years, they may invade the Sahel, where usually annual grasses with a quick germination dominate. After a major disturbance, such as a gradual decline in annual rainfall or soil nutrient exhaustion, these annual grasses may gradually replace the perennial grasses in the Sudan savanna. After such a disturbance in the Sahel these annual grasses themselves are replaced by slow-germinating annual species. Major abrupt disturbances (through arable or livestock farming, sudden occurrence or absence of fire or sudden cessation of rain in the rainy season) favour these slow-germinating species in both zones. The rate of regeneration is in general much slower than that of change due to disturbances. Subsequent series of years of above or below normal rainfall cause a shift of the distribution areas of all three groups to the north or south with the amount of rainfall.

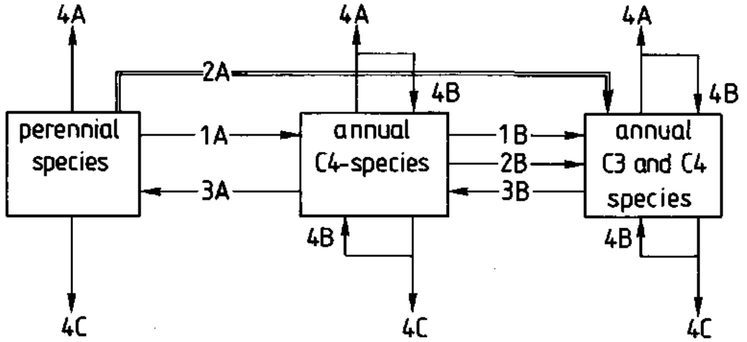


Fig. 3.4. Dynamics of the herbaceous vegetation in the Sahel and Sudan savanna (Breman et al., 1982)

1A,B : replacements through major gradual disturbances
2A,B : replacements through major abrupt disturbances
3A,B : regenerations in absence of disturbances
4A,C : migrations to the north or south during periods of wet or dry years
4B : replacement within groups

3.2.4. *Wildlife*

West Africa is rich in wild animal species with the mammals well represented (Happold, 1973a). Most species have a pan-African distribution, except for a few duiker species, for example *Cephalophus jentinki*, and only a few are really endemic to particular parts of Africa such as the giant eland and the pygmy hippopotamus *Choeropsis liberiensis* (Meester & Setzer, 1971). Most species are found within and around the tropical rainforest. Going north, into the Sudan savanna, the richness of species generally decreases and a strong relation with

Table 3.2. Mammal species in several West African national parks and game reserves[1])

national park/game reserve[2])	1	2	3	4	5	6	7	8	9	10	11
area (x 10^3km^2)	8.1	6.3	11.5	3.9	2.8	11.2	4.0	2.1	1.7	2.2	1.8
mean annual rainfall (x 10^3mm)	1.2	0.9	1.1	1.1	1.1	0.8	1.1	1.0	0.7	1.2	1.0
Papio cynocephalus	*	*	*	*	*	*	*	*	*	*	*
Cercopithecus patas	*	*	*	*	*	*	*	*	*	*	*
Cercopithecus sabeus	*	*	*	*	*	*	*	*	*	*	*
Canis aureus		*			*	*			*	*	*
Canis adustus	*	*			*	*	*	*			
Lycaon pictus	*				*	*	*	*		*	*
Crocuta crocuta	*	*	*	*	*	*		*	*	*	*
Hyaena hyaena		*							*	?	
Panthera leo	*	*	*	*	*	*	*	*	*	*	*
Panthera pardus	*	*	*	*	*	*	*		*	*	*
Acinonyx jubatus					*	*			*	*	*
Loxodonta africana #[3])	*	*	*	*	*	*	*	*	*	*	*
Diceros bicornis										*	*
Phacochoerus aethiopicus #	*	*	*	*	*	*	*	*	*	*	*
Potamochoerus porcus	*		*			*					*
Hippopotamus amphibius #	?	*	*		*	*	*	*		*	*
Giraffa camelopardalis #		*							*	*	*
Syncerus caffer #	*	?	*	*	*	*	*	*		*	*
Tragelaphus scriptus #	*	*	*	*	*	*	*	*	*	*	*
Tragelaphus derbianus	*									*	*
Cephalophus rufilatus #	*	*	*	*	*	*	*	*		*	*
Sylvicapra grimmia #	*	*	*	*	*	*	*	*	*	*	*
Kobus kob #	*		*	*	*	*	*		*	*	*
Kobus ellipsiprymnus #	*	*	*	*	*	*	*	*	*	*	*
Redunca redunca #	*	*	*	*	*	*	*	*	*	*	*
Hippotragus equinus #	*	*	*	*	*	*	*	*	*	*	*
Damaliscus lunatus					*	*			*	*	*
Alcelaphus buselaphus #	*	*	*	*	*	*	*	*		*	*
Ourebia ourebi #	*	*	*	*	*	*	*	*		*	*
Gazella rufifrons		?			*	*		*	*		
total number of species	22	22	20	18	25	26	20	20	20	26	27

[1]) Data from Happold (1973b), FAO (1981), Esser (1980), Child (1974) and this study; nomenclature and systematic classification according to Meester & Setzer (1971)

[2]) Numbers refer to Fig. 3.1.

[3]) #: species dealt with in this study

annual rainfall is supposed (see Delany & Happold, 1979). When several areas within the Sudan savanna are compared (Table 3.2), the number of species can be seen to increase towards the east, partly due to species invading from other bioclimatic zones such as the black rhinoceros, and partly due to less pressure from man.

Increase in cultivation and in the utilization of the savanna woodlands by cattle from the Sahel and a greater hunting pressure on wildlife are the main reasons for the fragmentation of animal populations (Geerling & De Bie, 1986; De Bie et al., 1987; De Bie & Geerling, 1988) and thus for the low numbers of animals. As a result the existence of several species is precarious. Consequently the preservation of wildlife in the Sudan savanna urgently requires an analysis of man's use of natural resources (Geerling & De Bie, 1986).

In this study we only consider certain ungulate species from the Sudan savanna belonging to the orders *Proboscidea*, *Perissodactyla* and *Artiodactyla*, listed in Table 3.2.

3.2.5. Land-use

A complete analysis of land-use in the Sahel and the Sudan zone with the possibilities and conditions for a sustainable utilization of the natural resources is given by Kessler & Ohler (1983) for the Sahel in west Mali, by Geerling & De Bie (1987) for the Mossi Plateau in Burkina Faso, by Kessler et al. (in press) for Burkina Faso and by De Bie & Geerling (1988) for the Sudan zone and by IUCN (1989) for the whole of Sahelian Africa.

Animal husbandry and arable agriculture are the most important types of land-use in the Sudan savanna (IUCN 1989). Animal husbandry is either nomadic, transhumant or sedentary. Nomadic pastoralism predominates at the fringe of the northern Sahel and the adjacent Sahara desert, where the occurrence of forage and water is scarce and unpredictable. Therefore farmers are continually on the move with their herds in search of both. The potential densities of these herds of sheep, goats and dromedaries are low, 7 TLU/km^2 (Kessler & Ohler, 1983) (TLU = tropical livestock unit, an hypothetical animal of 250 kg). During the wet season transhumant livestock grazes the good quality pastures (with a higher phytomass) of the northern Sahel. When the dry season starts, transhumant farmers are forced to move their Zebu cattle, sheep and goats south in search of water. Potential stocking rates in the northern Sahel, up to 29 TLU/km^2 in normal rainfall years, are considerably higher than those in the southern Sahel (Kessler & Ohler, 1983). In the southern Sahel and the Sudan savanna crop farming is usually more important than animal production, which is sedentary. N'dama cattle, sheep and goats are kept in the area around the settlements.

Animal production is low, especially in areas with moderate rainfall, and limited by the low availability of nutrients in the forage (Breman, 1986). Penning de Vries & Djitèye (1982) discuss how the quantity and quality of available forage in the Sahel is related to actual rainfall and soil fertility. Maximum stocking

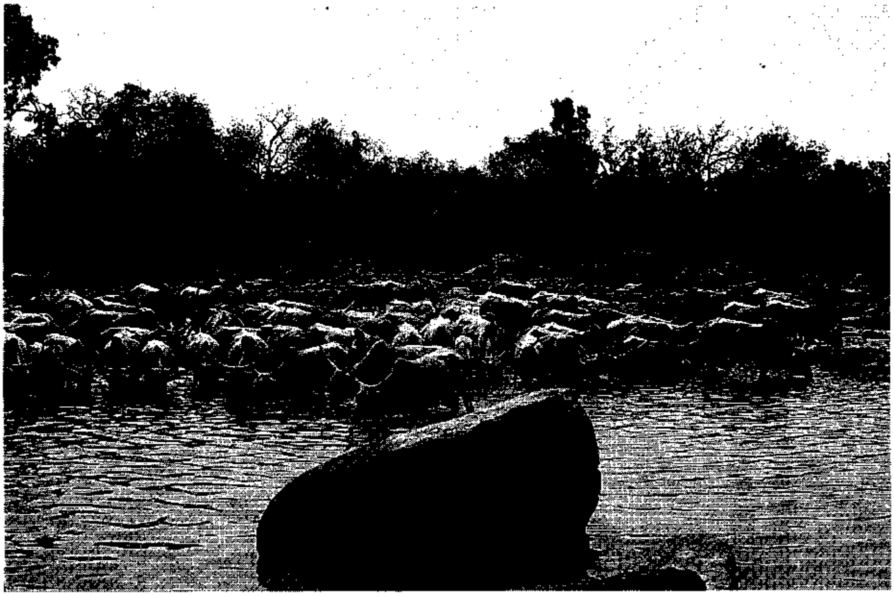


Plate 5. In the dry season transhumant farmers move their Zebu cattle to the savanna in search for water and forage.

rates of Sahelian pastures fluctuate with the series of wet and dry years (see also Breman & De Wit, 1983). The decrease in rainfall since 1970 (Fig. 3.3) has reduced the carrying capacity of the pastures (Penning de Vries & Djitèye, 1982). This has meant that the herdsmen have needed more land to meet animal requirements. In both the nomadic and sedentary livestock mortality rates have risen rapidly and animal numbers have fallen to a level fitting the actual carrying capacity: from 7 to 2 TLU/km^2 in the nomadic system and from 10 to 6 TLU/km^2 in the Sahelian sedentary livestock system (Kessler & Ohler, 1983). Transhumant farmers have solved the problem of shortage of pastures in the dry season by looking for pastures further south, in the Sudan savanna. The available pastures there were utilized and rapidly became overgrazed after which new pastures were sought. Until that time these grasslands in the Sudan savanna were largely unused because of the presence of trypanosomiasis and onchocercosis. Consequently animal numbers remained too high for the Sahelian wet-season pastures, which accelerated the process of degradation of the pastures (De Bie & Geerling, 1987). However in a very dry year mortality rates rose to a high level, for example 50-60% on the Mossi Plateau in Burkina Faso in 1985/1986 (Geerling & De Bie, 1987). At present most of the pastures in both the Sahel and the Sudan savanna are overgrazed; degradation of the natural vegetation continues and erosion gains ground. Furthermore, the transhumant livestock system is breaking down; increasing numbers of transhumant livestock farmers have moved south and become semi-sedentary: they have fewer animals and they move around over shorter distances. Frequently they lose the ownership of their herds, forced to sell on account of declining milk production.

These processes are aggravated by developments in crop farming. As the economic basis for inputs (e.g. fertilizer) is lacking, rain-fed agriculture is the most important type of agriculture dependent upon the natural fertility of the soil. Apart from the permanently cultivated fields in the vicinity of the villages, fields are cultivated for only 1-3 years after which a fallow period of four times the length of the cultivation period is necessary before the fertility of soil is restored (Kessler & Ohler, 1983). In the Sahel production is limited by the amount and distribution of rainfall and, when there is enough water, by soil fertility in the Sahel and the Sudan savanna (Penning de Vries & Djitèye, 1982).

Increase in the human population (Fig. 3.5) has led to three changes in crop practices: 1. extension of crop areas, 2. prolongation of the cultivation period at the cost of the fallow period and 3. neglect of non-productive activities such as soil protection. The resulting soil exhaustion and erosion continue to the present day and the breakdown of the natural ecosystem is obvious. The interests of animal husbandry and arable agriculture frequently clash. Farmers are increasingly forced to utilize marginally suitable land and therefore there is competition for the sparsely available areas (De Bie & Geerling, 1988). Besides, both types of farming negatively affect two other types of land-use: hunting and forest exploitation.

Although forbidden in most countries traditional hunting still continues: subsistence hunting is one of the pillars of the rural economy, 10-50% of animal protein coming from wildlife in rural areas (De Bie et al., 1987). The increasing demand on land by animal husbandry and arable agriculture coincides with a high hunting pressure, not only from the rural population but also from commercial hunters from the urban areas, armed with modern equipment. Larger mammals such as the topi and oryx have nearly all been exterminated in the Sahel and only remnant populations of gazelles are still present. In the Sudan savanna animal populations have been driven back to marginal land and are often too small for long-term viability.

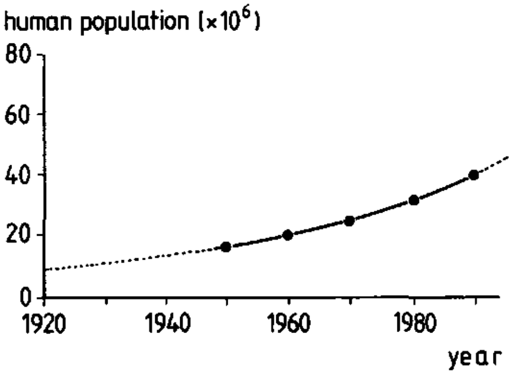


Fig. 3.5. Human population growth in six West African countries (source: United Nations, 1986).

Plate 6. Traditional hunting still continues in the Baoulé

By supplying wood for fuel, the natural vegetation in the Sudan savanna has an important economic function. For example it supplies 95% of all energy used in Burkina Faso. Overgrazing and the increase of arable farming have endangered this fuel supply: deforestation can be seen everywhere.

4. The study area: Biosphere Reserve 'Boucle du Baoulé' and its surroundings

4.1. General

The concept of a 'Biosphere Reserve' has been introduced as a tool with which to integrate a protected area into its environment (UNESCO, 1974). The main objectives of a biosphere reserve can be summarized as 1. to preserve the natural ecosystem for immediate and future benefit and for the conservation of genetic diversity of species, and 2. to provide areas for scientific research, especially for reference studies, but always within the limits set by the first objective (UNESCO, 1974; Batisse, 1982). Because this broad formulation of a biosphere reserve is less strict than that of a national park, there are two important consequences: 1. certain human activities, such as wildlife utilization and cattle grazing, can be allowed in the reserve, thus making integration with the area outside the reserve easier, and 2. guidelines for management demand a careful ecological and socio-economical analysis of both the actual and potential land-use (Heringa et al., 1987).

The Biosphere Reserve 'Boucle du Baoulé' and its surroundings (subsequently called the Baoulé), about 16,150 km^2, is situated in the western part of Mali, about 100 km north-west of the capital Bamako (Fig. 4.1). In this area are a former national park (Parc National 'Boucle du Baoulé') and three former game reserves (Réserve de Badinko, Réserve de Fina and Réserve de Kongossanbougou) (Fig. 4.1), which in 1982 received the official status of biosphere reserve. This reserve has an area of about 8,000 km^2.

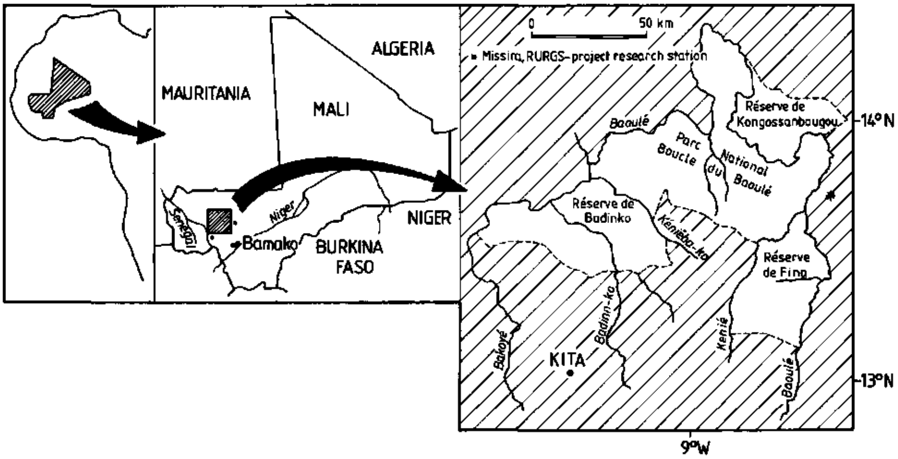


Fig. 4.1. Map of the Biosphere Reserve 'Boucle du Baoulé'

4.2. Climate

As elsewhere in the Sudan savanna, the climate is determined by the movements of the Inter Tropical Convergence Zone (ITCZ). There is one period of rain (June-September) and a long dry season almost without any rain. A clear distinction between these periods is apparent in the vegetation: at the end of the wet season annual grasses cease growth, whereas the perennial grasses, shrubs and trees may continue producing leaves well into February-March.

Before 1970 the long-term average rainfall was about 700 mm in the north and about 1100 mm in the south (Fig. 4.2). From 1970, when a long period of drought began, up to 1986, the average annual rainfall was below the average of the preceding 40 years (Fig. 3.3 and Fig. 4.2.). This reduction in rainfall is most noticeable in August and September (Fig. 4.3); furthermore the rainy season seems shorter. Yearly and regional variations in rainfall are sometimes considerable, being relatively larger in the more arid north. Temperatures are well above 40 °C in the dry season but more moderate in the wet season.

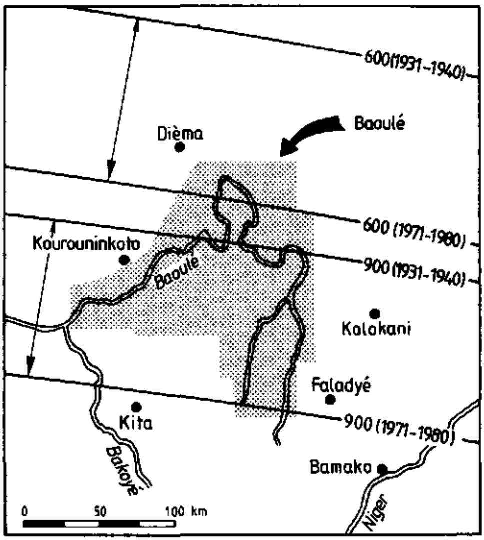


Fig. 4.2. Change in the position of two isohyets (average for 10 successive years) over the period 1931-40/1971-80 (Heringa, 1988)

4.3. Landscape and vegetation

The Baoulé is on the northern edge of the Mandigue plateau. In the study area this sandstone plateau is dissected from south to north. There are plains in between, that have deeper, loamy soils or shallow, gravelly soils on underlying laterite caps. Outcrops of dolerite and schist occur in the western part of the

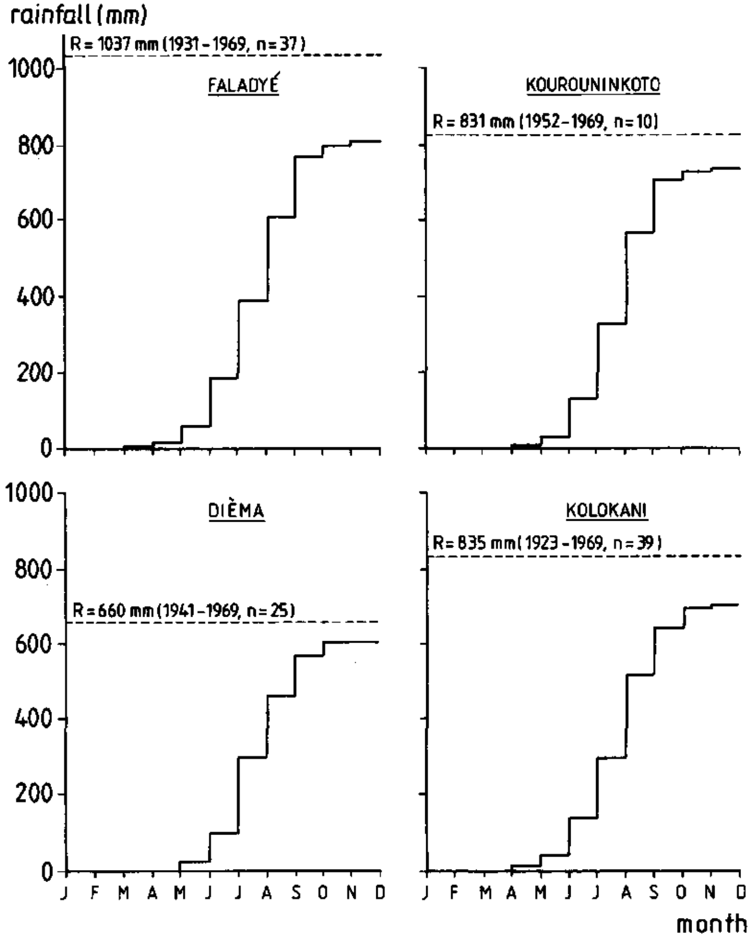


Fig. 4.3. Cumulative plot of average monthly rainfall in the period 1970-1982 compared to the average annual rainfall before 1970 (= R) for 4 weather stations around the Baoulé (for their location see Fig. 4.2)

Baoulé; in the north aeolic sands are found locally.

From the landscape-ecological map of the biosphere reserve, compiled in 1980-1981 (Van Wijngaarden, 1988), a number of landscape-ecological units can be distinguished (Table 4.1). Each of them is a mosaic, a combination of ecotopes (Table 4.2). For practical purposes the landscape-ecological units have been grouped into nine land-system units for this study (Tables 4.1 and 4.3). These units are ecologically significant, can be recognized from the air and on the ground, and are manageable: we were able to record the occurrence of animals in these units during survey flights. See Table 4.3 for a short description of these land-system units and the enclosed map for spatial patterns.

The vegetation, described in detail by Van Wijngaarden (1983,1988), is typical

Table 4.1. Landscape-ecological units of the Baoulé (Van Wijngaarden, 1983)

symbol	short description	contribution of ecotopes1) to the landscape-ecological units (%)				corresponding land-system unit
	HILLS AND UNDULATING TERRAIN					
CD	dolerite hills	50% D	20% S1	30% bare land		VI
CS	hills and undulating terrain on shale	60% S1	40% S2			CS
	PLATEAUS					
LG1	sandstone plateau	40% G1	40% G2	20% F		B
LG2	like LG1, but strongly dissected	40% G2	20% G1	30% Pn	10% F	B
LL1	laterite plateau	50% L2	30% L1	20% F		LSM
LL2	like LL1, but strongly dissected	50% L2	20% L1	20% Pn	10% F	LSM
LL3	like LL1, but with much bare laterite (bowals)	50% B	30% L1	20% L3		LSM
	FOOTSLOPES					
GP	footslopes with deep soils	40% Pn1	40% Pt1	20% G2		F
GL	footslopes, locally with laterite outcrops	50% Pn1	40% L2	10% G2		F
GG	footslopes, locally with sandstone outcrops	50% Pn1	40% G2	10% G1		F
	PLAINS					
PS	plains on shale	40% Pi1	30% S1	30% S2		F
PG	plains with many sandstone outcrops	70% G2	30% G1			SSP
PL1	laterite plains, locally with aeolic sands	50% L2	30% L1	20% Pe		F
PL2	laterite plains	60% L2	40% L1			F
PL3	like PL2, but higher canopy cover of trees	70% L3	30% L1			F
PE	aeolic sand plains	80% Pe	20% Pt1			F
PP1	plains with deep loamy soils	50% Pn1	30% Pt1	20% Pi1		F
PP2	like PP1, but slightly dissected	50% Pn1	30% Pi1	20% L2		F
PP3	like PP1, but associated with plateaus	50% Pn1	20% G2	20% Pt1	10% VI	F
PP4	like PP1, but higher canopy cover of trees	50% Pn2	30% Pt2	20% Pi2		F
PP5	like PP1, but dominated by *Isoberlinia doka*	80% Pn3	20% Pi2			F
PC	complex of PG, PL and PP1	30% Pn1	30% L2	30% G2	10% G1	F

	BOWALS							
B	bowal	80% B	20% L2					LSM
	TERRACES							
T1	lower terrace	40% Pn1	30% Pt1	20% Rf2	10% M			R
T2	higher terrace	50% Pn1	30% Pn2	10% Pt1	10% E			F
T3	like T2, but higher canopy cover of trees	50% Pn2	20% Pn3	20% Pt2	10% E			F
	VALLEYS							
V1	narrow valleys	50% V1	30% Pn1	20% E				R
V2	broad valleys	40% V1	20% V4	20% V6	20% M			R
V3	like V2, but with *Oxytenanthera*	70% V3	20% V2	10% M				R
V4	like V2, but with *Borassus* palms	50% V5	20% V1	20% V2	10% V6			R
V5	imperfectly drained valleys	70% M	20% V4	10% V6				R
	FLOOD PLAINS							
R1	narrow flood plain	40% R1 + Rb	20% Rf1	20% Rf2	20% E			R
R2	broad flood plain	20% R1 + Rb	30% Rf2	20% Rf1	10% Rf3	10% Rf4	10% E	R
R3	like R2, but with abundant *Borassus* palms	20% R1 + Rb	30% Rf3	20% Rf1	10% Rf2	10% Rf4	10% E	R

[1]) for description of ecotopes see Table 4.2

Table 4.2. Ecotope characteristics (Van Wijngaarden, 1983)

	Physical environment				Vegetation			
Symbol	**Parent rock**	**Terrain**	**Termite mounds**	**Soil**	**Structure^1)**	**Dominant woody species**	**Dominant herbaceous species**	**Bcpg^2)**
G1	sandstone	flat	rare	very shallow, rocky	WBG	Pterocarpus lucens Combretum micranthum	Loudetia togoensis	1
G2	sandstone	flat	rare	shallow, stony	WBG	Combretum glutinosum Combretum nigricans	Loudetia togoensis	2
L1	laterite	flat	rare	shallow, gravelly	WB	Combretum glutinosum Andropogon pseudapricus	Loudetia togoensis	2
L2	laterite	flat	common	shallow, gravelly	W +Bd	Combretum glutinosum Pterocarpus lucens	Loudetia togoensis Andropogon pseudapricus	2
L3	laterite	flat	common	shallow, gravelly	WB +Bt	Combretum glutinosum Combretum micranthum Grewia spp.	Schizachyrium exile Andropogon pseudapricus	4
Pe	aeolic sands	gently undulating	rare	well-drained, deep, sandy	W	Combretum glutinosum Sterculia setigera	Schoenefeldia gracilis Andropogon pseudapricus	1
Pn1	sandstone	flat	rare	well-drained, deep, loamy	W	Bombax costatum Combretum glutinosum	Andropogon gayanus Diheteropogon hagerupii	4
Pn2	sandstone	flat	rare	well-drained, deep, loamy	W	Pterocarpus erinaceus Combretum glutinosum	Andropogon gayanus	4
Pn3	sandstone	flat	rare	well-drained, deep, loamy	W	Isoberlinia doka	Andropogon gayanus Hyparrhenia spp.	5
Pt1	sandstone	flat	common	well-drained, deep, loamy	W +Bt	Bombax costatum Combretum glutinosum Anogeissos leiocarpus Boscia angustifolia	Andropogon pseudapricus Diheteropogon hagerupii	2
Pt2	sandstone	flat	common	well-drained, deep, loamy	W +Bt	Terminalia macroptera Combretum glutinosum Feretia apodanthera Grewia spp.	Andropogon gayanus Diheteropogon hagerupii Pennisetum pedicellatum	4
Pi1	sandstone or shale	flat	common	imperfectly drained, deep, loamy	W +Bt	Combretum glutinosum Acacia seyal Anogeissos leiocarpus Grewia spp.	Andropogon gayanus Andropogon pseudapricus	2
Pi2	sandstone or shale	flat	common	imperfectly drained, deep, loamy	W +Bt	Anogeissos leiocarpus Acacia seyal Tamarindus indica Feretia apodanthera	Andropogon gayanus Hyparrhenia spp. Pennisetum pedicellatum	4
J1	sandstone or aeolic sand	flat or gently undulating	rare	well-drained, deep, sandy or loamy	WB	Sclerocarya birrea Guiera senegalensis	Andropogon pseudapricus Sporobolus festivus	2
J2	sandstone or shale	flat	rare	well or imperfectly drained, deep, loamy	W	Acacia seyal Piliostigma reticulatum	Andropogon gayanus Andropogon pseudapricus	3
J3	sandstone	flat	rare	well or imperfectly drained, deep, loamy	W	Vitellaria paradoxa Ziziphus mauritiana	Andropogon gayanus Hyparrhenia spp.	4

S1	shale	flat to undulating	rare	well-drained, shallow to deep, clayish	WB	Acacia seyal	Andropogon gayanus Hyparrhenia spp.	5
S2	shale	undulating	rare	shallow, gravelly, clayish	W	Pterocarpus erinaceus	Hyparrhenia spp.	4
E	sandstone or alluvium	undulating	rare	various types	WB	Pterocarpus lucens	–	1
R	laterite	flat	rare	imperfectly drained, very shallow	G	Lannea microcarpa	various annual spp.	1
F	sandstone	mountainous	rare	shallow	Wd	variable	Pennisetum pedicellatum Andropogon gayanus	2
D	dolerite	hilly	rare	variable, but always with boulders or rocks	WG	Adansonia digitata various Ficus spp.	Pennisetum pedicellatum	1
V1	alluvium	flat	rare	well-drained, deep, loamy	Wd	Anogeissos leiocarpus Piliostigma reticulatum	Pennisetum pedicellatum Andropogon gayanus	2
V2	alluvium	flat	rare	well-drained, deep, loamy	W	Pterocarpus erinaceus Piliostigma reticulatum	Andropogon gayanus Hyparrhenia spp.	5
V3	alluvium	flat	rare	well-drained, deep, loamy	Wd	Oxytenanthera abyssinica	Pennisetum pedicellatum	1
V4	alluvium	flat	rare	imperfectly drained, deep, loamy	Wd	Anogeissos leiocarpus Mitragina inermis	Andropogon gayanus Pennisetum pedicellatum	3
V5	alluvium	flat	rare	imperfectly drained, deep, loamy	W	Borassus aethiopum	Andropogon gayanus Hyparrhenia spp.	4
V6	alluvium	flat	rare	poorly drained, deep, clayish	WG	Mitragina inermis Piliostigma reticulatum	Vetiveria nigritana	5
M	alluvium	flat	rare	very poorly drained, deep, clayish	G	–	Vetiveria nigritana Echinochloa stagnina	5
R1	alluvium	river bed	rare	variable	BG	Rotula aquatica	Cyperaceae spp.	3
Rb1	alluvium	river bank	rare	variable	B	Phyllanthus reticulatus	Vetiveria nigritana Pennisetum pedicellatum	3
Rb2	alluvium	river bank	rare	well-drained, deep, loamy	Bt	Acacia erythrocalyx	Pennisetum pedicellatum	1
Rf1	alluvium	rarely flooded flood plain	rare	well-drained, deep, sandy to loamy	F	Diospyros mespiliformis Combretum micranthum	Pennisetum pedicellatum Setaria spp.	1
Rf2	alluvium	rarely flooded flood plain	rare	well-drained, deep, sandy to loamy	Wd	Anogeissos leiocarpus Combretum micranthum	Pennisetum pedicellatum	1
Rf3	alluvium	rarely flooded flood plain	rare	imperfectly drained, deep, loamy	WBd	Borassus aethiopum	Andropogon gayanus	3
Rf4	alluvium	rarely flooded flood plain	rare	poorly drained, deep, loamy to clayish	W	Mitragina ilermis Cordia myxa	Andropogon gayanus Vetiveria nigritana	4

[1] Structure
G = Grassland
B = Bushland
W = Woodland
F = Forest
d = dense
t = thicket
+ = only on termite mounds

[2] Basal cover of perennial grasses
1 = 0%
2 = 0-2%
3 = 2-5%
4 = 5-10%
5 = >10%

for the Sudan savanna. The change of climate from north to south has a strong influence on the vegetation (see unit F, Table 4.3). Only in the southern valleys are conditions favourable for the growth of bamboo (*Oxytenanthera abyssinica*). A small grassy flood plain, the only one in the area, can be found on the western border of the former Fina game reserve. Every year, in November-December,

Table 4.3. Description of land-system units (after De Bie & Kessler, 1983 and Van Wijngaarden, 1988)

unit	geomorphology	name	vegetation	proportion of total area (%)
R	river + lower terraces	river	riverine forest, consisting of a fringe of large trees and shrubs with high, often closed canopy cover; rivers and streams have sandy or rocky beds which show a patchy cover of herbs, sedges and *Vetiveria nigritana* during the dry season.	7
F	shallow to deep soils, flat or gently undulating plains	Andropogon savanna	open canopy of trees and shrubs, in the north dominated by Combretaceae, in the south by *Isoberlinia doka, Vitellaria paradoxa*, etc.; a continuous grass cover consists of annuals (in the north) and predominantly perennials such as *Andropogon gayanus* (in the south).	72
LSM	non-elevated weathered laterite caps	Loudetia grass savanna	very open canopy of tall and small shrubs laterite caps (Combretaceae); grass layer consists mainly of annual species (e.g. *Loudetia togoensis*)	7
SSP	non-elevated sandstone pavements	Loudetia shrub savanna	rather similar to LSM.	5
CS	slopes of cindery-type sandstone (non-elevated)	shrub savanna	woody bushland in which *Acacia seyal* and perennial grasses dominate	3
VI	areas with exposed intrusive material	tree savanna	woodland; dominant woody species are *Adansonia digitata* and various Ficus species; *Pennisetum pedicellatum* is the dominant grass species	<1
B	(non-)elevated areas or escarpments of bouldary/layered sandstone	woodland savanna	dense woodland in which no specific woody species dominates; grass layer consists mainly of perennial grasses and *Pennisetum pedicellatum*	5

almost the entire area is burned off, either purposely to stimulate the regrowth of perennial grasses, to improve visibility or just by accident.

In general, soil fertility is low, especially concerning nitrogen, phosphorus and potassium; cation exchange capacity and base saturation are low (Van Wijngaarden, 1988).

There are no signs of large-scale erosion.

4.4. Land-use

In general crop farming around (and within) the study area can be described as being a rain-fed rotational agriculture (De Bie & Kessler, 1983): the amount of rainfall determines the types of agriculture and crops cultivated. Millet, sorghum and groundnuts are important crops. Cattle are kept as draught animals, for their manure and other purposes.

In the dry season large numbers of transhumant cattle, sheep and goats from the north visit the Baoulé (De Bie & Kessler, 1983; Van de Mandele & Roëll, 1988). Lack of water and forage in the north bring about these seasonal migrations despite the risk of various diseases (such as trypanosomiasis) and predators (lion and hyena). There is increasing irritation between arable farmers and the transhumant herdsmen, both groups competing for increasingly scarce uncultivated land. This is the result of a higher demand for agricultural crops through

Plate 7. Large numbers of transhumant goats visit the Baoulé in the dry season

the increase in rural population density as well as an increasing soil exhaustion of the agricultural fields.

Hunting is an important secondary land-use type supplying the human population with up to 30% of the animal protein they need (Havinga, 1988). Originally practised predominantly by farmers and certain tribes of transhumant cattle breeders, it is becoming more and more a commercial activity beyond the local and regional scale.

Gathering of forest products is still an important characteristic of the rural economy. Besides firewood the savanna provides other products such as food plants, honey, medicinal plants, timber for housing and wood for utensils.

5. General methods

5.1. Vegetation

5.1.1. Phenology

The phenology of plant species was recorded, as plant growth was expected to be related to the rainfall pattern.

Sprouting, flowering, withering of leaves, leaf fall and the growth in the dry season of savanna grasses were recorded at five stations (see Fig. 5.1). The following classes of phenological stages of over 30 woody species were recorded at several other stations (see Fig. 5.1), also at approximately monthly intervals:

Leaves	*Flowers*	*Fruits*
sprouting	in bud	unripe
young leaves	in full blossom	ripe
mature leaves, no further growth	past flowering	old
leaves drying out		
old leaves		
without leaves		

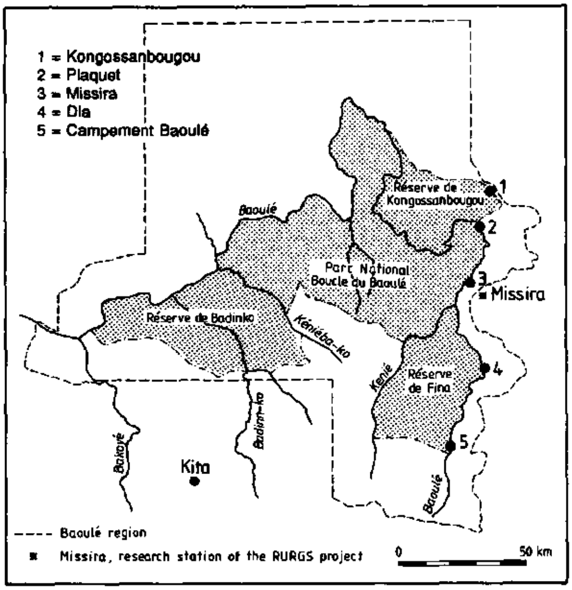


Fig. 5.1. Sampling stations in the Baoulé

5.1.2. Primary production

In order to examine the development of plant availability over the year, data on primary production were collected by the vegetation ecologists of the R.U.R.G.S.-project; four aspects of primary production of the vegetation were investigated (see Van Wijngaarden, 1983, 1988):

1 the phytomass of perennial and annual savanna grasses in 4 x 4 m plots at five stations was clipped at approximately monthly intervals for one year. Samples were taken to the laboratory in plastic bags, weighed to determine the fresh weight, dried for 24 h at 70° and weighed again for the dry-weight determination.

2 the dry-season growth of the perennial grasses in these plots was clipped at monthly intervals in one dry season; fresh and dry weights were determined as in (1).

3 peak phytomass of annual and perennial savanna grasses was harvested at the beginning of the dry season at a larger number of stations; fresh and dry weights were determined as in (1).

The results of the above measurements for the various ecotopes of each rainfall zone, published by the R.U.R.G.S-project (Van Wijngaarden, 1988), are used in this study for calculating the peak phytomass of savanna and riverine grasses per land-system unit per rainfall zone for years with a normal (= equal to the long-term average) annual rainfall, and with below normal annual rainfall, using the following formulas:

$$F_{a+p.i.j} = [(P_{h.i.j} \times 100 \times O_{i.j}) \times c_{gi.j}]$$

and

$$F_{p.i.j} = F_{a+p.i.j} \times c_{p.j}$$

where:

$F_{a+p,i,j}$ = phytomass (DM) of annual + perennial grasses in ecotope i in rainfall zone j

$F_{p,i,j}$ = phytomass (DM) of perennial grasses in ecotope i in rainfall zone j

$P_{h,i,j}$ = herbaceous phytomass, kg(DM).ha^{-1}, in ecotope i in rainfall zone j

$O_{i,j}$ = area of ecotype i in rainfall zone j, km^2

$c_{gi,j}$ = correction factor for the proportion of annual and perennial grasses in ecotope i in rainfall zone j

$c_{p,j}$ = correction factor for the proportion of perennial grasses in rainfall zone j

Adding ecotope estimates per land-system unit provided an estimate of the peak phytomass per land-system unit per rainfall zone.

In a comparable way the phytomass of the dry-season growth of perennial grasses was calculated and estimates per land-system unit per rainfall zone obtained:

$$F_{r,i,j} = R_{i,j} \times 100 \times O_{i,j}$$

where:

$F_{r,i,j}$ = phytomass (DM) of dry-season growth of perennial grasses in ecotope i in rainfall zone j

$R_{i,j}$ = phytomass of dry-season growth of perennial grasses, kg(DM).ha^{-1}, in ecotope i in rainfall zone j

$O_{i,j}$ = area of ecotope i in rainfall zone j, km^2

4 Leaf and young shoot phytomass of five shrub species at two savanna stations was measured at approximately monthly intervals; fresh and dry weights were determined as in (1).

In addition to this, I made measurements and collected samples as follows:

* samples of perennial grasses from the five stations were separated into categories of green leaf, dry (= brown) leaf, stem + sheath, and spike, to assess their relative proportion in the grass tussock and for subsequent chemical analysis.

* phytomass of *Cyperus* species on the dry river bed near Missira Research Station was clipped to measure plant growth; at approximately monthly intervals ten plots of 0.25 m^2 were clipped outside three exclosures and five inside them; samples were taken for chemical analysis;

* leaf and young shoot phytomass of woody riverine vegetation types growing on the river bank near Missira Research Sation was measured at approximately six-weekly intervals; ten plots of 1.50 m^2 each of *Acacia ataxacantha* and ten plots of 1.00 m^2 each of *Phyllanthus/Flemingia* vegetation were clipped.

* leaf + young shoot samples of 30 woody species were collected for chemical analysis.

5.1.3. Chemical analysis of plant material

In order to assess the nutritional value of plant material for herbivores plant samples were analysed chemically.

After harvesting the various plant groups and vegetation types (see 5.1.2), oven-dried samples were ground in a hammer-mill (1 mm mesh) and stored in sealed plastic bags for later analysis.

These samples were analysed for:

1 the percentage of organic material, using standard procedures.

2 the percentages of neutral-detergent fibre (NDF), acid-detergent fibre (ADF), acid-detergent lignin, cellulose and cutin, using the Van Soest-method (Goering & Van Soest, 1970; Van Soest, 1982).
We chose the sequential procedure of analysis, recommended by Mould & Robbins (1981), where the sample is first analysed for the concentration of NDF, after which the concentration of ADF is determined in the residue, then the concentration of lignin and finally the concentration of cellulose; in the alternative, parallel, procedure in which NDF concentrations are determined in separate samples, ADF concentrations are slightly higher (see Table

Table 5.1. Concentration (%OM) of ADF, hemicellulose, lignin and cellulose in 6 plant samples, using sequential (I) and parallel (II) analysis

	ADF		hemicellulose		lignin		cellulose	
	I	II	I	II	I	II	I	II
A356	37.2	43.6	38.0	31.5	7.4	5.7	32.3	34.6
A613	21.7	28.1	39.1	32.8	3.5	2.7	24.1	25.3
A612	36.4	37.4	38.0	37.0	5.8	4.2	30.6	33.4
A022	31.9	33.3	31.6	30.2	5.5	3.5	24.3	26.3
A252	40.7	42.3	39.5	37.8	8.6	6.4	32.0	35.3
A512	38.6	39.8	35.7	34.5	6.8	5.5	29.5	32.7

5.1), probably due to the precipitation of chemical compounds such as tannins from the cell contents in the acid environment (B. Deinum, pers.comm.; Mould & Robbins, 1981).

The proportion of cell content was assumed to be the difference between total organic matter and NDF (Van Soest,1982).

The percentage of hemicellulose was calculated by subtracting ADF from NDF although Mould & Robbins (1981) argue that this fraction represents more than hemicellulose alone.

If in the analyses of NDF and ADF duplicate samples were more than 5% above or below the average, these samples were not accepted; in the analyses of lignin and cellulose 10% deviation from the average was taken as a criterion.

3 the nitrogen concentration using the Kjeldahl analysis; crude protein concentrations were calculated by multiplying the percentage nitrogen by 6.25.

4 the concentration of tannins in a number of samples, using the formaldehyde method (Laboratory for Soil and Crop Research, Oosterbeek, the Netherlands).

5 the in-vitro digestibility, or more accurately the in-vitro rate of disappearance of dry/organic matter, following the procedure of Van Soest (1982). The rumen fluid of steers adapted to a roughage diet was used as inoculum in order to obtain maximum digestibility of cell-wall components. In-vitro values were *not* converted into in-vivo values using standard samples; these standards are of limited use in this study because they are derived from feeding trials with sheep which have a feeding strategy that differs from those of the herbivores studied. However these standards have been used to correct for variations in the donors inocula between successive series of analysis.

5.2. Fauna

5.2.1. Observations from the ground

In January 1980 we started observing animals and collecting faeces regularly in the Fina and Kongossanbougou game reserves, in the eastern part of the national park 'Boucle du Baoulé' and in the adjacent zone on the eastern bank of the river Baoulé (see Fig. 4.1). The western part of the Baoulé was very difficult to reach and research there demanded so much organization that we only made observations there once (February 1981). When observing animals the following notes were taken:

- * species, location, time and date;
- * total number, and if possible, sex and age of individuals, based on body size and horn development; three age classes were distinguished: calf/juvenile (< 0.5 adult size), subadult (> 0.5 adult body size and horns, if present, not fully grown) and adult;
- * activity, such as foraging, walking, and lying down;
- * plant category grazed (grasses, forbs, shrubs or trees); if possible, plants were identified to species level;
- * body condition; following Riney (1982) body condition was classified as:
  - I: poor = spinal ridge and ribs clearly visible, tail-base concave, flanks hollow;
  - II: fair = ribs just visible, tail-base flat;
  - III: good = ribs not visible, tail-base convex, filled flanks;
- * description of terrain; dominant plant species in the various vegetation strata, indications of recent fires, proximity of water.

The low incidence of actual sightings made the help of all colleagues necessary to obtain more information. They were asked to record all animals seen during their field trips on standard notation sheets.

Besides the field trips we made by car, more detailed surveys were carried out on foot near the Missira Research Station (see Fig. 5.1). Our familiarity with the area enabled us to observe animals for longer periods and obtain more data. The relative abundance of bushbuck and roan antelope in this area gave us the opportunity to collect additional data on, for example, home range size, stability of groups, and foraging behaviour of these species. The results of these two studies are reported elsewhere (Heitkönig, 1983b; Smits, 1982, 1986).

The data on the occurrence of animal species and their ecology, collected by the R.U.R.G.S.-project, prior to 1980, have been omitted from the analyses because the records were incomplete or inaccurate.

5.2.2. Aerial surveys

In order to obtain information on animal numbers on a comparable basis all over the Baoulé, two aerial surveys were made. These were conducted by Dr. R.M. Watson, Resource Management & Research, London; this paragraph describes the techniques, he employed in the inventories. These inventories aimed to supply the R.U.R.G.S.-project with total estimations of a number of features of the Baoulé, primarily the wildlife species and their distribution at the beginning of the wet season (1980) and in the late dry season (1981). Features were sampled using stratified random sampling. Methodology is as follows (for further details see De Bie & Kessler (1983).

Stratification: stratification was applied to break up the heterogeneous land into units that were ecologically, relatively homogeneous, enabling a more efficient sampling procedure and a smaller sampling error, i.e. a more precise estimation. Using a combination of satellite imagery, aerial photographs, high-altitude flying and criteria such as geomorphology, vegetation, drainage pattern and land-use, stratification produced 51 and 69 land and riverine units (LU/RU) for 1980 and 1981 respectively. Most units have been grouped into zones, where possible corresponding with already existing park or reserve boundaries (Fig. 5.2).

Samples: samples took the form of transects, flown in straight lines over a unit. The number of samples taken per unit depended on the density and distribution of the phenomena to be counted. Usually a certain average cover percentage is chosen below which observations cannot produce reliable estimates. In these surveys an average sampling cover of about 10% was aimed for in those areas where wildlife was expected; the remaining areas were sam-

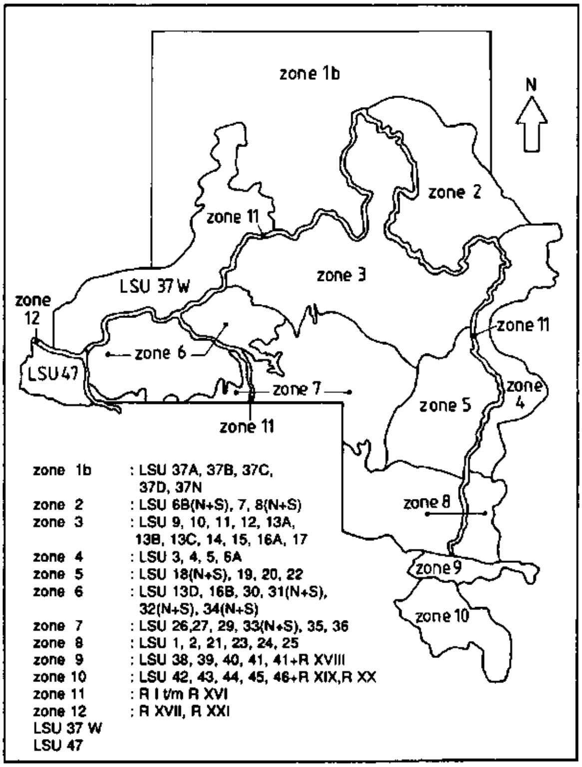


Fig. 5.2. Stratification of the survey area into zones, 1981 (De Bie & Kessler, 1983)

Table 5.2. Average sampling cover (% of total survey area)

year	area	sampling cover mean	s.d.
1980	zone 1a	3.6	0.5
	zones 2-8,11	10.4	2.5
1981	zone 1b	5.4	0.9
	zones 2-8,11,12	12.3	0.6
	zones 9,10	17.8	5.0
	LU 37W	6.4	–
	LU 47	10.9	–

pled less intensively, (see Table 5.2). The location of samples in a unit was selected at random. Samples were orientated at right angles to the ecological axis of the unit, i.e. parallel to the direction of maximum change in density of a feature. Such an orientation results in a transect with maximum heterogeneity; furthermore, differences between transects are reduced and thus also the sampling error.

Samples were demarcated by fixing two aluminium poles to the struts of the airplane wing so that the observer looked between them down to the ground in the area where the count was to be made. The width of the transect is determined by the position of the poles on the wing struts, the angle of banking and the altitude of the airplane, the nature of the terrain, and the position of the observer's head (see Table 5.3 for some operational details).

The counting of animals depended on whether an animal was inside or outside the demarcated area. If inside, it was counted. If a group extended beyond the width of a transect, the number of the whole group was noted as well as the number of the part inside the transect. Also, if there were too many animals, a photograph was taken from which the count was later made. Animals concealed by dense vegetation were counted and, if possible,

Table 5.3. Operational details of the aerial surveys

	1980		1981	
	survey area except 1a	zone 1a	survey area except 1b and LU 37W	zone 1b + LU 37W
survey speed	110 km/h	129 km/h	112 km/h	130 km/h
flight height	114 m	141 m	112 m	140 m
strip width	163 m	203 m	167 m	222 m

afterwards scared away into more open fields to be counted more accurately. All wildlife species were recorded according to group size, where possible, group composition with respect to age and sex, and to the land-system unit in which the animal was observed.

Abandoned, fallow or cultivated fields, as well as land-system units were enumerated by timing with a stopwatch as the area in question passes a fixed point on the inner pole. These times were converted to percentages of flying time along each transect.

Sample errors: there are various sources of error all which can influence the final estimation. Errors can be classified as:

- demarcation errors, due to the movements of both the airplane and the observer which cause deviations from the chosen transect width;
- enumeration errors, due to groups of animals, incorrectly counted when animals are concealed by vegetation or totally missed; correction factors have been calculated following Jolly & Watson (1979);
- identification errors: in mixed herds sheep and goats cannot be distinguished. Fallow and abandoned land is also often difficult to distinguish. There are sometimes problems in differentiating between the small herbivores, oribi, reedbuck and the two duiker species.

Calculations: estimates of the phenomena recorded were calculated as:

$$Y_a = \sum_i Z_i \text{ x } d_i \text{ x } R$$

where:

Y_a = corrected estimate for any item a recorded
Z_i = the area of any stratum i
d_i = the average density of the item a in stratum i
R = the total correction factor for item a

The standard error of any item is calculated as:

$$S.E._a = \sqrt{\frac{Z_i^2}{n_i} \times (R \times s)^2}$$

$S.E._a$ = the standard error of item a
n_i = the number of transects in any stratum i
s = standard deviation of item a in stratum i.

5.2.3. Analysis of diet composition

The food choice of wild ungulates was assessed by direct observations of foraging animals, the recording of feeding traces, rumen-content analysis and faecal analysis.

Direct observations produced very little information: the low densities of various species and their extreme wariness meant that animals were seldom seen foraging. Bushbuck in the near vicinity of the research station was the only species for which we were able to assess the frequency with which the various plant species were eaten, but only in the riverine habitat and during day-light. As bushbuck visit the savanna at night (Smits, 1982), our observations are of limited value for a quantitative assessment of the diet.

Careful examination of the vegetation can show which plant species are eaten by the wild herbivores, because grazing and browsing leave traces on shoots, leaves and bark which remain visible for up to several weeks depending on the growth stage and season. The advantage of this method over the direct observation of foraging animals is that patterns of vegetation use can be detected even when animals feed in thickets or at night. However, by this method it was impossible to ascribe feeding traces to a particular animal species unless clearly discernable foot prints were nearby. and this was rare.

The epidermal structure of plants is specific for each species. This epidermal layer is covered by a cuticle (consisting of cutin) which extends between the epidermal cells in a way characteristic of the species concerned. If the cuticle is separated, it provides an impression of the epidermal layer. The resistance of cutin to ruminal acids (Stace, 1965) is used in the analysis of rumen contents and faeces to identify the epidermal layers of the partly digested plants and provide information on the animal's diet.

The time different plants and plant parts are retained in the rumen differs. Therefore the quantitative analysis of rumen contents is normally limited to the identification of recently ingested particles, not or only slightly fragmented as a result of fermentation (Van de Veen, 1979). The quantitative reconstruction of the diet by rumen content analysis needs a considerable sample of dead animals. Although we were able to obtain permission to shoot bushbuck, warthog and roan antelope, this was only allowed in the dry season. We only shot 7 bushbuck and 2 roan antelope and therefore made a qualitative analysis of the rumen contents where all particles were included in the analysis regardless of their size. The following routine was used:

1 collection of a rumen sample, c. 100 ml, made up from various parts of the rumen of a freshly shot animal;
2 preservation of the sample in a 10% formalin solution;
3 taking a c. 5 g (fresh weight) sub-sample after thorough mixing;
4 boiling the sub-sample in 10 ml concentrated nitric acid (HNO_3) for 5 min;
5 adding 300 ml H_2O and boiling for 10 min;
6 pouring off the supernatant after fragments had settled down;
7 repeating steps 5 and 6;

8 taking 5 sub-samples of the fragments and mounting them in gelatin-glycerine on microscope slides.

About 100 fragments were identified on each microscope slide, using a 100x magnification, a key for vegetative characters and a reference collection of plant epidermes (Heitkönig, 1983a). Fragments that could not be identified at the species or family level, were classified as unidentifiable dicotyledons or monocotyledons.

It was relatively easy to collect faeces of the different animal species in the Baoulé, especially in the dry season. Using the faeces of known animal species for reference and checking the immediate surroundings of the droppings for foot prints, we had no problem in identifying species except the red-flanked duiker and Grimm's duiker as their faeces were too similar.

The general technique of maceration of faecal material is well known, see for example the reviews by Scotcher (1979) and Wesselo (1984), and need not to be described here. However, a problem often mentioned and also encountered in this study was the high proportion of fragments that could not be identified due to e.g lack of translucence, or fibrous material obscuring cuticle fragments. In order to achieve the maximum number of potentially identifiable fragments we deviated from normal procedures and applied the method of Goering & Van Soest (1970), originally designed for the assessment of plant cell-wall components, to the faecal samples. We prepared microscopic slides as follows:

1 faeces were collected whenever possible;
2 faeces were dried at 70° for 48 h and stored in sealed plastic bags for later processing;
3 10 droppings were randomly selected and soaked in water for about 10 min to make them easier to pull apart;
4 faeces were pulled apart by hand; seeds were stored separately for later identification;
5 about 1 g of the fragmented faeces was boiled in acid-detergent-reagent (ADR, see Goering & Van Soest, 1970) for 1 h in order to remove bacterial residues, animal excretion products, protein and hemicellulose;
6 the sample was filtered over a glass filter after which the residue, which contains cutin, lignin and cellulose, was washed with hot water; incubation of the residue with $KMnO_4$-solution followed at room temperature for about 3 h in order to remove the lignin components in the plant fragments (see Goering & Van Soest, 1970);
7 after washing the residue was incubated with 67% H_2SO_4 to remove the cellulose and leave the cutin;
8 the residue was quantitatively transferred into a petri-dish and evaporated till nearly dry;
9 10 sub-samples of 0.5 x 0.5 cm were taken randomly (using a paper with coordination system), and mounted on slides.

To identify all the plant fragments on the slides we made a determination key (Heitkönig, 1983a), a reference collection and photomicrographs of epidermes of the different parts of known plant species such as the stem, sheath, abaxial (= under) and adaxial (= upper) sides of the leaf. Unidentifiable fragments were described and encoded. Only fragments larger than 10,000 μ^2 were used for the qualitative assessment of plant species in the diet of an animal species as smaller fragments generally do not contain sufficient characteristics (such as glands and hairs) for their identification. However, smaller fragments but always larger than 5,000 μ^2, were used for quantitatively assessing the proportion of monocotyledons and dicotyledons in the diet (see 7.4.2).

The different rates of digestion of plant species is generally regarded as a source of error when quantifying plant species in the faeces of herbivores (Anthony & Smith, 1974; Putman, 1984). However, by limiting the quantification to only two classes, monocotyledons and dicotyledons, and by pooling the data per season, this problem is presumably overcome.

We identified seeds found in the faeces by comparing them with seeds from known species either that we had determined ourselves in Mali or those from the seed collections of the Department of Plant Taxonomy (Agricultural University of Wageningen, the Netherlands) and the Institute for Biological Archaeological Research (University of Groningen, the Netherlands).

Part II: Ecological characterization of wild ungulates in the West African savanna

Management of animal species, whether for sustainable utilization, which is utilizing animal production on a sustainable level, or for preservation, depends on an adequate identification of the resources needed by the animal species concerned (Owen-Smith, 1982a). Three basic needs can be distinguished: food, water and shelter, the last as protection against climatic stress and predators. Given the large diversity of animal species in the West African savanna, one may expect a differentiation of specific adaptations in order to meet these basic needs within the framework of the resources available. The species-specific adaptations (reflected in for example morphology, food choice, and digestive physiology) have consequences for other aspects of the species' biology such as social behaviour, range size and movements, and reproduction (Sinclair, 1977).

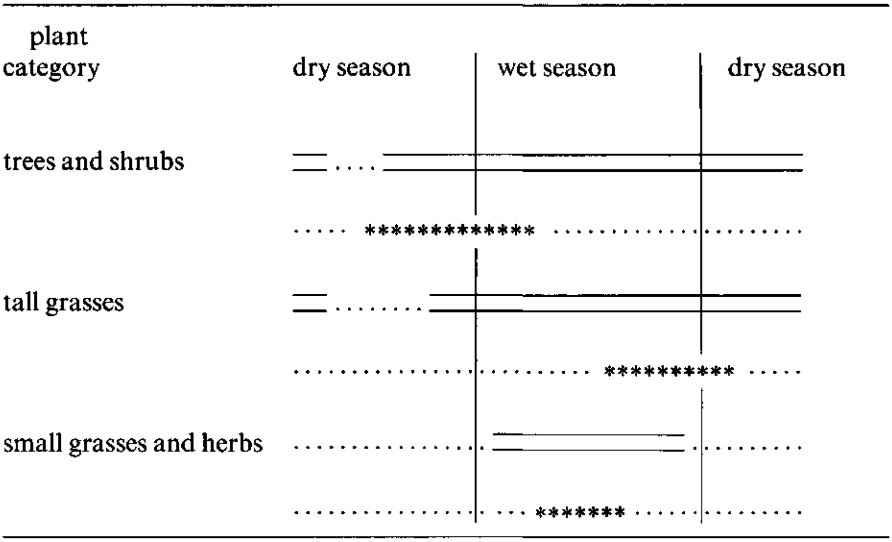
Chapter 6 describes the vegetation of the study area as a source of food. Chapter 7 deals with the biology of the ungulate species, concentrating on those aspects which lead to an ecological characterization of the ungulate community, the subject of Chapter 8.

6. The vegetation as a source of food

6.1. Introduction

To understand the ecology, distribution and potential abundance of the various ungulates in the Sudan savanna ecosystem, it is essential to know how plant phenological patterns vary over the year, as well as the patterns in plant availability and quality brought about by rainfall and soil fertility, and affected by bush fires. These aspects are dealt with in this chapter.

Certain patterns in plant availability can be derived from the relationships between the time of annual rainfall and temperature changes, and the various phases of plant development. During and just after the wet season the Sudan savanna grows abundantly but it provides a poor environment in the dry season: cover is minimum and food is scarce. This is a typical pattern for all savannas (Bourlière, 1983). A general scheme of the phenological patterns in the Sudan savanna is depicted below:



═ : in leaf
**** : flowering

Woody plants and perennial grasses are active throughout the year but more so during the wet season, whereas the growth of annual grasses is confined to the wet season (Bourlière & Hadley, 1983; Geerling, 1983). A rapid growth response to the first rains is characteristic for savanna grasses because then nutrients are released as litter accumulated during the dry season decomposes (Bourlière & Hadley, 1983).

Leaf-growth will continue in perennial grasses in the dry season if water is available in the soil. Unlike monocotyledons, woody trees and shrubs usually anticipate the first rains with the production of new leaves, which is triggered by factors such as longer photo-periodicity, change in temperature and increasing air humidity (Owen-Smith, 1982a; Sarmiento & Monasterio, 1983).

Thus as a source of food for both grazing and browsing herbivores the savanna shows important seasonal variations.

In general the primary production depends on the availability of water in the soil. Rainfall largely supplies the needs of the annual herbs whereas the deeper rooting perennial herbs, trees and shrubs also utilize subsurface water supplies. As pointed out by Penning de Vries & Djitèye (1982) and Breman & De Wit (1983) the availability of plant nutrients, especially nitrogen and phosphorus, is also important in determining the growth and quality of the herbaceous vegetation in the Sudan savanna of West Africa.

Gramineae are by far the most important contributors to the herbaceous primary production in the study area (92-98%, Van Wijngaarden, 1988) and with respect to weight *Andropogon gayanus* is the most important perennial. Although it has a high colonizing ability (Breman et al., 1982), its northern distribution limit of about 600 mm annual rainfall can change due to fire, changes in rainfall, or grazing (see 2.2.3). Moreover, just as other perennial grasses, its leaves continue to grow in the dry season and at this time *Andropogon gayanus* constitutes the bulk of herbaceous phytomass (Van Wijngaarden, 1988). Therefore I have focused my attention on this perennial savanna grass species.

The digestibility of a plant is related to the amount of insoluble complex carbohydrates in the cell wall such as cellulose and hemicellulose. Their fermentation is affected by the structure of the cell wall (such as the degree of lignification) and the species of microbes in the digestive tract of the herbivore. Microbial activity in turn depends upon an adequate protein supply (Van Soest, 1982). Hence, food intake is related to the protein content of the forage (Van Soest 1982). As plant protein is often available in limited amounts (Mattson, 1980; Owen-Smith, 1982a; Van Soest, 1982) the concentration of protein-bound nitrogen in the plants on offer to herbivores, is therefore one of the most critical parameters for nutritional quality.

Only in the last decades has the effect of tannins and toxic plant components such as saponins, glycosides and alkaloids (the so-called secondary plant components) on the plant-herbivore relationship become clear (e.g. McLeod, 1974; Cates & Rhoades, 1977; Rosenthal & Janzen, 1979). They interfere directly with the herbivore's physiology or with its microbial flora. Their defensive efficiency strongly depends on their concentration within the plant and on the susceptibility of the herbivore. There are two classes of tannins: hydrolysable tannins, which are supposed to inactivate the digestive enzymes of herbivorous insects, and condensed tannins, which are attached to protein of the plant's cell-wall and defend it against the attack of microbes of ruminant herbivores (Zucker, 1983). Moreover, the presence of these tannins causes an excessive production of proteolytic enzymes in the rumen which in turn results in a considerable faecal loss of nitrogen, a lower nitrogen balance and loss of weight (Robbins et al., 1987a). Their harmful effect on the animal's digestion warrants that some attention is paid to these components.

The production of foliage by woody plants in the West African savanna has been studied in much less detail than the phytomass of annual and perennial grasses (e.g. Kowal & Kassam, 1978; De Leeuw, 1979). The limited data is reviewed by LeHouérou (1980a). Data on the nutrient content of grasses and woody plants from other regions in West Africa is available but scarce (e.g. Diagayété, 1981).

6.2. Phenology

In general, information on phenological patterns is scarce for tropical regions (see review by Sarmiento & Monasterio, 1983). Existing systems of classifying especially woody plants into phenological groups are often highly detailed with the emphasis on the time of flowering. In this study we only analysed the period when shrubs and trees had green leaves, considering this to be a more functional approach to the analysis of the savanna ecosystem. We observed no periodicity in flowering and fruiting.

