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MODELLING OF EXTENSIVE LIVESTOCK PRODUCTION SYSTEMS

PROCEEDINGS OF THE ILCA/ARO/CABO WORKSHOP
HELD AT ARO, BET DAGAN, ISRAEL
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Preface

This document comprises the proceedings of the workshop on Modelling of Extensive Livestock Production Systems, held at the Volcani Centre of the Agricultural Research Organization (ARO) in Bet Dagan, Israel, from 5 to 9 February 1985. The workshop was jointly organised by the ARO, the Centre for Agro-biological Research (CABO) and the International Livestock Centre for Africa (ILCA), and was attended by 18 scientists from Ethiopia, Israel, Kenya, The Netherlands and UK.

The workshop originated out of a joint programme established in 1981 between the three centres already mentioned and the Institut du Sahel (INSAH) in Bamako, Mali. The purpose of the programme was to coordinate activities in modelling of primary and secondary production which were already taking place at the centres. The workshop presented the progress achieved in modelling at the centres, and desirable lines of development were discussed.

The workshop focused on four main items: modelling of primary production, feed intake, secondary production and management/economics of livestock production systems. This document contains the written presentations made at the workshop, and the summaries of the discussions of each paper. The general discussion at the end of the workshop focused on two items: the use of mathematical models and feed intake, the latter being a main subject of discussion and of concern to all participants.

We wish to acknowledge the ARO staff who assisted in running the workshop and organised two excursions, which were highly appreciated by the workshop participants. We also wish to thank Tezetta Gebeyehu who typed the proceedings, and Yalem Berhan Kebede who prepared the figures.

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ABSTRACT

These proceedings comprise 13 papers on modelling of extensive livestock production. The presentations were made by scientists working in Ethiopia, Israel, Kenya, The Netherlands and the UK. Aspects discussed include primary production, factors affecting feed intake and its prediction, secondary production, and management and economics. Livestock considered include cattle, sheep, goats and buffalo, and production systems in Africa, southeast Asia and Israel are discussed.

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ILCA's policy towards modelling in the framework of livestock systems research

L.J. Lambourne

Introduction

ILCA was established in 1974 with a mandate to "undertake a programme of research, documentation and training to support national institutions seeking to improve the sustained output of livestock production systems in sub-Saharan Africa."

As an international centre ILCA interpreted its responsibility as covering problems of regional rather than national scales and, as its founders required, has adopted a livestock systems research approach. This is derived from the earlier methods of farming systems research, and implies that ILCA's research teams are multidisciplinary in composition and training, and try to study all interacting aspects of the livestock production systems being investigated. They try, in collaboration with national bodies, to propose new methods and innovations drawn from available research findings or, if necessary, they undertake original research to identify and adapt technology capable of increasing animal production. Those ideas which are effective in controlled experiments conducted by ILCA and national research workers are tested on-farm with local animals, crops, pastures or farming methods. When they are shown to work in local farms and herds, ILCA hopes that national extension or development services will take them over and put them into increasingly large-scale practice, keeping in close touch with ILCA so that research workers know of the success of the innovations in other areas and can make further refinements or modifications to the methods.

Depending on the structure and motivation of local agricultural and livestock services, ILCA may work more closely with universities, research institutes or extension and development organisations, the latter being

closely involved in the on-farm testing stages of the work, its large-scale adoption, and the monitoring and feedback of results.

Structure of ILCA's activities

ILCA now has seven major systems research programmes in five African countries. These are backed up by several specialist research groups and a range of support services - laboratory, library, computing, printing, cartography, training, liaison and general administrative services - at Addis Ababa headquarters. ILCA also has established several information and research networks: one on trypanotolerance involves ILCA, ILRAD and national veterinary or animal production laboratories in 10 countries of central and West Africa; ILCA's African Research Network on Agricultural Byproducts, ARNAB, brings together researchers on agricultural by-products and crop residues in workshops and training courses, publishes a regular newsletter, and seeks to spread new ideas and better methods in this very important field. We also have a forage network in Ethiopia and hope soon to extend this so as to bring together agronomists and research workers in forage and animal production. In conjunction with the Plant Genetic Resources Centre in Ethiopia, we publish a germplasm newsletter and are now setting up networks in small ruminant production, animal traction and livestock economic policy analysis. Details of new activities, and many articles of interest to scientists all over Africa are published regularly in the ILCA Newsletter, Bulletin, specialist Research Reports, and conference and workshop proceedings. Several hundred African scientists will come to ILCA during 1985 for conferences, workshops or training courses.

Zonal distribution of ILCA's research programmes

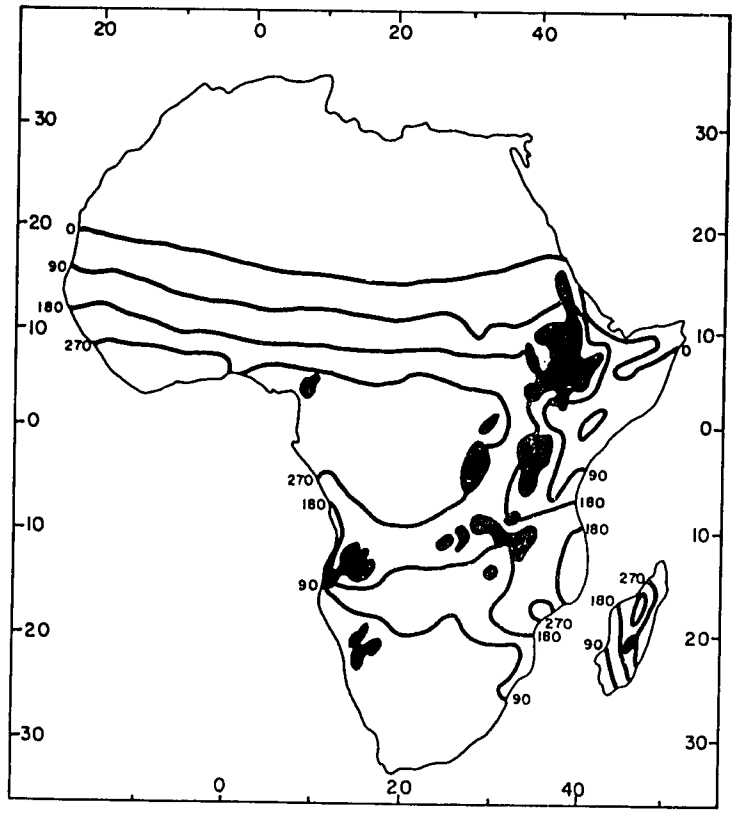
One of the early decisions concerned the structure of ILCA's research. It could have been organised by country, by product or commodity, by climatic zone, by geographic or economic subregion or in other ways. The experience of recent droughts may have decided the issue, but the decision to establish research teams by agroclimatic zones was soundly based.

The various agroclimatic zones are defined basically according to annual rainfall, but including also an appreciation of related climatic and soil features, so that the division into arid and semi-arid, subhumid, humid and highland zones is finally expressed in major differences in plant growth periods (Table 1, Figure 1). This is closely related to the possibility for cropping; at least 90 days of reliable soil moisture is needed for a grain crop, but it is a risky enterprise in many parts of the semi-arid zone because of large year-to-year variability. The growing period of 180-270 days in the subhumid zone gives reasonably assured yields for a wide variety of crops and forages. Livestock enterprises also can be more varied and productive; stock of greater genetic potential can be introduced into selected areas, where better nutrition and suitable health measures can be provided. The humid zone offers long plant growth periods, with the possibility of multiple cropping and high yields, but most of this zone is forested and harbours the tsetse fly, carrying the trypanosome blood parasite which makes this zone dangerous to cattle and, often, to man also. Other internal and external parasites, and a range of respiratory and other livestock diseases make this zone far less productive than it might be. The highlands are generally a much more benign environment - their altitude means that they tend to be subtropical to temperate, and have a rainfall generally more than 1000 mm.

Table 1. Zonal ecological classification.

Annual rainfall (mm)	Old description	Zone	No. of growing days/year	Moisture index
0	Saharan			-60
200		Arid	0-90	
400	Sahelian			
600				-40
800		Semi-arid	90-180	
1000	Soudanian			
1200				-20
1400	Guinean	Subhumid	180-270	
1600				
1800				
≥2000	Forest	Humid	>270	

Figure 1. Ecological zones of tropical Africa



Location of field programmes

Table 2 indicates several important points which explain the location of ILCA's teams.

Table 2. Livestock and human populations by zone in sub-Saharan Africa.

Zone	Percentage of					No. of humans (million AME[a])
	Area	Cattle	Sheep	Goats	All ruminants	
Arid	37	21	36	39	30	11.2
Semi-arid	18	31	22	26	27	30.9
Subhumid	22	22	14	16	19	20.6
Humid	19	6	8	9	6	20.3
Highlands	4	20	21	10	17	8.8
Total (millions)		148	104	125	377	91.7[b]

Source: Jahnke (1982).
[a] AME = adult male equivalents
[b] Total human population = ca. 240 million

1. The arid and semi-arid zones comprise 55% of the area of sub-Saharan Africa, and support 50-60% of the livestock and 40% of the people. In the arid zone proper, sheep and goats are relatively much more numerous than cattle, but cattle are better represented in the semi-arid zone. These are zones characterised by extensive pastoral livestock systems, often nomadic or at least transhumant, reflecting the bitter lesson that in the dry season and when the rains fail, herds and flocks must be able to move to somewhere with crop residues or forage reserves, either a swamp or a river flood plain or a regular dry season grazing area. ILCA has research teams in Mali, in the Ethiopian southern rangelands, and in the Kenyan Maasai rangeland system, reflecting the enormous extent and importance of this zone and its grazing systems.

2. The subhumid zone has relatively more cattle than sheep and goats, an indication of a greater reliability of forage supply, despite the fact that 2/3 of this zone is tsetse-infested or at least part of each year. ILCA's subhumid research team is based at Kaduna, but a new research project was recently started in central and southern Mali to extend legume forage production into that portion of the subhumid zone.

3. The humid zone, 19% of sub-Saharan Africa, has only 6% of the cattle, and 8 and 9% of the sheep and goats respectively. Its human population is 20% of the total, indicating the greater importance of cropping than of livestock production in this tsetse-infested region. ILCA has a research team based at Ibadan, working in close cooperation with IITA on the typical cropping and small-ruminant production systems of the zone.

4. The highlands are mostly in eastern Africa, and carry a much larger proportion of Africa's livestock - 20% of the cattle and sheep, 10% of the goats - than their relative area, which is only 4% of the total. This is substantially associated with intensive crop production in the highlands, often using draught oxen, and the availability of a range of crop residues and byproducts. This demand for draught oxen provides a valuable outlet for surplus male cattle reared in the adjacent rangeland areas. Ethiopia has the largest share of African highlands, and the largest livestock

population in the continent, and is thus an appropriate site for ILCA's highland zonal research team at Addis Ababa.

Livestock systems research and use of models

All of ILCA's programmes have adopted a systems approach to their task, but, because of the lack of a clearly defined standard method, each has felt free to adopt or develop its own variant of this. In each case there has been an initial period of analysis, in which a careful study of the literature, the results of preliminary surveys and often quite substantial field recordings have been incorporated into a system study. This description and evaluation of the livestock production system(s) of the zone, including their very important linkages with other agricultural systems, has served both to establish baseline production parameters and as the diagnosis for deciding where to focus more specific research in the ensuing phases. These constraints, or opportunities for improvement, have thus determined ILCA's component research interests.

This system analysis seems necessarily to be associated with either the use or development of a model as a way to understand and indicate the complexity of interrelationships and to derive mathematically-sound estimates of their outcome. This commonly requires computing resources. Several of ILCA's teams did this initially by setting up 'model farmlets' in which they proposed to study the effects on productivity of various alternative methods or enterprises, carried out generally by local farmers under research guidance and observation. This approach met with rather limited success - in the humid zone of southern Nigeria it quickly became evident that management of vigorous tropical grass and legume pastures for dwarf goats and sheep was a totally new experience for everyone, locals and research workers alike, for which published research literature provided no great help. The heavy mortality among ILCA's modest experimental flocks, too, convinced us that the risk of epidemics of PPR (peste des petits ruminants - a pneumonia-like respiratory disease) fully explained why villagers kept only three or four animals. 'Model farms' were used by ILCA's Highlands Programme in Ethiopia with rather more success.

Our research team in northern Nigeria used an existing CRED model as a pre-research model, and, coming to the initial conclusion that nutrition during the dry season would be the critical limitation to animal production, concentrated their efforts on that topic, with considerable success. Their results in improving dry-season nutrition by supplementary feeding and by use of special-purpose legume forages are now being incorporated directly into economic development models (von Kaufmann, 1984).

Another early decision was that, since cattle were the most important ruminant livestock in the arid, semi-arid, subhumid and highland zones, we should look for a simulation model to help us explore the factors influencing their productivity. This was of particular importance since ILCA had no research stations in the arid, semi-arid and subhumid zones, and thus could not set up experimental studies of cattle productivity. This led us to consider the general cattle herd model developed by TAMU (Sanders and Cartwright, 1979a; 1979b) and, after exploring one or two applications, to introduce some major changes and thus develop the ILCA model (Konandreas and Anderson, 1982) which is discussed in some detail by Wagenaar and Kontrohr (1986).

Past uses of simulation models by ILCA

The following list of applications of models indicates ILCA's interest in simulation models.

1. Botswana - Anderson and Trail (1978)
2. Anderson (1981) developed a model to investigate some of the problems of using milking cows for draught purposes.
3. Konandreas (1983) examined the problem of modelling intake from a sward having a range of components differing in palatability
4. Cattle production systems in Nigeria and Mali (de Leeuw and Konandreas, 1982)
5. Trade-offs between milk and meat production - Konandreas et al (1983)
6. ILCA/CABO/ARO modelling meeting, 1983
7. King (1983) modelled water and energy metabolism
8. Hiernaux (1984) developed a model of rainfall and pasture growth

9. Transhumant cattle in the Niger Delta (Wagenaar et al, 1984), and the Kenya Maasai land (Wagenaar and Kontrohr, 1986)

Models of pastoral productivity were given by:

10. Wilson (1984) and
11. De Ridder and Wagenaar (1984) in a paper to the 2nd International Rangelands Congress
12. Upton (1984)
13. Upton and Cossins (1984) in bio-economic models of small ruminant production in southern Nigeria and of pastoral livestock in the southern Ethiopian rangelands, respectively.

The latter two papers reflect a growing interest in including economic factors in the models.

14. McIntire (1984) used simple econometric modelling to study the productivity of alley farming in southern Nigeria
15. Von Kaufmann (1985) did the same for livestock enterprises in northern Nigeria
16. Henricksen and Durkin (1985) used water balance models to estimate growing periods for crops in several parts of Ethiopia.

These examples illustrate the wide range of ILCA's interests and involvement in modelling.

Experience has shown that livestock systems research is slow, for a variety of reasons. An initial description and productivity survey which proposes to follow reproductive performance of cattle must run for several years, and trends in, say, rangeland utilisation and possible changes resulting from grazing pressure or management require even longer to document, bearing in mind the great interannual variations in rainfall which effectively obscure small changes in vegetation and animal productivity.

For these reasons, among others, ILCA is giving increasing attention to methods for making rapid a preliminary system analysis. This permits the development of comparatively simple models (McIntire, 1984; Upton, 1986)

which may be used for sensitivity analyses to assess priorities for the next stage of research (Campbell and Arnold, 1973). This, too, is a subject for debate. Clearly an incorrect model could misguide the research, and, as pointed out by van Keulen (1976) and Arnold et al (1977), it is not just the values of particular coefficients that need to be varied in a sensitivity analysis, but perhaps also the basic concept of a relationship and the form of its algorithms. However, used with care, such pre-research models can be very useful and seem likely to save years of costly effort. As is often pointed out, formulating a model helps to focus attention on aspects of the system which are less well understood.

Some reflections on modelling in livestock systems research

The chemist, physicist and engineer have long used models, in the form of equations for chemical reactions, as descriptions of mechanical systems, of structures and stresses, and flow rates. Just as organic chemistry transcends inorganic chemistry in complexity, so too the discovery of enzymes introduced the vastly more complicated interacting world of biochemistry. This is analogous to the increasing complexity of models in agriculture - the interactions of climate, water and soil involve processes of physical impact, infiltration and runoff, evaporation according to air movement and temperature. The growth of plants introduces biological processes of greater complexity, and grazing animals involve the physiology and biochemistry of intake, digestion, energy and protein metabolism, growth, reproduction and lactation, all liable to modification by climate and disease.

