MODELLING THE DYNAMICS OF SEMI-ARID GRAZING SYSTEMS

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Contents

PREFACE

This is a report has two objectives: to review the current state of knowledge of semi-arid rangeland systems, and to present the results of a mechanistic model. The review covers a wide range of topics, and concentrates on areas we felt were critical to understanding and modelling rangeland dynamics. We welcome comments and suggestions.

ii   **SUMMARY OF REVIEW FINDINGS**

1. The review shows that an extensive body of literature on rangeland systems exists. There is considerable variation in the depth of knowledge of the key processes in such systems.

2. Relationships between rainfall, soil moisture and plant growth are fairly well understood, and detailed models can produce quite accurate results. There is less clear agreement on how herbaceous and woody plants differ in their water-use efficiency (itself an approximation of many physical and physiological processes), let alone at a finer taxonomic scale. The annual production of woody species is poorly known.

3. Variability of rainfall appears to be of considerable importance, not only being the main cause of variation in primary production, but also because it exceeds the impact of grazing intensity or fire on compositional change in vegetation.

4. Food intake and diet quality have a major effect on animal performance, but research on these variables is scarce and rather empirical in approach, or site-specific. This means that principles on which to base predictions of nutrient intake from the abundance and nutritive value of plants have been slow to emerge.

5. Spatial variation in the distribution of vegetation and in the accessibility to animals of surface water may constrain foraging behaviour and food intake.

6. Soil fauna, particularly termites, may have a surprisingly large impact on dry-season vegetation biomass, but also have effects on infiltration and nutrient cycling.

7. There has been an active debate on the management paradigms which are appropriate for rangeland systems. The difficulty of translating theoretical insights to the real world have perhaps been underestimated.

SUMMARY OF MODEL RESULTS

1   The model was successfully predicts many of the phenomena of semi-arid grazing systems. Predicted animal diets and performance levels, rainfall-stocking rate relations and bush encroachment are all reasonably close to those observed in reality. The current model omits an explicit treatment of soil nutrient status and other (*eg* hydrological) sources of spatial variation, and the does not yet include fire as a determinant of vegetation change.

2   The performance of semi-arid grazing systems was shown to be sensitive to climatic variability, and the separate effects of the mean and variance in annual rainfall were established. With increasing variability in annual rainfall cv from 0.2 to 0.4 (typical of semi-arid regions) and without changing the long-term mean annual rainfall, mean carrying capacity declines by a half. Measures to buffer climatic variability, particularly those designed to limit animal mortality in droughts, could certainly increase system output.

3   Diet quality was predicted to be the first limiting constraint on nutrient intake rates, animal production evidently being limited by the quantity of high-quality forage. Knowledge of the nutritive value of savanna vegetation components is surprisingly poor, and better information is required. Despite the importance of browse in heavily-utilised systems, there is inadequate knowledge of browse production and utilisation (especially of the highly nutritious pods and fruits of savanna trees). Better understanding of the diet selection of free-ranging animals is needed to assess the nutritional constraints on performance and to derive suitable interventions.

4   Bush encroachment is an important process, because it reduces grass yield and predicted diet quality. Bush utilisation by goats was shown to reduce encroachment.

5   The model offers a comprehensive basis on which to evaluate alternative management strategies, but further work needs to be done on the amalgamation of the many objectives of livestock keepers, as expressed in the chosen balance between economic output and the maintenance of high stocking rates.

6   Flexible stocking strategies designed to tackle climatic variation showed only limited scope for improving output over fixed stocking. The main reasons for this are that major losses of stock are associated less with one-year than with two-year droughts, which are difficult to track, and that de-stocking can be really effective only if the productive potential of the herd can be re-established more rapidly than is possible from depleted herds' own growth. If re-introductions of breeding stock are not possible, their numbers will lag behind climatic fluctuations, producing a succession of population crashes and missed opportunities.

7   Further analysis of the feasibility and effectiveness of adaptive management policies is required. Traditional policies of maintaining the maximum number of breeding stock, and of hoping that most of them will survive drought, may be as close as 'opportunistic' management can get to dealing with drought.

8   *Identified constraints.* Variation between years in the supply of sufficiently high-quality forage (caused by seasonal variation in rainfall) is the single most important constraint on production from semi-arid rangeland. The low quality of dry-season forage is the main constraint on nutrient intake by animals, and this directly affects mortality and hence output. Poor ability to predict severe droughts, and to rebuild herds following de-stocking or mortality, were identified as constraints on the adoption of flexible stocking policies.

INTRODUCTION

Understanding rangeland function is important for the development of management interventions which will lead to increased or more sustainable economic output. There are currently no scientific and objective methods of optimising the long-term utilisation of vegetation resources, of matching the mix of animal species to vegetation structure, of accounting for the impact of wildlife or of combining wildlife management goals with pastoralism. One of the reasons for this is the complexity of the rangeland systems. Semi-arid rangeland systems are complex in a number of ways. First, they contain a wide diversity of animal species and vegetation, with a correspondingly complex set of interactions between and within each. Second, semi-arid environments are characterised by high temporal and spatial variability, causing the production and utilisation of vegetation to fluctuate widely (Ellis & Swift 1988; Ellis *et al.* 1993; Stafford Smith & Pickup 1993). This poses particular problems in the analysis of system function and management (Behnke & Scoones 1993; Behnke & Kerven 1994).

Analysis of the dynamics of rangeland systems can best be undertaken by mathematical modelling. This is because modelling requires that the information about the components and interactions are brought together in a formal structure, and that decisions are made about what elements are essential and what can be omitted. It forces a critical approach to the assumptions underlying descriptions of the key processes in the system, and these assumptions are made explicit. Modelling serves to identify where knowledge is weak or lacking. The purpose of the work reported here is (1) to review and summarise what is known about the biological components of the system (as outlined in Fig. 1), from the perspective of what is required for modelling, and (2) to present results of a model of rangeland dynamics.

One of the fundamental questions in modelling concerns the level of detail required. A model must simulate the system's behaviour with sufficient accuracy to achieve the desired goal. The simplest type of model aims to capture the main properties of the system's behaviour with the smallest number of parameters by excluding both unnecessary detail and explicit description of the deeper causal relationships. Such 'phenomenological' models may be valuable for representing the surface phenomena, and for observing the system's behaviour in response to alteration of the parameter values, but their usefulness is limited to the scope of the original description. Detailed mechanistic models, in contrast, aim to go much further in describing the underlying causal relationships, and are, in principle, capable of representing the complexities of the system more faithfully, but risk becoming bogged down in detail and by parameters whose values are poorly defined. As more and more factors are included, it becomes harder to see which ones are important. A balance must be struck between these two approaches, by defining the level of detail which satisfies the goals of modelling, within the constraints imposed by the quality of information about the system.

The primary objective of the model to be developed here will be to assess the effect of climatic variation in affecting the output and dynamics of rangeland systems consisting of several animal and vegetation types. The model will provide a basis for investigating the way the mixture of animal species and vegetation types determines output and vegetation impact, and the scope for optimising system performance by flexible stocking policies. Faithfulness to a particular geographical location and use of the model for ongoing decision-support are, at present, beyond its remit.

The approach of the model will be mechanistic, because we want to understand how systems work, and to discover the critical limitations in current knowledge. Mechanistic models allow predictions to be made, for instance of animal performance under a given

management policy, or of how the system will respond to perturbation. Somewhat greater confidence can be placed on the predictions of mechanistic models than of phenomenological models, because of the more explicit treatment of causal relationships. An example of a mechanistic model of primary and secondary production in response to rainfall is shown in Fig 1
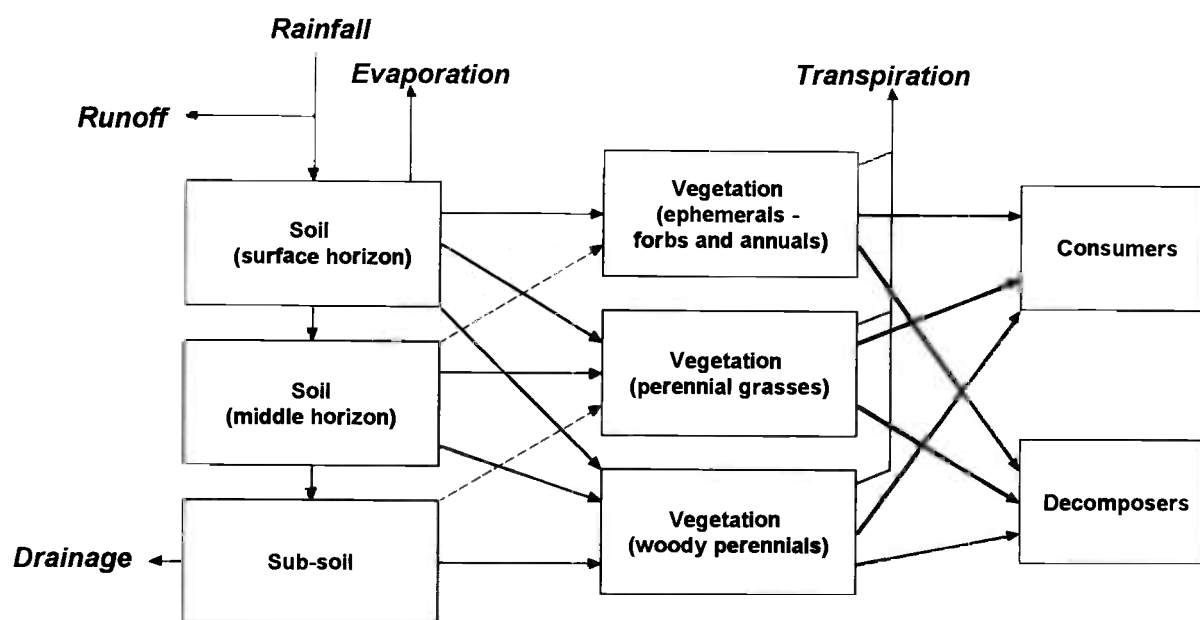

Fig 1 Outline of a grazing system, governed by rainfall and water use (thin lines) and flows of the resulting plant material (thick lines) to livestock and wildlife consumers, or lost to decomposers such as termites. Dashed lines indicate weak uptake of water, due to restricted rooting depth, of short-lived plants. Feedbacks (such as the effect of vegetation on runoff, or decomposers on nutrient cycling) have been omitted, for clarity.

The focus of our model is on animals, because of their economic importance, as well as on animals' interactions with the vegetation that supports them. We are concerned with the way semi-arid grazing systems are affected by environmental (particularly rainfall) variability and the feasible management responses. The review is therefore divided into sections dealing with *vegetation*, and the factors that determine its growth and dynamics; *animals*, particularly from the perspective of what determines diet selection; and *systems*, from the point of view of the current debate about the dynamics of semi-arid rangeland and the appropriate management paradigms.

It is important to realise that models evolve over time from simple beginnings to encompass greater complexity and detail. We have chosen to review broadly those subjects which seem important in rangeland systems, but it is inevitable that not all of them will be addressed by the model from the outset. For example, the response of animals' foraging behaviour to spatial heterogeneity, and the transmission of animal disease, are beyond the current scope of the model.

2 **VEGETATION**

2.1 Vegetation structure

Rangelands usually exhibit considerable botanical diversity, with a large number of plant species and growth forms. For simplicity, it is convenient to categorise plants into functional groups, according to growth form and life history, as follows: perennial grasses, annual grasses, forbs (together comprising the herbaceous layer) and woody plants (the browse layer, consisting of shrubs and trees). Plants of the herbaceous layer are generally short-lived, with correspondingly low allocation of primary production to storage tissues which are inaccessible to herbivores. At any given phenological stage, the digestibility of the various plant parts is fairly similar, and almost all the aerial parts of the plant die back at maturity and are replaced at the start of the next growth cycle. By contrast, the investment by woody plants in long-lived aerial structure creates marked divergence between the digestibility of newly-growing and old tissue. Woody plants have greater allocation of primary production to storage, from which re-growth is supported, and to maintenance respiration of tissue. These differences are of considerable significance for the production and potential utilisation of plant biomass by grazing and browsing herbivore species.

Vegetation composition in a typical semi-arid savanna is illustrated in Table 1. Trees form the great majority of the biomass, but contribute relatively little new growth, by comparison with the herbaceous and browse layers (Kelly & Walker 1976). No assessment was made of the utilisation of fallen tree leaves and fruits, which can be an important source of dry season forage.

Table 1. Composition and production of semi-arid bush savanna at sites in SE Zimbabwe differing in degree of utilisation by livestock and wildlife (Kelly & Walker 1976)

Utilisation rate	Rainfall (mm)	Above-ground biomass (kg/ha)				Annual production (kg/ha)				Utilisation by herbivores (%)	
		Herb.[1]	Shrub	Tree	Total	Herb.	Shrub	Tree	Total	Herb.[3]	Shrub
Nil	580	1728 (10)[2]	2802 (16)	12426 (74)	16956	1728 (52)	645 (20)	939 (28)	3312	4	<3
Light	620	2084 (12)	1706 (10)	13970 (78)	17760	2084 (58)	419 (12)	1073 (30)	3576	32	<3
Moderate	530	1217 (4)	2969 (11)	23676 (85)	27862	1217 (43)	741 (26)	895 (31)	2853	62	<3
Heavy	520	1238 (7)	1161 (7)	14762 (86)	17161	1238 (50)	256 (10)	960 (39)	2454	89	28
Mean	563	1567 (8)	2160 (11)	16209 (81)	19936	1567 (51)	515 (17)	967 (31)	3049	47	9

1. Peak herbaceous biomass. 2. Figures in parentheses are % biomass or production from each plant type at each site. 3. Utilisation of herbaceous biomass by end of dry season.

2.2 Primary Production

Available soil moisture and soil nutrient status are the most important influences on plant growth in African savanna systems (Dye & Spear 1982; Rutherford 1980; Scholes 1990, 1993) and hence on the biomass of animals present (Coe, Cumming & Philipson 1976; Fritz & Duncan 1994).

Annual variation in rainfall is a major source of variation in plant growth, as shown by the data collected over a period of 15-19 years on four soils varying in inherent fertility in SW

Zimbabwe (Dye & Spear 1982). Greater responses to increasing rainfall are seen on more fertile soils with higher clay contents than on infertile, sandy soils (Fig. 2 and Table 2). The effects of rainfall and soil type on primary production feeds through into secondary production, as can be seen in the geographical pattern of variation in animal biomass (Fritz & Duncan 1994). Their analysis showed that, for example, the combined biomass of wildlife and livestock on a fertile soil receiving 600 mm of rainfall annually would be 52 kg/ha, compared with 28 kg/ha at 400 mm. Biomass on a poor soil receiving 600mm of rainfall would be 25 kg/ha. (Equivalent stocking rates would be about 9, 16 and 18 ha/LSU). The dataset covered land areas under conservation and extensive pastoralism, but excluded areas under intensive management.
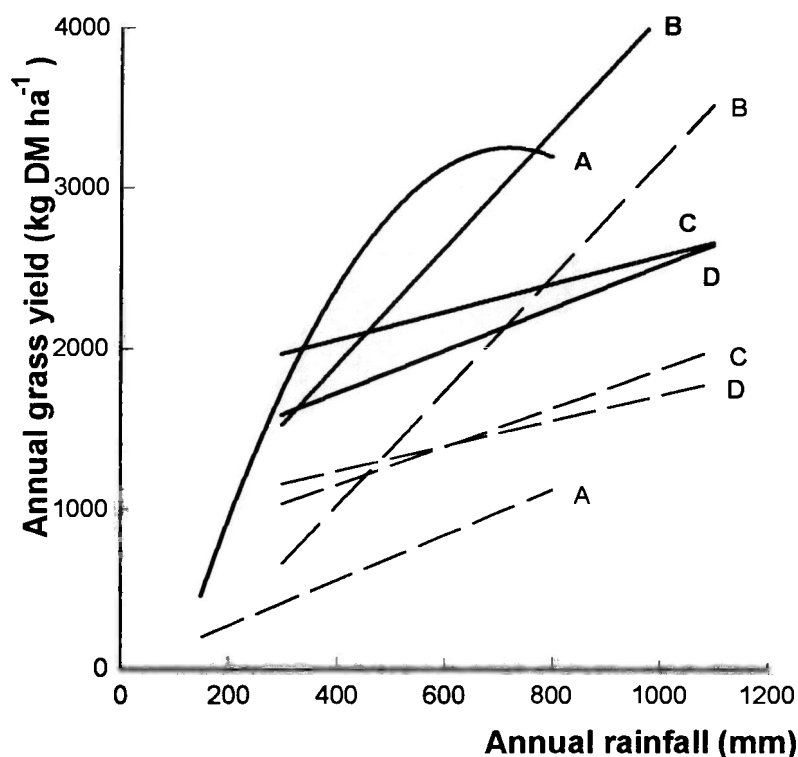
Fig. 2. Response of grass growth to rainfall on four soil types with bush present (– – – –) or cleared (———). Soils: A fertile clayey loam (Tuli lowveld); B loam (Matopos thornveld), C and D infertile sandy soils (sandveld).

Estimates of primary production in savanna systems are given in Tables 1-3. The assessment of plant production often takes place only once, at the end of the rainy season (eg Dye & Spear 1982). This measure has relevance to the potential of the biomass to support animals over the ensuing dry season, but underestimates the total growth throughout the growing season (Table 2; see also Scholes & Walker 1993; Fig 10.3), some of which is lost by tissue turnover *via* senescence and insect herbivory. Ongoing measurement, *eg* from monthly cutting, comes closer to estimating the amount of material entering the system. It is not always clear what methods were used in the literature.

Table 2. Net above-ground primary production (NAPP), recorded as peak biomass at the end of the growing season, of the herbaceous layer in SW Zimbabwe, with or without bush clearance (Dye & Spear 1982) and in Zambesi riverine woodland, recorded as monthly increments of growth (Dunham 1990).

Grassland type	Mean annual rainfall (mm)	Treatment	Mean annual NAPP (kg/ha)	Adjusted[1] annual NAPP (kg/ha)
Matopos thornveld	729	Bush present	2 194	1 733
		Cleared	3 093	2 623
Matopos sandveld	729	Bush present	1 545	1 391
		Cleared	2 157	1 988
Nyamandhlovu sandveld	652	Bush present	1 436	1 396
		Cleared	2 272	2 228
Tuli lowveld	491	Bush present	683	838
		Cleared	2 801	3 130
Zambezi riverine woodland: annual grassland	607	Annual grasses	6 220	-
		forbs	1 265	-
Zambezi riverine woodland: perennial grassland	412	perennial grasses	12 938	-

1. NPP adjusted to 600 mm rainfall per year, using regressions presented by Dye & Spear (1982).

Table 3. Annual production of woody plants: new stems and leaves.

Vegetation type	Mean annual rainfall (mm)	Mean annual NAPP (kg ha^{-1})	Reference	notes
Acacia xanthophloea Riverine woodland	800	5 000	1	Production below 5.75 m from ground.
Open alluvial woodland	-	2 254	2	50% higher than 5m, 38% below 2.5m
Acacia tortilis ridge-top thicket	800	1 725	1	49% of canopy volume of regenerated woodland
Dry miombo woodland	600	2 528	3	94% of total biomass was wood, remainder was browse.
Colophospermum mopane woodland	600	1 150	3	92% of total biomass was wood, remainder was browse.
Mixed tree and shrub *Burkea africana* woodland	586	1 336	4	Shrubs contribute 12% to total woody biomass
Broad-leaved dystrophic savanna	586	1934	5	Includes 10 % flowers and fruits; wood and root growth an extra 890 and 1865 kg ha^{-1}

1. Pellew (1980); Serengeti N. P. Tanzania. 2. Goodman (1975); Lutope River, Zimbabwe. 3. Martin (1974); Sengwa, N. W. Zimbabwe. 4. Rutherford (1979a); SW Africa savanna. 5. Scholes & Walker (1993); Nyslvley, N. Transvaal, South Africa.