6.2.1. Patterns in the growth of grasses and sedges

In the Baoulé various phenological patterns can be distinguished. The phenological pattern of *Andropogon gayanus* is presented for one sampling station (Dla) (Fig. 6.1). Growth responds to the first rains; within a few weeks after the first showers, sprouting starts. When the rain fails to continue after these showers, growth stops and the new phytomass withers. Apparently in *Andropogon gayanus* there is a long vegetative state with flowering more or less at the end of it. From December onwards leaf-fall occurs but in the study area only a small percentage of the plants reaches this stage as nearly all of the phytomass is destroyed by fire in October or November.

In the southern part of the Baoulé the rainy season generally starts a few weeks earlier than in the north (Fig. 3.3) and consequently growth of savanna grasses also starts up to 4 weeks earlier (see 6.3).

Once the new season's plants have produced seeds and senesced, continuation of growth is possible if sufficient water is stored in the soil (Fig. 6.1). This dry-season growth is characteristic of perennial grasses in the West African savanna (Menaut & César, 1982; Penning de Vries & Djitèye, 1982).

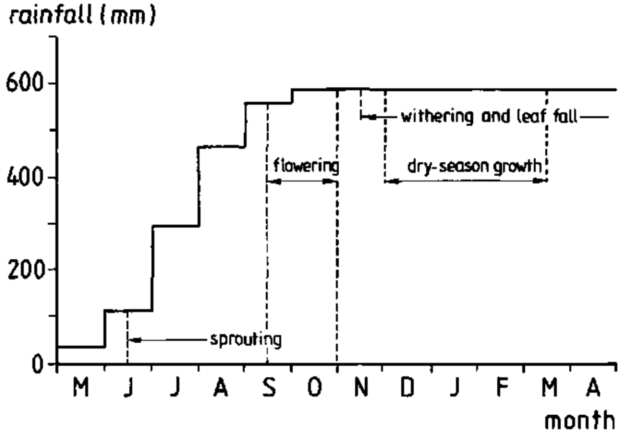


Fig. 6.1. Patterns of plant growth and flowering of *Andropogon gayanus* in relation to rainfall; sampling station Dla-1980/1981

Regrowth also occurs once the new season's growth has been destroyed by fires but this regrowth is also dependent on the water availability in the soil. Tall annual savanna grasses like *Andropogon pseudapricus* resemble *A. gayanus* with respect to their phenological pattern but they lack the ability of dry-season growth.

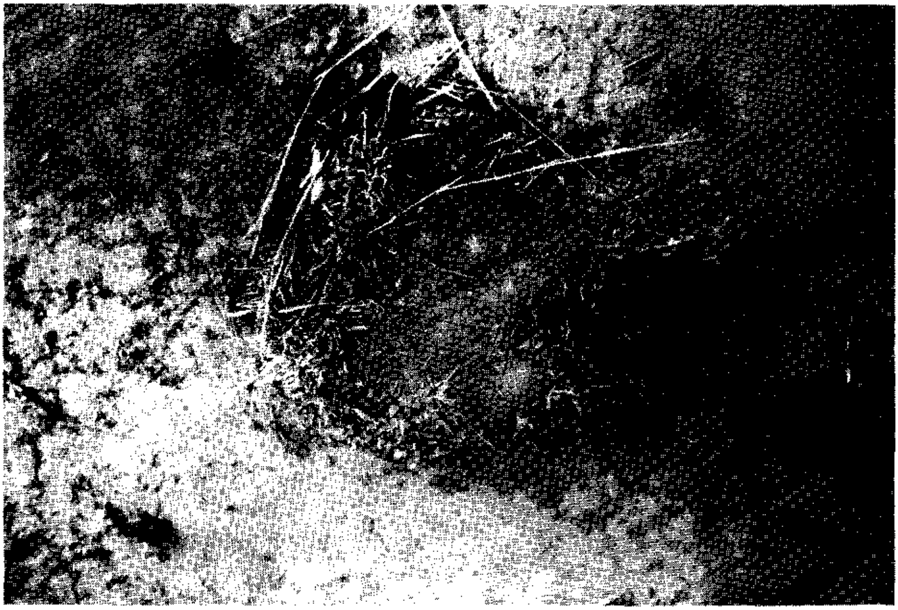


Plate 8. Fire stimulates the dry-season growth of perennial grasses

Perennial grasses in and along the rivers like *Vetiveria nigritana* and *Panicum anabaptistum* show a different growth pattern. Due to the continuous presence of sub-surface water, these riverine grasses grow throughout the year although the growth rate is higher in the wet season. Like the savanna grasses they flower in the late wet season. As the water-level of the river falls, Cyperaceae species growing on the river bed, colonize bare patches as they emerge (see also 6.3).

6.2.2. Patterns in the growth of trees and shrubs

The majority of woody shrubs and trees have leaves in the wet season and early dry season (Fig. 6.2). Only about 20% of the species observed are *evergreen*, with leaves throughout the year. After January the number of species with green leaves decreases sharply, rising again after May.

Trees and shrubs in the Baoulé can be divided into three main categories based on the pattern of presence/absence of green leaves (Table 6.1):

1. *deciduous species*, sprouting at or just before the start of the wet season and shedding their leaves just after the last rains or during the first months of the dry season. They are bare for at least two months. In a few species dried-up leaves stay on the branches until the end of the dry season.
2. *evergreen species*, with leaves all the year and new leaves gradually replacing old ones, or *semi-evergreen*, shedding leaves over a short period, sprouting taking place at the same time or directly afterwards.
3. *riverine species*, growing on the river bed and on the river bank. They are submerged during the wet season. In that period they are bare or with old leaves and sprout at the beginning of the dry season staying green until the next flooding.

The classification is mainly based on the criteria (a) in which period of the year woody species possess *green* leaves and (b) for which length of time. From the

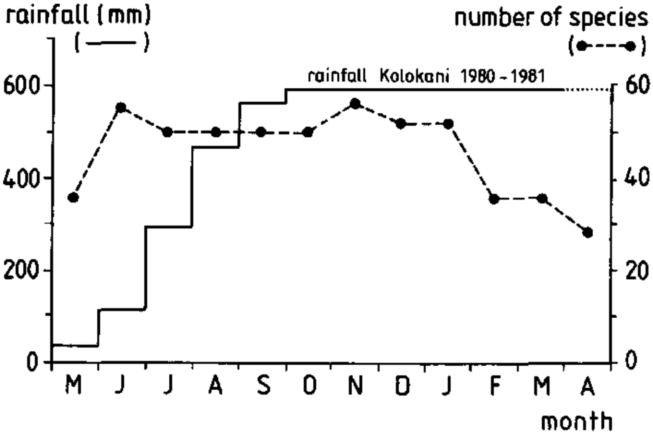
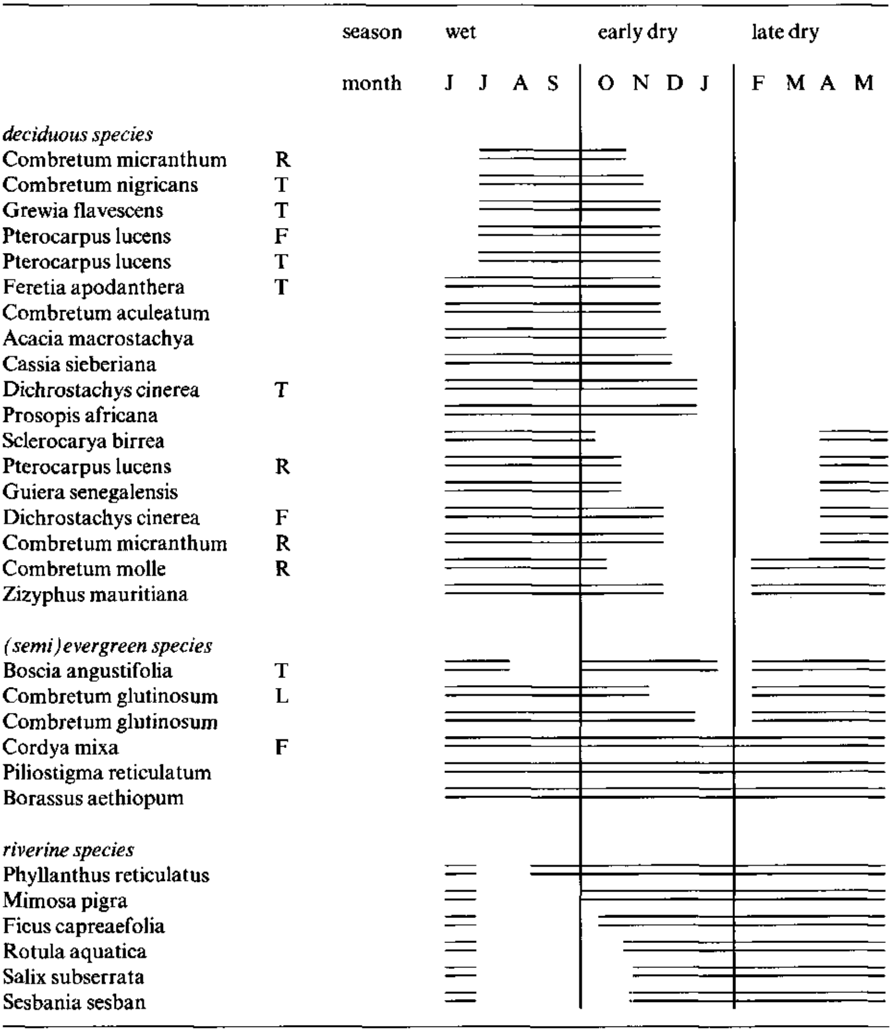


Fig. 6.2. Monthly number of woody plant species, bearing green leaves (n = 56)

Table 6.1. Phenology of some abundant woody plant species in the Baoulé



═══ period with green leaves

R = on rocky site; T = on termitary; F = near river; otherwise on sites with deeper soil

point of view of food availability, green leaves are considered more important for most herbivores (in terms of volume) than flowers and most fruits. Especially within category 1 a certain variation has been observed (Van Wijngaarden, 1988): from north to south species such as *Cassia sieberana*, *Guiera senegalensis* and *Sclerocarya birrea*, have green leaves for increasingly longer periods, corresponding with the increase in annual rainfall. Even at one locality, not all the individuals of a species belonging to one of these categories, closely follow the phenological pattern; depending on site characteristics such as fertility, or soil moisture content, individual trees and shrubs deviate from the general pattern (see Table 6.1).

6.2.3. Discussion

Considering the various types of phenological patterns that occur among the plant species in the Baoulé, it appears that despite the marked seasonality of rainfall, all three seasons have favourable conditions for certain plant groups. Apparently the availability of subsurface water is less critical because the two opposite phenological strategies of deciduous and evergreen are found.

Perennial grasses such as *Andropogon gayanus* and almost all taller annual grasses develop shoots gradually in the wet season. They flower when they reach their maximum phytomass late in the wet season (Fig. 6.1), at that time competing for light (Sarmiento & Monasterio, 1983). In the dry season perennial grasses stop growing unless soil humidity allows further growth from the base of the tussock as in more southern areas (Fig. 6.4). This flexible response enhances a species' performance when more humid conditions are met with in place or time.

Menaut & César (1982) discuss the phenological patterns of herbaceous plants in the Lamto area in Ivory Coast. As this area is situated in another bioclimatic zone, the Guinea zone, patterns are not strictly comparable as the amount of annual rainfall, about 1300 mm, and the length of the rainy season, 7-8 months, differ. However, trends in the growth cycle of some species such as *Hyparrhenia smithiana*, a tall perennial savanna grass, resemble those found for *Andropogon gayanus* in the study area: sprouting beginning at the start of the rainy season, flowering in the second half of that season, and withering and leaf fall immediately after the rains stop.

Data on phenological patterns found for woody plant species in the Baoulé agree well with the patterns we found in savanna trees and shrubs in forest reserves in Burkina Faso (Fig. 6.3 and Table 6.2).

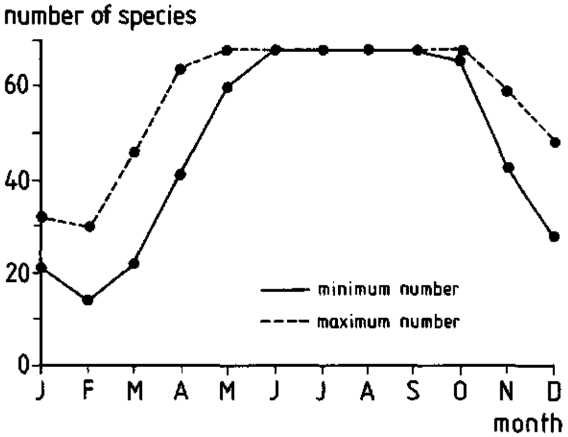


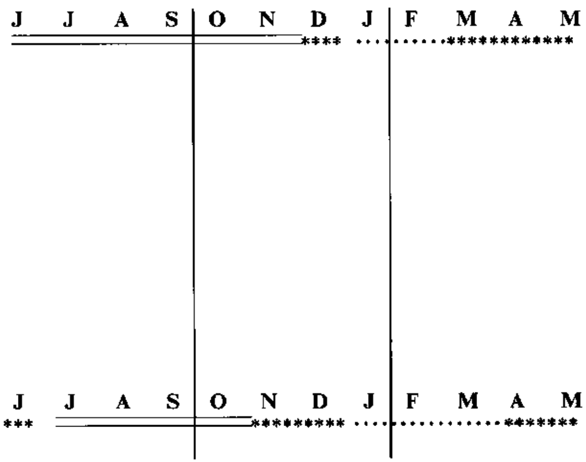
Fig. 6.3. Monthly number of woody plant species bearing green leaves during the year (n = 68). Data from observations in the forest reserves of Yabo, Bissiga, Sourou and Tissé in Burkina Faso

Table 6.2. Phenological groups of woody species in the forest reserves of Yabo, Bissiga, Sourou and Tissé in Burkina Faso

EVERGREEN RIPARIAN SPECIES		**season**	**wet**				**early dry**				**late dry**			
		month	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**
			=	=	=	=	=	=	=	=	=	=	=	=1)
Mimosa pigra	Mitragyna inermis													
Phyllanthus reticulatus	Rotula aquatica													
Sesbania sesban	Acacia ataxacantha													
Dichrostachys cinerea														
EVERGREEN UPLAND		**month**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**
			=	=	=	=	=	=	=	=	=	=	=	=
Boscia angustifolia	Boscia senegalensis													
Cadaba farinosa	Capparis sepiaria													
Diospyros mespiliformis	Maerua oblongifolia													
Saba senegalensis	Tamarindus indica													
SEMI-EVERGREEN		**month**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**
			=	=	=	=	=	=	=	=	****	****	=	=
Balanites aegyptiaca	Khaya senegalensis													
Piliostigma reticulatum	Sarcocephalus latifolius													
Ximenia americana	Zizyphus mauritiana													
Zizyphus mucronata	Guiera senegalensis													
SPROUTING IN MIDDLE DRY SEASON		**month**	**J**	**J**	**A**	**S**	**O**	**N**	**D**	**J**	**F**	**M**	**A**	**M**
			=	=	=	=	=	=	=	=**	****	****	*****	=
Combretum glutinosum	Vitellaria paradoxa													
Gardenia erubescens	Acacia seyal													
Prosopis africana	Piliostigma thonningii													
Acacia erythrocalyx	Gardenia ternifolia													
Terminalia laxiflora	Cassia sieberana													
Terminalia macroptera	Detarium microcarpum													
Pericopsis laxiflora	Combretum nigricans													

SPROUTING IN LATE DRY SEASON

month



Cassia singueana
Lannea acida
Acacia dudgeoni
Maytenus senegalensis
Hoslundia opposita
Parkia biglobosa
Lannea velutina
Stereospermum kunthianum
Grewia venusta
Feretia apodanthera
Pterocarpus erinaceus
Crossopteryx febrifuga

Combretum micranthum
Anogeissus leiocarpus
Lannea microcarpa
Acacia ataxacantha
Xeroderris stuhlmanni
Combretum aculeatum
Grewia bicolor
Strychnos spinosa
Entada africana
Dichrostachys cinerea
Securidaca longipedunculata

SPROUTING IN EARLY RAINY SEASON

month

Sclerocarya birrea
Pterocarpus lucens
Dahlbergia melanoxylon
Grewia flavescens
Securinega virosa
Sterculia setigera

Grewia lasiodiscus
Adansonia digitata
Burkea africana
Bombax costatum
Acacia macrostachya
Commiphora africana

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1) ═══ all species with leaves, ... all species without leaves, ****** some species with and some species without leaves

Deciduous species sprout earlier in the dry season in Tissé forest reserve with about 700 mm annual rainfall, than those more to the north in the the forest reserves of Yabo, Bissiga and Sourou with about 500 mm annual rainfall. This explains the difference between the maximum and minimum numbers of woody species with leaves shown in Fig. 6.3. When patterns are compared with those of species in the Baoulé such as *Cassia sieberana*, *Dichrostachys cinerea*, *Guiera senegalensis*, *Prosopis africana* and *Combretum glutinosum* (Table 6.1) differences become clear, emphasizing the strong influence of local and regional environmental characteristics, such as annual rainfall, on the phenology. Fig. 6.3 shows that in the middle of the dry season the number of woody species bearing green leaves, is low, comparable to what has been observed in the Baoulé.

The phenological patterns found in woody plants indicate that ground water remains available to the semi-evergreen and evergreen species for most of or even throughout the year. In their search for water they have to root deeper than the perennial grasses as these grasses, albeit deep-rooting, are the first to utilize infiltrating rainwater. The strategy provides the evergreen and semi-evergreen species with a photosynthetic apparatus which can be fully operative when favourable conditions arrive. Through this mechanism energy can be stored to pay for the maintenance of this apparatus in the dry season (Sarmiento & Monasterio, 1983). The same applies to those deciduous woody plant species which sprout in advance of the rainy season.

6.3. Plant production

Both the pattern and actual level of plant production are important for understanding the distribution of animal species in the Baoulé and their food selection. In both respects grasses and sedges differ considerably from trees and shrubs.

6.3.1. Grasses and sedges

Savanna grasses respond to the first rain showers rather quickly, but the peak in the phytomass is reached at the end of the rainy season or early dry season (Fig. 6.4).(The term phytomass is used to indicate all above-ground vegetative material, that is the standing crop present at a certain time. This approach underestimates above-ground primary production; for estimating this production phytomass measurements must be corrected for the loss of biomass by the death of plants or plant parts, or herbivory (Milner & Hughes, 1968)).

However, differences in annual rainfall are reflected in the peak phytomass: the more rain, the more phytomass. Fig. 6.4 shows this clearly for three sampling stations.

The proportion of leaves (dead + green) in the phytomass (% of total DM) decreases as the growing season advances, that of stem and sheaths rapidly increasing. Fig. 6.5 shows this for *Andropogon gayanus* and it has been observed in other tall grass species as well. Although green leaves are most important at the start of the wet season, from the late wet season onwards their proportion diminishes.

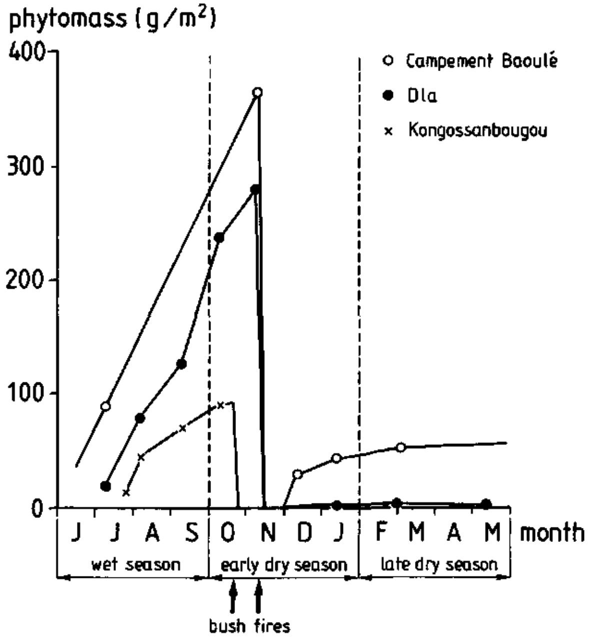


Fig. 6.4. Development of phytomass (gDM.m^{-2}) of *Andropogon gayanus* in three sampling stations Campement du Baoulé (800 mm), Dla (638 mm) and Kongossanbougou (517 mm), 1980-1981

Grasses at the sample stations with less than 800 mm rainfall per year (K, M, P, and D) showed no significant differences in the proportion of leaves and leaf/stem ratio (Fig. 6.5a, b). Average stem length at the end of the wet season did not differ significantly between four of these stations (Fig. 6.5c). Hence the increase in the phytomass from north to south, measured as an increase of weight per unit area (Fig. 6.4) in the zones with lower rainfall, has to be attributed to more stalks per tussock and/or to more plants per unit area. More phytomass in the higher rainfall zones as found at the station CB, can partly be explained by more leaves per stalk (Fig. 6.5a).

Thus, whereas in areas with a lower, more variable rainfall of below 800 mm, increasing rainfall results in more tussocks, which in turn increase the basal cover of tall perennial grasses, in higher rainfall zones plants also have more leaves on each stalk which stay green longer.

At the end of the wet season the phytomass of grasses is considerable, up to about 3,000 kgDM.ha^{-1} for *Andropogon gayanus* (see Fig. 6.4). Annual rainfall, soil type, ground cover of woody plants (De Leeuw, 1979; Breman, 1982a; Menaut & César, 1982) and the frequency of bush fires (De Leeuw, 1979) determine the phytomass produced by all savanna grasses. The total phytomass of savanna grasses per land-system unit (see Table 4.1) in each rainfall zone was calculated for years with normal (= long-term average) and below normal rainfall (Table 6.3 and Fig. 6.6), using data on rainfall, soil and vegetation characteristics (Van Wijngaarden, 1988) (for calculation see Chapter 5).

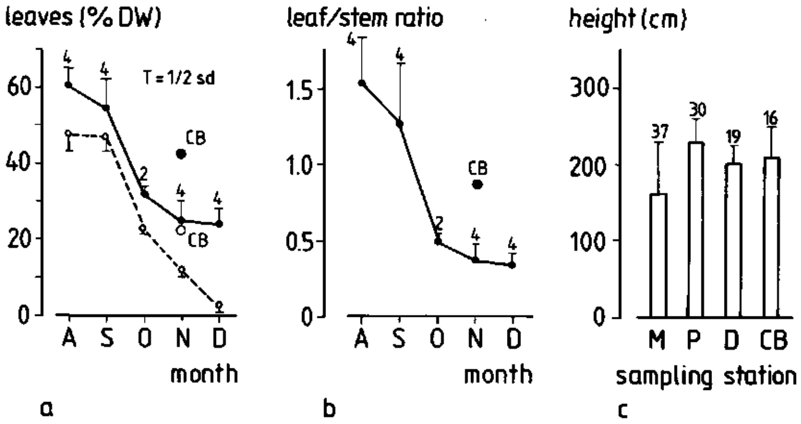


Fig. 6.5. Proportion of leaves (%, of total DM) (a), leaf/stem ratio (b), and length of stems (cm) at the end of the growing season (c) of *Andropogon gayanus*
—— = all leaves, ---- = green leaves only
(data from the sampling stations Missira (M), Plaquet (P), Dla (D) and Kongossanbougou (K) are shown as average trend lines, data for Campement du Baoulé (CB) (November only) are shown separately)

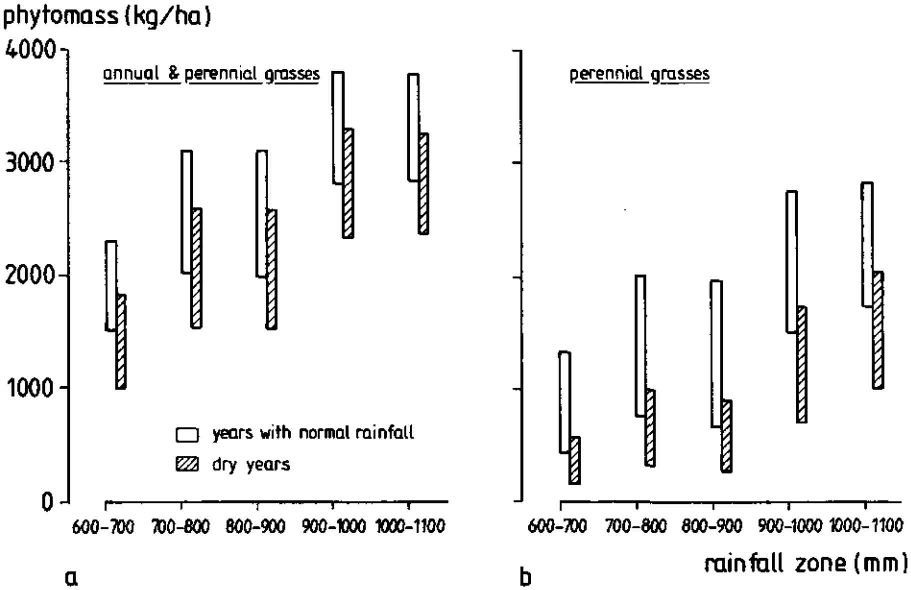


Fig. 6.6. Maximum phytomass of savanna grasses (kgDM.ha^{-1}) per rainfall zone

There is a gradual increase in the quantity of phytomass of annual and perennial grasses in the Baoulé from north to south, respectively from 1.2-2.3 tDM.ha^{-1} to 2.7-3.7 tDM.ha^{-1} in normal rainfall years and from 1-1.7 tDM.ha^{-1} to 2.3-3.3 tDM.ha^{-1} in dry years. Considered on their own, perennial grasses show a similar trend (Fig. 6.6b), the proportion in the total phytomass increasing from north to south, from c.45% to c.70% and from c.20% to c.50% in normal rainfall and dry years respectively. Comparing the phytomass of perennial grasses in the same area for different years, differences between years with normal rainfall and dry years are more pronounced (c.60% in the north, 40% in the south) due to tufts dying, fewer sprouts on each tuft and fewer leaves on the stalks. However, the reduction in rainfall has less effect on the total phytomass of all savanna grasses (15-25%) indicating that spaces not occupied by perennial grasses in dry years are largely filled by annual grasses through the germination of seeds already present. Thus, given a certain tuft density, the growth rate of perennial grasses determines whether the annual grasses will develop or not.

In October and November, there are frequent bush fires in the Baoulé (as nearly everywhere else in the Sudan savanna (Geerling, 1982)), and every year more than 95% of the study area is burnt (De Bie & Kessler, 1983). The plateaus (which are protected by steep escarpments), laterite caps and other rocky areas (where there is practically no combustible layer), and the riverine forest escape. One annual grass, *Pennisetum pedicellatum*, seems to be fire-resistant. It prefers sites shaded by trees and shrubs (Fig. 6.7) and is generally found in and along the riverine forest and around some types of termitaries (see Geerling & Diakité, 1988). In this way this species seems to protect such sites in the savanna from being burnt. Where bush fires occur, the other grasses are nearly all destroyed; a few patches escape but are of negligible importance. Thus there is a dramatic

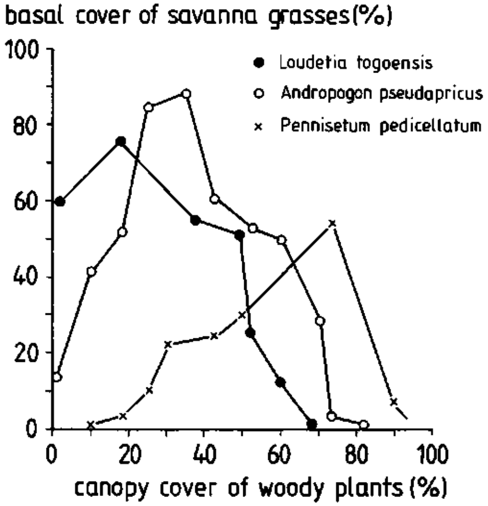


Fig. 6.7. Basal cover of savanna grasses (%) in relation to canopy cover of trees and shrubs (%), Tissé forest reserve (Burkina Faso)

Table 6.3. Maximum phytomass (kgDM × 10^5) of savanna grasses per land-system unit in the five rainfall zones in years with normal rainfall and dry years; O = area (km^2), A+P = annual and perennial grasses, P = perennial grasses, G = dry-season growth (in land-system unit R the river bed and the adjacent banks were not taken into account)

land-system unit		river	Andropogon savanna	Loudetia grass savanna	Loudetia shrub savanna	shrub savanna	tree savanna	woodland savanna
normal rainfall years								
		R	F	LSM	SSP	CS	VI	B
600- 700 mm	O	30	930	35	72	90	5	49
	A+P	64-96	1,358-2,125	46-76	92-153	115-191	0	65-107
	P	20-62	376-1,231	8-41	6-59	110-191	0	13-47
	R	0.3	8.1	0.2	0.3	3.6	0	0.3
700- 800 mm	O	145	2,743	105	250	101	15	263
	A+P	456-648	5,524-8,538	198-299	460-690	186-279	20-29	495-748
	P	211-460	2,264-5,763	40-168	32-263	178-279	6-10	79-323
	R	8.8	162.8	3.4	4.4	16.2	0.6	6.3
800- 900 mm	O	277	3,583	129	285	301	121	181
	A+P	957-1,329	7,336-11,645	237-356	524-787	554-831	156-234	3,361-5,054
	P	314-852	3,098-8,733	45-147	37-299	532-831	45-84	309-1,868
	R	12.4	193.5	3.5	5.0	48.2	4.8	32.2
900-1000 mm	O	138	2,375	46	223	63	12	577
	A+P	649-787	6,797-9,053	113-158	546-765	154-216	21-30	1,435-2,001
	P	188-359	4,661-7,753	21-59	38-291	147-216	5-10	153-753
	R	13.0	367.2	2.3	7.8	20.2	0.9	21.4
1000-1100 mm	O	61	727	92	14	0	0	129
	A+P	296-356	2,025-2,708	226-303	34-48	–	–	327-453
	P	72-128	1,625-2,483	48-102	2-18	–	–	55-189
	R	5.3	179.2	5.1	0.5	–	–	8.0

dry years

		R	F	LSM	SSP	CS	VI	B
600- 700 mm	O	30	930	35	72	90	5	49
	A+P	52-84	973-1,741	31-61	61-122	77-153	0	44-86
	P	6-27	129-502	2-11	0-9	57-147	0	4-15
	R	0	0	0	0	0	0	0
700- 800 mm	O	145	2,743	105	250	101	15	263
	A+P	386-581	4,269-7,348	150-251	345-575	139-232	15-24	374-627
	P	95-271	950-3,025	10-53	0-40	103-223	4-7	23-107
	R	1.8	31.0	0.3	0	4.0	0.2	0.6
800- 900 mm	O	277	3,583	129	285	301	121	181
	A+P	829-1,203	5,463-9,540	185-297	393-656	415-692	117-195	2,527-4,220
	P	105-345	1,213-4,268	14-55	0-46	312-664	30-56	50-403
	R	2.2	35.7	0.5	0	12.0	1.2	1.4
900-1000 mm	O	138	2,375	46	223	63	12	577
	A+P	585-758	5,680-7,873	90-135	437-655	124-185	17-26	1,153-1,718
	P	109-208	2,152-5,402	8-25	0-46	92-178	4-7	33-178
	R	6.5	183.6	1.1	3.9	10.1	0.4	10.69
1000-1100 mm	O	61	727	92	14	0	0	129
	A+P	265-326	1,686-2,365	181-271	27-41	–	–	263-390
	P	50-79	930-1,887	19-57	0-3	–	–	29-64
	R	2.7	77.4	2.6	0.3	–	–	4.0

fall in this source of forage early in the dry season, to nearly zero (Fig. 6.4).

Bush fires also have positive effects: by removing an enormous quantity of dead vegetative material from the perennial grasses, light can penetrate into the centre of grass tufts and stimulate dry-season growth. This growth is obvious within 14 days; the balance between shoots and roots is restored (Geerling, pers. comm.; see also Fisher, 1978). The quantity of growth is only substantial in the areas of higher rainfall (Table 6.3, Figs. 6.4 and 6.8).

The effect of less precipitation in dry years, with a fall of up to 200 mm (Fig. 3.2) is enormous: whereas in normal rainfall years dry-season growth is considerable in regions with more than 700 mm annual rainfall, in dry years this is only the case in regions which normally receive 900 mm or more (see also Table 6.3). This will certainly affect how much dry-season forage is available for grass-selecting herbivores.

Compared to the savanna grasses, the grass vegetation on the river bed and on the river-banks generally has a higher peak phytomass (see Table 6.4), which is rather constant over the different rainfall zones (except under 700 mm) and between normal and dry years.

Table 6.4. Average peak phytomass of grasses and sedges (kgDM.ha^{-1}) in and adjacent to the river bed per rainfall zone

	rainfall zone (mm/year)				
	600-700	700-800	800-900	900-1000	1000-1100
normal rainfall years	9-19	21-29	28-43	18-24	28-29
dry years	13-20	28-31	31-39	24-26	27-30

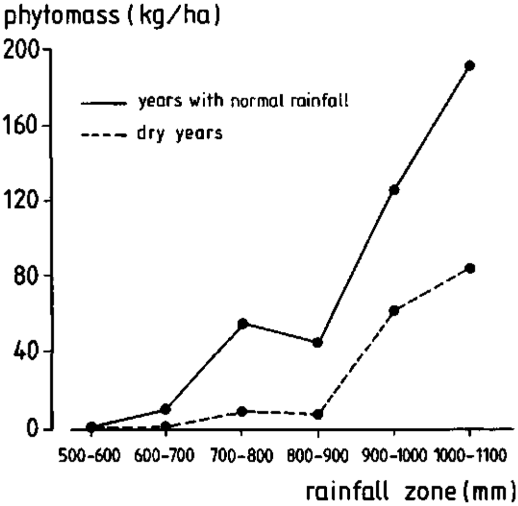


Fig. 6.8. Phytomass (gDM.m^{-2}) following dry-season growth of perennial grasses per rainfall zone

As however, the total area covered by the riverine land-system unit is very small, 345.5 km^2 (= 2.14% of the study area), the total quantity of this phytomass is only a small fraction of the total production of the herbaceous vegetation.

Perennial Cyperaceae species start to grow on patches that emerge when the water-level of the river falls at the beginning of the dry season; their growth rate is very constant (Fig. 6.9). As less than 5% of the river bed is covered with Cyperaceae, the total quantity of this phytomass certainly does not exceed 200 kgDM per ha. However, this type of vegetation, despite its limited distribution, is a valuable resource for wild ungulates.

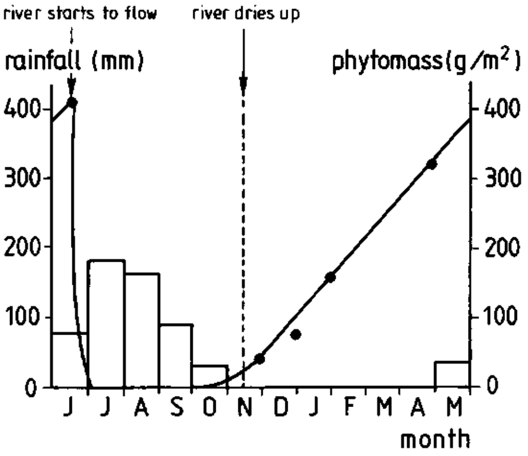


Fig. 6.9: Growth of Cyperaceae (gDM.m^{-2}) in the riverine land-system unit in relation to rainfall

6.3.2. *Woody foliage*

The phytomass of woody foliage, that is the leaves and twigs of the current season's growth, reaches its peak in deciduous, evergreen and semi-evergreen species late in the wet season (August-September) and in riverine species late in the dry season (March-April) (Fig. 6.10).

For evergreen and semi-evergreen species the maximum phytomass is about 300 gDM.m^{-2} when canopy cover is complete (= 100%), which is 30 kgDM.ha^{-1} per percentage point cover, decreasing to a minimum of about 50-70 gDM.m^{-2} (5-7 kgDM.ha^{-1} per percentage point cover) in the dry season. The production of deciduous species reaches a similar maximum but riverine shrubs do not exceed 100 gDM.m^{-2} (10 kgDM.ha^{-1} per percentage point cover).

The phytomass of the woody vegetation is thus considerable if canopy cover is 100%. However, in the savanna, shrubs and trees occur in patches or as individuals and the canopy cover is never complete. Hence the total phytomass per hectare is much lower. We have reanalysed data on canopy cover in the Baoulé, collected by Dekker (1980) to calibrate the relationship between canopy cover and foliage phytomass (Table 6.5). Species were classified as trees or shrubs, according to Geerling (1982).

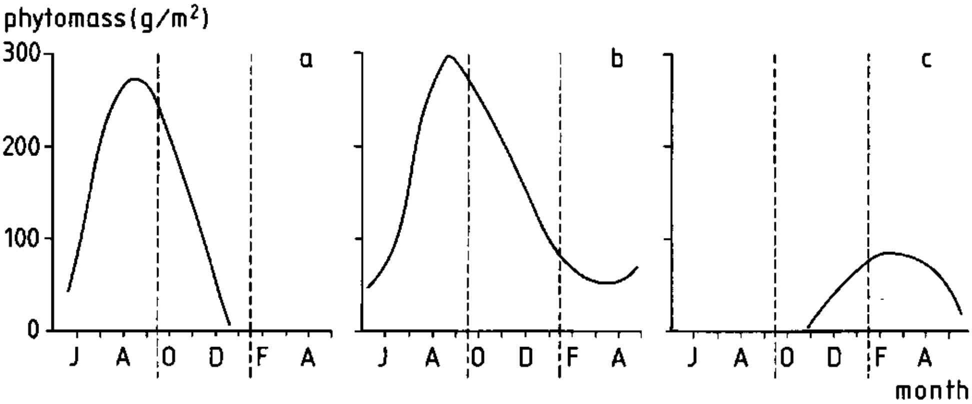


Fig. 6.10. Pattern of phytomass development (gDM.m^{-2}) in three groups of woody shrubs, (a) deciduous species, (b) evergreen and semi-evergreen species and (c) riverine species

The more rainfall, the greater the canopy cover of both trees and shrubs, but the proportion of shrubs decreases from 68% to 57%. Thus, as one goes south in the Baoulé, trees become increasingly dominant in the woody vegetation. The canopy cover of deciduous species of both trees and shrubs also increases with rainfall, from 33% to 40% and from 46% to 49% respectively.

Using the linear relation between the degree of canopy cover by woody species and the mean annual rainfall (see Breman, 1982; Van Wijngaarden, 1988) we calculated the peak phytomass of shrubs in the savanna in the wet and dry season (Table 6.6).

The peak phytomass of shrubs in the savanna is less than a fifth of the maximum phytomass of the herbaceous layer (Fig. 6.6a, Tables 6.3 and 6.6) with a considerable difference between the wet-season maximum and the late dry-season minimum. Thus there is a short period in the dry season that a very limited quantity of foliage is available from woody plants as a food resource

Table 6.5. Canopy cover (%) of woody vegetation in the north (700-800 mm rainfall) and in the south (900-1000 mm rainfall) of the Baoulé

	canopy cover (%)	
rainfall zone (mm)	700-800	900-1000
A: trees, total	9.4	20.7
– deciduous species	3.1	8.2
– evergreen species	6.3	12.5
B: shrubs, total	19.6	27.3
– deciduous species	9.1	13.3
– evergreen species	10.5	14.0

Table 6.6. Foliage phytomass (kgDM.ha^{-1}) of shrubs in the wet and dry seasons per rainfall zone[1])

rainfall zone (mm)	600-700	700-800	800-900	900-1000	1000-1100
			wet season		
shrubs, total	495	600	705	810	915
– deciduous species	210	270	330	390	450
– evergreen species	285	330	375	420	465
			dry season		
shrubs, total	57	66	75	84	93
– deciduous species	0	0	0	0	0
– evergreen species	57	66	75	84	93

[1]) calculated as actual percentage canopy cover x 30 kgDM.ha^{-1} and x 6 kgDM.ha^{-1} for the wet and dry season respectively

for herbivores, although quantities do not differ between the rainfall zones. No data were collected on the foliage production of the trees in the Baoulé nor are sufficient data known from other regions in the Sudan savanna to enable us to give values for the tree layer.

6.3.3. Discussion

In the wet and early dry season grass-eating herbivores have three to four times as much phytomass to choose from (although not all necessarily forage) as herbivores specialized in foraging on woody foliage (Fig. 6.11) This is apparently common in savannas (see e.g. Menaut & César, 1982). As a result of bush fires in the dry season, in November and December, this picture changes completely. Just after these fires there is much more woody foliage, or 'browse', than grass. This last is increased by regrowth of perennial grasses but only in the higher rainfall zones.

During the dry season there is an increase in the amount of both monocotyledons and woody foliage on the river bed and along the river banks. However, the grasses and sedges are distributed irregularly in patches in contrast with the thickets of *Acacia spp.* and other shrubs which fringe the rivers (in a strip of up to 20 m wide) without scarcely any interruption. In general these shrubs produce more leaf phytomass per unit area than the grasses and sedges, thus offering more potential forage for 'browse'-selecting herbivores.

From the data we presented on the annual production of phytomass of annual and perennial grasses in relation to rainfall, and the information on the dynamics of the herbaceous vegetation from Breman et al., (1982) (see also 2.2.3) it can be seen that the composition and the annual production of the herbaceous savanna vegetation are not at all constant. Moreover, it can be concluded that the changes in the composition of the vegetation, that is the proportion of perennial grasses in the herbaceous layer, and in the peak phytomass along the north-south rainfall transect also indicate the local variation in vegetation composition and maximum phytomass at a certain point on this transect in relation to changing amounts of annual rainfall. The amplitude of these changes, especially concerning the quantity of dry-season growth of perennial grasses, strongly deter-

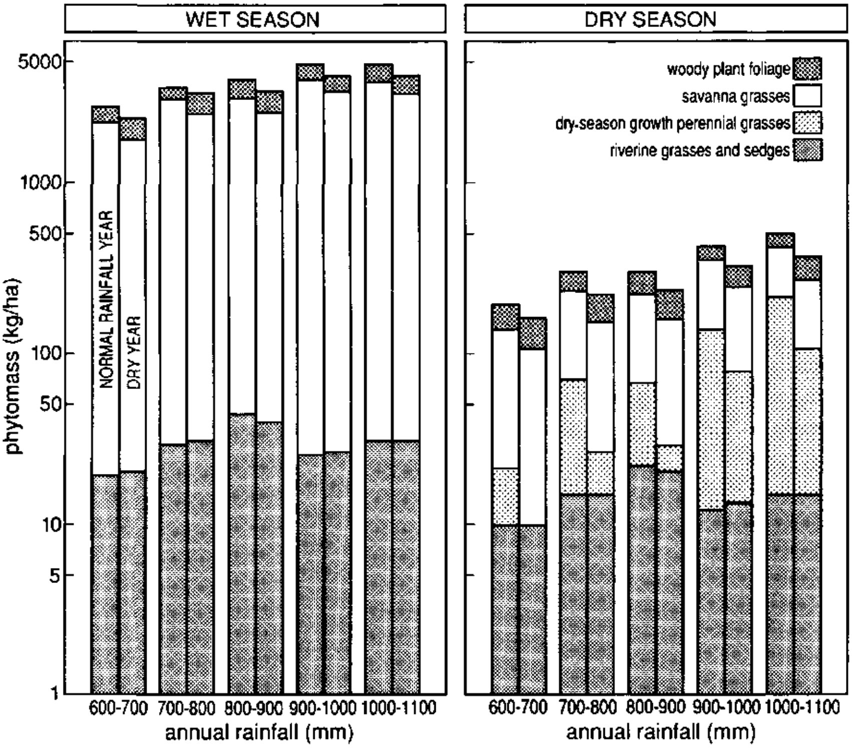


Fig. 6.11. Peak phytomass (kgDM.ha^{-1}) per rainfall zone

mines the long-term suitability of certain areas for sustaining viable populations of grazing ungulates. The changes in floristic composition and peak phytomass also occur at a specific site due to differences in topography and soil texture that affect the infiltration rate of rainwater.

Afolayan (1979) has shown that management such as burning and grazing can stimulate or suppress the annual production of savanna grasses (Table 6.7).

Table 6.7. Influence of management regimes on the annual production of savanna grasses (Afolayan, 1979)

management regime	annual production (gDM.m^{-2}) + 95% conf.lim.
early burning + grazing	1,084 ± 171
early burning − grazing	1,204 ± 145
late burning + grazing	1,082 + 130
late burning − grazing	1,667 ± 199
fire excluded + grazing	1,124 ± 67
fire excluded − grazing	845 ± 139

Patterns of seasonal production of *Andropogon gayanus* in the Baoulé strongly resemble those at the Niono-ranch in Mali (Breman, 1982) and at Shika in Nigeria (Haggar, 1970) (Fig. 6.12).

Our data on peak phytomass of perennial and annual grasses (Fig. 6.6) in the Baoulé correspond well with data from elsewhere in the Sudan savanna from several authors (Table 6.8).

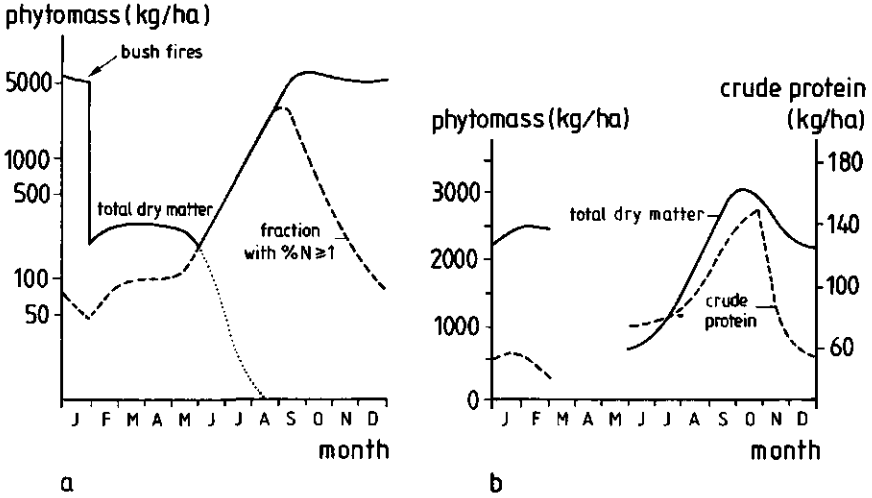


Fig. 6.12. Evolution of phytomass of *Andropogon gayanus* in (a) Mali (Niono ranch; Breman, 1982) and (b) Nigeria (Shika; Haggar, 1970)

Table 6.8. Peak phytomass of grasses (kgDM.ha^{-1}) in the Sahel, Sudan and Guinea zones as published by several authors

locality	vegetation	rainfall mm	peak phytomass	reference
Fété Olé, Senegal	Sahelian steppe	200	500	UNESCO, 1979
Mali	Sahelian steppe	200	1,000	Breman & de Wit, 1983
Richard-Toll, Senegal	Cenchrus/Chloris dominated steppe	200-400	900-2,400	Bourlière & Hadley, 1970
Mali	sahel-sudan transition	500	2,000	Breman & de Wit, 1983
Mali	Sudan savanna	800	3,000	Breman & de Wit, 1983
Mali	Sudan savanna	1000	4,000	Breman & de Wit, 1983
Nazinga, Burkina Faso	herbaceous savanna	1000	3,220	Fournier, 1987
Nazinga, Burkina Faso	shrub savanna	1000	3,450	Fournier, 1987
Leo, Burkina Faso	open Sudan savanna	1050	3,000	UNESCO, 1979
Leo, Burkina Faso	shaded Sudan savanna	1050	< 5,500	UNESCO, 1979
Shika, Nigeria	Guinea savanna	1100	3,350	Haggar, 1970
Ouango-Fitini, Iv.Coast	Loudetia savanna	1100	3,500	Fournier, 1982
Ouango-Fitini, Iv.Coast	woodland savanna	1100	5,500	Fournier, 1982
Olokomeji, Nigeria	derived savanna	1200	5,700- 8,000	Bourlière & Hadley, 1970
Lamto, Ivory Coast	Guinea savanna	1300	6,000-11,000	Menaut & César, 1982
Eruja, Ghana	derived savanna	1500	8,700	Bourlière & Hadley, 1970

LeHouérou (1980a) suggested 1 kg DM/mm rainfall/ha/year as a mean estimation of production of 'consumable' browse. Although a proper definition of 'consumable' browse is not given, it most probably refers to that part of the woody vegetation that *domestic* herbivores can reach, but it does not take the specific features of animal species such as the food choice and the digestive capacity, into account. The amounts obtained from this estimation are certainly lower than those given by Billé (1980) (Fig. 6.13), which also include the foliage production of trees. Breman (1982) estimated mean annual leaf production of shrubs and trees as ranging from 0.3 tDM.ha^{-1} at 600 mm annual rainfall (10% canopy cover) to 1.2 tDM.ha^{-1} at 1200 mm annual rainfall (40% canopy cover) (Fig. 6.13).

However, these measurements were made in a degenerated type of Sahelian woody vegetation and therefore the extrapolations to higher rainfall zones may underestimate potential foliage production (Breman, pers. comm.).

Breman (1982) pointed to the strong relationship between foliage production and canopy cover. The mean annual production of woody foliage per percentage

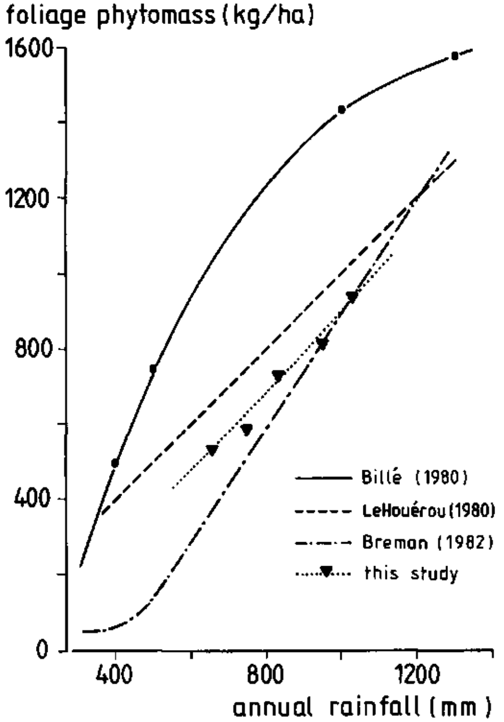


Fig. 6.13. Mean annual production of woody foliage (kgDM.ha^{-1}) in relation to rainfall as published by several authors.

canopy cover, 26-27 $kgDM.ha^{-1}$, is surprisingly constant along the north-south transect, and it corresponds quite well with the 30 $kgDM.ha^{-1}$ we found and used for calculating the total foliage production per rainfall zone (Table 6.6).

Table 6.9 shows the peak foliage phytomass in various parts of West Africa.

Table 6.9. Peak foliage phytomass of woody plant species ($kgDM.ha^{-1}$) in the Sahel and Sudan savanna as published by several authors

locality		rainfall mm	foliage phytomass	reference
Fété Olé, Senegal	shrubs + trees	400	120 (25-658)	Poupon, 1980
Niono Ranch, Mali	shrubs + trees	600	992 (2,100-3,500)	Hiernaux, 1980
Olokomeji, Nigeria	shrubs + trees	1200	1,200	Hopkins, 1966

Although in general there is an increase in the quantity of woody foliage with an increase in annual rainfall (see also Fig. 6.13), Table 6.9 shows that there can be a considerable variation at a specific site due to differences in topography and soil type that affect run-on and run-off of surface water (Hiernaux, 1980). Especially in the Sahelian steppe, variations in annual rainfall may cause up to 200% variation in the production of woody foliage (Billé, 1978). Both the peak phytomass of the herbaceous vegetation and the quantity of woody foliage increase along the north-south transect. However, as the canopy cover of trees and shrubs increases, it suppresses the productivity of the herbaceous layer (Ouedraogo, 1985). Hence the observed increase in the herbaceous phytomass is below its potential.

6.4. Plant quality

For ungulates, the change in the quality of the plants from season to season in their environment is most important from the nutritional point of view. To what extent this quality fluctuates is described for a number of grasses and woody plants growing in the Baoulé, in 6.4.1 and 6.4.2 respectively.

6.4.1. Grasses and sedges

In annual and perennial savanna grasses and in riverine grass species such as *Vetiveria nigritana* and *Panicum anabaptistum*, crude protein levels (= %N x 6.25) are highest at the start of plant growth in the wet season and decline afterwards (Fig. 6.14), when nutrients are diluted over the above ground parts to the minimum level required for physiological functions. Throughout the wet season and in the early dry season, leaves of perennial savanna grasses such as *Andropogon gayanus*, contain more protein than the stems and sheaths. This also applies to its dry-season growth; up to April the mean crude protein content

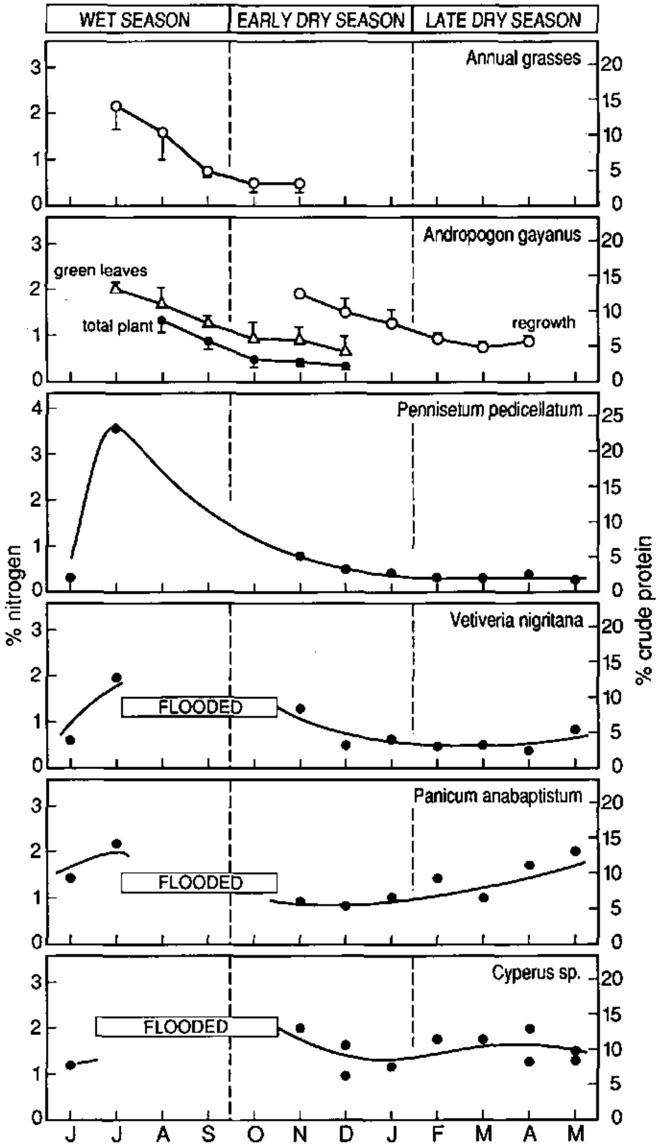


Fig. 6.14. Nitrogen content (%DM) of different monocotyledons during the wet and dry seasons

of this dry-season growth does not fall below 5% (Fig. 6.14). The annual savanna grass species *Pennisetum pedicellatum* has a very low crude protein content in the dry season. This species does not show the phenomenon of dry-season growth, and the difference with *Andropogon gayanus* from the nutritional point of view is clear. Hence we conclude that the growth of perennial grasses in the dry season considerably improves the availability of crude protein in the savanna, especially after bush fires. Riverine grasses, although less affected by water shortage than the savanna grasses, have a low crude protein content in the dry season, but unlike savanna grasses this increases just before the rainy season, especially in *Panicum anabaptistum*.

The crude protein content of riverine sedges is higher during the whole of the dry season and less varying than that of savanna and riverine grasses. These sedges grow continuously (see 6.2) due to the continuous presence of sub-surface water and high concentration of nutrients in their riverine habitat. In savanna and riverine grasses the decrease in crude protein content is not significantly correlated with changes in the level of other chemical plant components such as the proportion of all cell-wall components (NDF, Table 6.10). NDF levels are generally above 70% and fairly constant throughout the wet and dry seasons. Grasses contain more hemicellulose and cellulose but less lignin than woody plants (Table 6.11; De Bie, unpubl. data). Despite a decreasing crude protein content the in-vitro digestibility of leaves and dry-season growth of *Andropogon gayanus* remain relatively constant (Table 6.10); only the stems + sheaths show a declining in-vitro digestibility in the early dry season when the plants mature. In the other savanna and riverine grasses, the in-vitro digestibility of organic matter reaches a maximum in the early wet season (Table 6.10) coinciding with high nitrogen levels.

6.4.2. Woody foliage

Woody plants, regardless of the phenological group, have higher crude protein

Table 6.10. Monthly content of neutral detergent fibre (=NDF, % DM) and in-vitro digestibility of organic matter (=IVDOM,%) in several monocotyledons

season		wet				early dry				late dry			
month		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
Andropogon gayanus dry-season growth	NDF	–	–	–	–	–	70	73	70	68	70	70	–
	IVDOM	–	–	–	–	–	80	76	67	76	77	71	–
Andropogon gayanus green leaves	NDF	–	75	75	77	76	73	74	–	–	–	–	–
	IVDOM	–	81	75	76	81	79	78	–	–	–	–	–
Andropogon gayanus stem + sheath	NDF	–	81	85	81	88	85	86	–	–	–	–	–
	IVDOM	–	81	72	78	81	71	60	–	–	–	–	–
Pennisetum pedicellatum	NDF	88	55	–	–	–	88	87	87	83	84	84	90
	IVDOM	50	87	–	–	–	47	52	39	52	57	60	66
Vetiveria nigritana	NDF	84	82	84	–	–	80	83	90	84	85	84	82
	IVDOM	87	63	45	–	–	51	41	33	34	43	54	46
Panicum anabaptistum	NDF	71	61	72	–	–	68	70	74	72	76	–	74
	IVDOM	68	71	73	–	–	57	68	67	53	63	–	70
Cyperus spp.	NDF	67	–	–	–	–	–	68	69	64	66	71	68
	IVDOM	63	–	–	–	–	–	81	74	69	74	66	64

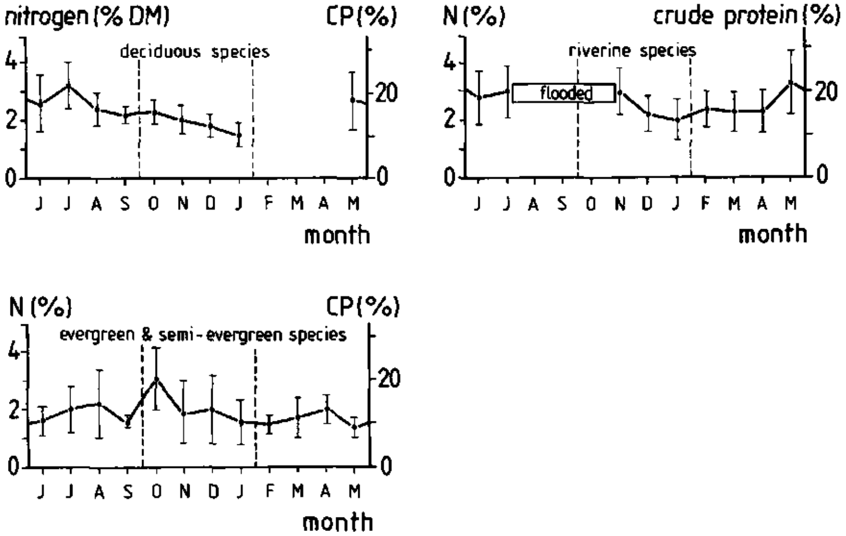


Fig. 6.15. Nitrogen content (% DM) in three phenological groups of woody plant species during the wet and dry seasons.

levels throughout the year than grasses (Fig. 6.15; Appendix II). Levels remain above 9% although there are considerable seasonal changes which show a close relationship with the phenological patterns of each group (Table 6.2): the highest levels of crude protein are found when plants are sprouting. Riverine species not only show high crude protein levels at the time of sprouting but also have a second peak just before the start of the wet season, comparable to deciduous species. This suggests an identical triggering mechanism.

In woody plants there is a negative relationship between the levels of lignin and crude protein. These plants show seasonal changes in lignin levels (Table 6.11) but inter-specific differences can be considerable (Appendix II).

Table 6.11. Average monthly levels of NDF (%OM) and lignin (%OM) and IVDOM (%) in three phenological groups of woody plants

season		wet				early dry				late dry			
month		Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May
deciduous species	NDF	43	46	56	52	51	49	48	43	–	–	–	41
	lignin	13	14	19	15	17	16	14	14	–	–	–	13
	IVDOM	61	64	53	58	47	51	55	57	–	–	–	65
evergreen and semi-evergreen species	NDF	58	59	57	57	47	57	51	54	60	55	55	53
	lignin	15	16	15	13	10	13	14	14	20	15	12	15
	IVDOM	56	57	53	53	66	54	49	57	39	52	50	54
riverine species	NDF	29	37	–	–	–	33	37	35	37	34	39	30
	lignin	5	8	–	–	–	6	7	7	9	8	9	5
	IVDOM	71	71	–	–	–	81	74	70	72	78	77	80

Woody plants have lower levels of NDF (< 60%) in the foliage than grasses (Table 6.11). Also in woody plants the in-vitro digestibility of foliage changes seasonally, but is on average lower than in grasses. This in-vitro digestibility is strongly influenced by the amount of fibre in the plant tissues (Fig. 6.16). The correlation diagrams in Fig. 6.16 show that mainly the lignin component of the fibre suppresses the in-vitro digestibility. Changes in the in-vitro digestibility are positively, although weakly, correlated to those in crude protein levels (Fig. 6.16).

As discussed in 6.1, phenolic components have to be taken into consideration when assessing the nutritional quality of plants. Phenolic tannins have been determined in a number of grasses and woody plants occurring in the Baoulé and were found in all plants examined. The data, presented in Table 6.12, indicate a certain pattern of seasonality in the tannin content of woody foliage, most obvious in deciduous species: this tannin content seems to show an increase with the age of the foliage. There appears to be no strong relationship between the in-vitro digestibility of organic matter and the phenolic tannin content of woody foliage (Fig. 6.17). However, an inhibiting effect of tannins on the digesti-

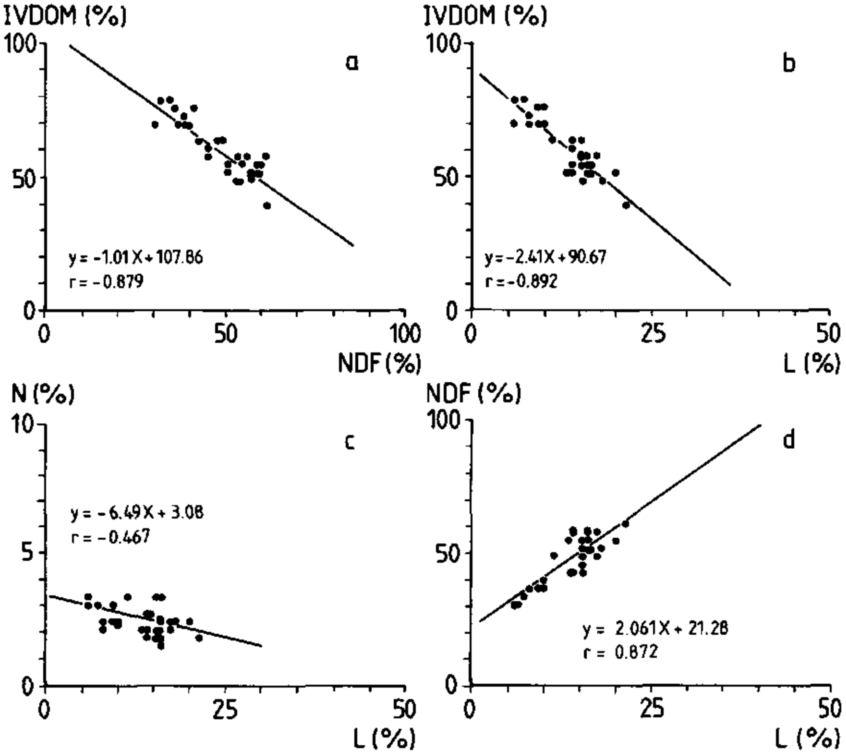


Fig. 6.16. Relations between nitrogen (N), lignin (L), in-vitro digestibility (IVDOM) and neutral detergent fibre (NDF) in woody plant species; (a) NDF-IVDOM, (b) IVDOM-L, (c) N-L, (d) NDF-L

Table 6.12. Phenolic tannins in the leaves of woody plant species in the early (I), mid (II) and late (III) growing season

	plant species	phenolic tannins (% DM) I	II	III
deciduous species:	Acacia seyal	–	3.2	0.5
	Combretum micranthum	1.7	7.1	9.7
	C. nigricans	7.0	9.4	11.8
	Feretia apodanthera	–	15.2	16.7
	Guiera senegalensis	2.1	8.0	12.6
	Zizyphus mauritiana	2.6	7.1	0.8
(semi)evergreen species:	Borassus aethiopum	8.4	9.0	7.2
	Boscia angustifolia	–	0.8	0.5
	Cadaba farinosa	1.8	9.5	–
	Maerua oblongifolia	0.8	–	1.6
	Piliostigma reticulatum	2.6	5.9	3.1
riverine species:	Acacia ataxacantha	9.0	9.2	2.8
	Mimosa pigra	3.2	4.6	6.1
	Sesbania sesban	5.0	2.9	3.5

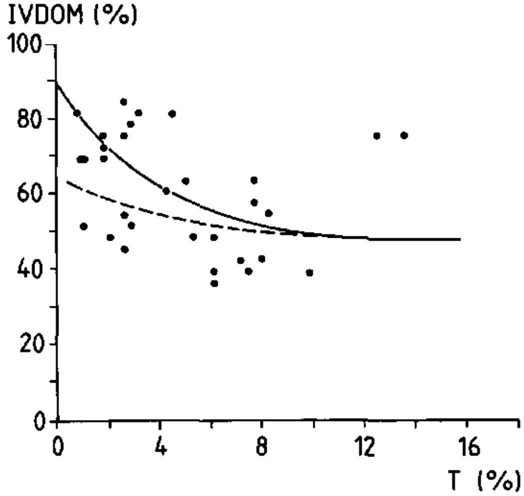


Fig. 6.17. In-vitro digestibility (IVDOM) in relation to phenolic tannins (T) in woody plant species; the broken line represents the relationship between the two variables found by Diagayété (1981)

bility of woody plant foliage can be detected: small quantities of tannins strongly reduces the in-vitro digestibility whereas this effect decreases with increasing levels of tannins.