The complexity and challenge of grassland livestock production perhaps explains the number and diversity of the models that have been published - Seligman (1976) gave a critical appraisal of 14 such models, and more recently Chudleigh and Cezar (1982) reviewed eight bio-economic models of beef-cattle systems. They, like Goodall (1976), made some thoughtful and constructive suggestions for future modellers to ensure better documentation, greater ease of interfacing with different user requirements and greater flexibility and adaptability in use of modular subroutines. A common problem is that for wider applicability, models need to be more generalised, whereas dealing in

fundamental tissue enzymic processes of animal (or plant) physiology, as in the work of Baldwin et al (1977), makes the models more complex in documentation and less user friendly. Simpler, more empirical models are easier to use but are more location-specific. It is notable that the Texas A & M University general cattle model (Sanders and Cartwright, 1979a; 1979b) has been modified (Sullivan et al, 1981) with the inclusion of improved forage intake routines (Smith and Williams, 1973) and some empirical location-specific elements to adapt it better to East African pastoral cattle production systems. The original TAMU model, like the ILCA one (Konandreas and Anderson, 1982), was open to the criticism raised by Whelan et al (1984), that it was insensitive to changes in pasture availability and did not include the very important feedback effect of selective grazing by animals on subsequent forage quality and availability. Wagenaar and Kontrohr (1986) in their paper to this meeting, discuss this and other features. It is still true that "Good scientific models are often too detailed or too speculative for those who want to apply them; whilst models used for predictive or management purposes are often too trivial or too crude to challenge scientific interest" (Penning de Vries, 1976). Thus despite the many excellent approaches to modelling ruminant digestive processes, notably the comminution of feed and passage of ingested nutrients and fluid flow through the rumen (Waldo and Smith, 1972; Mertens, 1973; Black et al, 1981), more effective use has so far been made of studies which treat the ruminant digestive tract as a 'black box' and model feed intake primarily as a function of forage quality and availability and the animal's physical capacity, as reflected in faecal output.

There has been a welcome and growing practical tendency to link together primary vegetative production and animal production, sometimes including stochastic routines to model the essentially random elements of annual rainfall variation, and the likelihood of conception or death. Guerrero et al (1984) provide a notable recent example, and in livestock systems research much use can be made of a simpler model which contains all the major elements of the climate, soil, plant, animal system plus the socio-economic aspects of management.

It is necessary to point out that Western economic criteria are not always, if indeed ever, relevant to decision-making by African nomadic

pastoralists or smallholders. There is a whole domain of research in the different value systems, the allocation of resources and authority, the economic and social obligations and the survival mechanisms of African societies, which has scarcely been tackled, even qualitatively.

The future of modelling in ILCA

ILCA's policy towards modelling will be determined largely by the needs of its research workers and there are clear indications that these needs have changed and will continue to do so. With the emphasis moving from system analysis to component research there will probably be increasing interest in specific, almost disciplinary, topics. For example, much agronomic interest is now centred on the role of legumes in maintaining or restoring soil fertility. Depending on how they are introduced, whether as a fodder bank or alley farm, in rotation or as an intercrop, they may compete to varying degrees with cereal crops for land, water and nutrients. Legumes greatly improve dry season forage quality and thus livestock performance, and this seems to be a subject where sufficient background information is now available to enable us to build or adapt a relatively simple model to look at promising alternatives.

In the crop/animal field too, there is a growing appreciation of the enormously important function of livestock as a bank account, capable of providing cash to invest in additional land, labour, fertilizer or seeds, and steadily multiplying and growing in the meantime. Upton (1986) and McIntire (1984) have already begun to interest themselves in this rich field, which is certain to expand and to incorporate, perhaps, some sociological or anthropological elements, which is long overdue.

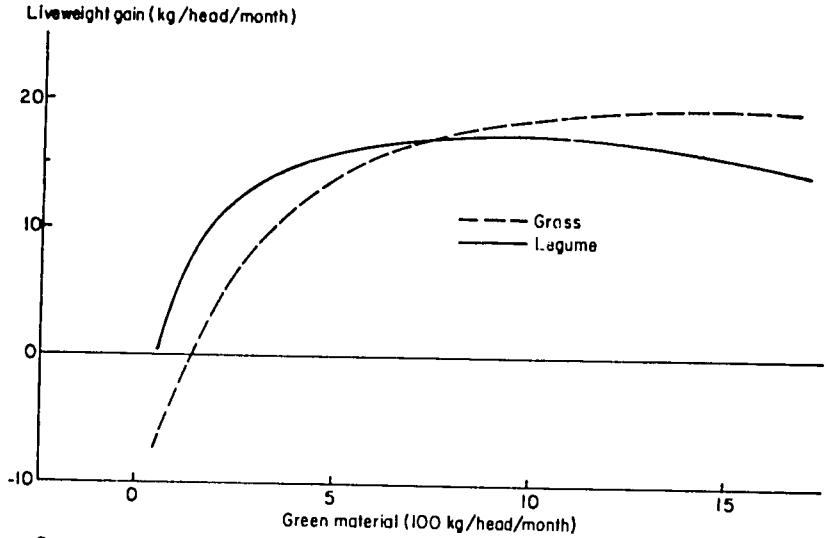
In the animal field ILCA will follow the lead of, for example, Levine et al (1981) in using data derived from Zebu and other indigenous breeds instead of European cattle (Wagenaar and Kontrohr, 1986). The factors affecting intake of these generally smaller and less productive animals on tropical pastures and crop residues are already under study and may require some modifications to the existing intake, growth and reproduction algorithms. A dominant feature of African livestock systems is the mixture

of animals kept, and the flexibility that this gives. The shorter gestation and higher fecundity of sheep and goats mean that their numbers increase more quickly than cattle after drought or disease, while the browsing habits of goats and camels gives them access to a second forage source with different patterns of growth and regeneration and rather different nutritional characteristics. Research is now under way at ILCA to determine how high-tannin content affects feed selection and intake and utilisation of browse plants, and no doubt this will yet-further complicate the modelling of some savanna grassland production systems. Many models have been published for sheep/grassland systems but none deals with African sheep and goats. The SR-CRSP programme is interested in small ruminant models (see for example Thomas 1984; Cartwright 1984a; 1984b) but the latest TAMU model (Blackburn, 1984) appears to be based on virtually the same nutritional physiology and arithmetic as the earlier sheep model of Graham et al (1976) once the forage has been eaten.

The problem of feed intake

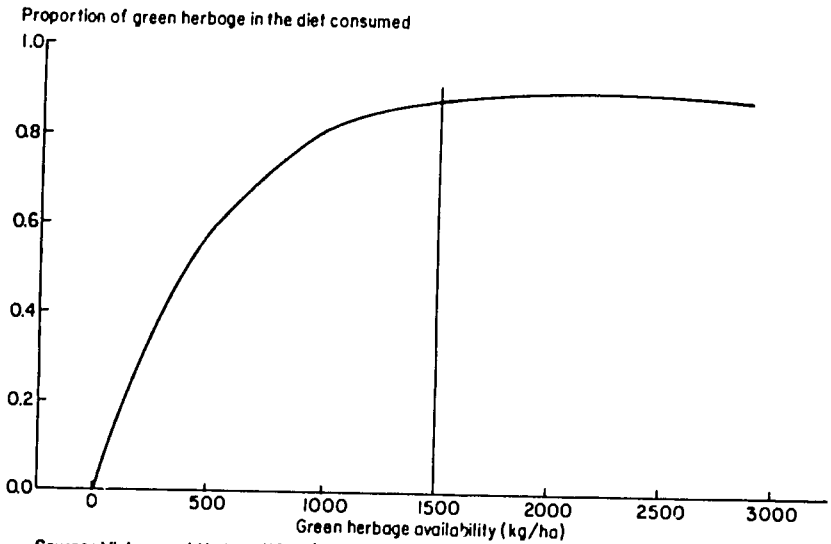
A recurring theme in these notes is the question of forage intake, which is the link between plant production and animal performance. Relationships between intake and forage quality are consistently found in experiments with sheep and cattle in temperate areas and on fairly uniform swards of improved pastures. The conditions in the tropics and subtropics are quite different, and in the realistic studies reported by 't Mannetje (1974) liveweight gain was found to be related to the total amount of green material, grass or legume or both, but not to quality attributes of the forage (Figure 2). The high rate of pasture growth in the wet season results for the rest of the year in a large excess of mature forage of steadily declining quality, from which sheep and cattle select a fraction, predominantly green while any persists, of much higher nutritive value than the rest. Models have been proposed, notably by Vickery and Hedges (1972) (Figure 3 and 4), Smith and Williams (1973) and Arnold et al (1977) (evaluated by Seligman, 1976) (Figure 5) to describe growth and senescence of pastures, and selection of green rather than dry material by animals, but these do not seem to have been widely followed.

Figure 2. Relationship between pasture attributes and liveweight gains on subtropical pasture



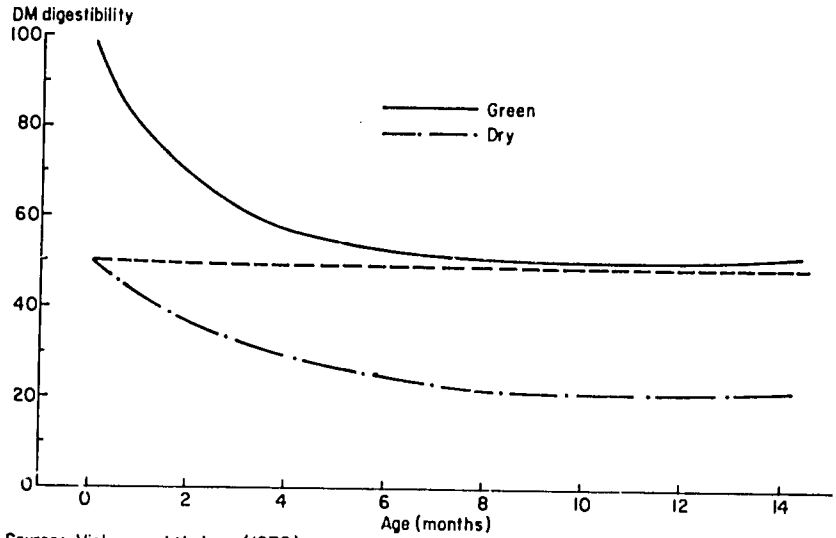
Source. 't Mannetje (1974)

Figure 3. Relationship between green herbage availability and diet



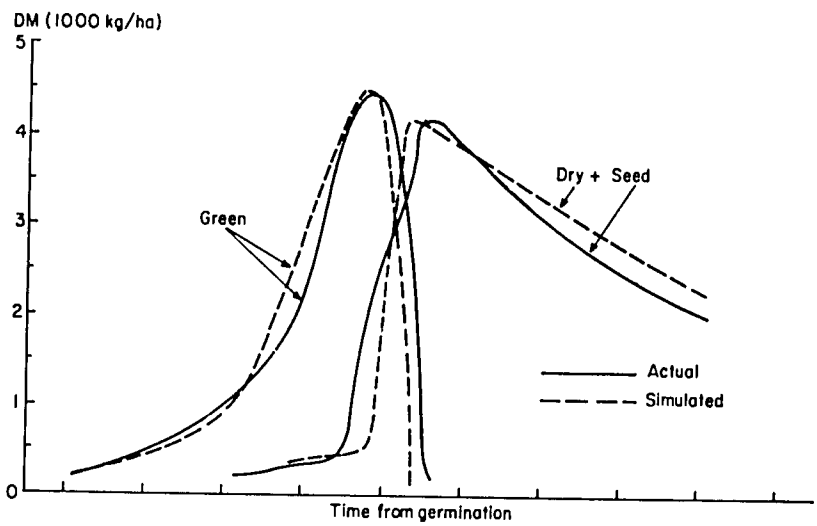
Source: Vickery and Hedges (1972)

Figure 4. Effect of age on digestibility of herbage



Source: Vickery and Hedges (1972)

Figure 5. Effects of grazing management on pasture/animal production: use of simulation model



Source: Arnold et al (1972)

Green is good

The most interesting recent development, and one which illustrates the merit of a broader approach, was that of McCown (1981). McCown combined a soil moisture and a temperature index to derive a 'growth index' which he used in conjunction with climatic records to calculate the start, end and duration of the growing period during which green feed is readily available. He was able to show that, over very large and heterogenous areas of tropical northern Australia, cattle weight gains were closely related to 'green' periods (Figure 6). He examined the effect of the relative numbers and timing of green and dry weeks throughout the year, noting the interesting facts that:

1. The relationship was clearer on all-grass pasture areas - legumes seemed to uncouple the relationship by prolonging weight gains into the dry season;
2. The main benefit of prolonging the green season is its effect of shortening the dry season; and
3. A dry week in the dry season increases liveweight loss more than a green week in the growing season increases liveweight gain.

The importance of this to ILCA lies in the availability of satellite imagery from Landsat or, the NOAA Tiros series, which enables us to record, over huge and inaccessible areas of Africa, the extent and timing of these 'green' periods and perhaps to develop from this an early warning system for bad seasons and possible drought.

Early warning: indicators of seasonal prospects - rainfall and plant growth

The development of satellite radiometry by NASA in the U.S. made available a method of monitoring vegetative green cover over large areas. Landsat satellites and their successors measure reflectance from the earth's surface in several spectral bands, of which the red and the infrared are the most useful for this purpose. These two measurements are combined into a ratio which varies according to the greenness of the reflecting surface, and is therefore called the 'vegetative index.' The numerical value of this index varies from zero to one, according to the proportion of the earth's surface that is covered by plants, and to their density and greenness (Tucker et al, 1985) (Figure 7).

Figure 6. Cumulative liveweight change of cattle from June to June in relation to total green weeks in this period

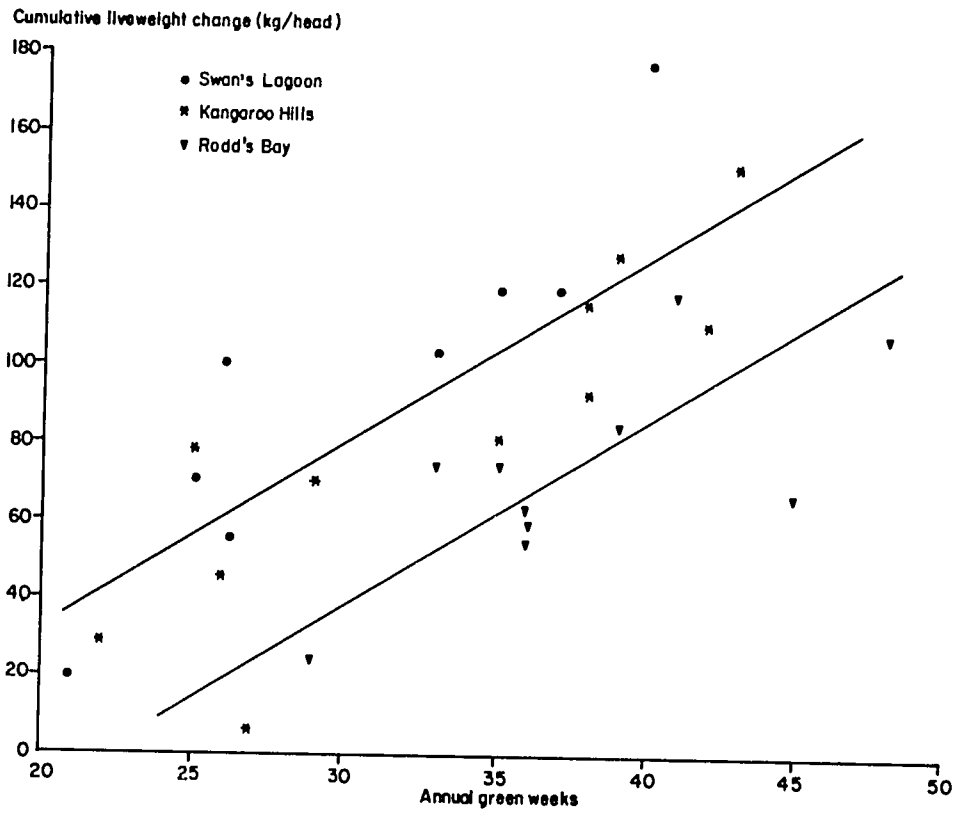
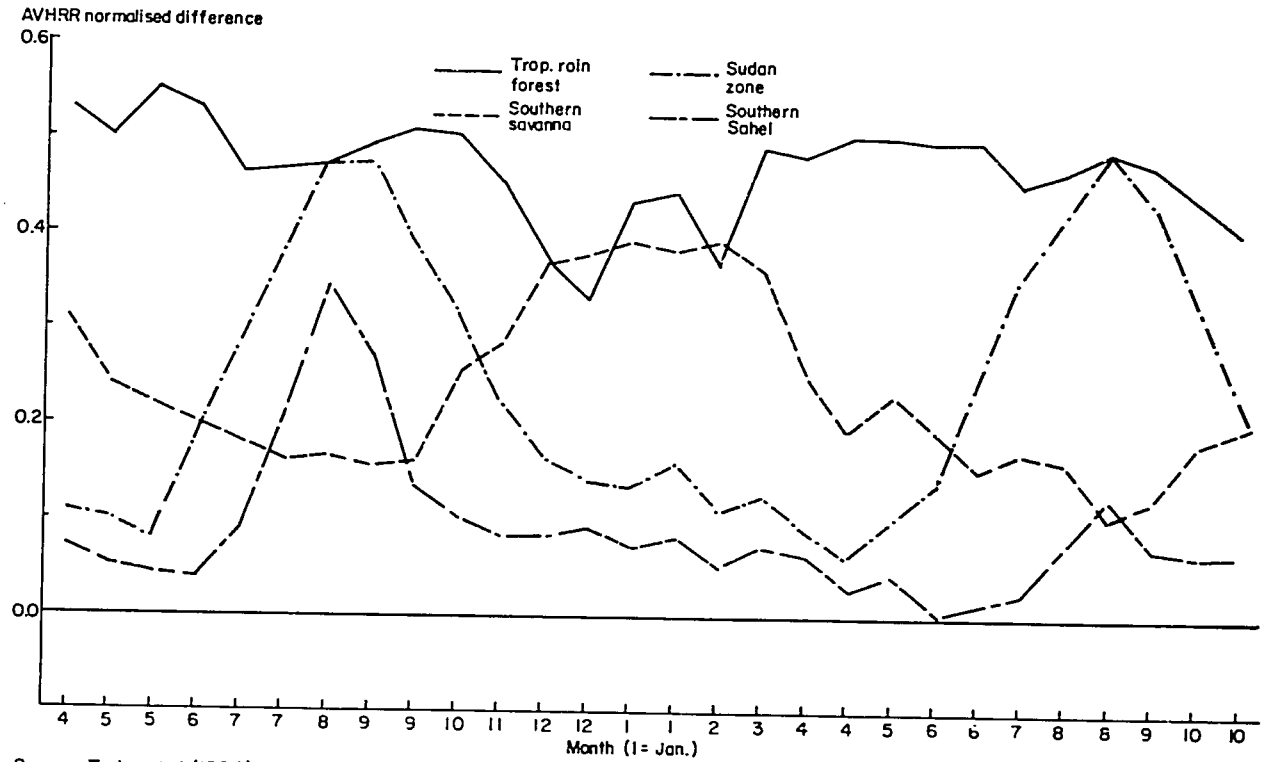


Figure 7. Spectral vegetation index at four African locations, April 1982 to November 1983



Source: Tucker et al (1985)

One value plotted per location for each 21-day period

Careful calibration of the vegetative index against measured crop biomass shows a good correlation during the growing season, but the relationship differs among crops, and between crops and pasture associations. Among pastures, grasses give less reflectance than dicotyledonous plants for the same vegetative biomass and, since the deeper-rooting trees in a savanna tend to remain green longer than the grasses, such an area may give a higher vegetative index than open grassland for a similar amount of available feed. Thus, research still needs to be done to find the appropriate equations for predicting plant biomass from vegetative index values for each pasture type.