The predominant reason why plants require water is to replace that lost while gas exchange is taking place through open stomata. The plant water pool and direct use of water in photosynthesis together constitute a very small proportion of the total water budget. By restricting water loss under dry conditions, plants necessarily restrict CO_2 uptake and photosynthesis. The relative rates of transpiration and CO_2 uptake depend on stomatal conductance, which is determined by anatomical, physiological and environmental factors. C assimilation is further modified by tissue respiration, which varies with plant biomass, growth rate and temperature, to leave net photosynthesis. Accordingly, the relationship between net C assimilation and transpiration, termed water use efficiency, is complex. Factors determining water use efficiency by vegetation underlie much of the variation in production which is not attributable to soil nutrient status. For example, comparison of grass production with bush present or absent shows that grass growth is reduced by competition from trees and shrubs (Table 2). Bush production was not recorded. Grasses are slightly more efficient converters of water to biomass than shrubs or trees, when compared at the individual plant level (Scholes &

Walker 1993; Table 6.7), but this is probably not the case at whole system level. Savannas with their tree component removed have never been found to have higher productivity than the combined productivity of grass and bush (Scholes & Walker 1993). It is argued that the different seasonal patterns of water-use by trees and grass gives savanna vegetation as a whole a higher water-use efficiency. The reduction in primary production under higher levels of utilisation by animals (Table 1, Fig 3) is not substantial after accounting for the differences in rainfall between sites, and seems to be due to a number of factors. At the heavily utilised sites, the proportion of bare soil was greater, and lower litter cover markedly reduced the infiltration and increased run-off of rainfall, reducing available soil moisture. Perennial grasses were declining in abundance, size and vigour, and possibly less productive annual grasses predominated. Annual differences in grass production, arising from variation in rainfall, were found to be greater under these conditions than at low-utilisation sites.
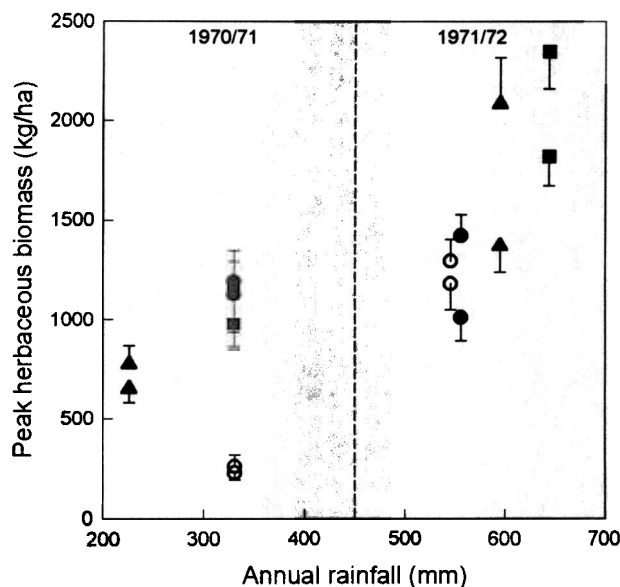
Fig 3. Annual production of herbaceous vegetation in two growing seasons (1970/71 and 1971/72) in SE Zimbabwe (data from Kelly & Walker 1976). In each season, two sites were used to estimate production under different intensities of utilization by livestock: nil (▲); light (■); moderate (●); and heavy (○). Error bars indicate sem.

High inter-annual variability in rainfall is a feature of semi-arid climates. Sites with low annual rainfall have, generally, greater annual variability in rainfall. The coefficient of variation for annual rainfall in Zimbabwe varies from 20% for stations with an average of about 800mm to more than 40% for stations with a mean of about 500mm or less (Denny 1983). In Botswana, the trend continues, with 80% cv at south western sites with 300mm average rainfall (Pike 1971, cited by Zumer-Linder 1976). A characteristic of longer-term data, corroborated by tree-ring data, is to show prolonged periods above or below the mean. A cyclic pattern of rainfall with a period of about 18 years is induced by the global shift in pressure belts (the Southern Oscillation).

Rainfall patterns for South Africa have been analysed by Zucchini *et al.* (1992) and the characteristics incorporated in a model which can generate daily rainfall patterns for any location. Such a model is useful for drought or rainfall risk assessment, but is also an ideal 'driver' for use in simulation models (*eg* Weigand *et al.* 1995). Rainfall patterns along the border with Zimbabwe approximate to those at sites from southern Matabeleland to

Mozambique. In Botswana, daily rainfall data for a number of sites can be obtained from the Meteorological office.

2.3 Models of primary production

Phenomenological models of primary production usually describe growth as being limited either by light interception or water use. In the former case, carbon budget models (eg Noy-Meir 1978; Johnson & Thornley 1983; Fryxell *et al* 1988) describe growth rate is a function of plant biomass through its association with light interception (and hence C gain) and respiration (C loss). For example, Fryxell *et al.* (1988) modelled daily growth of open Serengeti grassland with a linearly density-dependent, logistic expression,

$$growth = r(V + d)[1 - \frac{V + d}{k + d}]$$

(1)

where r is the intrinsic rate of increase, V is vegetation biomass, k is the peak vegetation abundance in the absence of grazing, and d is an offset to allow growth from reserves when $V=0$. This equation describes a parabolic growth response with increasing biomass, rising to a maximal growth rate for an abundance of $k/2$, and decreasing as the total biomass reaches the value of k. Similarly, Noy-Meir (1978) represented the plant growth season for permanent pastures of shrubs or perennial grasses as a triangular ramp function, with a maximal growth rate at its apex. Such functions model the pattern of net biomass accumulation observed by Bircham & Hodgson (1983). Seasonality of growth or the gross effect of rainfall could be introduced into the model by setting r to zero during the dry season or by defining r as a function of rainfall.

More complex models include both the C and N budget of plants. Coughenour *et al.* (1984) partitioned assimilates in terms of the physiology and morphology of perennial graminoids. Plant parts each incorporate a carbon pool and a nitrogen pool which act as sinks. C flux is determined by photosynthesis and reallocation of carbon to respiration and growth of crown, shoot and root. Nitrogen is reallocated to maintain the C/N ratio of the sink within limits. Photosynthesis is dependent on levels of leaf nitrogen, allowing a decrease in the rate of photosynthesis with time. The age and physiological status of an individual plant is thereby reflected by the strengths of its sinks. If there are sufficient stores of assimilate then primary production may occur. This is modelled by translocation of C to areas of growth for conversion to structural plant biomass. The photosynthetic rate is calculated in terms of the intensity and interception of solar energy by unit areas of leaf tissue. Impedance of light by self-shading is added by use of a derived form of Beer's law. Light intensity expressions may either include values for leaf area ratios (LAR) (Weltz *et al.*, 1992) or leaf area indices (LAI) (e.g., Johnson and Thornley, 1983; Prentice and Leemans, 1990). McMurtrie (1985), Prentice *et al.* (1987) and Leemans and Prentice (1989) have developed area-based growth (or 'gap') models in which bushes occupy individual microsites within a spatial frame. In place of a peak biomass (as in Eq. 1), they use a species-specific maximal area to limit canopy size. Maximum bush height is also moderated by bush area, simulating rapid vertical growth at first, followed by lateral spread and slower increases in height. Spatial interaction is included in the model *via* competition between microsites which may lead to growth impedance.

The simplest models of the dependence of growth on rainfall uses estimates of water use efficiency. Wagner (1976) calculated values of 4.12, 0.02 and 1.60 kg/ha/mm of rainfall for grassland, forest and desert, respectively. Zumer-Linder (1976) reports a similar average (4.3 kg/ha/mm) for the grassier regions of the eastern Kalahari. Uchijima and Seino's CHIKUGO model (reported in Jones *et al.*, 1992) is a large-scale model that derives growth from

evaporation. Annual precipitation and the latent heat of evaporation are compared to the net radiation levels to give a radiative dryness index. A non-linear regression model incorporates this and the annual net radiation in the construction of NAPP distribution maps for Japan. Berry and Hanson (1991) use soil drying times to take the place of evaporation terms. Soil drying time is a simple input to the model, defined as the time taken for saturated soil to dry to the wilting point. There is a similar treatment of soil moisture in IMAGES (Hacker *et al.*, 1991) in which a soil moisture index modulates plant growth and survival.

A more detailed approach involves separate calculation of available soil water. To model primary production explicitly in terms of precipitation requires a water budget model to allocate rainfall to evaporation, infiltration and runoff (Fig 1). A large number of such models exist (*eg* WATBAL, SWBBM/B, ESCALC, SWIM, SWEAT) and incorporate very similar and well-known principles.

Coughenour (1995) relates net primary production of shrubs and herbs to precipitation, water loss and water use efficiency in SAVANNA. The model is initialised with the spatial, temperature and rainfall characteristics of the study area which are extracted from GIS imagery. Monthly precipitation values are corrected for differences in elevation between the measurement site and the model co-ordinate. Water loss from the system is by evaporation from the soil surface depending on soil water content. Water loss from the plant surface is by transpiration, the rate of which is proportional to potential evapotranspiration, stomatal conductance, the vapour pressure deficit, day length and the green leaf biomass. Potential evapotranspiration is based upon the light intensity and leaf area index. Water that escapes runoff and evaporation is allowed to infiltrate the soil layers in sequence, providing each with its maximum water holding capacity before passing the excess onto the next layer. Water use efficiency is a measure of plant-specific conversion of soil water moisture into biomass. Dye incorporated a similar soil level structure into his VELD model of seasonal growth in savanna grasses (Dye 1984; Richardson *et al.* 1991). VELD's water budget submodel stores the soil moisture for the three levels resulting from a daily rainfall value. Infiltration, after runoff and evaporation from the soil surface, is sequentially allocated to each level in order of increasing depth. The plant-growth submodel assumes that net plant growth is related to transpiration rate, corrected for humidity, by a water-use coefficient and a coefficient of seasonal photosynthetic efficiency. Parameter values in VELD were tuned to experimental results for perennial grass growth at Matopos, SW Zimbabwe.

Bringing rainfall, photosynthesis and nutrients together requires expressions to describe each stage of the hydrological, physiological and morphological properties of an ecosystem. The Simulation of Production and Utilisation of Rangelands (SPUR) model (Hanson *et al.*, 1988) simulates the daily dynamics of given range sites. Water, carbon and nitrogen budget submodels use daily precipitation values, maximum and minimum temperatures, solar radiation levels and wind speeds. The carbon budget submodel calculates photosynthetically-active radiation to estimate net carbon assimilation rates from a calibrated light-response curve, dependent on the concentration of nitrogen, water availability, temperature, leaf age and light intensity. A nitrogen-use efficiency coefficient limits photosynthetic activity, and therefore carbon assimilation, at low leaf nitrogen. This forms a feedback loop with root nitrogen uptake. N uptake by roots and plant net C assimilation are assumed to occur only at times when the plant is transpiring. The SPUR model was used to test the effects of hypothetical variations in climate on NPP. A 6% reduction in NPP was found for each $^\circ$C reduction in temperature, implying a shortening of the growth season, and a similar magnitude of effect was found for light reduction.

McMurtrie & Landsberg (1992) applied light intensity formulae at a comparatively large photosynthetic scale when developing BIOMASS, an assimilate production and allocation model for forest stands. In BIOMASS, Lambert-Beer's law is applied to calculate interception of light energy by the forest canopy. By assuming that canopy respiration is proportional to canopy photosynthesis, McMurtrie & Landsberg (1992) derived an expression for biomass production, which was partitioned between foliage, fine root and wood. They found that the foliage and root components increased to an asymptotic weight while thickening processes continued linearly. Foliage and root growth were restricted by the shading effect of the canopy. Extending this model to a carbon-nitrogen model, McMurtrie& Landsberg (1992) found that growth may be limited by either assimilate or nutrient availability.

2.4 Nutritive value

As plant tissues mature, deposition of structural carbohydrates in cell walls and schlerenchyma causes them to predominate over the cell contents, which itself varies comparatively little in composition. These cytoplasmic constituents are an important source of fermentable substrates, including those containing nitrogen. The increasing content of structural tissue, together with its progressive lignification, causes a reduction in the digestibility of plant tissue. Greater differences in digestibility occur between plant parts on the same plant, particularly at advanced maturational stages (*eg* leaves and stem in grasses or leaves and twigs in browse; Table 4) than between leaves, stems or twigs of different species of the same plant type (*ie* grasses, or woody plants). Wilson (1982) reviews environmental effects on digestibility, the most important of which are the reduction in digestibility under high temperatures or drought. Frost brings about a rapid decline in the nutritive quality of tropical forages, primarily through the loss of leaf tissue.

Table 4. Seasonal variation in the digestibility (*in vitro* DMD) of plant parts.

Vegetation type		Wet season			Dry season			Reference
		Early	Mid	Late	Early	Mid	Late	
Perennial grasses	Leaf	68	53	49				1
		65	55	47	45			2
	Stem	63	49	45				1
			35	28		33		2
Mixed grasses	Leaf+stem	66	55			37		3
						35		2
Forbs		-	-	-	-	-	-	
Browse	Leaf	-	51	-	53	49	56	4
	Stem	-	28	-	31	27		4
	Whole shoot: new growth	-	-	-	-	53	56	5
	old growth	-	-	-	-	48	-	5
	Fruit/pods	-	-	-	-	56	-	6
	Fallen leaves							

1. Laredo & Minson (1973) estimated *In vitro* DMD; mean of 5 African grasses; Queensland, Australia. 2. Manuchi (1993) 3. Murray (1993) and unpublised; neutral cellulase digestibility; Tanzania. 4. Bamaulin (1981);mean of 28 mostly African species; Queensland. 5. Rees (1973); IVDMD estimated from MADF; mean of 10 species; Zambia. 6. Ncube and Mpufo (1994); mean of 4 species.

The data are surprisingly sparse, with many important components missing. Compared with grasses, there is less seasonal change in digestibility of browse plants (Jones and Wilson, 1987). There have not, apparently, been any comprehensive studies in a single location of the

digestibility of all the important components of animals' diets throughout the seasonal cycle. Skarpe & Bergstrom (1986) reported digestibility, N, P and Ca of grasses (all parts combined) and of browse leaves and twigs in vegetation of the Kalahari, Botswana, in relation to season and rainfall. Tolsma *et al.* (1987) reported the seasonal changes in mineral contents of tree and grass species in Botswana.

Nitrogen content, the great majority of which is in the cell contents (Jones & Wilson 1987), is usually closely correlated with digestibility (Table 5 and Fig 4).

Table 5. Relationship between N (%) and dry matter digestibility (DMD, %)

(a)   Perennial African grass species[1].

	Leaf & sheath	Stem
Green	N = -2.42+0.074 DMD	N = -0.32+0.019 DMD
Brown	N = 1.62+0.046 DMD	N = -0.83+0.027 DMD

(b)   Leguminous and non-leguminous African browse species.

	Shoot[2]	Leaf[3]	Stem[3]
Leguminosae (31 species)	N = 1.74 +0.019 DMD	N = 1.82+0.019 DMD	N = 0.80+0.019 DMD
Other taxa (24 species)	N = 0.89+0.019 DMD	N = 0.97+0.019 DMD	N = -0.05+0.019 DMD

1. MG Murray, unpublished. Combined regression: n= 148; r^2=0.75; residual SD = 0.37. 2. Bayer 1990. 3. Bamualin 1981, AW Illius, unpublished. Combined regression: n= 94; r^2=0.74; residual SD = 0.40
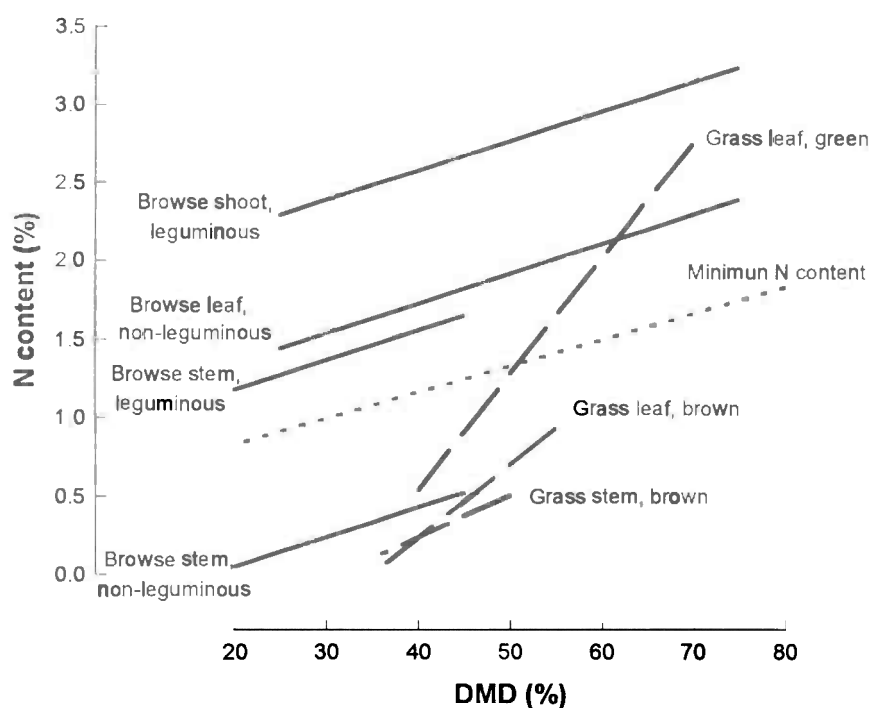
Fig 4. Relationship between N and DMD in African browse (——) and grasses (– – –), compared with the minimum N content required by microbes (· · · · ·), and ignoring the effect of tannins on N loss.

In browse plants, the N content at any value of DMD is lower in non-leguminous plants and in stems than in shoots or leaves. Nitrogen content declines rapidly in grasses as the tissue senesces and turns brown, as N is translocated, and is lower in stem than in leaf. Grasses have lower N than browse, especially in mature tissue with low DMD. The rumen microbial requirement for N is proportional to the supply of fermentable energy-yielding substrates (AFRC 1993), and the estimated requirement is plotted in Fig 4. Browse generally exceeds this requirement, except for non-leguminous browse stem, although the N balance of animals consuming browse is adversely affected by the presence of tannins (Hanley et al 1992). Amongst grasses, only green leaf exceeds the requirement.

Since the digestibility of dietary ingredients can vary by 2-3 fold, the inclusion of forage digestibility in grazing models is important for the accurate prediction of energy intake. Some rangeland models merely rely on forage DM allowances required by animals, without considering digestibility (eg Fryxell, Greever & Sinclair 1988). There have been very few attempts to model digestibility changes per se. Illius (1985) derived a phenomenological model of seasonal changes in digestibility of temperate grasses in relation to defoliation intensity, but the model does not describe the underlying changes in sward composition. Grazing models invariably use digestibility data recorded for the vegetation unit and over a time scale governed by the degree of resolution sought in the model: annual, seasonal or monthly means for the whole pasture, plant functional groups, individual species or plant parts within functional groups (eg Hacker et al. 1991; Richardson, Hahn & Wilkie 1991; Freer et al.). For example, the Texas A&M University (TAMU) beef cattle production model (ILCA, 1978) uses monthly values for DDM and N for 30 grass species, ranked according to observed selectivity. The Animal Production Simulation and Range Assessment Model for Botswana (APSRAMB) utilizes an extensive vegetation database which includes monthly digestibility data (Hoefsloot, 1995). Blackburn and Kothmann (1989; 1991) used a more detailed description of digestibility. The decline of forage quality over time was modelled by assuming a negative linear relationship with forage age, and live and dead leaf and stem tissue are treated separately. Hacker et al. (1991) assume a decline in the digestibility of ephemeral plants as they dry out after the end of rains. The actual number of measurements supporting these estimates is often rather small, and the source of data is seldom given, or the user is expected to supply them as an input.

2.5   Vegetation dynamics

A considerable literature exists on the determinants of vegetation state and its dynamics in semi-arid regions, and so only a very brief summary is provided here.