6.4.3. *Discussion*

The seasonal changes in the quality of savanna grasses are well documented for the subhumid savannas (900-1500 mm annual rainfall) in Nigeria (Haggar, 1970; De Leeuw, 1979; Zemmelink, 1974). De Leeuw (1979) found that both *Andropogon gayanus* and the total of all tall savanna grasses show a rapid fall in crude protein content during the wet season and, although initially significant differences exist between the crude protein content of the different parts of the plants, these disappear as plants grow older. The values are comparable to those found in the Baoulé. Experiments revealed that when protected against fires, the herbaceous vegetation contained less crude protein in the following growing season than when burnt: 3.6% compared with 6-7% DM (De Leeuw, 1979). This suggests that burning releases nitrogen which otherwise remains in the litter, reducing the amount available for next year's growth. In northern Nigeria where annual rainfall was 1000 mm, Zemmelink (1974) and De Leeuw (1979) found noticeably lower values of 44-60% for the in-vitro digestibility of *Andropogon gayanus* than the 60-80% we found for this plant species in the Baoulé. This can be attributed to a difference in analysis: they analysed whole plants, we analysed separate plant parts.

Afolayan & Fafunsho (1978) present information on the seasonal change in the crude protein content of some tall savanna grasses in Lake Kainji national park in Nigeria (annual rainfall 1100 mm). High levels of up to 9% crude protein were found at the beginning of the growing season, dropping to 2-3% in December as the grasses grow taller. Tall grasses appeared to have lower crude protein levels than short grasses, probably because of the higher proportion of stem material.

In Mali, Diagayété (1981) analysed the chemical composition of savanna grasses at two stations, Sotuba and Niono Ranch, with 1000 mm and 550 mm annual rainfall respectively. In all grasses, the crude protein content declines with age, other components such as cellulose and lignin increasing slightly. For *Andropogon gayanus* the values of crude protein content are somewhat lower than in the study area but as Diagayété (1981) does not distinguish between plant parts, values are difficult to compare.

After an extensive search of the literature, LeHouérou (1980b) brought together data on about 540 analyses of 105 woody plant species of 72 genera from 30 families, occurring in the Sahel, the Sudan and Guinea zones, from Senegal to the Central African Republic. Woody foliage appears to be richer in crude protein (8.2% on average, n = 540) than savanna grasses (3.1% on average, n = 18), as we found in this study, and also has less silica and a higher energy content of 6.0 MJ compared with 2.8 MJ per kg DM. Thus woody foliage seems to provide the protein and energy required by animals better than grasses. However, he did not use information on food intake or digestibility or tannins when calculating the availability of protein or energy. We found that the tannin content of woody foliage is often considerable, and the in-vitro digestibility variable and on average low. Hence, its classification as 'excellent fodder' (LeHouérou, 1980b) is, at best, optimistic!

Diagayété (1981) also analysed the chemical composition of the foliage and fruits of woody plants and found, as in the Baoulé, much more crude protein than in grasses, and less crude fibre such as cellulose. In woody legumes, the crude protein content, on average 20.4% DM, was higher than in other plant families which had 18.4% DM crude protein on average. Grasses contained more ADF and cellulose but less lignin than woody plants, agreeing with our findings for these plant groups. Furthermore herbaceous legumes showed higher in-vitro digestibility (OM) than grasses but the leaves of woody plants had much lower values than expected from their crude protein content. Some of the woody plants were found to have an extraordinarily high value for tannin content. In general his data fit in very well with our data in Table 6.12. There are two exceptions: *Acacia seyal* has a phenolic tannin content of 13-15% and *Guiera senegalensis* of 2- 5% according to Diagayété (1981) and there is no explanation for these differences. Diagayété (1981) found the following relationships between the in-vitro digestibility of protein and of the total organic matter, and the tannin content of plants (see Fig. 6.17):

$$\mathrm{IVEDP} = 54.4 - 23.1 \log \mathrm{T} \; (n = 31, r = -0.63) \text{ and}$$
$$\mathrm{IVDOM} = 57.3 - 8.2 \log \mathrm{T} \; (n = 42, r = -0.57)$$

in which:

IVEDP = in-vitro enzymatic disappearance of protein, %DM
IVDOM = in-vitro disappearance of organic matter, %
T = tannins, %DM

In this study:

$$\mathrm{IVDOM} = 70.03 - 15.0 \log \mathrm{T} \; (n = 31, r = -0.37)$$

The negative influence of the tannin content on the in-vitro digestibility of both protein and total organic matter is most obvious with a low tannin content (Fig. 6.17). Very small amounts of phenolic tannins (<5%DM) strongly inhibit the in-vitro digestibility of plant protein. Hay & Van Hoven (1988) fed steenbok *Raphicerus campestris* with experimental diets and found that when present in a concentration of 1%, tannins inhibit the digestion of protein and energy markedly. But the relationship above shows that digestibility is never completely inhibited by tannins.

6.5. The savanna vegetation: a fluctuating source of food

In this chapter we have presented information on phenological patterns, growth and quality of the vegetation of the Sudan savanna, information that is essential for the understanding of the ecology of ungulates in this ecosystem. Until now there has been no complete data on these aspects of the Sudan savanna.

The first conclusion is that despite the fact that rainfall is very seasonal in the Sudan savanna, this seasonality has not such an overriding effect that all plant species respond in the same way. Only annual grasses and deciduous shrubs and trees show phenological patterns that correspond with the rainy season. Semi-evergreen and evergreen woody plants and perennial grasses keep their leaves or produce new ones in the dry season, thus providing the ungulates with a food buffer in an otherwise less favourable period of the year. However, to what extent this buffer plays a role in the survival of animals differs between rainfall zones and also depends on the year-to-year fluctuations in annual rainfall.

From the described trends in the production, nutritional value and digestibility of savanna grasses it appears that, in general, the grassy component of the savanna vegetation shows a negative relationship between phytomass and nutritional quality (Fig. 6.18). From the nutritional point of view, we have shown that it is important to consider the different plant *parts* instead of the *whole plant*. Grasses respond immediately to the first rains and their low phytomass is characterized at this time by a high proportion of leaves with high levels of protein and digestibility. As the plants grow older and mature, the tall phytomass is usually low in protein, owing to minimum protein synthesis and heightened protein hydrolysis (Mattson, 1980) and rich in fibre, stems especially being much more lignified. Stems and sheaths form a high proportion of the phytomass at this time, and thus quantitatively determine its quality. Although the leaves have a higher quality, they form only a very small part of the phytomass.

This inverse relationship between the quality and quantity of phytomass of savanna grasses is generally recognized in African rangeland management (Pratt

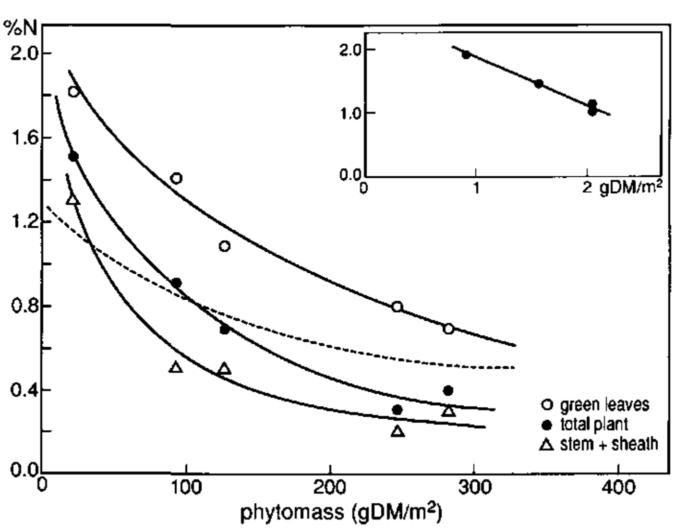


Fig. 6.18: Phytomass (gDM.m^{-2}) of *Andropogon gayanus* in relation to its nitrogen concentration (%) (Dla-station)
---- = minimum concentration of nitrogen required for maintenance in grasses (after Penning de Vries & Van Keulen, 1982)
Inset: relationship for dry-season growth

Plate 9. In the dry season the savanna provides a poor environment for herbivores: cover is minimum and forage is scarce

& Gwynn, 1977; Owen-Smith, 1982a; Penning de Vries & Djitèye, 1982).

Especially grasses of tropical origin are well known for their efficient utilization of nitrogen for growth and maintenance (Jones & Wilson, 1987). These grasses have a C4 photosynthetic pathway: the first product of this synthesis being a molecule with 4 carbon atoms. C4-grasses are characterised by a specialised leaf anatomy, higher tolerance of light intensity , higher growth rate and the higher efficiency in nitrogen-use (Jones & Wilson, 1987). Penning de Vries & Van Keulen (1982) have shown that, when nitrogen and phosphorus are available to C4-grasses in excess, once fully grown these grasses never contain more than 2% nitrogen in their tissues. When, however, these nutrients are limiting plant growth, such grasses always have 0.5% nitrogen, the minimum quantity necessary for tissue functioning at the end of the growing season, any excess being allocated to the tissues for seed production. Fig. 6.18 shows that the production of *Andropogon gayanus*, a C4-grass species (Penning de Vries & Van Keulen, 1982), is limited by the availability of nitrogen in the soil.

Bush fires greatly reduce the quantity of low-quality phytomass of savanna grasses. Dry-season growth improves the quality of the available phytomass (Fig. 6.18) and can thus be an important source of food for the grazing ungulates in that period. However, because this growth is determined by the availability of water in the soil, the amount available is very limited in the lower rainfall zones, i.e. 500-800 mm annual rainfall, and in years with below normal rainfall.

There is a considerable drop in quantity of the foliage of savanna trees and shrubs once the rainy season is over. The crude protein content of woody foliage is relatively constant throughout the year and higher than that of grasses, especially in the dry season. Semi-evergreen, evergreen and riverine shrubs and trees can thus be a source of supplementary protein for wild ungulates. Their use has also been suggested in animal husbandry to make up for the declining quality of pasture grasses and prevent weight losses in cattle (e.g. Billé, 1978; Bamualim et al., 1982).

However, woody foliage generally contains tannins, the amounts of which increase with age. These tannins reduce the availability of energy and nutrients to the herbivores (Robbins et al., 1987b; Hay & Van Hoven, 1988; see also Fig. 6.17) and therefore the actual digestibility of protein in many woody plants is much less than in herbaceous species (e.g. Diagayété, 1981; Jones & Wilson, 1987). Cooper & Owen-Smith (1985) showed that the palatability of 14 woody plant species for three browsing ruminants was clearly related to the content of condensed tannins in the leaves. The effect was a threshold one: plants with more than 5% condensed tannins were rejected as food during the wet season. As the dry season advances the increasing tannin content of the foliage makes the woody foliage less attractive to ungulates as food. Small amounts of hydrolysable tannins may also act positively by protecting plant proteins from bacterial degradation and making them available for absorption in the duodenum of the ungulate, and thus improving the quality of the diet. In this way plant protein is used more efficiently (Reid et al., 1974).

The quantity of forage on offer to ungulates that is nutritionally acceptable, varies between groups of plants, habitats and rainfall zones. Fluctuations in annual rainfall are unpredictable and may be considerable. They have a strong impact on the vegetation composition: dry years cause perennial grasses to retreat to more southern zones and to the lower parts of the topographical gradient, and hence the effect on the availability of food in the dry season can be considerable.

All the described characteristics of the different groups of forage plants have important effects on the populations of the various ungulates in the Sudan savanna. In the dry season grass-eating ungulates face a severe shortage of food, that has been strongly reduced, both quantitatively and qualitatively. Browsers foraging on woody foliage face a reduction of food abundance but probably less dramatic variations in its quality. The next chapter focuses on the ungulates themselves and how they cope with these changes in plant availability and quality.

7. The strategies of wild ungulates in the Baoulé

7.1. Introduction

The success of an individual animal to survive and to reproduce depends on its ability to cover its energetic and nutritional requirements and to provide a large enough surplus to allow it to reproduce (Clutton-Brock et al., 1982).

Large herbivores optimize the utilization of their environment by adapting their behavioural patterns: e.g. by selective foraging on different plant species and plant parts in plant communities and land-system units, according to what plants are available in space and time, or by adapting their social organization. However, this strategy (a behavioural policy, cf. Krebs & Davis, 1981) also depends on animal-specific characteristics such as body size, morphology, and physiology.

In the Sudan savanna of West Africa the availability of food fluctuates throughout the year: especially in the upland habitats it is scarce and of low quality in the dry season, but in the rainy season there is an abundance of highly nutritious food (Chapter 6). Flood plains always provide nutritious food outside the flooding season but its quantity available gradually decreases in time.

An analysis of the strategies the animals adopt in the savanna ecosystem to cope with this variation in the quantity and quality of the forage is the subject of this chapter.

7.2. Animal numbers and distribution

Despite the pressure from for example hunting, poaching, crop farming and livestock husbandry (Chapter 4; De Bie et al., 1987), the fauna of the Baoulé is still rich in species. A considerable number of ungulates present in the West African Sudan savanna can still be found in this area (see Tables 7.1 and 3.2).

However, species are represented by low numbers. Two aerial surveys provided population estimates for the Baoulé and its surroundings (De Bie & Kessler, 1983; Table 7.2). Comparison with ground data showed that some of the estimates had to be adjusted: ground observations on recognizable individuals during the dry season revealed a density of bushbuck higher than appeared from the aerial surveys, with 17 animals per km river bed in the pilot area 'Borassus' compared with 3 animals per km river bed in the same area from the air. Elephant and giraffe were not observed from the air but fresh dung and tracks were found on the ground. Aerial surveys indicated very low numbers for Grimm's duiker and oribi whereas ground inventories showed that these species are more com-

Table 7.1. Estimated population size of ungulate species occurring in the Biosphere Reserve 'Boucle du Baoulé' and surroundings, based on ground counts and aerial surveys[1]

English name:	Latin name:	population size
African elephant	Loxodonta africana	< 100
warthog	Phacochoerus aethiopicus	19,000 (± 3,000)
hippopotamus	Hippopotamus amphibius	100-200
giraffe	Giraffa camelopardalis	< 100
African buffalo	Syncerus caffer	Q[2]
bushbuck	Tragelaphus scriptus	15,000 (± 2,000)
giant eland	Tragelaphus derbianus	E[3]
red-flanked duiker	Cephalophus rufilatus	6,000 (± 2,000)
Grimm's duiker	Sylvicapra grimmia	
Bohor reedbuck	Redunca redunca	6,000 (± 2,000)
waterbuck	Kobus ellipsiprymnus	100-200
roan antelope	Hippotragus equinus	1,200 (± 600)
hartebeest	Alcelaphus buselaphus	100-300
topi	Damaliscus lunatus	E
oribi	Ourebia ourebi	6,000 (± 2,000)
red-fronted gazelle	Gazella rufifrons	Q

[1] Nomenclature and systematic classification according to Meester & Setzer (1971)

[2] Q = species may still live in the area but if so, then in very small numbers

[3] E = species no longer occurs in the area but did so until recently (see also Sayer, 1977)

Table 7.2. Population estimates of ungulates in the survey area, based on two aerial surveys; density in numbers per km^2

		area (km^2)	warthog	bush-buck	duikers	reed-buck	water-buck	roan antelope	harte-beest	oribi
wet season	number	18,561	22,244	10,348	7,241	9,520	63	1,548	116	3,264
1980	density		1.20	0.6	0.4	0.5	0.003	0.08	0.006	0.2
dry season	number	24,867	22,771	7,183	4,390	6,759	109	685	282	6,448
1981	density		0.9	0.3	4,390	0.3	0.004	0.03	0.01	0.3

mon. It is probably not possible to distinguish the two duiker species from the air.

In a limited area ground counts appear to give more reliable information on animal numbers than aerial surveys but require considerable time due to the shyness of the animals. Nevertheless, because of the vast area of the Baoulé (± 16,150 km^2) and its inaccessibility in the wet season, aerial surveys were the only means of estimating population size for all the animal species living there. The final estimates for each species in the Baoulé, a combination of ground and aerial observations, are given in Table 7.1. The large antelopes, elephant, giraffe and hippopotamus are rare. Warthog is still very abundant, probably because most of the inhabitants are of Islamic religion and are forbidden to eat it.

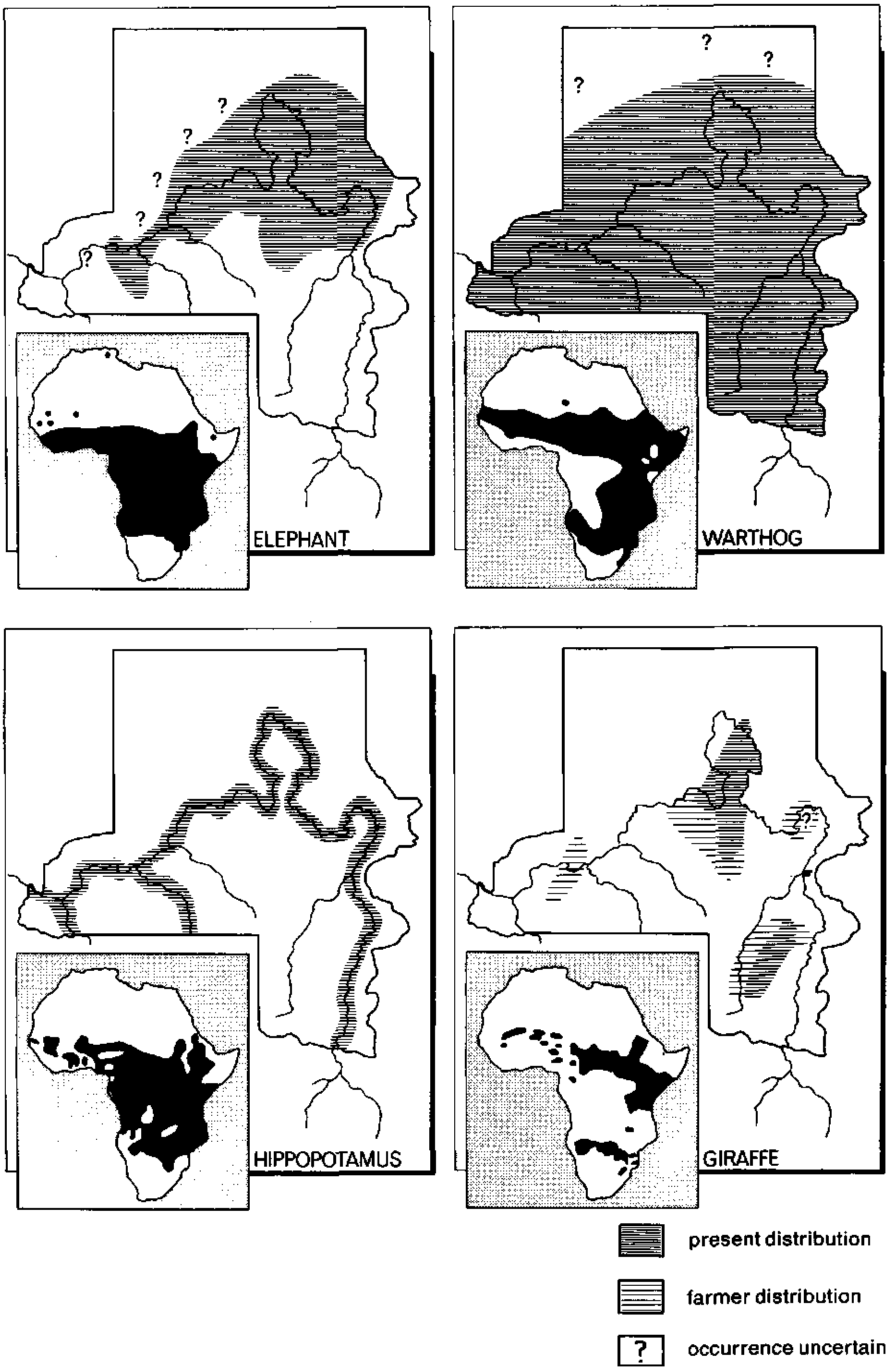


Fig. 7.1. Distribution of ungulates in the Baoulé

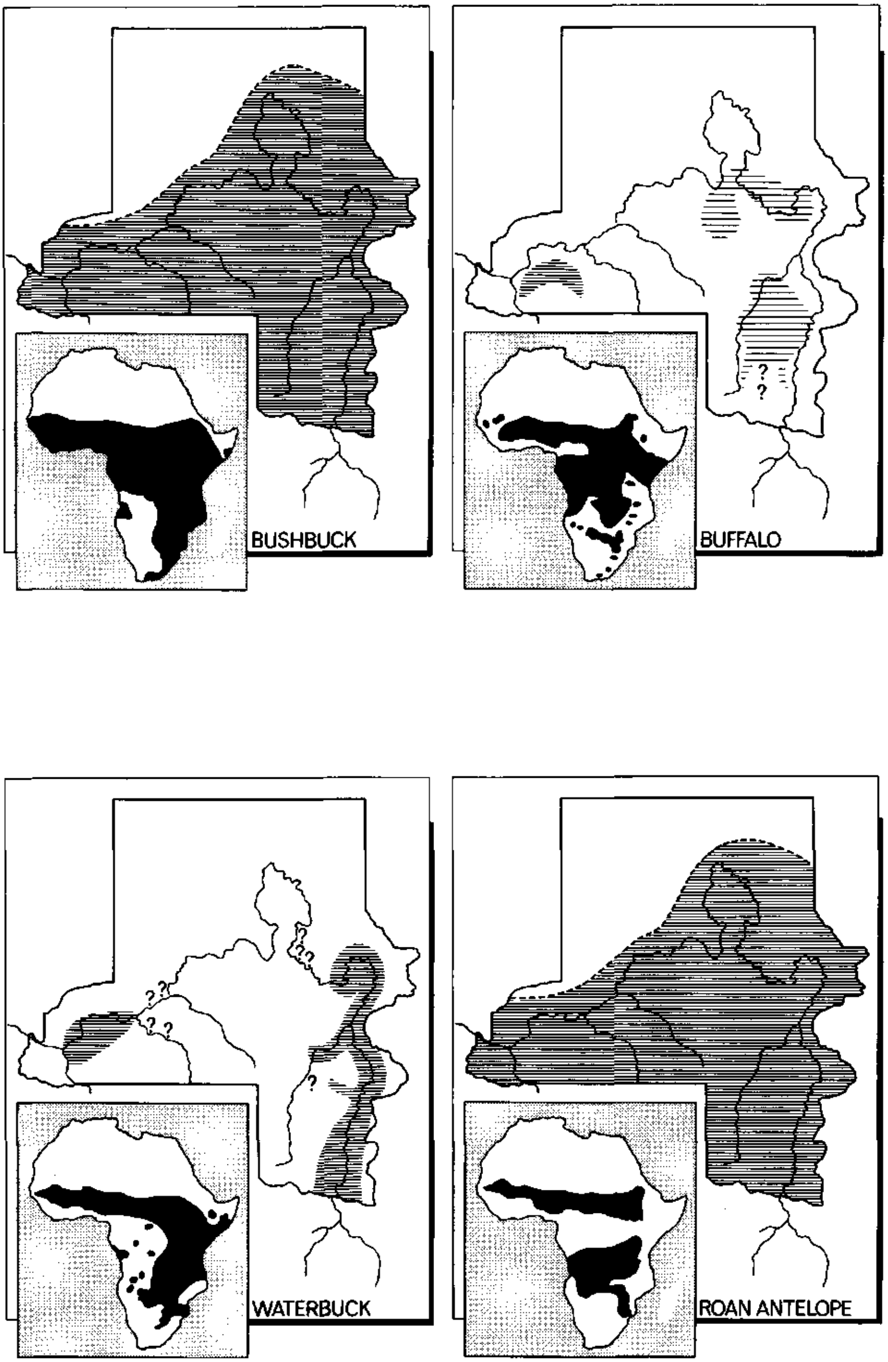


Fig. 7.1. (continued)

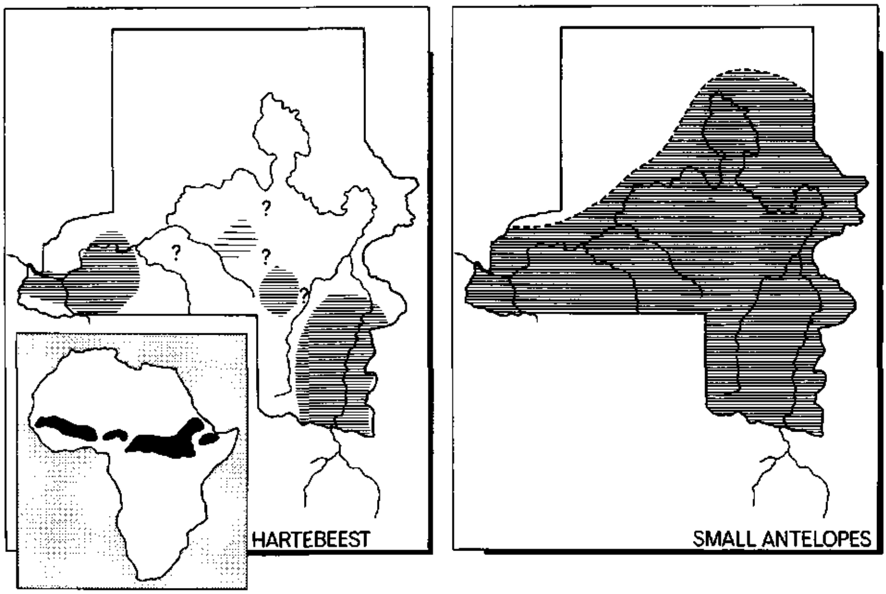


Fig. 7.1. (continued)

In Chapter 9 actual densities of the species, discussed in De Bie & Kessler (1983), will be compared with potential densities in order to evaluate the current status of the species concerned. Figures 7.1 give information on the distribution of the ungulate species in the Baoulé area.

7.3. Habitat selection

7.3.1. Introduction

Forage, water and shelter from climate and predators, basic needs for animals, are seldom evenly distributed but vary in space and time. Consequently, animals do not range freely. To study animal distribution, one should preferably first choose a set of resource parameters and describe animal distribution in relation to variations in these parameters (Duncan, 1983). Such an approach demands an intensive programme of measuring, that is often impossible to carry out. The alternative, a widely adopted approach and followed here, is to stratify the area a priori into units, mainly on the basis of geomorphological and vegetational characteristics, and describe how often an animal species uses a unit in relation to the resources in it.

Following Partridge (1978) habitat is defined as the complex of physical and biotic factors that make up the place in which an animal lives. Habitat selection then is the choice of a certain place.

In this study habitat selection is described according to what can be distinguished as a 'place' from the air. We used the land-system units (see Chapter

4 for a description) for recording animals. Each land-system unit is defined as a habitat type. As an animal species might use more than one unit, its habitat is formed by the total of all units used.

7.3.2. Specific methods

Information from ground observations, the occurrence of tracks, faeces, holes, and information from local hunters was limited to whether an animal species was present or not in a particular land-system unit. Furthermore this information was incomplete because of the uneven distribution of roads, low density and acute shyness of the animals. Aerial surveys provided quantitative information on the selection of land-system units. In the quantitative analysis of the patterns in habitat choice, we calculated:

Occupation of a land-system unit, being the percentage of all observations made in that land-system unit during each of the two aerial surveys.

Preference indices for the various land-system units in both the wet and the dry season for each species, based on the same data and using the formula:

$$P_{ij} = \log\left(\frac{(N_{ij} / N_i \times 100)}{(F_j)} + 1\right) \quad \text{(after Hunter, 1962 and Duncan, 1983)}$$

where:

P_{ij} = preference index of species i for land-system unit j
N_{ij} = numbers observed of species i in land-system unit j
N_i = numbers observed of species i in all land-system units
F_j = percentage of the area covered by land-system unit j

Values of P_i vary from 0 indicating total avoidance, 0.30 for no preference, up to values > 0.30 which indicates preference for the land-system unit concerned.

A *degree of overall selectivity*, S, for a comparison between species for all the land-system units combined:

$$S = \sum_{i=1}^{7} |(N_{ij}/N_i \times 100) - F_j| \quad \text{(Duncan, 1983)}$$

In theory, this index can vary from 0, where all land-system units are used in proportion to their area, to 200 with all observations occurring in one very small unit.

The existence of *spatial association* between the different species, i.e. aggregation of species due to passive or active behaviour, has been investigated using a 2x2 contingency table (Pielou, 1969):

		species 1		
		+	−	
species 2	+	A	B	N=A+B
	−	C	D	M=C+D
		R=A+C	S=B+D	

(+ = presence; − = absence)

From this table, a coefficient of spatial association between two species, V, has been calculated (Skogland, 1984):

$$V = \sqrt{\frac{AD - BC}{MxNxRxS}}$$

7.3.3. *Choice of habitat*

Qualitative observations show that in the wet season species occur in nearly

Table 7.3. Occupation (%) of the different land-system units by the various ungulates in the wet and dry seasons, based on aerial surveys;
Land-system units: R = river, F = Andropogon savanna, LSM = Loudetia grass savanna, SSP = Loudetia shrub savanna, CS = shrub savanna, VI = tree savanna, B = woodland savanna

	season	land-system unit								
		R	F	LSM	SSP	CS	VI	B		
warthog	wet	7	85	2	5	1	0	0		+
	dry	39	61	0	0	0	0	0	*	
hippopotamus	wet	100	0	0	0	0	0	0	*	
	dry	100	0	0	0	0	0	0	*	
bushbuck	wet	29	50	6	6	9	0	0	*	+
	dry	36	62	2	0	0	0	0	*	
red-flanked duiker	wet	14	76	6	4	0	0	0		
	dry	12	78	2	2	3	3	0		
reedbuck	wet	17	72	5	2	4	0	0		+
	dry	33	67	0	0	0	0	0	*	
waterbuck	wet	0	100	0	0	0	0	0	*	+
	dry	83	17	0	0	0	0	0	*	
roan antelope	wet	0	88	4	8	0	0	0	*	+
	dry	8	83	8	0	0	0	0	**	
hartebeest	wet	0	100	0	0	0	0	0	*	
	dry	0	100	0	0	0	0	0	*	
oribi	wet	4	96	0	0	0	0	0	*	
	dry	2	98	0	0	0	0	0	*	

* = significant from random distribution, P = 0.01 (Chi-squared test)
** = idem, P = 0.05
\+ = significant difference between wet-season and dry-season occupation of land-system units, P = 0.01 (Chi-squared test)

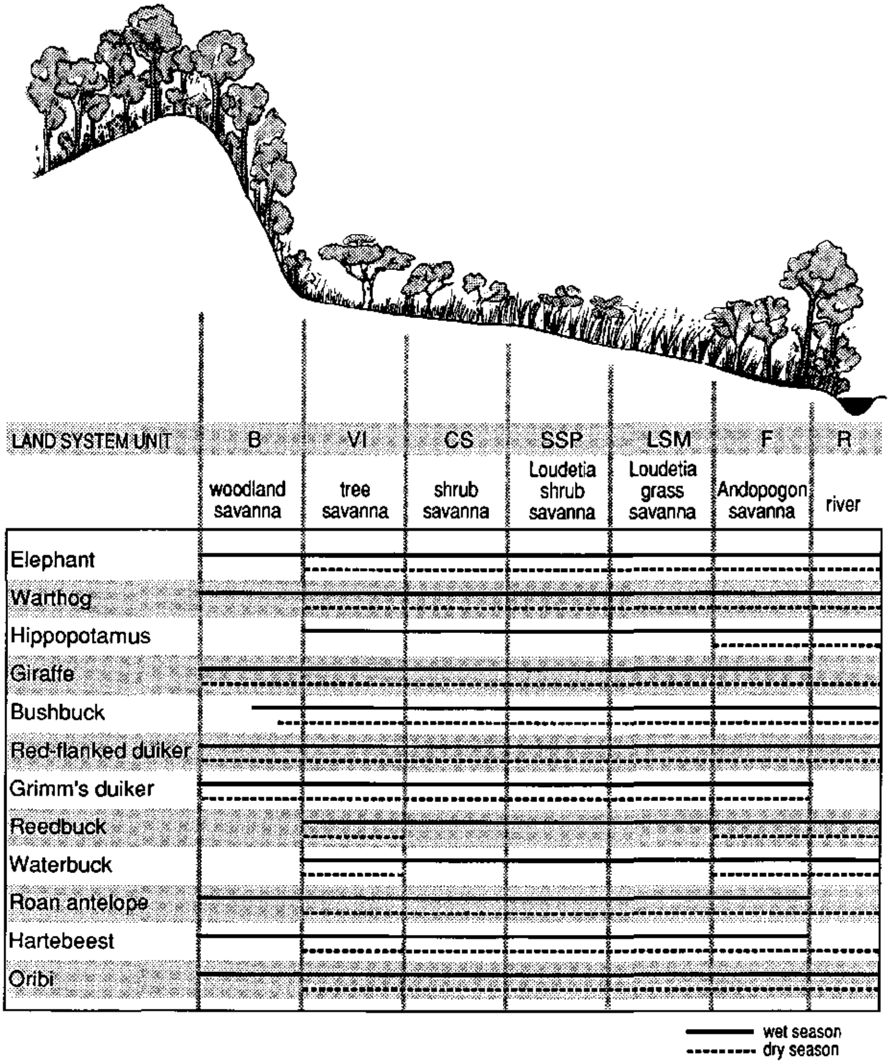


Fig. 7.2. Presence of ungulates in the various land-system units in the wet and dry seasons, based on qualitative observations

all units (Fig. 7.2), whereas in the dry season some species move along the topographic and drainage patterns to more low-lying units, a phenomenon named 'catena movement'.

Table 7.3 shows the occupation of the different land-system units in wet and dry seasons. A zero value for a land-system unit in Table 7.3 does not necessarily mean that animals do not use that unit: when densities are low, there is a big chance of being missed during an aerial survey. All observations of hippopotamus are of animals on the river bed itself.

A pattern is discernable: in general, fewer land-system units are used by the various ungulates in the dry season than in the wet season. Statistically, with the exception of the red-flanked duiker, the species' occupation of the various units is not random in either one or both seasons, showing that species are selective with regard to their use of different land-system units. Also five species significantly show a catena movement as had been noticed on the basis of qualitative ground information.

The indices for the degree of overall selectivity by the species for the land-system units is in general low (Table 7.4), except for hippopotamus and waterbuck in the dry season. Although most species show a slight increase in their overall selectivity during the dry season, a strong selection for one or more units cannot be observed on the basis of these indices.

Table 7.4. Degree of overall selectivity (S) for the land-system units by ungulates in the wet and dry seasons.

	species								
	wh1)	hi	bb	rd	rb	wb	ro	hb	or
$S_{\text{wet season}}$	26	186	58	22	22	56	38	56	48
$S_{\text{dry season}}$	62	186	58	26	52	152	27	56	52

1) wh = warthog, hi = hippopotamus, bb = bushbuck, rd = red-flanked duiker, rb = reedbuck, wb = waterbuck, ro = roan antelope, hb = hartebeest, or = oribi

Indices of preference for the different land-system units by the ungulates are given in Table 7.5 and show more clearly than the occupation data in Table 7.3 a seasonal trend in the pattern of habitat use.

In the wet season, the high-lying land-system units are visited more often than in the dry season; some of them are slightly preferred (underlined values). With the change to the dry season, warthog, bushbuck, reedbuck, waterbuck and roan antelope show a shift in their preference for low-lying units, especially the river (R), but hippopotamus, hartebeest and oribi do not. Red-flanked duiker not only uses more land-system units in the dry season but also prefers the tree savanna (VI) at the upper part of the catena.

To summarize, the results show that, in general, the animal species do not use the various land-system units randomly but are to some extent selective in their choice, although the degree of overall selectivity is low. There is a certain preference for some units, especially in the dry season.

We next assessed to what extent the various ungulates are spatially associated. From Table 7.6 it appears that, with the exception of the red-flanked duiker, all other species show an increase in the dry season in the number of species with which they are spatially associated, probably pointing to the limited availability of resources. Multi-species groups have never been observed which excludes the possibility of active aggregation behaviour among the species concerned. Because hippopotamus is restricted to the river in daytime and visits other land-system units only at night, its degree of association with other species is negatively influenced.

Table 7.5. Indices of preference by the ungulate species for the land-system units distinguished; underlined values indicate preference.
Land-system units: R = river, F = Andropogon savanna, LSM = Loudetia grass savanna, SSP = Loudetia shrub savanna, CS = shrub savanna, VI = tree savanna, B = woodland savanna

	season	land-system unit						
		R	F	LSM	SSP	CS	VI	B
warthog	wet	0.301	0.338	0.109	0.301	0.125	0.000	0.000
	dry	0.818	0.267	0.000	0.000	0.000	0.000	0.000
hippopotamus	wet	1.184	0.000	0.000	0.000	0.000	0.000	0.000
	dry	1.184	0.000	0.000	0.000	0.000	0.000	0.000
bushbuck	wet	0.711	0.229	0.269	0.342	0.602	0.000	0.000
	dry	0.788	0.270	0.109	0.000	0.000	0.000	0.000
red-flanked	wet	0.477	0.313	0.269	0.255	0.000	0.000	0.000
duiker	dry	0.434	0.319	0.109	0.146	0.301	0.602	0.000
reedbuck	wet	0.535	0.301	0.234	0.146	0.368	0.000	0.000
	dry	0.767	0.286	0.000	0.000	0.000	0.000	0.000
waterbuck	wet	0.000	0.378	0.000	0.000	0.000	0.000	0.000
	dry	1.109	0.092	0.000	0.000	0.000	0.000	0.000
roan antelope	wet	0.000	0.347	0.196	0.415	0.000	0.000	0.000
	dry	0.331	0.333	0.331	0.000	0.000	0.000	0.000
hartebeest	wet	0.000	0.378	0.000	0.000	0.000	0.000	0.000
	dry	0.000	0.378	0.000	0.000	0.000	0.000	0.000
oribi	wet	0.196	0.368	0.000	0.000	0.000	0.000	0.000
	dry	0.109	0.373	0.000	0.000	0.000	0.000	0.000

7.3.4. Discussion

To what extent can the observed patterns of habitat use, especially the shift to and preference for the land-system units at the lower end of the catena be explained by changes in the availability of the basic resources required by the species concerned?

In the wet season, herbaceous forage is available in large quantities everywhere (Table 6.3). Also in the dry season, all land-system units offer the dry-season growth of perennial grasses as potential food to grass-preferring ungu-

Table 7.6. Coefficients of spatial association.

		wet season								
		wh	hi	bb	rd	rb	wb	ro	hb	or
d										
r	warthog	*	0.26	1.00	0.73	1.00	0.26	0.55	0.26	0.40
y	hippopotamus	0.65	*	0.26	0.32	0.26	0.00	0.00	0.00	0.65
	bushbuck	0.73	0.47	*	0.73	1.00	0.26	0.55	0.26	0.40
s	red-flanked duiker	0.18	0.17	0.41	*	0.89	0.32	0.71	0.32	0.50
e	reedbuck	1.00	0.65	0.73	0.26	*	0.26	0.55	0.26	0.40
a	waterbuck	1.00	0.65	0.73	0.26	1.00	*	0.47	1.00	0.65
s	roan antelope	0.73	0.47	1.00	0.35	0.73	0.73	*	0.47	0.09
o	hartebeest	0.65	0.00	0.47	0.17	0.65	0.65	0.47	*	0.65
n	oribi	1.00	0.65	0.73	0.26	1.00	1.00	0.73	0.65	*

Table 7.7. Availability of dry-season growth of perennial grasses (kgDM.ha^{-1}) in the land-system units in normal rainfall years.

	land-system unit						
rainfall zone	R	F	LSM	SSP	CS	VI	B
600- 700 mm	10.0	8.7	5.7	4.2	40.0	0.0	6.1
700- 800 mm	60.7	59.4	32.4	17.6	160.4	40.0	24.0
800- 900 mm	44.8	54.0	27.1	17.5	160.1	39.7	177.9
900-1000 mm	94.2	154.6	50.0	33.5	320.6	75.0	37.1
1000-1100 mm	86.9	246.5	55.4	35.7	0.0	0.0	62.0

lates (Table 7.7) although in significantly lower quantities than in the wet season.

The area of Andropogon savanna (F) is much larger than that of the upper catena land-system units and hence the quantity of dry-season growth of perennial grasses on offer is much larger (Table 6.3). Moreover, the river (R) also provides the dry-season growth of grasses and sedges in the river bed and on the adjacent banks (see Table 6.4). Thus in the dry season these two land- system units are more attractive to grass-preferring ungulates than other units.

Most of the woody foliage is found in the riverine forest, around termitaries (in the Andropogon savanna), and on the shallow soils (Loudetia grass and shrub savanna (LSM, SSP), shrub and woodland savanna (CS, B)). Although its quantity drops during the dry season, there is enough in most of the land-system units to provide foliage as food for ungulates (Table 7.8).

On the river bed permanent water pools provide water in the dry season just as numerous (very) small springs in most of the rocky, shrub and woodland savanna do (CS,B) (Table 7.7; De Bie & Kessler, 1983). In the dry season permanent surface water is nearly always to be found within a distance of 15 km (Fig. 7.3).

Thus one should expect species requiring water daily or at least regularly (Table 7.9), and species needing green grass to fulfil their nutrient requirements, to descend to the lower part of the catena during the dry season. In general, the patterns found agree with this. Warthog, reedbuck, waterbuck, roan ante-

Table 7.8. Availability of woody foliage, shelter and surface water per land-system unit in the wet and dry seasons; 3 = available almost everywhere, 2 = locally available, 1 = not or sporadically available.

		land-system unit						
	season	R	F	LSM	SSP	CS	VI	B
woody	ws	3	3	3	3	3	3	3
foliage	ds	3	1	2	2	2	1	2
water	ws	3	2	2	2	2	2	2
	ds	3	1	1	1	2	1	2
shelter	ws	3	3	2	3	3	2	
	ds	3	1	1	1	1	2	2

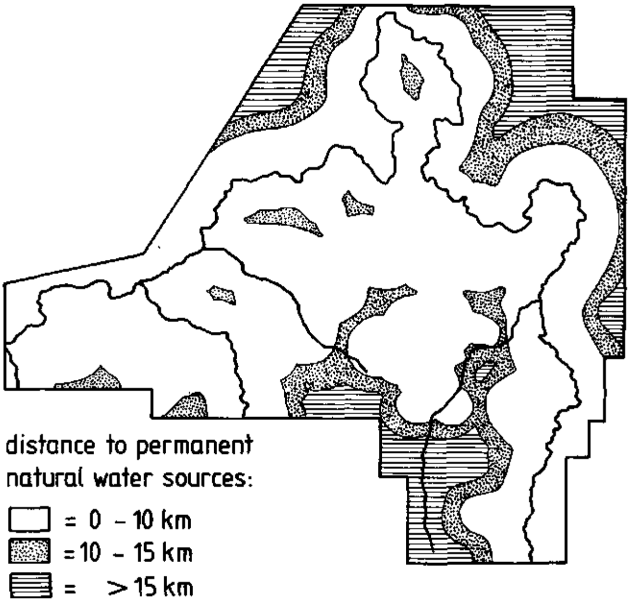


Fig. 7.3. Availability of surface water in the dry season

lope, hartebeest and oribi, that all need green grass to varying degrees (see 7.4) show a preference for the lower land-system units, warthog, reedbuck and roan antelope showing clear catena movements. For reedbuck, roan antelope and waterbuck this coincides with their water requirements.

Species that prefer browse such as giraffe, red-flanked duiker and Grimm's duiker, can survive in the upper catena. The small-bodied red-flanked duiker is only found where sufficient water and shelter are present. This species (and if necessary the Grimm's duiker as well) can probably fulfil its water requirements (Table 7.9) by using small springs. This in contrast with the larger bushbuck, also a browse-preferring species, which shows a considerable shift to the riverine unit.

The necessity of water for the functioning of its thermo-regulatory system

Table 7.9. Water requirements of West African ungulates in the Baoulé.

species, needing to drink daily or regularly:	species potentially independent of surface water
elephant	warthog
hippopotamus	giraffe
buffalo	Grimm's duiker
bushbuck	hartebeest
red-flanked duiker	oribi
reedbuck	
waterbuck	
roan antelope	

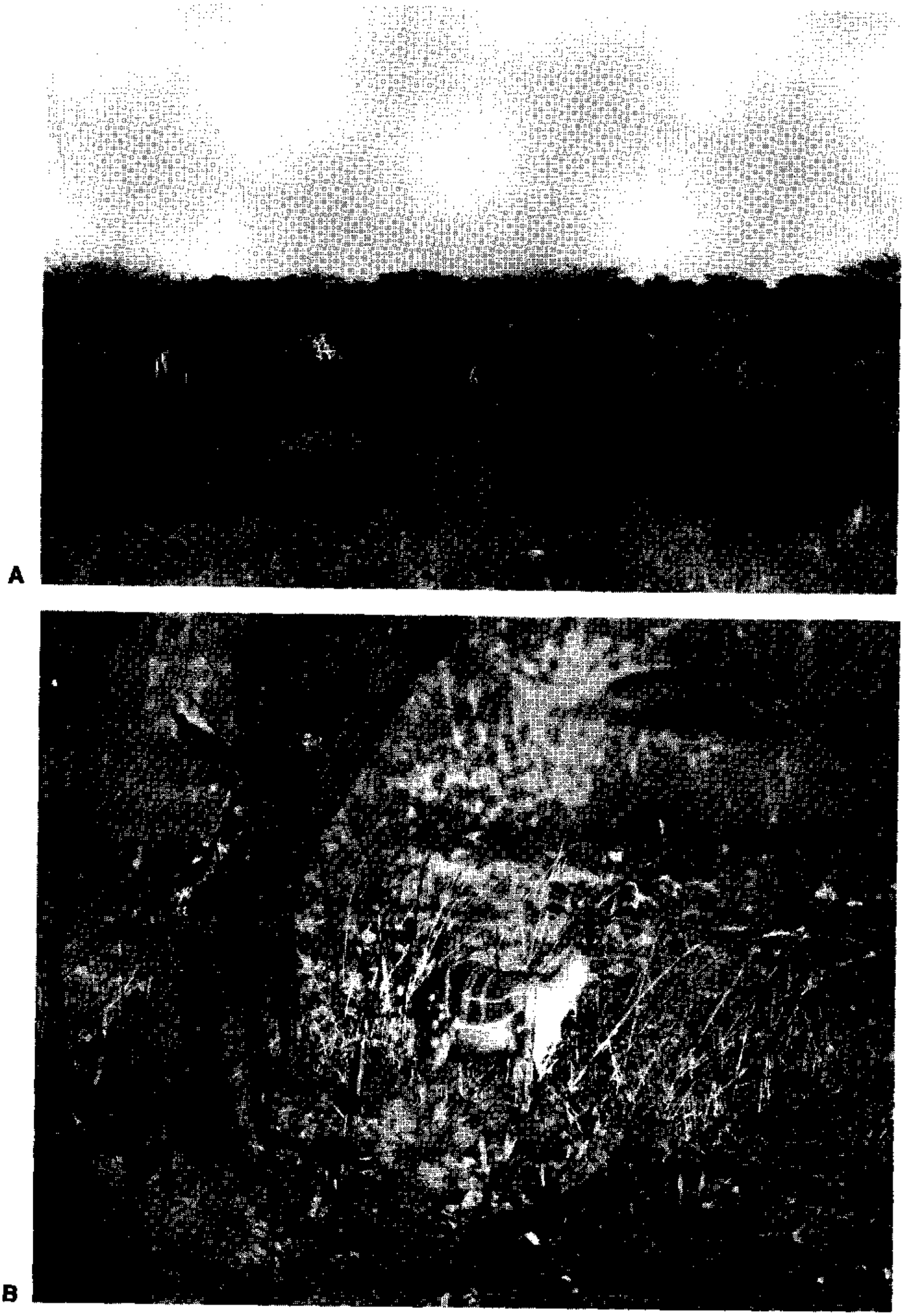


Plate 10. Giraffe (a) and bushbuck (b) have different water requirements

Plate 11. The presence of deep water is a characteristic of the hippopotamus' habitat

limits the distribution of hippopotamus to the lower catena units throughout the year. The elephant, living almost entirely on browse in the dry season, needs water at least once a day (Table 7.9) which explains its presence at that time in the lower units of the catena. None of our data suggest that these catena movements cover such large distances that one could regard them as large-scale movements or migrations. Although local hunters presume that elephants migrate, mapping of tracks from the air in the wet and dry seasons (Fig. 7.1) does not confirm this for the population we observed in the Baoulé.

The selection of places near the rivers (land-system unit R) by reedbuck and waterbuck, compared to that of roan antelope, may point to the importance of the third basic need that infuences the distribution of species: shelter against predators. The 'freezing' behaviour (where the animal stands or lies down motionless) to escape detection by a predator, as observed for waterbuck but also oribi and Grimm's duiker, requires cover, provided in this case by the riverine forest and the termitaries. Waterbuck are seldom found more than 3 km from the river in the dry season. This is in contrast with roan antelope and hartebeest which flee from their attacker and this asks for open country. They only use the riverine unit as a source of water and are nervous when forced to feed there (Geerling, pers.comm.).

It seems that northern subpopulations of roan antelope prefer more open, shrubby vegetation units, e.g. Loudetia grass savanna (LSM, with evergreen woody species) than southern subpopulations and hartebeest. This could be a consequence of a different diet (7.4).

Bushbuck use different habitat types during the day than at night. In the dry season bushbuck were seen feeding in daytime only on the river bed and in (the vicinity of) the riverine forest (see also Smits, 1986). However, as their faeces contain a number of plant species that are only found in the open woodland savanna (F), we concluded that the woodland is visited at night. This difference in habitat-type utilization is probably correlated with their anti-predation strategy (Leuthold, 1977).

There is a clear difference in the use of different habitat types by hippopotamus. It is the river itself which provides protection against climatic stress of high temperatures, whereas other units are visited to feed. Also for the warthog habitat types may have different functions. In the dry season the river bed provides surface water for drinking and, equally important, for wallowing. More rocky units function predominantly as feeding grounds. Warthogs usually modify burrows of aardvark *Orycteropus afer* for shelter. Burrows are only found where the soil is deeper such as in the Andropogon savanna (F).

A comparison of the distribution area of the ungulates (Fig. 7.1) with the map of land-system units suggests that for certain species e.g. hartebeest, other factors than the availability of habitat types limit their distribution. Such a factor could be the choice of food.

Much data have been published on the habitat selection of West African ungulates in other national parks (NP) or game reserves (GR): Child (1974, Borgu GR), Pelinck (1974, Borgu GR), FAO (1975, Yankari GR), Heisterberg (1975, Po NP), Bosch (1976, Bouba Ndjidah NP), Green (1977, Arli NP), FAO (1977, Waza NP), Milligan (1978, Lake Kainji NP), Esser & Van Lavieren (1979, Waza NP), Van Lavieren & Esser (1979, Bouba Ndjidah NP) and FAO (1981, Pendjari NP)(see Fig. 3.1 for location of the parks).

Summarizing this published information the pattern of habitat choice of ungulates in these parts of the Sudan savanna is (see also Fig. 7.4):

elephant : found in all types of shrub and woodland savannas but preferring the latter; in the dry season movements to and increasing use of riverine forest and flood plains;
warthog : occurring in all types of savanna with no clear preference and no clear distinction between wet and dry seasons;
hippopotamus : low-lying woodland savanna near permanent water, also utilizing flood plains in the dry season;
giraffe : preferring open shrub (e.g. *Acacia seyal*) savanna and woodland in wet and dry season;
buffalo : preferring all types of woodland savanna and flood plains near permanent water in all seasons;
bushbuck : preferring riverine forest but also utilizing patches of forest in the savanna where there is cover and permanent water; in the dry season also utilizing flood plains;

red-flanked duiker : especially found in riverine forest and dense patches of forest in woodland savanna near permanent water in all seasons;

Grimm's duiker : all types of woodland savanna with an understorey for cover but never found in riverine and riparian forest;

reedbuck : preferring low-lying woodland savanna and flood plain all year-round;

kob : in all seasons preferring open woodland savanna and especially flood plains, but always near permanent water;

waterbuck : preferring all types of low-lying woodland savanna, near permanent water (seldom observed more than 3 km away from water); in the dry season movements to and increasing use of river bed and flood plains;

roan antelope : found in all types of open woodland and shrub savannas but preferring woodland on poor, shallow soils (*Burkea/Detarium* woodland, *Combretum* woodland or shrub savanna); using flood plains only in the late dry season;

hartebeest : preferring all types of woodland savanna, both on deeper (*Isoberlinia* woodland) or on laterite or shallow soils (*Burkea/Detarium* woodland); using flood plains only in the late dry season;

oribi : found in all types of woodland savanna.

We can only compare this information superficially with our own data for the Baoulé region because it is qualitative rather than quantitative. Different methods and criteria are used to describe landscape and vegetational units. For example, although Milligan (1978) analysed the habitat choice of several ungu-

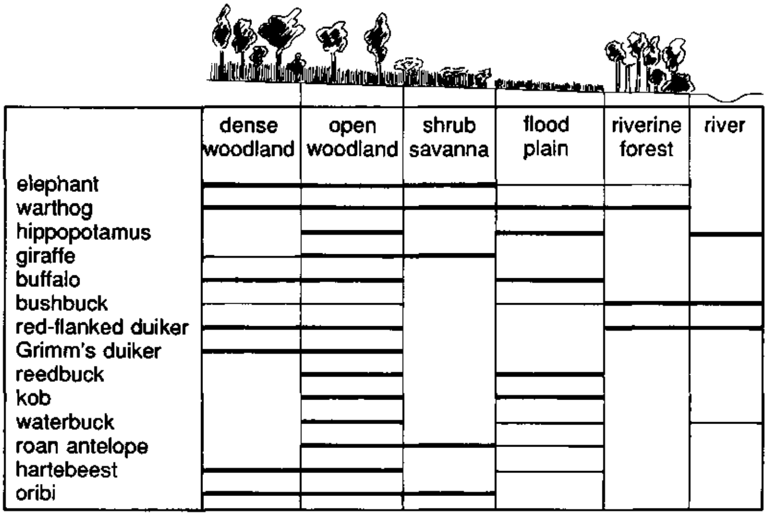


Fig. 7.4. A diagrammatic illustration of habitat choice of ungulates in various conservation areas in the Sudan savanna (see text)

Plate 12. Migration of elephant over large distances does sometimes occur when the seasons change

late species in the Kainji Lake national park quantitatively, he used another system of landscape classification. Furthermore, in general no clear distinction is made between the selection of habitat types in the wet and dry seasons. In some cases, the observed selection is biased towards those units situated near or along the tracks from where ground observations were made (e.g. Child, 1974; Pelinck, 1974; FAO, 1975).

However, we conclude that the pattern of habitat selection of ungulates we observed in the Baoulé (Fig. 7.2) is very similar to elsewhere in the Sudan savanna of West Africa.

The catena movements seen in species in the Baoulé have also been noticed by observers elsewhere in the Sudan savanna. There is no evidence of large-scale migrations although there are reports that elephant e.g. in the Gao region of Mali and in Burkina Faso migrate sometimes hundreds of kilometres to other places when the seasons change (Lamarche, pers. comm.; Heringa, pers. comm.; Jachmann, 1987b). Poché (1974b) reports the migration of elephant over distance of 50-150 km in and around 'W' national park in the dry season.

To summarize we conclude that because of the difference in resources needed by the animal species and the uneven distribution of these resources, animal species show a pattern of spatial separation. In the wet season, when there is food nearly everywhere, the presence of surface water and shelter mainly determine the degree of separation of species. Seasonal variations in resources may temporarily increase separation, for example the limited availability of good quality grass in the dry season, which means that 'browsers' and 'grazers' are more apart at that time.

Species that do not need surface water for drinking such as warthog and giraffe, show spatial flexibility in habitat selection as do species which maintain a certain level of nutrient intake in the dry season by increasing the proportion of woody foliage in their diet (e.g. roan antelope). The warthog, which is independent of water and supplements the nutrient content of its diet in the dry season with the roots of perennial grasses, shows the highest degree of plasticity. The Grimm's duiker also uses a wide range of ecological situations through its independence of water and the omnipresent woody foliage. Specialized species such as bushbuck and waterbuck are much less flexible.

7.4. Diet composition

7.4.1. Introduction

A number of options are open to the wildlife researcher for studying the food choice of wild ungulates (see summarizing review by Schwarz & Hobbs (1985)). The analysis of undigested plant fragments in the stomach contents and faeces, direct observations of wild or tame animals while they are feeding, comparison of marked plots before and after an animal has fed there, and free-choice feeding experiments are well-known techniques.

Before we started our research, there was no information on the food choice of the ungulates in the Baoulé.

It was relatively easy to collect faeces of most of the ungulate species during field work. The droppings of most species have characteristic shapes and especially in the dry season disintegrate very slowly. Except for bushbuck, low densities of the animals and their shyness meant that animals could seldom be observed while feeding and made it also very difficult to shoot individuals for examining the stomach content. The analysis of faecal material therefore forms the quantitative basis of this study of diet composition; the other techniques were applied whenever possible to add to the information from faecal analysis and the results integrated to classify species according to their diet composition.

7.4.2. Specific information on the analysis of diet composition

The diet of the various ungulates in the study area has mainly been reconstructed from the identification of undigested epidermis fragments of plant species in the faeces. This technique is outlined in Chapter 5 but more information on its application is essential for understanding the procedures followed in this study.

A major problem is the discernability of plant species on the basis of undigested plant fragments in the faeces, which depends on (see also Wesselo, 1984):

- the amount of cutin present in the middle lamella of the epidermal cells: when hardly any cutin is present, the cuticular layer shows few characteristics which makes determination more difficult, e.g. in herbs;
- the fragment size: small fragments possess few characteristics for determination;
- the digestion process;
- the treatment of the faeces.

Furthermore, this discernability might differ between plant species and with the season or growth stage.

Consequently there is always a proportion of the fragments which remains unidentifiable (Wesselo, 1984); Monro (1982) found 30-40% of the fragments unidentifiable in his study of the diet of impala *Aepyceros melampus*, and in our study this proportion is considerably larger (see 7.4.3) despite the procedure of faeces treatment (see 5.2.3). Hence, the botanical composition of the identifiable fragments is not representative of the composition of the total sample and of the diet: the proportion of plant species, that are difficult or not to identify, is underestimated and consequently the proportion of species that are more easily identified, overestimated.

Nevertheless, nearly always fragments can be classified into one of the three broad categories of mosses, monocotyledons and dicotyledons (Hansson, 1970). Therefore we used this classification for the quantitative assessment of diet composition but only the last two categories were used as mosses do not occur in the study area.

These epidermal fragments are from the surface of the plants. Therefore, if no surface fragments are lost during digestion or during the chemical treatment of the faeces, the total surface of all fragments in the faeces is equal to the surface of all plant material consumed. Certainly plant fragments will disappear between feeding by the herbivore and microscopical analysis. An analysis of the diet based on the surface area rather than the frequency of plant fragments is nevertheless recommended (e.g. Stewart, 1967), as it gives a better impression of the quantitative intake of the various plant species. Because plant species differ in 'fragmentability', counting of plant fragments in the faecal samples will give a bias towards the easily fragmentable species (Smith & Shandruck, 1979). Dry-milling of faecal droppings to constant fragment size is sometimes suggested as a solution to this problem (Putman 1984), but Holechek & Gross (1982) found that milling could cause excessive fragmentation of some plant species. We thus assessed the importance of plants by measuring the surface area of the fragments. We measured length and width of each fragment with a micrometer, estimated the surface area and divided them into five size classes (Table 7.10). The surface of fragments in size class V were determined individually. An estimation of the total surface of a group of plants was derived from the average fragment surface

Table 7.10. Size classes of plant fragments distinguished in faecal analysis.

size class	faecal fragment surface
I	5,000 – 19,999 μ^2
II	19,999 – 34,999 μ^2
III	35,000 – 49,999 μ^2
IV	50,000 – 64,999 μ^2
V	> 65,000 μ^2

per size class, the number of fragments per size class and the surface of all fragments in size class V. Particles smaller than 5,000 μ^2 were disregarded but this did not change the quantitative ratio of monocotyledons to dicotyledons significantly.

7.4.3. What do ungulates feed on in the Baoulé?

The distribution of faecal plant fragments over the different size classes does not differ between ruminating species nor between seasons within one species (Table 7.11). Non-ruminating herbivores have more large faecal fragments than true ruminants which suggests that they are less able to digest cell walls (7.5).

Analyses of faeces and rumen contents and direct observations of nearly all animal species in the area show a considerable variety of plant species in their diets (Tables 7.12 and 7.13; Appendix I).

The number of plant species occurring in the diets might have been overestimated as many faecal (and some ruminal) fragments could not be identified at the plant species level. Probably the fragments represent a smaller number of plant species than given in Table 7.12, because cuticles from different parts of the plant differ in appearance, e.g. the cuticle from the adaxial (= upper) and abaxial (= under) side of the leaf. Furthermore, some seeds could not be

Table 7.11. Frequency distribution (%) of faecal plant fragments over fragment size classes.

species	fragment size classes				
	I	II	III	IV	V
ruminants:					
bushbuck	43.6	23.3	12.9	7.9	12.3
duiker	49.7	27.4	9.0	8.2	6.0
waterbuck	38.4	26.9	13.2	9.0	12.5
hartebeest	30.9	30.5	13.8	8.6	16.2
reedbuck	43.9	24.9	11.5	7.1	12.6
roan antelope	45.4	25.8	12.7	6.5	9.6
oribi	38.2	31.9	12.6	8.7	8.6
non-ruminants:					
elephant	35.8	24.7	11.8	5.4	22.4
hippopotamus	16.4	20.3	13.2	14.7	35.4
warthog	19.7	22.1	14.8	15.3	28.1

Table 7.12. Number of plants species occurring in the diet of several ungulates, determined by direct observation, faecal and rumen content analysis.

	animal species							
	Wh	Bb	Du	Rb	Wb	Ro	Hb	Or[1])
dicotyledons								
identifiable	8	45	19	7	24	36	16	11
unidentifiable	14	23	9	3	10	65	17	1
monocotyledons								
identifiable	9	3	0	9	14	13	22	5
unidentifiable	22	1	1	16	19	30	37	18
total	53	72	29	35	67	144	92	35

[1]) Wh = warthog, Bb = bushbuck, Du = duiker, Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Hb = hartebeest, Or = oribi

Table 7.13. Plant groups and families occurring in the diet of ungulates in the Baoulé.

	number of plant species identified	Number of plant species eaten per animal species								
		El	Wh	Bb	Du	Rb	Wb	Ro	Hb	Or[1])
Trees and shrubs										
Anacardiaceae	2	2	1							
Apocynaceae	3	1		2	1	1	1	1	1	1
Balanitaceae	1			1						
Bombacaceae	2	2								
Boraginaceae	2	1		1						
Capparaceae	5	1		3	1		2	3	1	1
Celastraceae	1			1						
Caesalpinioideae	9	1		3	2		1	5	3	
Combretaceae	8		1	6	4		4	3 2	1	
Composeae	1			1						
Euphorbiaceae	1			1						
Mimosoideae	11	1		7	2	2	7	4	1	1
Moraceae	1			1		1				
Myrtaceae	1				1					
Palmae	1		1							
Papilionoideae	9	1		4	2	1	4	5	3	1
Polygalaceae	1							1		
Rhamnaceae	2			1				1		
Rubiaceae	7	1	1	2	1		2	3	3	1
Salicaceae	1			1						
Sapindaceae	1				1		1			
Sterculiaceae	1	1								
Herbs	18	2	4	8	3	1	2	6	2	3
Grasses										
– perennial	17	*	8	2		6	11	8	15	3
– annual	9	*				2	3	6	5	2
Cyperaceae			*	*		*	*			
Algae				*						

* = no identification made

[1]) El = elephant, Wh = warthog, Bb = bushbuck, Du = duiker sp., Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Hb = hartebeest, Or = oribi

identified, also causing an overestimation when other parts of the same species had been identified.