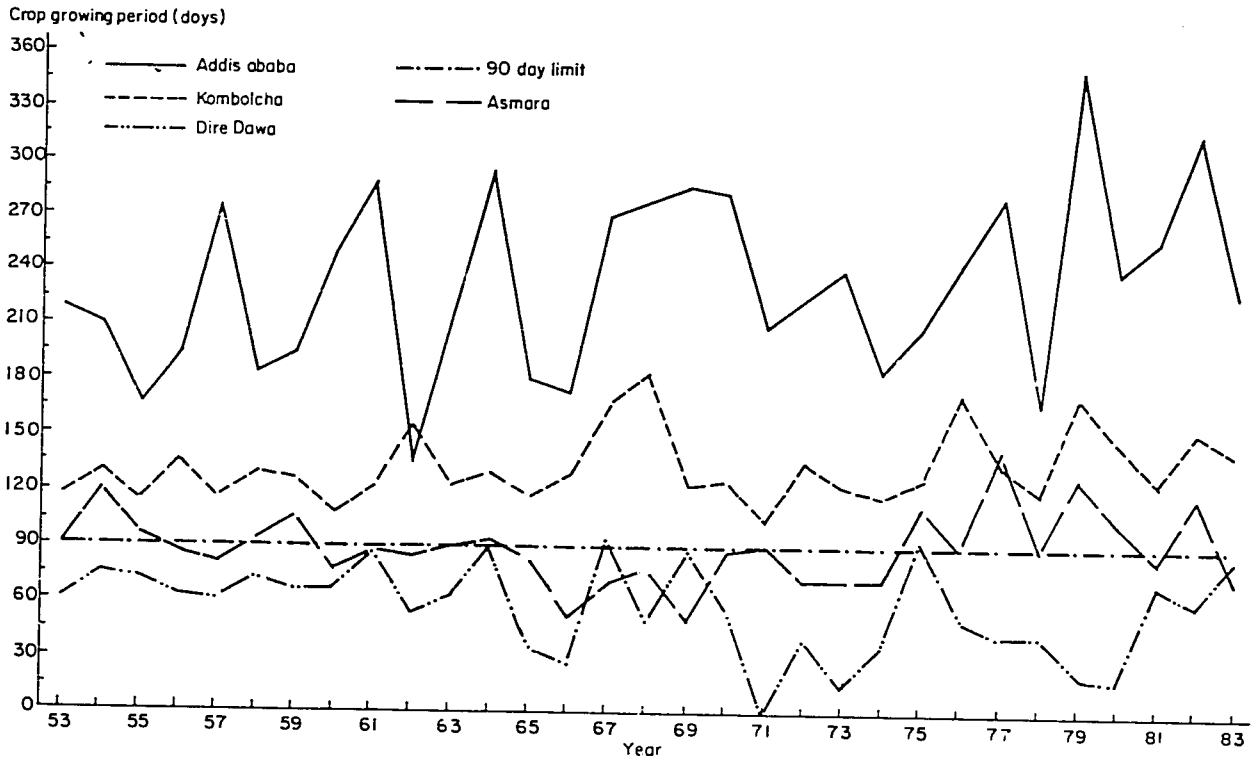
Satellite imagery has been widely used for monitoring greenness of the remote areas where rainfall may trigger hatching, development and migration of the desert locust. Satellite imagery has also been used to follow ocean temperatures and currents, to monitor the health of huge tracts of forest land and as a tool in land resource inventory.

This is an exciting prospect and much attention is now being given at ILCA to ways of relating satellite imagery, aerial survey records of vegetation and livestock numbers, and ground-truth observations of crop and pasture growth to livestock condition prices and economic indicators. It is too early to predict what form our models will take, but we believe that it will be possible to develop a method by which agricultural and economic planners may be warned in which areas there is likely, or certain, to be a deficit of grain or forage and where, on the other hand, there may be a surplus of food and livestock. Not only does McCown's work strengthen our belief that this can be done for purely pastoral areas, but recent work on water-balance models by Henricksen and Durkin (1985) suggests that a historical analysis of climate and soil moisture indices can pinpoint regions that are most liable to recurrent crop failures and can perhaps tell us a year or two ahead where the next drought is likely to be (Figure 8).

Summary and conclusions

1. ILCA has experimented with many types of simulation models in its livestock systems research work.
2. The mandate and the geographic location of ILCA's research programmes have given us a particular interest in grassland/livestock models and in their extension to economic and sociological decision-making.

Figure 8. Crop growing period at four Ethiopian sites 1953 to 1980



3. In simplified empirical forms these are proving valuable in assessing research priorities and we are likely to do more with such models.

4. In its current phase of component research ILCA will probably make more use of subsystems models, in its agronomic, livestock and socio-economic research.

5. Many published animal/pasture models are unsatisfactory for African use in their treatment of feed selection and intake and their use of parameters based on European-type livestock. Improved approaches to this problem are now available and current research at ILCA is expected to lead to more appropriate formulation perhaps of simplified empirical models linking climate-plant-animal.

6. Major new fields of interest include studies of climate-soil parameters for longer term land use and resource assessment. The linking of this with satellite imagery and aerial survey promises to make available early warning systems to relate rainfall or vegetative growth to agricultural and livestock productivity.

References

Anderson F M and Trail J C M. 1978. Mathematical modelling of livestock production systems: Application of the Texas A&M University beef cattle production model to Botswana. ILCA System Study No. 1.

Anderson F M. 1981. A simulation model to assist in the evaluation of cows as a practicable farm-level source of draught power. Unpublished Research Report. ILCA Highlands Programme.

Arnold G W and Campbell N A. 1972. A model of a ley-farming system, with particular reference to a submodel for animal production. Proc. Aust. Soc. Anim. Prod. 9:23.

Arnold G W, Campbell N A and Galbraith K A. 1977. Mathematical relationship and computer routines for a model of food intake, liveweight change and wool production in grazing sheep. Agric. Systems 2:209.

Baldwin R L, Koong L J and Ulyatt M J. 1977. A dynamic model of ruminant digestion for evaluation of factors affecting nutritive value. Agric. Systems 2:255.

Black J L, Beever D E, Faichney G J, Havarth B R and Graham N McC. 1981. Simulation of the effects of rumen function on the flow of nutrients from the stomach of sheep. Agric. Systems 6:195.

Blackburn H D 1984. Simulation of genetic and environmental interaction of sheep production in northern Kenya. Ph D thesis, Texas A & M University.

Campbell N A and Arnold G W. 1973. Use of a systems approach to establish research areas and priorities. Proc. III World Conf. Anim. Prod. Paper 2(a)-11.

Cartwright T C. 1984a. Systems analysis and synthesis of livestock herds. In: Partners in research, 5-yr report of Sr-CRSP Ed. Blond, Berkeley, VC. p. 92.

Cartwright T C. 1984b. Systems analysis research. Ibid. p. 187.

Chudleigh P D and Cezar I M. 1982. A review of bio economic simulation models of beef production systems and suggestions for methodological development. Agric. Systems 8:273.

Goodall D W. 1976. The hierarchical approach to model building. In: G W Arnold and C T de Witt, eds. Critical evaluation of systems analysis in ecosystems research and management. PUDOC Wageningen. p.10.

Graham N McC, Black J L, Faichney G J and Arnold G W. 1976. Simulation of growth and production in sheep. Model 1 - A computer programme to estimate energy and nitrogen utilization, body composition and empty liveweight change, day by day, for sheep of any age. Agric. Systems 1:113.

Guerroro J N, Wu H, Holt E C and Schake L M. 1984. Klein-grass growth and utilisation by growing steers. Agric. Systems 13:227.

Hiernaux P. 1984. Distribution des pluies et production herbacée au Sahel; une méthode empirique pour caracteriser la distribution des précipitations journali' .s et ses effets sur la production herbacée. ILCA Arid/Semi-Arid Zone Programme Document No. 98.

Henricksen B L and Durkin J W. 1985. Moisture availability, cropping period and the prospects for early warning of famine in Ethiopia. ILCA Bulletin 21:2-9.

Jahnke H E. 1982. Livestock production systems and livestock development in tropical Africa. Kieler Wissenschafts Verlag Vauk.

von Kaufmann R. 1985. The expected impact and future of the ILCA Subhumid Zone Programme. In: Livestock systems research in Nigeria's subhumid zone, 2nd ILCA/NAPRI symposium, 29 Oct - 2 Nov 1984, Kaduna, Nigheria. ILCA, Addis Ababa.

van Keulen H. 1976. Evaluation of models. In: G W Arnold and C T de Witt, eds. Critical evaluation of systems analysis in ecosystems research and management. PUDOC Wageningen. p.22.

King J M. 1983. Livestock water needs in pastoral Africa in relation to climate and forage. ILCA Research Report No. 7.

Konandreas P A. 1980. Modelling forage intake and animal performance when the quality of forage on offer is highly variable. Unpublished report, ILCA Highlands Programme.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: An integer and stochastic model for evaluating production alternatives. ILCA Research Report No. 2.

Konandreas P A, Anderson F M and Trail J C M. 1983. Economic trade-offs between milk and meat production under various supplementation levels in Botswana. ILCA Research Report No. 10.

de Leeuw P N and Konandreas P A. 1982. The use of an integer and stochastic model to estimate the productivity of four pastoral systems in West Africa. In: Proceedings of the National Beef Conference, Kaduna, Nigeria, July 1982. p. 184.

Levine, J M, Hohenboken W and Gene-Nelson A. 1981. Simulation of beef cattle production systems in the Llanos of Colombia. Pt 1: Methodology - an alternative technology for the tropics. Agric. Systems 7:37.

't Mannetje L. 1974. Relations between pasture attributes and liveweight gains on a sub-tropical pasture. In: Proc. XII Int. Grassl. Cong. Vol. III Pt 1. p.299.

McCown R L. 1981. Climatic potential for beef cattle production in tropical Australia. Part 1: Simulating the annual cycle of liveweight change. Agric. Systems 6:303.

McIntire J. 1984. Models of alley farming. Unpublished internal report. ILCA Livestock Policy Unit.

Mertens D R. 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph D thesis. Cornell Univ.

Penning de Vries F W T. 1976. Evaluation of simulation models in agriculture and biology: Conclusions of a workshop. Agric. Systems 1:99.

de Ridder N and Wagenaar K T. 1984. Comparison of the productivity of traditional livestock systems and ranching in eastern Botswana. In: Proc. 2nd Int. Rangelands Congr., Adelaide (in press).

Sanders J O and Cartwright T C. 1979a. A general cattle production systems model. Part I - Structure of the model. Agric. Systems 4:217.

Sanders J O and Cartwright T C 1979b. A general cattle production systems model. Part II - Procedures used for simulating animal performance. Agric. Systems 4:289.

Seligman N G 1976. A critical appraisal of some grassland models. In: G W Arnold and C T de Witt, eds. Critical evaluation of systems analysis in ecosystems research and management. PUDOC, Wageningen. p.60.

Smith K C G and Williams W A. 1973. Model development for a deferred-grazing system. J. Range Man. 26:456.

Sullivan G M, Cartwright T C and Farris D E. 1981. Simulation of production system in East Africa by use of interfaced forage and cattle models. Agric. Systems 7:245.

Thomas N. 1984. A small-ruminant production model on a programmable calculator. In: Partners in research, 5-yr report of SR-CRSP Ed. Blond: Berkeley, V C. p.82.

Tucker C J, Townshend J R G and Goff T E. 1985. African land-cover classification using satellite data. Science 227:369.

Upton M. 1984. Models of improved production systems for small ruminants. Seminar on small ruminant production in West Africa. Feb. 1984, ILCA, Ibadan.

Upton M. 1986. Modelling economic outcomes of livestock production systems. In: N de Ridder, H van Keulen, N G Seligman and P J H Neate, eds. Modelling of extensive livestock production systems. Proceedings of ILCA/ARO/CABO workshop, Bet Dagan, Israel, 5-9 Feb 1985. ILCA, Addis Ababa.

Upton M and Cossins N J. 1984. The productivity and potential of the Southern Rangelands of Ethiopia; Draft report, September 1984. Ethiopian Rangelands Programme, ILCA, Addis Ababa.

Vickery P A and Hedges D A. 1972. A productivity model of improved pasture grazed by merino sheep. Proc. Aust. Soc. Anim. Prod. 9:16.

Wagenaar K T and Kontrohr E. 1986. Appraisal of the ILCA cattle herd dynamics model using data from pastoral systems in Mali and Kenya. In: N de Ridder, H van Keulen, N G Seligman and P J H Neate, eds. Modelling of extensive livestock production systems. Proceedings of ILCA/ARO/CABO workshop, Bet Dagan, Israel, 5-9 Feb 1985. ILCA, Addis Ababa.

Wagenaar K T, Diallo A and Sayers A R. 1984. The productivity of transhumant Fulani cattle in the Niger inner delta in Mali. ILCA Arid, Semi-Arid Zone Programme Document (in press).

Waldo D R and Smith L W. 1972. A model of cellulose disappearance from the rumen. J. Dairy Sci. 55:125.

Whelan M B, Spath E J A and Morley F H W. 1984. A critique of the TAMU model when used to simulate beef cattle grazing pasture. Agric. Systems 14:81.

Wilson R T. 1984. Mixed species stocking and the vital statistics and demography of domestic animals in the arid and semi-arid zones of northern tropical Africa. In: Proc. 2nd Int. Rangeland Congr., Adelaide (in press).

Discussion

Statement - One of the things you refer to is the use of satellite imagery to understand what the situation is over large areas. Satellite imagery records greenness, but has the disadvantage that it does not give an indication of quality of the herbage, and both quality and quantity are of equal importance in judging the biomass as a feed resource.

Reply - Basically, satellite imagery measures greenness, i.e. the proportion of the area that is covered with herbage, modified by the density of that herbage. It becomes quite insensitive when the leaf area index is more than about three.

Statement - The relationships that you showed between the number of green weeks and animal performance may hold for a given situation in Australia, but when you apply that in different situations the relationship breaks down, because it is not only green that counts, but also how green.

Reply - This relationship has been applied in Senegal to analyse pastoral ecosystems. What is determined by satellite imagery is in effect the number of green days, and this value shows a very close correlation with biomass at the end of the wet season. It can predict the amount of biomass available for livestock at the end of the rains to within 200 kg/ha. However, the relationship is very location specific.

The result from satellite imagery is not just a measure of quantity or just quality, it reflects a number of features of the vegetative cover: but I go back to McCown, "If it is green it is good."

Comment - If you look at West Africa the number of green weeks increases from north to south, but that does not hold for gross cattle production. So the correlation between duration of green and animal performance does not hold in West Africa. Why it holds in Australia is difficult to understand.

Question - With regard to the question of process studies versus systems analysis, you sometimes come up against a problem without any recourse to making a complete system analysis, with or without a model. You gave the example of farmers keeping small numbers of animals because of the risk of PPR -- thus it is a veterinary problem that needs to be dealt with, and there is no need for a

detailed system analysis. That is the way that research has always worked, and no system analysis is going to replace that kind of problem perception. A balance is needed between the different approaches. So, in fact, whatever the approach, the aim is to identify the problem and determine whether it is relevant.

With regard to actual monitoring of vegetation, remote sensing offers a different way of approaching the situation, because here it presents a means for dealing with a problem. It seems that this method can provide data that would not have been available before, for areas which could not be surveyed. The question is, however, that when those data are available and are properly interpreted from the point of view of animal utilisation, what can be done with them?