The classical 'Clementsian succession' view of rangeland vegetation dynamics assumes that bare ground will become colonised by annual grass species, which will then be outcompeted by perennial grasses and woody species in a predetermined path towards a climax composition. 'Successional' forces were seen as being opposed by the effects of herbivory (via stocking rate) and fire, with vegetation state varying along a continuous axis between climax and 'degraded' vegetation (for a definition of degraded vegetation see below), according to the relative strength of successional forces, herbivory and fire. It is apparent that more complicated mechanisms than this determine the vegetation dynamics of rangelands. Abiotic influences may dominate the rangeland's biotic components in a way that succession models fail to take into account (Noble 1986). For example, one of the greatest influences on vegetation dynamics is that of soil moisture and the gradual drying out and re-wetting of the

soil, producing differential effects on established plant species and on seed germination (Westoby 1980).

Overview. Savannas are characterised as tropical and subtropical grasslands with a shrub or tree component. The composition of savanna vegetation is largely determined by rainfall and soil texture (being a convenient variable for representing both nutrient and hydrological properties) and modified by fire, grazing and the history of use (Fig 5, see review by Walker 1980).
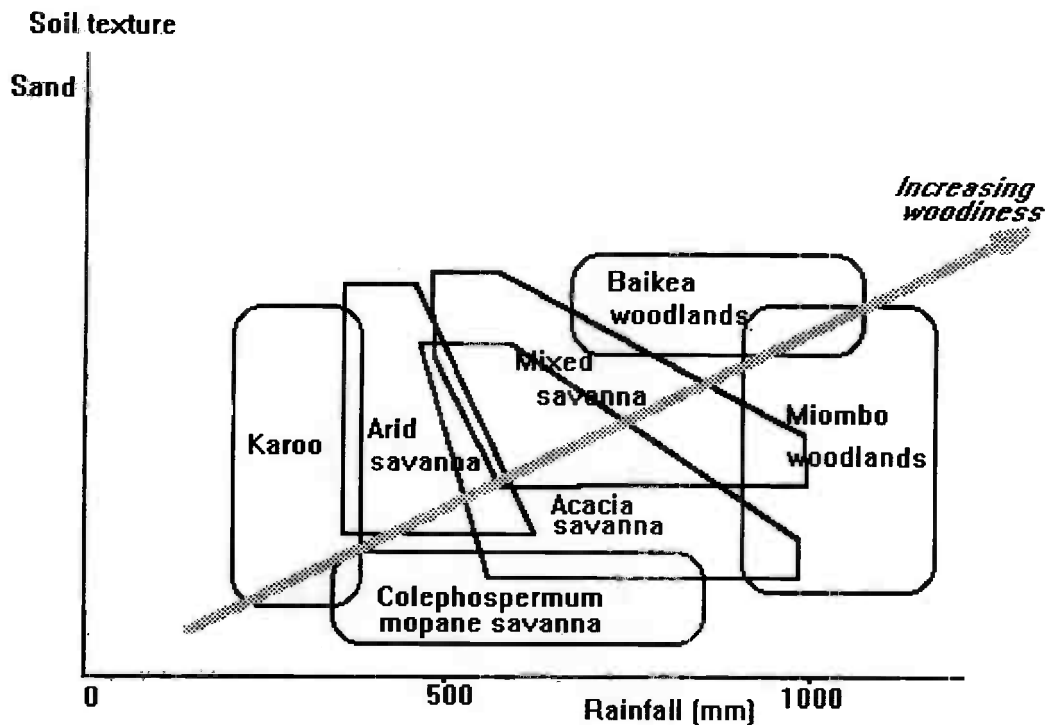
Fig. 5. Approximate description of the major types of savanna according to soil texture and rainfall (from Walker 1980).

To understand the response of vegetation to environmental and management influences, the main questions to be addressed concern the population ecology (establishment, recruitment, competition) and the ecophysiological characteristics of each plant species (water use efficiency, seasonal patterns of growth, storage, reproduction), and how these are affected by rainfall, herbivory and fire. In particular, interactions between the herbaceous and woody plants are a crucial determinant of savanna vegetation dynamics.

Tree-grass interactions and soil moisture. The ability of plants to compete for soil moisture is obviously important in water-limited environments, and so species interactions can partly be explained by differences in rooting depth in relation to the soil moisture profile. Shallow-rooted annual grasses are able to outcompete perennial plants in the upper soil layer, and therefore annuals respond better than perennials to erratic rainfall patterns, which do not allow much deep percolation. Grasses generally can compete successfully for water with woody species in the upper soil strata (Knoop & Walker 1985), but when bush reaches threshold density grasses are at a disadvantage and may not persist. Knoop & Walker (1985) argue that

the balance of herbaceous and woody species can be explained by the way rainfall intensity and soil properties determine the ratio of water in the topsoil as compared to that in the subsoil. Low rainfall especially on soils with a high silt and clay content reduce drainage to the subsoil, favouring herbaceous plants; conversely, on sandier soils there is deeper penetration of water, restricting its use by grasses and allowing relatively greater use by deeper-rooted woody plants. Another possible effect of trees on soil-water relations is by 'stem flow', in which interception of rain by the tree canopy and funnelling of it down the stem to the soil increases infiltration to the subsoil (Walker & Noy-Meir, 1982), but this process was not found to operate by Knoop & Walker (1985) or Smit *et al.* (subm).

Smit *et al.* (subm) examined the effects on soil water and plant growth of tree thinning in a semi-arid *Mopane* veld with 330 mm mean annual rainfall. The most striking effects of tree thinning were to increase peak grass biomass from about 90 to 1100 kg ha-1 (for no thinning and total clearance, respectively) and to reduce runoff of rainfall and increase infiltration. Partial thinning resulted in increased growth by the surviving trees, implying a reduction in inter-tree competition for water or nutrients. Smith & Goodman (1986) found similar results in *Acacia nilotica*. Smit *et al.* (subm) suggests that, as tree numbers increase, grass growth declines under direct competition for water, causing lower infiltration, due to the lower standing crop of litter. This reduces further the growth of grasses until they are replaced by bare ground, at which point the high runoff allows only drought-tolerant tree species to survive.

Plants vary in their responses to the drying out of the soil at the end of the growing season. Annuals may produce seeds several times throughout this period, thereby escaping any consequences of dry-season herbivory. Perennials drop their leaves and increase the depth of root growth through resource translocation. This may maintain a water column between the soil and each of the plant's meristems. Such actions preclude further high growth rates and represent a trade-off between growth and survival (Westoby 1980). It is thought that retaining access to deep soil water allows the early growth exhibited by woody species. Without this water column, time and resources would be spent rehydrating the meristematic tissues prior to growth. It is thought that this is how woody vegetation is able to pre-empt herbaceous growth by up to three months prior to the first rains. Even after the rains have started, perennials are able to respond before annuals can start their growth from seed (Tybirk *et al.* 1992). Woody species, and to a lesser extent perennial grasses, thus have an earlier and longer growing season.

Soil texture. Sandy soils, derived from granites, have low cation exchange capacity and concentrations of nutrients. Their coarse texture allows rapid infiltration of rain, promoting nutrient leaching, but more of the resulting soil moisture is removable by plants than from clay soils, and so in semi-arid savannas they may support more vegetation than clay soils. The latter are inherently more fertile, but percolation is slower, runoff higher and their higher matric potential means that less of the soil moisture can be extracted by plants. In the dry season, evaporation from the surface of sandy soils breaks the capillary column between the soil surface and soil water held below a few centimetres, greatly slowing further water loss to the atmoshere. In contrast, clay soils tend to crack and dry throughout the profile, with greater loss of water and slowing the process of re-wetting in later rains. Compared with sandy soils under mesic conditions, clay soils respond to the higher rainfall by supporting higher plant growth. The higher nutrient content of the litter promotes more rapid decomposition and thus speeds up nutrient cycling.

Rainfall variability is a primary determinant of compositional change (O'Connor 1985): 'Fluctuations in species abundances are the norm in savannas, and are related to the degree of rainfall variability. Available soil moisture, determined by rainfall, soil type and the woody/grass ratio, is the primary determinant of compositional fluctuations across all climatic regimes, but its effect is more pronounced in semi-arid than in mesic savannas, and on heavier textured than sandy soils. Correspondingly, the influence of fluctuations in the availability of nutrients, principally Nitrogen and Phosphorous, is greatest in the sandy soils of mesic savannas which are nutrient rather than moisture limited.' (O'Connor 1985). Rainfall variability clearly underlies the changes in species composition of more arid rangelands in which a substantial proportion of herbaceous vegetation is annual, and thus dependent on adequate rain for germination. For example, O'Connor & Roux (1995) describe the grassy dwarf shrub community of the Karoo, South Africa, as 'a matrix of longer-lived perennial grasses and dwarf shrubs within which dramatic variations in the abundance of annual grasses and ephemeral forbs took place'. Kelly & Walker (1976) noted that areas of bushveld in SE Zimbabwe dominated by annual grasses showed rainfall-induced fluctuations in annual growth which were up to four times larger than in swards dominated by perennials. Dye & Walker (1987) studied annual variation in patterns of perennial grass growth and concluded that differences in growth strategies and the timing of rainfall in relation to the growth phase of each species determined the extent of its growth and which species would predominate in a particular growing season.

Herbivory Although short-term rangeland dynamics are, generally, more prone to direction by abiotic factors, such as rainfall, than biotic factors such as grazing pressure (Noble, 1986, Milchunas et al., 1994), grazing does have significant long-term effects. In a comprehensive study, Milchunas and Lauenroth (1993) compared the effects of grazing on 236 globally-distributed sites. Changes in the species composition of the vegetation were found to be related to the duration of continuous heavy grazing, especially at more productive sites. There was a general tendency for a reduction in perennials in favour of annuals, an increase in annual and perennial forbs, and changes in the dominant species. They found that, when species composition changed due to grazing, there were a range of possible responses in above-ground or below-ground primary production. These inter-relationships would need to be understood further if species-based criteria in management are to reach the right conclusions about the long-term sustainability of production.

The effect of grazing during the growing season is, generally, to remove photosynthetic tissue and plant parts which contribute, directly or indirectly, to storage or seed production, and hence to persistence. Many species are especially sensitive to defoliation at the start of the growing season, because limited carbohydrate stores have often been expended to produce the first shoots of new growth. Outwith the growing season, most plants are much more resistant to defoliation, presenting only dormant or dead tissue above ground while mineral or nutrient reserves are stored below ground or as dispersed seed. Defoliation of woody species can stimulate replacement of lost tissue, provided carbohydrate stores or not exhausted. Acacia karroo, for example, is susceptible to defoliation during spring flush, when reserves are lowest, stimulated to regrow lost tissue during the growing season, and insensitive to defoliation while dormant (Teague & Walker 1988a, b).

The effect of grazing on species composition appears to be inversely related to rainfall with the greatest recorded effects at low rainfall sites (eg Tuli, Zimbabwe, 490mm) and almost no effect in higher rainfall savanna areas (eg Marondera, Zimbabwe, 940mm; O'Connor 1985). However, comparisons such as these may be confounded by differences in defoliation intensities between sites.

The maintenance of most savanna species is dependent on their being able to recolonize, largely by seed, gaps caused by grazing and drought. O'Connor (1991) showed how perennial grasses reproducing only by low numbers of large, poorly-dispersed seeds could become locally extinct under heavy grazing, due to increased adult mortality and reduced seedling recruitment. O'Connor & Pickett (1992) showed that grazing and intra-seasonal drought both reduced seed production in a number of African grasses, and sustained heavy grazing over more than 20 years eliminated seeds of long-lived 'palatable' perennials from the seed bank. O'Connor (1994) showed that species abundance, seedling recruitment, plant basal area and mortality in savanna grassland were more closely related to rainfall than to grazing during a five year period. Differences between species reflected such life history attributes as whether they were heavily grazed or produced seed prolifically.

Since these effects are at least partly mediated by grazing, the distinction has arisen between 'palatable' and 'unpalatable' species, the former necessarily being disadvantaged by grazing and thus being replaced by the latter. The classification of a plant's palatability is open to criticism (see section 3.1, para 2).

Woody plant establishment is a key process in bush encroachment. Under light grazing, herbaceous plants are able to prevent the establishment of woody plant seedlings, by competition for water and light. It is unclear how sensitive seedlings are to defoliation, and they may only be retarded by fire. Under heavier grazing, grasses are less able to compete for moisture and woody seedlings may become established. It appears that, as they grow, they become less susceptible to mortality from herbivory, and, when large enough, can also survive fire. Herbivory can, apparently, reduce seed formation, and thus affect population dynamics by reducing seedling number in the future. The lifetime patterns of competitive ability and of resistance to defoliation and fire with increasing plant size are clearly of interest but remain to be clarified for virtually all woody species found in savannas.

Fire has a modifying effect on savanna composition, somewhat like that of grazing, rather than being a controlling force (O'Connor 1985). Burning has long been thought of as beneficial, by preventing bush encroachment and maintaining grassland stability (Trollope 1982; Walker and Noy-Meir, 1982). Indeed, rather than soil water relations being the mechanism of bush encroachment, an alternative explanation is that the reduced herbaceous fuel load under grazing prevents the occurrence of fire from supressing woody seedling recruitment (Scholes 1993). It has also been suggested that burning can be counter-productive, by inducing the loss of perennial grasses and thereby actually encouraging invasive growth by the bush (eg Zumer-Linder, 1976). This is seen in long-term trials at Morale, Botswana. Paddocks are burned every 1, 2, 3, 4 and 5 years in September, when the bush is beginning to flush and burning is most effective. A control paddock is left unburned and all paddocks are ungrazed. To date, increasing the frequency of burns has reduced bush growth, but has also reduced perennial grasses and has increased annual grasses (G. Tacheba, 1995, *personal communication*). The review of grassland experiments by O'Connor (1985) suggested that the effect of fire on compositional change was complex, with an interaction of burning frequency and season with rainfall and soil texture.

Degradation. is a complex process, including the loss of plant species and the erosion and loss of soil. Degradation involves a long-term reduction in the ability of an area to support economic activity from primary and secondary production. Milton *et al.* (1994) have recently reviewed the subject.

Severe defoliation leads to the following progression. Preferred perennial grasses are grazed out first and replaced by less-preferred grasses, annuals and herbs. Eventually, deficient

seed production by preferred grasses leads to their extinction, and, of the ground vegetation, only annuals and herbs of low productivity and nutritive value are left. Further heavy grazing results in only bare ground or a few unpalatable bush species being left. The process of rangeland decline can become so severe that it amounts to desertification. Desertification implies aridity, but is not due simply to a decrease in rainfall, being primarily a disruption of ecology (Schlesinger *et al.*, 1990, Zimmer, 1995). The process involves a gradual redistribution of ground water, nutrients and microbes from the comparatively uniform grasslands into a mosaic of small nutrient rich patches growing at the expense of the surrounding land. Gradual depletion of the herbaceous layer exposes nutrient-carrying surface soil to wind erosion. The canopy can then act as a barrier, intercepting the wind-blown nutrients and depositing them at the foot of the bush. Without grass cover, the soil adsorbs more heat, slowing down nitrogen accumulation in the upper soil levels, thereby limiting nitrogen for grass growth. In addition, bare soils suffer increased runoff, also carrying away surface nutrients and grass seed deposits. The result of this nutrient redistribution is that nutrients cycles become concentrated around shrubs, creating nutrient-enriched patches (Blackmore *et al.*, 1990). Soil nitrogen is taken up by plants *via* an extensive root system, and returned by leaf fall, thereby maintaining localisation of the nutrient pool. Bush encroachment may thus limit erosion, and assist in regeneration, by shielding the soil surface.

According to Rapp (1976) "a common mechanism of desertization seems to comprise the following two phases. (1) Expansion and intensification of land use in marginal dry lands during wet years. These actions include increased grazing, ploughing and cultivation of new land, and wood collection around new camps or settlements. (2) Wind erosion during dry periods, or water erosion during heavy rain storms". Reynolds' (1995) model of the Jornada Basin desert, New Mexico, shows how grazing may precipitate desertification due to its effects on vegetation.

2.5 Synopsis and implications for modelling

Primary production on semi-arid rangeland is principally limited by moisture, with the implication that plant community structure is the outcome of competition for water. Soil texture is of importance in determining both hydrological and mineral nutrient properties. Rainfall variability seems to be the predominant agent of change in vegetation community composition. The effects of herbivory on vegetation dynamics could plausibly be ascribed to the loss of photosynthetic capacity of plants selected by animals, reducing the requirement for transpiration, and hence reducing the ability to compete for water.

A wide range of approaches has been adopted to modelling primary production. Description of water balance in more than one soil stratum appears to be the minimal specification consistent with the hypothesised role of soil water in determining both the production of and balance between woody and herbaceous vegetation components. Differences in the hydrological regime of herbaceous and woody vegetation, due to differences in their canopy structure and rooting zone, need to be resolved. Assumptions about similarity in the water-use efficiency of these components may be a weakness which cannot be resolved clearly, on the basis of present evidence. As with the response to soil moisture, plant allocation patterns are of fundamental importance to predicting forage supply, but these are poorly described, especially for browse.

3   **ANIMALS**

3.1   Foraging behaviour, intake and diet selection

Foraging behaviour and diet selection play a key role in grazing systems, not only by linking primary and secondary production, but also because it is the selectivity of herbivores which mediates and localises their impact on the population ecology of plant species (Brown & Stuth 1993). Yet, despite their importance, the mechanisms underlying diet selection remain obscure. Classical descriptions (eg Hunter 1962) distinguish broad botanical categories according to their use by grazing animals, and allude to the influence of plant phenology and biomass accumulation. Subsequent studies have supported these conclusions, but are largely descriptive and have not succeeded in providing a mechanistic basis for predicting diet choice (eg Arnold 1985; Grant et al. 1985b; Gordon 1989; Hodgson et al. 1991).

Classifying plants on the basis of their palatability has some attractions, operationally, but is flawed in attributing to individual species a unique value without regard for the other species present. Plant species which appear to be 'unpalatable' (ie they are rejected by animals) when present with more 'palatable' species may themselves be palatable under circumstances where the alternatives are avoided. 'Palatability' is thus relative, depending on the range of other plant species present. It is merely a description of a particular diet choice under particular conditions, rather than an explanation of it which can be generalised to other circumstances.

The point of going beyond mere descriptions of diet composition is to be able to <u>predict</u> how animals' diets will change in response to changing vegetation state and environmental influences (such as temperature, distance from water etc). The following is a review of some of the mechanisms which may be important in diet selection by ruminant livestock and wildlife.

Recent experimental approaches have suggested some of the functional and mechanistic bases for diet selection, by showing, for example, that diet choice may be influenced in diverse ways by animal state and by recent experience and constrained by the spatial distribution of resources (Newman et al. 1994; Parsons et al. 1994; Edwards et al. 1994). Yet the ability to predict diet composition still depends on rather few principles: plants with high concentrations of secondary metabolites are generally avoided; more is consumed from high biomass swards than from lower biomass swards of the same species and quality (Arnold 1985; Langvatn & Hanley 1993); there is some trade-off between biomass and digestibility (Illius et al. 1987; Wilmshurst et al. 1995; Shipley et al., subm); there is tendency towards frequency-dependent selection (Illius et al. 1987; Lundberg et al. 1989; Newman et al. 1994; Wallis de Vries & Daleboudt 1994).