Among the large number of plant species identified, only a few are eaten by most of the nine ungulates (Appendix I):

woody plants	:	*Gardenia* sp. eaten by eight, *Baissea multiflora* by seven, *Dichrostachys cinerea* by six, *Guiera senegalensis* by five and *Pterocarpus lucens* by five animal species;
herbs	:	*Borreria* sp. eaten by eight animal species;
grasses	:	*Paspalum polystachum* eaten by seven, *Andropogon gayanus* by six, *Andropogon pseudapricus* by five, *Hyparrhenia* sp. by five and *Panicum anabaptistum* by five animal species.

Especially *Gardenia* and *Borreria* seeds are often found in the faeces of most ungulates (Table 7.14). Both *Gardenia* and *Baissea* are (semi)evergreen, the rest are deciduous. Except for *Andropogon pseudapricus*, the grasses are perennial.

Some species such as hartebeest prefer monocotyledons (mostly grasses) while others such as the bushbuck prefer the leaves and twigs of shrubs and trees, and fruits. These preferences become more clear when the faecal fragments are analysed quantitatively (Fig. 7.5).

The proportion of monocotylenous plants varies seasonally: in general the grasses decrease in importance during the course of the dry season, Fig. 7.5,

Table 7.14. Plant seeds found in the faeces and rumen contents of various ungulates.

	animal species							
plant species	Wh	Bb	Du	Rb	Wb	Ro	Hb	Or[1]
Bauhinia rufescens						+		
Borreria radiata	+	+	+	+		+		+
Borreria stachydea	+	+	+	+	+	+	+	+
Cassia sieberana						+		
Cassia tora						+		
Coloquintus cf. vulgaris						+		
Dichrostachys cinerea		+		+		+		
Gardenia sp.	+	+	+		+	+	+	+
Hibiscus asper						+	+	+
Hibiscus cf. sabdariffa						+		
Indigofera sp.								+
cf. Acacia seyal						+		
cf. Boscia angustifolia						+		
cf. Caesalpinioideae					+	+		
cf. Feretia apodanthera						+		
cf. Labiatae	+	+	+	+	+	+		
cf. Mimosoideae	+	+		+		+	+	+
cf. Papilionoideae	+							+

[1] Wh = warthog, Bb = bushbuck, Du = duiker, Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Hb = hartebeest, Or = oribi

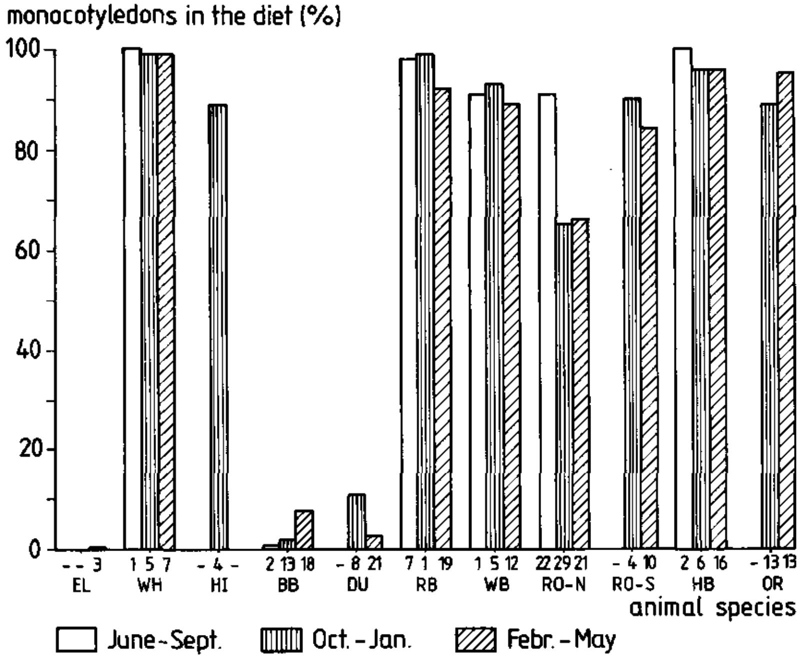


Fig. 7.5. Percentage of monocotyledons in the diet of several ungulates in the Baoulé, per season, based on faecal analysis.
El = elephant, Wh = warthog, Hi = hippopotamus, Bb = bushbuck, Du = duiker sp., Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Hb = hartebeest, Or = oribi

in spite of the nutritious dry-season growth of perennial grasses (especially that of *Andropogon gayanus*).

Although monocotyledons always form a minor part of the diet of the bushbuck, their proportion increases in the dry season (Fig. 7.5) due to a higher intake of Cyperaceae leaves and sprouts which become available in the river bed during this season when the water level falls.

Monocotyledons form almost 100% of the diet of the warthog (Fig. 7.5) but this may be an overestimation to some extent. Traces of digging showed other food plants such as tubers and bulbs (e.g. tubers of *Cochlospermum tinctorum*) in the diet during the dry season. However, these foods are not detected in faecal analysis because only fragments of epidermis and cuticle from the leaves and stems are examined.

A remarkable feature has been found in the diet of roan antelope: northern roan antelopes (i.e. north of Faliké) eat more woody foliage ('browse') during the dry season than those more to the south (Fig. 7.6). The percentage of monocotyledons in the diet of roan antelopes in the northern part of the biosphere reserve in the wet season differs significantly from that in the two other seasons (P = 0.05). This percentage also differs significantly (P = 0.05) between the northern and the southern subpopulations in both the early and the late dry

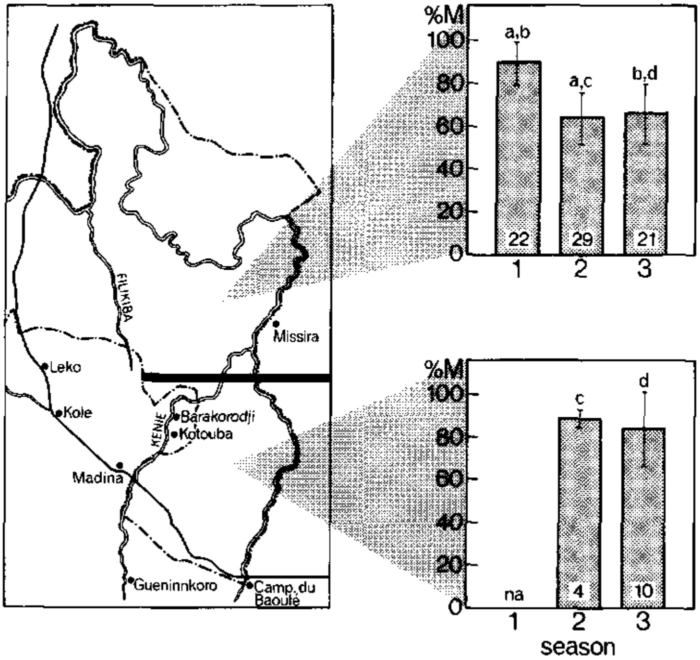


Fig. 7.6: Percentage of monocotyledons in the diet of roan antelope in the eastern part of the Baoulé based on faecal analysis. 1 = June-Sept; 2 = Oct-Jan; 3 = Feb-May; na = no data available; identical superscripts indicate significant difference between the two values concerned (Chi-squared test, P = 0.05)

season. These differences are related to differences in the availability of quality forage (see Chapter 8). No indications were found that this also occurs in other species.

Quantification of diet components was limited to the categories monocotyledons and dicotyledons (see 7.4.2). Faecal analysis is unlikely to give a true picture when the results are converted into a food intake ratio. Firstly, the percentage of monocotyledons may be slightly overestimated due to their higher surface/volume ratio (Anthony & Smith, 1974; Smith & Shandruck, 1979). Secondly, the percentage of dicotyledons might underrepresent the volume of woody plant intake: the quantification is only based on the analysis of epidermal and cuticular fragments of leaves and this does not take into account the parts of twigs that are eaten. These are found on the slide as totally unidentifiable fibrous material. Thirdly, differences in the digestibility of epidermal fragments of different plant parts affects the frequency of these fragments in the faeces (Van de Veen, 1979; Pulliam & Nelson, 1980; Putman, 1984).

These problems could be corrected for by establishing the relationships between ingesta and egesta in feeding trials with captive animals (Putman, 1984). As such facilities were beyond our reach, alternative methods were looked into.

By shooting animals and comparing the proportion of monocotyledons in the rumen and faeces, one could try to establish a correction factor. This method

Plate 13. Warthog feeds predominantly on grasses

assumes that the ruminal content (especially the larger fraction > 1 mm) correctly represents the food consumed. Only freshly ingested particles should be considered, in order to limit the risk of misinterpretation due to differential rates of digestion (Van de Veen, 1979). As in this study we only shot a few individuals of two species, we were unable to assess this correction method although our data (Table 7.15) suggest no great differences between ruminal and faecal contents with respect to the percentage of monocotyledons.

Table 7.15. Percentage of monocotyledons in rumen content and faeces of bushbuck and roan antelope (dry-season data).

	monocotyledons (%)	
	faeces[1])	rumen[2])
roan antelope	66% (s.d. = 13.9, n = 21)	59% (s.d. = 5.0, n = 2)
bushbuck	8% (s.d. = 8.4, n = 18)	2% (s.d. = 1.9, n = 6)

[1]): % of total cuticular area
[2]): % of total volume

Putman (1984) suggested using the digestibility of plant species to obtain a correction factor. He multiplied the number of faecal fragments of a particular plant species by 1/(1-digestibility) to obtain a figure representing its intake. This way of correction does in general increase the proportion of those plant species with high(er) digestibilities, unless their proportion in the faeces is very small. It can only be reliable if the plant species composition of the faeces is known quantitatively and the digestibility of all plant species known as well. As neither was known in our study we could not apply this correction method.

Because we had insufficient information to use a correction factor, we have used faecal analysis to get an impression of the diet composition and assumed it to be realistic.

Our results show that reedbuck, waterbuck, hartebeest, oribi and warthog in the Baoulé feed predominantly on monocotyledons throughout the year preferring short green grasses. Bushbuck and the two species of duiker select predominantly woody foliage and fruits. Roan antelope seems to hold the intermediate position of a mixed feeder preferring grasses in the wet season and shifting to a diet containing more woody foliage as the dry season advances. This shift is especially noticeable in the north of the Baoulé where perennial grasses produce scarcely any dry-season growth (Chapter 6). Although there is little quantitative data on the diet of elephant from faecal analysis, field observations of feeding traces suggest that elephant is a mixed feeder too.

The sole presence of epidermal fragments and cuticles of grasses in the few faecal samples we collected, confirms our observations in the field that hippopotamus in the Baoulé prefers grasses.

7.4.4. Comparison with other West African areas

Qualitative information on the diet composition of ungulates in several areas in West Africa is available in Geerling (1973, 1979, 1983), Child (1974), Afolayan (1975), FAO (1975, 1977, 1981), Heisterberg (1975), Bosch (1976), Milligan (1978), Wanzie (1978), Esser & Van Lavieren (1979), Okula & Sisé (1986) and Stark (1986a).

For practical reasons the information has been summarized as preferences for monocotyledons and dicotyledons in Table 7.16.

With regard to the choice of monocotyledons and dicotyledons, the preference of ungulates elsewhere in West Africa resembles that in our study area and thus the food choice of ungulates is very similar throughout the Sudan savanna.

The shift to woody foliage by the roan antelope during the dry season in the Baoulé has also been observed by Child (1974), Milligan (1978) and Geerling (1979) in the Sudan savanna of Nigeria (Table 7.17) and at the Nazinga Game Ranch in Burkina Faso (Fig. 7.7). Change in diet composition appears to follow changes in the development of the perennial grasses (see Figs. 6.3 and 6.9).

Poché (1974a) observed roan antelope in 'W' national park in Niger and found that their diet consists predominantly of grasses, 85% of all feeding records (n = 748) between 1970 and 1972. However, in the late dry season, from March to May, it ate considerably more browse, 27% of the feeding observations

Table 7.16. Summary of the preferences of ungulates for monocotyledons and dicotyledons in various areas in the West African savanna.

animal species	plant category monocotyledons	 dicotyledons	remarks	ref[1])
elephant	*	*	shifts to browse in dry season	1,3,4,6,7,8
warthog	*		tubers, etc, in dry season	1,2,4,6
hippopotamus	*		–	1,4,6
giraffe		*	–	1,3,6,7
buffalo	*	(*)	eats some browse in dry season	2,4,6,9
bushbuck	(*)	*	eats some regrowth of perennial grasses and some sedges	1,5,6
red-flanked duiker	(*)	*	–	1,4,6
Grimm's duiker		*	–	1,4,6
reedbuck	*	(*)	some browse in dry season only	1,4,6
waterbuck	*		–	1,6
roan antelope	*	*	proportion of browse in diet increases in dry season	1,2,3,4,5,6
hartebeest	*		–	1,2,4,5,6
oribi	*	*	see under roan antelope	1,4,5,6

[1]) 1 = Child (1974) 2 = FAO (1975) 3 = FAO (1977) 4 = FAO (1981) 5 = Heisterberg (1975) 6 = Bosch (1976) 7 = Esser & Van Lavieren (1979) 8 = Okula & Sisé (1986) 9 = Stark (1986a)

(n = 316), a figure comparable to those found for the Nazinga Game Ranch and the northern Baoulé (Fig. 7.7).

Contrary to our findings in the Baoulé, oribi in the Lake Kainji national park seem to prefer browse as a source of food (Child, 1974).

Table 7.17. The proportion of monocotyledons (% of total number of epidermal fragments) in the faeces of roan antelope and hartebeest, Lake Kainji national park (Nigeria) (Geerling, 1979).

month	percentage monocotyledons roan antelope	 hartebeest
December	89 (n = 10)	98* (n = 10)
January	73 ,,	77 ,,
February	87 ,,	91* ,,
March	58 ,,	79* ,,
May	96 ,,	99* ,,
June	99 ,,	100 ,,

* = significant difference between both animal species (Chi-squared test, P = 0.05)

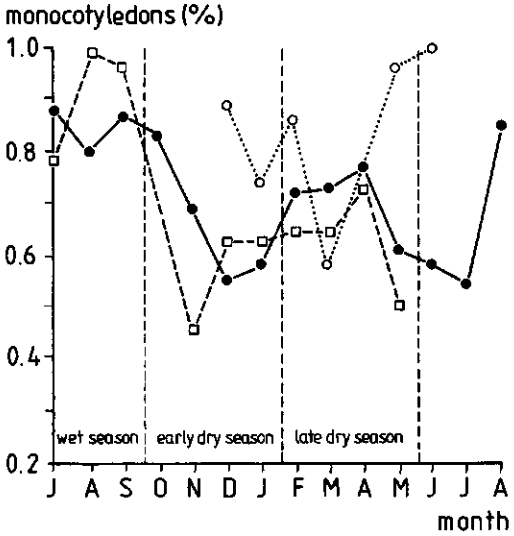


Fig. 7.7. Proportion of monocotyledons in the diet of roan antelope, based on faecal analysis

------- = Nazinga Game Ranch, Burkina Faso

– – – – = northern Baoulé

.... = Lake Kainji national park, Nigeria (from Table 7.17)

In the Yankari game reserve in Nigeria the diet of the larger herbivores is characterized by the large variety of plant species (FAO, 1975). Quantitative information is only available on the woody plant species browsed by the elephant during the dry season (Geerling, unpubl. data 1983). Of the 81 shrubs and trees examined (n = 4,082), only 29 species (19.4%) were utilized, with leaves, branches and/or bark eaten. Of only two species more than 50% of the individual shrubs and trees showed signs of elephant damage (Table 7.18).

Apart from the elephant, bushbuck and Grimm's duiker, all other species in this game reserve prefer grasses, both perennial and annual (FAO, 1975). There are, however, some differences with respect to the *structure* of the grasses they prefer (see Table 7.19). Hippopotamus, warthog and oribi prefer short green grasses. Besides these short grasses, waterbuck, hartebeest and roan antelope also eat parts of tall dry grasses (up to 3 m). Nearly all species graze on the dry-season growth of perennial grasses just as they do in the Baoulé.

In Bouba Ndjidah national park in Cameroon, elephant, roan antelope and oribi select a diet of grasses, sedges and woody foliage (Bosch, 1976) but as quantitative data are lacking no conclusion can be drawn concerning the exact proportion of woody foliage in their diet. The giraffe, bushbuck, Grimm's duiker and red-flanked duiker are typical 'browse' selecting species. The bushbuck and red-flanked duiker also eat fresh sprouts of the dry-season growth of perennial grasses (Bosch, 1976) and bushbuck search for sedges in the river bed during the dry season.

Hartebeest, waterbuck, warthog and hippopotamus mainly eat grasses.

Table 7.18. Utilization of woody plant species by elephant in the dry season, Yankari game reserve (Nigeria) (Geerling, unpubl. data 1983).

plant species	%	n	plant species	%	n
Mimosa pigra	72.6	146	Mitragyna inermis	18.8	64
Balanites aegyptiaca	60.3	78	Crossopterix febrifuga	15.4	39
Morelia senegalensis	45.0	20	Combretum molle	15.2	33
Combretum fragrans	30.8	26	Combretum glutinosum	15.0	254
Dichrostachys cinerea	30.8	91	Pteleopsis habeensis	10.0	30
Grewia spp.	30.8	39	Tamarindus indicus	9.3	43
Borassus aethiopum	29.7	239	Catunaregam nilotica	8.7	46
Acacia ataxacantha	29.6	307	Maytenus senegalensis	8.3	36
Ximenia americana	28.1	32	Guiera senegalensis	7.7	39
Acacia polyacantha	27.9	43	Boscia senegalensis	7.5	80
Vitellaria paradoxa	23.8	21	Securinega virosa	7.3	41
Detarium microcarpum	23.5	34	Combretum nigricans	5.8	865
Hymenocardia acida	23.2	56	Hexalobus monopetalus	2.8	36
Terminalia laxiflora	21.5	186	Antidesma venosum	1.7	59
Anogeissus leiocarpus	20.7	150			

Table 7.19. The preference of larger herbivores for different grass strata, Yankari game reserve (Nigeria) (adapted from FAO, 1975).

	animal species					
grass strata	Hi	Wh	Wb	Hb	Ro	Or1)
short green grass2)	+	+	+	+	+	+
tall dry grass			+	+	+	
regrowth perennial grass		+	+	+	+	
rhizomes perennial grass		+				

1) Hi = hippopotamus, Wh = warthog, Wb = waterbuck, Hb = hartebeest, Ro = roan antelope, Or = oribi

2) annual and perennial grasses unless stated otherwise

7.4.5. Discussion

With our data we are able to classify the animal species into the three commonly used categories of feeding habits, grazers, mixed feeders and browsers (Table 7.20). This facilitates the prediction of animal stocking rates from the phytomass production (Chapter 6).

According to this classification more species prefer monocotylenous plants to woody foliage. The elephant is a species with a typical mixed diet in which the dominant plants vary with the season.

From our field data and the literature, seasonality becomes a factor in the classification of both roan antelope and oribi. The shift they show in preference to woody foliage during the dry season can be considerable. According to their diet, in no part of their distribution area should these species be classified as pure grazers: mixed-feeding herbivores is more appropriate.

Table 7.20. Classification of ungulates in the Baoulé according to their diet composition.

grazers	*mixed-feeders*	*browsers*
Warthog	Elephant	Giraffe
Hippopotamus		Bushbuck
Reedbuck		Red-flanked duiker
		Grimm's duiker
Waterbuck		
______ Roan antelope ______		
Hartebeest		
______ Oribi ______		

______ : shifting seasonally

Plate 14. As the giraffe selects a diet of leaves and fruits of shrubs and trees, this species is classified as a browser

In the Baoulé as elsewhere in the West African savanna, ungulates face the problem of changing quantities of food.

We have shown that the development of the phytomass (Chapter 6) means that all species meet with a fall in the availability of food during the dry season.

If we consider only green leaves of grasses to be proper food for grazers, with regard to the quantity of forage these animals meet relatively fewer differences between seasons but more between rainfall zones. This is in contrast with woody foliage, where differences in quantity are more evident between seasons than between rainfall-zones.

7.5. On energy and protein requirements

7.5.1. Introduction

In order to calculate the potential animal densities in the Baoulé, in addition to knowledge of the diet of an animal and the availability of various types of forage, we need to know the amount of forage required per unit time by each species. More precisely, we need the energy and nutrient requirements per unit time for each species or group of species, both of which depend on their body size (Kleiber, 1961; Moen, 1973; Van Soest, 1982; McDowell, 1985) and digestive capabilities (Van Soest, 1982; R.A. Prins, 1987).

As described in Chapter 6, forage is characterized by a small proportion of readily digestible nutrients, the cell content, and a high but varying proportion of cell-wall components. All herbivores lack enzymes capable of degrading cellulose, hemicellulose and lignin, having failed to evolve mechanisms to extract energy directly from them (Van Soest, 1982).

Herbivores use the energy and nutrients fixed by plants in two ways: 1) by only using the cellular content of the plant parts consumed, neglecting the plant cell wall, and 2) by acting as a host to bacteria and fungi, which are able to break down these substances, in their gastro-intestinal tract. In all ungulate herbivores the second adaptation is found.

Microbial populations degrade cellulose, hemicellulose and pectins as well as the cell content to meet their own energy requirements; (part of) the micro-organisms and their waste products are a source of energy and nutrients to the herbivore (Van Soest, 1982). To enable micro-organisms to extract the available energy, the retention of these fibrous cell-wall components is an important condition to this adaptation, met by the development of a subdivided stomach in the true ruminants (*Ruminantia* and *Tylopoda*) and convergently developed non-ruminating species (e.g. *Hippopotamidae*) (Hofmann, 1973, 1982; Foose, 1982; Van Soest, 1982). In other non-ruminants (e.g. elephants *Perissodactyla*) retention of food occurs in folds of the intestinal tract: the large intestine and caecum.

In ruminants and other herbivores with forestomach fermentation (such as the hippopotamus) the food, once ingested, enters the rumen where it is attacked by the microbes. By fermentation, microbes transform a large part of the food into microbial cells and waste-products, mainly volatile fatty acids (VFA) and methane. Directly absorbed through the rumen wall, these VFA's are essential for the host, serving as a source of energy for biochemical processes. The rate of fermentation and food passage is high in the rumen of ruminants that select woody foliage but lower in the rumen of real grazers (Hoppe, 1984; Hoppe et al., 1977). Food particles unaffected by microbial fermentation in the rumen, together with part of the microbial cells pass through the gastro-intestinal tract where they undergo normal monogastric digestion (R.A. Prins, 1987). Undigested food particles leave the body as faeces.

The rumen 'ecosystem' is characterized by the absence of oxygen, a constant temperature of about 39 °C and a pH that varies between 6 and 7; this basic scheme is found in all ruminants, irrespective of their diet. (More detailed information on rumen physiology is found in the extensive studies by Hungate (1966,1975), Hofmann (1973) and Van Soest (1982)).

In non-ruminating hindgut-fermenters such as the elephant, comparable processes of fermentation are found in the colon and to some extent in the caecum. Normal enzymatic digestion occurs in the stomach and if microbes do occur in the stomach, they compete rather than cooperate with the host for the available energy and nutrients (Van Soest, 1982; R.A. Prins, 1987).

In ungulates, forage is thus partly digested in the digestive system, and partly excreted as faeces. The digestibility varies between animal species, depending on the chemical composition and structure of the forage and the digestive ability of the animal. A relatively constant proportion of the digestible energy (= DE) leaves the animal as urine and methane. What is left, the metabolizable energy (= ME), is used for maintenance, growth, work, reproduction and lactation. Thus in order to calculate the gross energy consumption necessary for maintenance, these requirements have to be corrected for the conversions from gross to digestible energy and from digestible to metabolizable energy. According to Moen (1973), ME is 82% of DE. Although generally considered as a constant, the proportion of DE available as ME depends on the nutritional quality of the forage. Furthermore, one needs to know the digestive ability of animal species before one can calculate the required intake of gross energy from the digestible energy.

7.5.2. Specific methods used to assess a species' digestive ability

When studying wild ungulates it is difficult to assess their digestive abilities by measuring their food intake and faeces production quantitatively. In this study we were unable to collect direct evidence either from feeding trials or by using external markers or indigestible internal indicators (see Van Soest, 1982).

Using the methodology of R.A. Prins et al. (1980), we estimated the in-vivo digestibility of dietary cell-wall components:

$$X = \frac{100(b\text{-}a)}{b} \quad \text{(R.A. Prins et al., 1980)}$$

where:

X = fraction of digested dietary NDR

a = fraction of indigestible dietary NDR
b = fraction of indigestible faecal NDR

Values for b were obtained as follows. Air-dried droppings were fragmented by hand to remove any seeds present in the faeces. 1 g was treated in the same way as the botanical samples (see Chapter 5) to determine the total fraction of faecal cell-wall components (NDR). Another 500 mg was incubated with rumen inoculum from domestic cattle for 96 hours, using standard procedures (Chapter 5). Afterwards we determined the fraction of the remaining indigestible fibre in a similar way as the total fraction of NDR in the non-incubated part of the faeces. We assumed that the incubation time was sufficient to achieve maximum digestion of the fibre. We expressed b as the fraction of total faecal NDR.

Tests revealed that the in-vitro digestibility of NDR in food plants measured after 48 hours incubation with rumen inoculum from cattle (Chapter 5) gives a good indication of the fraction of fibre that is potentially indigestible, see Fig. 7.8.

Therefore the values of NDR-digestibility after 48 hrs have been used to calculate values of a, using the data from 6.4 and 7.4, and the formulas:

$$a = 100 - V_{\text{dietary NDR}}$$

$$V_{\text{dietary NDR}} = [(IV_M x \%M) + (IV_D x \%D)]$$

where:
V = digestibility
IV = in-vitro digestibility of NDR after 48 hours
M = monocotyledons in the diet
D = dicotyledons in the diet

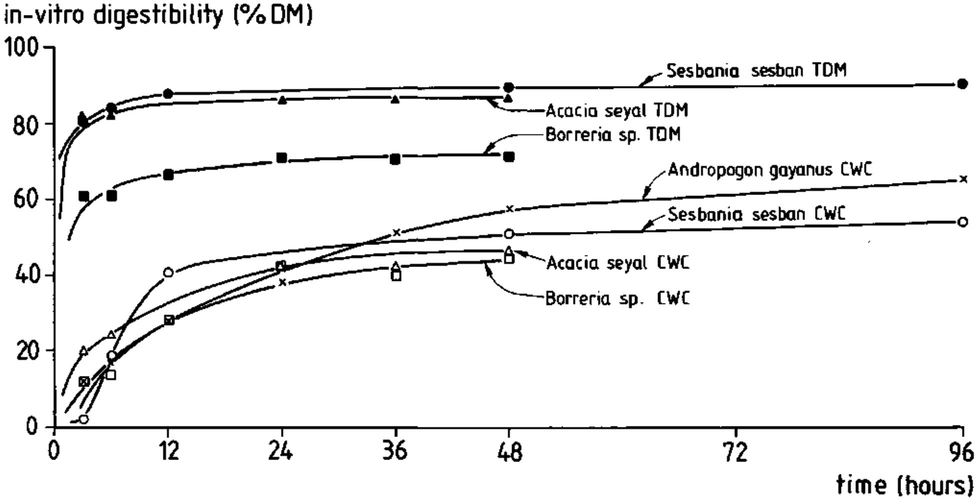


Fig. 7.8. In-vitro digestibility of NDR (% of total dry matter) of some plant species in relation to the length of incubation. TDM = total dry matter, CWC = cell-wall components

Digestive efficiency of total dietary material (DDM) has been calculated from the equation:

$$DDM = [(\%\ NDR_{diet} \times X) + (\%CC \times D_{CC})]$$

where:

CC = cell content

D_{CC} = digestibility of the cell content, assumed to be 100% (Van Soest, 1982)

7.5.3. Body size and energy requirements

In size, animal species in the Baoulé differ considerably, ranging from the duikers to the elephant. Larger species need less energy per kg body weight than smaller species (Van Soest, 1982). Hence live body weight is not a suitable measure for comparing the energy requirements of species. Instead the metabolic body weight, i.e. $W^{0.75}$ (W = live body weight) is used, as the energy requirements per unit metabolic body weight are equal for all mammalian species (Kleiber, 1961).

The different categories of feeders, the grazers, browsers and mixed feeders, are more or less evenly distributed over the metabolic weight classes (Fig. 7.9).

The relationship between body size (W, Kg) and the energy requirements for basal metabolism (NE, KJoules per day) can be expressed as $NE = 293 \times W^{0.75}$ (Kleiber, 1961). In free-living ungulates the actual costs for maintenance, the metabolizable energy requirements (= MEr, which is equal to the energy required for basal metabolism and unavoidable activities) demands about twice this amount of energy (Moen, 1973; Van Soest, 1982). Using this equation, Table 7.21 shows the relationship between body size and metabolizable energy requirements.

In order to calculate the gross energy consumption, needed to meet the metabolizable energy requirements (MEr), these requirements have to be corrected for the conversions from metabolizable to digestible energy (DE) and from digestible to gross energy.

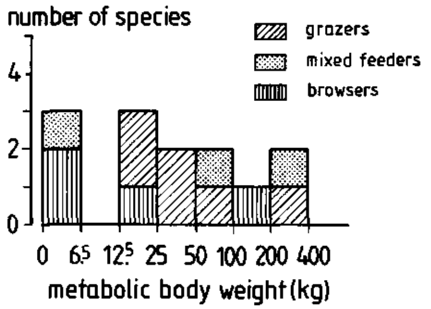


Fig. 7.9. The number of ungulate species in each feeding-style category per metabolic weight class.

Table 7.21. Metabolizable (MEr) and digestible (DEr) energy requirements for maintenance (MJ.day^{-1}) of ungulate species in the Baoulé.

	body weight (kg)[1]	metabolizable energy		digestible energy
		MJ/day	kJ/kg/day	MJ/day
grazers:				
hippopotamus	1400	134.1	95.8	163.6
buffalo	450	57.3	127.2	69.8
waterbuck	125	21.9	175.3	26.7
hartebeest	110	19.9	181.0	24.3
warthog	65	13.4	206.4	16.4
reedbuck	35	8.4	241.0	10.3
browsers:				
giraffe	1000	104.2	104.2	127.1
bushbuck	30	7.5	250.4	9.2
red-flanked duiker	11	3.5	321.8	4.3
Grimm's duiker	11	3.5	321.8	4.3
mixed feeders:				
elephant	1725	156.9	90.9	191.3
roan antelope	185	29.4	158.9	35.9
oribi	10	3.3	329.6	4.0

[1]) data on population mean body weight after De Bie & Kessler (1983) and Jachmann (1987a)

When ME is taken as 82% of DE, this factor tends to underestimate ME, especially in more digestible forages (Van Soest, 1982), but as it is widely used, we adhere to it. Table 7.21 presents the digestible energy required per species per day.

The duikers require about 3.5 times more metabolizable energy per kg of body weight than the elephant that is 160 times heavier, showing that larger ungulates can survive on a diet containing less energy per kilogram than smaller species (see Demment & Van Soest, 1985 for a more detailed discussion). Consequently both in general and within each feeding type (Table 7.21) smaller species have to feed more selectively than larger species.

7.5.4. Gross energy requirements

Efficiency of cell-wall digestion

Grazers are more capable of digesting cell-wall components than animals in the other feeding-style categories. Therefore, it was initially assumed that this efficiency would be reflected in a larger proportion of indigestible fibre (NDR) in the faeces after incubating with rumen micro-organisms for 96 hrs: the proportion of indigestible faecal NDR was thought to be an indication of the species' efficiency of cell-wall digestion. However, although the results show a difference between ruminants and non-ruminants, the fraction of indigestible faecal NDR in all ruminants is about 70-75% (Table 7.22) and does not vary significantly

Table 7.22. Fraction of indigestible faecal NDR (= b, expressed as a percentage of NDR before incubation, see 7.5.2).

species		indigestible faecal NDR mean	(range)	s.d.	n
ruminants:					
browsers:	bushbuck	75.8	(63.9-82.0)	5.1	14
	duiker	77.1	(66.5-82.3)	7.1	5
grazers:	waterbuck	70.3	(62.2-80.6)	5.6	15
	hartebeest	75.3	(60.1-84.5)	6.9	10
	reedbuck	72.9	(60.6-80.4)	5.4	13
mixed feeders:	roan antelope N	74.9	(60.3-84.7)	7.8	20
	roan antelope S	75.7	(68.0-80.8)	5.3	7
	oribi	72.0	(67.7-78.6)	4.1	5
non-ruminants:					
grazers:	hippopotamus	56.7	(50.8-62.3)	4.9	4
	warthog	65.0	(56.1-72.8)	5.8	6

between species. Northern and southern roan antelope have been treated separately as these subpopulations differ with respect to the percentage of monocotyledons in their diet (see 7.4).

The *in-vivo* digestibility of cell-wall components in the diet was therefore estimated by comparing the fractions of indigestible NDR in the food and faeces (see 7.5.2). Results, presented in Table 7.23 show that the grazers waterbuck, reedbuck and hartebeest have comparable and relatively high efficiencies of NDR-digestion.

Digestibility of NDR in late dry season is lower than that in the early dry season,

Table 7.23. Estimated in-vivo digestibility of dietary cell-wall components (%DM).

species		in-vivo digestibility of NDR (%DM) wet season	n	early dry season	n	late dry season	n
ruminants:							
browsers:	bushbuck	–		25.2	7	37.3	6
	duiker	–		–		0.2	4
grazers:	waterbuck	–		52.3	5	42.8	8
	hartebeest	–		55.7	5	47.2	5
	reedbuck	50.3	4	–		44.6	8
mixed feeders:	roan antelope N	43.5	5	36.1	7	33.3	8
	roan antelope S	–		51.8	2	43.3	5
	oribi	–		51.9	3	33.4	2
non-ruminants:							
grazers:	hippopotamus	–		14.7	3	–	
	warthog	–		25.6	3	26.4	3

but as the proportion of food plants rich in cellular content in the diet does not differ significantly between both seasons (7.4), these lower values are probably due to the increased indigestibility of the food as a whole (see 6.4).

To maintain a certain efficiency of fibre digestion when the digestibility of the fibre decreases, one should theoretically expect the retention of the ingested food in the rumen to be extended (Fig. 7.10, Van Soest, 1982) and this is what indeed actually happens in ruminants (Hoppe, 1984). However, food cannot be retained too long because of the risk of starvation through constipation. Thus less complete digestion of fibre is tolerated, as the values in Table 7.22 suggest.

The increased efficiency of NDR-digestion of the bushbuck in the late dry season is probably due to the higher intake of monocotyledons, especially the relatively more digestible leaves of *Cyperus* species (7.4).

Most interesting however, are the results found for the roan antelope and oribi. Roan antelope in the southern part of the study area show an efficiency of NDR-digestion comparable to those of the three other grazing antelopes. Much lower values are shown by oribi in the late dry season and northern roan

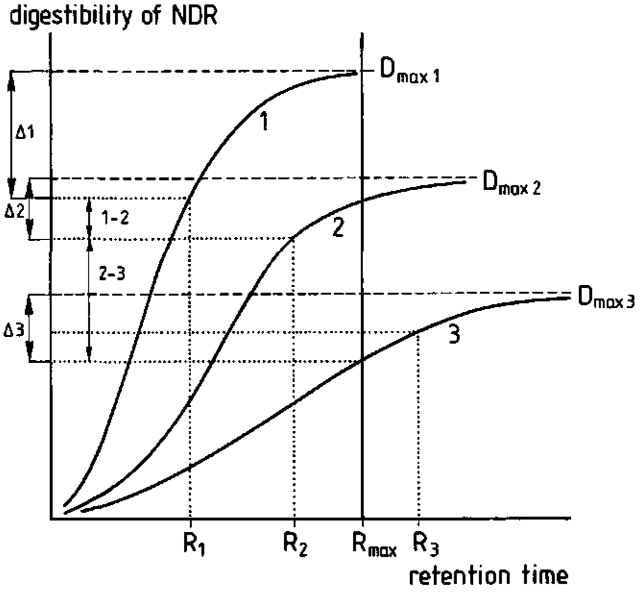


Fig. 7.10. Theoretical relationship between retention time in the rumen and digestibility of NDR of three plant growth stages; 1 = young, 2 = mature and 3 = old plants

R1, R2 : actual retention time of growth stages 1 and 2

R3 : retention time required for growth stage 3 to reach the same (relative) level of NDR digestibility as stage 2

R_{max} : maximum possible retention time

D_{max} : potential digestibility of growth stages 1, 2 and 3

Δ : difference between actual and potential NDR digestibility of growth stages 1, 2 and 3

1-2, 2-3 : difference between actual NDR digestibility of stages 1 and 2, and 2 and 3

(Based on Van Soest, 1982)

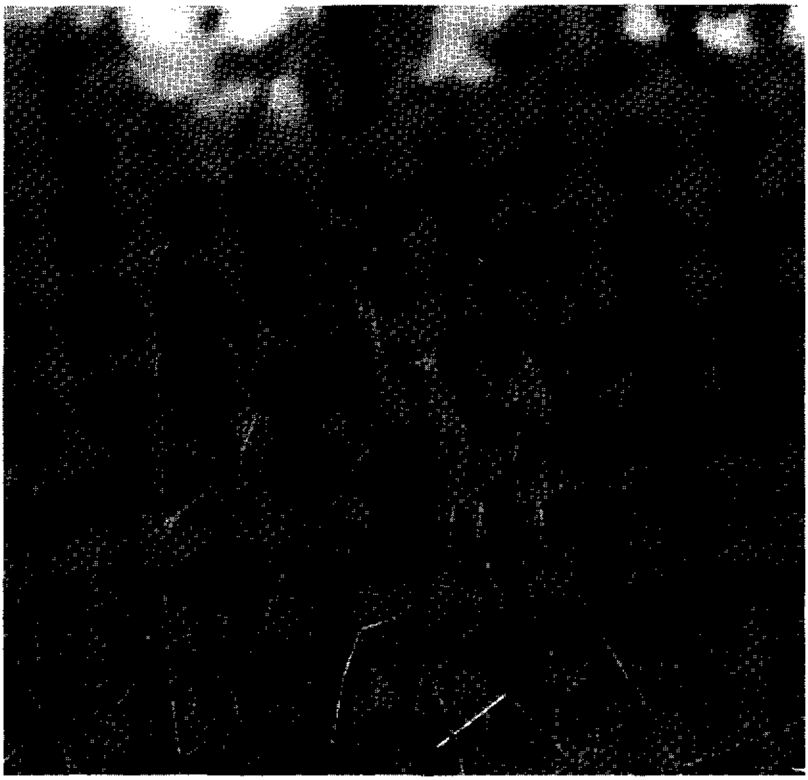


Plate 15. During the dry season the oribi feeds increasingly on woody foliage

antelope in the early and late dry seasons, suggesting a change to a more concentrated diet.

The results show that the hippopotamus and warthog, the non-ruminant grazers, have very low capability for digesting cell-wall components (Table 7.23), which is confirmed by the presence of large, undigested fragments of grasses in the faeces of these two species (see Table 7.11), thus showing the advantage of combining rumination with food retention.

Digestion of total dietary dry matter

We can compare the digestive efficiencies of species by converting the data in Table 7.23 into values for the efficiency of total dietary dry matter digestion (see 7.5.2) (Table 7.24).

There appears to be no pattern in the digestive efficiencies of the different ungulates in relation to their body weight or feeding style. In general, late dry-season values are lower due to an increased indigestibility of dietary cell-wall material at that time. Except for the duiker, hippopotamus and warthog, all species, no matter what their diet composition, maintain more or less compara-

Table 7.24. Efficiency of dietary digestion (%) of several ungulates in the Baoulé.

species		digestion of dietary dry matter (%)		
		wet season	early dry season	late dry season
ruminants:				
browsers:	bushbuck	–	73	76
	duiker	–	–	44
grazers:	waterbuck	–	67	54
	hartebeest	–	70	63
	reedbuck	63	–	64
mixed feeders:	roan antelope N	59	61	57
	roan antelope S	–	67	62
	oribi	–	57	52
non-ruminants:				
grazers:	hippopotamus	–	44	–
	warthog	–	52	49

ble digestion efficiencies.

The low digestive efficiency of the non-ruminating hippopotamus and warthog is explained by the absence of food retention.

The relatively low level of digestion of the almost exclusively browsing duiker may be attributed to the high levels of secondary plant components, mostly tannins, in the forage in the late dry season (Table 6.12). These compounds can inhibit digestion directly by forming complexes with plant protein (see Fig. 6.17 for the relationship between the percentage of tannins and the in-vitro digestibility in woody foliage). A quicker passage of food might reduce the effect of these components (Kay et al., 1979), but this would lower the already poor efficiency of cell-wall digestion in concentrate selectors. As the efficiency of cell-wall digestion in the duiker is zero (Table 7.23), such an increased rate of food passage is implied. It has been suggested that mammalian herbivores also reduce the effect of dietary tannins by producing proline-rich salivary proteins, which contain very low proportions of amino acids, nutritionally essential to the herbivore (Mole et al., 1988). The relatively large salivary glands found in African browsing ungulates such as the duiker (Hofmann, pers.comm.) suggest the presence of this mechanism as well.

We should emphasize that indirect methods were used for the assessment of digestive capabilities of animal species which could not be verified by more sophisticated experiments as feeding trials. Such data are not available from elsewhere in West Africa. However, our data (Table 7.24) can be compared with data (Table 7.25) compiled by Owen-Smith (1982a) for East and southern African ungulates and data from Foose's (1982) studies on zoo animals.

For all species except hippopotamus our values resemble those given by Foose (1982) and Owen-Smith (1982a). Differences should be attributed to the difference in method: captive animals versus animals in the wild. Furthermore, our

Table 7.25. Efficiency of digestion (%) of African ungulates given by Owen-Smith (1982a),a, and Foose (1982),b.

species	diet	DDM	DOM	DNDF[1]
hippopotamus, a	grass, 10% CP	68	–	–
hippopotamus, b	alfalfa hay	–	74	60
hippopotamus, b	grass hay	–	55	52
hartebeest, a	natural forage	62	–	–
waterbuck, b	alfalfa hay	–	68	54
waterbuck, b	grass hay	–	49	52
grimm's duiker, a	concentrate, 6-14% CP	62	–	–

[1] DDM = digestion of dry matter, DOM = digestion of organic matter, DNDF = digestion of cell-wall components (OM)

animals are subject to environmental stress caused by, for example, a shortage of drinking water and the risk of predation, which may affect the digestive performance. Higher digestive efficiency, more in line with values of other species but contradictory to our findings, have been found elsewhere for hippopotamus, suggesting that this non-ruminating species with its forestomach fermentation is as efficient as true ruminants in utilizing plant fibres (cf. Hoppe, 1984).

The data on the digestible energy required per day per species (Table 7.21) and the dry matter digestion efficiency (Table 7.24) enable us to estimate the gross energy intake required for maintenance of the various species (Table 7.26). The energy content of woody foliage and grasses is on average 18,187 $J.g^{-1}$ (DM) (s.d. = 1,071, n = 16). There is no significant difference between grasses and other plant categories. Therefore a value of 18,000 $J.g^{-1}$ (DM) has been used to estimate gross energy intake (I_1 in Table 7.26).

Table 7.26. Gross energy intake (I) required per day per animal species in the late dry season.
DEr : digestible energy requirements (from Table 7.21)
DDM : dry matter digestion efficiency (from Table 7.24)
I_1 : I, expressed as kg DM
I_2 : I, expressed as % of live body weight
I_3 : I, expressed as % of metabolic body weight ($W^{0.75}$)

species		DEr	DDM	I_1	I_2	I_3
ruminants:						
browsers:	bushbuck	9.2	76	0.7	2.3	5.5
	duiker	4.3	44	0.5	4.5	8.3
grazers:	waterbuck	26.7	54	2.7	2.2	7.2
	hartebeest	24.3	63	2.1	1.9	6.2
	reedbuck	10.3	64	0.9	2.6	6.3
mixed feeders:	roan antelope N	35.9	57	3.5	1.9	7.0
	roan antelope S	35.9	62	3.2	1.7	6.4
	oribi	4.0	52	0.4	4.0	7.1
non-ruminants:						
grazers:	hippopotamus	163.6	44	20.4	1.5	8.9
	warthog	16.4	49	1.8	2.8	7.9

For herbivores living in the Tsavo-ecosystem in Kenya, Van Wijngaarden (1985) proposed calculating the average food consumption (F, $kgDM.day^{-1}$) from the equation:

$F = 0.025 \times W$ (W = live body weight in kg).

The constant 0.025 is an average value, ranging from 0.039 in small-bodied herbivores to 0.022 in large ones such as elephant. When the gross energy intake (Table 7.26) is expressed in a comparable way, these values (I_2) also average at 2.5% (s.d. = 0.99) of the live body weight. However, this average value cannot be used satisfactorily in later calculations in this study (Chapter 9), because it overestimates daily food consumption in large herbivores and underestimates it in small ones.

In his study on the limiting effects of primary production on the herbivore density, Sinclair (1975) estimated daily food consumption of ungulates as 9% of their metabolic body weight ($W^{0.75}$, W = population mean body weight). H.H.T. Prins (1987), studying the ecology of African buffalo in Lake Manyara national park in Tanzania, derived the following estimation for dry matter intake per day for this species:

$F = 0.0635 \times W^{0.75}$

The results of our study, when expressed in a comparable manner (I_3), averaged at 7.1% of $W^{0.75}$ (s.d. = 1.05). The estimations of Sinclair (1975) and H.H.T. Prins (1987) differ considerably from Van Wijngaarden's (1985) in cases where daily food consumption is estimated for animals with higher body weights of 500 kg or more. The use of an average value of 2.5% of live body weight (kg) in the Van Wijngaarden's (1985) method results in an overestimation of intake for these heavier animals. Differences are strongly reduced when species- specific values of the coefficient are used.

In our calculations of potential stocking rates (Chapter 9) we kept to our result of the coefficient of 7.1% of metabolic body weight to estimate the daily gross energy consumption in the late dry season as it agreed quite well with that of Sinclair (1975) and H.H.T. Prins (1987).

7.5.5. Protein requirements

Not all the crude protein (CP) of plants is available to the herbivore, a certain proportion escapes digestion (Van Soest, 1982). According to H.H.T. Prins (1987) protein requirements ($g.day^{-1}$) can be calculated as:

$DP = 3.150 \times W^{0.75}$ for ruminant herbivores
$DP = 2.800 \times W^{0.75}$ for non-ruminant herbivores

in which DP stands for digestible protein, the proportion of plant protein available to the animal. According to Stobbs & Minson (1980) digestible protein can be derived for tropical grasses and legumes from the equation:

$DP = 0.90\,CP - 3.25$.

From this equation it appears that roughage should contain at least 0.6% nitrogen in order to supply the grazing herbivore with protein.

According to Crampton & Harris (1969) and elaborated by H.H.T. Prins (1987), the general relationship between DP and CP is:

$DP(\%) = 0.54 \times CP(\%)$ for roughage
$DP(\%) = 0.79 \times CP(\%)$ for concentrate forage

By combining the two sets of equations, one is able to assess the plant protein required (CP, $g.day^{-1}$) for each category of herbivore as:

roughage – ruminant : $CP = 5.83 \times W^{0.75}$
– non-ruminant : $CP = 5.19 \times W^{0.75}$
concentrate forage – ruminant : $CP = 3.99 \times W^{0.75}$
– non-ruminant : $CP = 3.54 \times W^{0.75}$

Thus to maintain their body weight grazers need more crude protein per day than browsers, and ruminants more than non-ruminants. As energy requirements are also correlated with the metabolic weight (see 7.5.4), the concentration of plant protein necessary for a balanced diet varies accordingly, from 8.2% and 7.3% for grazers to 5.6% and 5.0% for browsers, for ruminants and non-ruminants respectively. Both energy and protein requirements are correlated to the metabolic weight of animal species. Consequently, the plant protein concentrations for a balanced diet within a feeding style category are independent of body size!

7.6. Discussion: food supply versus requirements

From our estimations of the daily requirements of gross energy and protein we have assessed a balanced diet for each category of animal species although species seldom meet with circumstances in which the food supply completely matches this balanced diet. In Chapter 6 we have shown that the quantity and quality of the vegetation in the Sudan savanna shift with the seasons. Whereas the forage on offer in the wet season is of relatively high quality, with protein concentrations higher than necessary for a balanced diet, the quality of the vegetation, especially that of grasses, decreases during the dry season.

Fig. 7.11 compares the crude protein content of several grass species and phenological groups of woody plants in the different seasons with the crude protein required for a balanced diet in the different categories of ungulates.

In the early dry season the crude protein content of savanna grasses falls below the concentration required for a balanced diet of both ruminant and non-ruminant grazers but that of the riverine species *Panicum* and *Cyperus* remains adequate. Protein concentrations in woody foliage remain well above the required level for browsers.

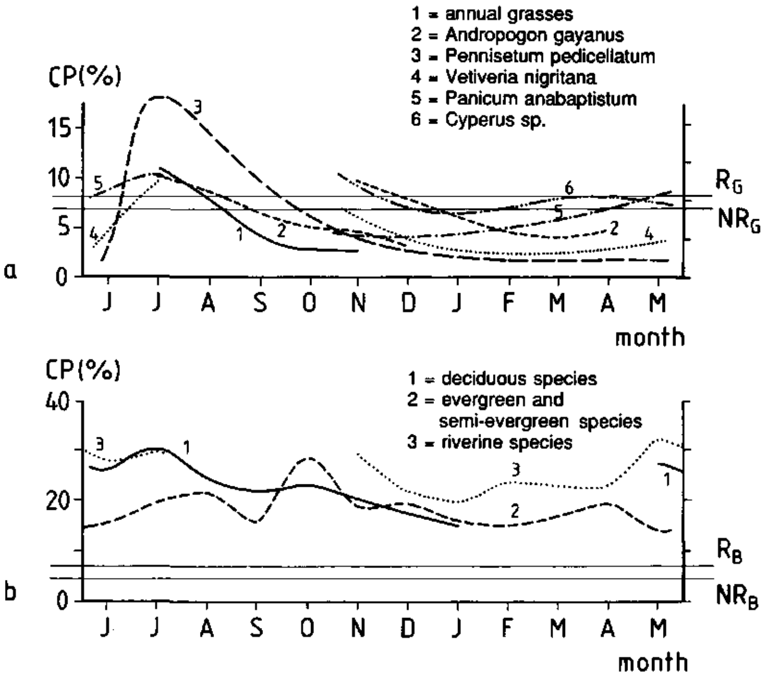


Fig. 7.11. Crude protein concentration in grasses (a) and in woody foliage (b) compared with the concentration required for a balanced diet in different categories of ungulates
R = ruminant, NR = non-ruminant, G = grazer, B = browser

Grazing animals are able to cope with lower levels of crude protein concentration by increasing their daily intake of food to a level above the quantity needed for energy requirements for maintenance. However, crude protein levels affect the maximum voluntary intake (Crampton & Harris, 1969; Alexander & Williams, 1973; Van Soest, 1982; Ketelaars, 1984), especially at concentrations below 8%: as there is insufficient nitrogen for microbial activity, digestive ability decreases. (Minson, 1981; Van Soest, 1982). (Note the conformity of 8% CP for a balanced diet for grazing ruminants with this level of plant protein required for adequate microbial activity in the rumen). Hence there is a critical level of crude protein concentration in the food, below which the daily protein requirement for maintenance is not met.

Fig. 7.12 shows the relationship between gross energy intake and crude protein intake:

* X denotes a daily intake of food, balanced with respect to energy and crude protein; the absolute quantity is well above the quantity required for maintenance allowing the herbivore to grow and to reproduce.

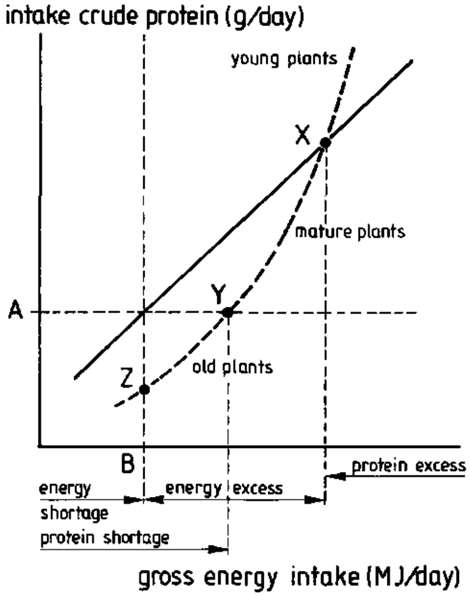


Fig. 7.12. Schematic representation of the relationship between crude protein intake (CP, g.day^{-1}) and gross energy intake (GI, MJ.day^{-1}) of a herbivore
A and B indicate the quantity of CP and GI required per day respectively
______ denotes the intake of a balanced diet
-------- denotes actual intake in relation to the energy and nitrogen content of the forage on offer
See text for further explanation

- Y indicates the point where intake meets the amount of crude protein required daily, below which protein deficiency occurs, but energy is still in excess of requirement.
- below Z the gross energy intake is also below the daily requirement.

H.H.T. Prins (1987) calculated that the minimum concentration of CP for maintenance is about 6% for the East African buffalo. As data are lacking for making these calculations for the ungulates of the Sudan savanna, we have adopted this value. It indicates that the ruminant and probably also the non-ruminant grazers face a *protein shortage* in the dry season, taking into account their relatively small body size and that most of the ungulates give birth to their calves in the dry season (see 7.7). Calving ushers in the lactation phase when energy demand doubles and protein requirement increases fivefold (Moen, 1973). This conclusion agrees with the assumption that generally protein is the limiting factor for ungulates in African ecosystems (Bell, 1971,1982; Sinclair, 1975). The limited availability of good quality forage (Chapter 6) allows only low numbers of grass-preferring ungulates to survive and demands selective feeding by these animals. Less selective species of comparable size such as wildebeest *Connochaetes taurinus* and zebra *Equus burchelli* are absent in the Sudan savanna but occur in the comparable woodland savanna of East and southern Africa (East, 1984). The greater homogeneity of the Sudan savanna may explain this absence.

In contrast to the grazers, browsers and elephants are apparently limited by the *quantity of food* available as the protein content never falls below the level of a balanced diet. Also Owen-Smith (1982b) concludes that energy rather than protein is the limiting factor for the browsing greater kudu *Tragelaphus strepsiceros.*

Species that mainly feed on the savanna grasses, i.e. warthog, hippopotamus, reedbuck, waterbuck, hartebeest, roan antelope and oribi, may thus be subject to both protein deficiency and a strong reduction in the availability of energy per unit area.

To cope with these problems various options are open such as:

* increase in selectivity, changing to other more nutritious plant parts (dry-season growth of perennial grasses);
* change of diet in favour of more nutritious plant species within the same plant community;
* moving to other plant communities within the same habitat or
* moving to other habitat types.

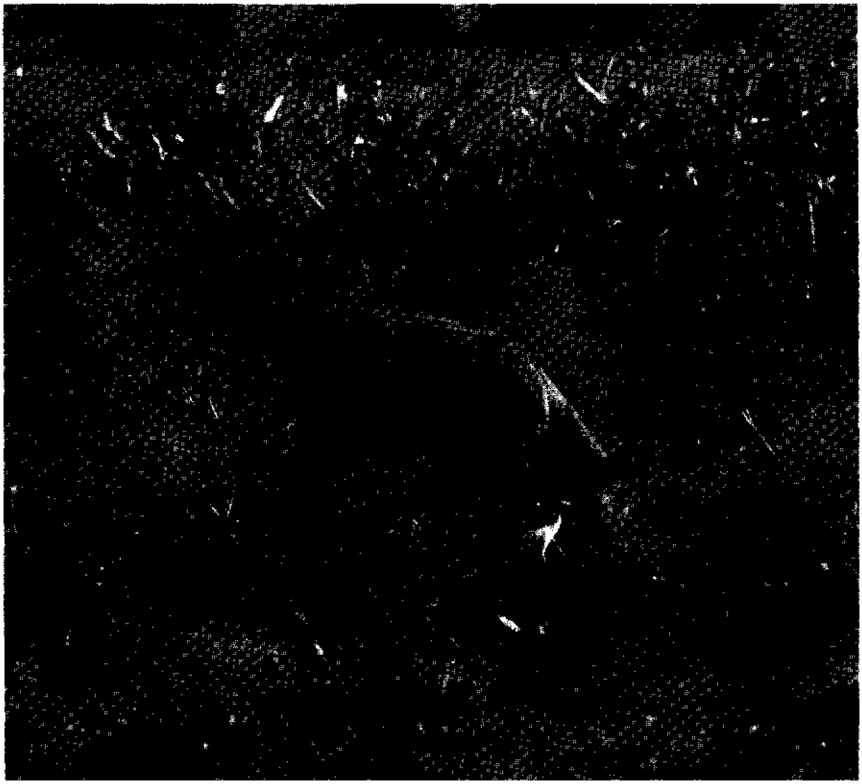


Plate 16. In the dry season the waterbuck visits the flood plain in search for fresh grasses

Waterbuck and reedbuck start to eat grasses and sedges in the river bed as soon as they become available to cope with the decrease in quality and quantity of the savanna grasses.

In the dry season the warthog eats bulbs, tubers and roots as well as riverine monocotyledons.

Hartebeest continues to feed predominantly on savanna grasses in the dry season, especially on the nutritious dry-season growth of perennial grasses, which sets a limit to its area of distribution (Chapter 8).

The roan antelope shows a high degree of adaptability to big changes in both forage quality and availability. This species, and to a lesser extent the oribi, is able to increase the proportion of woody plant leaves and twigs in the diet, if necessary.

The giraffe, the bushbuck and duikers, which feed on the more patchily distributed foliage of trees and shrubs, and fruits, are sure of forage of adequate quality. Although the availability of foliage phytomass is much less than that of monocotyledons and changes considerably over the year, it is more predictable in time and space (Owen-Smith, 1982a; Geerling & Diakité, 1988). Tannins and other comparable plant components can restrict the utilization of woody foliage and hence, these species need to select their food carefully. The elephant is much less affected by the fall in the quality of the savanna grasses. Like the hippopotamus this species is able to increase the rate of food passage to optimize

Plate 17. Roan antelope are adaptive feeders, varying their diet according to the seasons and the local conditions

the quantity of digestible plant nutrients (Van Soest, 1982). However, in the Baoulé in the dry season, these two species are probably also subjected to food shortage on the savanna, because of fires; the elephant strongly increases the proportion of woody plants in its diet, and the hippopotamus utilizes the patches of sedges and grasses in the river bed in addition to savanna grasses.

Thus when food quality drops below the level of a balanced diet, most animal species show an increase in selectivity combining it with either a change of habitat types (e.g. waterbuck and reedbuck) or a change of diet (e.g. warthog and roan antelope).

So far this chapter has concentrated on the energy and protein content of forage as limiting factors for the maintenance of animals. However, levels of nutrients other than nitrogen might well be deficient, especially minerals.

West African soils are low in phosphorus (Penning de Vries & Djitèye, 1982) and low phosphorus levels in the vegetation are commonly associated with them (Brinkman & De Leeuw, 1977; Penning de Vries & Djitèye, 1982). Phosphorus levels in plants generally decrease as the plant matures resulting in phosphorus deficiency in dry-season forage (Brinkman & De Leeuw, 1977, Table 7.27). The concentration of phosphorus in woody foliage is higher than that in grasses and generally sufficient to cover the maintenance requirements of cattle. Concentrations of calcium, potassium and magnesium are above those needed for maintenance (Table 7.27). Large populations of wild herbivores live in areas where phosphorus deficiency is so common that wild herbivores must either differ substantially from cattle with respect to their mineral requirements or be highly selective concerning habitats and forage in different seasons (McNaughton, 1987, 1988). Although there is selectivity with respect to habitat choice and diet composition (7.3, 7.4), this would probably not improve the intake of phosphorus to such a level that concentrations comparable to those required for cattle are met (Table 7.27). Probably the mineral requirements of wild African ungulates differ as well, but they have not yet been measured critically to make it possible to derive criteria for the minimum concentrations required. It should be realized that in ruminants the recycling of phosphorus is very efficient: about 80% of endogenous phosphorus entering the digestive system with saliva, is reabsorbed (Suttle, 1987) as phosphorus is essential for the functioning of nucleic acids.

Furthermore, there are large reserves of phosphorus, calcium and magnesium in well mineralized bone, which are mobilized in periods of deficiencies (Suttle, 1987). Hence to predict how much phosphorus a herbivore needs and the adequacy of forage in this respect, the measurement of phosphorus should be standardized. Moreover, the effects of forage intake on endogenous phosphorus should be looked at (see Suttle, 1987).

The optimum ratio Ca/P is between 1 and 2 and the values found exceed this this optimum, indicating a mineral imbalance. The deliberate consumption of soil by large herbivores is often thought to be a behaviour by which the animals concerned supplement their diet with nutrient minerals, or compensate

Plate 18. Soil consumption is a common feature of the feeding behaviour of roan antelope in the Baoulé

for mineral imbalances. This behaviour has been observed in several ungulate species in the Baoulé, such as roan antelope, bushbuck, elephant and reedbuck, and elsewhere in the Sudan savanna, e.g. in the Benoué national park (Stark, 1986b) and Yankari game reserve (Ayeni, 1977). Faecal pellets consisting entirely of soil have been found regularly. In their review on the ingestion of soil by large herbivores in arid rangelands, Kreulen & Jager (1984) concluded that the evidence for soils supplying nutrient minerals is meagre, except for sodium which appears to be a major attracting element in many soil licks, as is the case in the Baoulé and in the Benoué national park (Stark, 1986b). There is no information on the concentration of sodium in West African savanna plants but Stobbs & Minson (1980) mention sodium deficiency in this zone besides a deficiency of phosphorus, calcium, copper and molybdenum. The licks we found were very poor in phosphorus, and hence animals do not benefit from soil ingestion in this respect.