Answer - As an example, we are involved in a project in Niger at the moment in which we hope to integrate data from satellite imagery, low level aerial survey and ground-truth measurements on cattle numbers, condition, reproductive performance, markets, prices, and economic welfare of the people involved. The hope is that this will provide a tool for planners and decision makers on which to base their decisions about development and use of resources, since there is not much that the individual pastoral herder in the sub-Saharan zone can do. He does not have any land, he has livestock, but he is hundreds of miles from any sort of services for most of the time. The most help that can be given to the pastoralists is through guiding government policy decisions, which is the aim of this work. However, we do not really know if we can convince governments. We have argued that all countries in sub-Saharan Africa are increasingly dependent upon aid. We have told the governments that this type of work will provide them with an objective and comparatively quantitative assessment of the prospects for the year, whether for crops or pastures or both. This could help them in making decisions on the allocation of resources or in asking for aid. In addition, it ought to help to convince the international agencies that are involved.

Statement - In a meeting on the use of satellites to monitor food resources a number of years ago, the conclusion seemed to be that this was a technology that was useful to countries that were reasonably developed, because they have the means to adjust the use of their resources, whether through a forestry service, a bureau of land management or whatever agencies that they have. Recent developments seem to be leading to improving the efficiency of the more

developed countries, rather than helping the under-developed ones, which are just watching the developments.

Reply - May be, but this is not a technology that we are in a position to restrict to a particular client. It may be another top down approach, but at least it does seem to have a client or series of clients, even if they are not the clients we would most like to get at.

Question - Regarding the work in southern Nigeria, you say that the risks of PPR fully explained why villagers kept only three or four animals. I wonder whether this is the case, as one might expect that the risk of losses would lead to keeping more rather than fewer animals.

Answer - There was not enough time in this presentation to go into details, but the history is that whenever more than a handful of animals were together, disastrous outbreaks of PPR or similar diseases occurred. This is probably why it has remained a back-yard type of operation, in which there is never a sufficient concentration of animals for effective transmission of the virus. The animals can survive in the presence of PPR if only a few animals are kept.

Question - Well, with animals mixed together in a sort of village flock, there may be hundreds of animals and they are not segregated in any way, so I am not sure.

Answer - They are never herded as a flock. They always stay in small groups of two or three animals.

Models and the analysis of productivity in extensive livestock systems in Israel

N. G. Seligman

Introduction

There are no wide open ranges in Israel and not very many extensively managed herds of cattle or flocks of sheep. Possibly that is why we have so many models of pastoral systems. It seems that when development problems are particularly complex and essentially insoluble through benevolent intervention, the urge to challenge the obduracy of the system with a model becomes overpowering. In a sense, system modelling is a relatively easy way to avoid facing real problems. It seems as if almost anybody who really wants to can build a simulation model and become a creator, albeit of a flimsy world of computer output.

In Israel models, particularly those of livestock systems, seem to have the property of spontaneous generation since the historic workshop on simulation modelling led by the late Professor George M. van Dyne in the early seventies. Even though no problems seem to be solved, few are deterred from going ahead and building a new model. Sometimes older models are cannibalised, often ignored (probably just as well) and the result is a glorious proliferation, especially for a community which produces only about 10% of its red meat consumption from herds based on the range.

Table 1 lists pastoral models in Israel, complex and simple, biological, economic and bio-economic, that have been published. Efforts were not limited to extensive herds and a promising analysis of dairy herd nutrition was discontinued because of in-house conflicts (Goldman et al, 1977; Talpaz et al, 1980). The list makes up a mixed bag which is rather difficult to review. In order to evaluate these models we need to define criteria for classification and possibly even evaluation.

Table 1. Extensive livestock production models in Israel.

Ecosystem-type models of the IBP type:

- NEGEV (Seligman et al, 1981): agropastoral system.
- ZABAN (Zaban, 1981): sheep herd management.
- KAHN (Kahn, 1982; Kahn and Spedding, 1983 and 1984; Kahn and Lehrer, 1984): cattle herd simulation, development of the TAMU model.
- BENJAMIN (Benjamin, 1983): sheep and herd management.
- UNGAR (Ungar, 1984): agropastoral system management.

Process models:

SIMPLE (Noy-Meir, 1975a; 1975b; 1976; 1978a; 1978b): application of predator-prey dynamics to analysis of stability and productivity of different types of grazing systems.

INTAKE (originally Noy-Meir, developed by Ungar, 1984): a mechanistic model of intake by ruminants grazing a homogeneous pasture.

Input/output models:

PSG (Spharim and Seligman, 1983): a pasture system generator used in conjunction with a multi-period linear programming model applied to regional planning of agropastoral development.

Graphical (Seligman and Spharim, 1984; Seligman et al, 1983a; 1983b; Seligman, 1983; Seligman et al, 1984; Spharim and Seligman, 1985): multiple socio-economic goal analysis of agropastoral system feasibility.

BEEFX (Weitz and Seligman, 1985): annual balance of beef herd nutrition, pasture utilization, population dynamics and production from cow-calf herd to feedlot.

Classification and evaluation

The time-tested criterion for biological taxonomy is sex, and it would be gratifying to be able to classify simulation models on such a universally useful basis. Unfortunately, this is not possible. A number of criteria can be used to classify models including the generality or specificity of the model, how widely applicable it is, and its complexity. Probably a more interesting approach would be to classify models by their objectives. That would also provide a recognisable measure of success, assuming that the objective was worthwhile in the first place.

Livestock systems models can serve a number of purposes, the most common of which are research, management and planning.

Research objectives of modelling aim at testing how well we understand the functional nature of complex systems in terms of known or hypothesised processes. A special aspect is the study of the sensitivity and stability characteristics of the system in question. The general assumption is that the functions that define the model are a good representation of the relevant characteristics of the system, so that analysis of the model has relevance to the physical system that is the subject of the study. We will see that when the objectives are clear and the model definition is short and concise, its use can lead to insights that can be classified as 'advance in knowledge'. The Israeli models that can be classified as research models, by nature or by declaration, are the NEGEV, KAHN, SIMPLE and INTAKE models.

The NEGEV model was a class exercise that started off in the van Dyne simulation workshop during 1971 and continued for more than a year at the Hebrew University and ARO. It was meant to show that, with a little training, simulation modelling of complex systems is feasible and can be done by a well-run interdisciplinary team and that it can produce workable tools that can be used for presumably useful system analysis. The NEGEV model had all the classical components of the IBP ecosystem models: Abiotic, primary producers, secondary producers, decomposers and managers. It described a sheep grazing system in the northern Negev based largely on data from Migda. The model indicated that when unmanaged and confined to a given area, sheep would die out in severe drought years, and that this could be avoided only by managerial adjustment of sheep numbers (Tadmor et al, 1977). No doubt, further work on the model could have produced a richer harvest of insights but it seems that the 'post-natal depression' that follows many massive modelling efforts had a

deadening effect on further involvement. The decease of one of the moving spirits of the exercise certainly reduced motivation and NEGEV did not extend far beyond the bounds of the exercise it was originally intended to be.

The KAHN model is a fairly complex cattle simulation model that concentrates on describing animal performance, including both growth and reproduction, as a function mainly of feed quality, and of animal and breed characteristics. It is a development of the TAMU model, but is based on single animals rather than on classes in a herd and has been used mainly to validate some of the assumptions underlying the process definitions. It has been carefully constructed and has raised questions regarding the appropriateness of some of the equations used in the TAMU model. It can be used as a herd management tool, but to date has been used mainly for research. This model will be discussed in greater detail during this workshop.

The Noy-Meir SIMPLE model is a reductionist model taken to the extreme. Basically it defines only a growth function and a grazing (or consumption) function, in such a way that graphical and analytical methods of investigation can be used to solve problems of system stability. Certain problems like rotational grazing or seasonality, which cannot be treated analytically, are fairly easily solved by numerical methods.

By defining the problem as concisely as possible, these models have achieved a generality that has both added significantly to the understanding of grazing dynamics and provided a strong link between pasture management and classical population dynamics in ecology. The central issues of grazing system stability are treated in detail and provide a theoretical basis for rational pasture management. The SIMPLE model is our best example of an analysis that has attained a worthwhile scientific objective. It almost suggests that the impact of a model will bear an inverse relationship to its complexity. I say almost, because the analysis of the SIMPLE model is, conceptually at least, rather more sophisticated than that of many more-complex models.

The INTAKE model is a mechanistic model which will also be discussed during this workshop. It is also a research model but even though it is concisely formulated, it is considerably more complex than the SIMPLE model. INTAKE mainly deals with behavioural aspects of intake and has been used to generate consumption functions. Problems of parameterisation and validation involve considerable experimental effort that can not always meet model needs, especially if precision is important.

The next set is the management models. These as a rule have practically-oriented management objectives. The management problems stem from the complexity of the interactions between climate, pasture, animal, nutrition and economic factors. Consequently, most of the management models are open-ended, in the sense that there is no conceptual limit to their complexity. Only the competence, patience and perseverance of the modeller set a limit. This group of models includes MIGS1, ZABAN, BENJAMIN, and BEEFX. UNGAR is also a management model, but is based on a more careful formulation and analysis of objectives.

The first attempt at setting up a full-blown agricultural system model resulted in the Migda system model (MIGS1). It involved a concerted effort by a group of livestock and pasture specialists and, in fact, translated the current views on the functioning of the main components of the system into an operative continuous simulation model. By the time the model was completed, most of the problems that the model was meant to address were almost forgotten. Some new problems, such as timing of weaning, were analysed with the model and influenced the herd-management decisions taken at Migda, but only to a very limited extent. ZABAN and BENJAMIN are sheep husbandry models of the same genre. They too have been developed and analysed and have since remained on the shelf. Their effect on management practices has been no greater than that of MIGS1.

The UNGAR model, or rather set of models, will be discussed in more detail during the workshop. It treats separate problems that face the manager of agropastoral systems of the type developed at Migda. The problems are clearly and concisely defined and their nature exhaustively analysed, both analytically and graphically. Among the insights obtained is the division of the management space into areas of relative stability that are separated by areas, often rather narrow, where decisions are very sensitive to parameter changes or to data accuracy. Recognition of these different areas of robustness and instability can help to rationalise decision making under the conditions of uncertainity that are typical of the systems studied. Unfortunately, there has been little opportunity to implement the insights gained from this study, mainly because it has only recently been completed. Whether the impact of this model on management practices will be any different from its fore-runners remains to be seen. But if its application remains limited, it would, in no small measure also be due to the fact that the agropastoral systems which it is meant to serve are mainly experimental as yet and are only now being developed on a farm scale.

BEEFX can barely be called a model. It is essentially a feed and performance calculator that can produce an annual balance of a beef herd grazing a seasonal Mediterranean pasture. The feed requirements, pasture and feed values and performance parameters are all empirical table data, taken from the NRC manuals and from local farm data. Its special characteristic is that it is totally farm oriented and uses parameters that describe the herd, pasture, available feed, prices and performance standards as registered by the manager of the herd being analysed. When these data are available various management options can be tested for profitability or for production efficiency. The management options include herd size, cow size, feeding strategies, timing of breeding and weaning, supplementary feeding options and target sale weights as well as other sensitivity analyses. It calculates the evaluation parameters for one-year cycles and does not explicitly consider carry-over effects from one year to the next. Conceptually, the model is rather crude and does little more than what a rancher, concerned about improving his herd management, would do on the back of a match box. However, it does it on a much grander scale and allows much greater resolution than is normally possible with a heterogeneous herd and many management options. This model has been developed in close cooperation with the extension service and consequently has been introduced to a number of ranches. It has only recently been launched after an (over-) extended period of development, but has provoked interest among extension workers and herd managers. It has already been used as an aid to determining whether to increase a herd and to what extent. But how much impact it will have on wider problems of herd management in Israel remains to be seen.

The group of planning models includes PSG and GRAPHICA. They are both input/output models that define a wide range of system conformations. They are also based on agropastoral systems appropriate to the northern Negev of Israel and were conceived as a means for determining appropriate planning and research objectives in fostering livestock and crop integration under dryland conditions. Both models can be divided into two main components: system definition and system evaluation. The system definition is a flexible accounting algorithm that defines the input/output relations of the system as a consequence of changing herd performance levels, pasture utilisation methods and other management parameters. The system evaluation component is basically different in both models. In PSG, the input/output model is combined with a multiperiod linear programming model to determine the optimum course of system selection over a development period, normally 15 years. The program takes into

account regional resources and constraints and defines regional consumption as the basic target function. GRAPHICAL is a static model but can, however, be run over a series of years. Its main characteristic is that it evaluates the systems in a multiple-goal setting. The goals that have been defined are basically farmers' income, regional trade balance and regional employment.

The PSG linear-programming model has been analysed in some detail and has indicated the relative advantages and disadvantages of the three sheep breeds that are potentially useful in the area. GRAPHICAL has been applied to a number of management and planning problems and has helped clarify the system characteristics that would probably prevent wide-spread acceptance. It also indicates what the conditions are for acceptance and the direction for further research. Recently, PSG has also been developed into a multiple-goal model in a study planned to investigate feasible development scenarios in a Mediterranean-type setting. Both models will be discussed in more detail during the workshop.

Neither of these models has had much impact on development in the northern Negev. That would safely classify them with the other models except for two recent developments. The Migda research results are being tested in a farm-scale project, sponsored by the Ministry of Agriculture and the Settlement Department. The project was planned with some of the model analyses in hand. If the project gets off the ground, it will also provide an opportunity to test the UNGAR management models. Too much depends on a rather shaky project plagued with an uncertain future.

The multiple-goal GRAPHICAL model has been used in designing a research project on forage shrubs, funded by USAID. Despite doubts as to the value of forage shrub development under local conditions, the model indicated that even a small positive effect of the shrubs on weaning rates, whether because of greater ewe fertility or greater lamb survival, would justify their introduction on purely economic grounds. Consequently, a set of experiments was designed to test this hypothesis.

Lessons

If proof is needed that some people do not learn from experience, then the Israeli experience in livestock modelling could serve. However, this may not be a bad thing, because so often past experience is not much use in a rapidly

changing world where so many problems solve themselves, generally by becoming worse, irrelevant or overshadowed by greater problems. In addition, galloping technology inflation constantly fosters the illusion that a whack of megabytes concentrated into a nanosecond will crack at least some of the painful problems that prevent us managing our affairs more rationally. So even if it is futile to learn the lesson, there may be a point in drawing some conclusions that could serve as an ad hoc basis for discussion if not as a guideline for future modelling activities.

Firstly we need to correct the third law of simulation which says that "simulation modelling will go on until the budget runs out." With computer costs pulmmeting and with in-house minis and in-office micros proliferating, there is, unfortunately, no serious budgetary constraint. So today it seems that simulation modelling goes on until retirement or decease unless the modeller is fired previously or has given up of his own accord. So if the activity is inevitable, let us try to make it as useful and, as interesting as possible. Mainly, this means finding a worthwhile objective that can be attained by a model analysis better or sooner than by other means. The difficulty with this is that partisan interests tend to cloud the issue so that it is often easier to build a model than it is to obtain concensus on an objective that meets these criteria. Nevertheless, there is virtue in trying to formulate good questions for all the glib answers we tend to generate.

Secondly, it would appear that complex methodology is not necessarily the most effective means of solving complex problems. If our experience is any indication, the most powerful and significant models have been the simpler ones. Most of the more complex models seem to get bogged down in their own complexity. However, complexity in itself would not be so heavy a burden if the model was sound conceptually. If this is the case, the wider generality of the model could possibly justify its cumbersome structure. On the other hand, the difficulty with simple models is that they generally require greater intellectual effort. They depend on the ability to perceive the essence of a problem and to pose the significant questions. They usually require more than a modicum of mathematical ability in order to derive their full implications, and they tend to leave one in the lurch when facing specific management problems.

Thirdly. if a model is meant to be used in herd management, it has far more chance of meeting this objective if it is developed in close liaison with the managers or consultants or extension officers who are going to use it.

Whether this is because of the obligation that goes with involvement and identification with the model or whether it is because the model is more sharply focused on a real problem is not immaterial, but the chances are that both the motivation to use the model and its usefulness will be enhanced. At least, it makes the definition of the objective a collective responsibility which requires a considerable degree of concensus.

All this has been said before and, at this stage, borders on triviality. Does this mean that such conclusions are misleading? Or that they are valid, but difficult to practise? Or that, in fact, they are being practised to varying degrees; and that the modelling of livestock production is indeed maturing; and that we'll hear about major advances and achievements in the course of this workshop? That would be gratifying and justification enough for the effort involved in organising it. Regarding the Israeli experience, we can point to a significant achievement in the elaboration of theory in grazing dynamics and to some extent in system management. The impact of the management models in practice has been far less impressive. Yet one cannot conclude that all the effort has been in vain because there are signs that the need for these models and an appreciation of their special contribution is growing. How soon system analysis will become routine in management and planning of extensive livestock production is difficult to estimate. There are a number of definitions of a wise man in the Hebrew tradition. One of them asks: "Who is the wise man?" and answers: "He who foresees the course of events." That definition would make any estimate of mine a mere guess. I am sure that the wiser among us will point the way more clearly.

References

Benjamin Y. 1983. A management model of a grassland sheep system under Israeli conditions. M. Phil. thesis, Univ. of Reading, UK.