In foraging theory, animals are generally assumed to be making decisions which enable them to maximise their long-term average rate of energy intake (Stephens & Krebs 1986). Although intake rate maximisation is assumed to apply in many optimality models of ruminant foraging (Belovsky 1978; Owen-Smith & Novellie 1982; Ungar & Noy-Meir 1988, Parsons et al. 1994b) there is little direct evidence that herbivores select diets which do actually maximize intake rate (Crawley 1983), even though harvesting difficulty is certainly the special feature of grazing. Amongst the few reports of animals selecting diets which maximized intake rate are those of Black & Kenney (1984) and Demment et al. (1993), and in neither case is the evidence particularly striking. Under closely controlled conditions, goats offered a range of temperate grass species have been shown to select those from which they obtained the highest intake rate (Illius et al., subm). More often, herbivore diets are characterised by the diversity of constituents: that is, they contain a mixture of food items with apparent disregard for the

intake rate each offers (Westoby 1974; Crawley 1983; Illius & Gordon 1993; Newman *et al.* 1994). This has led to doubt over the validity of the rate maximisation premise for herbivores, and factors such as obtaining a balance of nutrients, dilution of toxins, state dependence of diet selection, sampling, and perceptual constraints on recognition of the profitability of food items have been suggested as explanations (Westoby 1974, 1978; Pulliam 1975; Belovsky 1978; Illius, Clark & Hodgson 1992; Illius & Gordon 1993; Parsons *et al.* 1994a; Newman *et al.* 1994; Newman *et al.* 1995). As Stephens & Krebs (1986) point out, none of these factors defy analysis or suggest that herbivore diets fall outwith the paradigm of optimality. Unfortunately, the study of herbivores in complex natural environments must inevitably be limited to a descriptive approach, because the scope for selection is likely to be of greatest importance to animal and vegetation alike, but where closely controlled experimentation is infeasible. It is virtually impossible to infer the either the functional or mechanistic bases of foraging behaviour, especially when it is highly variable in space and time, from observations which are unsupported by controlled experimentation and detailed measurements.

Forage of low digestibility is avoided by ruminants when higher-quality alternatives are equally available. *Ad libitum* intake is reduced by low digestibility and it is assumed that low rate of ruminal digestion and passage impose physical constraints on intake (*eg* Laredo & Minson 1973). Although low quality vegetation (such as dead grass and browse twigs) can only be eaten in limited daily quantities, its abundance is usually high, and it can be eaten rapidly. In contrast, the intake of more digestible plant parts is less likely to be limited by digestive capacity than by the low rate of intake which results from their small size and sparseness. The trade-off between instantaneous intake rate and digestive capacity which maximizes daily energy intake can be used to predict foraging behaviour, and shows good agreement with experimental observation (*eg* Wilmshurst *et al.* 1995; Shipley *et al.*, subm).

An example of species differences in the digestibility of the diet selected is given in Fig 6. The diets of goats, Dorper and Merino sheep and cattle were compared when grazing together, at fixed stocking rate, on False Upper Karoo vegetation (dwarf shrubs and grasses). The rains (November to April) allow increased intake of new growth, with digestibility declining, especially in the larger-bodied animals, as the dry season progresses. Smaller animals appear less sensitive to declining biomass of high-quality plant tissues, unless vegetation becomes depleted after poor rains (*ie* after June 1977 in Fig 5).
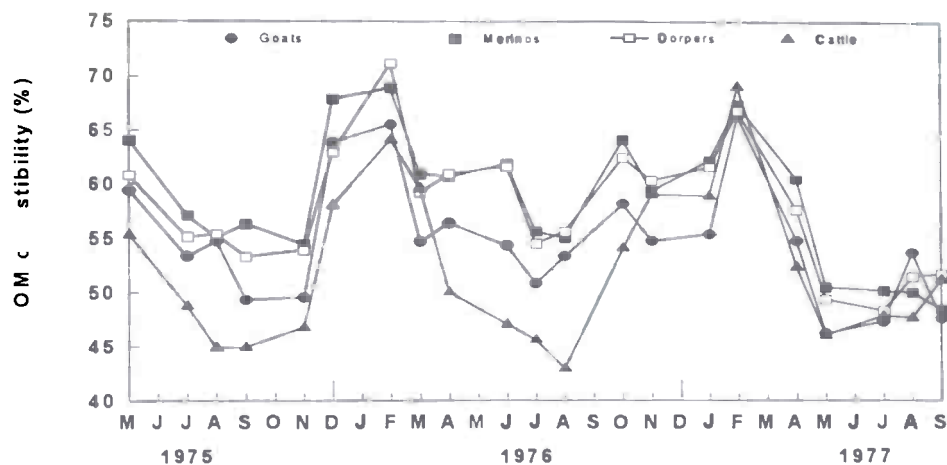
Fig. 6. Seasonal changes in the digestibility of diet selected by goats, sheep (Dorpers and Merinos) and cattle grazing karoo veld (Zeeman et al. 1983)

The occurrence of secondary plant metabolites in woody browse is clearly related to rejection by herbivores (Bryant & Kuropat 1980; Provenza & Malachek 1984), but the very low concentrations of these compounds in short-lived gramineous vegetation suggests they have little influence on selection amongst grasses (Iason & Waterman 1988). Other plant taxa show clear cases of deterrence of herbivory by allelochemicals, which act variously as toxins, (to which the animal may not be susceptible other than by having to bear the metabolic costs of detoxification), by reducing energy, protein or mineral digestion or retention, or simply by diluting the nutrient content of plant tissue. Indeed, lignin could be seen as acting on diet selection as an inert diluent. Allelochemicals are just one of a number of classes of plant attribute, along with the physical, structural and chemical properties which influence intake rate (Burlison et al. 1991; Laca et al. 1992; Illius et al. 1996) and digestion and metabolism.

The main problem in assessing the importance of secondary plant metabolites for diet selection is in not knowing how the animal integrates or balances the various positive and negative attributes of the vegetation. For example, how much of the variation in diet composition, after controlling for variation in allelochemical content, is due to variation in digestibility and nutrient content, and in the rate at which they can find and ingest a particular plant species? What is the response of animals which take mixed grass-browse diets (and this seems to include all classes of livestock at some time or place) to the seasonal changes in the digestibility/allelochemical trade-off of grasses and browse plants? Do animals integrate all positive and negative effects of dietary constituents to maximize long-term rate of energy and nutrient intake, subject to avoiding being poisoned? Clearly, to put the biochemical aspects of diet selection in context requires consideration of both the deterrent (allelochemical-related) and attractive (nutrient-related) plant attributes, and of the possible interactions between the two. Illius & Jessop (1995) modelled the interaction between allelochemical concentration and nutrient content, and suggested that the diminution in energy yield as a result of the dilution effect and the metabolic costs of detoxification is not substantial, by comparison with the potential effects of lignification on daily intake. Instead, it seems more likely that allelochemical deterrence acts via amino acid and nitrogen loss, arising as costs of controlling acid-base balance. The interaction between nutrient intake rate and detoxification capacity was hypothesized to result from the limited ability of animals to detoxify allelochemicals when under nutritional stress.

Less attention has generally been given to the positive goals which animals may seek to achieve when selecting a diet than about the avoidance of negative effects (but see reviews by Provenza 1995 and Illius & Jessop, subm). Evidence that animals can select diets to meet their potential rates of nutrient utilization comes from experiments on the effect of animal state on diet selection under choice feeding. For example, growing pigs offered iso-caloric feeds differing in protein content selected a combination with a protein concentration which matched their declining requirements for protein deposition as they increased in size (Kyriazakis et al. 1990). When both feeds on offer had a higher protein content than that required, the pigs avoided excessive protein intake by choosing predominantly the feed with the lower protein content. This showed clearly that pigs could select a diet which matched their changing requirements and could avoid nutrient imbalances. It might be thought that ruminant animals face a more complex problem in selecting a diet, since digestion and metabolism in the rumen is interposed between the nutrient ratio of foods eaten and the nutrient ratio absorbed. However, Cropper (1987) and Hou (1991) demonstrated that sheep selected a diet whose protein content varied consistently with degree of maturity and with time, and, using operant conditioning, that sheep were prepared to perform work to maintain the composition of their diet (Hou et al. 1991). Further evidence of the association between nutrient requirements and

diet selection in sheep was provided by Kyriazakis & Oldham (1993), who offered lambs one of six isocaloric diets with metabolisable protein:energy ratios ranging from 4 to 14 g/MJ either alone or as a choice with the highest-protein feed. Comparison of protein deposition in the sheep offered single diets with that in sheep selecting between two feeds showed that, given a choice, sheep selected diets which maximized their growth rates by avoiding diets too high or low in protein relative to energy.

The ability of animals to avoid nutrient imbalances may involve the same process as the avoidance of toxins, namely, via sensations of malaise induced by post-ingestional consequences (Provenza 1995). Animals appear to use these sensations and other aspects of 'post-ingestional feedback' to avoid nutrient imbalances and toxins and to modify nutrient intake if they are given the opportunity to select from an adequate range of dietary ingredients (Burritt & Provenza 1992; Provenza et al. 1994). For ruminants, the response to absorbed nutrients is mediated by rumen processes, and the synchrony of supply of metabolites to rumen microbes can exert a considerable effect (Dove & Milne 1994). In this sense, the distinction between energy and protein consumed is somewhat arbitrary, given the intervention of microbial metabolism and N recycling. This can, for example, cause an increase in the fermentable energy intake to result in increased microbial protein supply to the small intestine.

3.2   Animal species interactions: Complementarity and competition in resource use.

Because of the diversity of vegetation present in much rangeland, there may exist the potential for many animal species to coexist with limited competition, thereby increasing the potential for economic output. Balanced vegetation use also offers the promise of greater persistence of desirable vegetation components and less bush encroachment, which is a common consequence of cattle selectively using the grass fraction of the vegetation. The question, then, is of the relation between species differences in foraging behaviour and the extent of competition in resource use.

Sympatric animal species often show differences in diet composition, and hence a degree of niche separation (eg Gwynne & Bell 1968; Jarman & Sinclair 1979; Murray & Brown 1993) and there is some evidence that ungulate species diversity is related to habitat heterogeneity (Turpie & Crowe 1994). Species differences in foraging strategy are presumed to arise from differences in the efficiency or manner in which they obtain their metabolic and habitat requirements from a given vegetation type. For example, goats eat more gorse than do sheep when stocked together (Clark et al. 1982), and this can partly be explained by differences in their digestive physiology. The superiority of goats in consuming and digesting gorse and other low-quality forages is attributed to greater particulate outflow rate from the rumen, and to higher rumen NH_3 from better N recycling supporting higher fibre digestion rates (Howe et al. 1988; Domingue et al. 1991). Illius & Gordon (1987, 1993) and Gordon & Illius (1988, 1989, 1996) discuss some of the ways animals are adapted to a particular feeding niche, where their foraging efficiency is, hypothetically, maximized. Whether or not dietary specialization implies some degree of past or present competition for resources, increasing specialization will reduce niche overlap and thus may reduce competition with other species. It is not clear how far the evolution of foraging efficiency has been affected by interspecific competition, nor is there particularly good evidence, because of the difficulty of obtaining it, for feeding competition being an important factor determining herbivore community structure. Predation, disease and parasitism may be equally or more important determinants of animal abundance (see Sinclair 1985).

The existence of intraspecific competition is clearly seen in the negative response of individual animal performance to increased stocking rate (Jones & Sandland 1974). But even here, the degree of competition, and hence the slope of the response, will be a function of the intraspecific variance in diet composition. Given additional variance in herbivore diets, from the presence of other animal species, the slope of the response would be expected to be shallower still. The slope can thus be regarded as an index of competition. In one of the few attempts to quantify such effects, Connolly (1987) and Nolan & Conolly (1989) analysed a series of mixed grazing experiments with sheep and cattle, using response equations with coefficients both for the effect of species density on itself and for the effect of companion species. Results from 3-month grazing trials showed that, from the sheeps' viewpoint, each additional steer was equivalent to 4.3 sheep, while from the steers' viewpoint, an extra steer was equivalent to 8.8 extra sheep. Each species affected the other rather less than expected, since, in terms of metabolic mass, one steer would be equivalent to about 5 sheep. Results from 6-month trials showed that the addition of one steer affected the performance of lambs to the same extent as an extra 2.9 ewes with their lambs, while it took the addition of 4.8 ewes with lambs to affect the performance of steers as much as an extra steer would have. In both trials, mixed stocking improved output over equivalent stocking with single species, suggesting a degree of niche separation.

While it might be expected that the degree of heterogeneity of the vegetation affects the scope for complementary use of vegetation by different animal species, much of the evidence for niche separation comes from apparently quite homogeneous grassland systems. Further evidence is required of the response of one species, in a given environment, to increasing numbers of other species; of the ability of a species to diversify its diet under feeding competition; and of the seasonal incidence of dietary overlap and therefore of potential competition. It may then be possible to move further towards matching animal species mixtures to vegetation structure. Until then, an appraisal of the potential for complementarity could be undertaken by modelling, given a knowledge of species differences in foraging behaviour.

3.3   Exploiting habitat heterogeneity: the question of spatial scale

The problem of what is the appropriate scale for measuring and studying ecological processes has long been recognised (eg Greig-Smith 1952). The importance of spatial scale for herbivore foraging is now well established, and is having an impact on modelling (Senft et al. 1987; Coughenour 1991; Laca & Demment 1991; Laca & Ortega 1995). 'Heterogeneity' is itself scale-dependent; that is, what may be perceived at one scale as heterogeneous may be homogeneous at other levels - the difference between the beetle's and the buffalo's view of the prairie. This requires that space be defined from the herbivore's point of view (Morse et al. 1985; Pickett et al. 1989; Kotliar & Weins 1990). Variation exists at each of a range of spatial scales - from the local (variation between successive bites) through the scale of whole plant communities and up to landscape and regional scales. Herbivore impacts are also scale sensitive, being dependent on the scale of the analysis, spatial distribution of plants, and distribution of defoliation (Brown & Allen 1989; Brown & Stuth 1993; Laca & Ortega 1995). Moreover, since much of the difference between animal species in foraging behaviour and mechanisms of diet selection can be attributed to variation in body size, it can be predicted that species will differ in the spatial scale at which heterogeneity in the vegetation can be exploited, according to their body size and morphology. Therefore, species differing in size would be expected to have different effects on habitat heterogeneity, especially at the boundaries

between vegetation types, where the colonising plant species is present at low biomass, and likely only to be accessible to the smaller animal species.

Two recent examples of the importance of spatial scale are the studies of Scoones (1993, 1995), on the use by cattle of heterogeneous habitats, and the study of Ash *et al.* (in prep), both of which suggest that the decline in animal performance during drought or with increasing stocking rate is sensitive to the spatial scale of the area in which animals are permitted to forage. Scoones (*ibid*) argued that livestock survival was critically dependent on access to localised key resources during the dry season. Ash, comparing studies from a number of sites, found that the decline in cattle gains with increasing stocking rate was steeper in 5-15 ha paddocks than in 15-50 ha paddocks, while in 400-1200 ha paddocks there was no significant decline. The likely explanation is that there is greater habitat heterogeneity at larger spatial scales, which serves to buffer variation in herbivore competition for resources and impact. Walker *et al.* (1987), comparing ungulate mortality from a two-year drought in four wildlife conservation areas in southern Africa, concluded that mortality was greater where the establishment of watering points led to reduced spatial heterogeneity of grazing impacts and abolition of reserve stands of lightly-grazed grassland. Although this effect is confounded by the higher animal biomass in watered sites, it was argued that spatial patterning of resources acted as a buffer during drought.

3.4   Surface water

Access to surface water is an important limitation on the foraging behaviour of livestock and, by regulating their movements, localises the impact of defoliation and trampling on the vegetation, and also of treading and nutrient cycling on the soil (Pickup, 1994). Cattle require drinking water every 1 or 2 days, whereas goats can go for longer without, and indigenous breeds are often more tolerant than exotics. Wildlife are generally less dependent on surface water. Where domestic animals need a supply in areas of sparse surface water, boreholes are sunk. Water points therefore impose a spatial patterning of livestock impacts on rangeland.

Landsat images of the Kalahari clearly show the influence of point water source locality as a radial depletion emanating from each borehole. Closer inspection of the denuded zone shows a system of concentric vegetation bands, where the grazing pressure leading away from the borehole can be seen as a gradient running to the extent of its influence. Lange (1969) introduced the name "piosphere" to describe this zone of influence. In an arid chenopod shrubland in South Australia, Andrew (1988) recorded a clearly-demarcated 'zone of attenuating stocking pressure', stretching about 800m from the nearby *sacrifice zone*, less than 50m from the water point. Andrew and Lange (1986a, b) linked physical stresses on the soil surface with temporal and spatial changes in the underlying ecosystem. Breaking up of the the soil's lichen crust, soil compaction and intensive defaecation modified soil condition and mineral status, with erosion along animal tracks. Surface compaction and grazing pressure had a significant effect on grass biomass, grass and shrub mortality and seed germination, with patterns of defoliation and mortality radiating out from the water source.

Perkins and Thomas (1993) reviewed the impacts associated with boreholes in the Kalahari, and concluded that degradation is complex, being affected by topography and drought, as well as by stocking rates and duration of establishment. Zumer-Linder (1976) reported an average inter-borehole distance for the central Kalahari of 10-15km, the maximum walking distance for cattle. Perkins (*personal communication*) estimates that it has now been reduced to as little as 8km . This clearly has implications for the peripheral vegetation of the outer bands as the piosheres become merged.

The consequences of water supply are also observed for fenced land. Enclosures with a water supply soon become over-used, in contrast to distant paddocks that do not have a water supply have plentiful stocks of fodder which cannot be used (N. Kombani, 1995, *personal communication*).

3.5 Soil fauna

The rôle that invertebrates play in grazing systems dynamics has, generally, been ignored. They represent a second class of herbivores (ruminants being the first) with a surprisingly similar ecological repertoire: patterns of diet selection, impacts on the standing biomass in competition with each other and with ruminants, together with wider effects on the soil water regime, nutrient cycling, and vegetation dynamics (Whitford 1986 and references therein). Standing herbaceous biomass present at the start of the dry season is of vital importance to the support of livestock and wildlife until the next rains, so removal of this resource by soil fauna needs to be accounted for.

Termites can be divided into foraging and humus-eating species. With the exception of *Hodotermes mossambicus*, which can harvest large quantities of green grass, foraging termites and millipedes consume dead leaves and litter which might otherwise be used by ruminants during the dry season. It is hard to find reliable estimates of the biomass of invertebrates, but in some systems it may exceed that of the ruminants, and may even be 10 times higher (Whitford 1986). Dunham (1990) estimated that termites and large mammals *each* removed about 25% of herbaceous net annual primary production during the dry season in Zambezi riverine woodlands. Ohaigu & Wood (1979) estimated that the fungus-growing *Macrotermitinae* removed 42% of grass production, (70% of which was during the dry season), compared with 4% by *Trinervitermes* and 45% by cattle. In contrast, on a sandy soil in Northern Transvaal, South Africa, the low biomass of termites only accounted for less than 2% of litter removal Scholes & Walker 1993).

Macrotermes mounds can be found in woodlands at about 3-5 per ha. (Trapnell *et al.*, 1975), and foraging may still take place up to 50m away from a mound. Territorial control (Schuurman & Dangerfield 1995) may restrict the influence of any one colony to a limited area. Even where there is no surface nest (*e.g. Microtermes)*, there is an extensive subterranean gallery system. By removing a significant proportion of the litter standing crop, invertebrates may have a significant effect on rainfall infiltration rates. Infiltration is higher for littered ground than bare ground (Kelly & Walker 1976), but infiltration is also increased by colonial tunnel networks (Whitford 1986).

Invertebrates play a significant rôle in the cycling and concentration of soil nutrients. Studies have shown the significant influence that termites (especially the mound-forming *Macrotermes*) and millipedes have on soil composition and fertility (*eg* Trapnell *et al.*, 1975, Dangerfield, 1991). Nutrient cycles are modified by the subsequent redistribution of organic matter and nutrients to the soil (Trapnell *et al.* 1975; Dangerfield, 1993) and the breaking down of mammalian dung. The high concentrations of nitrogen and phosphorous that are present in the faecal pellets of invertebrates certainly modify the local environment. For example, phosphorus concentration is double that of background levels in termite mounds and colonies of *Cubitermes* have a pronounced effect on the distribution of soil organic carbon in local above-ground samples (Dangerfield 1991). Nutrient effects are concentrated within the mounds, whereas infiltration effects occur more widely, throughout the foraging zone.