Is the phosphorus content of the forage then a limiting factor for the occurrence of wild herbivores? I have not considered phosphorus a factor to be taken into account in calculating the ecological carrying capacity for the following

Table 7.27. Calcium, phosphorus, magnesium and potassium content (% DM) in grasses and woody foliage in West Africa.

plant species	season	country	Ca	P	Mg	K	Ca/P	ref.
'grasses'	ws		0.34	0.22	0.23	2.56	1.55	Kapu, 1975
'grasses'	lds		0.22	0.03	0.11	0.37	7.33	id
annual grasses:								
Ctenium elegans	lds		0.26	0.04			6.50	LeHouérou, 1980b
Diheteropogon hagerupii	eds		0.34	0.03			11.30	id
Pennisetum pedicellatum	eds		0.17	0.04			4.20	id
Schoenefeldia gracilis	eds		0.22	0.03			7.30	id
	lds		0.19	0.03			6.30	id
perennial grasses:								
Echinochloa stagnina	lds		0.35	0.03			11.60	LeHouérou, 1980b
Hyperthelia dissoluta	eds		0.36	0.08			4.50	id
woody plants:								
Acacia ataxacantha	ds	Sen1)	0.50	0.16			3.13	LeHouérou, 1980b
Acacia seyal	ds	Sen	1.15	0.28			4.11	Billé, 1978
	eds	Sen	1.58	0.16	0.30	0.73	9.88	LeHouérou, 1980b
Acacia sieberana	ws	Sen	1.13	0.15	0.30	0.80	7.53	id
	eds	Sen	2.50	0.10	0.43	0.33	25.00	id
Balanites aegyptiaca	eds	Mal	0.86	0.03			28.67	Billé, 1978
	eds	Nig	3.90	0.10	0.80	1.50	39.00	LeHouérou, 1980b
Bauhinia rufescens	ws	BF	2.90	0.15	0.50	0.90	19.33	id
	lds	BF	3.30	0.24	0.40	0.80	13.75	id
Bombax costatum	ds	Sen	1.60	0.13			12.31	id
	ds	Sen	1.70	0.09			18.89	id
Boscia angustifolia	eds	BF	0.60	0.11	0.20	1.30	5.45	id
	ds	Sen	1.24	0.06			20.67	id
Cadaba farinosa	ds	Sen	1.66	0.07			23.71	Billé, 1978
	eds	BF	1.80	0.12	0.80	1.60	15.00	LeHouérou, 1980b

Combretum aculeatum	ws	BF	1.40	0.50	0.30	2.30	2.80	id
	eds	BF	2.80	0.12	0.30	0.50	23.33	id
Combretum micranthum	ds	BF	1.10	0.03	0.30	0.60	36.67	id
Dichrostachys cinerea	eds	BF	1.40	0.11	0.40	1.20	12.73	id
Feretia apodanthera	ds	Sen	1.05	0.07			15.00	Billé, 1978
	lds	BF	0.80	0.20	0.60	1.20	40.00	LeHouérou, 1980b
Grewia bicolor	eds	Sen	3.77	0.09	0.70	0.80	41.89	Billé, 1978
Guiera senegalensis	ws	BF	0.80	0.30	0.20	1.00	2.67	LeHouérou, 1980b
	eds	BF	1.60	0.20	0.40	0.80	8.00	id
Piliostigma reticulatum	ds	Sen	0.37	0.14			2.64	Billé, 1978
Pterocarpus erinaceus	ds	Sen	0.56	0.22	0.42	2.70	2.55	LeHouérou, 1980b
Pterocarpus lucens	ws	BF	0.90	0.20	0.40		4.50	id
	lds	Mal	1.50	0.08	0.50	0.80	18.75	id
	ds	Sen	1.47	0.08			18.38	Billé, 1978
Tamarindus indica	ws	Sen	3.30	0.04	0.45	0.50	82.50	LeHouérou, 1980b
	lds	Sen	2.12	0.10	0.56	0.80	21.20	id
Zizyphus mauritiana	ws	Mal	1.80	0.21	0.20	1.40	8.57	id
	eds	BF	2.30	0.13	0.40	1.00	17.69	id
	lds	BF	3.20	0.20	0.30	0.70	16.00	id
	lds	Sen	2.49	0.14	0.46	0.70	17.79	Billé, 1978
required concentrations for cattle			0.24	0.18	0.10	0.50		McDowell et al., 1983

[1]) Sen = Senegal, Mal = Mali, Nig = Nigeria, BF = Burkina Faso

reasons. Wild herbivores have evolved in areas poor in phosphorus, the recycling of phosphorus is very efficient in ruminants and large quantities of phosphorus can be stored in their bones, assuming that these stocks can be added to when phosphorus concentrations are above the concentrations required for the animal species.

Soil ingestion may have other beneficial effects, as discussed by Kreulen (1985). Acidosis resulting from the abrupt change from roughage to the first flush of growth, providing animals with protein-rich forage with readily fermentable carbohydrates, may be a threat to ungulates early in the wet season; soil ingestion can provide the animal with buffering salts. Faecal pellets from antelopes such as roan antelope and oribi, consisting entirely of soil, found in the Baoulé in that period, may suggest that these animals are liable to acidosis. Also disorders caused by digestive inhibitors such as tannins, that reduce the quality of the forage, may be prevented or alleviated by eating soil: clay minerals may compete with tannins for plant protein or inactivate tannins and toxic alkaloids directly. Also, when the quality of ingested forage declines, the presence of soil in the rumen may improve energy and nitrogen utilization by stabilizing the cation absorption complex. The use of mineral licks in the Baoulé in the dry season may also indicate this effect.

8. The ungulate community in the Baoulé

8.1. Introduction

A striking feature of African herbivores, noted by Leuthold (1978) and others, is that relatively large numbers of species coexist in the same area. Consequently, the study of ecological separation within, or rather the structure of herbivore communities has received much attention (e.g. Lamprey, 1963; Bell, 1970; Dunbar, 1978; Leuthold, 1978; Sinclair & Norton-Griffiths, 1979; French, 1985).

Given the large variation in the availability of resources and their limited extent especially in the dry season, one might speculate whether there is competition for resources. Competition is a symmetrical process: both competitors are adversely affected and this tends to result in the evolution of mechanisms or processes which reduce the interaction (Cowie & Krebs, 1979). Competition can only occur when the resources utilized are finite or when resources are renewed at a lower rate than that at which they are used up (Dunbar, 1978).

This chapter gives an ecological characterization of the ungulate community of the West African savanna, and of the Baoulé in particular, and analyses the main physical determinants by which coexistence of species is achieved and is maintained (8.2).

The social organization and timing of reproduction of the species of the ungulate community is briefly treated (8.3 and 8.4) because it is also important for judging the carrying capacity of the Sudan savanna and the conservation and management of its ungulate community.

8.2. The ecological separation of ungulates

8.2.1. Specific methods

Indices of overlap in habitat use in the dry season were calculated for pairs of animal species, using the formula:

$$a_{jk} = \frac{\Sigma\, p_{ij} \times p_{ik}}{(\Sigma\, p_{ij}^2 \times \Sigma\, p_{ik}^2)^{1/2}} \quad \text{(Pianka, 1973)}$$

in which p_{ij} and p_{ik} is the proportion of the i-th habitat type utilized by the j-th and k-th species, respectively. This index assumes values between 0 = total niche separation and 1 = total overlap. Dietary overlap between two species was simply calculated as the sum of the percentage points from both monocotyledons and dicotyledons which are common to both species (Dunbar, 1978). As habitat and food were considered to be biologically independent resources, indices for combined overlap were obtained by multiplying the uni-dimensional values (Leuthold, 1978; Putman, 1986).

8.2.2. Mechanisms of ecological separation

There are several mechanisms by which separation between species can be achieved (see Lamprey, 1963; Sinclair, 1985):

- * separation by habitat, by the occupation of different land-system units at the same time, or the same units at different times;
- * separation by food, by the selection of different plant categories or different plant parts, or by feeding at different levels in the vegetation;
- * separation in space by differences in dependence on water.

Using our data from Table 7.3 and Fig. 7.5, the overlap between species with respect to the choice of habitat and diet composition, have been analysed for the dry season when the resources are more limited than in the wet season (see Chapters 6 and 7).

The analysis shows a considerable overlap in diet composition (Table 8.1) but this was because only two plant categories were used in the calculation of indices. Nevertheless, separation between the browsers, such as the red-flanked duiker and bushbuck, and the other species is clear.

Table 8.1. Indices of overlap in diet and habitat among ungulates in the Baoulé.

		diet								
		wh	hi	bb	rd	rb	wb	ro	hb	or
	warthog	*	0.90	0.10	0.02	0.86	0.83	0.67	0.97	0.76
h	hippopotamus	0.54	*	0.20	0.12	0.96	0.93	0.77	0.93	0.86
a	bushbuck	1.00	0.50	*	0.92	0.24	0.27	0.43	0.13	0.34
b	red-flanked duiker	0.91	0.15	0.93	*	0.16	0.19	0.35	0.05	0.26
i	reedbuck	0.99	0.44	1.00	0.95	*	0.97	0.81	0.89	0.90
t	waterbuck	0.55	0.98	0.67	0.35	0.62	*	0.84	0.86	0.93
a	roan antelope	1.00	0.10	0.91	0.99	0.93	0.29	*	0.70	0.91
t	hartebeest	0.84	0.00	0.86	0.99	0.90	0.20	0.99	*	0.79
	oribi	0.85	0.02	0.88	0.99	0.91	0.22	0.99	1.00	*

Apart from the hippopotamus, there is in general a large overlap in habitat utilization. However, as daytime observations are the only source of information, the time this species spends in the riverine unit is exaggerated. Species which utilize the Andropogon savanna (land-system unit F) show considerable overlap except for species such as the waterbuck that were frequently observed in the riverine unit.

The combination of diet and habitat utilization already leads to an ecological separation among some but not all species (Table 8.2).

There are other mechanisms which, although they could not be assessed quantitatively, also lead to a separation of species. A *horizontal separation* results within each feeding style because of the difference in degrees of dependence on surface water for drinking, or in the case of hippopotamus, for shelter. Further-

Table 8.2. Indices for combined resource overlap between ungulates.

	wh	hi	bb	rd	rb	wb	ro	hb	or
warthog	*	0.49	0.10	0.02	0.85	0.46	0.67	0.81	0.65
hippopotamus		*	0.10	0.02	0.42	0.91	0.10	0.00	0.02
bushbuck			*	0.86	0.24	0.18	0.39	0.11	0.30
red-flanked duiker				*	0.15	0.07	0.35	0.05	0.26
reedbuck					*	0.60	0.75	0.80	0.82
waterbuck						*	0.24	0.17	0.20
roan antelope							*	0.70	0.90
hartebeest								*	0.79
oribi									*

more species are *vertically* separated by differences in the level at which they feed, most noticeable in browsers: giraffe feeds at levels of up to 5 m above the ground, and its potential competitor the Grimm's duiker of up to 0.75 m; wheras woody foliage up to 1.75 m is available to the bushbuck, the red-flanked duiker does not reach foliage above 0.75 m.

Especially in the grass-preferring species, separation may occur by difference in *degrees of selectivity* in the utilization of the grass layer. The narrow muzzles and thus smaller bite size of reedbuck and oribi enable these species to graze the small tufts of dry-season growth and to reach higher intake than larger species grazing on the same sward (Illius & Gordon, 1987).

Plate 19. Vertical separation of species: giraffe feeds at levels up to 5 m above the ground

Table 8.3. Mechanisms operating in the dry season leading to ecological separation between the ungulates in the Baoulé[1]).

species	el	wh	hi	gi	bb	rd	Gd	rb	wb	ro	hb	or
elephant	X	1	1	3	2/4	2	2	1	1	1	1	1
warthog		X	1/3	1	1	1	1	3	3	5	5	5
hippopotamus			X	1	1	1	1	5	5	1	3	3
giraffe				X	4	4	4	1	1	1	1	1
bushbuck					X	4	4	1	1	1	1	1
red-flanked duiker						X	3	1	1	1	1	1
Grimm's duiker							X	1	1	1	1	1
reedbuck								X	5	5	3	3
waterbuck									X	2	2	2
roan antelope										X	3	4
hartebeest											X	5
oribi												X

[1]) 1 = different diet composition 2 = different habitat choice
3 = different water requirements 4 = different feeding levels
5 = different degree of selectivity concerning plant parts

In Table 8.3 each species is compared with all other species in the Baoulé and the mechanism supposed to be the most important with respect to the separation of species is given per species pair. Difference in diet composition operates most frequently, in more than 50% of all cases, followed by difference in dependence on water and selectivity concerning plant parts.

Fig. 8.1 shows how these three mechanisms lead to an ecological separation of the ungulates in the Baoulé, with body size indicating different degrees of selectivity and vertical zonation of feeding levels. It does not imply that interspecific competition does not occur at all: species that are more successful in utilizing a resource under competitive conditions will have larger populations than the less successful competitor. But by these mechanisms large-scale changes in the total number and biomass of the ungulate community are avoided. In this way the ungulate community achieves a state of stability in which the proportion of the various species differs with variations in the availability of the resources.

8.2.3. Discussion

As explained in Chapters 3, 4 and 6, rainfall and bush fires are the most important determinants in maintaining the structure and composition of the Sudan savanna vegetation. In Chapter 6 we have shown that the wet-season growth of perennial grasses is strongly related to the amount of rainfall (Fig. 6.6). In general, no tall savanna grasses, either annual or perennial, occur in areas with less than 500 mm annual effective rainfall (= 100% infiltration, i.e. no run-on or run-off).

In the absence of bush fires, the phytomass of savanna grasses in areas with higher annual rainfall is potentially available to grazing ungulates during the dry season. However, only a small part of it is of sufficient quality (about 1% N, see Chapter 7), to be characterized as food. In the tall savanna grasses this

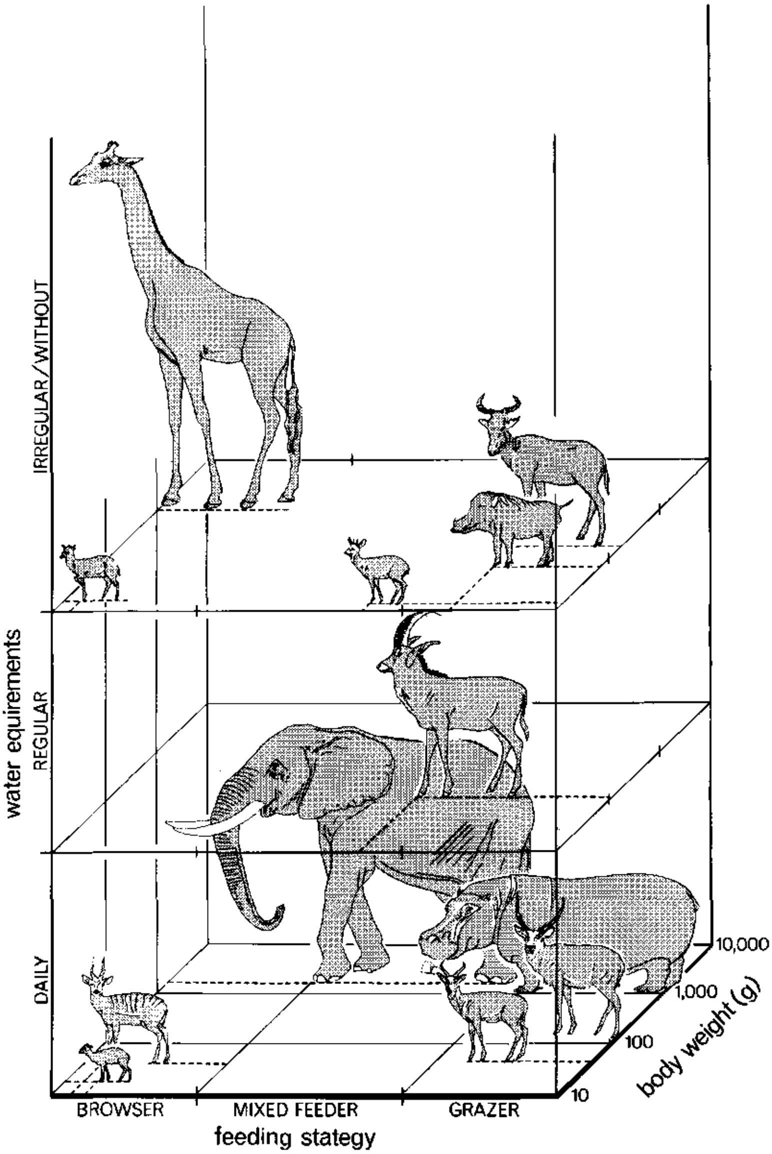


Fig. 8.1. Ecological separation of ungulates.

fraction is about 10%, further increased by the dry-season growth of perennial grasses, but only considerably when annual rainfall exceeds 700 mm. However, the savanna is usually set on fire, which results in a nearly total absence of food in areas with 500-700 mm annual rainfall and leaves virtually only the dry-season growth of perennial grasses as forage in areas with more than 700 mm rainfall.

How does this affect the composition of the ungulate community of the savanna? The northern limit of the distribution area of grazing ungulates such as hartebeest, waterbuck and reedbuck, coincides more or less with the 800-mm isohyet. However in reality, 800 mm rainfall does not equal 800 mm effective rainfall, because of differences in topography (causing run-on or run-off) and in soil texture (resulting in differences in infiltration). Thus in shallow depressions there is more water for plant growth and on hill tops less. Consequently the distribution area of the above species can locally deviate north or south from the 800-mm isohyet. This 'rule of distribution' is less strict for waterbuck and reedbuck than for hartebeest. These two species are able to cope with a decreasing quantity of nutritious savanna grasses by eating more riverine monocotyledons. Thus the occurrence of riverine monocotyledons north of the 800-mm isohyet enables these ungulates to survive, but only locally because to the north these plants become increasingly rare (Chapter 6).

Fluctuations in the amount of yearly rainfall determine the balance between perennial grasses, annual grasses and herbs in the West African savanna (Fig. 3.4). Prolonged periods of unfavourable conditions, such as the drought in West Africa between 1970 and 1985, influence not only the distribution of perennial grasses, i.e. a replacement to more southern regions (and to lower parts of the catena), but especially their dry-season growth (Fig. 6.8). In dry years grasses produce less phytomass in the wet season, with a reduction of about 20% in the northern and about 10% in the southern Sudan zone, and perennial grasses

Plate 20. The distribution of hartebeest is strictly limited by the availability of the dry-season growth of perennial grasses

only have dry-season growth at lower latitudes. Drought thus results in both lower densities of grass-preferring ungulates and in the total disappearance of species in certain regions. This has happened with hartebeest (see Fig. 7.1) and buffalo (De Bie & Kessler, 1983) in the Baoulé. We should expect to find ungulates, such as elephant and roan antelope, that are able to compensate for the absence or scarcity of grass of adequate quality in the dry season by extensive feeding on woody foliage in more northern areas, and this has been observed (Fig. 7.1). Rather, their distribution is limited by the availability of drinking water and the total quantity of dry-season forage.

Bush fires are another important feature of the Sudan savanna that affect the structure of the ungulate community. Through fire a balance is maintained between the canopy layers of woody plants and grasses. Early fires especially preserve the grass component (see Chapter 4) and furthermore stimulate the dry-season growth of perennial grasses, and make it easier to obtain for grazing herbivores by destroying the lignified stems and sheaths of the wet-season growth. Early fires perpetuate the grazing ungulates and lessen the impact of elephants on the woody stratum (Jachmann et al., 1989) because resprouting is limited. Late fires do not stimulate dry-season growth. Without fires the savanna itself would gradually change into a dry forest. The effects of animals, particularly elephants, upon the woody stratum, although often considerable, are generally insufficient to convert such a dry forest into a savanna (Norton-Griffiths, 1979), although elephants may facilitate the entry of fire into the forest (Cumming, 1982).

Hence the occurrence and timing of bush fires on the savanna are crucial to the preservation of the ungulate community. The composition and structure of the whole ungulate community and in particular the presence of grazers and mixed feeders such as reedbuck, waterbuck, roan antelope, and hartebeest depend largely on the regular occurrence of early fires. Hence I conclude that not only the savanna vegetation but also the ungulate community should be characterized as a 'fire-climax'. A summary of these interrelationships and thus processes of regulation is presented as a model in Fig. 8.2.

In the Sudan savanna the ungulate community is dominated by four species: elephant, buffalo, hartebeest and roan antelope (see Chapter 9, Fig. 9.3). With respect to the vegetation structure we may label the elephant as a 'structure-modifier' and the other species 'structure-followers', as they are largely dependent on the regular occurrence of fire. Long-term absence of fires will therefore have a considerable effect on the populations of certain species: grazers will gradually disappear from the area, browsers will remain. Sinclair & Norton-Griffiths (1979) have shown this clearly for the ungulate community in the Serengeti national park in Tanzania. Elephants are expected to remain as the forage availability for this mixed-feeding species will probably increase (3.2.3, Jachmann et al., 1989).

Biological factors such as a large change in the number of one of the four dominant species, such as elephant, may considerably affect the populations of other species (see Van Wijngaarden, 1985).

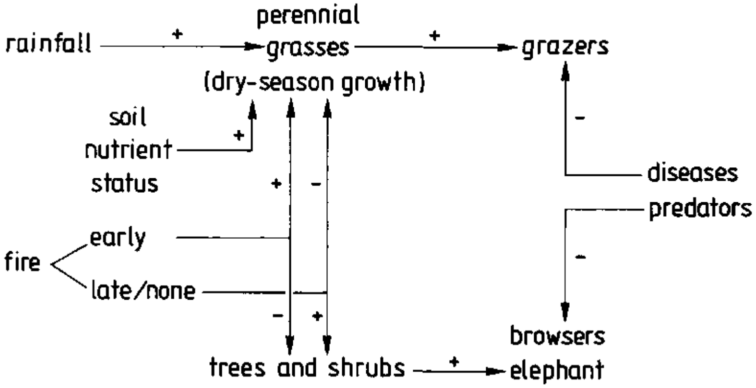


Fig. 8.2. Model illustrating the interrelationships between environmental factors and ungulates in the Baoulé; plus signs indicate that higher values in the preceding feature result in higher values in the succeeding one, whereas minus signs result in lower values.

Within the limits set by the above physical determinants (rainfall and fire), the ungulate community is structured by mechanisms discussed in 8.2.2. The availability of quality forage mainly determines both species composition and the numbers of the ungulate community in the West African Sudan savanna.

The mechanism of migration to avoid a shortage of dry-season forage has not been observed in the West African wild ungulates. Especially for grazers the strategy of migration seems very adaptive. However, as grazers in the Sudan savanna are limited through the availability of quality forage in the dry season (Chapter 7), which is much less than in the wet season (Chapter 6), migration is not a necessary behavioural trait. Migration is an adaptive strategy only if wet and dry season ranges are able to supply more or less comparable amounts of food and thus to sustain comparable densities of animals. Such situations are seldom found in the Sudan savanna, only where uplands (wet-season range) meet flood plains (dry-season range). In such cases not only wild ungulates show seasonal migration (e.g. white-eared kob *Kobus kob leucotis* in Sudan (Fryxell & Sinclair, 1988)): many pastoralists in the Sahel in Mali move their cattle between the Sahelian pastures and the flood plain of the Inner Delta of the river Niger.

Larger species can also make food more available to smaller ones: facilitation (see Bell, 1970, 1971). In Benoué national park, kob feed on swards maintained by hippopotamus (Geerling, pers. comm.). If the hippopotamus disappears the swards change into bush, which is of no use to the kob. Thus interactions such as facilitation help to shape the ungulate community.

The various mechanisms described reduce the potential competition between the species in the Baoulé in the dry season. Considering the seasonal variation in resources, especially food, this competition is probably periodical. The mechanisms provide the community with a certain degree of resilience (or flexibility) to environmental changes. Large variations in environmental features such as in rainfall, do not eliminate the total ungulate community but they certainly affect its species composition.

These conclusions, however, are based on the patterns of resource utilization and their seasonal variation, and not on the process itself which requires a more experimental approach. The migration of wildebeest into the Mara-ecosystem enabled Sinclair (1985) to adopt such an approach. From his analysis it appeared that predation also played a role as important in structuring that ungulate community as interspecific competition. This may apply to the West African Sudan savanna with traditional hunting replacing or complementing predation.

Differences in body weight, feeding styles and dependence on water in relation to food supply bring about a separation between species that minimize (potential) competition. The next two paragraphs discuss how food supply and habitat structure influence elements in the social organization and reproduction of the different species.

8.3. On social organization

8.3.1. Introduction

For optimal use of the resources within the habitat, individuals arrange themselves both socially and spatially (Leuthold, 1977). The main components of *social arrangements* are group formation and group composition. Extremes of group formation are found, ranging in size from the solitary animal through different types of social units such as pairs, female herds with solitary males to large mixed herds (Estes, 1974; Leuthold, 1977). In addition to social arrangements, *spatial arrangements* such as the (non)exclusive home-range, (pair)territory and non-territorial society, can be observed (Leuthold, 1977).

Both social and spatial arrangements provide the species' population with a 'structure', the social organization (Leuthold, 1977). Following Leuthold (1977) social organization is defined as the result of all social interactions and spatial relations among the members of a single-species population. As the resources vegetation, water and shelter in the Baoulé show seasonal variations (Chapter 6 and 7.3), social organization is expected to be flexible, to be reflected by changes in the social and spatial arrangements.

This paragraph gives information on the social organization of ungulates in the Baoulé, especially their social arrangements, by describing (changes in) group size and group composition, and compares results with data from other regions within the Sudan savanna. Because of the shyness of the animals in the study area it was not possible to distinguish between stable social units and temporary aggregations. Therefore we use the neutral word 'group'.

8.3.2. Group size

We made 640 observations of 1378 animals of several ungulate species in the Baoulé in the wet and dry seasons, arbitrarily choosing a minimum of ten observations of groups per season to minimize bias towards a certain group size.

Consequently no mean group size could be calculated for Grimm's duiker, waterbuck, roan antelope and red-flanked duiker in the wet season, and for hippopotamus, elephant, hartebeest and giraffe in both the wet and dry season (Table 8.4).

The frequency of group size for each species is given in Fig. 8.3. From the

Table 8.4. Mean group size of some ungulate species (ground observations) in wet (=ws) and dry (=ds) season.

species			group size		total number of groups
			mean	range	
browsers:	red-flanked duiker	ds	1.0	1	24
	Grimm's duiker	ds	1.2	1-2	18
	bushbuck	ws	1.2	1-2	17
		ds	1.4	1-4	125
mixed feeders:	roan antelope	ds	5.1	1-16	42
	oribi	ws	1.5	1-3	14
		ds	1.4	1-3	104
grazers:	reedbuck	ws	1.3	1-3	21
		ds	1.6	1-4	65
	waterbuck	ds	2.3	1-7	21
	warthog	ws	3.4	1-7	27
		ds	3.0	1-8	161

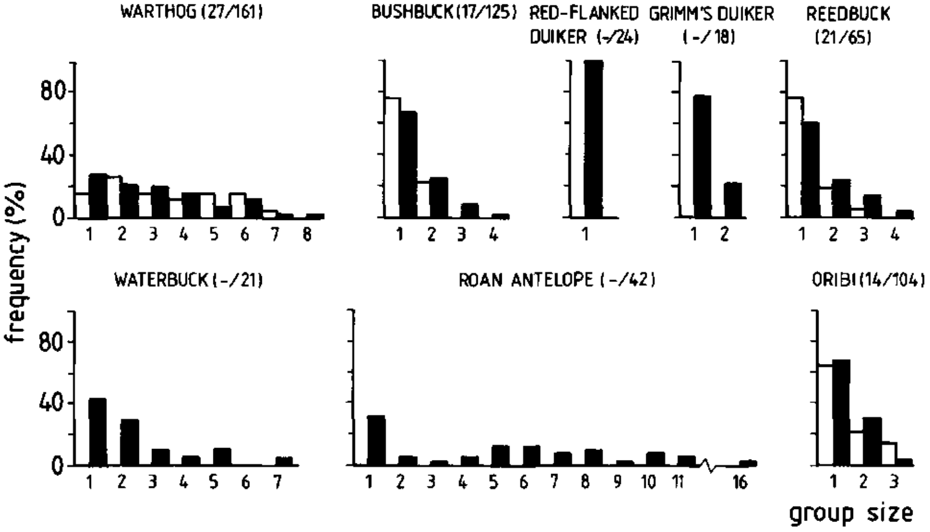


Fig. 8.3. Group size frequency of several ungulates in the wet (white bars) and dry season (black bars); (n1/n2): number of groups observed in each season

data it follows that species can be divided into two main categories:

* species living solitarily or in pairs: bushbuck, red-flanked duiker, Grimm's duiker, reedbuck and oribi;
* species living in aggregations of more than two individuals: warthog, waterbuck and roan antelope.

Although few, our observations on elephant, hippopotamus, hartebeest and giraffe indicate that these species can also be placed in the second category.

It appears that, independent of their feeding style, the smaller species with a body weight below 50 kg, fall into the first category and the larger ones into the second. No significant changes in group size during the year were found although in the dry season animals tended to occur in slightly larger groups (Table 8.4 and Fig. 8.3). The data from aerial observations in Table 8.5 seem to confirm this.

Table 8.5. Mean group size of several ungulate species in the Baoulé in the wet and dry seasons determined by aerial survey.

species		wet season 1980		dry season 1981	
		mean group size	number of groups	mean group size	number of groups
browsers:	red-flanked duiker	1.1	50	1.1	45
	bushbuck	1.3	77	1.4	84
mixed feeders:	roan antelope	5.4	25	5.8	16
	oribi	1.3	24	1.6	60
grazers:	reedbuck	1.1	77	1.5	81
	waterbuck	2.5	2	3.5	6
	hartebeest	4.3	3	4.6	3
	warthog	2.6	288	2.7	158
	hippopotamus	1.9	10	3.5	24

8.3.3. Group composition

In order to describe the social structure of various species one has to define the social units. As males are generally easier to recognize than females, the absence or presence of one or more males has been taken as the criterion for describing social units and four units have been distinguished:

social unit I : one or more males (adult or subadult);
social unit II : one or more females (adult or subadult), with or without juveniles;
social unit III : one adult male with one or more females (adult or subadult), without juveniles;
social unit IV : more than one adult male, with one or more females (adult or subadult), with or without juveniles.

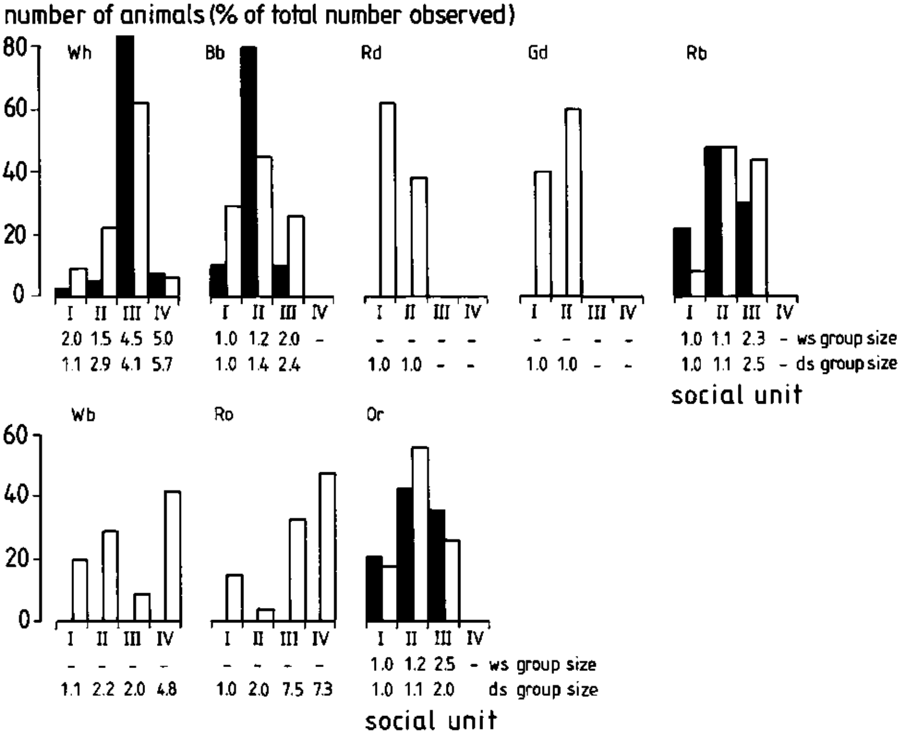


Fig. 8.4. Distribution of observed animals (% of total number) over the social units in the wet season (= white bar) and dry season (= black bar);
Wh = warthog, Bb = bushbuck, Rd = red-flanked duiker, Gd = Grimm's duiker,
Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Or = oribi

From Fig. 8.4 we see that:

- * both duiker species are solitary; the lack of observations of social unit III probably indicates that sexes only meet for mating;
- * bushbuck, reedbuck and oribi live both solitarily and in pairs (= male with female, sometimes accompanied by a juvenile); pairs are more frequent in reedbuck and oribi;
- * warthog live predominantly in family groups ('harem');
- * a large proportion of waterbuck and roan antelope live in mixed herds (social unit IV); in waterbuck solitary or aggregated males (social unit I) and female groups (social unit II) are also important units; in roan antelope social unit III, the harem, is second in importance.

The frequency of these social units may be influenced by a skewed sex ratio. The presentation of data in Fig. 8.4 suggests that the sex ratio is in favour of females, in at least the bushbuck, reedbuck, waterbuck, roan antelope and oribi. Ground and aerial observations confirm this (Table 8.6). The difficulty in dis-

Table 8.6. Adult sex ratio.

species	number of males per female	N	type of survey[1])
warthog	0.9	205	G
bushbuck	0.6	174	G
	0.7	183	A
Grimm's duiker	0.7	10	G
roan antelope	0.6	133	A
reedbuck	0.5	92	G
waterbuck	0.5	26	A
oribi	0.5	98	G
hartebeest	0.4	11	G

[1]) G = ground observation, A = aerial survey

tinguishing between the sexes in red-flanked duiker and Grimm's duiker is probably the reason that we found different proportions of social units I and II where one should expect equal proportions.

According to Fig. 8.4 the social structure is rather stable: the same social units are observed in both the wet and dry season and no major shifts occur.

The limited observations suggest that the social structure of elephant, hippopotamus, giraffe and hartebeest resemble those of waterbuck and roan antelope. However, it should be remarked that although the social units are the same, their frequencies often differ between species which perhaps is related to the distribution and quantity of the resources they depend on (see below).

Detailed observations made by Smits (1982) on individually recognizable bushbuck over 6 months at the study site 'Borassus' showed that, with respect to the stability of social units in this species:

* the association between female and juvenile is very stable;
* the male-female association is of short duration; males were regularly observed with different females and never with the same female on two consecutive occasions;
* some female-female (perhaps mother-daughter) associations are strong;
* males only associate with each other for a short period.

8.3.4. Discussion

Results on the mean group size of ungulates in the Baoulé (Table 8.4) agree quite well with data from other regions in the Sudan savanne (Table 8.7). The maximum group size for all grazing species is larger in Lake Kainji national park (Milligan, 1978) than in the Baoulé, perhaps because there is more dry-season growth of perennial grasses in Lake Kainji national park due to the higher annual rainfall of 1000-1250 mm.

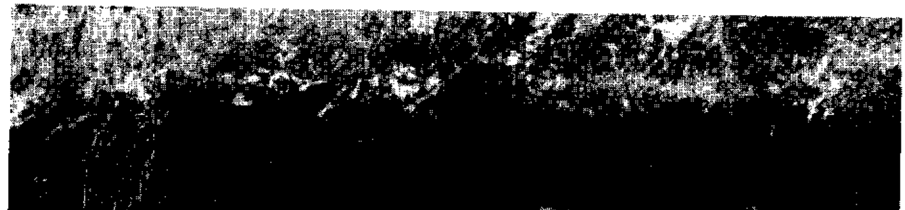
Compared to the more mosaic structure of the corresponding vegetation zones in East and southern Africa, the vegetation of the Sudan savanna is rather monotonous over the whole of its range (White, 1983). Thus as group size can

Table 8.7. Mean group size of ungulate species in West African conservation areas.

area:	Borgu GR		Lake Kainji NP[3])		Bouba Ndjidah		Benoué NP[6])	Yankari GR[7])		Po NP		Arli NP[9])	Deux Balé[10]	'W' NP[9])	St. Floris NP[11])
	a[1])	b[2])	a	b	a[4])	b[5])		a	b	a[8])	b[9])				
species:															
elephant	7.0	4.8	16.2	6.3	–	–	–	16.0	11.1	–	4.4	–	5.3	–	12.4
warthog	3.2	3.3	2.6	1.5	–	2.0	3.1	3.9	2.6	3.5	1.4	2.7	8.0	2.5	2.4
hippopotamus	–	5.6	–	–	–	–	–	–	–	–	–	–	–	–	29.1
giraffe	–	–	–	–	2.5	–	–	–	–	–	–	–	–	–	2.6
bushbuck	1.3	1.2	1.2	1.4	1.0	1.5	1.4	1.2	1.1	1.2	1.0	1.0	1.0	1.8	–
red-flanked duiker	–	1.1	1.1	1.0	1.0	–	1.1	1.0	1.0	1.0	–	–	–	–	–
Grimm's duiker	1.1	1.1	1.2	1.2	1.0	1.1	1.0	1.1	1.0	1.3	1.2	1.0	1.0	1.0	1.1
reedbuck	–	1.7	–	–	1.8	1.5	1.4	–	–	1.4	1.0	1.5	1.0	1.2	1.8
waterbuck	3.0	3.0	3.5	1.0	–	2.0	4.2	5.1	3.9	4.6	2.0	4.0	–	3.3	6.5
roan antelope	4.9	5.0	5.6	2.9	–	2.5	4.0	7.2	4.9	3.3	3.2	6.3	7.8	5.2	6.1
hartebeest	5.9	5.0	5.1	4.5	–	7.2	5.4	5.2	5.3	8.2	8.0	5.0	3.0	4.3	6.3
oribi	1.7	1.6	1.7	1.6	2.1	1.7	2.5	1.3	1.5	1.6	1.6	1.0	1.0	1.0	1.7

1) dry-season data 1970-1972, Child (1974)
2) dry-season data 1973, Pelinck (1974)
3) dry-season (a) and wet-season (b) data 1976, Milligan (1978)
4) dry-season data 1973-1976, Bosch (1976)
5) dry-season data 1978, Geerling (pers. comm.)
6) dry-season data 1976-1978, Esser (1980)
7) dry-season (a) and wet-season (b) data 1970-1972, FAO (1975)
8) dry-season data 1972-1974, Heisterberg (1975)
9) dry-season data 1981, Bousquet et al. (1982)
10) dry-season data 1982, Bousquet et al. (1982)
11) dry-season data 1969-1970, Loevinsohn (1977)


A


B

c

Plate 21. Three types of group formation: (a) a pair of oribi, (b) a female herd of waterbuck and (c) a mixed herd of topi

be regarded as an indicating parameter for optimal habitat use, large variations in mean group size are not to be expected throughout the Sudan savanna (see 7.3.1). This is confirmed by only slight differences in mean group size over several years (Table 8.7). Even the large mean group size for elephant in Lake Kainji national park in 1976 is not significantly different from values in previous years because of the great variation in herd size (Milligan, 1978).

The larger group size of ungulates in the dry season compared to that in the wet season, observed in the Baoulé, is also evident in other areas e.g. Lake Kainji national park and Yankari game reserve. Which factor is responsible for this increase? As this question largely parallels that of which factor or factors are responsible for the difference in the mean group size between the categories of species, they will be discussed together.

As shown in Chapter 7, smaller species have to select a more nutritious diet than larger species. Both in the grass compartment of the vegetation and in the lower shrubs, these more nutritious plant parts are sparse and/or patchily distributed (Chapter 6). Their utilization by one animal strongly reduces the availability for the one that follows. Two options are open to the second one (Jarman, 1974): he can spend more time on foraging at the same spot or look for his own 'honey-pot'. Both options prevent group formation through the spatial separation of individuals. Thus not surprisingly one finds the smaller species, bushbuck, reedbuck, oribi and duiker living solitarily or in pairs whereas the larger species are gregarious. During the dry season, all forage becomes more localized (Chapter 6). One should thus expect group size to *decrease* in all species through the mechanism described, but this contrasts with the observed increase in group size. Therefore, although food dispersion cannot be excluded as a factor, we have to conclude that other factors must have overriding effects.

Firstly, in the Baoulé as elsewhere in the Sudan savanna, the availability of surface water for drinking is more localized in the dry season. This might be the reason that populations of water-dependent species, such as elephant, hippopotamus, bushbuck, red-flanked duiker, reedbuck, waterbuck and to some extent roan antelope, are limited to smaller areas which results in larger aggregations of individuals. The dry-season concentrations of reedbuck in the Dinder national park in the Republic of Sudan, but still located within the Sudan savanna, can be mentioned as an extreme example. Along the banks of the Dinder river, Holsworth (1972) observed 4,500 animals with about 50% in herds of 100 or more, the largest herd consisting of 400 individuals. He thought that this gregarious behaviour was induced by the distribution of water in the dry season, being very limited compared to that in the species' range in the wet season. This example is a good illustration of the effect of a resource on the social organization of a species.

Secondly, loss of cover due to fires or shedding of leaves might induce an increase of group size to provide a better protection against predators (see Alexander, 1974; Estes, 1974).

However, probably the most important factor responsible for the increase in group size of most species in the dry season is their reproductive behaviour. For optimum calf survival (see 8.4), females generally give birth to the calf in the early to mid dry season. Calves strongly associate with their mother and as a female with her calf is usually counted as two individuals, obviously the mean group size increases.

Besides, mating behaviour may affect group size as sexes have to associate for a certain time. Species that calve in the early to mid dry season, mate in the preceding late dry season, which contributes to the observed increase of mean group size of ungulates in the Sudan savanna in the dry season. Observations on mean group size in hartebeest and roan antelope in Lake Kainji national park (Milligan, 1978) support this explanation (Fig. 8.5).

According to the literature referred to in Table 8.7, species are organized in the same social units throughout the Sudan savanna as in the Baoulé, with only minor differences with respect to their relative proportions. A major difference is found in oribi in the Benoué national park, where 78% of all individuals live in pairs (Esser, 1980).

Some reports (Child, 1974; FAO, 1975; Bosch, 1976) mention the existence of a 'nursery herd' in waterbuck and hartebeest: a group of several calves attended by one adult animal. Observations were too few to say whether this type of social unit occurs in the Baoulé, or that hartebeest leave their calves behind when they move to rivers and large pools for drinking as reported by Child (1974), FAO (1974), Bosch (1976) and Geerling (pers.comm.).

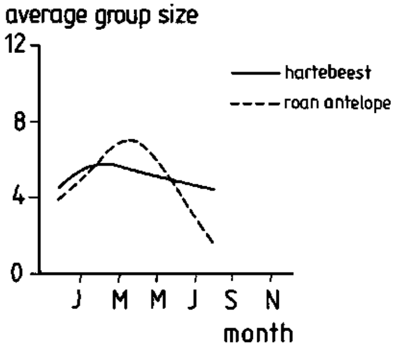


Fig. 8.5. Mean group size in hartebeest and roan antelope in Lake Kainji national park in Nigeria, dry season 1977-1978 (after Milligan, 1978)

Although all social units have been observed in elephant, hippopotamus, giraffe, waterbuck, roan antelope and hartebeest in the Baoulé (8.3.3), differences exist in the social structure between the species, as elsewhere in the zone. In roan antelope and hartebeest social units I and III are more frequent while in waterbuck social units I and II are comparatively more important. As the waterbuck depends on surface water for daily drinking, its range movements are rather limited. Probably it is energetically more favourable for adult males to establish a territory and try to keep the young males out which consequently keeps these young males on the move. Because of the independence of water of hartebeest and the flexible food choice of roan antelope, these species can move over larger areas. As their food is thinly spread (Chapter 6), it should therefore be more advantageous for a male of these species to link up with a moving herd of females and defend his 'harem' against other males on the spot than to defend a fixed area with an ample food supply. Thus differences in the availability and use of resources can explain differences in social structure. No precise information can be given on the social structure of the other three species due to insufficient observations over the whole Sudan zone but Child (1974) mentions bachelor herds in elephant where 14% of the observed animals are mature males, in groups of one to three individuals.

I conclude that the availability of resources in space and time determines the size and composition of ungulate aggregations and how space is utilized and is thus responsible for seasonal fluctuations in social organization.

8.4. Reproduction: the effect of food supply

8.4.1. Introduction

Various aspects such as physiological cycles of reproduction, sexual behaviour, length of gestation, parturition and litter size, maternal care and seasonality of reproduction, all of which are more or less interrelated, can be placed under the heading 'reproduction'.

Environmental factors such as rainfall, day-length, food availability and temperature have major influences on reproduction (Sadleir, 1969; Bronson, 1985). Because all these factors show a cyclic variation over the year (Chapters 3,4 and 6) in the Baoulé, one should expect the reproductive aspects mentioned to be tuned to these environmental cycles in such a way to achieve maximum reproductive success (see Weir & Rowlands, 1973).

Reproduction is defined as successful if the calf of an ungulate species is weaned, after which no direct care is given by the parent or parents. Therefore we expect parturition to take place in the Baoulé at a time of the year most favourable for the subsequent lactation and weaning.

8.4.2. Period of parturition in the Baoulé

All ground and aerial observations were analysed with respect to the occurrence of young. From the results, species-specific parturition periods in the Baoulé have been determined, which are compared in Fig. 8.6 with periods of parturition at four sites elsewhere in the Sudan savanna, combining the available data per species in one diagram. The data are arranged in order of increasing average rainfall. The average length of the wet season is also indicated.

Warthog piglets are seen throughout the year but two peaks are easily distinguished, one around February and another in July (Fig. 8.7). Very few piglets are seen at the end of June but within a few days at the beginning of July the number rapidly increases, first in southern areas and later in the north (Watson, pers. comm.). As the piglets stay in the denning hole for three to four weeks (Rodgers, 1984) parturition must peak around January/February and in June (Fig. 8.6). The January/February peak is quantitatively more important than the one in June. Furthermore it seems that peaks are more pronounced in lower rainfall areas (De Bie & Kessler, 1983). Mean observed litter size is 2.5 (s.d. = 0.77, range 1-4) but it has to be borne in mind that more piglets could have been born of which one or more died within the first weeks of life.

Only one calf per female has been observed in the bushbuck. All our observations indicate that females give birth throughout the whole year. However, male-female associations are more frequently seen between January and April (Smits, 1982), suggesting a period of more sexual activity and thus a higher number of conceptions. As the gestation takes about 180 days (Morris & Hanks, 1974), proportionally more calves should be born in the second part of the wet season from August to October.

As no female reedbuck were observed with calves before February, reproduction is apparently seasonal. Each female has only one calf and as the calf does not accompany its mother for the first 2 to 4 months (Jungius, in Lent, 1974), parturition must start in November/December.

From March to June, small calves of waterbuck, one per female, are seen. Similar to reedbuck, the female waterbuck hides her calf for about 4 weeks (Spinage, in Lent, 1974), which means that calves are born from February onwards.

The roan antelope also appears to have one calf at a time. Parturition is be-

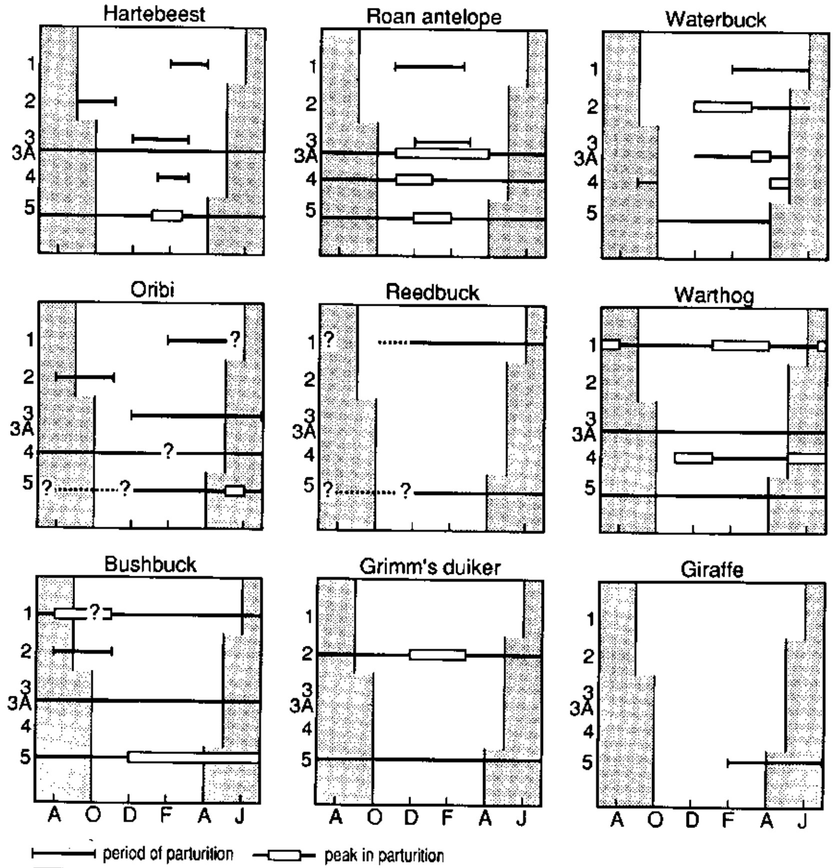


Fig. 8.6. Periods of parturition of several ungulate species in West Africa.
1 : Baoulé (600-900 mm; this study),
2 : Pendjari NP (900 mm; FAO, 1981),
3 : Borgu GR (1000-1200 mm; Child, 1974),
3A: Lake Kainji NP (1000-1200 mm; Milligan, 1978),
4 : Yankari GR (1000 mm; FAO, 1975),
5 : Bouba Ndjidah NP (1200 mm; Bosch, 1976).
shaded: wet season.

tween November and February.

In hartebeest there seems to be a strict calving season, from February to March, although our observations are very few.

No newborn oribi calves have been observed before February, thus parturition does not occur throughout the year.

For the remaining species no data could be collected on parturition.

Three types of reproduction patterns are to be recognized in the above species:

1. a very restricted period of parturition: waterbuck, roan antelope and hartebeest;

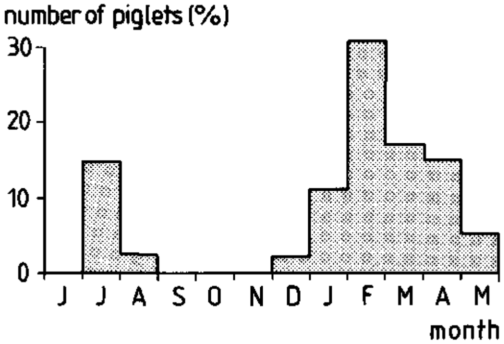


Fig. 8.7. Occurrence of warthog piglets per month in the Baoulé (expressed as the percentage of the total number of animals observed per month).

2. a period of parturition with a well-defined start but a gradual decrease in frequency: reedbuck and oribi;
3. continuous breeding, with or without peaks in parturition: bushbuck and warthog.

Body size and feeding style (as an indication for resource utilization) are closely related to these patterns (Table 8.8).

Table 8.8. Reproduction pattern in relation to feeding style of ungulates in the Baoulé.

reproduction pattern	feeding style		
	grazer	mixed feeder	browser
very restricted period	waterbuck hartebeest	roan antelope	–
distinct start	reedbuck	oribi	–
continuous breeding	warthog	–	bushbuck

8.4.3. Discussion

Substantial information on periods of parturition in ungulates in the Sudan savanna is provided by Child (1974) and Milligan (1978) for Lake Kainji national park, FAO (1975) for Yankari game reserve, FAO (1981) for Pendjari national park and Bosch (1976) for Bouba Ndjidah national park (Fig. 8.6). Combining this information with our data, the data reveal that:

* the more rainfall in an area, the more that parturition is spread over the year, e.g. hartebeest, roan antelope and waterbuck;

Plate 22. Roan antelope calves are of a similar size, suggesting a strict calving season

- * species foraging on woody foliage such as bushbuck and Grimm's duiker breed the whole year round regardless of the annual rainfall;
- * large ungulate species have more restricted calving seasons than small species: e.g. hartebeest and waterbuck compared to oribi and reedbuck;
- * the more parturition is restricted to a certain period, the more it is concentrated in the dry season, e.g. hartebeest, roan antelope and waterbuck.

How can these patterns be explained?

As concluded in Chapter 7, ungulates foraging on grasses meet a sharp fall in forage quality and quantity late in the wet season and in the dry season. Although pregnancy puts a heavy burden on the female, lactation costs even more energy (Millar, 1977; Sadleir, 1969,1984) with a peak coming some months after parturition (e.g. 1-2 months in the white-tailed deer *Odocoileus virginianus* (Moen, 1973)); energy requirements of lactating females may be 40% greater than those of non-reproductive animals (Owen-Smith, 1982a). One would therefore expect parturition to take place in the wet season when most food is available (Sadleir, 1984), but the calf would then have to be weaned in the dry season under much less favourable circumstances. As the calf is smaller in size than the adult animal when it is weaned, at most 60% of adult body weight (Millar, 1977), it has higher energy requirements, about 15% more than that of the adult.

Thus in grass-preferring ungulates, weaning at the beginning of the wet season, when large quantities of nutritious young grass are available, will maximize reproductive success. Consequently, parturition in these species should take place in the dry season, as apparently happens. It also becomes clear that in higher rainfall areas where dry-season growth of perennial grasses of adequate or good quality continues for a longer period and the growth period is longer in the wet season, parturition of the grass-preferring ungulates does not need to be so restricted.

There is good quality woody foliage for browsing ungulates throughout the year (Chapter 6). Weaning, and thus parturition, could therefore take place in every month of the year, as indeed is the case, for example in bushbuck and Grimm's duiker. Perhaps the energy cost of lactation acts as a second determinant, causing peaks in parturition.

The narrow muzzles of species such as oribi and reedbuck, enable them to select the more nutritious parts of grasses in the dry season and they can maintain an intake of relatively nutritious forage for a longer period than the larger ungulates. Parturition could therefore be less restricted to a particular season, although its start should be well defined, and this is suggested by our data.

I conclude that, in addition to the energy requirements of lactating females, time of parturition is geared to allow the maximum chance of survival of the calves after weaning, i.e. when there is suitable forage for the young. This is most pronounced in the larger grass-preferring ungulates.

Fig. 8.6 indicates that species do not have fixed periods of reproduction over the whole Sudan savanna, but that food availability, and therefore ultimately rainfall, has a large influence on the time of parturition. Thus in areas with a low annual rainfall, there is very little variation in the time of parturition within species, especially in grass-preferring species.

Next to the fulfilment of energetic and protein requirements of the female during pregnancy and lactation (see Sadleir, 1984) or, as argued by Sinclair (1983) her body condition during pregnancy, the survival of the calf after weaning apparently acts as an important selection mechanism in determining the period of parturition. However, when asking which factor triggers the timing of parturition, it must be realized that birth is the outcome of conception. The question is thus which factor triggers the time of conception in such a way that both lactation and weaning of the calf take place in the favourable season. Bronson (1985) suggests three possibilities: opportunism, with no 'predictors', photoperiodism or nutritional parameters. That it is a case of opportunism agrees well with Sinclair's (1983) hypothesis, that there is no trigger to reproduction, and that peaks in births reflect differences in calf survival. As concluded above, this may be the case in higher rainfall areas, but in a harsher environment restricted breeding periods would nevertheless eventually evolve. Response to a particular photoperiod is widely recognized as the reason for the start of breeding cycles and is found in some African ungulates such as the wildebeest (Sinclair, 1983). Nutritional parameters may also proximately and ultimately stimulate breeding cycles as in lechwe *Kobus lechwe* (Sinclair, 1983).

Part III: Ecological carrying capacity

In Part III the ecological carrying capacity of the Baoulé area is assessed by calculating the dry-season stocking rates using the data from Part II, and our results are compared to known densities of ungulates in other West African areas and converted into potential animal numbers in the Baoulé (Chapter 9). Other ways of assessing the ecological carrying capacity in West Africa are discussed in Chapter 10, as well as what is known about other savannas in Africa and Australia in this respect.

9. Ecological carrying capacity of the Baoulé

9.1. Introduction

Bell (1984) distinguishes three types of approach for estimating the ecological carrying capacity:

- the *analytical* approach: estimates are based on the analysis of components and processes in the plant-herbivore system;
- the *comparative* approach: estimates are derived by comparison with areas with similar physical and biotic features, assuming that such areas have similar carrying capacities;
- the *manipulative* approach: estimates are derived by analysing the response of a population to manipulation (i.e. various intensities of harvesting).

We had to choose the analytical approach in this study because:

- the manipulation of animal populations was neither practical nor possible because of the low animal densities, the unsuitable terrain, and the shortage of time, personnel and finances;
- the comparative approach could also not be used as one of the objectives of this study is to examine if 'rules of thumb', used elsewhere for estimating the carrying capacity of an area, are applicable to the West African savanna and in particular to the Baoulé.

In its most *simple* form, the analysis of the ecological carrying capacity is often regarded as the calculation of the potential stocking rate for an area over an indefinite period of time, that is, the availability of a resource required by an animal species or group of animal species in that area, divided by the species' requirements of this resource.

Available forage is nearly always the only resource taken into account as it affects animal density directly, but other factors, such as shelter, available surface water for drinking, geomorphology, presence of predators and diseases, can affect animal density as well. Where forage is the main limiting factor, not all of the phytomass produced is available to the animals, part of it may be unpalatable or out of reach for the animals or its nutrient content may be well below the required minimum level. Moreover, because of yearly variation in external factors, such as rainfall, and the dynamic nature of the interactions between the main components of the ecosystem (the vegetation and the herbivores), the ecological carrying capacity of a certain area can only be assessed after long periods of careful analysis of (trends in) both vegetation and herbivores in situations without human interference. It can thus be seen that there are many sides to the relationship between ungulates and the ecosystem they live in and hence, the analytical approach to estimate the ecological carrying capacity is often very complex.

As shown in Chapter 6, the quantity of grass forage in the dry season is greatly reduced by bush fires. Of what remains, only a small part is at least moderately digestible (> 50%) and nutritionally adequate (Chapter 6), containing at least 6% crude protein, the minimum for maintenance for grazing ungulates (Sinclair, 1975; H.H.T Prins, 1987; see also 7.5). Dry-season growth of perennial grasses increases the quantity of grass forage, but only significantly in the higher rainfall zones. Also there is much less woody foliage in the dry season than in the wet season, although it is of reasonable to good quality with at least 7% crude protein (Chapter 6). Hence on the basis of these findings it was argued (see 7.5) that the quantity of quality forage in the dry season is the main factor limiting the maximum number of animals. Research in other African savanna ecosystems, e.g. in the Serengeti national park in Tanzania, has shown that the availability of food resources is the predominant factor regulating animal numbers (Sinclair, 1977, 1979) which supports the assumption adopted here.

The definition of ecological carrying capacity in Chapter 2 can now be written more specifically as: the level of natural equilibrium between the availability of forage of adequate quality and its consumption by wild ungulates. This equilibrium can be indexed by the total live weight of the animals. The complex links between ungulates and their environment are thus simplified to the relationship between forage availability and forage consumption. Consequently, the limited availability of forage of adequate quality in the dry season is used as the simplified basis for the calculation of the potential dry-season stocking rate, or grazing capacity (see Chapter 2), for the various rainfall zones in the Baoulé. These stocking rates then serve as conservative but realistic estimates for the ecological carrying capacity in the Baoulé (see Fig. 9.1).

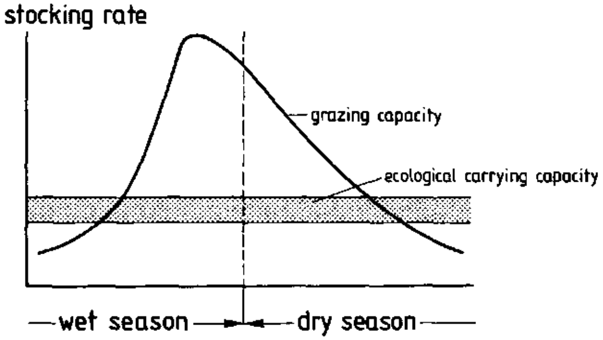


Fig. 9.1. Schematic representation of the theoretical stocking rates in the wet and dry season, based on the availability of adequate quality forage, compared to the theoretical level of ecological carrying capacity

As the availability of quality forage is directly related to the variability in annual rainfall, the calculations are based on a variable with relatively short-term fluctuations. Therefore we give an estimation of the ecological carrying capacity for years with normal and below normal rainfall.

9.2. Methods

Using the approach outlined in 9.1, the dry-season stocking rates have been calculated using a slightly modified version of Thalen's (1979) formula:

$$DSR_i = \frac{(F_g \times q_g \times p_g) \times c_g + (F_b \times q_b \times p_b)}{R_i}$$

in which:

DSR_i = dry-season stocking rates for animal species i

F_g = grass phytomass in the dry season

q_g = proportion of grass phytomass with adequate quality

p_g = proportion of grass phytomass removable on a sustained basis

c_g = proportion of grasses in the species' diet

F_b = availability of woody foliage in the dry season

q_b = proportion of woody foliage with adequate quality

p_b = proportion of woody foliage removable on a sustained basis

c_b = proportion of woody foliage in the species' diet

R_i = forage requirements of animal species i in the dry season

Thus the numerator represents the availability of forage, the denominator the animal requirements.

Availability of forage

Not all of the vegetation of adequate quality present in the dry season is available to the animals. Therefore, the data in Chapter 6 have to be corrected.

In perennial savanna grasses potentially all dry-season growth is food as its crude protein content meets the level required for maintenance (Chapter 6). However not all of it can be grazed. Stobbs (1973a,b) found large variations in the bite size of cattle in relation to the structure of grassy vegetation, especially concerning the proportion of stems and the density of the sward. The intake of forage by sheep appears to be related to the height of the sward: consumption increased with increasing leaf length (Allden & Whittaker, 1970). As the grass tufts are small in the north of the Baoulé but larger and taller in the south, the proportion of the plant that can be removed by grazing increases from north to south. On the basis of qualitative, comparative observations of grazed and ungrazed tufts and grazing animals, we assume that in normal rainfall years net availability (p_g in the formula) is at most 30, 50, 50, 90 and 90% of the grass tufts that could be grazed, calculated per rainfall zone from north to south respectively. In dry years these values are 0 (no dry-season growth available), 30, 30, 50 and 75% respectively. Only leaves of the wet-season growth of perennial grasses are suitable as forage, about 10% of the phytomass (Chapter 6). However, in all rainfall zones this quantity is reduced by over 90% by bush fires.

The quality of tall annual grasses, if they survive the bush fires, is not sufficient to consider them as dry-season forage (Chapter 6).

The vegetation of short annual grasses is dominated by *Loudetia togoensis*, a grass species which for unexplained reasons, is hardly eaten. Herbaceous dicotyledons are scarcely present in the dry-season phytomass (see Van Wijngaarden, 1988).

According to the data in Fig. 6.12 only the riverine grass *Panicum anabaptistum* is suitable. Estimated to be about 50% of the riverine phytomass (Smits, 1982) it has enough protein to be considered as dry-season forage. Also Cyperaceae on the river bed are of adequate quality and, as shown by grazing cattle in broken-down exclosures (Fig. 9.2), up to 75% of the phytomass can be grazed.

We assume that all savanna shrubs, bearing leaves in the dry season provide potential forage (Chapter 6) and that 50% of these leaves can be eaten by animals without being detrimental to the shrubs. We estimated that only about 10% of the woody foliage of riverine species is within reach of the animals, and this is confirmed by observations on bushbuck, the largest browsing species in this habitat type (Smits, 1982). However, the net available quantities are very small: less than 1 kg.ha^{-1} per average km^2 rainfall zone.

In contrast with deep rooting perennial grasses for which the northern zones of the Baoulé are a marginal area (see Chapters 3 and 6), a succession of several dry years has no immediate effect on the foliage production of shrubs in the savanna; usually it takes longer before a reduction in annual rainfall is reflected in the production of woody foliage (Geerling, pers.comm.). Therefore we applied the same phytomass values for normal and dry years.

Table 9.1 gives the net available quantity of forage per rainfall zone, based on the data from Chapter 6 but calculated with the DSR-formula given above.

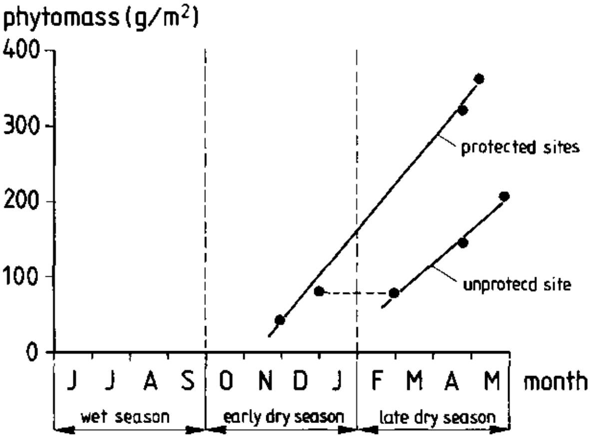


Fig. 9.2. Growth of riverine Cyperaceae in grazed and ungrazed areas

Table 9.1. Quantity of net available forage per rainfall zone in the dry season (kg DM.ha^{-1}).

	rainfall zone (mm)				
	600-700	700-800	800-900	900-1000	1000-1100
grasses and sedges					
normal rainfall years	16.4-31.3	50.8-68.4	48.2-70.3	164.2-198.2	235.7-263.5
dry years	12.1-20.3	24.5-33.7	24.6-35.6	55.0- 67.7	106.1-133.6
woody foliage					
all years	29	33	38	42	47

Animal requirements

As larger animals are cheaper per unit body mass in terms of daily energy and nutrient requirements (see Chapter 7; Moen, 1973; Van Soest, 1982) the problem arises of which body weight to choose for calculating these requirements and thus potential stocking rates. This problem has been solved by analysing the total daily consumption of dry matter by ungulates in various national parks and game reserves in the Sudan savanna. Assuming that the daily intake of food is 7.1% of their metabolic body weight (Chapter 7), animal densities have been converted into daily consumption of dry matter per km^2 to find out the proportion of the total consumption that can be attributed to the different species. It appeared that in the Sudan savanna, a few species accounted each for 10% or more of the total consumption, Fig. 9.3, and when the different areas are compared, four species dominate the ungulate community with respect to the dry matter consumption:

elephant (body weight 1,725 kg, mixed feeder)
buffalo (body weight 450 kg, grazer)
roan antelope (body weight 185 kg, grazer/mixed feeder)
hartebeest (body weight 110 kg, grazer)

Elephant + buffalo and elephant + hartebeest were chosen as representative ungulate combinations of the ungulate community for further calculations of the potential stocking rates. Although it might be argued that the selectivity of the three ungulate species for certain plant species is not taken into account in these calculations, as far as the *potential* herbivore biomass per rainfall zone is concerned we assume that this factor can be neglected because:

* the dry-season growth of perennial grasses forms the bulk of the available phytomass in the herbaceous layer and without doubt is eaten by all grazing ungulates;
* the diet of elephant contains a large number of woody plant species despite sometimes high levels of secondary plant metabolites such as tannins (Geerling, 1973; Croes, 1987; Rood, 1988); only very few species are not eaten at all (Geerling, 1973; Rood, 1988; Jachmann et al., 1989).