Goldman A, Seligman N G, Amir S, Drori D and Halevi A. 1977. A nutrition model of dairy cattle and its possible uses. Special Publication No. 98, ARO, Bet Dagan (Hebrew with English summary).

Kahn, Hava E. 1982. The development of a simulation model and its use in the evaluation of cattle production systems. Ph.D. thesis, Univ. of Reading, UK.

Kahn, Hava E and Spedding C R W. 1983. A dynamic model for the simulation of cattle herd production systems: I. General description and the effects of simulation techniques on model results. Agric. Systems 12:101-111.

Kahn, Hava E and Spedding C R W. 1984. A dynamic model for the simulation of cattle herd production systems: II. An investigation of the various factors influencing the voluntary intake of dry matter and the use of the model in their validation. Agric. Systems 13:63-82.

Kahn, Hava E and Lehrer A R. 1984. A dynamic model for the simulation of cattle herd production systems: III. Reproductive performance of beef cows. Agric. Systems 13:143-159.

Noy-Meir I. 1975a. Primary and secondary production in sedentary and nomadic grazing systems in the semi-arid region: analysis and modelling. Final research report submitted to the Ford Foundation (Project 7/E-3). Department of Botany, Hebrew Univ., Jerusalem, Israel.

Noy-Meir I. 1975b. Stability of grazing systems: an application of predator-prey graphs. J. Ecol. 63:459-481.

Noy-Meir I. 1976. Rotational grazing in a continuously grazing pasture: a simple model. Agric. Systems 1:87-112.

Noy-Meir I. 1978a. Stability in simple grazing models: effects of explicit functions. J. Theor. Biol. 71:347-380.

Noy-Meir I. 1978b. Grazing and production in seasonal pastures: analysis of a simple model. J. Appl. Ecol. 15:809-835.

Seligman N G, Tadmor N H and Dovrat A. 1972. An exercise in the simulation of a semiarid Mediterranean grassland. Bull. Rech. Agron. Gembloux: Volume extraordinaire édité à l'occasion de la semaine d'étude des problèmes Méditerranéens: 138-144.

Seligman N G, Benjamin R W and Eyal E. 1981. Migda Systems (MIGS1). A model for studying management systems of an integrated sheep-wheat farm in the semi-arid zone of Israel. Special publication no. 207. Division of Scientific Publications, Volcani Center, ARO, Bet Dagan, Israel.

Seligman N G. Spharim I, Harel Dalia, Eyal E, Benjamin R W and Benjamin Y. 1983a. Economic evaluation of agropastoral systems based on wheat and sheep husbandry applied to the northern Negev of Israel: 1. Effect of area of pasture in relation to area of wheat. Hassadeh 63:877-880; 2. The effect of three-year legume pasture and of cheaper recycled feed on economic feasibility. Hassadeh 63:1126-1128. (Hebrew, with English summary.)

Seligman N G, Spharim I, Eyal E and Benjamin R W. 1983b. Definition of a feasible agriculture technology in terms of multiple socio-economic goals: A graphical method applied to dryland agro-pastoral development in the reviewed northern Negev of Israel. Pamphlet no. 226, Division of Scientific Publications, Volcani Center, ARO, Bet Dagan, Israel. (Hebrew with English summary.)

Seligman N G. 1983. Forage shrubs and the economic viability of agropastoral systems in the Mediterranean semiarid zone. AID/CALAR/FOPAR Research Report 2-83, United States-Egypt-Israel Cooperative Arid Lands Agriculture Research Program: Fodder Production and Utilization by Small Ruminants in Arid Regions.

Seligman N G and Spharim I. 1984. Socio-economic feasibility of development in agropastoral systems: a quantitative approach. In: Proceedings of the 2nd International Rangeland Congress, Adelaide, Australia. (in press).

Seligman N G, Spharim I and Benjamin R W. 1984. Nitrogen fertilizer application and income stability in semi-arid pastoral systems. In: Proceedings of the 2nd International Rangeland Congress, Adelaide, Australia. (in press.)

Spharim I and Seligman N G. 1983. Identification and selection of technology for a specific agricultural region: A case study of sheep husbandry and dryland farming in the northern Negev of Israel. Agric. Systems 10:99-125.

Spharim I and Seligman N G. 1985. A graphical method for relating multiple socio-economic goals to R & D objectives in agriculture. Res. Policy. (in press.)

Tadmor N H, Noy-Meir I, Safriel U, Seligman N G, Goldman A, Katznelson J, Eyal E and Benjamin R W. 1977. A simulation model of a semi-arid Mediterranean grazing system. Israel J. Bot. 26:161-171.

Talpaz H, Seligman N G, Goldman A, Sklan D and Horwitz S. 1980. Optimal trajectory of lactation and nutrition for the dairy cow. In: D Yaron and C Tapiero, eds. Operations research in agriculture and water resources. Proceedings of an International Conference, Jerusalem, 1979. North Holland Publishing Co., Amsterdam. pp. 285-294.

Ungar E D. 1984. Management of agropastoral systems in a semi-arid region. Ph. D. Thesis, Hebrew University of Jerusalem, Israel.

Weitz M and Seligman N G. 1985. BEEFX-Management analysis of a beef herd grazing seasonal Mediterranean range. Research Report, Division of Range and Forage Crops, ARO, Bet Dagan, Israel.

Zaban H. 1981. A study to determine the optimal rainfall land use systems in a semi arid region of Israel. D. Phil. thesis, University of Reading, UK.

Discussion

Question - From a farm manager's point of view, should not one ask what the aims of the model are: does it in fact help the farmer, improve his knowledge or hindsight?

Answer - These are questions that should always be asked, i.e. what are we aiming at? What are we doing it for? Who is our target audience? Is it the scientific community that we want to impress, is it the economic investor whom we want to influence, is it the farmer in the field we want to change or help? Very often, one may find that if we can determine clearly who the target is, many of the other problems are going to fall into place, simply because the audience determines what the preferences, what the priorities are.

Question - Is there any danger, as perhaps there has been in the past, of the model being the objective?

Answer - Very often, if you don't really determine who or what it was being done for, the actual activity itself becomes quite addictive. It is a responsibility of the modeller and of the people around to see that his effort is actually serving some useful purpose. Sometimes people just stop, and that's where it ends; sometimes it is taken up and seems to help other people carry on doing their modelling. Whether they come up with anything better is also often dependent on who is doing it, how intelligently it is being done, and how much luck a person has in striking the happy combination of a problem which is manageable and having the necessary environment and data and people who are able to carry things on. A very good example would be the TAMU model that started off by people taking the initiative in Texas, using a lot of public relations, and getting the model applied on a very large scale in many other parts of the world. The model apparently had a fairly sound fundamental basis, because quite a number of people have used it as a basis for developing their models further, such as the Kahn and ILCA models. There we have an activity that has provided a sort of framework for quite a lot of subsequent modelling activities in the world at large.

Prediction of actual primary production under nitrogen limitation

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Introduction

The value of natural rangeland as a feed source for ruminants is a function of both the quantity and the quality of forage present. These two characteristics alone may not suffice to give an adequate description of the feed source, because such factors as the distribution in space of the quantity (spatial heterogeneity), and quality (different organs) may exert a major influence on the feed value, but the former constitute the minimum required information. Extensive research in semi-arid regions, which are characterised by low and erratic rainfall, has shown that the two characteristics are not independent. There appears to be a much greater variability in the amount of water available for plant growth than in the amount of plant nutrients, both in time and in space. As a consequence, in years with favourable rainfall, production (quantity) will be determined by the availability of plant nutrients. Under such conditions, the concentration of the limiting element in the vegetation will reach some species-specific minimum value (quality). In unfavourable rainfall years, on the other hand, water will be the constraining factor and the element concentration in the tissue will remain well above the minimum value, thus providing higher-quality forage.

To characterise continuously the vegetation as a feed source it is necessary to keep track of the accumulation of both dry weight of the vegetation, which is a function of both moisture and nutrient availability, and the element content, which is a function of its availability in the soil. Models at various levels of detail describing the water balance in the soil have been developed, and, depending on the purpose of the model, provide adequate predictions of moisture available for the vegetation and its influence on production. Models of the nitrogen balance in the soil, its consequences for the availability of the element to the vegetation and the ensuing effect on growth and production are far less developed.

In the first instance the aim of developing the present model was to predict the depth and duration of soil wetting, in an attempt to use those characteristics as an indicator for nutrient availability to the vegetation. Moreover, those characteristics may be of importance for the distribution of annuals and perennials in semi-arid regions. So far, these attempts have not been entirely successful, but efforts in this direction are being continued.

As a parallel effort, a simple nitrogen model was added in an attempt to predict primary production under variable conditions of moisture and nutrient availability.

Description of the model

Water balance

To describe the water balance, the total soil depth is subdivided into a number of compartments. In the present version, a total depth of 3 m is considered, consisting from the top downwards of 10 compartments of 0.05 m, five of 0.10 m and eight of 0.25 m. Both the total depth and the number of compartments can easily be changed.

A provision is built-in to take into account layered soils with a heterogeneous profile. In the present version restricted to five horizons. For each horizon, the depth below the soil surface has to be defined, as well as its properties with respect to the water-holding capacity, characterised here by the volumetric soil moisture content at field capacity, at wilting point and at air dryness, respectively. From a soil physical point of view, these characteristics are only loosely defined, because they are not inherent soil properties, but are co-determined by the boundary conditions (notably the depth of the groundwater table), and possibly plant properties (especially the lower value at which moisture is readily available to the plants). Such detail is, however, not considered in the present model.

Rainfall is introduced as a forcing function, derived from the nearest site where rainfall is gauged. If the site considered is far removed from the measurement site, a correction factor can be introduced, either based on intelligent guesswork, or on a more formalised procedure to generate rainfall data ('trend surface analysis').

Infiltration is derived from rainfall, taking into account interception by the vegetation, and the effect of soil surface properties, as expressed in run-off or run-on. Interception is difficult to quantify, but it is assumed that 1 mm of rainfall is intercepted by the vegetation irrespective of rain intensity or vegetation density. Run-off is calculated taking into account both average long-term run-off for a particular site, defined by a coefficient based on measurements, or on prior knowledge of the site and its soil properties, and the effect of rainfall intensity. The latter is described by an empirical relation that assumes a higher value for the run-off factor if rainfall intensity is higher. Implicitly the use of this function assumes that rainfall distribution over the day is always identical. The relation between rainfall intensity and run-off can be derived on the basis of a detailed, physically-based model of infiltration, as affected by soil hydraulic properties and surface characteristics (Rietveld, 1978). Application of such a model, however, requires detailed information on both soil properties and rainfall intensity. For most practical purposes, therefore, direct measurement of run-off seems more appropriate. In cases where such measurements are not available the run-off coefficient may be estimated on the basis of analogy, taking into account the effects of soil texture (Hoogmoed and Stroosnijder, 1984; Stroosnijder and Kone, 1982).

For the calculation of 'effective infiltration' an additional problem arises, related to the fact that the time resolution of the model is one day. If, in reality, rainfall occurs at the beginning of the day, i.e. between 0.00 and 9.00 hours, evaporation from the soil surface proceeds at the potential rate during that day and a substantial part of the water is lost. If, on the other hand, rainfall occurs after 18.00 hours, evaporation from the soil surface is negligible until the start of the following day, resulting in smaller losses (Stroosnijder and Kone, 1982). Because the timing of rainfall is not specified in the present model, it is assumed that it always takes place at the beginning of the day. As a consequence, the difference between potential soil evaporation and soil evaporation based on the actual top soil moisture content is subtracted before the water enters the soil profile. This formulation may lead to overestimation of soil evaporation, but at the present level of resolution any formulation will be arbitrary.

The moisture that enters the soil profile is distributed over the various soil compartments in such a way that they are filled to field capacity from the top downwards (van Keulen, 1975). This formulation thus assumes instantaneous equilibrium, i.e. within the time interval specified by the model. Subsequent compartments are filled up until total effective infiltration is dissipated or until the remainder has drained below the specified profile depth. Transport of moisture under the influence of gravity or under the influence of developing potential gradients is not taken into account. Of course, some redistribution of moisture will take place (Stroosnijder, 1976), and that can be described by defining field capacity at a somewhat lower value, resulting in slightly deeper infiltration.

The present model is intended for use in perma-dry conditions, where a water table is either absent or, if present, at such a great depth that it does not contribute to the moisture in the rooting zone. Hence, upward transport is not accounted for in the model.

Direct evaporation from the soil surface is an important source of non-productive water loss, especially under semi-arid conditions (Stroosnijder and Kone, 1982; van Keulen et al, 1981; van Keulen, 1975). For a proper description of the water balance, this process must therefore be described with some accuracy. A description based on physical processes is not possible in the framework of the present model, because the time constants of these processes are too small for time intervals of one day (van Keulen, 1975). Therefore, a parametrised description has been developed.

Potential evapotranspiration is introduced in the model as a forcing function. These values are calculated with a Penman-type equation, outside the model, but the calculation can also be incorporated in the model if the required meteorological data are available.

Potential evaporation from the soil is derived from potential evapotranspiration by subtracting potential transpiration by the vegetation. Thus, when the vegetation forms a closed surface, covering the soil completely, all available energy will be dissipated by transpiration and evaporation from the soil is negligible. As the next step, the influence of dessication of the top soil on evaporation from the soil is taken into account. This effect is derived from the assumption that, after an initial period, when soil evaporation is determined by energy availability (the 'constant-rate' stage), a 'falling-rate' stage follows, during which evaporation is determined by the rate at which

moisture can be supplied to the soil surface. During the falling-rate stage a linear relation is assumed between cumulative soil evaporation and the square root of time (Stroosnijder and Kone, 1982; Ritchie, 1972). Hence, actual evaporation from the soil is derived from the slope of the relation between cumulative soil evaporation and square root time, and the time that has elapsed since the last effective rain shower, i.e. a shower that resulted in soil wetting.

As said before, transport between soil compartments under the influence of developing potential gradients is not explicitly incorporated in the model. However, evaporation from the soil surface results in redistribution of soil moisture by transport from deeper layers. In the present model that process is 'mimicked' following the procedure developed by van Keulen (1975), in which it is assumed that the total moisture withdrawal due to evaporation from the soil surface is distributed over the various soil compartments, following an exponential extinction function, and is moreover influenced by the actual moisture distribution in the soil profile. The extinction coefficient is a soil characteristic and can either be derived from experimental data, or from a detailed model of soil evaporation (van Keulen, 1975). The procedure has been described in detail by Stroosnijder (1981) and van Keulen (1975).

Potential transpiration is also derived from potential evapotranspiration, taking into account the effect of vegetation density and that of the nitrogen status of the vegetation. The influence of vegetation density is described under the assumption that potential transpiration by vegetation that does not cover the soil completely is proportional to its relative energy interception. The latter is calculated under the assumption of exponential extinction of irradiance (Goudriaan, 1977), with an extinction coefficient depending on vegetation type typically varying between 0.5 for erect gramineous vegetation and 0.7 for more planofile herbaceous vegetation. The degree of soil cover is mainly determined by the leaf area of the vegetation, but because that characteristic is not separately tracked in the present model, soil cover is related here to total above-ground biomass by a function that essentially describes the combined effect of specific leaf area and leaf-weight ratio (Watson, 1947).

The effect of the nitrogen status of the vegetation on potential transpiration is related to the mode of stomatal regulation. It appears that some species regulate stomatal opening in such a way that the CO_2 concentration inside the stomatal cavity is maintained at a near-constant value (Goudriaan and van Laar, 1978). Any condition that interferes with CO_2 assimilation then leads to partial stomatal closure in an attempt to reduce the influx of CO_2 into the stomatal cavity. One such condition is nitrogen shortage, the rate of CO_2 assimilation being proportional to the nitrogen concentration in the leaves over a wide range of concentrations (van Keulen and Seligman, 1985; Goudriaan and van Keulen, 1979; Wong, 1979). Hence, suboptimum nitrogen concentration in the leaf tissue results in lower CO_2 assimilation, followed by stomatal closure and consequently lower transpiration rates. In the model it is assumed that in the first period after germination sufficient nitrogen is available in the soil to maintain optimum nitrogen conditions in the vegetation, and that gradually the nitrogen store in the soil is depleted, leading to suboptimum levels. Potential transpiration is reduced in proportion to the ratio of actual growth rate and potential growth rate of the vegetation, taking into account the maintenance requirements.

Actual transpiration is derived from potential transpiration, taking into account the effect of root distribution and activity and soil moisture distribution. It is assumed that root density decreases linearly from the soil surface to the root tip. Root activity is calculated from root density, taking into account the moisture status of the various soil compartments. The latter is described by a schematic function that is zero when the soil moisture content is below wilting point, one when the soil moisture content is higher than 40% of the total plant-available moisture storage capacity (defined as the difference between wilting point and field capacity) and increases linearly in the intermediate range. Total root activity is then normalised in such a way that when the soil moisture status of the various compartments is favourable actual transpiration equals potential transpiration. In reality, some of the soil compartments may be too dry to allow unimpeded uptake of moisture by the roots. A reduction factor is introduced to account for the effect of suboptimum soil moisture conditions. This reduction factor is derived following a 'Veihmeyer-type' approach, i.e. soil moisture is readily available when soil moisture content exceeds 40% of the storage capacity, it is unavailable at wilting point, and availability decreases linearly in the intermediate range. For each soil

compartment water uptake by roots is calculated as 'root activity factor' multiplied by the 'reduction factor' and potential transpiration. The sum of water uptake by the roots in the various compartments is equal to actual transpiration.