Other invertebrates that may have a significant effect on rangeland ecology are: ants (infiltration and seed predation); and beetles (infiltration, root herbivory, faecal decomposition and nutrient redistribution).

3.6   Disease transmission

One important aspect of the interaction between domestic livestock and wildlife is the transmission of disease (Pastoret *et al.* 1988; Grootenhuis 1990; Rossiter 1990). Wildlife, which are likely to be able to range widely, unless game fences are erected, form an important reservoir of infectious diseases and parasites. The following brief review considers some of the most significant ones, economically and pathologically, and those of local importance where wildlife-livestock transmission is a problem. We are indebted to our colleague, Michel de Garine-Wichatitsky, Dr.Vet., of CIRAD-EMVT, Zimbabwe, for helping us compile this.

Diseases in Africa fall into two categories, according to origin (Bengis & Erasmus, 1988; Pastoret et al. 1988). Endemic African diseases, which have evolved and cycle with indigenous wildlife which in turn act as reservoirs. They usually cause minimal debility and mortality in wildlife, but have severe effects on livestock. Trypanosomiasis, Theileriosis, Foot and Mouth Disease (SAT virus Type) and Bovine Malignant Catarrh are typical examples. The second category contains diseases which have probably been introduced onto the African continent by domestic animals, and are capable of infecting some wildlife species, often causing large scale morbidity and mortality. Rinderpest is the most spectacular example, along with Rabies, Anthrax and Brucellosis.

Trypanosomiasis is caused by protozoa (*Trypanosoma* spp) transmitted by tsetse fly (*Glossina* spp). Wild bovids are resistant to the species of trypanosomes which affect domestic livestock. Mechanisms of resistance include a reduced attractiveness for tsetse of wildlife species compared to cattle, as well as immunological defences (limited skin reaction, trypanocidal components in serum). Wildlife are considered to be the reservoir for domestic livestock and extermination of wildlife has been used in the past for control.

Theileriosis. The most important group of livestock diseases in eastern Africa, from an economic point of view, are the tick borne diseases, of which Theileriosis (East Coast Fever and Corridor Disease) is the most important. ECF is caused by *Theileria parva parva*, a protozoan parasite transmitted by the brown ear tick, *Rhipicephalus appendiculatus*. The costs of treatment against ticks and mortality due to ECF may annihilate cattle ranching, as the disease is almost always fatal for cattle. It is likely that the parasites originated from buffalo, which are all infected within the distribution area of the tick vector. Corridor Disease, the name of the buffalo form of Theileriosis caused by *Theileria parva lawrenci*, is transmitted by *Rhipicephalus appendiculatus* and *Rhipicephalus zambeziensis*. Wild animals live in balance with the parasites, but cattle can be severely affected, and CD is a major cause of cattle mortality where it is endemic.

Rinderpest was introduced to the African continent and resulted in a pandemic from 1898-1903 (Meltzer 1993). Severe mortality occured in cattle and also in susceptible wildlife species, such as buffalo (*Syncerus caffer*), bushbuck (*Tragelaphus spekei*), eland (*Taurotragus oryx*), reedbuck (*Redunca spp.*), waterbuck (*Kobus spp.*), and wildebeest (*Connochaetes taurinus*). Some of these species, such as buffalo, have never been as numerous as before the pandemic.

Foot and Mouth Disease More than 70 species of mammals, representing over 20 families, have been described as being receptive to the virus of Foot and Mouth Disease. In

Africa, buffalo and kudu (*Tragelaphus strepsiceros*) act as an important reservoir of the virus. Althought the disease is not usually fatal for southern African ungulates, it must be controlled to protect meat and agricultural exports. The zonation of Zimbabwe into areas from which the EU will or will not import beef, due to the presence of Foot and Mouth Disease, and the veterinary cordon fences in Botswana have both had significant impacts on wildlife and the opportunities for multi-species production. Theoretically, the movements of cattle and game-meat are restricted from endemic to disease-free areas, and buffalo cannot be kept in disease-free areas.

Malignant Catarrhal Fever is a disease of cattle caused by the alcelaphine herpes-virus ACV-1, carried by wildebeest. There is presently no other solution than separation of the two species, and in some areas, the disease as become the major cause of mortality of cattle in mixed ranches.

Bovine Petechial Fever is a disease of cattle for which bushbuck is a reservoir host. This ricketsial disease, of which the vector has not been identified yet, is ecologically confined to mountainous woodland, and can cause high mortality of cattle.

Parasites Seasonal prevalence surveys indicate that many instances of cross-infestation of parasites between wild and domestic mammals in African savannas are possible (*eg* Lightfoot & Norval 1981; Horak 1983; Bengris & Erasmus 1988). Many species of helminths can be transmitted between wild and domestic herbivores (*eg Haemonchus contortus* in sheep and blesbok ; *H.placei, Trichostrongylus colubriformis* and *T. falculatus* in impala, *Aepyceros melampus*, and cattle; *Oesophagostomum columbianum* in impala and sheep), but usually these nematodes establish only small populations in the alternate host. Other parasites, such as the larvae of *Gedoelstia* ssp. flies, which normally partasitize alcelaphine antelope, if deposited in the eyes of sheep can lead to severe ocular, vascular and nervous complications. The rate of transfer of most of these parasites between the hosts is largely unknown, as well as their real effects on both populations.

Ticks Considerable cross-infestation with immature ticks occurs between cattle and impala, and kudu harbour tick species usually encountered on cattle. There is still a controversy on host resistance for wildlife species, which would limit tick population growth, because only a proportion of the female ticks could fully engorge, and thus be successful in reproduction. The role of reservoir of ticks played by wildlife has often been evoked, but rarely demonstrated, as population studies have seldom been performed on ticks from different hosts. The deleterious effects of ticks on ungulates hosts can be divided into five categories : tick-borne diseases, tick toxicoses, metabolic debilitation, secondary infection and tick worry.

Tick-borne diseases: There is increasing evidence that wild ungulates frequently harbour tick-borne disease organisms and do occasionally succumb to tick-borne diseases. Heartwater, caused by *Cowdria ruminantium* and transmitted by ticks of the genus *Amblyomma*, Babesiosis (*Babesia* spp, transmitted by several species of ticks), have been described in various species of wild herbivores, which could play the role of reservoir for these diseases (*eg* Cowdriosis in eland, Anaplasmosis in giraffe and buffalo, Babesiosis in waterbuck and kudu). But it seems that tick-borne diseases are less serious than the direct effect of ticks in wildlife populations. Theileriosis has been discussed above.

Tick toxicoses: Several forms of toxicosis as a result of tick bites have been described in domestic animals, and suspected in wild herbivores. These include paralysis -caused by many species of ticks-, rhipicephaline toxicosis - caused by heavy infestations of *R. appendiculatus*, - and sweating sickness caused by *Hyalomma truncatum*.

Metabolic debilitation: Reduction of mass gain of animals infested with ticks, compared to similar animals regularly dipped with acaricides, can be severe (sometimes as much as 46% reduction over 27 weeks for cattle in Australia). About 35% of this has been attributed to the loss of blood induced by engorging ticks. The remaining 65% were due to reduced food intake, as it appeared that salivary secretions of ticks contain toxins with an anorectic effect.

Secondary infection: Tick bite lesions can become secondarily infected.. The most serious secondary infestation are those of maggots (larvae of flies of the family *Calliphoridae*) which are known to have caused the death of eland, kudu, sable and Burchell's zebra.

Tick worry: All species, when annoyed by ectoparasites, spend time on self-grooming. These activities involve time and energy cost to the host, which may become prohibitive when the animal is weakened through any cause.

3.7 Synopsis and implications for modelling

Existing empirical and theoretical work provides a basis for the mechanistic modelling and prediction of diet selection and intake. Much of the species differences in diet selection can probably be accounted for by mechanisms related to body size. Species- and population-specific factors such as animal learning and experience may affect foraging behaviour in a manner which is hard to account for in predictive models.

Spatial heterogeneity in vegetation abundance, or location of water points and fences, are clearly important influences on foraging behaviour, but require a considerable addition in complexity over a first-generation model, in which spatial homogeneity would be assumed.

Soil fauna clearly can exert a marked influence through plant consumption, mineral cycling and infiltration rate, yet most of these are too poorly quantified, in relation to faunal biomass and environmental factors, for any but fixed estimates to be incorporated in models.

Systems

To provide some background to the mechanistic modelling of grazing systems, this section reviews current understanding of them, of how they change over time (*ie* their dynamics) and of some of the management challenges they pose. Mechanistic modelling is not, of course, the only way of trying to understand rangeland systems' dynamics, and they have been the subject of considerable debate between empiricists, managers and theoreticians. For at least the last 20 years, there has existed an uneasy relationship between theoretical and field approaches to understanding grazing systems dynamics, with theory providing a number of concepts and predictions for field ecologists and managers to grapple with. Current issues in the debate about the behaviour and management of semi-arid grazing systems need to be seen in the light of the theoretical background and because of this, the contribution of theory and its current usefulness are reviewed in some detail.

4.1   Management paradigms

Rangeland management and the attainment of desired goals is perhaps a more complicated task than almost any other area of agricultural practice, in which control of the production process is more amenable to scientific input. Unlike pastoral systems in cool, temperate regions, with dependable rainfall and intensive physical and management inputs, the arid rangelands suffer capricious rainfall and low productivity. Systems which are predictable and productive are inherently controllable and reward the development and prescription of sophisticated and reliable techniques for managing production for specified goals. In arid and semi-arid rangeland systems, which have quite different dynamics, the ability of managers to exert control is subject to a number of constraints, such as the unpredictability of events, the adverse economics of extensive systems and their enormous physical scale.

One of the obvious contrasts between intensive and extensive grazing systems is in their dynamical response to, and likelihood of experiencing, perturbations. Much of this is accounted for by differences in rainfall, being the primary determinant of plant growth, and the generally negative relationship between the mean and variance of rainfall. With increasing aridity comes increasing stochastic domination of the conditions for plant growth, and hence of ecosystem dynamics. High variability implies the occurrence of rare, extreme events, such as a drought year followed by one of unusually high rainfall. These can drive episodic changes in plant species composition, and are therefore thought to underlie the discontinuous shifts in state documented for semi-arid rangelands (Griffin & Friedel 1985; Westoby *et al.* 1989; Walker 1993; O'Connor & Roux 1995; Weigand, Milton & Wissell 1995). For example, fire or exceptional rainfall may be prerequisites of germination. In eastern Australian shrub grassland, unusually (*ie* 2-5 times per century) good rainfall in two or more years allows the establishment of many shrub seedlings and a substantial fuel of ephemerals and perennial grasses. Removal of the fuel by heavy grazing prevents fire, and this allows shrubs to grow, establish a seed bank, suppress grass growth and become dominant within 10-20 years (this and many other examples in Westoby *et al.* 1989). Events and behaviour such as this are described in terms of grazing ecosystems experiencing transitions between alternative stable states.

Much of the debate about appropriate methods of rangeland management thus reflects the inadequacy of paradigms based on the notion that systems are in some sort of equilibrium or balance (Westoby 1980; Behnke *et al.* 1993). Previously, vegetation state was seen as being held between the opposing forces of succession and competition by the effect of grazing, and therefore controllable by stocking rate. Instead, the focus has shifted to techniques suitable for

systems which are subject to high variability, and which are, necessarily, often not at equilibrium (see Scoones 1994; Behnke & Kerven 1994), and which may be prone to shift between alternative states. This has led to the development of the state-and-transition approach to management, which addresses as threats and opportunities the series of stochastically-driven changes of state which characterise the dynamics of such systems (Westoby et al. 1989; Walker 1993). For example, Walker, Matthews & Dye (1986) identified the need for event-oriented management approaches for southern African systems which are dominated by external events, principally the sporadic seasonal pattern of rainfall. Frame-based dynamic modelling for studying ecosystem dynamics have been developed, based on the AI concept of 'frames' representing vegetation alternative states, with event-driven changes between states (Starfield et al. 1993).

4.2   Theory

The following is a review of the origin and meaning of the concepts of stability, nonequilibrium and resilience, intended to ask what part they play in our current view of grazing ecosystem function.

Theoretical investigations of the dynamics of Lotka-Voltera models of predator-prey systems form the basis of our understanding of the conditions for the stability of ecosystems (Rosenzweig & McArthur 1963). For a given model of the predator-prey (or, more generally, consumer-resource) interaction, there generally exists a parameter space which yields some type of stable solution, in the form of a dynamic equilibrium. Crawley (1983) gives a helpful account of how, in a simple model linking plant growth and consumption to plant biomass, and animal population growth to intake, the stability of the system is increased by increasing plant intrinsic growth rate or by reducing asymptotic plant biomass (thereby increasing density-dependent regulation of growth) or by decreasing herbivore growth efficiency. There exist various combinations of parameters which have stable equilibria, stable limit cycles, or violent oscillations which lead to herbivore or plant extinction. Stability, as a theoretical concept, is thus intimately tied to the deterministic dynamic equilibrium, where the mutually dependent consumer and resource are in balance. Pimm (1984) provides a clear set of definitions of ecosystem variables. 'A system is deemed stable if and only if the variables all return to the initial equilibrium following their being perturbed from it. A system is locally stable if this return is known to apply only certainly for small perturbations and globally stable if the system returns from all possible perturbations.'

The dynamic equilibrium of a model system is obviously dependent on the structure of the model, and is altered by, for instance, choosing a different type of herbivore functional response or introducing plant reserves which allow plant recovery from total depletion. Take, for example, Noy-Meir's (1975) treatment of plant-herbivore dynamics, which provides a celebrated example of the way modelled interactions can predict the existence of more than one stable state, and which is cited as explanation of why rangeland systems may occupy more than one state (Westoby et al. 1989). In using this type of model to ask the question of how many steady states there are, we must be careful to make the distinction, that is often overlooked, between two alternative models, either with constant or variable herbivore numbers. For fixed stocking rates, as in Noy-Meir's (1975) original model, or where herbivore population dynamics is not linked to vegetation state, the quantity of vegetation at which the herbivore population is static can occur at either low or high vegetation biomass, which are alternative stable states. The existence of two alternative stable states also depends on the vegetation isocline (all points where dV/dt=0 on a graph of vegetation against herbivores)

being convoluted, as can result from various assumptions about density-dependent plant growth, plant reserves and the exact shape of the herbivore functional response (Noy-Meir 1975). In an interesting recent development, Reitkerk & Van de Koppel (in prep) argue that a humped resource isocline may underlie vegetation growth, as a result of feedbacks between vegetation and rainfall infiltration rate, and between vegetation and nutrient loss *via* runoff. Now consider a model of the herbivore population that differs by allowing their numbers to vary, by linking their fecundity to vegetation biomass. In this case, the herbivore population will be stable at the vegetation biomass which will exactly allow them herbivores to maintain their numbers, and the system has only one stable state (see Noy-Meir 1982, Figs 3 & 4).

The unsurprising conclusion of this comparison is that the choice of model determines the stability conditions revealed. Wang & Gutierez (1980) argue forcefully that stability analyses reflect model assumptions rather than testable field biology, having shown the arbitrariness of stability characteristics of models with varying degrees of realism - age structured populations and seasonality, for instance. It would not seem unfair to conclude that the correspondence between the stability conditions of simple models and the set of meta-stable 'states' observed in real systems is largely metaphorical. This is not to say that simple models are wrong, for they are successful *in their own terms* at describing the behaviour of coupled plant-animal interactions in an imaginary homogeneous environment, but to caution against extrapolation beyond these conditions. Indeed, the problem lies with the very simplicity of such models, which do not incorporate quite obvious influences on real ecosystems, such as spatial and temporal variation, which affect their stability (see DeAngelis & Waterhouse 1987; Crawley 1983 p 213). The question here is what modifications are required to model the essential properties of real systems, both natural and managed.

Transitions between states in rangeland systems do not merely involve quantitative changes in vegetation biomass, but involve qualitative changes in plant community structure and in the potential future changes of the same order. For modelling, the crucial difference between classical multiple equilibria and the catalogue of alternative states in rangeland systems is that the former can be expressed in terms of a continuous vegetation axis (eg plant biomass) whereas the latter need to be represented either on a catalogue of new axes, corresponding to each new state, or some fairly creative thinking has to be done to represent them on a new axis that can then be related to herbivore response. The work of Hardy & Mentis (1986), relating plant community composition to its effects on animal production, is a guide to how this might be attempted.

The foregoing considered some of the deterministic and biotic elements in system stability. A second class of disruptive influence on ecosystems, and one which is thought to raise questions about the usefulness of equilibrium concepts themselves, is that due to stochastic, abiotic effects on systems that would be stable under constant conditions. In seasonal systems which are continuously grazed, herbivore numbers are usually limited by their ability to survive periods of weight loss during the dormant season of plant growth, both by using plant residues from the growing season and body reserves established then (eg Milner & Gwynne 1974; Sinclair 1975; Ellis & Swift 1988). Density-independent population processes are relatively important (eg Langvatn et al. 1996; Albon, Coulson & Clutton-Brock, in press), often associated with climatic extremes such as poor winter weather or lateness of rains in arid systems. Animal populations are therefore small, relative to that supportable during the growing season, with the result that there is weak or no density-dependent regulation of either animal or vegetation population processes occurring then. Vegetation biomass shows wide positive and negative excursions from the annual mean, and only a small proportion of it is consumed by mammalian herbivores, the remainder being lost through senescence and micro-

faunal herbivory. In such systems, the coupling of animal and plant processes appears to be weak, compared with climatic and density-independent determinants of animal and plant abundance. The weakness of linkages between systems processes, due both to extreme seasonality and to stochastic environmental factors, has given rise to the view that such systems do not obey classical equilibrium dynamics, as defined by coupled consumer-resource dynamics, but exhibit nonequilibrial dynamics (Chesson & Case 1986; DeAngelis & Waterhouse 1987; Ellis & Swift 1988; Behnke *et al.* 1993). Weins (1984) suggested that all ecological systems fall somewhere on a continuum from equilibrial to nonequilibrial, and characterised the latter as showing weak biotic coupling, independence of species, abiotic limitation rather than resource limitation, density independence and large stochastic effects.