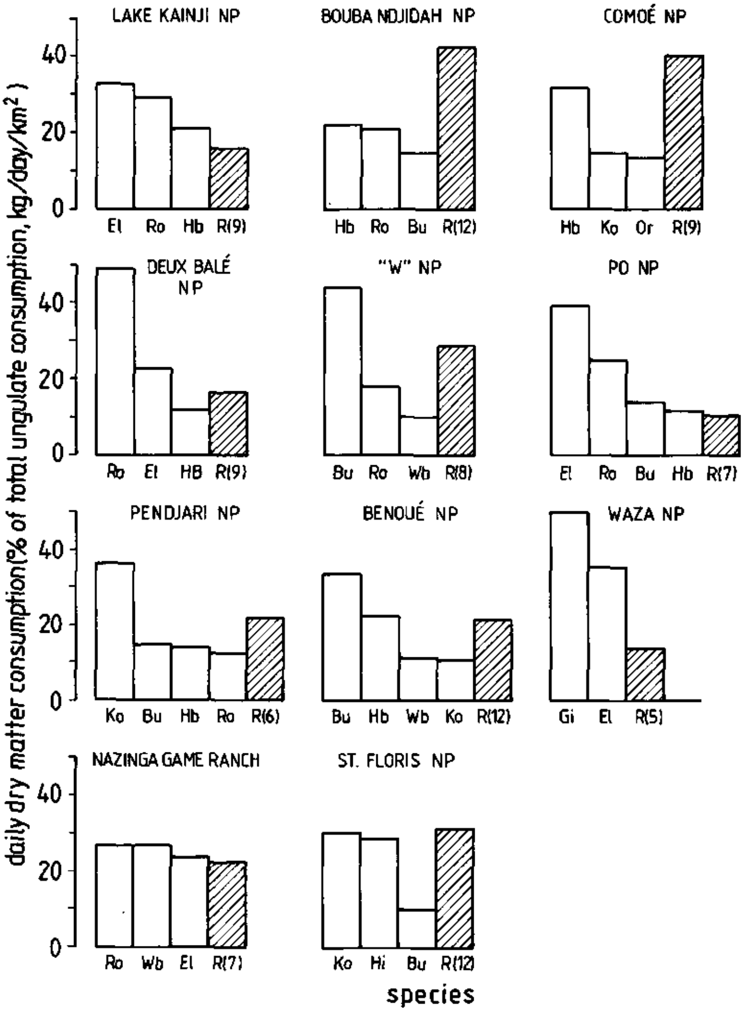


Fig. 9.3. Histograms showing animal species with a daily dry matter consumption exceeding 10% *of the daily dry matter consumption of the total ungulate community in different areas in the Sudan* savanna. Data from Esser & Van Lavieren (1979), Barber et al. (1980), East (1984) and Jachmann (1987a). El = elephant, Ro = roan antelope, Hb = hartebeest, Bu = buffalo, Ko = kob, Or = oribi, Wb = waterbuck, Gi = giraffe, Wh = warthog, Hi = hippopotamus, R = remaining species, () = number of remaining species

Concerning the quantity of forage, a further adjustment is called for. We assume that the requirements of energy and nutrients are fulfilled when the daily intake of food of sufficient quality (for hartebeest and buffalo containing not less than 6% crude protein and for elephant not less than 5%) is at least 7.1% of their metabolic body weight (Chapter 7). Moreover, we assume that these requirements are constant throughout the dry season. The required intake of elephant

Plate 23. African buffalo is one of the four ungulate species which dominate the ungulate community of the West African savanna

was doubled in order to take into account secondary plant compounds such as tannins. These are found in considerable quantities in the dry-season woody foliage and reduce plant digestibility by up to 50% (see Chapter 6).

Concerning the dry-season availability of grasses and sedges, the length of the dry season is set at 220 days in years with normal rainfall and at 250 in years with below normal rainfall (Chapter 3). For woody foliage, the length of the minimum period is shorter, 90 and 120 days respectively. That the length of the dry season is generally longer to the north and shorter to the south is not accounted for.

Animals may loose some body weight in the dry season by using stocked-up energy reserves (fat). However, there is no information on the physiological tolerance to weight loss of particular species. Therefore this was not taken into account in the calculations (see also 9.5).

9.3. Potential stocking rates

Assuming that all of the net available forage is consumed, the dry-season stocking rates were calculated for the species selected (Table 9.2 and Fig. 9.4).

The data indicate a situation in which *all* potential net available forage is consumed by the species concerned but under natural circumstances this does

Table 9.2. Potential dry-season stocking rates ($kg.km^{-2}$) for two combinations of ungulate species per rainfall zone.

	rainfall zone (mm)				
	600-700	700-800	800-900	900-1000	1000-1100
normal rainfall years					
hartebeest	331-632	1,026-1,382	974-1,420	3,317-4,004	4,762-5,323
or					
buffalo	496-947	1,534-2,071	1,459-2,128	4,971-6,000	7,135-7,977
elephant	1,462	1,664	1,916	2,118	2,370
dry years					
hartebeest	215-361	436-599	437-633	978-1,204	1,886-2,375
or					
buffalo	322-541	653-898	655-948	1,465-1,804	2,827-3,559
elephant	1,097	1,248	1,437	1,588	1,778

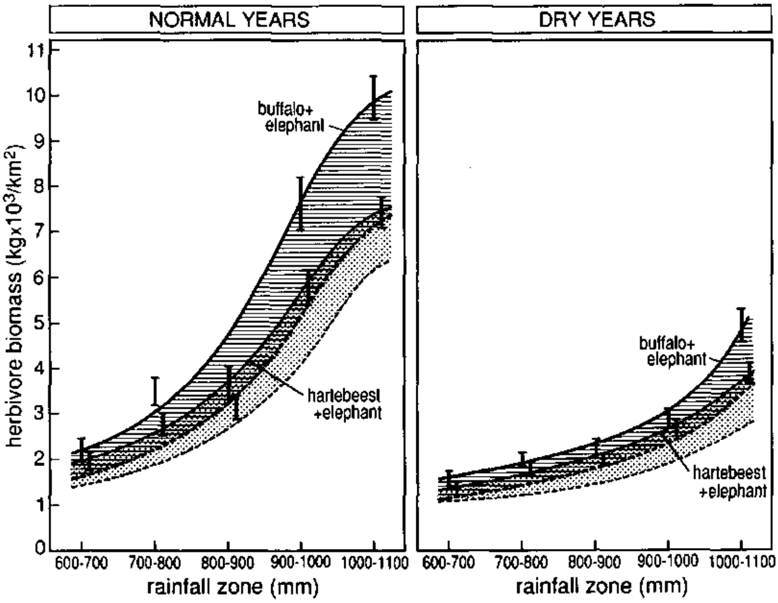


Fig. 9.4. Relationship between rainfall and potential biomass of two combinations of ungulates in years with normal is rainfall and in dry years; shaded areas indicate the 75-100% range of potential biomass

not generally occur: animals nearly always overlook some forage, even in times of limited availability. Moreover, sometimes the quantity of net available forage may be slightly overestimated (e.g. the quantity remaining after fire). As a conservative estimate of the potential carrying capacity is safer than one that is too optimistic (see Fig. 1.1), it is more realistic to say that the potential dry-season stocking rates, and thus the potential carrying capacity, will be in the range of 75%-100% of the values presented in Table 9.2.

The results from the DSR-formula for calculating the animal requirements show that the heavier the animal species, the higher the biomass of this species that can be maintained on one km^2. Hence, we conclude that at the same level of food availability the potential carrying capacity of an area in terms of biomass per km^2 can be influenced by the *composition* of the ungulate community.

A comparable dry-season ungulate biomass in years with normal rainfall is found in dry years in zones with about 200 mm more rainfall, because of a similar trend in the dry-season growth of perennial savanna grasses (see Chapter 6). For the elephant it is the longer period of minimum available woody foliage which contributes to this effect.

The most important conclusion, however, is that both in years with normal rainfall and dry years, the total dry-season stocking rates strongly increase with increasing mean annual rainfall though not linearly. The effect of the dry-season growth of perennial savanna grasses and its quantity obvious: in lower rainfall zones, animal biomass is kept down by the lack of nutritious forage for grass-preferring species, and increases strongly in the higher rainfall zones where this type of forage is produced in substantial amounts.

To summarize we conclude that:

* from north to south the ecological carrying capacity increases; for grass-preferring ungulates this increase is particularly the result of an increase in the quantity of dry-season growth of perennial savanna grasses (Fig. 6.8);
* the lower rainfall zones are mostly unsuitable for the larger grazing ungulates as there is none or very little nutritionally acceptable forage, especially in dry years; this is confirmed by the behaviour of transhumant cattle visiting the Baoulé in the dry season: they show a rapid migration from the southern pastures of the Sahel to the higher rainfall zones (800 mm annual rainfall or more); these zones have substantial quantities of dry-season growth (De Bie & Kessler, 1983).

9.4. Validity of the potential ecological carrying capacity

Ideally, the validity of the calculation of the potential ecological carrying capacity should be obtained from information on actual ungulate biomass in the Baoulé. However, actual data on animal numbers is not representative of a response to natural conditions. The numbers are too low because of:

Table 9.3. Ungulate biomass ($kg.km^{-2}$) in several conservation areas in West Africa.

area	rain-fall (mm)	1 Green (1973)	2 Child (1974)	3 Heister-berg (1975)	4 FAO (1975)	5 Bosch (1976)	6 Greling & Toni (1976)	7 Esser & Van Lavieren (1979)	8 Bousquet et al. (1982)	9 Barber et al. (1980)	10 Milligan et al. (1982)	11 East (1984)	12 Stark (1986)	13 10+11 corrected
1 Waza NP	700	–	–	–	–	–	–	A:4,268 B:2,098 C:1,247	–	1,785	–	–	–	–
2 'W' NP	730	–	–	–	–	–	–	–	1,080	–	1,121	1,341	1,344	1,261
3 Po NP	900	–	–	1,822	–	–	1,572	–	306	1,562	1,812	1,806	1,806	1,817
4 Deux Balé NP	970	–	–	–	–	–	–	–	533	1,130	1,045	1,029	1,029	1,041
5 Arli NP	1000	A:3,015 B:2,202	–	–	–	–	1,679	–	1,583	2,386	1,831	1,756	2,202	1,777
6 Yankari GR	1000	–	–	–	357	–	–	–	–	–	349	–	–	359
7 Pendjari NP	1050	–	–	–	–	–	–	–	–	–	2,746	–	2,746	2,751
8 Benoué NP	1100	–	–	–	–	–	–	–	–	–	–	–	1,325	–
9 Borgu GR	1100	–	839	–	–	–	–	–	–	710	–	–	–	–
10 Lake Kainji NP	1100	–	–	–	–	–	–	–	–	–	1,274	1,284	1,284	1,288
11 St. Floris NP	1150	–	–	–	–	–	–	–	–	A:3,533 B:1,551	4,032	–	4,032	2,600
12 Bouba Ndjidah NP	1200	–	–	–	–	2,012	–	–	–	2,548	2,321	2,342	2,342	2,416
13 Comoé NP	1200	–	–	–	–	–	–	–	–	290	213	247	247	253

- hunting and poaching, considered to have a severe impact (Geerling & Diakité, 1988), but no reliable information exists which enables corrections;
- increasing competition with both sedentary and transhumant livestock, the latter invading the area in the dry season in very large numbers (De Bie & Kessler, 1983);
- decrease of habitat types as they are turned into arable land.

Historic data is lacking, fragmentary or inaccurate (e.g. Sayer, 1977).

Thus, it was necessary to obtain validity for the potential ecological carrying capacity by comparing our data with that from other sources and areas. In Part I and Part II we have shown that the West African savanna is a rather uniform landscape and that its ungulate communities are comparable. In several national parks and game reserves in the Sudan savanna, animal populations have been counted in the recent past, thus providing data for comparison (Table 9.3). Explanation of Table 9.3:

- Columns 1-8 give data from original publications. Sometimes however, it is not clear which counting methods were used for population estimates.
  Also the biomass may have been calculated with slightly different weight units per species.
- Barber et al. (1980) and Milligan et al. (1982) were the first to present comparative biomass figures of different areas (columns 9 and 10). East (1984) also provides data of ungulate biomass in conservation areas in West Africa (column 11) as part of an overview concerning the whole of Africa south of the Sahara. Using the original population counts he arrived at somewhat different figures than Milligan et al. (1982) who used the same sources. However, Milligan et al. (1982) did not include hippopotamus, and East (1984) excluded the duiker species. Column 13 gives the corrected figures using the information provided by both. Stark (1986c) mainly used these two sources for his overview (column 12).
- As all original surveys were carried out at least 4 years after 1970 (unless otherwise indicated), animal densities and biomass represent ungulate populations living in a period with below normal rainfall.
- In column 8, biomass figures calculated from the results of ground surveys made by Bousquet et al. (1982) in 1980-1982, are given. Their data (Bousquet et al., 1982) show the severe decline in animal numbers in this zone between successive counts. In the four conservation areas concerned hunting and poaching were named as the prime causes for this decline which ranged from 20% to 80%,
- The effect of hunting and poaching is also clear from the data of Barber et al. (1980) for St. Floris national park in the Central African Republic. Whereas the total national park (2,643 km^2) has an ungulate biomass of 1,551 kg per km^2 (11B in Table 9.3), the best guarded area (853 km^2) with virtually no hunting or poaching activities has more than twice this biomass (11A in Table 9.3).

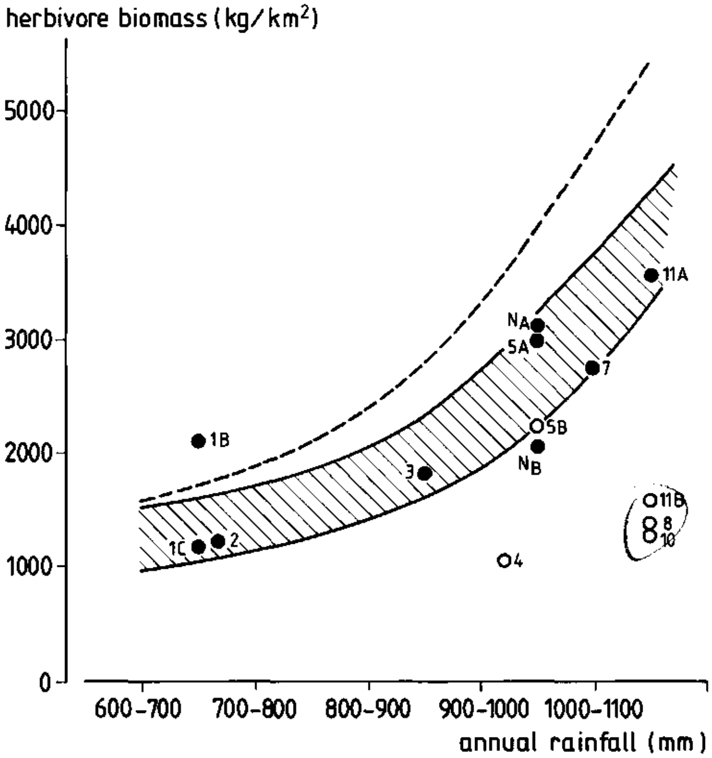


Fig. 9.5. Ungulate biomass (kg.km^{-2}) of several West African conservation areas in relation to annual rainfall (mm) in the dry years following 1969.
filled circles : areas without any serious poaching
open circles : areas with considerable poaching
potential ecological carrying capacity in dry years in the Baoulé
: elephant-buffalo line
: elephant-hartebeest line, shaded area is the 75-100% range
for area codes, see Table 9.3 and text

In Fig. 9.5 the herbivore biomass data from Table 9.3 is plotted against rainfall, with the potential stocking rates for the Baoulé in dry years for comparison. All counts in these conservation areas took place at least three years after the start of the severe and long drought of 1969/1970. It is concluded that conservation areas (or parts of them) with hardly any or no poaching, have an ungulate biomass which agrees well with the hartebeest-elephant biomass curve for dry years in the Baoulé. Hence they support the validity of this curve of potential carrying capacity in the Baoulé and confirm that potential ungulate biomass in this area can be quantified by considering the availability of quality forage.

The buffalo-elephant curve appears to be too optimistic to predict herbivore biomass, especially in the higher rainfall zones.

The validity of the hartebeest-elephant curve is also strengthened by Jachmann's (1987a) calculations of animal densities at the Nazinga Game Ranch in Burkina Faso. The animal numbers are stable, and the ungulate biomass of this ranch is just above 2,000 kg per km^2 ($N_B$in Fig. 9.5), and in its best protected area about 3,000 kg per km^2 ($N_A$in Fig. 9.5). These figures correspond very well with the range of values predicted by the hartebeest-elephant curve (Fig. 9.5).

Data for Waza national park (Esser & Van Lavieren, 1979) shows the ungulate biomass of a flood plain before and after the construction of a dam. Until 1979, when a dam was built in the Logone river, vegetation growth was not only determined by rainfall but also by seasonal flooding that inundated the plain. Values for the ungulate biomass were well above the predicted values of carrying capacity for a 700 mm savanna in both normal and below normal rainfall years (1A (1961-survey) and 1B (1978-survey) in Table 9.3 and Fig. 9.5). However, since flooding has been prevented, the area is now comparable to the other 700 mm savanna biotopes. The kob, a flood plain species (see Part II), has decreased in number dramatically and is near to extinction (Geerling, pers. comm.). When the ungulate biomass in 1977 is corrected for this decline of kob, the result, about 1,200 kg per km^2, fits the predicted dry-year ecological carrying capacity (1C in Fig. 9.5).

Although there is a relationship between annual rainfall and vegetation com-

Plate 24. Kob in Waza national park before the building of a dam in the Logone river

position and production, limiting animal numbers through the availability of quality forage, this does not mean that the animal species composition or their density is always comparable. Within the conservation areas in West Africa, the availability of habitat types varies. As species show clear habitat preferences (7.3), the composition of the ungulate community and the numbers of each species vary although generally the same few species dominate (see 9.2). Whereas the Nazinga Game Ranch, Arli national park and Pendjari national park have roughly a similar ungulate biomass, there is hardly any kob and no korrigum on the Nazinga Game Ranch whereas these species are common in the two national parks. In contrast, the elephant is rare in Arli national park and Pendjari national park and more numerous on the Nazinga Game Ranch (Green, 1979; East, 1984; Jachmann, 1987a).

9.5. Potential animal numbers in the Baoulé

Now that the validity of the estimates of the potential ecological carrying capacity has been shown for the Sudan savanna and in particular for the Baoulé, we can speculate on what this information means in terms of composition and potential animal numbers for each rainfall zone in the Baoulé. The assortment of species and their respective numbers must be known before sustainable exploitation of wildlife in the area can start.

To translate herbivore biomass to numbers of each species, we have to consider some aspects of the availability of basic resources (9.2) with respect to the species' specific requirements.

Although *shelter* is limited in the Baoulé (Van Wijngaarden, 1988), there is always shelter for species that need it.

Surface water is available everywhere in the dry season (Fig. 7.3) but is limited, especially in regions with less than 700 mm annual rainfall or in dry years less than 700-800 mm. Consequently, the water-dependent species, hippopotamus, reedbuck, waterbuck and buffalo, cannot live in these regions (De Bie & Kessler, 1983). Although elephant is also water-dependent, it is able to cover long distances to water points (Van Melle, pers.comm.).

Dry-season growth of the perennial savanna grasses is the main food source for the grazing ungulates as well as for the mixed-feeding but grass-preferring roan antelope and oribi. Consequently grass-preferring ungulates, both domestic and wild, cannot survive in regions with less than 800 mm annual rainfall or in dry years less than 900 mm (Chapters 6 and 7; De Bie & Kessler, 1983). Reedbuck and waterbuck are exceptions, sometimes living on relatively small patches of regrowth in the 700-800 mm rainfall zone and supplementing their diet with riverine grass species (see Chapter 7).

Bearing these restraints in mind, not all species occur throughout the area. Table 9.4 gives the occurrence of the grass-preferring species in each rainfall zone. The African buffalo has been included in this table as it is known to have occurred in the Baoulé and probably still does in very small numbers. The Baoulé

Table 9.4. Presence of grass-preferring species per rainfall zone[1]).

	rainfall zone (mm)									
	normal rainfall years					dry years				
	600-700	700-800	800-900	900-1000	1100-1000	600-700	700-800	800-900	900-1000	1100-1000
Wh	*	*	*	*	*	*	*	*	*	*
Hi		*	*	*	*			*	*	*
Rb		*	*	*	*			*	*	*
Wb		*	*	*	*			*	*	*
Ro	*	*	*	*	*	*	*	*	*	*
Hb			*	*	*				*	*
Or	*	*	*	*	*	*	*	*	*	*
Bu			*	*	*				*	*

[1]) Wh = warthog, Hi = hippopotamus, Rb = reedbuck, Wb = waterbuck, Ro = roan antelope, Hb = hartebeest, Or = oribi, Bu = buffalo

is potentially suitable for this species but it has disappeared, mainly through hunting and the strong influx of transhumant cattle in the area since the drought started in 1969-1970.

The next step is to determine the proportion of the dry-season growth in the diet of the various species and what proportion of the dry-season growth available will be used by each species.

Insufficient quantitative observations with respect to these aspects of dry-season growth of perennial grasses has forced us to make assumptions. Because the bulk of the grass phytomass in the dry season consists of this dry-season growth, especially in the higher rainfall zones, the first assumption is that 90% of all monocotyledons found in the diet of these ungulates is dry-season growth of perennial savanna grasses (the percentage of dietary monocotyledons is derived from data in Chapter 7). Current observations at the Nazinga Game Ranch in Burkina Faso show that at least for roan antelope and hartebeest this assumption approaches reality (Legemaat, pers.comm.).

It is even more difficult to assess what proportion of this dry-season growth each species will take. Considering that the large species, hippopotamus and buffalo, are less selective than the smaller species, and that the smaller species take proportionally less when there is more phytomass per grass tussock, an allocation for each species was made (Table 9.5). This is based on the assumption that the larger the species the more it can take from a tuft of grass. The difference between northern and southern roan antelopes (see Chapter 7) has been set at 800-900 mm annual rainfall (900-1000 mm in dry years).

For each rainfall zone the biomass of each species was calculated using the formula:

$$N_i = \frac{\text{net quantity of dry-season growth x } a_i}{(b_i \text{ x } \%M) \text{ x } (0.071 \text{ x } W^{0.75}) \text{ x } T}$$

Table 9.5. Proportion of dry-season growth of perennial grasses allocated to each animal species (% of net availability).

rainfall zone (mm)		species	proportion of allocated dry-season growth per animal species
normal years	dry years		
600-700	600-800	warthog, oribi:	40%
		roan antelope:	20%
700-800	800-900	hippopotamus:	35%
		roan antelope, waterbuck, warthog:	15%
		reedbuck, oribi:	10%
800-1100	900-1100	hippopotamus, buffalo:	25%
		roan antelope, waterbuck, warthog, hartebeest:	10%
		reedbuck, oribi:	5%

in which:
N = number of species i
a = proportion of dry-season grass growth allocated to species i
b = proportion of dry-season grass growth in diet of species i
M = percentage of monocotyledons in diet of species i
W = mean population body weight (see note under Table 7.21)
T = length of the dry season in days

The potential numbers of grass-preferring species are given in Table 9.6. Numbers of browsing ungulate species have been calculated in the same way. However, before their potential numbers could be calculated, the amount of woody foliage available had to be adjusted for the proportion taken by grazing ungulates, because in the dry season these species take their share as well (within the grazer guild the refinement of sequence has not been undertaken). As it was difficult to differentiate between the various browsing ungulate species with respect to their diet, elephant was chosen as the representative of the large ones. Giraffe, although also large, was unsuitable as it not only utilizes the shrub layer but also the tree layer for which we have no data on foliage production nor could it be found in other studies made in West Africa. We chose the bushbuck to represent the small browsers, which also include the red-flanked duiker

Table 9.6. Potential numbers of grass-preferring ungulates per rainfall zone in the Baoulé.

	rainfall zone (mm)						
	600-700	700-800	800-900	900-1000	1000-1100		
area (km^2)	1,231	3,716	6,670	3,484	1,041		
						Total number	animals per km^2
normal rainfall years							
warthog	600	5,900	5,400	13,800	6,300	32,100	2.0
hippopotamus	–	1,300	1,300	3,400	1,600	7,500	0.5
reedbuck	–	5,900	4,400	11,200	5,100	26,700	2.0
waterbuck	–	3,600	3,500	9,000	4,100	20,100	1.0
roan antelope	200	3,400	2,600	6,700	3,100	15,800	1.0
hartebeest	–	–	3,300	8,600	3,900	15,800	1.0
oribi	2,400	15,800	11,600	29,900	13,700	73,800	5.0
buffalo	–	–	2,700	6,900	3,200	12,800	0.8
dry years							
warthog	0	1,500	800	3,400	2,000	7,800	0.5
hippopotamus	–	–	200	800	500	1,500	0.1
reedbuck	–	–	800	2,800	1,700	5,200	0.3
waterbuck	–	–	500	2,200	1,300	4,000	0.3
roan antelope	0	400	500	1,600	1,000	3,500	0.2
hartebeest	–	–	–	2,100	1,300	3,400	0.2
oribi	0	4,600	2,100	7,300	4,400	18,500	1.0
buffalo	–	–	–	1,700	1,000	2,700	0.2

and the Grimm's duiker with comparable diets. The dry season was calculated as 90 days in normal rainfall years and 120 in dry years. In this period the elephant's diet consists entirely of browse, and that of the bushbuck of half grasses and sedges, half browse (Chapter 7).

The potential numbers of browse-preferring species for each rainfall zone are given in Table 9.7.

Fig. 9.6 shows the relationship between the total dry-season stocking rates (kg.km^{-2}) of all ungulate species and rainfall.

The numbers of a particular species should be considered as indicative, as changes in our assumptions will result in different numbers, especially concern-

Table 9.7. Potential numbers of browsing ungulates per rainfall zone in the Baoulé.

	rainfall zone (mm)						
	600-700	700-800	800-900	900-1000	1000-1100	Total number	animals per km^2
area (km^2)	1,231	3,716	6,670	3,484	1,041		
normal rainfall years							
elephant	1,000	3,300	7,000	3,700	1,200	16,100	1.0
bushbuck	700	3,200	3,900	900	400	9,200	0.6
dry years							
elephant	800	2,600	5,400	3,100	1,000	12,800	0.8
bushbuck	500	2,400	3,000	700	300	7,000	0.4

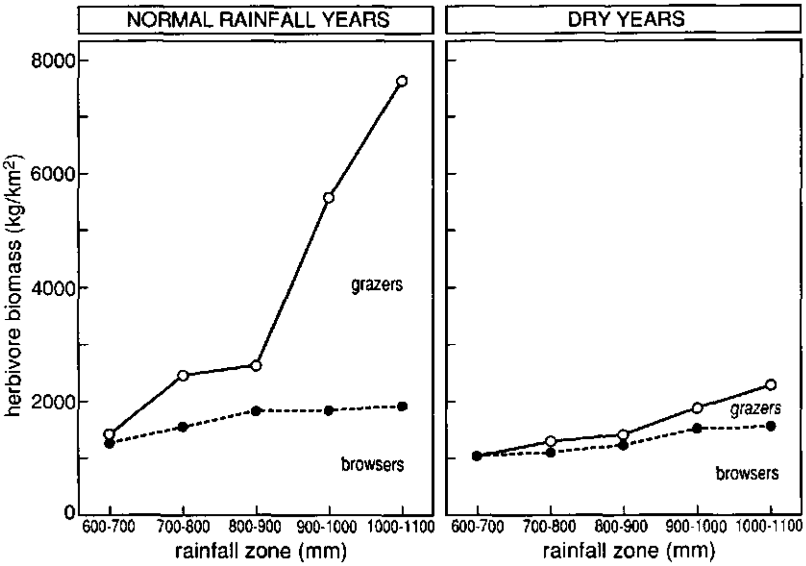


Fig. 9.6. Relationship between total dry-season stocking rates (kg.km^{-2}) and rainfall in the Baoulé

ing the grass-preferring species. In particular, the allocation of the dry-season growth of perennial grasses over the various grazers might be called speculative but is the best guess we can make until the results of future research on this aspect.

Nevertheless, these calculations of the dry-season stocking rates for the various animal species in the Baoulé show that:

* the numbers of grass-preferring ungulates increase from north to south as a result of an increase in the quantity of dry-season growth of perennial savanna grasses;
* as smaller grass-preferring ungulates are less affected by a decrease in this type of forage during a series of dry years, these species become relatively more numerous at that time;
* in normal rainfall years, browsers dominate the ungulate community in the northern and central parts of the area. In the southern part the grazers utilize a substantial proportion (increasing with rainfall) of woody foliage thereby reducing the quantity 'left' for the browsers. It seems that above 800 mm annual rainfall grazers directly compete with browsers for woody foliage and we have assumed that the grazing species are the more successful. If the reverse is true, this will certainly have an effect on the dry-season stocking rates, but this will be slight with respect to the total ecological carrying capacity of the area, not exceeding 500 $kg.km^{-2}$ more in the highest rainfall zone in normal rainfall years.

Tropical ungulates do not stock large quantities of fat, especially not subcutaneous fat (Table 9.8; Ledger, 1963). Therefore, the utilization of these energy reserves could influence the estimates only marginally on a year-round basis.

Table 9.8. Condition indices of bushbuck (Bb) and roan antelope (Ro), shot in the Baoulé in 1981; measurements were taken following Riney (1982). KFI = kidney fat index, BMI = bone-marrow fat index

animal	sex	date	field index	mean KFI	BMI	BMI class	percentage bone-marrow fat	depth back fat
Bb I	M	15-1-81	III¹)	24.7	64.7	II²)	85.5	1 mm
Bb II	F	8-2-81	III	109.2	67.1	II	82.4	1 mm
Bb III	F	10-2-81	III	15.6	61.5	II	76.8	1 mm
Bb IV	M	14-2-81	III	23.4	26.6	I	22.2	1 mm
Bb V	F	9-3-81	III	11.9	63.9	II	85.6	1 mm
Bb VI	M	23-3-81	III	16.7	45.8	I	80.4	1 mm
Bb VII	M	3-4-81	III	6.6	35.1	I	63.3	1 mm
Ro I	F	14-4-81	III	29.2	61.6	II	92.2	1 mm
Ro II	M	29-4-81	III	5.7	10.9	I	23.4	1 mm

¹) general body condition; good (III), fair (II) or bad (I)

²) III: BMI > 85% (good), II: BMI = 50%-85% (fair), I: BMI < 50% (bad) after Brooks (1978)

Table 9.9. Potential and actual dry-season densities (number.km^{-2}) of ungulates in the Baoulé[1]).

	potential density	actual density[2])
warthog	0.5	0.9
hippopotamus	0.1	< 0.01
bushbuck + duikers	0.4	0.5
reedbuck	0.3	0.3
waterbuck	0.3	< 0.01
roan antelope	0.2	0.03
hartebeest	0.2	0.01
oribi	1.2	0.3
total biomass (kg.km^2)	1,773	< 100

[1]) elephant and buffalo: no census data

[2]) source: Table 7.2

Also predation, one of the complications when calculating the ecological carrying capacity, mentioned by Bell (1984), has not been taken into account.

If we ask to what extent do the potential numbers compare to the actual numbers of the various species in the Baoulé, we see in Table 9.9, that numbers differ markedly. Only for the reedbuck and the smaller browsers (the bushbuck and the duikers) are the figures in the same order of magnitude. Except for the warthog, which is present in higher numbers than expected, the potential numbers for all other species are much higher than the actual numbers. Heavy poaching and uncontrolled subsistence hunting are considered to be the main causes for this decline in animal numbers (De Bie et al., 1987). These activities perhaps also explain the increase of warthog numbers. Considered an impure species by the Mohammedan society it is hunted in only very small numbers. Other grass-preferring species are hunted instead, thus improving the availability of forage for the warthog, and allowing its numbers to increase.

9.6. Conclusions

The most important conclusion from the foregoing paragraphs is that between 600-700 mm and 1000-1100 mm annual rainfall the ecological carrying capacity of the Baoulé increases with rainfall. In the lower rainfall zones animal numbers are kept down through a lack of forage in the dry season of a quality acceptable for grass-preferring species. Where this type of forage reaches substantial quantities in the higher rainfall zones, the ecological carrying capacity increases sharply. Years with below normal annual rainfall result in lower potential animal numbers because of a decline in the quantity of dry-season growth of perennial grasses. This effect is not direct but a time-lag of several years is apparent as shown by the correlation between livestock numbers and rainfall in the Sahel (Table 11.4 and Fig. 11.2). A series of dry years affects the ecological carrying capacity much more than one dry year.

As daily forage requirements are related to the metabolic mass ($W^{0.75}$) of the individual species, the predicted level of the ecological carrying capacity of an area with a certain annual rainfall will be affected by animal species composition.

The ungulate biomass of other conservation areas in the West African savanna provides evidence for the validity of the presented relationship between rainfall, primary production and 'hartebeest-elephant' biomass in the Baoulé. I therefore conclude that this relationship between the ecological carrying capacity and rainfall applies generally to the West African savanna.

Animal species can be classified into nine groups, according to their weight and feeding style. When the potential numbers of each animal species in Table 9.6 are converted into herbivore biomass for each group (Table 9.10), it appears that the Sudan savanna is dominated by large herbivores. The pattern corresponds rather well with the distribution of herbivore biomass in the comparable moist-dystrophic savanna of Kasungu national park in Malawi (southern Africa) (Bell, 1984). Although there are differences in habitat and vegetation structure between these areas, the similarity in the distribution of herbivore biomass points to compensatory feeding between species, especially those in different weight classes.

In the lower rainfall zones in the Sudan savanna, the ungulate biomass tends to be dominated by browsing ungulates. Above 800 mm annual rainfall, grass-preferring species are in the majority but in dry years the proportion of browsing species increases as there is much less grass for grazers. The possibility of using domesticated herbivores with comparable feeding styles instead of wild grass-preferring herbivores as in livestock husbandry is therefore also limited.

The low level of the ecological carrying capacity in the lower rainfall zones and the large difference in capacity in all rainfall zones between normal rainfall years and after a series of dry years have two important consequences for the management of the savanna ungulate community.

Table 9.10. Percentage of total herbivore biomass per animal species group in the Baoulé (normal figures) and in Kasungu national park, Malawi (Bell 1984)(italic figures).

feeding style	grazer	mixed feeder	browser	total
weight class				
large > 1,000 kg	20	50	0	70
	1	*55*	*1*	*57*
medium 100-1,000 kg	17	5	0	22
	33	*3*	*1*	*37*
small < 100 kg	6	1	1	8
	1	*1*	*4*	*6*
total	43	56	1	100
	35	*59*	*6*	*100*

Plate 25. True grazers such as the hartebeest, are vulnerable to small reductions in annual rainfall

Firstly, subpopulations of the larger, especially grazing herbivores in the lower rainfall zones are very vulnerable to the consequences of climatic change. No dry-season growth of perennial grass is produced following a small reduction in the annual rainfall. Hence these subpopulations can only be protected effectively if corridors are made to southern subpopulations from where a build-up of numbers can be supported or, in the worst case, can start. Secondly, uncontrolled hunting could drive the northern subpopulations more easily into extinction than the southern subpopulations because of their generally lower overall densities and vulnerability due to the environment in which they live. Any management, aiming at the long-term survival of these populations has to take these aspects into account.

In the Sahel where the annual rainfall is below 600-700 mm, the tall perennial and annual savanna grasses are replaced by short annual grasses. As shown by the project 'Production des Paturages Saheliens' (Penning de Vries & Djitèye, 1982), the quality of short annual grasses generally remains higher throughout the year than that of the grasses in the savanna, and this allows a higher density of animals (see also Chapter 10). Hence the transition from short annual grasses in the Sahel to the taller annual and perennial grasses in the Sudan savanna causes a strong reduction in the ecological carrying capacity when entering the

Sudan zone from the north. Observations on the movements of transhumant cattle confirm the absence of suitable forage in the 600-800 mm rainfall zone of the savanna: during migration large numbers pass quickly through this zone to more southern regions (De Bie & Kessler, 1983). The carrying capacity in more southern rainfall zones, where the annual rainfall is 800 mm or more, is improved for grazers by the dry-season growth of the perennial grasses.

In zones with an annual rainfall above 1100 mm the number of trees increases but the quantity of woody foliage per tree remains the same (Geerling pers. comm.). Consequently woody phytomass moves up vertically at the expense of shrubby phytomass, and we can expect the opportunities for browsers to decrease, even for elephant, which prefers all sizes of shrubs and small trees, as shown by observations on the Nazinga Game Ranch (Croes, 1987; Rood, 1988). In the herbaceous layer perennial savanna grasses are replaced by other species, e.g. *Andropogon tectorum*, *Hyparrhenia* spp. and *Imperata cylindrica*. There is little information on their ecology, especially with regard to quality parameters. Because of a longer wet season and less frequent burning we expect the ecological carrying capacity to decline in these zones.

10. The ecological carrying capacity of the West African savanna: comparisons with other approaches and regions

10.1. Introduction

As the relationship between rainfall and primary production is clearly visible in the field, several studies have focussed on the mathematical aspect of this relationship (e.g. Whittaker, 1970; Sinclair, 1975; De Leeuw, 1976, 1977; LeHouérou & Hoste, 1977). These studies were followed by explorations of the relationship between rainfall and herbivore biomass and its use for predicting animal stocking rates, not only in West Africa but also in East and Southern Africa (Coe et al., 1976; Bell, 1984; East, 1984).

This attention for carrying capacity partly originated from the objective in cattle husbandry and game ranching to produce maximum sustainable yields. Interest in animal abundance and in populations in equilibrium with their environment, resulted from more emphasis on research into the population dynamics of large animals. Knowledge on African ecosystems has increased in the last decades and ecosystems with large ungulates have received special attention e.g. Serengeti national park (Sinclair & Norton-Griffiths, 1979), Nylsvley nature reserve (several papers in Huntley & Walker, 1982), Tsavo national park (numerous publications by Leuthold and others). It has become apparent that to understand the regulation of populations of large ungulates, one has to consider their environment explicitly as part of the total ecosystem (Botkin et al., 1981). The mechanisms by which the environment affects the birth and death rate particularly need analysis (Botkin et al., 1981).

In this chapter, the ecological carrying capacity of savanna ecosystems in Africa and Australia as predicted by various methods is discussed in view of the potential ecological carrying capacity as calculated for the Baoulé.

10.2. Other approaches for the assessment of carrying capacity of the West African savanna

This paragraph describes the approaches of several authors for assessing the ecological carrying capacity of the West African savanna for grazing herbivores, in this case cattle. It analyses similarities and differences with our results in the Baoulé.

A. De Leeuw (1976,1977) assessed the potential carrying capacity of the northern Nigerian rangelands for cattle, by examining the species composition of the herbaceous layer and considering its forage yield, found by clipping experiments. He found that :

$$\text{primary production (kg.ha}^{-1}) = 2.36 \times \text{rainfall (mm.year}^{-1}) + 34.7$$

De Leeuw assumed that an animal of 300 kg requires about 15 kg forage per day and applied a correction for plant losses and a proper use factor to conserve plant production potential. He predicted that the potential carrying capacity increases with rainfall (Fig. 10.1).
However, his values for the savanna zone are much higher than predicted by the 'hartebeest'-curve in our study (Fig. 10.1). This difference is mainly caused by:

- * De Leeuw's (1976,1977) assumption that all herbaceous phytomass is potential forage, which does not take quality parameters such as the protein content, into account;
- * the calculation, based on the maximum standing crop of the herbaceous vegetation, disregarding the effect of fires on the total phytomass and the dry-season growth.

Consequently potential carrying capacities are largely overestimated, especially in the lower rainfall areas.

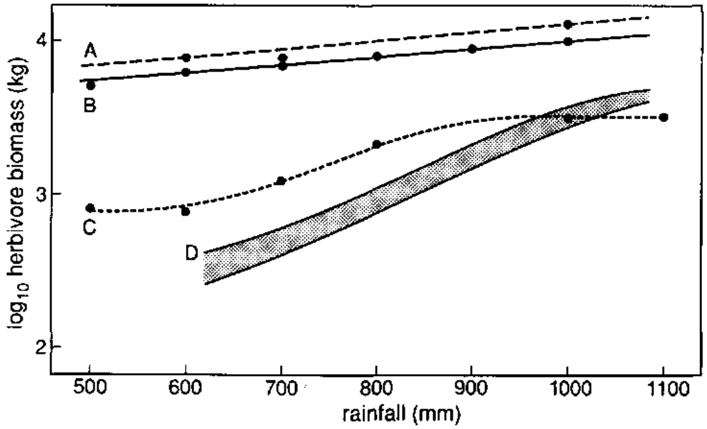


Fig. 10.1. Relationship between biomass (kg.km^{-2}) of grazing herbivores and average annual rainfall (mm) according to
A: De Leeuw (1976,1977),
B: LeHouérou & Hoste (1977),
C: Penning de Vries & Djitèye (1982) (normal rainfall years)
D: this study (hartebeest-curve, normal rainfall years)

B. By bringing together data on the average annual rainfall and primary production of the herbaceous layer from 44 sites in eight Sahelian and Sudanian countries, LeHouérou & Hoste (1977) examined the relationship between average annual rainfall and pasture production for the Sahel and the Sudan savanna. Assuming that one TLU (Tropical Livestock Unit = animal of

250 kg) needs 6.25 kg DM of forage per day containing 156 g DP, they arrived at the equation:

$y = 0.0004\,x^{1.001} \quad r = 0.89 \quad n = 44$

in which:
y = TLU per ha
x = average rainfall (mm.year^{-1})

Again, compared to our predictions (Fig. 10.1), this equation overestimates the potential ecological carrying capacity of the savanna, especially in the lower rainfall zones, because the calculations are based on the total annual production of the herbaceous vegetation, disregarding the seasonal differences and the effect of fire.

In contrast with De Leeuw (1976,1977), LeHouérou & Hoste (1977) corrected the available phytomass for quality: on a year-round basis they estimated that 40% of the herbaceous layer could be consumed. They noted (LeHouérou & Hoste, 1977) that the carrying capacity also varies with other environmental variables apart from rainfall such as soil type and range conditions, and that as a result the herbivore biomass may vary by a factor of five at the same rainfall level.

C. Penning de Vries & Djitèye (1982) published the results of an extensive research programme on soil-plant relationships of the steppe vegetation of the Sahel, especially regarding the role of plant nutrients. One of the important conclusions of this research is that in the Sahel and the adjacent Sudan savanna, plant production is determined by the availability of nitrogen (N) and phosphorus (P) in the soil when water is not limiting. They translated their results into a prediction of the carrying capacities of these rangelands for cattle. For this prediction Penning de Vries & Djitèye (1982) state that a sustainable pastoral livestock husbandry is only possible if those factors which limit vegetation production are quantified:

- in the Sahel and the Sudan savanna vegetation growth is subject to the limited availability of N, P or water;
- if N is limiting vegetation growth, sustainable grazing is only possible if the annual input of N (brought about by fixation by legumes and by micro-organisms and algae in the soil, and deposition from the air) equals annual losses (through for example grazing, fire, and volatilization).
  When input and loss are in equilibrium, the proportion of N available for grazing is translated into the proportion of phytomass available as quality forage;
- if P is limiting vegetation growth, the phytomass at the end of the growing season should be used to calculate carrying capacity as this is when the least P is available;

- if water is the limiting factor, which generally is the case in areas with less than 250 mm effective annual rainfall, the availability of the forage determines the carrying capacity as in fact all vegetation is of sufficient quality.

Taking these conditions into account, Penning de Vries & Djitèye (1982) calculated the herbaceous phytomass available to cattle, per rainfall zone for the area with between 100 and 1000 mm average annual rainfall. Assuming that the forage requirements of an animal of 250 kg (= 1 TLU) are 6.25 kg DM per day containing at least 1.0% N, they arrived at the estimates of the carrying capacity for cattle shown in Fig. 10.1. The predicted stocking rates for the range between 600 and 1000 mm annual rainfall are especially interesting with respect to our study, as despite an increase in phytomass with rainfall, Penning de Vries & Djitèye (1982) predict that the carrying capacities will level off and stabilize around 3,100 $kg.km^{-2}$ (2,200 $kg.km^{-2}$ in dry years) (Fig. 10.1).

Our predictions clearly differ:

- when annual rainfall is below 1000 mm, we predict a lower ungulate biomass than Penning de Vries & Djitèye (1982), and
- above 1000 mm we predict comparable or higher values.

The condition of ecosystem equilibrium as implemented by Penning de Vries & Djitèye (1982) means that the quantity of N which can be taken from the system by for example grazing, fire, and volatilization, has to equal the quantity of N, entering the system by such means as rainfall or fixation. They calculated the carrying capacity of West African rangelands from the net quantity of N available to grazing animals, using the formula:

$$N_i = \frac{f_b \times N_b}{0.525}$$

in which:

N_i = quantity of N ($kg.km^{-2}$), net available to grazing animals

N_b = quantity of N ($kg.km^{-2}$) in the above-ground herbaceous phytomass

f_b = fraction of N_b, disappearing annually due to grazing

In the higher rainfall zones the availability of P limits plant growth more than that of N, and should therefore be used when the carrying capacity of these zones is calculated with regard to ecosystem equilibrium. However, Penning de Vries & Djitèye (1982) used the net availability of N throughout, stating that as a result the carrying capacity of the higher rainfall zones may be overestimated.

Penning de Vries & Djitèye (1982) assessed the availability of N on a year-round basis but corrected it for the seasonal fluctuations in phytomass. They assumed that the ratio between late dry-season forage and maximum phytomass declines from 0.15 in the Sahelian steppe to 0.05 in the Sudan savanna. This ratio may apply to those areas where annual grasses dominate the herbaceous layer as in the natural steppes of the Sahel. However, we found that in the Sudan savanna there is a tremendous fall in the quantity of phytomass in the herbaceous layer due to fires (Chapter 6). Moreover, although between 600 and 800 mm annual rainfall perennial grasses show a dry-season growth, this growth is quantitatively insignificant. Hence, in the zone with between 600 and 1000 mm annual rainfall, the quantity of edible vegetation in the dry season is much lower than the 5% of the maximum wet-season phytomass assumed by Penning de Vries & Djitèye (1982) (Table 10.1). It is this, and not the quantity of N net available that limits the number of grazing ungulates (see Chapter 7). Consequently, the maximum number of grazers potentially able to live on the savanna with an annual rainfall below 1000 mm, is much lower than predicted by Penning de Vries & Djitèye (1982) because they consume only a fraction of N, that according to these authors is available for grazing (see Table 10.2).

Table 10.1. Dry-season forage (savanna grasses only), expressed as a fraction (%) of the maximum phytomass.

rainfall zone	Andropogon savanna	all land-system units	
	normal years	normal years	dry years
600- 700 mm	0.5	0.4	0
700- 800 mm	2.3	2.2	0.5
800- 900 mm	2.0	1.8	0.4
900-1000 mm	4.6	3.8	2.2
1000-1100 mm	7.6	5.8	3.0

To conclude, we have shown that the approach of Penning de Vries & Djitèye (1982) overestimates the quantity of forage available to grazers in the dry season on the savanna in zones with between 600 and 1000 mm annual rainfall: it overestimates the potential growth of perennial grasses and disregards the effect of fire. The limits to the consumption of N as imposed by the equilibrium-idea are never met.

We have predicted a comparable to higher ecological carrying capacity for

Table 10.2. Annual availability of N (calculation following Penning de Vries & Djitèye (1982), see text) and annual consumption of N (kg.km^{-2}) by grazing ungulates (this study) per rainfall zone for normal rainfall years.

rainfall zone (mm)	600-700	700-800	800-900	900-1000	1000-1100
$N_{consumed}$	52	114	117	328	437
$N_{available}$	119	194	289	338	353
ratio	0.44	0.59	0.40	0.97	1.24

grazing ungulates in the higher rainfall zones, partly due to a difference in methodology. The dry-season forage available to grazers is slightly more than 5% of the maximum phytomass (Table 10.1). In our calculations we used a dry-matter intake per day equal to 7.1% of the animal's metabolic weight, while Penning de Vries & Djitèye (1982) used a dry-matter intake of 2.5 % of the live weight which, given a similar quantity of forage, results in a lower number of animals. Table 10.2 shows that our calculations of the annual consumption of N in the higher rainfall zones equals or exceeds the presumed annual availability of N. The data on the stocking rates in other West African conservation areas confirm that animal densities can indeed be higher (Table 9.3, Fig. 9.5) than those predicted by Penning de Vries & Djitèye (1982). However, higher carrying capacities can only be reached if there are more nutrients available to grazing ungulates than these authors assumed.

Recent discussion centres on the importance of a 'biotic factor' as a further complication. In 1962 Scott published the results of an interesting study on the relationship between mean annual rainfall and the percentage base saturation in well-drained soils in East Africa with a clayey or sandy texture. Up to 800 mm average annual rainfall, because of leaching, the more the rainfall, the lower the percentage base saturation (see Fig. 10.2). Above ± 800 mm, regardless of soil texture, the base saturation increases reaching a peak at ± 1200 mm mean annual rainfall (Fig. 10.2) and decreases again with further increase in rainfall.

To explain this discontinuity, Scott (1962) found evidence for his hypothesis that this increase in the percentage soil base saturation is the result of the release of bases from decomposing plant material. Below 800 mm average annual rain-

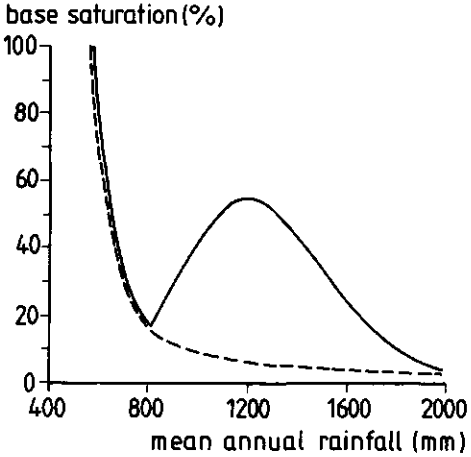


Fig. 10.2. Relationship between soil base saturation (%) and mean annual rainfall (mm) (adapted from Scott, 1962 and Botkin et al., 1981)
---- : only abiotic factors involved
—— : abiotic + biotic factors involved (see text)

fall the small quantity of organic plant material means that its decomposition plays a minor role in modifying the percentage soil base saturation. Although leaching also increases with an increase in average rainfall above 800 mm per year, the dominant factor determining the base saturation is the breakdown of organic matter, the quantity being larger due to denser plant growth. This results in an increase in the base saturation of the soil. Above 1200 mm annual rainfall, although bases are still released by the decomposition of plant material, the amount does not increase and leaching again becomes the dominant factor. Hence Scott (1962) concludes that a biological factor intrudes into an otherwise abiotic leaching process. In Fig. 10.2 the effect of this biological factor in terms of soil base saturation is the difference between the dotted line and the solid line.

Botkin et al. (1981) considered the nutrient status of the ecosystem as a whole and its relationship with animal abundance, and they included an animal factor in their explanation of the discontinuity of soil base saturation, rather than only an increase in the breakdown of organic plant material (Scott, 1962). They suggest that organisms, such as termites and microbes, as well as large herbivores act together with plants so that nutrients are retained in the ecosystem in spite of hydrological and eolian leaching forces. They concluded that the storage and flux of nutrients in ecosystems in East and southern Africa are strongly influenced both by the vegetation and herbivorous organisms (see also McNaughton & Georgiadis, 1986).

This probably applies to West African savanna ecosystems as well. Herbivorous arthropods (e.g. ants and termites), earthworms and microorganisms play an important role in the energy and nutrient flow of the West African savanna ecosystem (Lamotte, 1982; Menaut et al., 1985). For example, in moist savannas earthworms ingest huge amounts of soil, about 1,000 $t.ha^{-1}$ annually (Menaut et al., 1985); their density and period of activity have a major effect on microbial activity and consequently on the availability of nutrients to plants. No earthworms are found in areas with below 900 mm average annual rainfall. Although Penning de Vries & Djitèye (1982) studied the effect of termites, ants and microorganisms on the retention and loss of N in the natural pastures of the Sahel, they did not look at the retention of soil nutrients in the Sudan zone, the result of activities by earthworms and termites. Hence the extrapolation of their findings from the Sahelian steppe to the Sudan savanna is unjustified. In view of more research it appears that in the Sudan savanna, especially above 900 mm annual rainfall, the 'biological factor' can assume dominance in determining nutrient balance.

I conclude that the methodology applied by Penning de Vries & Djitèye (1982) for estimating carrying capacity is sound for the natural pastures of the Sahel. However, for the Sudan savanna, it grossly overestimates the availability of forage for grazers in the lower rainfall zones because it does not take into account the discontinuity in forage availability caused by the transition from annual to perennial grasses in combination with fires. Also, it probably underestimates the availability of N and other nutrients in the higher rainfall zones.

Breman et al. (1987) recently elaborated the approach of Penning de Vries & Djitèye (1982) for both the Sahelian steppe and the Sudan savanna. The availability of forage as the average over the whole dry season (including that provided by trees and shrubs and by the leftovers from crop farming) was used to calculate the carrying capacity (Breman, pers.comm.) instead of the extreme minimum forage situation at the end of the dry season used by Penning de Vries & Djitèye (1982). As a result their carrying capacities are higher than those of Penning de Vries & Djitèye: herbivore biomass increasing from 3,000 $kg.km^{-2}$ at 300 mm rainfall to about 12,500 $kg.km^{-2}$ at 1000 mm rainfall. These values exceed those of the hartebeest-elephant curve in our study over the whole of the rainfall gradient (Fig. 9.4) as well as the information presented on the maximum numbers of wild herbivores given for other West African conservation areas (see Table 9.3). These higher values are partly due to the inclusion of leftovers from crop farming in the quantity of available forage, and perhaps also because of the overestimation of N, available to grazing herbivores, as explained in this section.

10.3. The carrying capacity of the West African savanna compared to other savannas

This paragraph discusses the relationship between rainfall and secondary production as examined for the Sudan savanna ecosystem against approaches for assessing the ecological carrying capacity of savanna ecosystems in other parts of Africa and in Australia. In most cases lack of information on the productivity of the vegetation in the various areas prevents a direct comparison of the relationship between rainfall and primary production. To overcome this problem we assumed that herbivore populations in the other areas are limited by food as those in the Baoulé (see also Chapter 7).

10.3.1. East and southern Africa

The comparative approach of Coe et al. (1976) is one of the best known and earliest examples of the use of average annual rainfall to predict herbivore biomass. Using data from 20 wildlife areas in Eastern and southern Africa they derived the following equation (see also Fig. 10.3):

$$Y = 1.552\,(\pm\, 0.329)\,X - 0.62\,(\pm\, 0.903)$$

in which:
Y = log herbivore biomass ($kg.km^{-2}$)
X = log average annual rainfall (mm)

This equation was widely used in Africa to predict the biomass of large herbivores (also West Africa, see e.g. Milligan, 1978). Compared to our results, the animal densities predicted by this formula are high, especially for areas with more than 800 mm annual rainfall. The narrowness of the relationship suggests

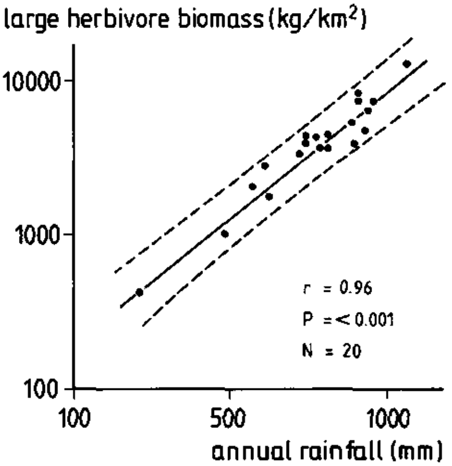


Fig. 10.3. Relationship between large herbivore biomass (kg.km^{-2}) and average annual rainfall (mm) (after Coe et al., 1976 and Jewell, 1980)

that rainfall alone is a reliable predictor of the carrying capacity. As the data used by Coe et al. (1976) concern herbivore densities in areas characterized by soils of recent volcanic origin with high fertility, and disregard the effect of rainfall distribution on primary production and forage quality, these environmental differences explain the higher densities compared to those of the West African Sudan savanna.

Moreover, according to Bell (1982), the data from which the equation is derived, are biased towards the higher end of the biomass spectrum, indicating a bias in the density of biologists and their interests as well. Areas with a low biomass are underrepresented in the sample taken by Coe et al. (1976) and, as these authors have already indicated, the validity of the herbivore biomass/rainfall relationship above 1000 mm average annual rainfall may be weak due to the small number of observations. Bell (1982, 1984) continued on the path set by Coe et al. (1976) and collected a larger set of data from 46 wildlife areas and from a wider range of average annual rainfall, geomorphological situations, soil types and vegetation systems. He concluded that the relationship between the biomass of large wild herbivores and the average annual rainfall is much better described by a *set* of curves (Fig. 10.4a), each curve describing a particular combination of environmental characteristics. Highest herbivore biomass is found on volcanic and alluvial soils with a high nutrient status, and it is this situation which corresponds with the relationship worked out by Coe et al. (1976), representing savannas of high soil nutrient status, relatively low annual rainfall, and a low phytomass of high quality. These so-called arid/eutrophic savannas have relatively high densities of small to medium-sized, mainly grazing herbivores. If annual rainfall is above 1200 mm, herbivore densities become lower due to the decreasing forage quality.

Moist/dystrophic savannas have soils of lower nutrient status, mainly weath-

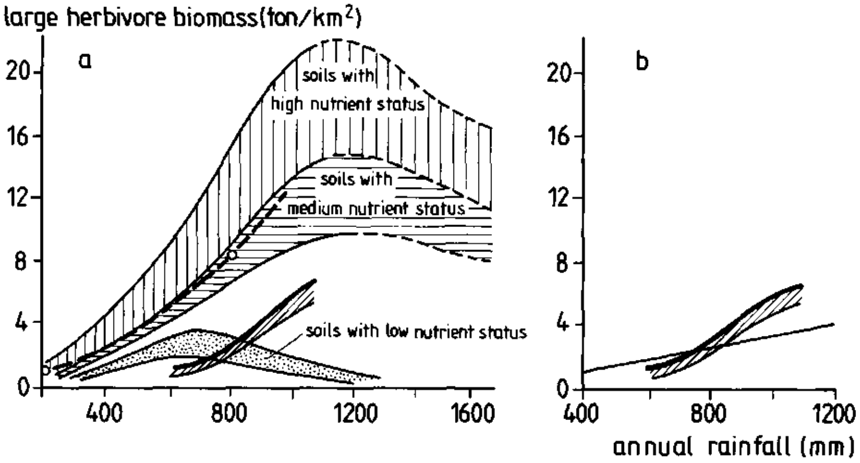


Fig. 10.4. Relationships between large herbivore biomass (kg.km^{-2}) and average annual rainfall (mm) in different soil types
a : after Bell (1984)
– – – – = curve derived by Coe et al. (1976)
—— = this study (hartebeest-elephant curve, normal rainfall years)
b: after East (1984), see Table 10.3
—— = this study (hartebeest-elephant curve, normal rainfall years)

ered basement areas (granite shields, sandstone and Kalahari sands); they generally receive much more rainfall, have high phytomass of low quality and have low biomass of, usually the larger, herbivore species. Furthermore, the data in Fig 10.4a indicate that the maximum herbivore biomass in this type of savanna is reached at lower levels of annual rainfall than in the arid/eutrophic savannas with high nutrient soils. Bell (1982) concluded that animal density is related to the availability of plant and soil nutrients, but modified by diseases such as trypanosomiasis transmitted by tsetse flies (*Glossinidae*).

On the basis of the analysis of his own data Bell (1982) concluded that the relationship between rainfall and large herbivore biomass, found by Coe et al. (1976), and their interpretation is an oversimplification of the real situation in East and southern Africa.

To what extent are Bell's (1984) relationships applicable to the natural rangelands in West Africa? We have to bear in mind that despite the size of the data set, it only covers conservation areas in East and southern African (Bell, 1982: Tables 2 and 3).

Concerning the geological parent material, West African savannas can be classified as moist/dystrophic savannas as they have a low nutrient status (Part I). Thus the lower curve in Fig. 10.4a should be compared with the hartebeest-elephant curve, our prediction of the ecological carrying capacity of the Sudan savanna.

The differences are:

- we found the highest herbivore biomass at the higher rainfall levels, 1000-1200 mm annual rainfall, whereas Bell's low nutrient status curve indicates an optimum at about 700 mm annual rainfall;
- we found lower herbivore biomass between 600 and 800 mm annual rainfall in the Sudan savanna;
- the discontinuity imposed on the carrying capacity by the change in vegetation in the transition from Sahelian steppe with short annual grasses to the Sudan savanna with its tall annual and perennial grasses, is not found in Bell's (1982, 1984) herbivore biomass/rainfall relationship for soils with low nutrient status.

Bell's (1984) indication of a fall-off in large herbivore biomass above 700 mm annual rainfall is partly due to the exclusion of data points representing three low nutrient status wildlife areas which he regarded as 'representing a genuine discontinuity in the biomass spectrum equivalent to the distinction between arid/eutrophic and moist/oligotrophic communities'. Our information on herbivore biomass in West Africa (Chapter 9 and Fig. 10.4a) shows that higher herbivore biomass is possible in areas with more than 700 mm annual rainfall. This has also been shown by the density of cattle in relation to rainfall, worked out by Rodgers & Randolph (1986) using the same data set as Bell (1984) for cattle (Fig. 10.5). This curve has an optimum at around 1000 mm annual rainfall, but in areas with more than about 900 mm annual rainfall, especially in West Africa, cattle densities are kept down through trypanosomiasis. Hence a cattle census probably does not reflect the level of potential carrying capacity.

Secondly, the data sets from which the herbivore biomass on soils of low nutrient status has been derived, are from moist/dystrophic savannas in East and southern Africa, the so-called 'miombo' savannas, which compared to the higher stocked arid grasslands have received relatively little scientific attention (McNaughton & Georgiadis, 1986). Consequently the data points may not represent systems at carrying capacity due to species being missed, an unmeasured

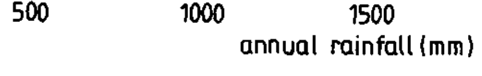


Fig. 10.5. Relationship between cattle biomass (expressed as a percentage of the biomass at 1000 mm rainfall) and annual rainfall (mm) (after Rodgers & Randolph, 1986)

off-take of poaching or census errors. These problems occur particularly in savanna woodland as a result of poor lateral visibility.

With respect to the vegetation, West Africa is less diverse than East and southern Africa, the vegetation zones neatly arranged according to rainfall (White, 1983). In East and southern Africa where the geomorphology and geological parent material are much more diversified, so also are the habitat types. This heterogeneity may be the reason for the smaller differences in forage availability between the wet and dry seasons in these parts of Africa. The seasonal differences in forage availability in the Sudan savanna, which are characteristic for this zone (Chapter 6), lead to low animal densities, especially in the lower rainfall zones (Chapter 9). Consequently, the impact of the transition from short annual grasses to tall annual and perennial grasses on the carrying capacity is less clear in East and southern African savannas than in the Sudan savanna, because the spatial scale on which this transition occurs is much smaller. Moreover, compared to the climate in East and southern Africa, the Harmattan, the characteristic hot north-eastern winds from the Sahara, is an extra factor to be considered as it makes it more difficult for the animals to survive the dry season.