For each soil compartment the water balance is now completed, and the rate of change is calculated as: rate of inflow - rate of outflow - rate of soil evaporation - rate of root water uptake.

For special purposes, some auxilliary variables are calculated subsequently, such as the total amount of available moisture in the soil profile and the moisture status of the profile (a value being zero when no moisture is available in the root zone, or one otherwise). The number of days the soil moisture status is above wilting point is calculated for each compartment, which is used later to define the total wetting duration of the profile. That total wetting duration should be related to availability of nitrogen to the vegetation.

Growth of vegetation

The vegetation considered in the model is a mixture of annuals that starts from seed each year. For each site initial biomass after germination is defined, based on an estimate of the total seed stock in the soil and its germination characteristics.

Germination is assumed to take place in the upper 5 cm of the profile, whenever soil moisture in that soil layer is above wilting point. To calculate the moisture status of the soil layer for any particular day, infiltration on that day is also taken into account (rain is assumed to take place at the beginning of the day). If these conditions are fulfilled, the day is considered a germination day. Germination is considered complete when the number of germination days equals the total time required for germination, which is a species characteristic (Breman and Krul, 1982), in the present model an average value being used. For specific situations where the composition of the seed stock is known, a more accurate value can be introduced. If the top- soil dries out before germination is completed, the seedlings are considered to be dying and plant growth resumes only after a rainfall event rewets the top- soil.

At completion of germination, total above-ground biomass is initialised with the predefined initial value. The increase in biomass is defined by a relative growth rate in the early stages of plant growth. In the present version a value of 0.15/d is defined, being typical for a mixture of annuals in Sahelian conditions (Penning de Vries, 1982). These growth rates can be realised, because in the initial stages sufficient plant nutrients are available in the soil to ensure optimum concentrations in the vegetation (Penning de Vries and van Keulen, 1982). When the growth rate calculated on the basis of the constant relative growth rate exceeds a predefined maximum value, that value is substituted.

For both situations, the growth rate is corrected for the ratio of actual and potential transpiration, under the assumption that CO_2 assimilation is reduced in proportion to the reduction in transpiration. That assumption is based on extensive experimental evidence and theoretical treatment of the processes (cf Tanner and Sinclair, 1983; de Wit, 1958).

If the soil dries out, transpiration gradually declines until the whole root zone is at (or below) wilting point, at which point stomata are fully closed and CO_2 assimilation ceases. When such conditions last for some time the vegetation will react with processes that decrease transpirational demand, such as leaf rolling and leaf shedding. In the present model these phenomena are not taken into account in a dynamic way. The number of days on which there is no transpiration is tracked in the model and if it exceeds a certain predefined value, characterising the buffering capacity of the vegetation, the vegetation is assumed to die completely in one day. If a rainfall event occurs before that day is reached, the accumulated stress days are zeroed and accumulation starts again after that moisture has been depleted.

The total number of growing days of the vegetation is tracked by integrating each day that actual transpiration assumes a non-zero value.

Dry-matter accumulation in the roots is not considered in the model, because the growth rate is defined on an above-ground basis only. Rooting depth is, however, considered: the rooting depth at emergence is assumed to be 0.075 m, and under optimum conditions the rate of root extension is 0.04 m/d. Root extension proceeds at that rate until the root tip reaches a soil compartment that is at or below wilting point, after which root extension ceases. Root extension also ceases when a predefined maximum rooting depth has been reached.

The nitrogen balance

The major characteristic of the nitrogen balance, as described in the present model, is that it is highly empirical, which means that it can only be used with extreme caution outside the range of conditions for which the model has been calibrated. In this first approximation several assumptions have been introduced that simplify reality substantially and it may well be necessary to replace some of these during further development of the model.

The mineral nitrogen in the soil is assumed to be in nitrate form, even though in reality some may be present in the form of ammonium (Krul et al, 1982).

At the start of the simulation, an initial amount of mineral nitrogen is assumed to be present in the soil, originating largely from the previous year's root material that has partly decayed. The amount present is therefore proportional to the amount of roots present, for which a typical value for annual vegetation in the Sahel has been chosen (Penning de Vries and van Keulen, 1982).

Mineral nitrogen in a soil compartment can increase by decomposition of organic material, it being assumed that during the growing season the microbial population is more or less in equilibrium, so that all nitrogen in the decomposing material contributes to the mineral nitrogen store. The rate of decomposition is derived from the total amount of organic material present, assuming a constant relative decomposition rate, and taking into account the effect of soil moisture status on microbial activity. In the present model, essentially the relation as given by Beek and Frissel (1973) is used, although conflicting evidence is available in the literature (Stanford and Epstein, 1974; Robinson, 1957).

In the first soil compartment two more processes contribute to mineral nitrogen. Firstly, the influx by rain, which also represents fixation by blue-green algae and free-living bacteria. The concentration of N in rainwater is assumed to be 0.0125 kg/mm. Secondly, decomposition of litter on the soil surface, which consists of plant remnants from the previous season, also provides inorganic nitrogen to the top soil compartment. The rate of decomposition of litter is described in a similar way as for the organic matter in the soil, i.e. a constant relative decomposition rate, corrected for the moisture content in the top soil compartment.

It is assumed that the contribution of stable organic material to the supply of mineral nitrogen is negligible.

A major problem in the description of the processes of the nitrogen balance treated so far is that estimates have to be made of the initial size of the various components. In the calibration runs most of the values were derived from experimental data collected in the Sahelian zone (Penning de Vries and Djitèye, 1982).

Mineral nitrogen will move with water flow. Hence, during a rainfall event, leaching of nitrogen may take place. The rate of outflow of nitrogen from any compartment is calculated as the rate of water flow from that compartment multiplied by the average concentration of nitrogen in the 'outflow' and the 'inflow' compartment. Finally, that value is multiplied by a 'leaching efficiency' (van Veen et al, 1981).

Uptake of nitrogen by the vegetation is assumed to take place only passively, i.e. with the transpiration stream. The rate of uptake from each compartment is thus obtained as root water uptake multiplied by the concentration of N in that compartment, multiplied by a nitrogen uptake efficiency. Total uptake of nitrogen by the vegetation is the sum of uptake from the various compartments in the root zone. This formulation may be an oversimplification, because in reality it seems that if the demand for nitrogen of the growing vegetation is higher than can be supplied by passive uptake, additional uptake can take place by diffusion of nitrogen to the root surface (van Keulen et al, 1975).

For each soil compartment, the nitrogen balance is now completed by formulating the rate of change as: rate of mineralisation plus rate of inflow from the overlying compartment minus rate of outflow to the underlying compartment minus rate of root nitrogen uptake.

Some model specifications

A complete listing of the model, formulated in the simulation language CSMP is given in Appendix 1, while a glossary is provided in Appendix 2.

As explained earlier, the time interval of integration is one day, and integration is performed according to the simple rectilinear integration method.

Results and discussion

It should be stressed that the results presented are of a preliminary nature, because the model is still under development and further adaptations and changes are certainly necessary.

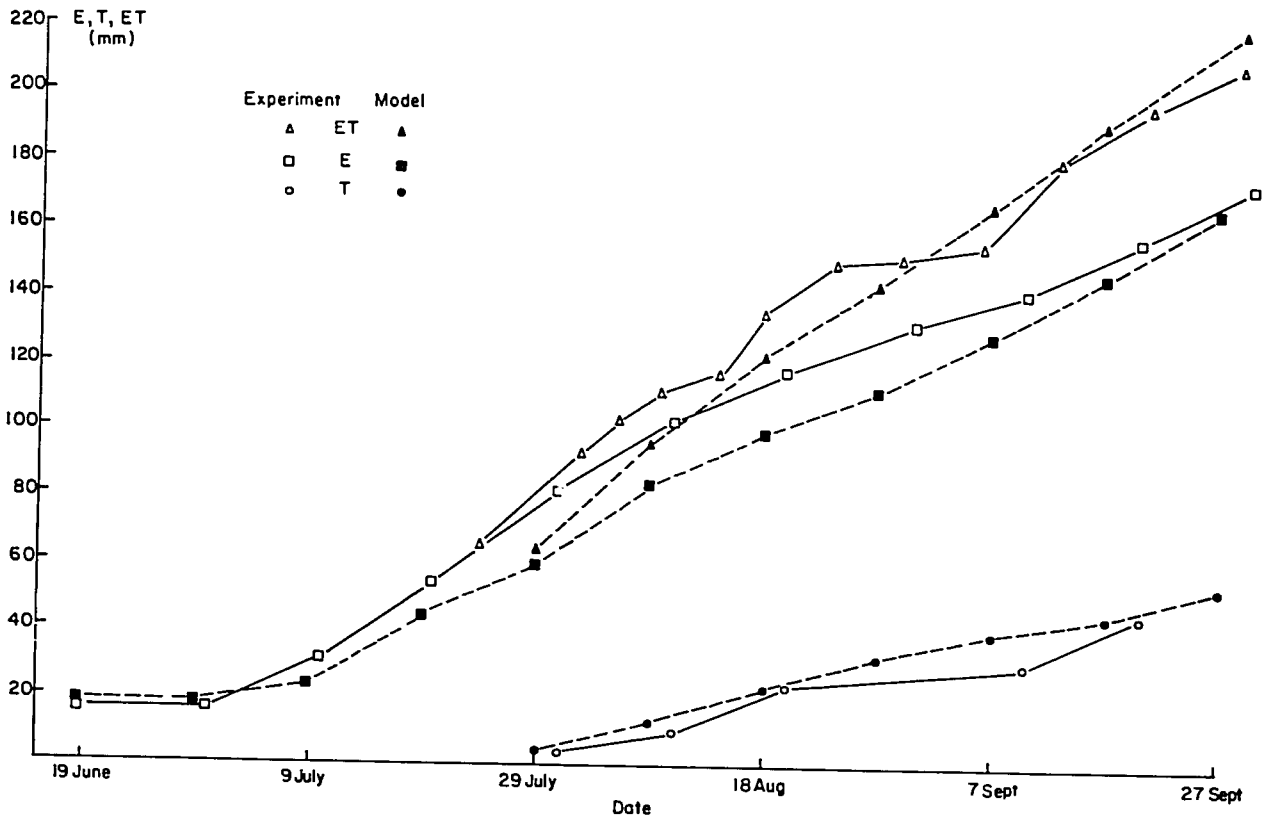
Calibration runs were carried out with data from an experiment carried out in Niono, Mali (5° 45'W, 14° 30'N), in 1978 on a sandy soil (Stroosnijder and Kone, 1982).

The measured and calculated terms of the water balance are given in Figure 1. In the experiment total evapotranspiration was determined by measurement of total soil moisture by neutron moderation, taking into account infiltration as measured at the site. Evaporation from the soil was determined separately and the difference between the two terms was calculated as crop transpiration. This results in the observation that cumulative transpiration sometimes declines, a situation that in reality will not have occurred.

Measured and simulated values are of the same order of magnitude, although individual values sometimes deviate up to 15%. However, taking into account the simple description of the water balance and the fact that the soil at the experimental site is rather heterogeneous, whence it is difficult to define soil physical parameters unequivocally, the results are satisfactory.

The calculated biomass at day 268 (25 September) was 1860 kg/ha, which is substantially higher than the 1400 kg/ha measured in the experiment. However, at that particular site the vegetation consisted predominantly of Zornia glochidiata, a leguminious species with a relatively short growth cycle and hence a low total dry-matter yield. The average yield on the sandy soil of the ranch was substantially higher that year and may have approached the calculated value. In the Zornia plot growth of the vegetation ceased before day 268, not because of moisture shortage (even after that day there was sufficient moisture in the soil to sustain plant growth) but due to photoperiodic effects. It has been observed in the Sahelian region that most of the plant species are very photoperiod-sensitive. In the model this effect is not incroporated, so that only moisture shortage causes cessation of growth. Evidently, this omission affects the degree of realism of the model, and, if possible, some sort of quantitative description of the effect of photoperiodism on phenological development of the vegetation should be included.

Figure I. Measured and calculated values of evaporation (E), transpiration (T) and evapotranspiration (ET), Niono, Mali, 1978



From a comparison of the measured and simulated soil moisture profiles on three dates during the growing season (Figure 2), it appears that the model predictions are not very accurate. The depth of wetting is much deeper in reality than calculated by the model. However, simulated ET values are similar to the measured values (Figure 1), so the main difference is in the distribution of soil moisture. The reason(s) for these discrepancies are not clear: it could be speculated that redistribution of moisture takes place under the influence of gravity, a process not accounted for in the model. Such an effect could be mimicked in the model by assuming a somewhat lower value for field capacity, thus inducing deeper infiltration. Experimentation with the model has shown, however, that to achieve the measured depth of wetting, unrealistically low values would have to be introduced. It seems, therefore, that at this stage the various terms of the water balance and their description in the model need to be reconsidered. These results are somewhat disappointing, because one of the aims of the model is to predict total nutrient uptake by the vegetation as a function of the depth and duration of soil wetting, based on the assumption that nutrient supply from the soil is mainly determined by that characteristic (cf Harpaz, 1975).

In Figure 3 measured and simulated uptake of nitrogen are compared using data from a transect in the Sahel studied for four consecutive seasons (Breman and Krul, 1982). There is considerable scatter in the data, but this may be partly attributed to the fact that no attempt was made to include site- or year-specific information for the description of the nitrogen balance in the model.

The relationship with integrated soil wetting is illustrated in Figure 4, using the same data. Despite the fact that the moisture distribution in the calibration runs was not very satisfactory, it seems that a relationship exists between the calculated product of depth and duration of soil wetting and total nitrogen uptake as measured in the field. Longer wetting generally leads to higher nitrogen availability, up to a value of about 1500 layer.d, after which levelling off occurs. These results indicate that the length of the period during which conditions are favourable for microbial activity, and hence for decomposition of organic material, is a major determinant of the soil nitrogen supply.

Figure 2. Measured and simulated soil moisture profiles on three dates during the growing season, Niono, Mali, 1978

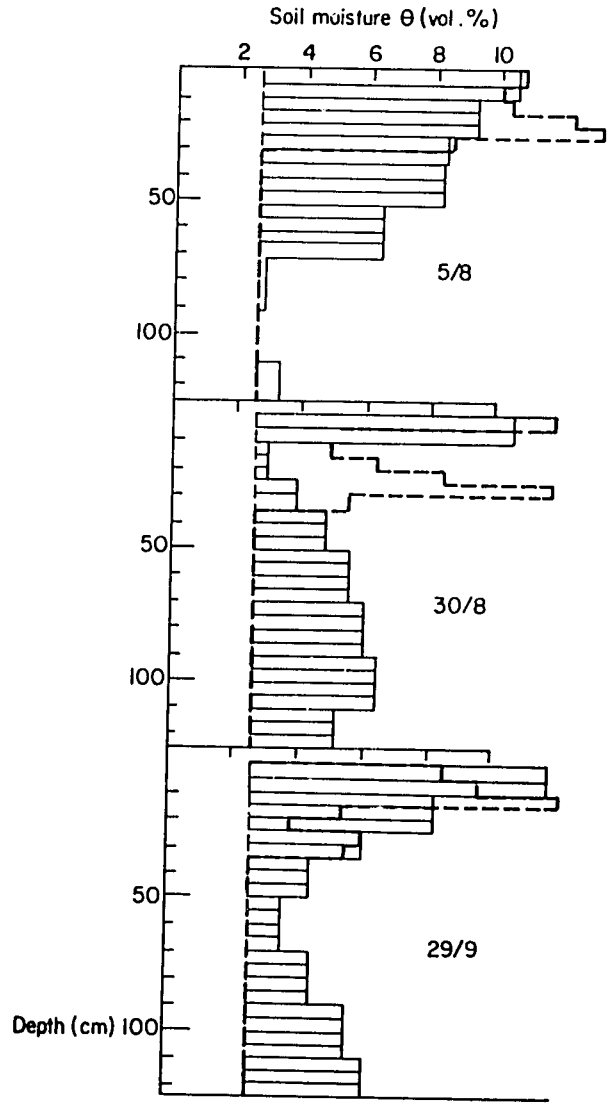


Figure 3. Relationship between measured and simulated uptake of nitrogen of vegetation, with and without a legume component, from a transect in the Sahel, 1976-79