Nonequilibrial systems could be defined as those lacking or having only weak inter-dependence of consumer and resource dynamics, but the term is generally used to describe systems which are merely not at equilibrium. However, there is a sense in which all natural systems are nonequilibrial, insofar as environmental fluctuations and stochastic variation in parameter values, such as birth or death rates, are constantly redefining the dynamic equilibrium, and sometimes at a rate faster than the system can respond (according to its resilience; see below). Then, the system will be in permanent orbit around a moving attractor, never coming to rest at an equilibrium which, nevertheless, does exist (see Fig 7). This is the soft case of nonequilibrium, where density-dependent effects on herbivore fecundity and mortality are present, but their severity is defined by current seasonal conditions. They will be more severe than average about half the time, in years when plant growth is poor and the animal and plant processes become tightly coupled, and relaxed or lacking in the remaining, better-than-average years, when coupling of the processes becomes looser. For example, Caughley & Gunn (1993) showed that short-term unpredictable fluctuations in rainfall are the cause of long-term aperiodic fluctuations in kangaroo numbers. Note that their model, in which vegetation and animal dynamics are linked, would, under constant rainfall, have a stable point (at V=230 kg/ha and H=2.9R-103 kangaroos/km^2, where R is 3-monthly rainfall in mm). The hard case of nonequilibrium is where, under conditions of extreme seasonality, predation or disease, there is really no relationship between the vegetation and the rate of change of herbivores, nor *vice versa*. These are, simply, non-interactive systems (Caughley & Lawton 1981) for which no equilibrium state exists strictly as a result of plant-animal interactions. What actually does govern the dynamics must lie in relations with other agents. The Turkana rangeland system in East Africa is considered to be an example of a nonequilibrium system, due to its extreme seasonality, with animals having minimal impacts on plants and animal mortality being determined largely by the length of the dry season (Ellis & Swift 1988). In terms of animal numbers, humans supported and economic output (if not land occupied), most rangeland systems must, by definition, fall well short of this extreme and are quasi-equilibrial, or, to put it more simply, seldom at equilibrium. Coppock (1993), comparing the Borana and Turkana systems, suggests that drought frequency and degree of aridity mark the border between quasi-equilibrial and nonequilibrial systems. Likewise, Ellis (1994) argues that environments experiencing rainfall with greater than 30% interannual coefficient of variation are so dominated by variability that they can be distinguished from equilibrial systems. This defines nonequilibrium in quantitative terms, according to whether stochastic influences are considered to be dominant. The management implications of variability are examined in Scoones (1994).
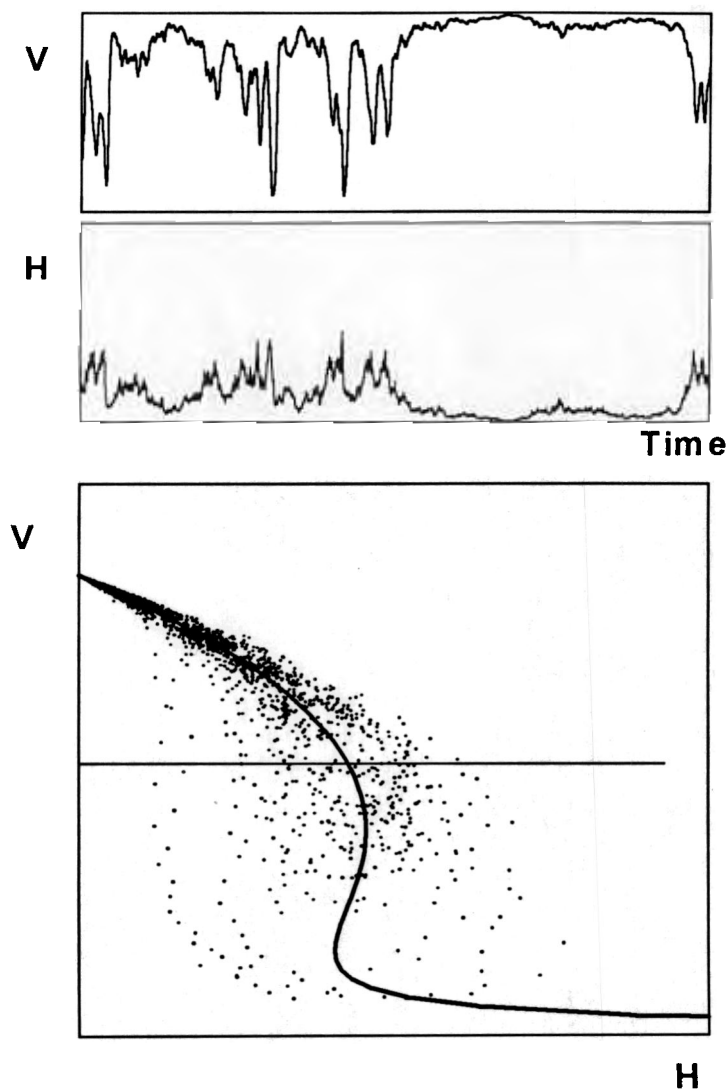
Fig 7. Vegetation-herbivore relations which appear nonequilibrial, under conditions where herbivore mortality is stochastic. The model, relating herbivore intake and population growth to vegetation biomass, and with density-independent mortality (Crawley 1983 eqn 4.7), was modified by setting the rate of *per capita* mortality to a positive random variable with cv=50%.

Top two graphs: Changes in vegetation biomass (V) and herbivore numbers (H) over a simulation of 2000 timesteps. Bottom graph: Combinations of V and H (•) over the duration of the simulation, showing departures from the stable equilibrium which, under a constant mortality rate, would lie at the intersection of the vegetation isocline (curve) and the herbivore isocline (horizontal line). Note that the herbivore numbers tend to be lower than the equilibrium, and vegetation higher.

An alternative, qualitative, view of nonequilibrium concerns the disparity between population-regulating processes at small and large spatial scales. At small spatial scales, even small perturbations can cause local extinctions. The population could then be regarded as comprising a collection of transient patches, whose dynamics can best be described by gap models in which colonization and extinction are probabilistic. It can be shown that the stable equilibrium state is a property that can emerge asymptotically from extrapolation to sufficiently large spatial scales (DeAngelis & Waterhouse 1987). A nonequilibrial community is one where non-deterministic population fluctuations on a small spatial scale are an essential part of community phenomena at a larger scale (Chesson & Case 1986). Alternatively, population fluctuations at the larger scale may be the result of processes at the same scale. Grazing systems may possess some of the features of both, for while plants and the impact of herbivory may be highly localised, the mobility of herbivores allows them to avoid the consequences of purely local plant extinctions and be more affected by community-scale plant population dynamics.

Whatever links there might have been between theoretical conceptions of stability and that observed in nature were severely questioned by Connell & Sousa (1983). In a review of 49 sets of long-term census data, they sought to assess whether, in populations followed for at least one complete turnover of all individuals, there was a subset that exist in an equilibrium state or states. The results showed a continuum of temporal variability in dynamics, only a few cases of stable limit cycles, and no evidence of multiple stable states in unexploited natural populations or communities. They found 'no evidence to show that following a disturbance any community has adjusted back to an original species configuration which then resisted change beyond one complete turnover' (Connell & Sousa 1983, p 806). The study could be criticised for ignoring, or not having access to, suitable data. For example, Schoener (1985) responded by showing that some lizard populations were, by comparison with other taxa considered by Connell & Sousa, unusually constant over time. Silvertown (1987) pointed out that data from the Park Grass Experiment at Rothamstead, England had been overlooked. These provide good *prima facie* evidence of stability in plants grouped as grasses, legumes and miscellaneous, although there is considerable variability at finer scales of taxonomic resolution. Stability, like so much else, is a scale-sensitive phenomenon. By excluding cases where populations were kept at different, possibly stable states by human intervention (*eg* Noy-Meir 1975), and demarcating 'appropriate scales of space and time', Connell & Sousa's study could be also be criticised for being too stringent in its criteria. These exclude the timescales relevant to rangeland management, which recognises changes of state (Laycock 1991), whether or not these correspond to stable equilibria.

Much is made of the 'resilience' of rangeland systems to disturbance, but here again, the analogy with the original concept may be misleading. Resilience is usually meant in the sense that rangeland systems are more resistant to degradation than was first thought, especially by the colonial administration (see Abel & Blaikie 1989; Behnke & Scoones 1993; Tapson 1993), despite exhibiting some of the worst examples of degradation. Resilience was first defined by Holling (1973) as 'a measure of the ability of these systems to absorb changes of state variables, driving variables, and parameters, and still persist'. Without a means of quantifying resilience, the concept remains merely a useful metaphor which 'characterises the magnitude of the population perturbations the system will tolerate before collapsing into some qualitatively different dynamical regime' (May 1981). Beddington *et al.* (1976) used the rates of return to equilibrium after a perturbation as a measure of resilience, thus defining it in terms of the steepness, rather than the size, of the basin of attraction. The concept of return time is, of course, meaningless for unstable equilibria. A useful corollary of this definition is that highly

resilient systems will show less 'nonequilibrial' properties, because they track more rapidly the environmentally-induced vagueness in the equilibrium point. Pimm (1984) defines resilience as 'the characteristic return time, being the time taken for a perturbation to return to $1/e$ (~37%) of initial value'. As such, it is amenable to field determination. DeAngelis (1992) applies this definition to a wide range of consumer-resource models. Most recently, Ives (1995) has developed a method of estimating resilience in stochastic systems as the variability in population densities relative to environmentally-driven variability in population growth rates.

The *quantitative* definition of resilience is somewhat at odds with continued use in its original, *qualitative* sense (*eg* Walker & Noy-Meir 1982; Holling 1986). This definition incorporates, and thus confuses, notions of stability, the size of the domain of attraction, the resistance of a system to perturbation, and its variability. For example, Abel & Blaikie (1989, p114) interpreted resilience as the ability to recover from disturbance, and to be a property of unstable systems. Of semi-arid rangeland, they concluded (p120): 'because it is unstable, rangeland is also intrinsically 'resilient' compared to more 'stable' ecosystems. Degradation occurs when rangeland is perturbed beyond its ability to recover. Resilience varies with land type'. Faced with this confusion over definitions, one is inclined to redirect Caughley's (1979) famous question about carrying capacity and ask 'what is this thing called resilience?'. In its loose definition, expressing the ecologist's intuitions about semi-arid rangeland, resilience seems to come down to the greater susceptibility of herbivores to starvation than of plants to herbivory or soil to erosion. This differential mortality of the components of the system in response to a stress, together with the relatively slow rate of recovery of the herbivore population, has the effect of allowing some sort of plant community to regenerate or establish from seed banks at low herbivore pressure. Systems with plants less tolerant of severe herbivory and so having a narrower differential between animal and plant mortality would be expected to show more comprehensive collapses during drought.

Conclusions. The implications of all this are as follows. Theoretical approaches reveal the range of possible ecosystem behaviour, but field ecologists perhaps take too lightly the difficulties of translating these insights to the real world. Theoretically-derived concepts of stability, equilibrium and resilience may not be useful and may indeed be quite misleading in the search for understanding real systems, especially those under management. The conditions for stability of simple models are highly sensitive to model assumptions, and it is arguable that the multiple stable states predictable by them have little bearing on the significant qualitative changes that characterise shifts between vegetation communities in many rangeland ecosystems. Instead of using such concepts as metaphors for system behaviour, endeavour should focus on a mechanistic understanding of the underlying nature of grazing systems, in all their specificity. For example, O'Connor (1991) adopted Connell & Sousa's (1983) proposal 'to study the broader class of mechanisms which ensure population persistence regardless of whether equilibria can be identified' to elucidate the conditions for local extinction in perennial grassland. Stafford Smith's (1996) call for a functional classification of rangeland types is an example of how progress is likely to be made, by seeking the particular from which to generalise. Likewise, the point of elucidating the concept of resilience is to enlighten the investigation of the biological basis or nature of resilience in grazing systems. In other words, what properties of the system determine how fast it recovers from perturbation? As our mechanistic understanding of the systems components and processes improves, there is obviously increased scope for learning from mechanistic modelling of systems responses to environmental and management inputs. It is this approach, allied to field experimentation, which is likely to produce the fastest progress in the future.

Lastly, spatial scale makes all the difference to the perception of ecological concepts, and its importance is often overlooked. There is no spatial uniformity in stability, persistence or resistance. This is important because degradation is a process which starts locally and expands. Stafford Smith (1995) points out that state-and transition models are deficient in assuming a landscape with a uniform management impact, and blind to the greater susceptibility of spatially-diverse landscapes to localised perturbations, which may become foci of degradation. The challenge here is to relate the spatial scale of diversity to the appropriate scale of management.

4.3   Synopsis and implications for modelling

In semi-arid grazing systems, there seldom exists an equilibrium between animal numbers and vegetation biomass, because of the high intra- and inter-annual variability of rainfall. Arguments about whether this constitutes a qualitatively different dynamical regime can be by-passed by mechanistic modelling.

Vegetation changes in rangeland systems are evidently subject to stochastic events, such as fire or rainfall, or the concatenation of them. This poses severe challenges to modelling, and a frame-based or probabilistic approach would be rquired to accomodate the state-and-transition approach to rangeland dynamics.

A MODEL OF SEMI-ARID GRAZING SYSTEMS

5.1 Objectives

(a)   The primary objective of modelling semi-arid grazing systems was to find out how far the existing knowledge of the underlying processes could account for and replicate the dynamics of the system. Thus, subsidiary objectives include the prediction of animal performance in response to variation in rainfall and to stocking rate, and the effects of animal type and vegetation conditions on system performance.

(b)   Modelling will to be used to assess the components and processes to which the system is most sensitive, and to identify inadequacies in current knowledge which limit our understanding and ability to predict system performance. An important objective, therefore, is to identify future research needs.

(c)   The model will be used to explore management policies and interventions which would repay further study as techniques for increasing economic output and coping with climatic variability.

5.2 Model description

The model is based closely on the information reviewed (Illius, Derry & Gordon 1995). Its main features are described briefly here. The model runs on a daily iteration interval, and calculates, from daily rainfall data, vegetation growth and its allocation to plant parts, the selection and intake of these by animals, the animals' consequent energy and protein balances, body growth, reproduction and mortality. It therefore simulates animal population dynamics by coupling them to vegetation biomass dynamics, allowing the underlying mechanisms to dictate the performance of the system over the chosen time scale.

Most simulations were run for 20 years, after an initial running-in period of 5 years (to minimise the effects of the chosen initial values) using mean daily rainfall for the particular site. 20-year runs of daily rainfall from 4 sites in Botswana and 5 sites in Zimbabwe can be chosen, and replicates of these can be run by randomising the order in which each year's data are taken. Runs longer than 20 years can be achieved by repetition of the rainfall data set, or by using output from the Zucchini rainfall generator.

The main components of the model were initially programmed in BASIC, which is excellent for rapid prototyping, and subsequently incorporated into a comprehensive model programmed in C++. This is an object-oriented language which allows definition of data-types (classes) representing groups, such as animal types, which share certain properties. The result is considerable power and flexibility in specifying the number of plant and animal species to be included in the simulation, provided sufficient is known about each to distinguish them from a generic type. The model results described (below) were based on single herbaceous and woody vegetation types, and on cattle and goats as representative animal types. Given sufficient data, an almost infinite number of other vegetation and animal components, such as annual grasses, herbaceous dicots, sheep, impala and kudu could be included without further programming.

Vegetation.   The vegetation component of the model is based on that of Dye (1983), who modelled grass growth in a semi-arid savanna in SE Zimbabwe. His model was applied to growth in two vegetation components: perennial grasses and woody browse. The phenology and allometric relations between the plant parts of these components (Poupon 1976, Dye and

Walker 1987, Rutherford 1984) was used to predict the daily growth of green leaf, stem and seed (grasses) and green leaf, twig, wood and fruit (trees). Trees were assumed to have the same rain-use efficiency as grasses, in the absence of clear evidence to the contrary. Literature estimates of tissue senescence, decomposition and invertebrate herbivory were included in the prediction of tissue flow from net photosynthesis through to loss from the system. The state variables were, for grasses: carbohydrate stores, green leaf, dead leaf, green stem plus seed, dead stem, fallen seed; and for trees: carbohydrate stores, green leaf, fallen leaf, current season's twig, wood, fruit, fallen fruit.

Animals.   The animal component is based on previous models described by Illius & Gordon (1991), Illius & Jessop (1995) and Illius & Clutton-Brock (in prep). Each species is specified by the mature size of each sex, and allometric functions of body mass are used to calculate such physiological and morphological properties as the maximum rate of protein deposition, maximum fat mass, duration of pregnancy and lactation, and incisor breadth. The number of age classes can be specified, and was chosen to be four for cattle (*ie*, >1 y.o, yearlings, 2 y.o, adults) and two for goats. Suckling animals are classed as neonates until the end of lactation, when they are added to the juvenile (>1 year old) class. For each sex, age class and species, the model calculates the daily selection of the diet, energy and nitrogen intake, and their metabolic consequences for two state variables: fat-free mass and fat mass. The other animal state variables are the numbers in each sex and age class for each species.

Diet selection and intake are calculated on the assumption that, each day, each animal species will choose either grass or browse according to which allows maximum daily energy intake, net of the energy costs of foraging. Daily intake for each vegetation component (grass: green and dead leaf and stem; browse: green leaf, shoot, fallen leaf, fallen fruit) is calculated according to the equations of Spalinger & Hobbs (1992), which use the abundance and potential bite size of these components. Selection between grass components is calculated from incisor breadth (based on Illius & Gordon 1987) and a limit, imposed by mouth size, on the ability to select the highest-digestibility component while rejecting those of lower digestibility. Daily potential intake, when abundance is not limiting, is calculated from equations summarising the digesta kinetics model of Illius & Gordon (1991, 1992) which shows good agreement between predicted intake of tropical grasses and that observed in a range of ruminant species. Actual intake is the lesser of that calculated subject to the constraints of food abundance, digestive capacity or ability to deposit protein and fat in animals of each age, sex and reproductive status.

Reproduction in females is determined by animal state (conception can take place if animals have >50% of the maximum fat mass for mature females of the species; pregnancy costs and lactation yield are calculated from body condition and nutrient intake). Mortality is deemed to occur when fat mass reaches zero. Mean body fat in each age class, sex and reproductive status is obtained daily from the calculated energy balance, and is assumed to be normally distributed. Mortality occurs in the proportion of animals in the tail of this distribution that projects below zero. Note that reproduction and mortality are *state-dependent* (their occurrence is dependent on fat-free mass and fat mass, and not according to a prescribed rate). Birth season is thus a consequence of body condition, although the model allows mating seasons to be defined.

To make comparisons between different animal species, it was assumed that animals are equivalent when compared on the basis of the metabolic live weight (LW) of the mature animal, with immature animals rated in proportion to their degree of maturity. We therefore defined animals in terms of the Livestock Equivalent (LE), where 1 LE is the (live weight)$^{0.75}$

of a mature bull of 450 kg. Given the range of ages and weights in the average herd, there are about 1.5 'average' cattle per LE and about 7.6 'average' goats.

Management. The model can be run without animal sales, in which case the ecological carrying capacity of the system is expressed (as the size of the animal population maintained by intake-dependent birth and mortality), or with a range of animal sales policies. These include a constant percentage offtake of animals on a chosen date each year, annual sales designed to limit stocking rate to a chosen quantity, pre-emptive sales triggered by insufficient rainfall by a chosen date, and a variable stocking-rate regime determined from the current season's rainfall..

5.3   Model performance

To illustrate the behaviour of the model, the results of a simulation of 40 years are shown in Fig 8. The simulation used a 20-year run of rainfall data from Bulawayo, Zimbabwe, repeated once, and continuous stocking with 0.1 cattle of 450 kg per ha (*ie* 0.1 LE/ha). The pattern of grass and tree growth can be seen to follow annual rainfall (Fig 8a). The balance between trees and grass is determined by competition for soil water in the model, and this depends on the mass of green leaf, and hence transpiration. Trees come to predominate over herbaceous biomass within 10 - 15 years, leading to bush encroachment (Fig 8b, c), due largely to earlier leaf emergence in trees and their greater carbohydrate stores, together with the reduced competition for water from grasses which are subject to reduced leaf mass from grazing. The diet of the cattle, initially predicted to be solely grass, shows increasing amounts of browse as the grass biomass declines, and there is a commensurate reduction in the daily energy intake, expressed as multiples of the daily energy requirement (Fig 8d).

These patterns are consistent with field experience (WS Trollope, TG O'Connor, pers. comm) and show the model to be capable of replicating the main features of semi-arid system dynamics. Some of the important components are examined in greater detail, below.

Rainfall.   The effect of mean annual rainfall on predicted ecological carrying capacity (defined by Caughley 1979 as the equilibrium animal density in the absence of offtake) is shown in Fig 9. The 20-year mean carrying capacities of 8 sites in Botswana and Zimbabwe, along a SW-NE transect from 300 to 870 mm mean annual rainfall were predicted by allowing herbivore numbers to be determined by the supply of vegetation (*via* food intake, birth and mortality), without animal sales. Two conditions were simulated, with low (100 kg/ha) and intermediate (2000 kg/ha) starting values for the biomass of trees, with the result that carrying capacity is restricted by tree encroachment (see below, *Bush encroachment*). Predicted carrying capacity increases with rainfall, in broad agreement with the carrying capacities observed by Fritz & Duncan (1994). In particular, it is reassuring that the predicted and observed carrying capacities are of the same order of magnitude. Note that the only parts of the model adjusted to match known output concerned the vegetation: grass yield was adjusted in relation to rainfall to match that observed by Dye & Walker (1987) at Bulawayo. The prediction of animal intake, growth, birth and mortality was not adjusted to conform to any output but were independently derived, being based on the principles outlined above.