East (1984) examined the herbivore biomass/rainfall relationship for individual species using a larger set of data than Bell (1984) and that included information from West Africa. Taking the occurrence and abundance of animal species in savannas of *low nutrient status*, he divided species into two groups: arid and moist-savanna herbivores. On these soils the biomass of arid savanna species peaks at an annual rainfall of less than 800 mm, and that of moist savanna

Plate 26. Roan antelope, a moist-savanna species

species at above 1000 mm annual rainfall.

Arid-savanna species dominate the herbivore biomass, especially in the arid/eutrophic savanna, where they make up more than 90% of the total herbivore biomass. In the moist/eutrophic savannas of East and southern Africa these arid-savanna species, especially elephant and buffalo, also comprise on average about 80 % of the total herbivore biomass; this proportion is reduced to about 50% in the West African moist/dystrophic savanna, agreeing with our data (Chapter 9). The total biomass of arid-savanna species is positively related to rainfall, except in moist/dystrophic savannas with soils of low nutrient status (Table 10.3). At a given amount of annual rainfall the total biomass of arid-savanna herbivores, as well as that of individual species, tends to be positively related to the availability of soil nutrients.

The biomass of moist-savanna species (hartebeest, roan antelope, sable antelope *Hippotragus niger*, warthog, waterbuck, kob, reedbuck, Southern reedbuck *Redunca arundinum*, oribi and bushbuck) is positively related to rainfall, and apparently not limited by nutrient availability as it is similar for areas of low and high soil nutrient status (Table 10.3). The relatively high herbivore biomass of moist-savanna species in West African conservation areas hardly influences the relationship of all sites with low nutrient status (Table 10.3). Discussing the moist/dystrophic savannas, East (1984) concludes that the low total herbivore biomass reflects the limiting effect of vegetation quality rather than quantity which corresponds with our findings (Chapter 7, Fig. 10.4b).

To summarize the various approaches, we can see that no general relationship between rainfall and herbivore biomass can be applied throughout Africa nor can areas be compared solely on the basis of annual rainfall. As Bell (1982, 1984) and East (1984) have shown, soil nutrient status is also a major determinant of the total herbivore biomass. Comparing West African conservation areas with those with a similar rainfall range in East and southern Africa, East

Table 10.3. Regressions between herbivore biomass (y, log biomass) and rainfall (x, log rainfall); n = number of conservation areas (after East, 1984).

	n	$y = bx + a$	r^2	P
arid savanna herbivores				
soil nutrient status:				
high	9	$y = 2.03(\pm 0.29)x - 2.0(\pm 0.8)$	0.87	<0.001
medium	6	$y = 1.56(\pm 0.22)x - 0.7(\pm 0.6)$	0.93	<0.01
low (<700 mm.year^{-1})	8	$y = 2.10(\pm 0.31)x - 2.5(\pm 0.8)$	0.87	<0.001
low (all sites)	20	–	0.19	ns
moist savanna herbivores				
soil nutrient status:				
high	9	$y = 2.65(\pm 0.70)x - 5.3(\pm 1.9)$	0.67	<0.01
medium	6	–	0.17	ns
low (<700 mm.year^{-1})	7	–	0.47	ns
low (all sites)	19	$y = 2.40(\pm 0.41)x - 4.6(\pm 1.2)$	0.67	<0.001
low (W. African sites excluded)	17	$y = 1.93(\pm 0.41)x - 3.5(\pm 1.1)$	0.69	<0.001

(1984) has pointed out that the species spectrum differs. He has shown that as the arid/eutrophic savannas are dominated by arid-savanna ungulates, the herbivore biomass/rainfall relationship is very precise to predict the total herbivore biomass in these savannas, which explains the close fit of the original correlation of Coe et al. (1976). In moist/dystrophic savannas the arid-savanna species are less dominant, especially in West Africa (East, 1984; Chapter 9). Consequently, any general herbivore biomass/rainfall relationship predicts the total herbivore biomass less precisely. Dividing the species into two categories, arid and moist- savanna species, improves the prediction; thus it is clear that the composition of the ungulate community should also be taken into account.

Comparisons should be made with caution. McNaughton & Georgiadis (1986) warn that assigning a single biomass value to vast areas such as the Serengeti national park, can obscure its heterogeneity with respect to rainfall and geology.

East (1984) attributes the lower total herbivore biomass in the West African savanna compared to that of other African savannas partly to hunting pressure from high-density human populations and partly to differences in the structure of ungulate communities due to the long history of intense land-use. But East (1984) has also shown that the present hunting pressure alone cannot account for the observed low herbivore biomass. We have shown that the homogeneity of the West African savanna leads to larger differences in forage availability between the wet and dry seasons than in areas with comparable soil nutrient status and rainfall in East and southern Africa. In my opinion this explains the lower herbivore biomass, especially with respect to the grazers, which are all moist-savanna species. Finally, comparisons are not always fair as data on herbivore biomass in moist savanna ecosystems in East and southern Africa may well be less accurate than those from comparable areas in West Africa.

10.3.2. Australia

The Australian subhumid and semi-arid savannas extend in a wide arc from the tropical north to the subtropical southeast (Mott et al., 1985). Rainfall is highly seasonal, falling mainly in the summer months and decreasing from the coast to the inland. Soil fertility is generally low although in some areas clays give the soil a high nutrient status.

The natural savanna vegetation has evolved under the primary constraints of climate and soil, but fire has also played an important role (Tothill et al., 1985).

Due to the seasonality of rainfall and its variability, the biological productivity is strongly seasonal and highly variable.

Mott et al. (1985) mention that in terms of functional adaptations to the environment, many plants show similarities to those in other continents in comparable situations. Especially in the functioning of the subhumid savanna ecosystems, the shortage of nutrients is more important than climatic limitations and parallels those conditions in the savannas in West and Central Africa. In Australia the annual production of herbaceous forage is positively related to rainfall

(Wheeler & Hutchinson, 1973) but when the mean annual rainfall increases above 600 mm, production is slowed down increasingly, as nutrient availability becomes the dominant factor for plant growth. In the subhumid savannas the quality of forage decreases rapidly in the dry winter months. As a consequence vertebrate biomass is low in all these types of subhumid savanna.

Within the Australian subhumid and semi-arid savannas, Mott et al. (1985) distinguished six main types of savanna vegetation on the basis of the herbaceous vegetation:

subhumid:	* monsoon tallgrass savanna	> 750 mm	annual	rainfall
	* tropical tallgrass savanna	> 500 mm	,,	,,
	* subtropical tallgrass savanna	> 750 mm	,,	,,
	* midgrass savanna	> 500 mm	,,	,,
	* midgrass savanna on clay soils	> 500 mm	,,	,,
semi-arid:	* tussock grasslands	< 500 mm	,,	,,

Winter drought and plant growth predominantly limited by nutrient availability characterize the tallgrass savannas, although within the tropical and subtropical grassland savannas, the higher soil fertility on the east coast compensates to some extent for the less favourable climatic conditions. A combination of low rainfall and low soil fertility probably limits plant production in the midgrass savannas. In all these subhumid savannas fires occurs annually. The arid climate limits plant production on the tussock grasslands, especially on the better soils, and the great variability in rainfall causes large fluctuations in annual herbaceous production.

Within all savanna types low levels of available nitrogen and phosphorus in the soil are reflected in a rapid depletion of these elements during the growing season of the vegetation. The availability of both elements appear to limit plant growth. Evidence suggests that, although locally phosphorus is often the primary limiting element, in general it is nitrogen.

The native vertebrate fauna of Australia is rich in herbivorous species, especially kangaroos and wallabies. However, their overall biomass is low compared to that of the fauna of savanna ecosystems in other parts of the world. Mott et al. (1985) calculated 100 kg.km^{-2} of native fauna for the arid savannas and considered it unlikely that its biomass in other types of savanna would be very different.

Of the domesticated herbivores that have been introduced into the Australian savannas, cattle and sheep are the most important. Whereas cattle are found in all types of savanna, sheep occur mainly on the tussock grasslands. Feral goats are also found on the semi-arid tussock grasslands and feral pigs on the subhumid savannas (Reece et al., 1979). Table 10.4 shows the distribution of the biomass of introduced herbivores over the different types of savanna.

The total biomass values of native and domesticated herbivores are comparable to those of some African savannas although the tussock grasslands carry higher densities than for example the Sahelian steppe. However, unlike the sub-

Table 10.4. Biomass ($kg.km^{-2}$) of the most important introduced herbivores in Australian savannas (after Mott et al., 1985).

savanna type	biomass
monsoon tallgrass savanna	800
subtropical tallgrass savanna	6,000
midgrass savanna	3,000
tussock grasslands	4,400

humid savannas, the semi-arid grasslands have degraded considerably this century (Tothill et al., 1985) indicating that they are permanently overstocked. There are, however, indications that the native fauna may occur in high densities in these tussock grasslands. Caughley (1983) described the population growth of the red kangaroo *Macropus rufus* and the western grey kangaroo *M. fuliginosus* in Kinchega national park (235 mm annual rainfall) after the exclusion of sheep in 1967. After ten years, numbers tended to stabilize at about 2,000 $kg.km^{-2}$, suggesting a natural equilibrium between plant production and consumption.

In the management of all types of Australian savanna, when assessing the carrying capacity, not the quantity but the quality of the available forage is the limiting factor (Mott et al., 1985); this also applies to the majority of African savannas. In the arid regions the variability in the quantity of forage caused by the high year-to-year variability in rainfall, results in extra management problems (Wilson & Harrington, 1984). Moreover, the absence of permanent drinking water in all types of savanna limits animal biomass unless it is provided by man-made watering holes (Tothill et al., 1985).

The best-known approach for estimating the livestock carrying capacity in the arid rangelands of Australia is that of Condon (1968). He assesses the grazing capacity of a given area by relating it to an area with a known grazing capacity, the reference area. Environmental characteristics, such as rainfall, soil type and soil fertility, topography, the presence of trees and the type of herbaceous vegetation and its production, are weighted to adjust the grazing capacity of the reference area to that of the area in question. From this grazing capacity the ecological carrying capacity can be assessed as well as the carrying capacity for exploitation.

10.4. Conclusions

In broad outline, the herbaceous phytomass of savanna ecosystems in Africa and Australia generally decreases from the higher to the lower rainfall zones, while the quality of the vegetation increases along this gradient. The same trends are found in the North American savannas (Stoddart et al., 1975). Most savannas have a low soil fertility; only a few have soils with high or medium fertility. As a consequence, herbivores in the subhumid savannas face the problem of a declining forage quality whereas in the more arid regions the quantity of forage is often limited, although its quality meets the animal species requirements.

Wild African ungulates can be classified into those that are more numerous in the arid savannas and those that reach their highest densities in the moist savannas. However, herbivore biomass may differ considerably because of local and regional differences in, for example, rainfall, soil fertility status and topography. Wilson & Harrington (1984) showed that the carrying capacity of arid grasslands in Australia is strongly influenced by the seasonality of rainfall: winter rains lead to higher herbivore biomass than summer rains. East (1984) has shown that, with the same amount of annual rainfall, an increase in soil nutrient status results in higher herbivore biomass. Not the total amount of annual rainfall, but the amount reaching the plants, affected by the local geomorphology, determines the type of vegetation and its quality: whereas run-on of surface water might result in a vegetation of perennial grasses, annual grasses might result from run-off (see Penning de Vries & Djitèye, 1982).

Although insufficient knowledge of the savanna ecosystem may make the assessment of the ecological carrying capacity by the analytical approach premature (Bell, 1984), we have shown that its estimation by the comparative approach is not without pitfalls either, for example when different regions within Africa are compared.

Condon's (1968) method seems to be the most promising approach for the management of the African savannas, although it needs to be developed for the different regions and situations within Africa (10.2). This approach demands a specific programme to be set up to choose reference sites, collect the necessary data and to select weighing factors, in relation to each herbivore species or group of herbivore species. In addition, the methodology for monitoring a particular ecosystem should be developed in order to be able to account for environmental oscillations and fluctuations. Although such a programme seems ambitious, we should realize that knowledge is building up about the functioning of savannas (see e.g Penning de Vries & Djitéye, 1982; Tothill & Mott, 1985). Moreover, practical experience gained on livestock and game ranches may be very useful.

Part IV: Conservation and management

Animal husbandry and arable agriculture are expanding rapidly in the Sudan savanna, driving the last populations of wild ungulates into less suitable areas where their existence is threatened. Actual numbers of wild ungulates are low in the Baoulé and elsewhere in the Sudan savanna. These remnant populations are becoming more and more isolated making them more vulnerable to illegal hunting and competition from livestock.

The information on the ungulate community and ecological carrying capacity of the Sudan savanna in this study, enables us to suggest management options for the conservation and management of the wild ungulate populations and the natural savanna ecosystem.

11. Conservation of wild ungulate populations in the West African savanna

11.1. General introduction

More and more the belief is gaining ground that nature conservation and especially the conservation of wild ungulates, cannot be considered in isolation. In tropical countries conservation of nature means the conservation of natural resources on which the human population depends. Wildlife is such a natural resource. Hence the conservation of the wild ungulate populations will only be successful if it is part of the broader approach to conserve land and natural resources, i.e. the 'environment'. This approach takes full account of and is integrated with human development need (Estes, 1989). Therefore, the conservation of wild ungulates should no longer be considered as just the preservation of species in a designated area, such as a national park or game reserve.

There are two categories of conservation:

1 non-consumptive utilization of species, when species are preserved with respect to their value as parts of an ecosystem which has a regulation or information function for mankind;
2 consumptive utilization of species where wild animals have a production function just as other natural resources such as soil, water and vegetation.

In practice, the first category implies the protection of ecosystems in national parks and/or game reserves whereas the second means that wildlife conservation has to be considered in the same way as other types of land- use with a production function, such as animal husbandry, and arable agriculture.

However, whether conservation concerns the preservation of ecosystems or the utilization of species for production, choices always have to be made about what should be done where, why and how.

11.2. The design of conservation areas

11.2.1. Introduction

Animal husbandry, arable agriculture and exploitation of the forest for firewood show clear signs of rapid expansion over yet unoccupied areas. Trends are not independent, an increase in the area of arable land forcing livestock to move to other, often less favourable pastures. These pastures were not utilized earlier for various reasons, such as the occurrence of river-blindness and sleeping-sickness, the presence of less suitable forage or lack of water, and were the 'natural' reserves where the wild fauna could survive. Medical care for both humans and livestock, provision of wells and the cultivation of fodder have enabled people to settle in these areas. The friction between pastoralists, or their representatives, and the authorities in charge of the protection of natural areas is growing, both in the Baoulé (Havinga, 1988) and in general. Moreover, the relative fixed size of the domestic herds (up to about 300 animals, being larger than those of the wild ungulates) in combination with the retarded response to drought (see 11.2.2), and the resulting overgrazing and erosion cause many management problems. If conservation is to be an objective of the central government, the conservation of populations of wild ungulates should thus primarily focus on the protection of suitable areas.

The conservation of wild ungulate populations within specific areas demands explicit decisions with respect to:

* the necessity of their conservation
* which species or group of species does one intend to conserve
* the location, size and number of conservation areas

These aspects will be discussed with respect to the Baoulé; this area serves as an example for all other conservation areas in the West African savanna.

11.2.2. The necessity of conserving wild ungulate populations

Conservation can be justified in two ways, by the belief that all living creatures have a right to exist, and secondly by the assumption that through conservation benefits can be derived for mankind, such as the genetic diversity of food crops which enable them to resist various diseases (the so-called information, production and regulation functions of nature) (Margules & Usher, 1981; see also Soulé & Simberloff, 1986).

The pragmatic approach to decide whether conservation of wild ungulate populations is necessary or not, can be divided into a group of scientific criteria (Margules & Usher, 1981) and one of more political criteria. With respect to the Baoulé, the following scientific criteria can be distinguished (see Margules & Usher, 1981):

* diversity
* area
* rarity
* naturalness
* representativeness

Diversity:	if diversity is defined as the number of species, the Baoulé is highly diverse (see Table 3.2) although the abundance of most species is at present very low.
Area:	the number of species increases with the size of an area, the so-called species-area relationship. East (1981) found

that this relationship could be applied to the herbivores and carnivores in African conservation areas; the Baoulé is among the largest areas within the Sudan savanna (see Table 3.2).

Rarity: although rarity has several definitions and depends on scale (Margules & Usher, 1981), it can relatively easily be quantified. The ecosystem of the Baoulé is relatively intact and nowadays such natural areas are difficult to find; until recently it was one of the last refugia of the giant eland in West Africa, its population representing a specific subspecies.

Naturalness: the Baoulé is natural in the sense that over large areas it is free of significant recent human impact. The ecosystem has only changed over small areas due to crop farming, but this area is increasing (De Bie & Kessler, 1983). Although there is hunting and animal husbandry, the spectrum of animal and plant species is not severely affected by them.

Representativeness: regarding the composition of the ecosystem, its geomorphology, vegetation and wild fauna, the Baoulé is one of the best examples of Sudan savanna, especially as it covers most of the rainfall gradient.

Judged by these criteria, there are sufficient reasons for considering the conservation of wild ungulate populations in the Baoulé. In Mali it has now become an unique area; this combination of animal species is no longer found elsewhere in the country.

However, the Baoulé is not the only area in the Sudan savanna for which these criteria can be answered positively. Elsewhere in the Sudan zone such areas can still be found, see Fig. 3.1. But it is the only bloc in the western Sudan savanna, which covers an ecological gradient formed by annual rainfall ranging from about 700 mm in the north to about 1100 mm in the south. Thus the position of the Baoulé as an ecological-geographical unit is exceptional and warrants conservation, as it gives more weight to its value on a local and national scale.

However, the conservation of the Baoulé has to be also justified from the political point of view. The central government may aim to protect nature as a part of the natural heritage. Conservation in the form of national parks and game reserves attracts foreign currency by tourism. Moreover, attention for conservation is increasingly used as an effective tool for appeasing foreign governments and international organizations: more and more environmental issues are made the conditions for development programmes. If a country can show that efforts are made towards the conservation of species and ecosystems, they have more chance of success with their applications for financial support. However such a strategy is not stable: as soon as the attitude of potential donors changes, the government policy will, and has to, change as well, and the conservation aspect will probably be disregarded.

More secure is the argument that in large parts of the Sudan savanna, as in Mali, bush meat is an important source of animal protein (see Chapter 3). In order to protect this natural resource, refugia are needed from where populations of wild animals can build up again when numbers become low due to the combination of hunting and drought.

It is not easy to convince people that the conservation of natural ecosystems is a necessity, especially in poor countries where the survival of the human population in the short-term has high priority. Ultimately the decision of whether or not attention has to be paid to the conservation of natural ecosystems is, despite scientific arguments, a political one.

11.2.3. How large should a conservation area be?

Under the heading 'single large or several small' or its acronym SLOSS there has been a long discussion about the optimal size of conservation areas (see Soulé & Simberloff, 1986), but this is no longer an issue. First there is evidence building up that a single large area can contain as many species as several small ones (East, 1981; Soulé & Simberloff, 1986; Boecklen & Bell, 1987). More important however in the West African context is the fact that such choices cannot be made any more. Outside the main conservation areas no empty areas exist; man has invaded all those that were available (see 11.3). Furthermore, of the natural areas with a conservation status, it is difficult to preserve what is left. Hence, in West Africa non-biological factors dictate the size of conservation areas.

As we need large areas, the areas at present under conservation management should be preserved in their entirety as far as is possible. In a conservation area, subpopulations form a mosaic in which the individual subpopulations are in different phases of population dynamics, due to local variation in rainfall, topography and vegetation. Some subpopulations may decline whereas others will increase in number (Owen-Smith, 1983); some may even become extinct. As long as these empty spaces can be filled up again through immigration from other subpopulations there is no problem. It can even be an advantage for the population as a whole as genetic information can be exchanged (see also Miller, 1979). However as soon as the conservation area becomes fragmented, emigration and immigration can no longer take place. Opinions on the effect of fragmentation on the ecosystem as a whole are still contradictory (Usher, 1987). Often arguments have been derived from the 'island theory' (MacArthur & Wilson, 1967) to demonstrate that small areas have higher rates of species extinction and lower rates of immigration than large ones. At this point it suffices to say that conservation areas should be large enough to encompass the full range of spatial and temporal processes (such as succession and subpopulations in different cycles of population dynamics) and of ecological gradients (Usher, 1987).

The ecological gradient in the Baoulé from north to south means that the conservation of a small area in the north has less value than one of the same size in the south, as due to the variability in rainfall, a series of dry years affects the northern subpopulations of grazing ungulates much more than those in the south (see Chapter 9). Thus for the viability of the northern ungulate subpopulations, corridors are necessary or preferably their conservation area should be linked up with a larger one that extends further south. With regard to their habitat, the southern subpopulations have a much greater chance of survival, because of the higher probability of sufficient rainfall, and thus of forage supply. Therefore, the southern zone of the Baoulé is more important for the conservation of wild ungulate populations than the northern one.

But can the southern subpopulations of ungulates survive in isolation? Apart from the argument that the more subpopulations present in the mosaic of the population, the greater the viability of the population as a whole (see above), the minimum number of individuals needed for the survival of a species is directly related to the minimum area needed (Soulé & Simberloff, 1986). The forces which determine this minimum population size are extremely complex.

Soulé & Simberloff (1986) concluded that for many species this minimum number is seldom below a few hundred. East (1981) analysed the species composition of 17 African conservation areas and, on the basis of the species-area relationship, concluded that if the minimum population size of large mammals exceeds 100 individuals for large herbivores and 25 for carnivores, very large reserves of more than 10,000 km^2 are needed to ensure the existence of the species communities characteristic of the African savanna. Soulé & Simberloff (1986) came to the same conclusion.

From our calculations of the overall potential stocking rates (Table 9.6), it appears that for an ungulate community in which each species is represented by at least 100 individuals, a minimum area of about 1,000 km^2 is needed. This is an average, in the northern part of the Baoulé a larger area is required than in the south (for example, the hippopotamus needs about 3,000 km^2 in the 800-900 mm rainfall zone and about 200 km^2 in the southernmost rainfall zone). The minimum area required depends on the animal species, smaller browsing ungulates demanding smaller areas than the large grazing species (Table 9.6). In general predators require much larger areas than their prey (East, 1981). Which species does a country wish to conserve? Again, this is a political rather than a scientific decision and depends on how the justification for conservation is formulated.

The Biosphere Reserve 'Boucle du Baoulé' is large enough to provide resources for viable populations of the wild ungulate species living there today according to the criteria of minimum area and minimum population size, even though it is becoming more isolated.

11.3. The compatibility of the conservation of wild ungulate populations with other land-use

11.3.1. Introduction

Increasingly more attention is given to finding out under which conditions

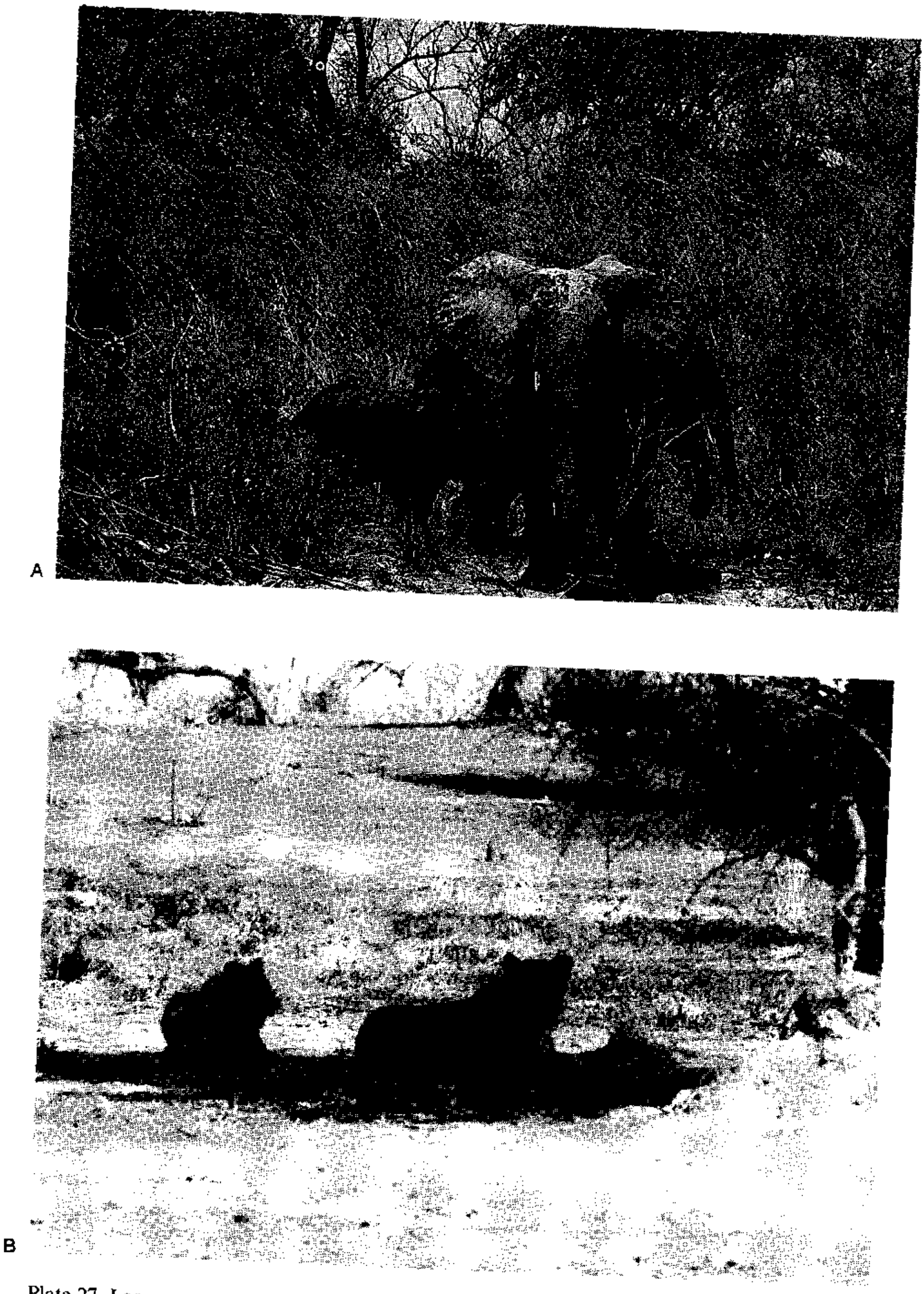


Plate 27. Large areas are needed for the conservation of herbivores such as the elephant (a) and carnivores such as the lion (b)

human and wildlife populations can coexist. Making buffer zones around conservation areas is an example of this recent trend in land-use planning. The analysis of the potential compatibility of the conservation of wild ungulate populations with other types of land-use is, or should be, an important part of all land-use planning programmes.

The analysis of this compatibility of wildlife conservation with other land-use types is the subject of this paragraph. The compatibility concerns the potential joint occupation of land, the territorial compatibility, and not the professional compatibility, such as the farmer who is also a hunter, although this practice is common in the Sudan savanna.

11.3.2. Animal husbandry

A short outline of the animal husbandry practised in the Baoulé and in the Sudan savanna was given in Chapters 3 and 4. Van der Mandele & Roëll (1988) describe the system of transhumant livestock in the Baoulé in more detail, and Havinga (1988) gives information on the sedentary system of animal husbandry. Information on animal husbandry in Mali is given by Wilson (1986), Wagenaar et al., (1986), Breman et al., (1987) and Roëll (1989) and for the whole of Sahelian Africa by IUCN (1989).

Animal numbers and distribution

As the Baoulé is one of the relatively empty savanna areas in West Mali, large numbers of transhumant livestock visit the area in the dry season (Table 11.1). Numbers differ because a larger area was surveyed in 1981 than in 1980 (see

Table 11.1. Total numbers and densities (number per km^2) of livestock in the Baoulé in 1980 and 1981, based on aerial surveys (compiled on the basis of data from De Bie & Kessler, 1983 and Van de Mandele & Roëll, 1988).

		1980	1981
transhumant cattle (zebu)	number	87,000	176,100
	density	4.4	7.1
sedentary cattle (mainly N'dama)	number	35,200	25,300
	density	1.8	1.0
transhumant sheep + goats	number	127,000	304,500
	density	6.5	12.3
sedentary sheep + goats	number	62,000	64,700
	density	3.2	2.6
donkeys	number	5,700	12,800
	density	0.3	0.5
horses	number	3,200	4,900
	density	0.2	0.2
camels	number	30	500
	density	0.001	0.02

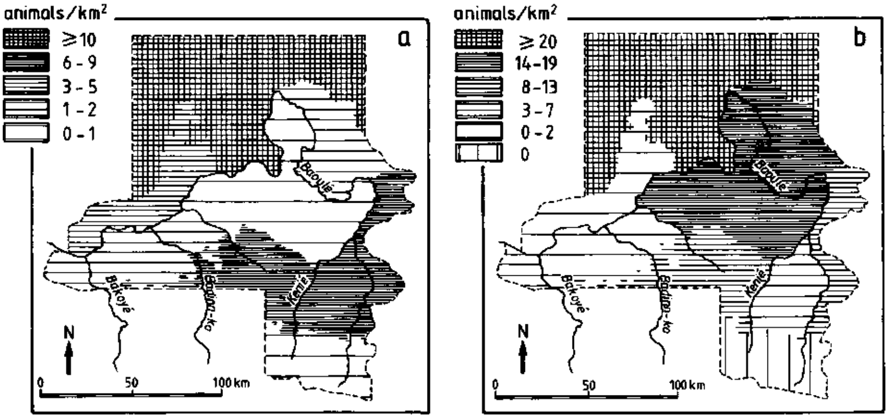


Fig. 11.1. Distribution of (a) transhumant cattle and (b) sheep + goats, in the Baoulé in 1981 (from Van de Mandele & Roëll, *1988*)

Chapter 5). Moreover, the area was surveyed at different times of the year: in June 1980 part of the transhumant livestock was already on its way up to the southern Sahel, whereas in April 1981 the transhumant livestock was at the most southern point of its migration (in fact large numbers had migrated to areas south of our survey area). Furthermore there was slightly more forage and water in the southern Sahel in 1980 than in 1981, which resulted in a larger proportion of livestock staying in that zone in the dry season or only migrating south to the Baoulé for a short period (Van de Mandele & Roëll, 1988); the higher densities of transhumant livestock in 1981 indicate migration further south.

Herds of transhumant livestock are not evenly distributed over the area (see Fig. 11.1). Zebu cattle receive medical treatment with Berenil against trypanosomiasis (Van de Mandele & Roëll, 1988); sheep and goats are more susceptible to trypanosomiasis than cattle but in general are not treated. Cattle densities are high in the Sahel and in the southern zones of the savanna where quality forage in the form of dry-season growth of perennial grasses is available despite the risk for trypanosomiasis. The densities of the small transhumant ruminants, sheep and goats, gradually decline towards the south.

Considering the distribution of transhumant livestock in Mali, Table 11.2 shows

Table 11.2. Distribution of livestock in Mali before 1982 (from Wilson, 1986).

zone		camels		cattle		sheep + goats	
		N	%	N	%	N	%
arid,	< 600 mm	164,000	91	939,000	21	3,596,000	43
semi-arid,	600-1000 mm	15,000	8	1,468,000	32	2,418,000	25
sub-humid,	> 1000 mm	–	0	1,009,000	22	790,000	10
Inner Niger delta		–	0	1,114,000	25	1,439,000	18

Table 11.3. Distribution of livestock biomass (% of total TLU's) of livestock in Mali in 1982 (after Breman et al., 1987).

zone [1])	total livestock	camels	cattle	sheep	goats
northern Sahel, < 300 mm	32	93	24	47	47
southern Sahel, 300-600 mm	27	7	28	25	25
northern Sudan savanna, 600-1000 mm	30	0	34	22	22
southern Sudan savanna, > 1000 mm	11	0	13	6	6

[1]) Inner Niger delta excluded

that sheep and goats are mainly found in the arid zone, the Sahel, and cattle are more evenly distributed over the various climatic zones.

These data in Table 11.2 are from before 1982 when herds were recovering from the impact of the first period of drought. According to Breman et al. (1987), in 1982 numbers were the highest ever reached in Mali; at that time the distribution shows the same pattern as in earlier years (Table 11.3).

Livestock husbandry is concentrated in the drier areas (< 600 mm annual rainfall) where the pastures with annual grasses provide good forage. Also in the Inner Niger delta large numbers of livestock are found. About 55% of the cattle grazing in the savanna consists of N'dama cattle or related mixed races, that show a certain tolerance to trypanosomiasis.

Since 1965, the number of livestock has changed little, from 37 to 45 million head, in the western Sahelian countries of Senegal, Mauritania, Mali and Niger (IUCN, 1989). However, as the annual rate of increase of 0.6% is below that of the human population (IUCN, 1989), the number of livestock animals per capita has decreased from 2.9 to 1.9 in this period (IUCN, 1989).

In the countries situated more to the centre of the Sahel, Burkina Faso, Chad and Sudan, numbers more than doubled to about 76 million head, an annual rate of increase of 3%; the number of livestock per capita increased slightly from 2.0 to 2.2 (IUCN, 1989).

In the countries of the western Sahel the effect of a long series of dry years is very noticeable (Fig. 11.2), and to a lesser extent in those in the centre. The effect was not immediate but a time-lag of 3 years is apparent (Table 11.4), indicating that a series of dry years have more effect on herd mortality than one dry year such as 1983.

Table 11.4. Correlation (r) between livestock numbers and rainfall in the Sahel (from IUCN, 1989); $y = 0, -1, \ldots$ indicates the time-lag between both the variables.

region	y 0	y-1	y-2	y-3	y-4	y-5
western countries	–0.05	0.39	0.53	0.58	0.43	0.29
central countries	–0.28	–0.09	0.14	0.45	0.44	0.33

$p < 0.05$ for $r > 0.42$

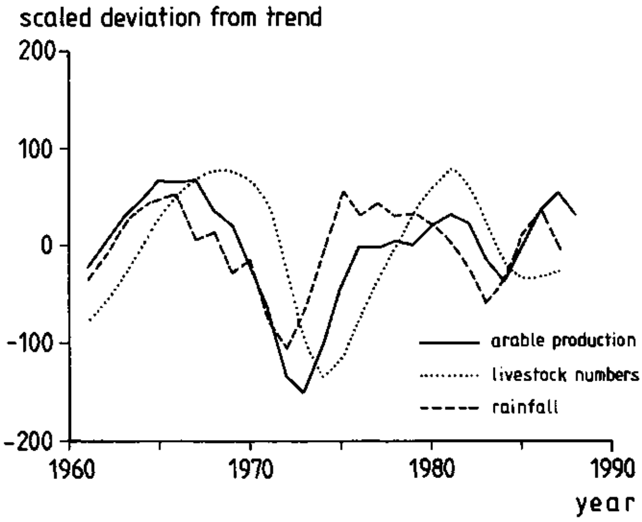


Fig. 11.2. Influence of rainfall on livestock numbers and arable production (IUCN, 1989).

During the last decade, the following trends in animal husbandry can be seen:

* change from transhumant to sedentary pastoralists, especially in the empty areas in the savanna; herds only move around locally; crop farming is increasingly important to secure a basis for existence;
* more and more herds are sold to people from outside the area (such as merchants and civil servants) as the ultimate way to survive in drought periods with the result that the acquisition of grazing rights by non-pastoralists is growing;
* overexploitation of pastures as a result of 1: the time-lag between decreasing rainfall/primary production and livestock numbers, and 2: herds being forced into smaller, often less fertile areas due to an rapidly extending arable agriculture.

Forage competition with wild ungulates
The diet composition of livestock visiting the Baoulé has been qualitatively described by Van de Mandele & Roëll (1988) and is summarized in Table 11.5.

Zebu cattle can be classified as pure grazers (Hofmann & Schnorr, 1982; Coppock et al., 1986). They prefer green grasses, avoiding dried grasses as much as possible. Cattle in the Baoulé only eat significant quantities of woody foliage in the dry season, up to about 25% of their total intake. In the forest reserve Sourou in Burkina Faso, they eat a similar proportion of woody foliage except in April and May (Table 11.6). In April the intake of litter, such as straw, fallen leaves, flowers and seeds, reaches its maximum, about 50%. As a large part of this area is set alight at the end of April, destroying the litter and perennial grasses, providing high quality regrowth, the amount of forage at ground level

Table 11.5. Forage preferences of Zebu cattle, sheep and goats in the Baoulé (after Van de Mandele & Roëll, 1988).

forage type	cattle	sheep	goats
annual grasses	xxx	xxx	xx
perennial grasses,			
wet-season growth	xxx	xx	xx
dry-season growth	xxx	xxx	xx
herbs	xxx	xxx	xxx
woody foliage	x	xx	xxx

x = low preference, xx = medium preference, xxx = high preference

rapidly decreases in May, forcing the animals to feed upon woody plants (about 90% of their total intake). This also explains the sudden increase in time spent on walking (see Table 11.6), as trees and shrubs occur in small patches in the savanna.

In addition to feeding on natural forage, cattle in the Baoulé graze on what is left after the harvest in arable fields near the villages in November and December (see also Table 11.6).

Goats are selective mixed feeders (see Hofmann & Schnorr, 1982; Coppock et al., 1986) preferring woody foliage, which makes up about 60% of their daily intake in the dry season, and herbs. The data on goats in the forest reserve Sourou give a similar picture (Table 11.6). In the late dry season, February and

Table 11.6. Activity pattern and diet composition of cattle and goats in the forest reserve Sourou (Burkina Faso)
activity: % of observation time (daytime only)
W = walking, F = feeding, O = other
diet composition: % of total bites observed
G = grasses, B = woody foliage, L = litter, H = harvest leftovers

	cattle							goats						
month	activity			diet composition				activity			diet composition			
	W	F	O	G	B	L	H	W	F	O	G	B	L	H
June								57	41	2	0	100	0	0
July	50	49	1	100	0	0	0							
August	53	43	4	100	0	0	0							
September	69	30	1	100	0	0	0							
December	41	54	5	51	26	0	23	43	53	3	27	64	9	0
January	37	58	5	80	20	0	0	38	53	9	15	74	11	0
February	32	62	6	61	27	13	0	37	62	1	0	27	73	0
March	38	56	6	56	29	15	0	37	56	7	0	53	47	0
April	56	44	0	42	9	49	0	32	66	2	1	73	26	0
May	86	14	0	2	90	8	0	25	71	4	0	78	22	0

Plate 28. Goats prefer the foliage of shrubs and trees.

March, flowers and seed pods of *Acacia* species such as *Acacia seyal*, appear attracting the goats. Moreover the herdsmen often make more of this type of forage accessible through lopping branches. However, at the beginning of the wet season when many shrubs start to sprout again (see Table 6.2), the goat's diet consists entirely of young leaves.

Sheep, like cattle, are grazers but are more selective (Hofmann & Schnorr, 1982). Their intake of woody foliage increases to about 25% in the dry season.

Livestock eat many species of woody plants in the dry season despite their limited availability at that time (Chapter 6), see Table 11.7.

To maintain their body weight, cattle need to consume forage with a minimum concentration of nitrogen of 1.0% DM (Penning de Vries & Djitèye, 1982), which is comparable to the needs of wild ungulate grazers (Chapter 7). As protein requirements are not related to body size, sheep need similar concentrations but browsers, such as goats, lower concentrations of plant protein (see Chapter 7). Similarity in feeding styles and energy and protein requirements leads us to conclude that livestock faces similar problems to wild ungulates in the dry season regarding forage quality and quantity. Due to their narrow muzzles sheep and goats compete with the smaller, more selective grazers and browsers, and cattle with the larger, less selective ones (see Table 11.8). Hence livestock competes with wildlife for the same forage resources (Chapter 9).

Only the elephant and giraffe are free from competion with livestock for woody foliage, as because of their height they are able to feed on woody foliage higher than 1.75m above the ground, the maximum height that livestock can reach.

Hence, the introduction of livestock into an area occupied by populations

Table 11.7. Preferences of livestock for woody plant species in three forest reserves in Burkina Faso: Yabo (dry season), Bissiga (dry season) and Sourou (whole year);
N = number of species eaten, P = number of species preferred (Chi-squared test, P = 0.05),
C = number of preferred species in common, n = total number of bites observed.

		cattle	sheep	goats	c/s	c/g	s/g
Yabo							
	N	24	38	32			
	P	14	13	16			
	C				6	6	10
	n	60	188	263			
Bissiga							
	N	23	39	23			
	P	10	16	9			
	C				5	5	4
	n	148	510	588			
Sourou							
	N	32	–	26			
	P	14	–	6			
	C				–	5	–
	n	1,087	–	3,494			

– = no data available

Table 11.8. Potential forage competition between wild and domestic ungulates.[1]

	cattle	sheep	goats
grazers:			
hippopotamus	+	–	–
buffalo	+	–	–
waterbuck	+	+	+
hartebeest	+	+	+
warthog	–	+	+
reedbuck	–	+	+
browsers:			
giraffe	–	–	–
bushbuck	–	+	+
duiker	–	+	+
mixed feeders:			
elephant	–	–	–
roan antelope	+	+	+
oribi	–	+	+

[1] + = potential competition; – = no potential competition

of wild ungulates can have severe negative consequences for the composition of the ungulate community.

Another limiting factor for livestock distribution is the presence of drinking water. Cattle need to drink at least once a day, about 20 l per head daily, which limits their walking distance from water to 10-15 km (Van de Mandele & Roëll, 1988). Sheep need 2-6 l and goats 2-4 l per head daily (Van de Mandele & Roëll, 1988) and can be watered once in 2-3 days, allowing them to a larger range of movements than cattle. However, in the Baoulé the distribution of permanent water (see Fig. 7.3) poses no problem to the utilization of the area by all species of livestock. As several wild ungulates depend on the presence of drinking water as well (Table 7.9), livestock competes with these species for the same water resources.

We calculated the potential densities of grazing livestock for the Baoulé in a similar way as for the wild ungulates (see Chapter 9) (as accessibility, a factor limiting the use of certain land-system units to cattle, was not taken into account, these stocking rates are maximum values). It appears that in 1981 there was a serious overstocking with respect to cattle and sheep (Table 11.9).

If overstocking recurs it will not only pose problems to the wild fauna with respect to the immediate availability of their forage, but it will also result in a gradual change in the composition and structure of the vegetation. Overstocking on the Sudan savanna has resulted in the death of perennial grasses because tufts are overgrazed and trampled. During our study in the Baoulé we have seen such signs of overstocking. In contrast with annual grasses which reproduce by seed, perennial grasses spread mainly by vegetative reproduction and thus depend heavily on the survival of the tufts. When pastures are overgrazed, tall annual grasses take over (see Fig. 3.4) and as a result the availability and quality of forage in the dry season decline (Chapters 6 and 7).

11.3.3. Other land-use types

Arable agriculture

The main characteristic of arable agriculture is that the natural vegetation is replaced by cultivated species which have a high yield per plant. As cultivation

Table 11.9. Livestock stocking rates, dry season 1981 (from Table 11.1) and potential stocking rates in years with normal rainfall and dry years (stocking rates in TLU.km^{-2}).

actual stocking rates in 1981:	
cattle:	5.7 TLU
sheep + goats:	1.5 TLU
all livestock:	7.3 TLU
potential stocking rates for cattle + sheep:	
normal rainfall years:	13.4 TLU
dry years:	5.0 TLU

1 camel = 1 TLU, 1 zebu = 0.7 TLU, 1 sheep = 0.1 TLU, 1 goat = 0.1 TLU,
1 donkey = 0.2 TLU (Wilson 1986)

aims to produce food for the human population, it is obvious that this is not compatible with the conservation of wild ungulates.

Ungulates such as warthog, bushbuck, duikers and elephant, damage crops; at the boundaries of the Biosphere Reserve 'Boucle du Baoulé' this damage can be considerable (Havinga, 1988). This has prompted active protection of the arable fields by guarding and, although officially forbidden, by hunting. About 50% of the arable farmers also hunt, often using inferior equipment (Havinga, 1988).

Arable agriculture around, and also in the Baoulé, shows signs of expansion, more in the north than in the south (Table 11.10 and De Bie & Kessler, 1983).

North of the Baoulé more fields were cleared in 1980/1981 than in the Baoulé and south of it. In the Baoulé the fallow period is longer than in the other zones (Table 11.10, columns 2 and 4), which indicates a rather short cycle of using agricultural fields and probably points to the low soil fertility of this area. Fig. 11.3 shows the areas with arable agriculture in the Biosphere Reserve 'Boucle du Baoulé' in 1981.

The expansion of arable agriculture in the lower rainfall zones has also been observed elsewhere in Mali by Kessler & Ohler (1983). Their analysis of land-use in the Sahel and Sudan savanna showed that rain-fed agriculture rapidly expanded due to the increase in the human population, the introduction of ploughs which facilitated the cultivation of more land, the need for more land because of the reduced yield per field caused by decreasing rainfall, and due to a change from food crops to ground nuts and other cash crops. As the best areas are already under cultivation, land which is marginal from the point of soil fertility, is brought into use. As land becomes scarce, fallow periods become shorter and the risk of degradation increases by soil exhaustion and erosion.

Contrary to the conclusions of Bell (1986) these trends are apparent in the whole of Sahelian Africa (IUCN, 1989): between 1960/1965 and 1985/1987 the area under cultivation increased by 33% in the western countries of the Sahel and 36% in the central ones. Although there was also an increase in the total yield of agricultural produce, this was due to the increase in cultivated area; the yield per ha decreased in the western countries and remained approximately constant in the central countries (IUCN, 1989). Both the agricultural production

Table 11.10. Indices for trends in land-use (after De Bie & Kessler, 1983).

Cl/H: ratio of new land in 1981 to land under cultivation in 1980

F/Cr: ratio of fallow land to land under cultivation

(F+A)/F: ratio of fallow + abandoned land to fallow land, which is a relative index for the length of fallow period

(F+A)/Cr: ratio of fallow + abandoned land to land under cultivation

	Cl/H	F/Cr	(F+A)/F	(F+A)/Cr
north of the Baoulé	0.23	0.56	2.36	1.09
Baoulé	0.08	1.05	3.71	3.30
south of the Baoulé	0.09	0.62	3.29	1.90

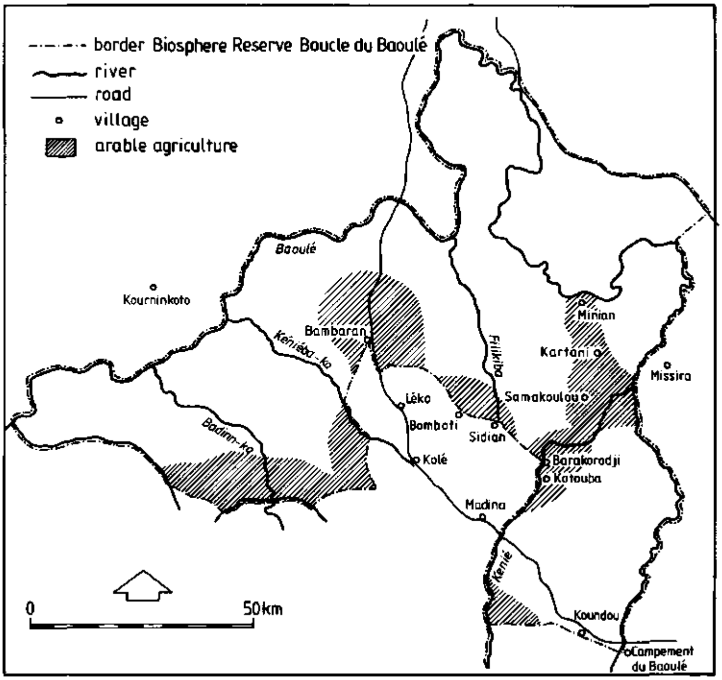


Fig. 11.3 Areas under arable agriculture in the Biosphere Reserve 'Boucle du Baoulé'

and land under cultivation decreased per head of the human population. In the western countries which are more susceptible to climatic variability, agricultural production is more directly correlated with rainfall than livestock numbers are: agricultaural production responds after a time-lag of 1 year (Fig. 11.2). Hence, the consequences of a decrease in annual rainfall on agricultural production and livestock numbers become apparent in different years and have hardly any direct connections.

Exploitation of firewood and timber

Wood collected in the savanna is the most important source of energy (Kessler & Ohler, 1983), other sources being hardly available to the rural population. The annual requirement of firewood, including charcoal, is about 1 cubic metre per person for those living from arable agriculture or in cities and 0.1-0.2 cubic metre for those living from animal husbandry (Kessler & Ohler, 1983). Kessler & Ohler (1983) calculated that (with the annual production of wood in the savanna) to supply the annual needs of one person living from arable agriculture, about 4 ha of natural vegetation and fallow land is required in the southern Sahel, 1.6 ha in the northern Sudan savanna and 0.6 ha in the southern Sudan savanna. There is a growing demand for firewood due to the increase in the human population. In West Africa the impact of deforestation around cities and major villages is increasing. Although collecting firewood affects the composition and structure of the shrub and tree layer, the effect is limited. Only stems of a certain diameter are felled: those too thin are of no use, and those too thick are left as they cannot be cut with traditional implements. Only when land is being cleared for crop farming are thick trees burnt to make their removal easier. Moreover, dead wood is preferred as it weighs less and is thus easier to collect. Grazing reduces the risk of fire and thus protects the (lower) shrubs and trees (De Bie & Geerling, 1988).

11.3.4. Conclusions

Options for the integration of different land-use types are limited. Arable agriculture is not compatible with the conservation of the large ungulate community.

With respect to the forage resources in the dry season, cattle, sheep and goats are serious competitors with most of the wild ungulate species in the Sudan savanna, having similar feeding styles and range of body weights.

Also the integration of firewood collection and conservation of the wild ungulates is questionable: on low fertility soils there is the risk of soil nutrient exhaustion as the potential off-take of nutrients is limited.

Thus it should be clear that the conservation of the large ungulate community in the Baoulé precludes simultaneous livestock husbandry and the exploitation of the forest for firewood. Whether this biological argument can be translated into management decisions, guaranteeing the priority of providing an optimal habitat for the wild ungulates, is in essence a political decision. To what extent in the current situation, this, perhaps utopian view can be applied to the whole of the Baoulé will be explored in 11.4.

11.4. Conservation and management: towards a management strategy for the Biosphere Reserve 'Boucle du Baoulé'

Potentially, the Biosphere Reserve 'Boucle du Baoulé' offers a durable opportunity for large ungulate species to live in the area. According to East (1984), the minimum number of animals required for long-term viable populations, is several hundreds to a thousand for larger ungulates. Potential stocking rates (Tables 9.6 and 9.7) are well above this number. Not only international criteria can be found for the conservation of the area and its wild ungulate populations, it is also justifiable on both the local and national scale (11.2). The Baoulé is an unique example of the Sudan savanna ecosystem in Mali with a high value as a site of natural heritage. At present, however, this value is rapidly diminishing: in common with virtually every other conservation area in the Sudan savanna it is not free from the impact of man. This is because of the lack of law enforcement and management (De Bie et al., 1987; Heringa et al., 1987) and the increasing pressure from animal husbandry and arable agriculture (see 11.3). Moreover, the rural population regards the hunting of the wild fauna and the gathering of firewood as their traditional rights.

Given the objective of the Biosphere Reserve 'Boucle du Baoulé', the preservation of the natural ecosystem with its populations of large herbivores (see Chapter 4), a management policy is needed that will safeguard what is left and to attempt to restore what has been lost. Doing nothing means the legalization of ongoing processes of land degradation that result from illegal land exploitation, and the end of the natural ecosystem. Hence, early decisions are unavoidable.

11.4.1. Management of the core and peripheral area

The present status of the governmental service responsible for the management of the Baoulé, the lack of infrastructure and lack of confidence of the local rural population in the management service (Heringa et al., 1987) mean that bringing the management up to the desired level all over the area in one step is physically, socially and financially impossible. A phased strategy is more appropriate, i.e. the zoning of management in space and time. One should start by managing a *core area*: the area with the highest ecological potential and viability within the present boundary of the biosphere reserve. The core area requires strict protection and therefore most management should concentrate on it. Subsequently, depending on the results achieved with regard to the protection of the ungulate populations and their increase in numbers, it should gradually be enlarged. The question is where to locate the core area? The two most important criteria are:

- the presence of animal populations;
- the presence of a sufficient range of climatic diversity to ensure the viability of animal populations through ecological diversity.

The core area indicated in Fig. 11.4, meets these criteria. It encompasses both northern and southern areas which at present have different compositions of animal species (compare with Fig. 7.1) and a considerable stretch of the river Baoulé which is a vital habitat type. It also covers a climatic gradient, that is sufficiently large to absorb long-term changes in climate and hence in forage availability. Moreover, the high ornithological value of this area (De Bie & Morgan, 1989) enhances its importance. An extra advantage, compared to the more western areas, is its relative accessibility from the capital Bamako which makes its management easier.

We should mention that there is a proposal to declassify some areas in the biosphere reserve that have been under cultivation for a long time either resulting in irreparable damage to the natural ecosystem or having a high economic value for nearby villages, thus excluding them from the reserve (Heringa et al., 1987). This loss can be compensated for by the inclusion of other more natural areas outside the present boundary (see Heringa et al., 1987).

The remaining area where traditional land-use is temporarily allowed under strict conditions (see below), has been designated a *peripheral zone*.

The core area measures 4,099 km^2, comprising 50% of the Biosphere Reserve 'Boucle du Baoulé'. Table 11.11 lists the animal species to be found in this core area and their potential numbers, calculated from data presented in Chapter

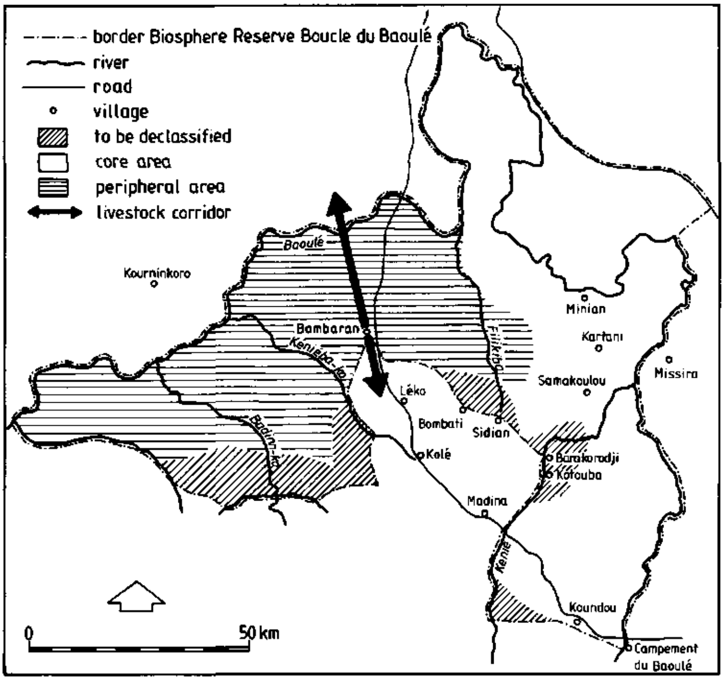


Fig. 11.4. Lay-out for the Biosphere Reserve 'Boucle du Baoulé'

9. The core area can meet the requirements of all large ungulates. Their potential numbers during short periods of successive dry years are above the minimum population size required for long-term viability as mentioned by various authors (see 11.2). However, a larger area is required if longer series of dry years occur,

Table 11.11. Potential animal numbers per species in normal rainfall years and in dry years in the proposed core area.

animal species	normal rainfall years	dry years
warthog	8,000	1,900
hippopotamus	1,800	200
reedbuck	7,000	1,000
waterbuck	5,100	800
roan antelope	4,100	800
hartebeest	3,200	700
oribi	18,900	4,700
buffalo	2,600	500
elephant	4,000	3,200
bushbuck/duikers	2,700	1,800
total numbers	57,400	15,600

which cause large-scale replacement of perennial grasses by annual grasses (see Fig. 3.4). This need for a larger area is enhanced if the area is becoming more isolated (see 11.2). The conservation of the large ungulate community of the West African Sudan savanna can be achieved by proper management of this core area. The same is probably true for some carnivore species with relatively small hunting ranges such as lion, leopard and both hyena species, if the minimum population size required is 25 (see East, 1984).

The concentration of management activities, such as anti-poaching control, on the proposed core area will not reduce the value of the whole biosphere reserve as a conservation area. The potential of the core area to maintain a complete and viable ungulate community is comparable to that of the total biosphere reserve, mainly due to its lay-out by which it encompasses a climatic gradient. Therefore this core area in itself will also have an exceptional value in the western Sudan savanna through its position in the ecological-geographical unit (see 11.2.2), rating high on the list of other conservation areas (see Table 3.2 and Fig. 3.1).

The peripheral area comprises all of the remaining area of the Biosphere Reserve 'Boucle du Baoulé', not being declassified (Fig. 11.4). Its management policy implies the temporary continuation of those traditional land-use activities which do not directly conflict with the ultimate management objective of the reserve as a whole: the conservation of the natural ecosystem. Therefore, incompatible land-use activities should be discouraged in order to make the extension of the core area easier in the future, for example in about 20 to 30 years.

Arable agriculture and animal husbandry should be banned from the peripheral area as soon as possible, as they are not compatible with the conservation of the large ungulate community (see 11.3). Only a narrow zone north of the village Bambaran (see Fig. 11.4) should continue to function as a corridor for livestock, permitting their migration from northern pastures to southern markets.

Hunting small or non-threatened game species such as guinea fowl, porcupine and warthog, might be permitted (to continue) on a limited scale and carried out by a master plan. The guidelines we developed for such a master plan (De Bie et al., 1987) involve local hunters with their traditional methods and revalue their former hunting associations.

Similarly, the collection of firewood and forest products should be strictly regulated.

Strict protection of the core area is important to ensure the continued existence of the ungulate community but other specific management activities, as well as a sound monitoring system, are also needed. However, the formulation of a management plan for the core area and peripheral area is beyond the scope of this thesis. Elements for such a plan are published in detail in De Bie et al. (1987) and Geerling et al. (1988). A few important subjects for the management plan follow directly from this study and I therefore discuss them briefly.

In Chapter 8 I have concluded that the ungulate community can be characterized as a fire-climax community, its existence depending on the regular occur-

Plate 29. Hartebeest: a key-species in the preservation of the ungulate community of the West African savanna.

rence of fire. Hence the application of fire is an important tool in managing the preservation of the ungulate community. In this respect both hartebeest and elephant are important species to be monitored and studied. Hartebeest is the most explicit grazer and the condition of its population with respect to number, reproduction, mortality and distribution, might serve as an sound indicator for the viability of all grass-preferring species. Elephants play an role in maintaining the balance between grasses and woody plants (Chapter 8). Information on their feeding ecology, population dynamics and their impact on the vegetation is thus essential for good management.

11.4.2. The human factor

The proposed management strategy has far-reaching consequences for the local population. Not only does it mean that several villages would have to be moved out of the biosphere reserve, but also it would certainly affect the economy of those living outside the reserve or in those areas which should be declassified.

About a thousand people would be forced to find another place to live and work (Heringa et al., 1987). Are there empty areas outside the biosphere reserve where they can resettle? If there are, to what extent would this evoke resistance from the local people already there, who would thus face increasing competition for natural resources, which are already scarce?

Although some measures can be taken to divert the attention of the local population from the conservation area, their implementation is often beyond the competence of the nature conservation authorities. However, in my opinion these activities should be part of the management policy: a sound management of the interior of the conservation area is possible only if the local population can find a means of existence outside the boundary of that area.

Thus the conservation of the biosphere reserve demands a management policy that is firm and clear in its dealings with the rural population and organizations representing those for whom other types of land-use are essential. Obviously, such a management policy demands the cooperation of the local population.

However, the main problem is that there is often a gap between the objectives of the central authorities and their local representatives (the management staff and wardens of the area) and those of the local population. For the locals it is not the conservation of the ecosystem that is important, but its utilization with a minimal interference from 'above'. This gap thus concerns the difference between the long-term interests of the government and the short-term benefits demanded by the local population. Normally, the local population is not consulted and hence does not participate in the process of decision-making (see also Bell, 1986). As a result the local people do not feel any concern or responsibility for the plans imposed from above.

Consequently, there are frictions and conflicts as observed in the Baoulé (see Havinga, 1988). To avoid such problems, conservation should take the needs and development of the local population into account because conservation inevitably affects their traditional rights of hunting, grazing and gathering.

Firstly, a well-considered management of the adjoining areas is important in this respect. Any attempts to increase the sustainability of land-use (De Bie & Geerling, 1988) by measures such as soil and water conservation, to be followed by increasing the production potential by, for example, supplying fertilizers (see Breman & De Wit, 1983), will lower the pressure on the nature conservation area and thus increase its viability. In the short-term the supply of fertilizers may be more effective for both the rural population and nature conservation than e.g. expensive technical innovation or reafforestation projects. This policy can be supported by measures such as improving living conditions and providing health care and education. To avoid a pressure on the land beyond its agricultural carrying capacity due to the increase of the human population, paying a premium for moving to other areas and setting up small-scale industrialization projects are necessary incentives.

Secondly, some continuation of traditional land-use such as the combination of animal husbandry with the cropping of wildlife, might be an option in zones separating these agricultural areas from the conservation area, the so-called buffer zones. However, the potential for such strategies is limited (11.3). Furthermore, it should always be clear that although some other types of land-use are possible in these buffer zones, the ultimate objective is conservation and therefore the land falls under the responsibility of the management authority.

11.5. Conclusions

No matter what kind of criteria are used to justify the conservation of wild ungulate populations on the West African savanna, or in what way wildlife is considered (either as a natural resource or as part of the natural environment), there is an immediate need for the protection of those areas which harbour the last remnant populations.

Most of these conservation areas are large enough to sustain viable populations. However, presently they enjoy hardly any protection, or none at all, against the pressures from outside. Poaching, illegal land occupation, competition with livestock and habitat degradation all endanger the survival of the ungulates.

Without the involvement of the local population there is little chance of conservation being successful, especially when potential animal densities are low, as in the West African savanna. The slaughter of elephants in Tsavo national park in Kenya is an example (Parker, 1983a). We have to compromise between the long-term objective of conservation and the short-term interests of the local population (Parker, 1983b; Bell, 1986).

All over the West African savanna zone, there is an urgent need for a management programme to be implemented by those who are responsable for the conservation and management of these areas. Essential elements of such a programme are: the protection of animal populations against poaching and the negative effects of other types of land-use, the management of the area by e.g. the regular application of fire, and the monitoring of the vegetation and the ungulate populations. These activities should be actively supported by international donors by long-term financial and, if necessary, personal commitments. It should be accompagnied by applied ecological research in order to enable the management authorities to correct and adapt their policies according to the dynamics of the ecosystem. Furthermore, the management programme could demand a change of the present regulations and laws in order to facilitate law enforcement.

For the conservation of the Biosphere Reserve 'Boucle du Baoulé' such a programme must be met as well. The project 'Recherche pour l'Utilisation Rationnelle du Gibier au Sahel' provided the authorities in Mali with a basis for the formulation of a sound management programme. Besides protection, a regular aerial census (i.e. once in every five years) of the area should be an important element of this programme to provide realistic estimates of the animal populations. Moreover, regular monitoring work (by local management agents) of the trends in the vegetation and in the number of animals, with a periodic evaluation of their results, is a prerequisite for a sound management programme.

The formulation and implementation of such a management programme deserves continued international support. The initiative of the Netherlands' government towards the conservation of the West African ungulate populations urgently requires a follow-up. Unless a programme for census work, vegetation and animal population monitoring, and habitat management is developed, the conservation perspectives of our project will not be realized.

Summary

Introduction

In large parts of Africa land-use predominantly consists of the traditional use of the natural renewable resources soil, water, vegetation and fauna. The level of production depends on the regenerative capacity of the resource; inputs such as fertilizers are hardly available.

The repercussions of economic realignment in combination with other factors such as a rapid human population growth and technical innovation, have caused an increase in the exploitation of the natural resources. Aggravated by environmental uncertainties such as variability in rainfall, overexploitation of the natural resources has accelerated, initially without detrimental effects on the level of production. With an increasing pressure on land, reinforced by an accumulation of the effects of different land-use types, production levels decreased because the regenerative capacity of the natural resources was negatively affected.

The wild fauna in Africa forms such a renewable resource. In West Africa its overutilization has led to a depletion of animal populations: several species live on the brink of extermination. Only in national parks and game reserves are sizeable populations found, but even there their existence is not at all certain as man is invading these areas looking for 'empty' land.

The conservation of savanna ecosystems with representative populations of wild animals has become a matter of high priority. Not only their preservation as a part of the natural heritage but also their contribution to the rural economy justifies this attention.