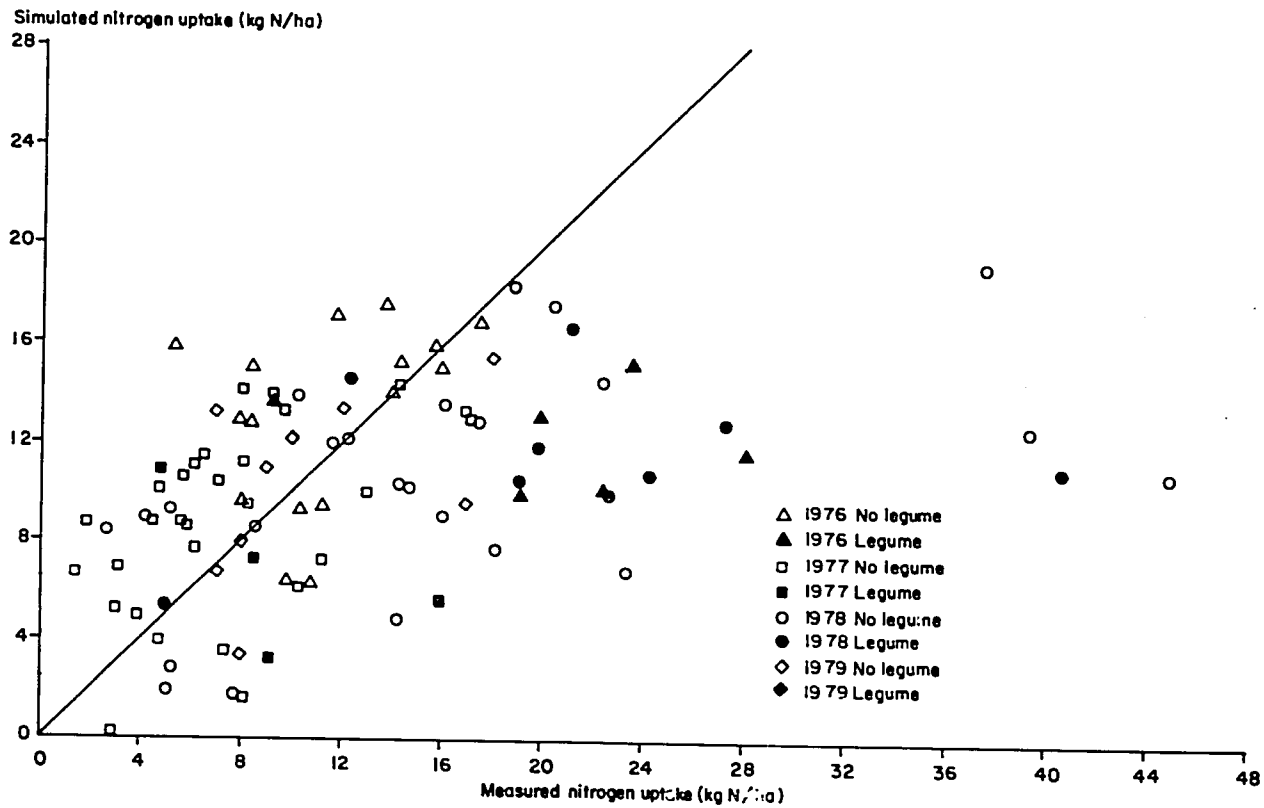
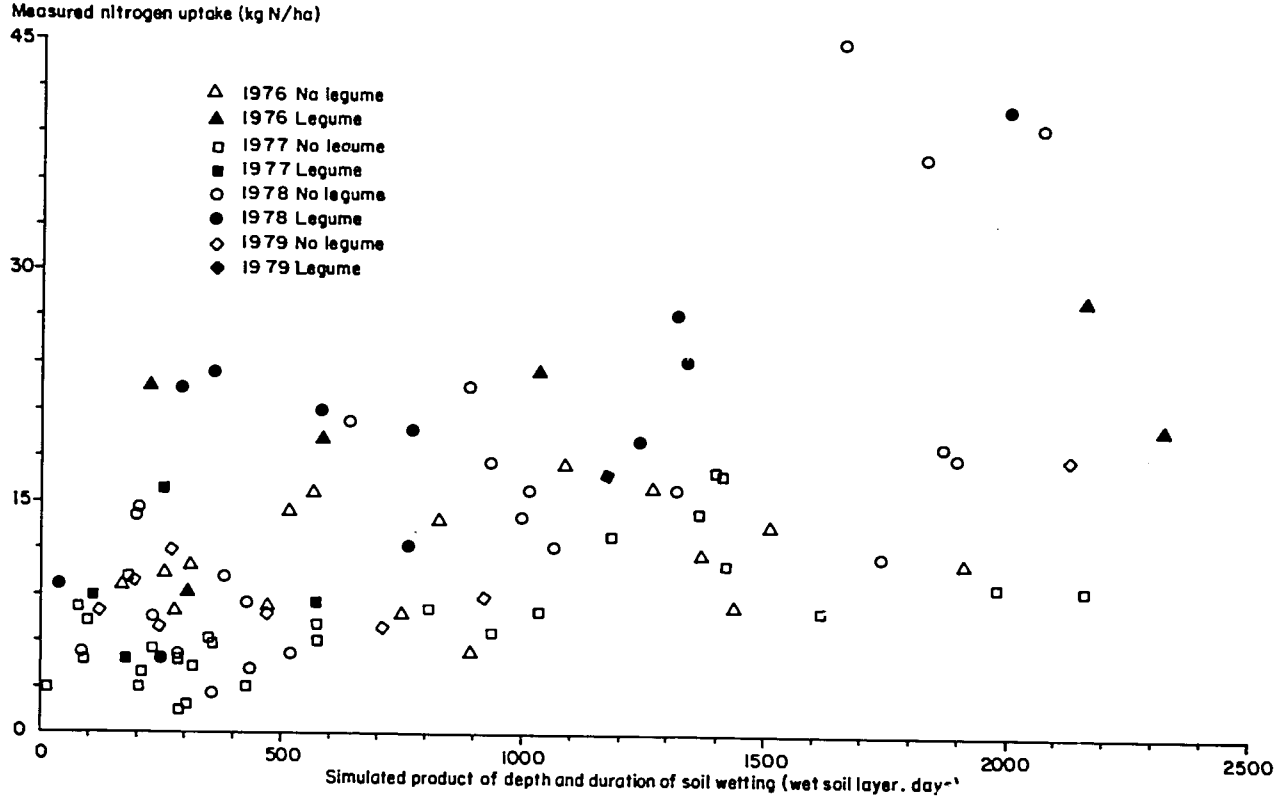


Figure 4. Relationship between the simulated product of depth and duration of soil wetting (wet soil layer. days) and measured nitrogen uptake (kg N/ha) of vegetation, with and without a legume component, from a transect in the Sahel, 1976-79



The scatter of the data is still rather large for which there are a number of possible reasons:

1. In the present description no distinction is made between soil wetting in the surface horizons, where most of the organic material is concentrated, and in deeper layers. Improvements in the relation could possibly be expected if the wetting depth and duration were weighted for organic matter content of the soil.
2. The field data, covering many different sites and a number of years, cover a large variety of vegetation types. The composition of the vegetation differs considerably from year to year and from site to site. This phenomenon has consequences for the nitrogen economy as well, because different species may mature at different times. Therefore, it could be that, at harvest time at the end of the rainy season, some of the nitrogen that was taken up by the vegetation was lost already by seed shedding, especially because those organs act as a strong sink for nutrients at the end of the plant's life cycle (de Ridder et al, 1981). One of the factors that causes discrepancies is the proportion of legumes in the final biomass. Most data points for which more than 20% of the final biomass consisted of legumes are at the upper side of the graph, indicating the contribution of nitrogen fixed from the atmosphere.
3. In the present formulation it is assumed that practically all the nitrogen available to the vegetation in the current season originates from plant remnants from the previous season. Thus, more nitrogen would be available after a relatively favourable season with a large biomass than after a relatively unfavourable season, while in a favourable season following a drought year there could be some contribution from residual nitrogen that was not taken up in the water-limited year. None of these differentiations have been taken into account in the model.

Concluding remarks

The model as presented in this paper can be considered partly as a summary model (Penning de Vries, 1982), comprising simple descriptions of processes that are relatively well understood. Partly, however, the model is highly empirical and therefore speculative, especially for the soil- and vegetation-nitrogen balances.

In some respects, particularly (evapo)transpiration and dry-matter production, the performance of the model is reasonable; in other aspects, for instance moisture distribution, its performance is rather weak. More work is needed on these.

Another aspect that needs further study is the relationship between the nitrogen status of the vegetation and its growth and production. In the present formulation these two characteristics are completely independent, the growth rate being derived from experimental data. A more fundamental approach, whereby the processes of assimilation and respiration as influenced by the nitrogen status of the vegetation are considered, could be an attractive alternative (cf van Keulen and Seligman, 1985).

All-in-all it may be concluded that the present model is a useful first approximation for the description and understanding of natural vegetation in semi-arid regions, but that for wider application further development is necessary.

REFERENCES

Beek J and Frissel M J. 1973. Simulation of nitrogen behaviour in soils. Simulation Monographs, PUDOC, Wageningen, the Netherlands. 76 pp.

Breman H and Krul J M. 1982. La pluviosité et la production de fourrage sur les pâturages naturels.. In: F W T Penning de Vries and A M Djiteye, eds. La productivité des pâturages sahéliens. Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle. Agricultural research report 918, PUDOC, Wageningen, the Netherlands.

Goudriaan J. 1977. Crop micrometeorology: A simulation study. Simulation Monographs, PUDOC, Wageningen, the Netherlands. 249 pp.

Goudriaan J and van Keulen H. 1979. The direct and indirect effects of nitrogen shortage on photosynthesis and transpiration in maize and sunflower. Neth. J. Agric. Sci. 27:227-234.

Goudriaan J and van Laar H H. 1978. Relations between leaf resistance, CO_2-concentration and CO_2-assimilation in maize, beans, lalang grass and sunflower. Photosynthetica 12:241-249.

Harpaz Y. 1975. Simulation of the nitrogen balance in semi-arid regions. Ph D thesis, Hebrew University, Jerusalem. 134 pp.

Hoogmoed W B and Stroosnijder L. 1984. Crust formation on sandy soils in the Sahel. I. Rainfall and infiltration. Soil Till. Res. 4:5-23.

van Keulen H. 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs, PUDOC, Wageningen, the Netherlands. 176 pp.

van Keulen H and Seligman N G. 1985. Simulation of water use, nitrogen nutrition and growth of a spring wheat crop. Simulation Monographs, PUDOC, Wageningen, the Netherlands. (In prep.)

van Keulen H, Seligman N G and Benjamin R W. 1981. Simulation of water use and herbage growth in arid regions - A re-evaluation and further development of the model Arid Crop. Agric. Syst. 6:158-193.

van Keulen H, Seligman N G and Goudriaan J. 1975. Availability of anions in the growth medium to roots of an actively growing plant. Neth. J. Agric Sci. 23:131-138.

Krul J M, Penning de Vries F W T and Traore K. 1982. Les processus du bilan d'azote. In: F W T Penning de Vries and A M Djiteye, eds. La productivité des pâturages sahéliens. Une étude des sols, des végétations et de l'éxploitation de cette ressource naturelle. Agricultural research report 918. PUDOC, Wageningen, the Netherlands.

Penning de Vries F W T. 1982a. La production potentielle des pâturages naturels. In: F W T Penning de Vries and A M Djiteye, eds. La productivité des pâturages sahéliens. Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle. Agricultural research report 918, PUDOC, Wageningen, the Netherlands.

Penning de Vries F W T. 1982b. Phases of development of models. In: F W T Penning de Vries and H H van Laar, eds. Simulation of plant growth and crop production. Simulation Monographs, PUDOC, Wageningen, the Netherlands.

Penning de Vries F W T and van Keulen H. 1982. La production actuelle et l'action de l'azote et du phosphore. In: F W T Penning de Vries and A M Djiteye, eds. La productivité de pâturages sahéliens. Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle. Agricultural research report 918, PUDOC, Wageningen, the Netherlands.

de Ridder N, Seligman N G and van Keulen H. 1981. Analysis of environmental and species effects on the magnitude of biomass investment in the reproductive effort of annual pasture plants. Oecologia 45:263-271.

Rietveld J J. 1978. Soil non-wettability and its relevance as a contributing factor to surface runoff on sandy dune soils in Mali. Report, Department of theoretical production ecology, Agricultural University, Wageningen, the Netherlands.

Ritchie J T. 1972. Model for predicting evapotranspiration from a row crop with incomplete cover. Water Res. Rep. 8:1208-1213.

Robinson J B D. 1957. The critical relationship between soil moisture content in the region of the wilting point and mineralization of native soil nitrogen. J. Agric. Sci. 49:100-105.

Stanford G and Epstein E. 1974. Nitrogen mineralization-water relations in soils. Soil Sci. Soc. Am. Proc. 38:103-107.

Stroosnijder L. 1981. Simulation of the soil water balance. In: F W T Penning de Vries and H H van Laar, eds. Simulation of plant growth and production. Simulation Monographs, PUDOC, Wageningen, the Netherlands.

Stroosnijder L. 1976. Infiltration and redistribution of water in soils. Agricultural research report 847, PUDOC, Wageningen, the Netherlands. 213 pp. (Dutch with English summary).

Stroosnijder L and Kone D. 1982. Le bilan d'eau du sol. In: F W T Penning de Vries and A M Djiteye, eds. La productivité des pâturages sahéliens. Une étude des sols, des vegetations et de l'exploitation de cette ressource naturelle. Agricultural research report 918, PUDOC, Wageningen, the Netherlands.

Tanner C B and Sinclair T R. 1982. Efficient water use in crop production: Research or re-search. In: H M Taylor, W R Jordan and T R Sinclair, eds. Limitations on efficient water use in crop production. Am. Soc. Agron., Monograph. ASA Monographs Inc., Madison, Wisc., USA.

van Veen J A, McGill W H, Hunt H W, Frissel M J and Cole C V. 1981. Simulation models of the terrestrial nitrogen cycle. In: F E Clark and T Rosswal, eds. Nitrogen cycling in terrestrial ecosystems. Processes, eco-system strategies and management impacts. Ecol. Bull., Stockholm.

Watson D J. 1947. Comparative physiological studies on the growth of field crops. I. Variation in net assimilation rate and leaf area between species and varieties, and within and between years. Ann. Bot. 11:41-76.

de Wit C T. 1958. Transpiration and crop yields. Agricultural research report 648, PUDOC, Wageningen, the Netherlands. 88 pp.

Wong S C. 1979. Elevated atmospheric pressure on CO_2 and plant growth. I. Interactions of nitrogen, nutrition and photosynthetic capacity in C3 and C4 plants. Oecologia 44:68-74.