To separate the effect of variability in rainfall from the effect of mean annual rainfall on system performance, simulations were carried out which varied the annual rainfall while holding the long-term mean approximately constant. The 20-year mean daily rainfall at Bulawayo was determined, and used as the baseline data set. Annual variation was then generated by multiplying each day's rainfall by a random number with mean 1 and with the

chosen coefficient of variation (cv). The same random number was used throughout one year, so increasing or decreasing the whole mean rainfall pattern. Carrying capacity was determined as before, and the results are shown in Fig 10. The steep decline in carrying capacity - by about half when comparing an annual rainfall cv of 33% with no variation - is primarily due to the frequency and severity of livestock population crashes during drought. Frequent droughts mean that animal populations spend little time at the densities which the mean annual rainfall would support if annual variation were absent, spending most of the time building up between crashes. Note that the decline in carrying capacity with increasing rainfall variability is continuous, and does not exhibit a discontinuity at about 33% cv, which some authors have held to be the threshold beyond which rainfall variability dominates systems' dynamics (see Ellis & Swift 1988, Ellis 1994).

Diet selection and animal type   To compare diet selection in cattle and goats, and its effect on grass/tree dynamics, simulations with the same conditions as in Fig 8 were run for 20 years, and the mean proportion of grass in the vegetation (peak biomass in March) and in the mean diet selected were recorded for the last five years of each run. Stocking rate was varied between runs.

The dietary differences between cattle and goats, and the effects on the vegetation, were most marked at high stocking rates, with goats suppressing tree growth by more heavy browsing (Fig 11a, b). Greater selection of grass by cattle allowed trees to dominate the vegetation. This pattern closely mirrors the observed effects of the two species in savanna systems, giving rise to the recommended use of goats to control bush encroachment (du Toit 1972, Sweet & Mphinyane 1986). Goat diets in Zimbabwe have been observed to contain 30-80% grass, depending on browse availability (Sibanda 1986; Nyamangara & Ndlovu 1990)

It is important to note that these animal differences were not due to programmed assumptions about greater browsing by goats, but to differences in body size between two animal types both expressing the same foraging strategy of maximising daily energy gains net of maintenance costs. The dietary differences are accounted for in the model by the fact that the nutritious growing tips and fallen fruits of browse are scarce, small in size, and take longer to harvest, giving lower rates of energy intake to larger animals than they can obtain by grazing, confirming the predictions of Illius & Gordon (1987).

Bush encroachment   One particularly noticeable feature of the way the model predicts bush encroachment is its dependence on the starting values for tree biomass. The general pattern, which accords well with field experience, is that once a critical tree biomass is reached, bush encroachment is likely to take off. This happens because trees become more able to compete with grasses at higher biomass, and because some of its leaves are held above the browsing range of animals. Fig 12 shows the dependence of browse biomass after a 20-year simulation on the initial wood biomass, with or without goats. At low initial biomass (as would be the case after a fire), competition from grass is sufficient to suppress tree growth, especially with goats present, but if trees start the simulation at >400 kg/ha, encroachment ensues. The sharpness of the threshold between these two outcomes is probably exaggerated by the model, but the phenomenon is real enough.

The main reason why bush encroachment is deleterious for system performance appears to be because browse offers animals lower rates of nutrient intake than grass. More knowledge of browse nutritional quality and intake rate is needed to be confident of this. In subsequent simulations, we avoided the problem of sensitivity to the pattern of bush encroachment by using a low initial value for tree biomass.
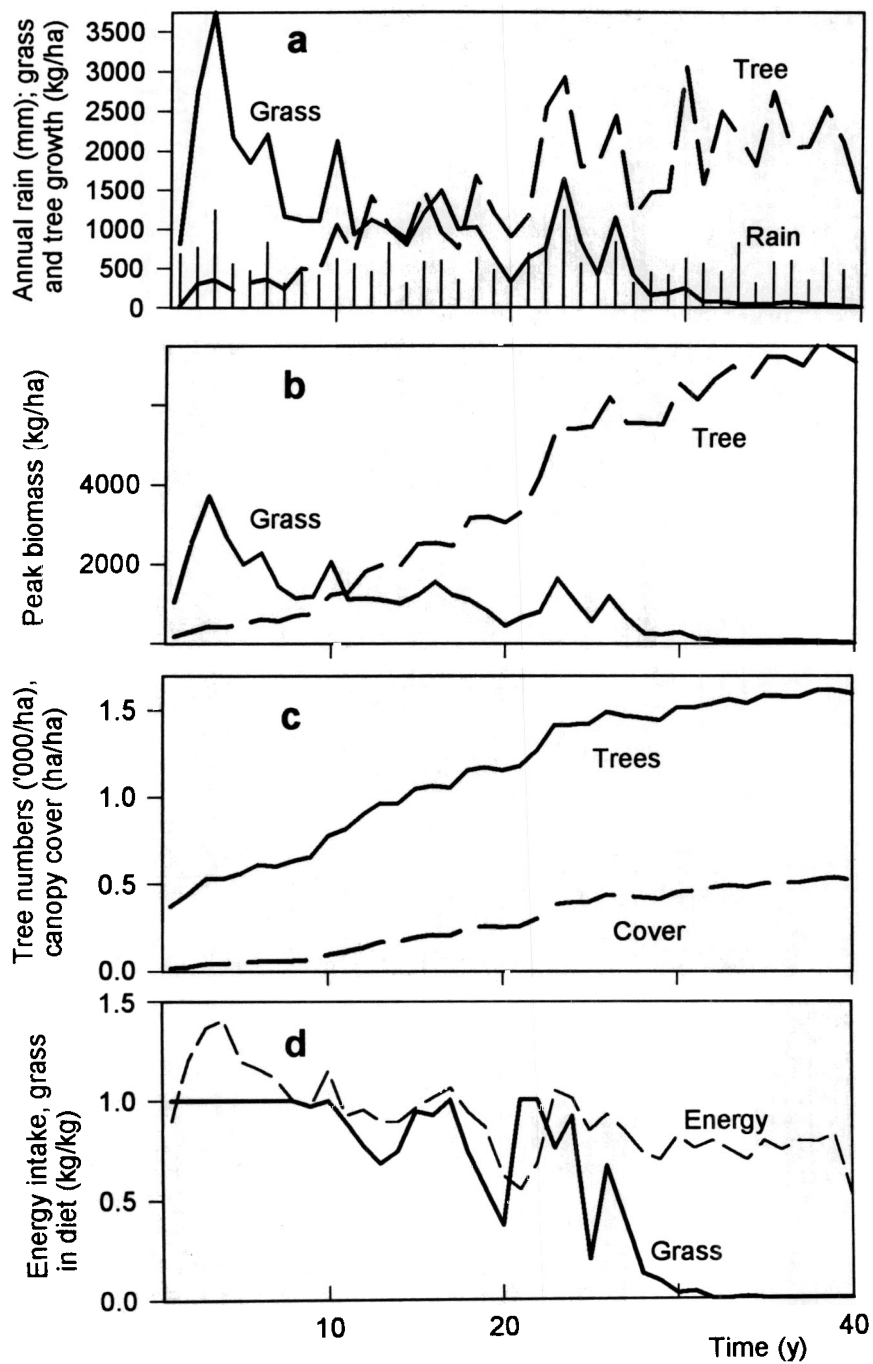
Fig 8. Results of a 40-year simulation of a semi-arid grazing system, continuously stocked with 0.1 Livestock Equivalent (450 kg cattle) per ha. (a) Annual rainfall, annual grass and tree growth; (b) herbaceous and tree biomass; (c) the increase in tree numbers and canopy cover; (d) the energy intake, expressed as multiples of the daily energy requirement, and diet composition expressed as the proportion of grass.
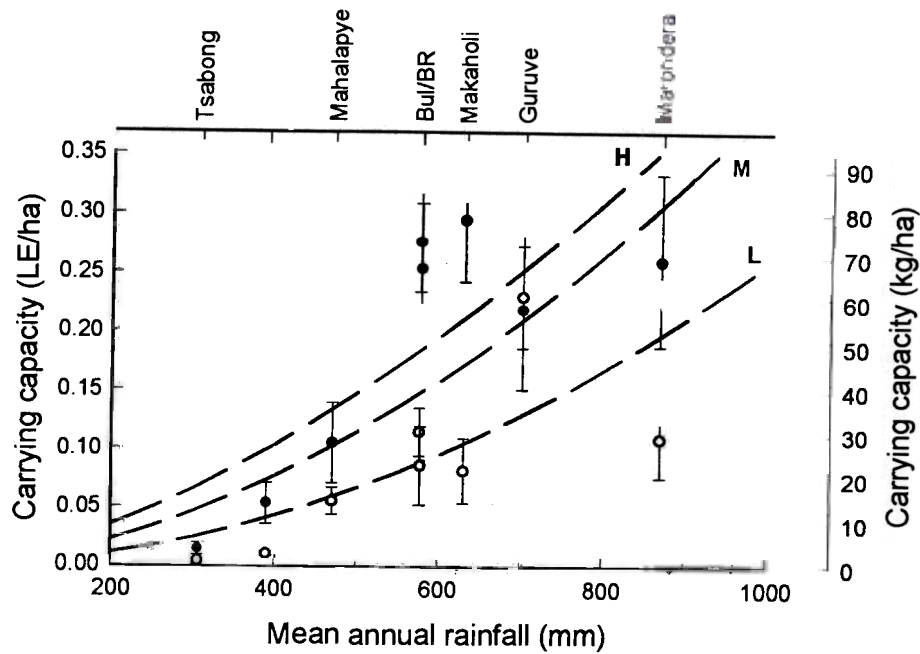
Fig 9. Predicted 20-year mean ecological carrying capacity (± sem) in relation to the rainfall at 7 locations from SW Botswana to NE Zimbabwe (Tsabong, Palapye, Mahalapye, Bulawayo and Buffalo Range, Makaholi Guruve, Marondera). Closed symbols: 100 kg/ha starting tree biomass; Open symbols: 2000 kg/ha starting tree biomass. For comparison, the curves (right axis) show the carrying capacity observed by Fritz & Duncan (1994) in relation to rainfall at sites of high, medium or low soil nutrient availability (H, M, L).
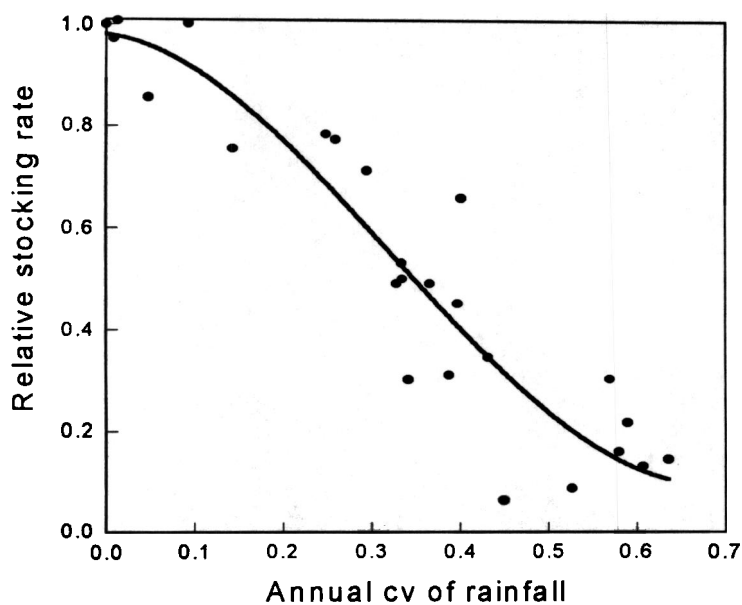

Fig 10. Decline in stocking rate with increasing variability in mean annual rainfall, with the latter held approximately constant.
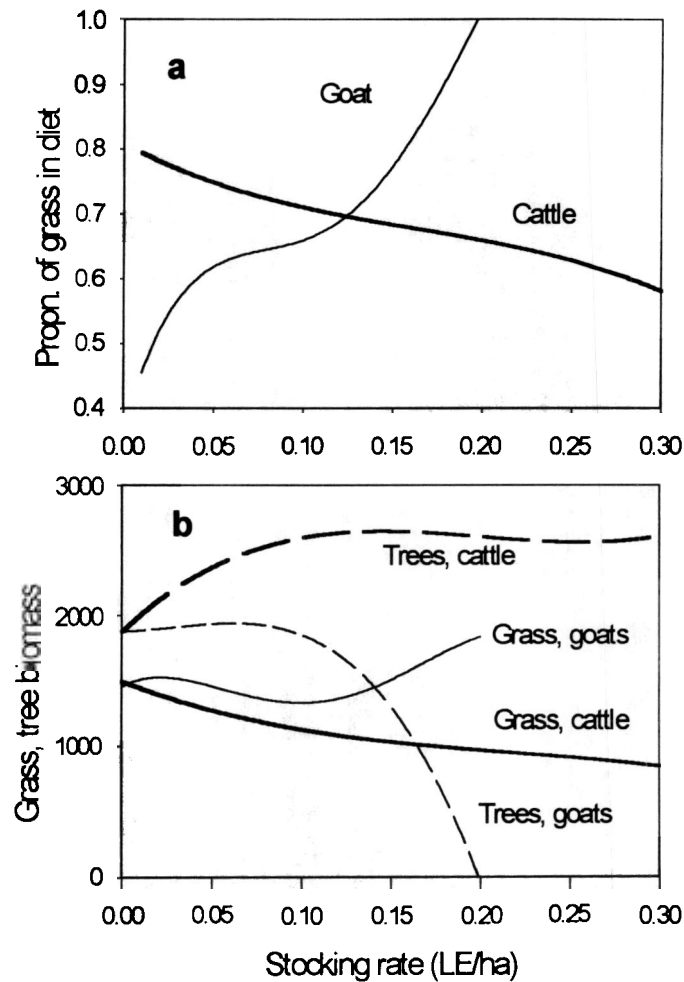
Fig 11. Comparison of cattle and goats utilising mixed grass/tree vegetation and the effects of stocking rate on the proportion of grass (a) in the predicted diet and (b) in the vegetation.

Cattle have a high proportion of grass in the diet, suppressing grass growth and allowing trees to dominate the vegetation. Goats eat more browse, at stocking rates up to about 0.1 LE/ha, and severely suppress browse growth at higher stocking rates.
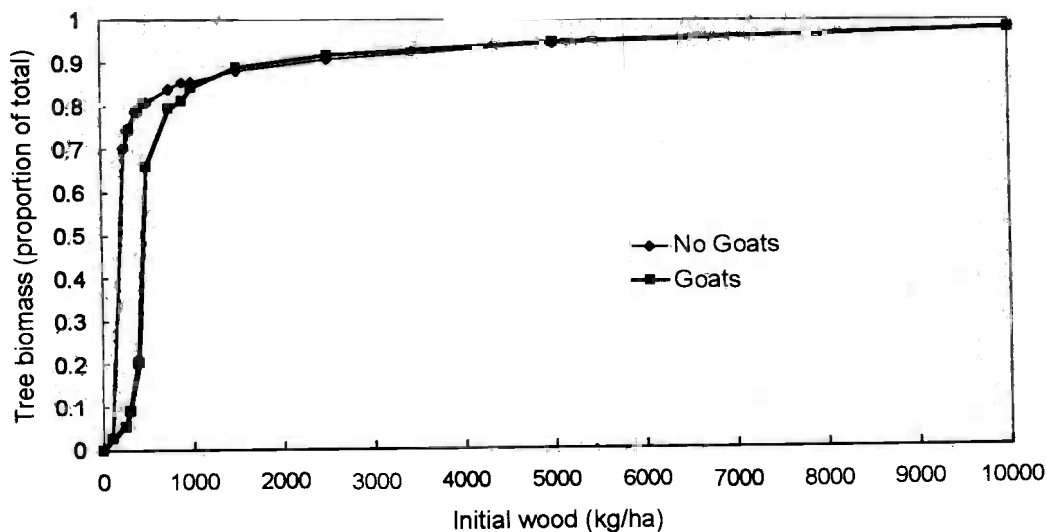

Fig 12. The domination of the vegetation by trees (20-year means) depends on initial tree biomass. At ecological carrying capacity, goats have a limited effect on this.

5.4   System sensitivity

Here, we wish to identify the components and processes to which the system is most sensitive (ie for which a given change in input produces a relatively greater change in output). Sensitivities can be recognised, broadly, as those which are fundamental properties of the natural system, and those which are more likely to be attributes or artefacts of the model itself. It is obviously important to recognise the former, in order to understand the constraints to development, while overcoming deficiencies in the model will improve the ability to use it for prediction, planning and investigating management strategies.

Climatic variability   The effects of the mean and variance in annual rainfall have been established (Figs 9 and 10). Model predictions of carrying capacity increase roughly as the cube of rainfall, in comparison with observed carrying capacities varying with approximately the square of rainfall (Fig 9; Fritz & Duncan 1994). A doubling in mean annual rainfall from 300 to 600 mm would increase predicted carrying capacity tenfold, from 0.012 to 0.12 (model) or, according to data of Fritz & Duncan (1994) fourfold, from 0.03 to 0.12. Natural systems are clearly sensitive to mean annual rainfall. The model overestimates sensitivity, mainly due to under-prediction of carrying capacity at low rainfall, and sensitivity to bush encroachment in the absence of fire, which would tend to stabilise the vegetation of natural systems. Better understanding of vegetation dynamics is required, particularly in relation to the rainfall-growth responses of diverse vegetation types (eg forbs, ephemerals) which are important in low-rainfall regimes.

The importance of annual rainfall variability *per se* is clear from Fig 10. To put it in perspective, an increase in the cv from 0.2 to 0.4 (which covers much of the natural range in semi-arid regions) and without changing the long-term mean annual rainfall, would reduce mean carrying capacity by a half. Measures to buffer climatic variability, particularly those designed to limit animal mortality in droughts, could certainly increase system output.

Vegetation dynamics   Bush encroachment has been considered above, and is clearly an important process, because it reduces grass yield and predicted diet quality (Fig 8). The prediction that it takes about 20 years for encroachment to become a problem coincides closely with field experience (WS Trollope, *pers com.*), and once bush gets established it is extremely difficult to suppress by herbivory alone. That said, the model is probably unduly sensitive to initial values for bush, and to the absence of fire and spatial variation in soil hydrology, both of which would tend to stabilise the system. Additionally, the modelling of growth allocation in herbaceous and tree components showed considerable sensitivity to the parameter values controlling phenology and the use and replenishment of stores. Further understanding of browse growth and allocation is needed to improve prediction of tree-grass balance, which is a fundamental aspect of savanna systems.

Vegetation utilisation and animal performance   Animal   responses   to vegetation, *via* foraging behaviour, diet selection and intake, are critical components of grazing systems. Model predictions of diet selection, intake and performance are realistic, and the model is really only sensitive to the digestibility of the vegetation components available. Diet quality was predicted, consistently, to be the first limiting constraint on cattle nutrient intakes at all but high levels of tree encroachment, when the time taken to forage on small browse items began to be important. For goats, digestive constraints remained the limitation throughout. Animal production is evidently limited by the quantity of high-quality forage. Knowledge of the nutritive value of savanna vegetation components is surprisingly poor, and better information is required. Better understanding of the diet selection of free-ranging

animals is needed to assess the nutritional constraints on performance and to derive suitable interventions.

5.5   Investigation of management strategies

Four aspects of management were investigated: stocking rate, choice of species mix, sales policy and flexible stocking policies aimed at minimising drought effects. The investigation of optimal stocking rate and of species choice was carried out together, as was the investigation of the policy on the composition and timing of sales in relation to drought.

Stocking policy   The model allows the stocking rate of each animal species to be set, by selling surplus animals on a given date. The sales date was chosen to be in mid-March, at the end of the rainy season. The initial sales policy applied was that only animals older than one year could be sold, excluding lactating females, and selling males first followed by females until stock numbers were sufficiently reduced to achieve the chosen stocking rate. The response of animal sales (measured by the mean annual LW sold per LE) to stocking rate was determined for cattle and goats stocked on the own or in various ratios. Simulations were run for 20 years, after a 5-year run-in, using the Bulawayo rainfall data, and the 20-year means of model performance were recorded for analysis.