The aim of this study is to contribute to the ecological knowledge required for the conservation and management of wild animal populations in West African savanna ecosystems.

Field work was mainly carried out in the Biosphere Reserve 'Boucle du Baoulé' in Mali. Additional observations were made in Burkina Faso.

An ecological characterization of the West African savanna

The vegetation as a source of food

The analysis of phenological patterns and trends in plant availability and quality in relation to environmental factors such as rainfall, soil fertility and fires, is essential for the understanding of the ecology of wild ungulate species.

Although rainfall is very seasonal in the West African savanna, not all plants reflect this seasonality. Every season has favourable conditions for certain plant groups. Only annual grasses and deciduous trees and shrubs show phenological patterns corresponding with the rainy season.

Perennial grasses dominate the savanna when the average annual rainfall is above 700 mm; annual grasses are abundant in zones with lower annual rainfall. Perennial grasses show a gradual development of shoots in the wet season. The growth of annual and perennial grasses is entirely determined by the availability of soil nitrogen. Perennial and tall annual savanna grasses flower when maximum phytomass is reached in the late wet season. Maximum phytomass reaches considerable quantities, and reflects the amount of rainfall received by the site. More rainfall results in more tufts per unit area but in the higher rainfall zones (i.e. above 800 mm annual rainfall) plants also invest in more leaves per stalk that remain green for a longer period. Variability in rainfall is relatively larger in the drier zones, as a result of which differences in phytomass between average and below average rainfall years are more pronounced. The quality of both annual and perennial savanna grasses slowly decreases during growth. The leaves, however, maintain a higher quality than other plant parts. In the dry season perennial grasses may show a dry-season growth if permitted by soil humidity. A substantial amount of dry-season growth of perennial grasses is found in zones which receive more than 900 mm annual rainfall. The quality of this dry-season growth is much higher than the remaining wet-season phytomass. Bush fires strongly reduce the phytomass of savanna grasses but stimulate dry-season growth.

Trees and shrubs can be classified into three groups with respect to the timing of sprouting and site of occurrence. Peak phytomass of deciduous and (semi)-evergreen species is reached in the late wet season and that of riverine species in the late dry season. There is a positive relationship between the quantity of woody foliage produced and annual rainfall.

The quality of this woody foliage is higher than that of the savanna grasses and more constant; the quantity available in the wet season is only one quarter. In the dry season the availability of woody foliage exceeds that of the savanna grasses. The presence of secondary plant compounds that depress the digestibility of woody foliage, seems to be positively correlated to the age of the leaves. Herbivorous animals in the savanna thus face a large variation in both forage quantity and quality.

The ecology of wild ungulates

Despite the severe hunting pressure and decreasing area of distribution, the West African savanna is still rich in ungulate species, but numbers are low.

Species do not use the various habitat types according to availability but show a degree of preference, especially in the dry season. However, the degree of overall selectivity is low. Species follow the catena in the landscape: in the dry season they concentrate at the lower end of the catena, which is often situated near a river. These movements and their distribution in general are correlated to their forage and water requirements. Warthog shows the highest degree of plasticity with respect to the spatial utilization of the savanna; species that feed more selectively, such as the bushbuck and waterbuck, are much less flexible.

No large-scale migrations have been observed nor are there indications that such movements have been a general feature of West African ungulates.

According to the proportion of grass in the diet and its seasonal change, species are classified as grazers, browsers and mixed feeders. More species prefer grass to woody foliage. In contrast with current literature it is concluded that both roan antelope and oribi should be classified as mixed feeders as both species can show a considerable shift to woody foliage in the dry season.

If only green leaves of grasses are considered as appropriate forage for grazers, these species meet fewer differences between seasons than between rainfall zones with respect to the quantity of available forage. For browsers the difference in forage availability between seasons is more pronounced than between rainfall zones.

Digestible energy, required per day per species, and the dry matter digestion efficiency were calculated permitting an estimate of gross energy intake required per day for maintenance. This intake appeared to be 7.1% of their metabolic weight. Grazers need more protein per day to meet their requirements than browsers, and ruminants more than non-ruminants. Plant protein concentrations in a balanced diet, i.e. a diet that meets both energy and protein requirements, are found to be independent of body size within each feeding strategy category. Integration of the data on forage quality and availability with the information on diet shows that the number of grazers is limited by the availability of plant protein in the dry season and that browsers are apparently limited by the quantity of available forage.

Most species show selective feeding to cope with this phenomenon of forage quality dropping below the minimum level dictated by a balanced diet, either by selecting different plant species, or by moving to other habitat types.

The ungulate community of the West African savanna

Given the large variations in the availability of resources such as forage and water, and their limited distribution in especially the dry season, competition between animal species can expected. Overlap in the diet of species is considerable, but this is mainly because in the quantitative analysis of diet composition only two plant categories were distinguished. Also there is a large overlap in the choice for the different habitat types. However, the combined overlap index shows a separation among some but not all species. Other mechanisms also lead to separation between species, such as separation through difference in feeding levels (animal size) and through different degrees of feeding selectivity (muzzle width).

Quantitatively, difference in diet composition is the most important mechanism leading to an ecological separation between most of the species examined, followed by differences in water dependency and in feeding selectivity. These mechanisms reduce the potential competition for resources through which the ungulate community achieves a certain stability. Large fluctuations in numbers are thus not to be expected.

Rainfall and bush fires are the main determinants of the structure and composition of the savanna vegetation. The availability of dry-season growth of perennial grasses determines the distribution of grass-preferring ungulates. In the lower rainfall areas these species become less numerous and more vulnerable to the variations in annual rainfall. Series of drought years do not eliminate the entire ungulate fauna but shift the relative proportion of species in the community to the woody foliage-preferring species, and may even cause the local extinction of grazing ungulates. Ungulates, such as elephant, roan antelope and oribi (mixed feeders), which can compensate for these variations in grass availability in space and time, are thus expected to have a more northern distribution than the real savanna grazers, which is indeed the case.

Fires maintain an equilibrium between the canopy layer of trees and shrubs and the cover by grasses. Fires preserve the existence of savanna grasses and stimulate the dry-season growth of the perennial grasses and increase its obtainability. Grass-preferring ungulates depend on the regular occurrence of fire. Long-term absence of fires will therefore have considerable influence on the abundance of certain ungulate species. Fire structures the composition of the ungulate community. The ungulate community of the West African savanna should therefore be characterized as a fire-climax.

The period of reproduction of the ungulates in the West African savanna is strongly determined by their feeding strategy: grazers have more restricted periods of reproduction than browsers. In both feeding strategy categories body size affects this periodicity as well: the larger the species, the more restricted the calving period.

In addition to the energy requirements for lactation, time of parturition is geared to allow the maximum chance of survival of calves after weaning. Weaning in the beginning of the wet season probably results in maximum calf survival in grazers, especially for the larger-bodied ones. For browsers that face the problem of a decreasing forage quality over the seasons to a lesser degree, this 'necessity' of timing is less important.

Ecological carrying capacity of the West African savanna

The different approaches for the estimation of the ecological carrying capacity are discussed. The method chosen in this study is to use the limited availability of quality forage in the dry season as a conservative but realistic estimate for the ecological carrying capacity as ungulates in the West African savanna ecosystem face the problem of a limited availability of quality forage in that period. From north to south the ecological carrying capacity increases, from c.1,000 (c.500) kg.km^{-2} to c.8,000 (c.3,550) kg.km^{-2} for grazers and from c.1,500 (c.1,100) kg.km^{-2} to c.2,400 (c.1,800) kg.km^{-2} for browsers in normal rainfall (dry) years. The lower rainfall zones are largely unsuitable for the grass-preferring ungulates throughout the year.

The validity of the relationship found between annual rainfall and herbivore biomass has been obtained through the comparison of these estimates of the ecological carrying capacity with information on animal stocking rates in other areas in the West African savanna. These areas, which have no or only minor poaching activities, have animal densities comparable to those calculated as the potential stocking rates for the Baoulé. This provides strong proof for the relationship of the ecological carrying capacity with annual rainfall in the Baoulé.

These potential stocking rates have been converted to potential numbers per species. When these figures are compared to the actual numbers, there are marked differences. For nearly all ungulate species actual numbers are far below their potential, indicating the severity of hunting pressure and of competition with livestock in the Baoulé.

In the lower rainfall zones of the West African Sudan savanna the ungulate biomass tends to be dominated by browsing ungulates. Above 800 mm annual rainfall grass-preferring species constitute the majority. Grass-preferring ungulates are vulnerable to climatic changes in the lower rainfall zones, especially as they depend on the dry-season growth of perennial grasses. In areas below 600 mm annual rainfall, short annual grasses provide good quality forage, higher in quantity than that available in the zone between 600 and 800 mm rainfall from dry-season growth of perennial grasses. Hence the transition of the Sahel pastures to the northern Sudan savanna shows a strong reduction in the ecological carrying capacity.

Because it is concluded that northern populations of especially grass-preferring species are very vulnerable to climatic changes, their protection will be effective and their long-term viability guaranteed only if corridors to more southern populations are available. Furthermore, uncontrolled hunting can drive northern populations more easily into extinction than southern populations of the species concerned.

When other approaches for the assessment of the carrying capacity in the West African savanna zone are analysed it appears that some methods do not incorporate the quality of the vegetation nor the large seasonal fluctuations in its quantity. Most methods take the quantity and/or quality of the vegetation as a starting point for the calculation of the carrying capacity. Discussion then centres on the limiting factors for vegetation growth. However, aspects concerning the feeding ecology and behaviour of the ungulates are not or only in a generalised form taken into account. This results in an overestimation of the carrying capacity of the lower rainfall zones, and sometimes in an underestimation in the higher rainfall zones.

Comparisons with the ecological carrying capacities of other savanna ecosystems in Africa reveal that in general the ecological carrying capacity of the West African savanna is lower than that of comparable regions elsewhere. Differences in soil nutrient status are responsible. Moreover, West Africa is less diversified with respect to the vegetation than East and southern Africa: the vegetation zones are neatly arranged according to rainfall. This leads to lower animal densities in the lower rainfall zones than in other parts of Africa with comparable rainfall, where the impact of the transition of short annual to tall perennial grasses is less detectable. Also the Harmattan is a phenomenon which lays extra physiological stress on the ungulates in the West African savanna in the dry season.

An analysis of the carrying capacity of Australian rangelands shows that in general they differ from the West African savanna in a comparable way to the savannas of East and southern Africa.

Conservation and management

With the present trends in land-use in West Africa it is obvious that the conservation of natural ecosystems should have a high priority. Areas, which have been the domain of wild ungulates for centuries are becoming scarce. The political decision to protect areas for the conservation of wild ungulate populations, for both consumptive and non-consumptive utilization, deserves a more extensive scientific basis.

The development of management programmes is urgently needed. Actual protection of conservation areas should have high priority. Furthermore, in the savanna ecosystem the systematic application of fire early in the dry season is an important tool in the preservation of the ungulate community. Hartebeest and elephant are key-species: they should carefully be monitored as they serve as indicators for the well-being of all ungulate species.

The active support by international donors in the development and implementation of these programmes is a necessity.

The Baoulé is an unique area: it supports a valuable combination of animal species due to the presence of an ecological gradient from north to south. This exceptional position on the national and international level warrants conservation efforts.

Fragmentation of suitable areas is becoming a problem which severely threatens conservation areas. The consequences of such fragmentation for the viability of ungulate populations and their conservation in the Baoulé are described. The present size of the biosphere reserve is large enough to provide resources for viable populations of ungulate species if various criteria for the long-term persistence of these species are applied.

The potential compatibility of the conservation of wild ungulate populations with other land-use types is considered but it is concluded that the conservation of the large ungulate community of the West African savanna in the Baoulé precludes simultaneous animal husbandry, arable farming and other land-use types.

A phased strategy for the conservation of the wild ungulate populations in the Baoulé is proposed. The management of a core area should have high priority; the ongoing traditional land-use in the peripheral areas should be discouraged in order to facilitate the extension of the core area in future. The formulation of a management programme is urgently required; it should be actively supported by the Netherlands' government.

Unless such a programme for census work, regular monitoring of animal populations and vegetation, and habitat management is developed and implemented in the very near future, our work for the conservation of wild ungulate populations in the Baoulé will have been in vain.

Samenvatting

Wild als natuurlijke bestaansbron in de West-afrikaanse savanne

Inleiding

In grote delen van Afrika maakt het landgebruik op voornamelijk traditionele wijze gebruik van de natuurlijke hernieuwbare bestaansbronnen bodem, water, vegetatie en fauna. Het produktieniveau van dit landgebruik hangt af van het regeneratievermogen van de bestaansbron; toevoegingen van buitenaf zoals kunstmest zijn nauwelijks beschikbaar.

De gevolgen van economische veranderingen in samenhang met andere factoren zoals een snelle groei van de bevolking en technische innovatie, hebben geleid tot een toename van de exploitatiedruk op de natuurlijke bestaansbronnen. Versterkt door onzekerheden inherent aan het milieu, zoals variabiliteit in de regenval, nam de overexploitatie van de natuurlijke bestaansbronnen toe. Aanvankelijk waren er geen negatieve gevolgen voor het produktieniveau te bemerken. Echter, met een toename van de druk op het land, en versterkt door een opeenstapeling van de effecten van de verschillende vormen van landgebruik, daalde de produktie van het landgebruik aangezien het regeneratievermogen van de natuurlijke bestaansbronnen negatief werd beïnvloed.

Wilde dieren in Afrika vormen zo'n natuurlijke bestaansbron. In West Afrika heeft de overexploitatie ervan geleid tot een uitdunning van de wildpopulaties. Sommige soorten verkeren zelfs op het punt van uitsterven. Alleen in nationale parken en wildreservaten treft men nog populaties van enige omvang aan maar zelfs daar is hun voortbestaan onzeker omdat de mens deze gebieden binnentrekt op zoek naar ongebruikt land.

De aandacht voor de bescherming van savanne-oecosystemen met representatieve populaties wilde dieren heeft een hoge prioriteit gekregen. Niet alleen hun bescherming als deel van het natuurlijk erfgoed maar ook de bijdrage die de wilde fauna levert aan de economie van het platteland rechtvaardigt deze aandacht.

Het doel van deze studie is bij te dragen aan de kennis die noodzakelijk is voor het behoud en beheer van populaties wilde dieren in de West-afrikaanse savanne-oecosystemen.

Het veldwerk is hoofdzakelijk uitgevoerd in het biosfeerreservaat 'Boucle du Baoulé' in Mali en directe omgeving. Aanvullende gegevens werden verzameld in Burkina Faso.

De vegetatie als voedselbron

De analyse van fenologische patronen en van het verloop in de beschikbaarheid en kwaliteit van planten in relatie tot omgevingsfactoren zoals regenval, bodemvruchtbaarheid en vuur, is noodzakelijk voor het begrip van de oecologie van wilde hoefdieren.

Hoewel de regenval een sterk seizoenkarakter heeft, is dit aspect niet in alle plantensoorten terug te vinden. Elk seizoen biedt gunstige omstandigheden voor de groei van bepaalde groepen planten. Alleen de eenjarige grassen en de bladverliezende struiken en bomen vertonen fenologische patronen die overeenstemmen met het optreden van regen.

Meerjarige grassen overheersen in de vegetatie wanneer de jaarlijkse hoeveelheid regen meer bedraagt dan 700 mm; eenjarige grassen zijn rijk vertegenwoordigd in gebieden met minder neerslag. Meerjarige grassen vertonen een geleidelijke groei van scheuten in de regentijd. Deze groei, evenals die van de eenjarige grassen, is geheel onderhevig aan de beperkingen opgelegd door de beschikbaarheid van stikstof in de bodem. Meerjarige en eenjarige grassen bloeien wanneer de maximale fytomassa is bereikt, aan het einde van de regentijd. Deze maximale fytomassa kan aanzienlijk zijn en weerspiegelt de hoeveelheid regenval op een bepaalde plaats. Meer regenval resulteert in meer pollen gras per oppervlakte-eenheid maar in gebieden met hogere regenval (i.e. meer dan 800 mm per jaar) vormen planten ook meer blad per stengel; dit blad blijft langer groen. De variabiliteit in de jaarlijkse regenval is relatief groter in de drogere gebieden en daardoor zijn er de verschillen in fytomassa tussen jaren met normale hoeveelheden regenval en drogere jaren meer uitgesproken.

De kwaliteit van zowel eenjarige als meerjarige grassen loopt langzaam terug tijdens de groei van de planten. De bladeren behouden echter steeds een hogere kwaliteit dan andere delen van de plant. In de droge tijd kunnen meerjarige grassen doorgroeien indien er voldoende vocht in de bodem beschikbaar is. Deze droge-tijd groei vormt aanzienlijke hoeveelheden in zones die meer dan 900 mm regen per jaar ontvangen. De kwaliteit van deze in de droge tijd gevormde fytomassa is veel hoger dan die van de fytomassa die dan nog resteert uit de natte tijd. Bosbranden reduceren de fytomassa van de savanne grassen in sterke mate maar bevorderen tevens de groei van de meerjarige grassen in de droge tijd.

De voorkomende soorten bomen en struiken kunnen in drie groepen worden ingedeeld op basis van het moment van uitlopen en plaats van voorkomen: de bladverliezende soorten, de altijd-groene of bijna-altijd groene soorten, en soorten die bij de rivieren groeien. De maximale hoeveelheden blad worden bij de eerste twee groepen aangetroffen tegen het einde van de regentijd, die van de soorten die bij de rivier groeien, in de tweede helft van de droge tijd. De hoeveelheid blad die wordt geproduceerd neemt toe met de hoeveelheid jaarlijkse regenval.

De kwaliteit van het blad van bomen en struiken is hoger dan dat van de grassen en varieert minder in de tijd; de hoeveelheid in de regentijd beschikbaar blad is slechts een kwart van dat van de grassen. In de droge tijd is er daarentegen meer blad van houtige planten beschikbaar dan fytomassa van savanne grassen. De aanwezigheid van secundaire plantestoffen zoals tanninen, die de verteerbaarheid van het blad voor de herbivoor doen verminderen, neemt toe met de leeftijd van het blad.

Herbivoren die in de savanne leven, zien zich dus geconfronteerd met een grote variatie in voedselaanbod en voedselkwaliteit.

De oecologie van wilde hoefdieren

Ondanks de zware jachtdruk op en een kleiner wordend verspreidingsgebied van hoefdieren is de West-afrikaanse savanne nog steeds rijk aan soorten hoefdieren maar de aantallen zijn laag.

Met name in de droge tijd vertonen de verschillende soorten hoefdieren een voorkeur voor bepaalde typen habitat. De diersoorten volgen de hoogtegradiënt in het landschap: in de droge tijd concentreren zij zich in de lagere delen ervan, vaak in de nabijheid van een rivier. Deze bewegingen en de ruimtelijke verspreiding in het algemeen zijn in verband te brengen met de behoeften aan water en voedsel. Het wrattenzwijn vertoont de grootste plasticiteit in relatie tot het gebruik van de savanne; soorten die selektiever eten zoals de bosbok en de waterbok, zijn minder flexibel. Migratie van hoefdieren over grote afstanden is nooit waargenomen noch is er enige evidentie gevonden dat een dergelijke migratie bij West-afrikaanse hoefdieren algemeen voorkomt.

Op basis van het aandeel grassen in het dieet en de fluctuaties daarin over de seizoenen zijn de diersoorten geclassificeerd als 'grazer', 'browser' en 'mixed feeder'. Het merendeel van de hoefdieren geeft voorkeur aan grassen boven blad van bomen en struiken. In tegenstelling tot wat de huidige literatuur leert, is geconcludeerd dat zowel de paardantiloop als de oribi geclassificeerd moeten worden als 'mixed feeders' omdat beide soorten in de droge tijd een aanzienlijke verschuiving in het dieet ten gunste van het blad van bomen en struiken kunnen laten zien.

Indien alleen de groene bladeren van grassen als geschikt voedsel voor grazende hoefdieren worden aangemerkt, zijn voor deze dieren de verschillen in de hoeveelheid beschikbaar voedsel tussen de seizoenen geringer dan die tussen de verschillende regenvalgebieden. Voor de 'browsers' is juist het omgekeerde het geval.

De verteerbare energie die per dag benodigd is voor onderhoud, en de verteringsefficiëntie van de opgenomen droge stof zijn per diersoort berekend om tot een schatting te komen van de bruto energie opname per dag benodigd voor onderhoud. Deze opname blijkt gelijk te zijn aan 7.1% van het metabolische lichaamsgewicht. 'Grazers' hebben meer plantaardig eiwit nodig per dag om in de behoefte aan eiwit te voorzien dan 'browsers' en herkauwers meer dan niet-herkauwers. De concentratie plantaardig eiwit in een gebalanceerd dieet, i.e. een dieet dat zowel voorziet in de behoefte aan eiwit als in dat aan energie, is binnen elke groep van voedselzoekstrategieën onafhankelijk van de lichaamsgrootte van een diersoort. Wanneer de gegevens aangaande het aanbod aan voedsel en de kwaliteit ervan geïntegreerd worden met die betreffende het dieet, blijkt dat voor de 'grazers' de *kwaliteit* van het beschikbare voedsel de beperkende factor is; hun aantallen worden bepaald door de beschikbaarheid van kwaliteitsvoer in de droge tijd. Voor de 'browsers' is klaarblijkelijk de *hoeveelheid* aan beschikbaar voedsel de beperkende factor.

De meeste diersoorten vertonen enige mate van selectiviteit in het voedselzoeken wanneer de kwaliteit van het voedsel daalt onder de minimum waarde zoals die door het gebalanceerde dieet wordt gesteld. Zij doen dit door andere plantensoorten te gaan eten of door zich naar andere habitattypen te begeven.

De hoefdier-gemeenschap van de West-afrikaanse savanne

Gezien de grote variatie in het aanbod aan primaire levensbehoeften zoals voedsel en water, en de beperkte aanwezigheid ervan in met name de droge tijd, kan competitie tussen diersoorten worden verwacht. Er is een aanzienlijke overlap in de samenstelling van het menu van soorten maar deze overlap is vooral het gevolg van het onderscheiden van maar twee typen voedsel in de kwantitatieve analyse van het dieet. Ook is er een grote overlap in de keuze voor de verschillende typen habitat. Gebruik van een index waarin de voedsel- en habitatkeuze zijn gecombineerd toont een scheiding aan tussen soorten, zij het niet tussen alle. Andere mechanismen dragen ook bij tot een scheiding van soorten in ruimte en tijd, zoals scheiding tengevolge van verschil in hoogte waarop voedsel wordt gezocht (diergrootte) en tengevolge van verschillende mate van selectiviteit bij het voedselzoeken (bekbreedte). Verschil in menusamenstelling is echter in kwantitatieve zin het belangrijkste mechanisme dat tot oecologische scheiding van soorten leidt, gevolgd door verschillen in drinkwaterbehoefte en in selectiviteit in voedselzoeken. Deze mechanismen beperken de potentiële competitie om primaire levensbehoeften tussen soorten waardoor de hoefdier-gemeenschap een zekere mate van stabiliteit verkrijgt. Grote fluctuaties in aantallen zijn dientengevolge niet te verwachten.

Regenval en bosbranden bepalen in belangrijke mate de structuur en samenstelling van de savannevegetatie. De beschikbaarheid van de droge-tijd groei van de meerjarige grassen bepaalt de verspreiding van de hoefdieren die een voorkeur hebben voor gras. In de gebieden met een lagere jaarlijkse regenval zijn deze diersoorten minder talrijk en kwetsbaarder voor variaties in de jaarlijkse regenval. Een serie van opeenvolgende droge jaren doet niet de gehele hoefdier-gemeenschap verdwijnen maar heeft tot gevolg dat het aandeel van de 'browsers' in die gebieden relatief groter wordt; lokaal kunnen 'grazers' uitsterven. Hoefdieren zoals de olifant, paardantiloop en de oribi ('mixed feeders'), die voor deze ruimtelijke en temporele variaties in de beschikbaarheid van grassen kunnen compenseren, zouden dus een noordelijker verspreiding moeten hebben dan de echte 'grazers' op de savanne en dat is inderdaad het geval.

Door branden blijft een evenwicht bestaan tussen de boom/struiklaag van de savanne en de grassen. Bosbranden garanderen het voortbestaan van savannegrassen en stimuleren de groei van de meerjarige grassen in de droge tijd en vergroten de bereikbaarheid ervan. Hoefdieren met een voorkeur voor grassen zijn dus afhankelijk van regelmatig optreden van vuur. Langdurige afwezigheid van branden zal dientengevolge een aanzienlijke invloed hebben op de talrijkheid van bepaalde hoefdiersoorten. Vuur geeft structuur aan de hoefdier-gemeenschap. Deze hoefdier-gemeenschap moet daarom gekenschetst worden als een vuur-climax gemeenschap.

Het moment waarop de hoefdieren in de West-afrikaanse savanne hun kalveren werpen wordt sterk bepaald door hun voedselzoekstrategie: bij 'grazers' is de periode in het jaar waarin dit plaatsvindt sterker afgebakend dan bij de 'browsers'. In beide categorieën is de lichaamsgrootte mede van invloed: hoe groter de diersoort, hoe korter de werptijd.

Het tijdstip waarop het kalf wordt geworpen is zodanig gesteld dat naast het voorzien in de energiebehoeften voor het zogen van kalf, er ook een maximale overlevingskans voor het kalf na spening wordt bereikt. Spening van de kalveren in het begin van de regentijd resulteert waarschijnlijk in een maximale overlevingskans voor kalveren van grazende hoefdieren, met name voor de grotere soorten. Voor 'browsers' die in mindere mate met het probleem van afnemende voedselkwaliteit worden geconfronteerd, is deze timing van werpen minder belangrijk.

De oecologische draagkracht van de West-afrikaanse savanne

Verschillende benaderingen voor het schatten van de oecologische draagkracht worden besproken. In deze studie is gekozen voor de methode die de beperkte aanwezigheid van kwaliteitsvoedsel in de droge tijd gebruikt als basis voor een conservatieve maar realistische schatting voor de oecologische draagkracht van de savanne, omdat hoefdieren in de West-afrikaanse savanne zich gesteld zien voor het probleem van een beperkte aanwezigheid van dit voedsel in die periode. Van noord naar zuid neemt de oecologische draagkracht van de savanne toe, van ca 1000 (ca 500) kg.km^{-2} tot ca 8000 (ca 3500) kg.km^{-2} voor 'grazers' en van 1500 (ca 1100) kg.km^{-2} tot ca 2400 (ca 1800) kg.km^{-2} voor 'browsers' in normale regenval (droge) jaren. Over het gehele jaar gerekend zijn de zones met de lagere jaarlijkse regenval in sterke mate ongeschikt voor de grazende hoefdieren.

De validiteit van de gevonden relatie tussen biomassa van de hoefdieren en jaarlijkse regenval is verkregen door deze schattingen voor de oecologische draagkracht te vergelijken met dierdichtheden in andere gebieden in de West-afrikaanse savanne. Deze gebieden, die geen of nauwelijks activiteiten van stropers kennen, hebben dierdichtheden die in dezelfde orde van grootte liggen als die welke als potentiële dichtheden voor de Baoulé berekend zijn, hetgeen een sterk bewijs is voor de gevonden relatie van de oecologische draagkracht met de jaarlijkse neerslag in de Baoulé.

Deze potentiële dierdichtheden zijn omgerekend naar potentiële aantallen dieren per soort. Wanneer deze aantallen vergeleken worden met de nu aanwezige aantallen, dan blijken er grote verschillen te bestaan. Bijna alle soorten hoefdieren komen in veel lagere aantallen voor dan die welke er op grond van de berekeningen zouden kunnen leven, hetgeen aangeeft hoe zwaar de jachtdruk is in de Baoulé alswel de competitie met vee.

In de lagere regenval zones van de West-afrikaanse savanne neigt de hoefdiergemeenschap gedomineerd te worden door de 'browsers'. Wanneer de jaarlijkse regenval meer dan 800 mm bedraagt, vormen de grazende hoefdieren de meerderheid. Deze laatsten zijn kwetsbaarder voor klimatologische veranderingen in de gebieden met minder regenval, vooral als soorten afhankelijk zijn van de droge-tijd groei van meerjarige grassen. In gebieden met een jaarlijkse neerslag onder de 600 mm leveren de lage eenjarige grassen voedsel van voldoende kwaliteit en de hoeveelheid ervan is groter dan dat wat aan droge-tijd groei van meerjarige grassen beschikbaar is in de gebieden met een jaarlijkse regenval tussen 600 en 800 mm. Dientengevolge gaat de overgang van de Sahel-weiden naar de savanne gepaard met een sterke verlaging van de oecologische draagkracht.

Omdat de noordelijke populaties van de grazende hoefdieren kwetsbaar zijn voor klimaatsveranderingen, zal de bescherming van deze noordelijke populaties slechts dan effectief kunnen plaatsvinden en de levensvatbaarheid ervan ook op lange termijn worden gegarandeerd, wanneer er corridors naar zuidelijker populaties beschikbaar zijn. Eveneens kan een ongecontroleerd uitoefenen van de jacht de noordelijke populaties gemakkelijker doen uitsterven dan zuidelijker populaties van deze soorten.

Wanneer andere benaderingen voor de vaststelling van de oecologische draagkracht in de West-afrikaanse savanne worden bestudeerd, blijkt dat sommige van deze methoden niet de kwaliteit van de planten of de grote verschillen in de beschikbaarheid ervan over de seizoenen in de berekening meenemen. De meeste methoden gebruiken de hoeveelheid en/of de kwaliteit van de planten als uitgangspunt voor de berekening van de draagkracht, waarna men zich dan concentreert op die factoren die beperkend zijn voor de groei van deze planten. Echter, aspecten als de voedseloecologie en het gedrag van de hoefdieren worden niet of slechts in zeer algemene zin in de berekening betrokken. Dit mondt uit in een overschatting van de draagkracht voor de gebieden met lagere regenval en soms in een onderschatting ervan voor gebieden met hogere regenval.

Vergelijkingen met de oecologische draagkracht van savanne-oecosystemen elders in Afrika tonen aan dat over het algemeen de oecologische draagkracht van de West-afrikaanse savanne lager is dan die van vergelijkbare gebieden elders. Verschillen in bodemvruchtbaarheid zijn hiervoor verantwoordelijk. Bovendien is de vegetatie van de West-afrikaanse savanne minder divers dan die van Oost en zuidelijk Afrika: de vegetatiezones in West Afrika liggen netjes gerangschikt, in overeenstemming met de hoeveelheid jaarlijkse regenval. Dit leidt tot lagere wilddichtheden in de gebieden met lagere jaarlijkse regenval dan in andere delen van Afrika met vergelijkbare hoeveelheden regen, waar de invloed van de overgang van eenjarige naar meerjarige grassen minder te bespeuren is. Ook de Harmattan is een verschijnsel dat ten opzichte van andere delen van

Afrika een extra fysiologische belasting vormt voor de hoefdieren in de West-afrikaanse savanne.

Een analyse van de draagkracht van de natuurlijke graslanden in Australië laat zien dat zij in grote lijnen op overeenkomstige wijze verschillen van die van de West-afrikaanse savanne als die in Oost en zuidelijk Afrika.

Behoud en beheer

Gezien de huidige ontwikkelingen in het landgebruik in West Afrika is het duidelijk dat het behoud van natuurlijke oecosystemen een hoge prioriteit moet hebben. Gebieden die eeuwenlang het domein zijn geweest van de wilde hoefdieren zijn schaars aan het worden. De politieke beslissing om gebieden te beschermen voor het behoud van populaties wilde hoefdieren, voor zowel consumptieve als niet-consumptieve benutting, behoeft uitgebreider wetenschappelijk onderzoek.

De ontwikkeling van programma's voor het beheer is dringend noodzakelijk. Daadwerkelijke bescherming van natuurgebieden heeft de hoogste prioriteit. Eveneens is het gebruik van vuur, vroeg in de droge tijd een belangrijk hulpmiddel bij het beschermen van de hoefdier-gemeenschap. Het hartebeest en de olifant zijn als sleutelsoorten aan te merken: hun populaties moeten zorgvuldig gevolgd worden omdat zij de leefsituatie van alle soorten hoefdieren kunnen duiden.

De actieve ondersteuning door internationale donoren bij de ontwikkeling en uitvoering van deze programma's is onontbeerlijk.

De Baoulé is een uniek gebied: het bevat een waardevolle combinatie van diersoorten tengevolge van de aanwezigheid van een oecologische gradient van noord naar zuid. Deze op nationale en internationale schaal uitzonderlijke positie rechtvaardigt inspanningen gericht op het behoud ervan.

Fragmentatie van gebieden vormt in toenemende mate een probleem dat natuurgebieden bedreigt. De consequenties van een dergelijke fragmentatie voor de levensvatbaarheid en het behoud van populaties hoefdieren in de Baoulé worden beschreven. Afgemeten aan verschillende criteria voor het voortbestaan van dieren op lange termijn, zijn de huidige afmetingen van het biosfeerreservaat voldoende om mogelijkheden voor bestaan te bieden voor levensvatbare populaties wilde hoefdieren.

De mogelijkheid is onderzocht in hoeverre het behoud van populaties wilde hoefdieren te verenigen is met andere vormen van landgebruik. Geconcludeerd wordt echter dat het behoud van de hoefdier-gemeenschap van de West-afrikaanse savanne in de Baoulé gelijktijdig gebruik van het gebied door veehouderij, akkerbouw en andere vormen van landgebruik uitsluit.

Een fasering in het behoud van de populaties wilde hoefdieren in de Baoulé wordt voorgesteld. Het beheer van een kerngebied moet hoge prioriteit krijgen; daarnaast moet het huidige, traditionele landgebruik in de periferie ontmoedigd worden teneinde een toekomstige uitbreiding van het kerngebied te vergemakkelijken. Het formuleren van een programma voor het beheer is dringend gewenst en dient daadwerkelijk ondersteund te worden door de Nederlandse overheid. Zo'n programma voor tellingen, voor het volgen van de ontwikkelingen in de vegetatie en in dierpopulaties, en voor het beheer van het gebied als leefgebied voor tal van soorten planten en dieren moet op zeer korte termijn worden opgezet en in uitvoering worden genomen, anders zal ons werk voor het behoud van populaties wilde hoefdieren in de Baoulé voor niets zijn geweest.

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Appendix I:

Plant species, eaten by ungulates in the Baoulé, based on field observations, ruminal and faecal analyses.
Nomenclature of woody species after Geerling (1982).
Explanation of life form (lf) code:
t = tree, pa = palm, s = shrub, su = suffritex, l = climber, p = perennial grass, a = annual grass
EL = elephant, WH = warthog, BB = bushbuck, DU = duiker
RB = reedbuck, WB = waterbuck, RO = roan antelope, HB = hartebeest, OR = oribi

Plant species	lf	EL	WH	BB	DU	RB	WB	RO	HB	OR
woody plants										
Acacia ataxacantha	l			x	x		x			
A. erythrocalyx	l			x			x		x	
A. hockii	s						x			
A. macrothyrsa	t			x				x		
A. nilotica	s			x						
A. seyal	t	x								
A. sieberana	t			x			x	x		
Adansonia digitata	t	x								
Adenium obesum	t	x								
Albizia chevalieri	t						x	x		
Anogeissus leiocarpus	t				x					
Baissea multiflora	l			x	x	x	x	x	x	x
Balanites aegyptiaca	t			x						
Bauhinia rufescens	s							x		
Bombax costatum	t	x								
Borassus aethiopum	pa		x							
Boscia angustifolia	t	x			x			x		
B. senegalensis	s							x		
Breonadia salicina	t								x	
Cadaba farinosa	l			x			x	x	x	
Canthium cornelia	l								x	
Cassia sieberana	t			x				x	x	
Combretum aculeatum	s				x					
C. glutinosum	s			x			x	x		x
C. micranthum	s			x			x	x	x	
C. nigricans	s			x	x			x		
Cordya mixa	t	x								
Cordyla pinnata	t							x		
Crossopterix febrifuga	s							x		
Detarium microcarpum	t								x	
Dichrostachys cinerea	s			x	x	x	x	x		x
Erythrina senegalensis	t							x		x

Plant species	lf	EL	WH	BB	DU	RB	WB	RO	HB	OR
Feretia apodanthera	s							x		
Ficus capreaefolia	s			x		x				
Flemingia faginea	s			x			x			
Gardenia erubescens	s	x						x		
G. ternifolia	t		x	x	x		x	x	x	x
Guiera senegalensis	s		x	x	x		x		x	
Hippocratia africana	l			x						
Isoberlinia doka	t				x			x		
I. tomentosa	t						x			
Lannea microcarpa	t	x								
Lonchocarpus laxiflorus	t			x			x	x		
L. cyanescens	l								x	
Maerua angolensis	t			x						
M. oblongifolia	su			x			x			x
Millettia thonningii	t				x					
Mimosa pigra	s			x		x				
Paullinia pennata	l				x		x			
Pericopsis laxiflora	t				x				x	
Phyllanthus reticulatus	s			x						
Piliostigma reticulata	s	x		x				x	x	
P. thonningii	s				x					
Prosopis africana	t						x			
Pterocarpus erinaceus	t							x		
P. lucens	s	x		x		x	x	x		
Rotula aquatica	s			x						
Saba senegalensis	l			x						
Salix subserrata	s			x						
Sarcocephalus latifolius	t			x						
Sclerocarys birrea	t	x	x							x
Securidaca longipedunculata	s							x		
Sericanthe chevalieri	s						x			
Sesbania sesban	s			x						
Sterculia setigera	t	x								
Syzygium guineense	s				x					
Tamarindus indica	t			x						
Terminalia avicennioides	t			x			x			
T. laxiflora	t			x						
Vernonia colorata	s			x						
Xeroderris stuhlmannii	t						x	x	x	
Zyziphus mauritiana	t							x		
Z. mucronata	s			x						
forbs										
Ageratum conyzoides				x						
Borreria chaetocephala								x		
B. radiata		x	x	x	x	x		x	x	x
B. stachyda			x	x	x	x	x	x		x
Cassia orientalis				x						
C. tora								x		
Cochlospermum tinctorum	su		x							

Plant species	lf	EL	WH	BB	DU	RB	WB	RO	HB	OR
Coloquintus vulgaris								x		
Courbonia virgata	su			x						
Cucumis spec.			x							
Dipcadi longifolium							x			
Hibiscus asper								x	x	x
H. sabdarifa (?)								x		
Hygrophila pobeguinii				x						
Indigofera spec.		x			x					x
Ipomoea spec.				x						
Lepidagathis spec.				x						
Meriammia spec.								x		
Oldenlandia corymbosa				x						
Zornia glochidiata				x	x					
grasses/sedges										
Andropogon gayanus	p		x			x	x	x	x	x
A. pseudapricus	a					x	x	x	x	x
Brachiaria jubata	p					x	x	x	x	
B. lata	a						x			
Ctenium neewtonii	p?							x	x	
Cynbopogon giganteus	p		x			x		x		
Cyperus spec.	p		x	x		x	x			
Digitaria ciliaris	a?							x		
Diheteropogon hagerupii	a							x		
Elymandra androphyla	p						x			
Eragrostis gangetica	a							x	x	
Hypparhenia dissoluta	p							x	x	
H. rufa	p		x			x	x	x	x	
Imperata cylindrica	p								x	
Leersia hexandra	p		x						x	
Loudetia hordeiformis	a								x	
L. simplex	p						x	x	x	
L. togoensis	a								x	
Panicum anabaptistum	p		x	x		x	x		x	
Parahypparhenia perennis	p		x				x	x	x	
Paspalum polystachyum	p		x	x		x	x	x	x	x
Pennisetum pedicellatum	a					x				
P. polystachyon	a								x	
P. subangustum	a							x	x	
Schizachirium exile	p?								x	
S. sanguinum	p?								x	
Sporobolus pyramidalis	p							x	x	x
Vetiveria fulvibarbis	p		x			x	x			
V. nigritana	p						x		x	
algae										
unidentifiable specis				x						

Appendix II:

Chemical composition and in-vitro digestibility of woody plant species eaten by various ungulates in the Baoulé; all species sampled in woodland savanna near Missira Research Station, unless otherwise indicated.

Legend: M : month (1 = january, etc)
T : tannins (% of dry matter)
N : nitrogen (% of dry matter)
V_{om} : in-vitro digestibility of organic matter
V_{cwc} : in-vitro digestibility cell wall components (organic matter)
NDF : neutral detergent fiber (% of organic matter)
ADF : acid detergent fiber (% of organic matter)
HEMI : hemicellulose (% of organic matter)
CELL : cellulose (% of organic matter)
LIGN : lignin (% of orgnaic matter)
*.** : no data available
FL : riverine site
TE : on ant hill
ML : on shallow soil with laterite caps
MP : on very deep soil
RO : rocks

ACACIA ATAXACANTHA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.59	*.**	37.4	3.4	48.6	29.5	20.2	15.1	10.5
2	2.41	*.**	45.2	–1.9	45.9	29.5	17.4	15.7	10.7
3	1.95	9.15	56.8	11.0	46.0	30.5	15.3	14.2	12.4
4	2.82	*.**	66.5	28.3	47.0	38.0	9.1	21.1	16.6
5	4.33	*.**	72.6	30.8	30.1	17.2	13.6	8.3	6.4
6	4.40	*.**	33.5	**.*	23.2	13.5	10.2	7.7	4.1
7	4.10	*.**	68.6	31.0	48.2	30.8	18.4	16.0	11.5
8	2.99	2.83	43.6	8.1	62.3	42.4	21.1	17.8	20.6
9									
10									
11	3.52	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
12	2.64	9.03	64.3	12.5	43.0	25.9	17.3	13.3	9.3

ACACIA SEYAL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.62	*.**	74.1	38.8	31.3	12.2	19.9	7.3	3.3
2	2.45	*.**	76.5	30.3	24.8	13.3	11.8	7.4	4.3
3	2.13	*.**	84.1	50.3	22.7	11.8	10.9	7.1	3.3
4									
5	2.63	*.**	75.8	30.0	27.0	11.8	15.8	8.8	2.1
6	3.08	*.**	83.7	48.0	20.6	8.6	12.4	7.0	.9
7	2.89	*.**	72.6	33.5	32.1	15.0	17.7	9.0	4.4
8	1.95	3.21	81.6	56.1	31.5	15.4	16.7	8.8	5.4
9									
10	1.94	*.**	76.0	35.1	32.7	17.5	15.6	10.1	6.0
11	2.07	*.**	74.7	31.5	33.1	16.9	16.6	8.1	6.9
12	2.92	0.48	84.7	64.7	29.7	13.4	16.8	8.7	3.7

BORASSUS AETHIOPUM

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.10	*.**	33.6	47.5	63.5	43.5	19.8	29.7	11.7
2	1.08	*.**	26.0	10.4	64.0	41.6	22.4	26.6	12.5
3	1.14	*.**	36.0	37.8	69.6	49.7	19.8	32.3	14.6
4	0.99	8.97	38.7	40.3	67.8	49.3	18.4	30.0	14.6
5	0.99	*.**	33.5	8.8	69.2	46.4	22.8	31.1	12.2
6	0.97	*.**	34.8	8.7	68.3	45.1	23.2	31.9	11.7
7	1.26	*.**	54.6	38.9	62.2	44.5	17.7	29.0	13.0
8	1.54	7.21	39.3	15.1	71.2	46.9	24.7	29.6	14.9
9									
10									
11	1.39	*.**	42.2	35.5	66.3	46.1	20.1	31.0	13.0
12	1.02	8.37	43.2	38.6	63.7	44.8	18.8	30.2	12.6

BOSCIA ANGUSTIFOLIA TE

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	3.13	*.**	52.6	7.4	64.3	40.5	24.0	23.4	8.4
2									
3	3.16	0.79	51.2	21.2	61.1	37.7	23.6	23.5	9.1
4	2.23	*.**	31.0	17.8	63.9	41.5	22.6	24.4	9.5
5									
6	2.28	*.**	56.8	24.4	68.2	41.3	27.1	24.3	10.7
7	2.96	*.**	50.8	29.1	55.6	34.1	21.7	20.1	9.1
8	2.64	0.48	**.*	**.*	**.*	**.*	**.*	**.*	**.*
9									
10	3.56	*.**	61.1	61.5	57.1	35.3	21.6	20.8	8.1
11	2.85	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
12	2.74	*.**	30.7	49.0	64.3	40.7	23.4	23.4	9.0

CADABA FARINOSA TE

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1									
2									
3									
4	2.81	9.50	**.*	**.*	*.**	*.**	11.2	5.7	3.3
5									
6									
7	*.**	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
8	5.01	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
9									
10	4.71	0.83	75.3	44.1	28.0	18.4	9.4	10.4	4.7
11	4.97	*.**	**.*	**.*	**.*	**.*	15.3	10.4	5.5
12	5.06	1.67	76.4	21.7	24.6	14.0	10.5	7.9	4.8

CASSIA SIEBERANA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.40	*.**	45.4	2.0	41.0	30.3	10.4	16.6	11.4
2	1.27	*.**	56.3	26.2	43.6	32.3	11.1	16.9	10.6
3									
4	2.03	*.**	68.9	31.7	38.9	25.2	14.1	11.7	9.2
5									
6	2.57	*.**	67.5	23.1	45.7	29.2	16.5	10.5	15.9
7	1.77	*.**	68.3	32.2	47.8	33.5	14.2	15.6	12.0
8	2.05	*.**	53.1	23.2	60.7	42.2	18.4	15.5	17.5
9									
10									
11									
12									

COMBRETUM GLUTINOSUM ML

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	0.76	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
2									
3	1.77	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
4	1.70	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
5	1.09	*.**	44.8	5.1	42.1	28.9	13.3	19.8	8.4
6	1.28	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
7									
8	1.16	*.**	60.2	17.1	40.2	26.9	13.5	16.7	8.0
9	1.36	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
10									
11	0.85	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
12	1.05	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*

COMBRETUM GLUTINOSUM MP

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	0.67	*.**	48.6	11.3	42.4	30.2	12.4	19.9	8.6
2									
3	1.73	*.**	63.9	9.7	28.2	19.5	8.9	12.6	5.2
4	1.89	2.97	65.2	22.0	32.6	23.6	9.2	15.5	4.9
5	1.50	*.**	56.8	12.2	35.1	25.4	9.9	16.2	7.1
6	1.10	*.**	55.1	18.9	47.4	33.2	14.5	22.7	8.4
7	1.21	*.**	42.5	15.3	49.4	33.7	16.1	22.4	9.1
8	1.16	2.73	54.7	13.5	44.0	30.0	14.3	19.6	8.2
9	1.98	*.**	52.7	19.6	51.6	33.0	18.8	22.3	8.8
10									
11	1.02	5.35	**.*	**.*	**.*	**.*	14.4	23.3	8.7
12	1.12	*.**	56.6	13.5	38.2	24.8	12.5	15.5	7.8

COMBRETUM MICRANTHUM RO

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.78	*.**	76.6	48.4	43.0	28.4	14.9	13.0	12.2
2	2.12	*.**	54.2	22.0	43.4	30.3	13.5	13.5	14.8
3	1.47	*.**	77.1	49.3	34.1	24.2	10.1	11.5	11.3
4	2.16	*.**	**.*	**.*	**.*	**.*	13.4	13.2	15.1
5	3.10	*.**	**.*	**.*	**.*	**.*	14.5	6.9	21.4
6	2.30	*.**	70.8	29.9	37.8	22.9	14.9	7.8	12.3
7	3.47	*.**	67.5	24.0	48.6	28.7	20.1	9.2	14.0
8									
9									
10									
11									
12									

COMBRETUM MICRANTHUM TE

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.70	*.**	57.6	23.2	41.1	28.3	13.4	12.7	13.2
2									
3	1.69	*.**	72.7	43.0	42.3	31.2	11.5	15.6	12.4
4	2.34	1.70	75.1	50.8	39.6	27.2	12.8	12.5	12.8
5									
6	1.66	*.**	**.*	**.*	**.*	**.*	9.2	14.8	17.5
7	4.33	*.**	**.*	**.*	**.*	**.*	24.1	9.2	15.4
8	3.16	7.13	**.*	**.*	**.*	**.*	27.6	13.5	16.5
9									
10	2.62	*.**	**.*	**.*	**.*	**.*	13.6	16.5	19.1
11	2.50	*.**	36.3	20.5	53.2	40.3	13.3	17.3	20.5
12	2.06	9.74	54.5	26.3	55.7	37.5	18.2	14.6	18.8

COMBRETUM NIGRICANS TE

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.37	*.**	29.0	5.3	58.7	48.6	9.9	14.6	23.4
2									
3	1.62	*.**	54.5	20.8	53.5	43.8	9.6	15.2	22.0
4	1.49	7.01	35.9	8.8	55.2	44.8	10.2	15.4	21.0
5									
6	1.80	*.**	59.6	21.9	59.6	48.2	11.3	15.9	24.1
7	4.07	*.**	74.4	44.3	43.8	21.8	22.2	5.9	13.5
8	3.05	9.42	43.4	1.4	54.3	42.7	13.1	13.3	23.4
9									
10	2.65	*.**	42.4	−6.4	56.9	44.6	11.9	14.2	22.9
11	2.69	*.**	45.0	5.2	56.5	49.5	6.2	9.6	27.6
12	1.70	11.76	37.7	10.1	63.3	53.9	9.3	11.8	27.0

DICHROSTACHYS CINEREA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.29	*.**	64.6	24.0	50.2	41.2	9.3	10.0	24.8
2	1.62	*.**	33.9	7.6	53.4	41.7	12.0	16.7	14.5
3	2.46	*.**	56.3	23.5	52.7	40.1	12.8	14.7	16.3
4	2.50	*.**	57.2	24.4	52.6	39.7	13.2	14.6	15.8
5	4.87	*.**	71.7	41.3	40.2	21.8	18.6	8.0	10.4
6	4.53	*.**	73.3	32.5	32.4	20.5	12.2	9.6	5.9
7	3.34	*.**	**.*	**.*	**.*	**.*	16.5	**.*	9.8
8	2.74	3.81	44.2	33.3	58.6	40.4	18.0	13.8	16.4
9									
10									
11	2.27	*.**	49.4	1.9	51.1	40.1	11.6	13.7	15.8
12	1.51	12.59	**.*	**.*	43.0	32.0	10.4	15.6	7.7

DICHROSTACHYS CINEREA TE

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	*.**	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
2									
3									
4	2.09	9.38	55.7	21.0	52.8	37.2	15.7	1.4	11.2
5									
6	4.11	*.**	75.6	43.9	42.4	21.7	20.8	10.5	6.4
7	3.60	*.**	58.9	22.8	61.0	45.3	15.6	14.7	19.1
8	2.05	12.32	47.0	13.0	61.2	48.0	13.5	17.3	19.2
9									
10	2.17	*.**	17.8	11.6	70.8	61.4	9.6	17.3	26.2
11	2.40	*.**	54.3	7.3	47.8	31.4	16.5	11.5	8.7
12	1.48	*.**	56.3	18.8	44.1	30.4	13.7	14.2	13.6

FICUS CAPREAEFOLIA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.88	*.**	85.7	72.6	38.9	20.3	19.1	15.4	3.2
2	2.56	*.**	91.2	66.6	37.2	17.7	20.3	13.1	3.9
3	2.10	*.**	88.3	62.6	37.9	19.8	18.8	14.4	4.3
4	2.54	4.64	89.6	68.1	36.2	17.2	19.9	13.9	2.9
5	3.44	*.**	88.6	62.4	34.3	19.5	15.2	13.4	3.4
6	2.72	*.**	88.7	64.5	36.5	18.9	18.3	15.4	2.4
7	3.23	*.**	88.4	71.6	34.3	16.6	18.5	13.3	2.7
8	1.44	0.48	54.2	9.0	36.9	27.2	10.0	9.7	12.8
9									
10									
11	3.07	*.**	86.1	60.6	41.1	19.9	22.1	14.5	4.8
12	3.06	1.43	89.8	71.4	37.7	19.3	19.1	14.5	4.1

GUIERA SENEGALENSIS MP

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.29	*.**	42.0	−23.9	56.5	47.2	9.6	15.7	23.0
2									
3	1.07	2.14	47.3	− 1.5	62.5	50.5	12.5	23.7	20.9
4									
5	1.93	*.**	54.4	0.0	53.4	39.7	14.2	17.2	18.8
6	1.66	*.**	42.5	21.4	63.0	47.3	15.9	16.2	24.9
7	1.49	*.**	45.5	4.9	69.9	55.8	14.5	23.6	23.4
8	1.48	7.95	**.*	**.*	66.4	52.3	14.6	18.7	22.9
9	2.00	*.**	**.*	**.*	69.4	48.3	21.7	17.7	21.7
10									
11	1.60	*.**	41.4	−30.0	54.9	43.1	12.2	17.0	19.5
12	1.44	12.59	**.*	**.*	54.9	44.7	10.8	18.1	20.7

ISOBERLINIA DOKA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.87	*.**	41.6	28.4	70.4	60.9	9.7	16.7	25.2
2									
3	2.01	*.**	44.5	10.6	60.5	44.7	16.0	18.7	17.6
4	2.56	*.**	52.9	37.4	61.5	40.5	21.3	20.5	12.2
5									
6	2.34	*.**	53.8	35.3	59.7	40.0	20.0	20.8	12.6
7									
8									
9									
10									
11	1.54	*.**	47.5	13.9	64.9	48.3	16.9	23.6	17.8
12	2.89	*.**	68.6	43.1	48.9	30.6	17.7	11.9	11.5

MAERUA OBLONGIFOLIA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.88	0.24	64.0	26.0	39.5	24.9	15.0	14.3	5.5
2									
3									
4	2.29	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
5									
6	4.46	*.**	79.3	31.9	34.1	20.2	14.2	10.1	3.9
7	*.**	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
8									
9	3.77	1.55	70.3	36.6	42.3	25.8	17.0	13.9	6.8
10									
11	3.05	*.**	66.8	19.4	41.6	25.5	16.4	13.9	5.3
12	2.42	0.83	69.7	16.8	47.7	29.4	18.5	17.7	7.4

MIMOSA PIGRA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.49	*.**	40.0	14.6	52.7	28.8	24.2	14.9	11.1
2	2.50	*.**	47.5	22.5	58.0	36.6	21.8	17.9	15.9
3	2.37	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
4	2.18	4.63	61.2	22.4	50.1	32.0	18.5	18.3	10.9
5	2.70	*.**	62.5	18.7	40.5	23.3	17.5	14.3	6.7
6	2.68	*.**	57.6	5.9	40.0	25.1	14.9	15.4	8.2
7	2.76	*.**	41.7	−83.7	38.4	23.4	15.2	15.4	6.4
8	2.45	6.11	49.8	8.3	52.8	33.7	19.1	17.0	13.9
9									
10									
11	2.81	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
12	2.05	3.21	50.0	11.0	46.9	28.3	18.9	16.6	8.9

PHYLLANTHUS RETICULATUS FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	2.53	*.**	86.0	52.6	24.8	12.5	12.7	8.2	3.8
2	2.53	*.**	85.3	66.3	26.3	10.8	16.3	6.7	2.8
3	2.53	*.**	86.5	66.7	23.5	11.6	11.9	7.8	2.9
4	2.21	*.**	**.*	**.*	*.*	*.*	12.9	7.9	2.5
5	2.92	*.**	86.9	71.3	28.8	11.4	18.2	7.9	2.7
6	2.25	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
7	3.51	*.**	88.6	75.3	21.1	9.8	11.7	6.3	2.9
8	2.18	0.84	74.9	36.2	30.1	15.1	15.5	9.0	5.6
9									
10									
11	2.90	*.**	78.6	42.2	32.2	14.6	18.3	8.2	4.8
12	2.69	1.31	84.6	69.6	28.8	12.9	16.7	8.7	3.3

PILIOSTIGMA RETICULATUM MP

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	0.90	*.**	61.7	13.2	51.9	37.5	14.8	16.0	17.9
2									
3	0.91	*.**	61.8	13.1	51.3	38.5	13.5	17.6	17.7
4	1.59	5.94	64.0	33.7	63.3	48.7	15.1	14.1	23.2
5	1.24	*.**	56.0	18.7	64.1	48.3	16.3	19.5	20.4
6	1.31	*.**	42.6	20.8	63.8	53.8	10.4	17.6	31.2
7	1.04	*.**	55.3	16.9	64.8	50.8	14.5	17.8	24.3
8	1.31	3.09	**.*	**.*	66.2	50.3	16.4	26.3	19.8
9	1.53	*.**	**.*	**.*	63.4	45.7	18.3	23.9	17.0
10									
11	1.04	2.61	56.4	12.3	60.3	47.2	13.6	18.3	20.9
12	1.26	*.**	24.0	−58.3	59.9	45.7	14.7	17.9	20.3

PROSOPIS AFRICANA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.86	17.10	64.7	6.1	39.2	29.1	10.5	10.2	10.4
2									
3									
4									
5									
6	*.**	*.**	50.0	13.2	41.0	26.4	14.6	9.5	10.9
7	2.67	*.**	60.2	9.7	47.8	35.6	13.0	10.9	19.7
8	2.31	15.20	57.0	5.3	42.2	31.9	9.6	8.9	13.5
9									
10	2.26	*.**	36.6	1.6	45.9	35.3	9.7	11.4	13.3
11									
12	1.67	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*

PTEROCARPUS LUCENS FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.57	*.**	67.0	22.5	46.8	34.3	13.0	14.3	10.9
2	1.75	*.**	42.8	14.2	52.3	37.5	15.1	15.1	14.4
3	1.47	*.**	57.2	21.7	54.8	43.1	12.1	16.7	18.7
4	2.03	*.**	60.1	27.5	54.4	38.7	16.1	14.6	16.6
5	2.21	*.**	52.2	20.9	57.1	39.4	17.8	15.0	20.0
6	2.81	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
7	3.85	*.**	58.9	23.3	41.0	31.6	9.4	11.2	15.5
8	2.85	0.83	33.0	17.9	62.9	45.4	17.5	13.0	24.8
9									
10									
11	2.47	*.**	47.0	1.4	53.2	44.2	9.4	15.2	18.1
12	1.90	2.14	42.9	8.1	47.3	33.7	13.6	12.4	12.4

PTEROCARPUS LUCENS RO

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1									
2	2.22	*.**	53.2	2.2	58.7	40.1	19.1	15.8	16.7
3									
4									
5	*.**	*.**	**.*	**.*	**.*	**.*	**.*	**.*	**.*
6	2.36	*.**	21.9	−48.6	38.6	27.3	11.4	9.4	11.7
7	3.15	*.**	60.1	17.0	47.2	33.5	14.0	10.8	14.3
8	2.00	2.49	45.5	11.5	61.6	43.9	17.7	12.9	23.9
9									
10	1.83	*.**	43.3	2.1	57.9	45.4	12.5	16.1	21.0
11	1.88	*.**	37.7	−17.3	52.6	40.0	12.3	15.2	20.0
12	1.37	2.62	60.1	19.3	53.4	42.5	11.2	15.1	17.7

ROTULA AQUATICA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.70	*.**	87.2	65.7	32.7	23.4	9.0	16.5	6.9
2	1.75	*.**	84.2	65.9	36.5	28.7	8.0	17.2	12.7
3	1.48	*.**	84.3	62.2	2.6	24.7	8.2	17.5	6.8
4	1.33	3.45	83.4	59.4	33.9	28.2	6.3	16.0	11.5
5	1.47	*.**	86.4	60.4	26.2	18.8	7.4	13.5	4.7
6	1.90	*.**	86.3	66.2	23.7	18.7	5.6	13.8	4.5
7	1.94	*.**	48.5	32.5	55.0	39.7	15.2	8.0	22.1
8									
9									
10									
11	2.51	2.61	79.2	45.7	32.0	25.9	6.4	15.0	8.5
12	1.55	4.37	72.7	32.6	39.5	27.4	11.9	17.3	9.1

SABA SENEGALENSIS FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.67	*.**	78.7	48.3	32.9	23.3	10.1	9.5	14.2
2	1.74	*.**	42.2	8.1	45.4	36.0	9.3	9.9	19.2
3	1.46	*.**	34.7	1.9	64.0	58.9	4.1	16.7	24.1
4	2.15	*.**	49.8	16.7	57.9	53.6	4.8	11.4	25.6
5	1.65	*.**	80.5	57.7	37.8	24.0	14.0	8.6	14.5
6	1.68	*.**	75.5	40.6	32.9	20.3	12.9	9.3	10.5
7	2.39	*.**	90.9	76.5	48.1	29.3	19.0	11.6	18.6
8									
9									
10									
11	1.81	*.**	**.*	**.*	59.8	51.5	7.5	10.9	24.6
12	1.95	*.**	69.5	38.1	35.3	25.8	9.8	8.6	16.7

SALIX SUBSERRATA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.83	*.**	64.6	17.5	29.3	24.9	4.7	11.2	10.2
2	1.80	*.**	63.4	13.2	34.5	27.7	6.9	11.9	11.2
3	2.07	1.82	68.7	26.1	35.5	24.9	10.4	10.2	9.6
4	1.84	*.**	72.3	42.0	41.4	30.8	10.2	11.7	11.4
5	2.06	*.**	70.1	38.7	42.4	25.8	16.6	10.6	11.0
6	1.79	*.**	68.8	33.1	34.3	27.4	6.8	11.0	4.8
7	1.41	*.**	56.4	21.5	40.4	29.1	11.3	12.5	10.4
8									
9									
10									
11									
12	2.08	5.94	64.9	19.2	32.3	25.3	7.2	12.2	11.1

SCLEROCARYA BIRREA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1									
2									
3									
4									
5	3.05	*.**	71.1	41.0	37.2	18.7	19.0	10.6	5.4
6	1.68	*.**	72.9	35.3	36.3	14.9	22.2	9.1	4.0
7	2.38	*.**	87.2	60.0	30.7	19.8	11.1	10.9	6.3
8									
9	2.00	9.38	68.7	28.2	38.4	19.2	19.8	7.3	9.4
10									
11									
12									

SESBANIA SESBAN FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	0.60	*.**	82.2	26.3	14.7	10.9	4.6	6.7	4.0
2	3.63	*.**	83.4	38.4	17.7	14.6	3.7	8.0	4.7
3	3.77	*.**	88.4	60.7	15.3	9.3	5.9	6.2	2.5
4	4.20	2.85	86.3	68.6	26.4	15.7	11.3	10.6	5.0
5	4.62	*.**	87.8	56.4	14.7	12.1	3.3	7.8	3.6
6	3.92	*.**	88.0	56.1	16.8	13.1	4.4	8.5	4.4
7	3.31	*.**	87.9	46.9	12.9	9.5	4.2	6.4	2.8
8	3.51	3.45	83.9	45.5	19.4	12.6	7.7	7.1	5.1
9									
10									
11	4.57	*.**	86.2	52.3	17.7	13.0	5.4	7.4	5.1
12	*.**	4.99	84.9	40.6	17.8	11.2	6.6	5.9	3.8

ZIZIPHUS MAURITIANA

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1									
2	2.13	*.**	72.0	30.3	35.6	23.1	12.7	11.8	8.3
3	2.12	*.**	80.9	56.8	38.2	22.9	15.6	12.1	7.6
4	1.30	2.61	76.6	36.3	30.3	20.5	10.0	10.5	6.3
5	1.36	*.**	67.9	15.1	33.3	22.4	10.8	11.8	8.8
6	3.07	*.**	74.2	33.6	33.9	21.9	12.2	13.7	5.8
7	2.87	*.**	82.1	57.6	36.6	21.1	15.9	12.2	6.4
8									
9	2.70	7.13	47.6	17.1	49.4	33.3	16.1	15.5	12.5
10									
11									
12	2.16	0.83	70.2	40.5	40.0	30.9	8.8	14.1	13.6

ZIZIPHUS MUCRONATA FL

M	%N	%T	Vom	Vcwc	%NDF	%ADF	%HEMI	%CELL	%LIGN
1	1.68	*.**	75.3	51.8	40.5	21.7	19.2	10.3	9.6
2	1.81	*.**	76.9	52.0	37.3	20.9	16.7	10.4	9.0
3	1.69	*.**	71.9	43.8	47.2	29.5	18.0	11.6	15.7
4	1.39	1.90	80.3	55.0	38.1	22.3	16.1	10.9	9.1
5	4.77	*.**	84.1	45.8	19.4	12.0	7.2	7.1	4.1
6									
7	3.66	*.**	83.9	69.2	44.3	20.9	23.7	10.0	8.0
8									
9	1.86	*.**	54.1	29.8	52.5	33.1	19.7	12.1	16.9
10									
11	1.90	*.**	78.1	52.7	43.8	22.1	22.0	10.7	9.3
12	1.27	2.73	77.3	49.3	45.9	26.6	19.7	12.1	11.9