The results were analysed according to Connolly & Nolan (1976), by determining animal performance as a function of the stocking rates of its own and of its companion species, if present. Fig 13 shows fitted curves for the predicted performance of each species in the presence of varying stocking densities of the alternate species.
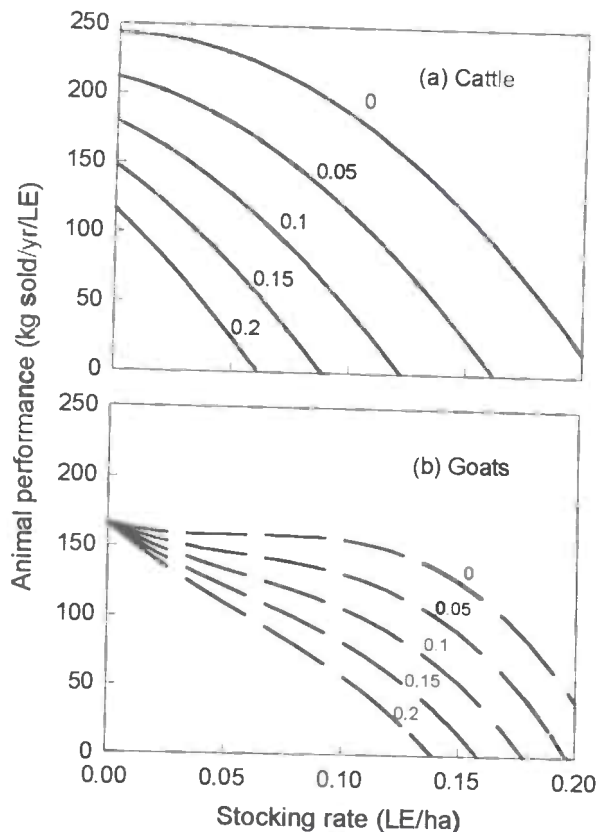

Fig 13. Response of animal performance to stocking rate in (a) cattle and (b) goats, when stocked with animals of the alternate species at a range of stocking rates (separate curves, labelled with stocking rates, in LE/ha, of the alternate species).

Assuming 1.5 cattle and 7.6 goats per LE, the maximum performance predicted is, respectively, about 170 and 20 kg of LW sold per animal present in the system.

The results show that animal performance declines with increasing stocking rate, in the classical manner (Jones & Sandland 1974). The difference in maximum performance of the species at low stocking rate is largely an artefact of the differences in the age structure of the species and the goats' higher reproductive rate: a greater proportion of the population is less than the saleable age of one year. Comparison of cattle and goats shows that goats can be maintained at higher stocking rates than cattle before performance is reduced. The effect of goat stocking rate on cattle performance is greater than *vice versa* (the lines are further apart and steeper in Fig 13a than b). This reflects the superiority of goats at utilising scarce resources, as discussed above (*Diet selection and animal type*). Further evidence of this is shown in Table 6, where the predicted ecological carrying capacities (*ie* without animal sales) of cattle and goats are compared when the species are stocked either alone or together. Alone, cattle achieve a 20-year mean of 0.15 LE/ha (cf 0.27 by goats) but when goats are introduced, they displace the cattle, whose stocking rate falls to only 0.015 LE/ha. These are the predicted population consequences of mixing animals of different body size but similar feeding strategies. If goats were to use less grass, less competition would result, and higher cattle numbers could be maintained for a given goat stocking rate.

The combined animals sales per ha are shown in Fig 14 in relation to the stocking rate of each species, obtained by multiplying sales/LE by stocking rate (LE/ha). Maximum output was 19.8 kg LW/ha, compared with observed values for steers grazed alone of 16 kg/ha in SE Botswana (APRU, cited by Abel & Blaikie 1989) and 25 kg/ha in SE Zimbabwe (Carew 1976). There was no statistically significant optimal combination of species, in the sense of a mix which produced greater output than could be obtained from cattle alone (19.4 ± 0.67 kg LW/ha at 0.12 LE/ha), goats alone (19.0 ± 0.64 kg LW/ha at 0.14 LE/ha), or any combination of cattle or goats. The present evidence, limited as it may be by the simple vegetation structure in the model, does not suggest much scope for increasing saleable output by manipulating stocking ratios.

We have not, so far, attempted to devise more sophisticated measures of system performance, which would combine the value of sales with other livestock outputs such as traction, transport, milk and manure. Insofar as the combination of livestock keepers' goals appear to be met by maximising the numbers of animals kept, stocking rate itself may be a useful measure of performance, since stocking rate is almost directly equivalent to total livestock holdings.

Table 6. Predicted ecological carrying capacity (*ie*, without sales) of cattle and goats stocked alone or together.

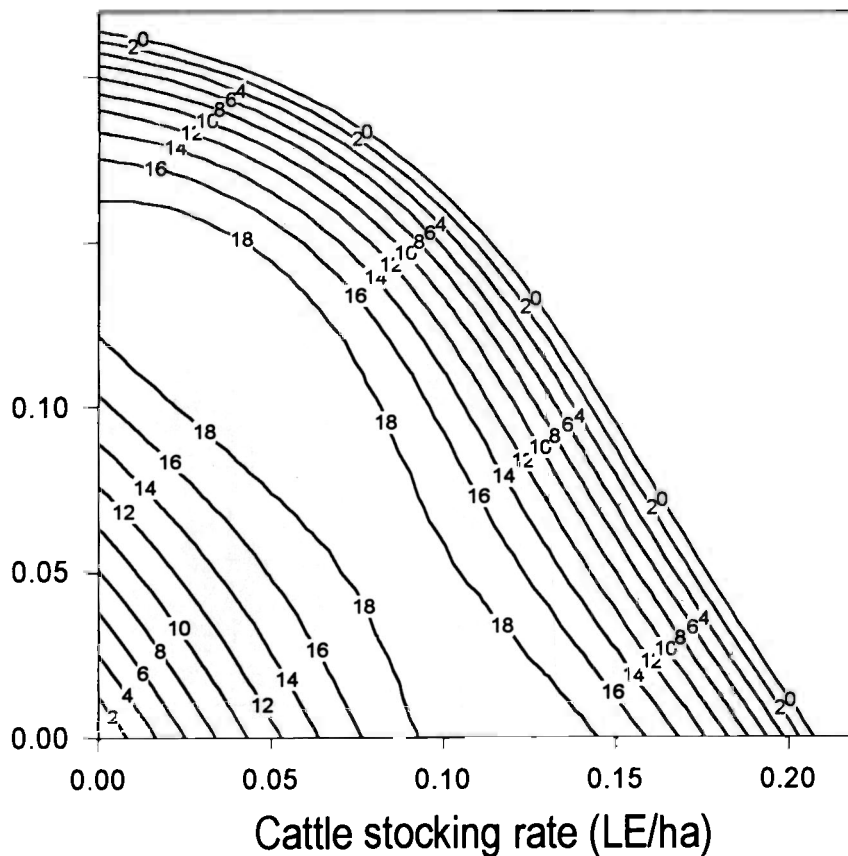| | Predicted carrying capacity, LE/ha | | |
	Cattle (sem)	Goats (sem)	Combined
Cattle only	0.15 (0.010)	0	0.15
Goats only	0	0.27 (0.043)	0.27
Mixed stocking	0.015 (0.0016)	0.16 (0.019)	0.175

Goat stocking rate (LE/ha)

Fig 14. Annual sales of cattle and goats combined (kg LW/ha) in relation to the stocking rate of each species. Iso-product contours connect combinations of species' stocking rates which give equal output (kg LW/ha).

Sales policy and flexible stocking   Ways of 'tracking' environmental fluctuations could be of value in limiting drought-induced mortality. While investigating methods of adapting stocking rate to the current season's rainfall, we also varied the rules governing livestock sales, chiefly by allowing weaned animals under one year of age to be sold and not selling any females of breeding age. We found that the composition of the allowable sales had a significant bearing on whether reduced stocking rate targets could be met and on how rapidly the population could recover. These effects, together with those of tracking policies, are described below, and summarised in Table 7.

The first decision-rule we implemented in the model was to sell a chosen percentage of the animals ('pre-emptive sales') if the rainfall on a chosen date was below some threshold proportion of the long-term average rainfall on that date. Regular sales ('stock sales') still took place to re-set the target stocking rate in mid-March, as before. Simulations were all carried out with goats at a target 0.15 LE/ha, with the Bulawayo rainfall data. The effects on the 20-year mean annual sales were very similar for the different decision dates and rainfall thresholds investigated, and examples are shown in Fig 8 of the effects of varying the percentage of stock sold to pre-empt mortality following poor rains. Whether these pre-emptive sales occurred at

the beginning of December or the end of February, the main effect was to reduce the later stock sales and not to achieve a significant increase in output. As the percentage of the current stock sold pre-emptively was increased to 80%, mortality was slightly reduced, with the main consequence being that the low resulting stocking rate reduced overall output (Fig 15a). The effect of varying the sales policy to exclude the sale of female breeding-stock was to increase output (Fig 15b), but pre-emptive sales still served no significant purpose.
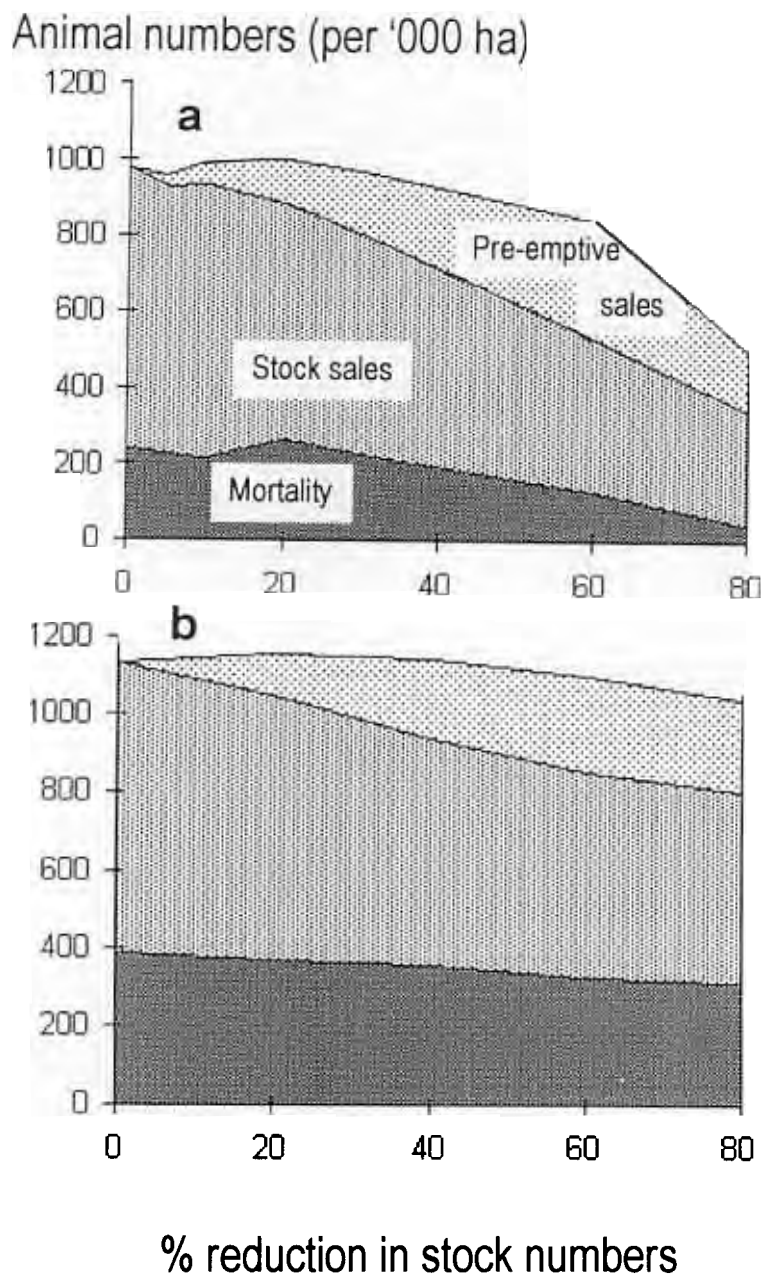
Animal numbers (per '000 ha)

Fig 15. The effect of varying the percentage of the current animal population sold pre-emptively on the mean numbers dying or sold at mid-March stock sales. Pre-emptive sales were triggered at the end of February in years when rainfall was <70% of the long term mean

(a) Allowing sales of female breeding stock reduces mortality but leads to severe reductions in stocking rate when pre-emptive sales >60%, limiting mean output.

(b) Without sales of female breeding stock, stocking rate reductions cannot be achieved, mortality is not reduced, but output is maintained.

% reduction in stock numbers

We then turned to a tracking policy which adapted the target stocking rate, set each March, as a function of the current season's rainfall, using a relationship derived from the ecological carrying capacities predicted for a range of mean annual rainfall (Fig 9, closed symbols). To prevent stocking rates becoming so high that a crash was bound to be severe, the rate was either capped to 0.3 LE/ha, or varied in accordance with previous as well as current

year's rainfall. Lastly, we investigated a policy designed to coincide with the period of mortality, by selling animals in proportion to the current mortality rate, with mid-March stock sales designed to return to a fixed stocking rate (0.15) or using the adaptive stocking rate, as above.

Table 7. Comparison of inflexible and flexible stocking policies.

Female sales policy*		POLICY							
		Fixed stocking (control)	Pre-emptive sales, based on rainfall by Dec	Pre-emptive sales, based on rainfall by Feb	Adaptive stocking, based on annual rainfall	Adaptive stocking, capped at 0.3 LE/ha	Adaptive stocking, variable cap	Fixed stocking with mortality tracking	Adaptive stocking with mortality tracking
	(a)	Mean stocking rate (LE/ha)							
+		0.14 #	0.159	0.147	0.15	0.138	0.086	0.154	0.169
		0.17 #	0.184	0.181	0.21	0.205	0.137	0.134	0.177
	(b)	Mean annual sales (kg LW/ha)							
+		19.4	20.5	19.8	22.2	20.6	15.0	18.5	20.5
		19.9	21.1	21.5	22.4	23.0	16.6	18.5	18.4
	(c)	Mean annual sales (kg LW/ha), compared at 0.18 LE/ha stocking rate							
+		22.5	22.6	23.1	23.1	24.8	24.3	21.1	25.0
		20.9	20.7	21.4	19.2	20.5	20.8	19.6	18.7
	(d)	Mortality (%)							
+		14.3	15.6	15.7	13.3	11.6	7.0	15.8	10.7
		21.9	25.3	24.9	28.1	27.5	22.2	22.9	24.1

* Sales of female breeding stock allowed (+) or not (-).
# Fixed stocking rate chosen to be comparable with mean stocking rates of the flexible stocking policies.

Table 7 summarises the results of the 50 combinations of sales and tracking policy investigated, compared with inflexible stocking policies. Stocking rate was the most important influence on output, followed by the sales policy on female breeding stock (both p<0.001). Differences between fixed, pre-emptive and tracking policies were also significant (p=0.003) with a significant interaction with female sales policy (p<0.001). Higher output was almost always associated with policies which maintained high average stocking rates, as was higher mortality.

By using some of the tracking policies and by retaining all breeding females, both of which increased mean stocking rate, increases in output of 15 - 20% were obtained, compared with fixed stocking (Table 7b). Tracking policies designed to limit mortality and so increase output were less effective than expected, for three main reasons. First, for large stock reductions to be achieved inevitably requires that breeding females be sold, which in turn reduces future productive potential and offsets the benefits of reduced mortality. Second, if breeding females are never sold, or sales coincide with mortality (as in the 'mortality tracking' policy) then the average size of the animals sold is reduced, leading to lower output. Third,

while tracking the current season's rainfall was effective in reducing mortality in the following dry season, it could not avoid the frequently larger mortality occurring as a result of late or low rain in the following season. In agreement with this, Ellis & Swift (1988) noted that two-year and not one-year droughts were the major source of mortality in the semi-arid Turkana system, E. Africa. The mortality tracking policies were designed to overcome this, but they generally failed by having to sell animals at a light weight, yet in large numbers.

The failure of tracking policies to improve on the underlying balance between reduced stocking and maintaining productive potential is reflected in the analysis of sales compared at constant stocking rate (Table 7c; LSD~ 1.6) at which the best tracking policies were only about 10% better than fixed stocking. Nevertheless, tracking policies modestly fulfil the twin goals of obtaining increased output while allowing greater numbers of animals to be kept (ie, maintaining high stocking rates) better than do fixed stocking policies. It would appear that, in the absence of an ability to restock after droughts, the traditional policy of maintaining the maximum size of breeding herd is well founded, provided that the total weight of animal sales is not the highest priority.

5.6   Conclusions

Recalling that the object of this exercise has been to establish the feasibility of modelling semi-arid grazing systems, to determine limitations in current knowledge and understanding, and to explore what lessons about management might be gained, the following conclusions can be drawn.

Modelling

The model successfully predicts many of the phenomena of semi-arid grazing systems: animal diets and performance levels, rainfall-stocking rate relations and bush encroachment are all reasonably close to those observed in reality. This is made possible by the existence of a substantial literature on savanna systems, as well as by a well-established modelling approach to describing the mechanisms of animal-plant interactions.

Models are intended to be simplifications of the real world, or they would not be tractable. Nevertheless, major omissions of the current exercise include the absence of an explicit treatment of soil nutrient status and other (eg hydrological) sources of spatial variation, and the absence of fire as a determinant of vegetation change.

The model offers a comprehensive basis on which to evaluate alternative management strategies, but further work needs to be done on the amalgamation of the many objectives of livestock keepers, as expressed in the chosen balance between economic output and the maintenance of high stocking rates.

2.   Future research needs

The literature on **browse production and utilisation** is weak, despite the importance of browse in heavily-utilised systems. Current estimates of browse diet quality suggest that it is usually more profitable for animals to select grass. Either browse quality is underestimated, or animal species for which browse is a major dietary constituent must actually depend on non-grass herbaceous components (ie forbs, as shown in kudu by Owen-Smith & Cooper 1989), for which few production and quality data are currently available.

The prediction that mixed stocking shows no benefit over using single animal species is not in strong disagreement with the current literature, even though it would be expected that diverse vegetation offers scope for complementary utilisation by a range of animal types. The

usefulness of our conclusions may be limited by the simple description of vegetation structure (single generic herbaceous and browse components) and by the assumption that animals forage on the basis of economic choices, rather than on some sub-optimal or instinctual basis. Because of the potential benefits of **matching vegetation resources with animal types**, these possible deficiencies need to be evaluated and rectified.

Further analysis of the **feasibility and effectiveness of adaptive management** policies is required, in the light of our findings that their benefits may be modest (see below).

3.   *Policy implications*

The flexible stocking strategies we designed to tackle climatic variation have so far shown only limited scope for improved output over fixed stocking. The main reasons for this are that major losses of stock are associated less with one-year than with two-year droughts, which are difficult to track, and that de-stocking can be really effective only if the productive potential of the herd can be re-established more rapidly than is possible from depleted herd resources.

If re-introductions of breeding stock are not possible, their numbers will lag behind climatic fluctuations, producing a succession of population crashes and missed opportunities. Inadequate infrastructure (*eg* absence of national drylot schemes to store animals over droughts) is likely to be a constraint on re-stocking. Indeed, there is some scepticism about the feasibility of de-stocking/re-stocking schemes (Sandford 1994). Schemes to distribute supplements to livestock *in situ* during droughts would break the regulating effect of drought on animal numbers, an effect, some argue, which limits the capacity of high stocking rates to cause degradation (Scoones 1994). Traditional policies of maintaining the maximum number of breeding stock, and of hoping that most of them will survive drought, may be as close as 'opportunistic' management can get to dealing with drought.

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