Appendix 1 Model listing.

```
      TITLE SAHEL MODEL
      SYSTEM NPOINT = 2000.
      SYSTEM BCD
      INITIAL
      NOSORT
      STORAGE AIRDR(25),  AIRDRY(5),  BOUND(5),   DPTH(25), ...
              DPTHC(25),  EVAPR(25),  F(25),      FLDCAP(5), ...
              FLDCP(25),  MF(25),     NCONC(25),  NLEACH(25), ...
              NUPTAK(25), RDENF(25),  RDSUBS(25), RNMIN(25), ...
              RRDENF(25), STORC(25),  TCK(25),    TRAN(25), ...
              VAR(25),    WIN(25),    WLTPNT(5),  WLTPT(25)
      FIXED I,N,K
      PARAM N = 23
      TABLE TCK(1-23) = 10*50.,5*100.,8*250.
      TDEPTH  = 0.
      DEPTH(1) = 0.
      DO 10 I  = 1,N
      DPTH(I+1) = DPTH(I)+TCK(I)
      TDEPTH    = TDEPTH +TCK(I)
      DPTHC(I)  = DPTH(I)+0.5*TCK(I)
   10 CONTINUE
      K      = 1
      DO 30 I = 1,N
      WLTPT(I) = WLTPNT(K)
      FLDCP(I) = FLDCAP(K)
      AIRDR(I) = AIRDRY(K)
      STORC(I) = FLDCP(I)-WLTPT(I)
      IF(DPTH(I+1).LT.BOUND(K)) GOTO 20
      K        = K+1
   20 CONTINUE
   30 CONTINUE
      DO 40 I = 1,N
      WI(I) = TCK(I)*AIRDR(I)
   40 CONTINUE
```

```
      INCON CROPSI = -1.
      RTDI  = RTDG
      TABLE SUBSTI(1-23) = 2*325.,2*100.,2*65.,2*35.,2*10.,3*7.,...
                           2*5.,4*3.,4*0.
      DO 50 I = 1,N
      INI(I) = IFRMN*SUBSTI(I)
50    CONTINUE
      DYNAMIC
      NOSORT
      DAY    =    STDAY+TIME
      RAIN   =    ISOHC*AFGEN(RAINTB,DAY)
      INTC   =    INSW(1.0-RAIN,1.0,RAIN)
      RNOFF  =    RNOFFC*AFGEN(ROFINT,RAIN)*RAIN
      INFR   =    RAIN-RNOFF-INTC
      PETNR  =    AFGEN(PETNRT,DAY)
      PETR   =    AFGEN(PETRT,DAY)
      RNPAR  =    INSW(RAIN-0.001,-1.,1.)
      EVAPTR =    INSW(RNPAR,PETNR,PETR)
      SCOV   =    1.0-EXP(-0.5*BIOM/AFGEN(SSWTB,BIOM))
      PDGRT  =    LIMIT(0.,1.,BIOM/2500.)*PDGRTM
      NFACT  =    AMIN1(1.0,(1.5*DGRATE+.015*BIOM)/...
                  (1.5*PDGRT+.015*
                  (BIOM+NOT(BIOM))))
      TRANP  =    SCOV*INSW(CROPST,0.,EVAPTR)*NFACT
      EVAPP  =    AMAX1(0.,EVAPTR-TRANP)
      DSLER  =    INTGRL(90.001,1.-INSW(RAIN-0.001,0.,...
                  INSW(EVAPP-INFR,DESLER-0.001,0.)))
      AEVAP  =    AMIN1(EVAPP,EVAPC*(SQRT(DSLER)-SQRT(DSLER-1)))
      SUMRRD =    0.
      DO 60 I = 1,N
      EFFAC   =  AFGEN(EFFACT,AMIN1(1.0,(W(I)/TCK(I)-WLTPT(I))/...
                 STORC(I)))
      RRDENF(I) = TCK(I)*EFFAC*AMAX1(0.,(RTD-DPTHC(I))/...
                  (RTD+NOT(RTD)))
      SUMRRD   =  SUMRRD+RRDENF(I)
```

```
   60 CONTINUE
      DO 70 I = 1,N
      RDENF(I) = RRDENF(I)/(SUMRRD+NOT(SUMRRD))
      TRAN(I)  = 0.
      EVAPR(I) = 0.
   70 CONTINUE
      STRAN = 0.
      DO 80 I = 1,N
      REDF = LIMIT(0.,1.,(W(I)/TCK(I)-WLITPT(I))/(LMF*STORC(I)))
      TRAN(I) = RDENF(I)*REDF*TRANP
      STRAN =  STRAN+TRAN(I)
      IF(DPTH(I+1).GT.RTD) GOTO 90
   80 CONTINUE
   90 CONTINUE
      SUMT   = 0.
      DO 100 I = 1,N
      VAR(I) = AMAX1(W(I)/TCK(I)-AIRDR(I),0.)*EXP(-0.001*PROP...
               *DPTHC(I))
      SUMT   = SUMT+VAR(I)*TCK(I)
  100 CONTINUE
      SEVAP  = 0.
      DO 110 I = 1,N
      F(I)   =  TCK(I)*VAR(I)/(SUMT+NOT(SUMT))
      EVAPR(I) = AMIN1(W(I)-TCK(I)*AIRDR(I),F(I)*AEVAP)
      SEVAP  =  SEVAP+EVAPR(1)
  110 CONTINUE
      EVAPPR = AMAX1(0.,EVAPTR-INTC-STRAN)
      WIN(1) = AMAX1(0.,INFR-EVAPPR)
      SEVAP  = INSW(WIN(1)-0.001,SEVAP,EVAPPR)+INTC
      DO 120 I = 2,N+1
      WIN(I) = AMAX1(0.,WIN(I-1)-(FLDCP(I-1)*TCK(I-1)-...
               (W(I-1)-INSW(WIN(1)-0.001,EVAPR(I-1),0.)-...
               TRAN(I-1)))/DELT)
  120 CONTINUE
      DO 130 I = 1,N
```

```
      RCW(I) = WIN(I)-WIN(I+1)-INSW(WIN(1)-0.001,...
               EVAPR(I),0.)-TRAN(I)
130   CONTINUE
      W      = INTGRL(WI,RCW,23)
      WGER   = 0.
      DO 140 I = 1, N
      IF(DPTH(I+1).GT.GDPTH) GOTO 150
      WGER   = WGER+W(I)
140   CONTINUE
150   CONTINUE
      WGER   = WGER+INFR
      WTOTR  = 0.
      MSSTAT = 0.
      DO 160 I = 1,N
      WTOTR  = WTOTR+W(I)*LIMIT(0., TCK(I),RTD-DPTH(I))/TCK(I)
      MSSTAT = MSSTAT+INSW(W(I)-WLTPT(I)*TCK(I)-.001,0.,1.)*...
               LIMIT(0.,TCK(I),RTD-DPTH(I))/TCK(I)
      IF(DPTH(I+1).GE.RTD) GOTO 170
160   CONTINUE
170   CONTINUE
      GERD   = FCNSW(WGER-GDPTH*WLTPT(1),1.,1.,0.)
      MSFG   = INSW(CROPST, INSW(WGER-GDPTH*WLTPT(1),0.,1.),0.)
      EMPTR  = AND(GERD,MSSTG)*MSSTG/DELT
      PUSHE  = AND(-CROPST,MSSTG-GERMT)
      MSSTG  = INTGRL(0.,MSFG*(1.-PUSHE)-PUSHE*MSSTG/DELT-EMPTR*...
               (1.-PUSHE))
      KILD   = FCNSW(STRAN,0.,0.,1.)
      PUSHD  = AND (CROPST,MSSTD-DEADT)
      MSFD   = INSW(-STRAN,0.,1.)*INSW(CROPST,0.,1.)*(1.-PUSHD)
      EMPTRR = AND(KILD,MSSTD)*MSSTD/DELT
      MSSTD  = INTGRL(0.,MSFD-PUSHD/DELT*MSSTD-EMPTRR*(1.-PUSHD))
      SWPDS  = 0.
      DO 180 I= 1,N
      SWPDS  = SWPDS+AND(RTD-DPTH(I)+0.001,DPTH(I+1)-RTD)*...
               INSW(W(I)-WLTPT(I)*TCK(I),0.,1.)
```

```
180  CONTINUE
     GRTD     = INSW(CROPST,0.,INSW(MXRTD-RTD,0.,OGRTD*SWPDS))*...
                (1.-PUSHD)
     RTD      = INTGRL(0.,RTDI*PUSHE/DELIT+GRTD-PUSHD/DELIT*RTD)
     GRRATE   = AMIN1(RGR*BIOM,DGRATE)*STRAN/(TRANP+NOT(TRANP))
     RGROW    = GRRATE/(BIOM+NOT(BIOM))
     TRR      = STRAN/(TRANP+NOT(TRANP))
     BIOM     = INTGRL (0.,IBIOM*PUSHE/DELIT+GRRATE*(1.-PUSHD)-...
                PUSHD*BIOM)
     TDBIOM   = INTGRL(0.,PUSHD*BIOM)
     CROPST   = INTGRL(CROPSI,PUSHE*2.-PUSHD*2.)
     GROWD    = INSW(CROPST,0.,1.)*INSW(MSSTAT-.001,0.,1.)
     TGROWD   = INTGRL(0.,GROWD)
     TOTNUP   = 0.
     DO 190 I= 1,N
     NCONC(I)= NI(I)/W(I)
     NUPTAK(I) = AMIN1(NI(I),NUE*NCONC(I)*TRAN(I))
     TOTNUP   = TOTNUP+NUPTAK(I)
190  CONTINUE
     DO 200 I= 1,N
     NLEACH(I) = AMIN1(NI(I)-NUPTAK(I),LE*WIN(I+1)*(NCONC(I)+...
                 NCONC(I+1))/2.)
     MF(I)    = AFGEN(MFT,AMAX1(0.,(W(I)/TCK(I)-WLITPT(I)))/...
                STORC(I))
     RDSUBS(I) = RDR*MF(I)*SUBSTR(I)
     RCSUBS(I) = -RDSUBS(I)
200  CONTINUE
     RCLIT    = RDLIT*MF(1)*LITTER
     RNMLIT   = FRNLIT*RCLIT
     RNMIN(1)= FRNR*RDSUBS(1)
     RCN(1)   = NCR*INFR+RNMLIT+RNMIN(1)-NLEACH(1)-...
                NUPTAK(1)
     TRNMIN   = RNMIN(1)
     DO 210 I= 2,N
     RNMIN(I) = FRNR*RDSUBS(I)
```

```
      TRNMIN  = TRNMIN+RNMIN(I)
      RCN(I)  = RNMIN(I)+NLEACH(I-1)-NLEACH(I)-NUPTAK(I)
210   CONTINUE
      TMINR   = INTGRL(0.,TRNMIN)
      TMINL   = INTGRL(0.,RNMLIT)
      TMINRL  = INTGRL(0.,TRNMIN+RNMLIT)
      LITTER  = INTGRL(ILIT,-RCLIT)
      SUBSTR  = INTGRL(SUBSTI,RCSUBS,23)
      NI      = INTGRL(INI,RCN,23)
      NDBIOM  = INTGRL(0.,PUSHD*TNITUP)
      TNITUP  = INTGRL(0.,IFRNB*IBIOM*PUSHE/DELT+TOTNUP*(1.-PUSHD)-...
                PUSHD*TNITUP)
      NCBIOM  = TNITUP/(BIOM+NOT(BIOM))
      TSUBST  = 0.
      TOTNI   = 0.
      DO 220 I= 1,N
      TSUBST  = TSUBST+SUBSTR(I)
      TOTNI   = TOTNI+NI(I)
      RAVW(I) = FCNSW(W(I)-WLTPT(I)*TCK(I),0.,0.,1./DELT)
      RAVW1(I) = RAVW(I)*MF(I)
220   CONTINUE
      AVW     = INTGRL(IAVW,RAVW,23)
      AVW1    = INTGRL(IAVW,RAVW1,23)
      TAVW    = 0.
      TAVW1   = 0.
      DO 230 I= 1,N
      TAVW    = TAVW+AVW(I)
      TAVW1   = TAVW1+AVW1(I)
230   CONTINUE
      GERWAV  = INTGRL(0.,PUSHE)
      GDAY    = INTGRL(0.,PUSHE*TIME-PUSHD/DELT*GDAY)
      EGDAY   = INTGRL(0.,PUSHD*TIME-PUSHD/DELT*EGDAY)
      DRAIN   = WIN(N+1)
      TDRAIN  = INTGRL(0.,DRAIN)
      TRAIN   = INTGRL(0.,RAIN)
```

```
      TOTINF  = INTGRL(0.,INFR)
      TEVAP   = INTGRL(0.,SEVAP)
      TOTRAN  = INTGRL(0.,STRAN)
      ET      = INTGRL(0.,SEVAP+STRAN)
      FUNCTION RAINTB = 0.,0.,4.,0.,5.,25.,6.,0.,9.,0.,10.,25.,...
                        11.,0.,14.,0.,15.,25.,16.,0.,19.,0.,20.,...
                        25.,21.,0.,24.,0.,25.,25.,26.,0.,29.,0.,...
                        30.,25.,31.,0.,34.,0.,35.,25.,36.,0.,39.,0.,...
                        40.,25.,41.,0.,44.,0.,45.,25.,46.,0.,49.,0.,...
                        50.,25.,51.,0.,54.,0.,55.,25.,56.,0.,59.,0.,.
                        60.,25.,61.,0.,64.,0.,65.,25.,66.,0.,69.,0.,.
                        70.,25.,71.,0.,74.,0.,75.,25.,76.,0.,79.,0.,.
                        80.,25.,81.,0.,84.,0.,85.,25.,86.,0.,89.,0.,.
                        90.,25.,91.,0.,94.,0.,95.,25.,96.,0.,99.,0.,.
                        100.,0.
*     FUNCTION EVPTB =  0.,4.,31.,4.,32.,5.,59.,5.,60.,6.,90.,6.,...
*                       91.,6.5,151.,6.5,152.,6.,212.,6.,213.,5.,...
*                       243.,5.,244.,5.5,304.,5.5,305.,4.5, 334.,4.5,.
*                       335.,4.,365.,4.
      FUNCTION PETINRT = 91.,6.3,105.,6.3,135.,7.0,166.,6.9,196.,6.1,...
                         227.,5.9,258.,5.8,288.,5.3,304.,5.3
      FUNCTION PETRT  = 91.,4.3,105.,4.3,135.,5.0,166.,4.9,196.,4.1,...
                         227.,3.9,258.,3.8,288.,3.3,304.,3.3
      FUNCTION ROFINT = 0.,0.,5.,0.2,10.,0.5,20.,1.2,30.,1.55,...
                         70.,1.7,200.,1.7
      FUNCTION EFFACT = -10.,0.,0.,0.,0.4,1.,1.1,1.
      FUNCTION SSWTB  = 0.,500.,250.,500.,400.,600.,15000.,600.
      FUNCTION MFT    = 0.,0.,.25,.05,.5,.3,.75,.75,1.,1.,1.5,.5
      TABLE FLDCAP(1-3) = 0.225, 0.145, 0.09
      TABLE WLTPNT(1-3) = 0.075, 0.055, 0.028
      TABLE AIRDRY(1-3) = 0.025, 0.018, 0.009
      TABLE BOUND(1-3)  = 150, 1200, 3001
      TABLE IAVW(1-23)  = 23*0.
      PARAM STDAY  = 0.
      PARAM ISOHC  = 1.
```

```
PARAM RNOFFC = 0.2
PARAM EVAPC  = 3.3
PARAM PROP   = 15., LMF    = 0.4
PARAM GERMT  = 1.5, GDPTH  = 50.
PARAM IBIOM  = 15., RGR = 0.15, DGRATE = 35., PDGRIM = 250.
PARAM RTDG   = 75., OGRTD = 40., MXRTD = 1500.
PARAM IFRNB  = 0.025, IFRMN = 0.010, NUE = 0.9, LE = 0.7
PARAM FRNLIT = 0.0075, FRNR = 0.0092, NCR = 0.0125
PARAM RDR    = 0.05, RDLIT = 0.05, ILIT = 500.
PARAM DEADT  = 4.
PARAM HRVST  = 300.
PRINT W(1-23),  TDRAIN,   TRAIN,   TOTINF,   TOTRAN,   TEVAP,  ...
      ET,       RTD,      TGROWD,  GDAY,     GERWAV,   GRRATE, ...
      TDBIOM,   TNITUP,   NCBIOM,  NDBIOM,   TMINR,    TMINL,  ...
      TMINRL,   TSUBST,   TAVW,    TAVW1,    STRAN,    TRANP,  ...
      SEVAP,    AEVAP,    WTOTR,   LITTER,   BIOM,     WIN(1), ...
      EVAPPR,   EVAPP
OUTPUT RGROW,TRR,BIOM,SCOV,NFACT
PAGE NTAB = 3, SYMBOL = (R,T,B,S,N)
OUTPUT TNITUP, NCBIOM,NDBIOM,TMINR,TMINRL
PAGE NTAB = 5, SYMBOL = (T, L, D, R, M)
TIMER FINTIM = 0., DELT = 1., PRDEL = 1., OUTDEL = 1.
METHOD RECT
END
```

Appendix 2. WBNLIM variable definitions.

AEVAP	Actual soil evaporation rate not considering daily rainfall-enhanced evaporation (mm/day)
AIRDR	Volumetric water content of a soil layer when air dry (m^3/m^3)
AIRDRY	Volumetric water content of a soil horizon when air dry (m^3/m^3)
AVW	Number of days water content of a soil layer is above wilting point (d)
AVW 1	AVW weighted by function relating rate of decomposition of organic material to soil moisture content (d)
BIOM	Weight of live shoot (kg DM/ha)
BOUND	Depth of boundary between soil horizons (mm)
CROPSI	Initial crop status (CROPST) (-)
CROPST	Crop status indicating live standing crop present (CROPST = 1) or not (CROPST = 0)
DAY	Number of days in the year from 1 January
DEADT	Duration of no transpiration before death (d)
DELT	Time step of calculations
DGRATE	Nutrient limited potential shoot growth rate (kg DM/ha/d)
DEPTH	Depth of top of a soil layer (mm)
DEPTHC	Depth of center of a soil layer (mm)
DRAIN	Water drained below the deepest soil layer (mm)
DSLER	Number of days plus 1 since last effective rain (d)
EFFAC	Reduction factor for root effectiveness as a function of soil moisture content (-)
EFFACT	Table of EFFAC versus reduced soil moisture content (-)
EGDAY	Day number of end of last growing period
EMPIR	Rate seed imbibition period is reduced when soil becomes too dry prior to germination (d/d)
EMPIRR	Rate drought period without transpiration is reduced when transpiration resumes (d/d)
ET	Cumulative sum of evapotranspiration (mm)

EVAPC	Experimentally determined evaporation constant (mm/d)
EVAPP	Soil evaporation rate potential (mm/d)
EVAPR	Actual evaporation rate from a soil layer (mm/d)
EVAPTR	Potential evapotranspiration rate (mm/d)
EVPTB	Table of Penman potential evaporation rates (mm/d)
F	Normalized fraction of soil evaporation from a soil layer (-)
FINTIM	Last simulation day number
FLDCAP	Volumetric water content of a soil horizon at field capacity (m^3/m^3)
FLDCP	Volumetric water content of a soil layer at field capacity (m^3/m^3)
FRNLIT	Fraction of nitrogen in litter (-)
FRNR	Fraction of nitrogen in dead root organic matter (-)
GDAY	Last germination day number
GDPTH	Seed depth (mm)
GERD	Indicator that seeds are being wetted (GERD = 0) or not (GERD = 1) (-)
GERMT	Number of days seeds need to be wetted before germination (d)
GERWAV	Germination wave number
GROWD	Indicator that the day is a growth day (GROWD = 1) or not (GROWD = 0)
GRRATE	Shoot growth rate (kg DM/ha/d)
GRTD	Root extension rate (mm/d)
IAVW	Initial available water index (AVW) (d)
IBIOM	Initial weight of shoots (BIOM) (kg DM/ha)
IFRMN	Initial fraction of nitrogen mineralised from dead root organic matter (-)
IFRNB	Fraction of nitrogen in IBIOM (-)
ILIT	Initial weight of litter (kg DM/ha)
INFR	Soil water infiltration rate (mm/d)
INI	Initial mineralised nitrogen in a soil layer (kg/ha)
INTC	Rainfall interception rate by litter and plants (mm/d)
ISOHC	Isohyet correction factor (-)
K	Soil horizon number

KILD	Indicator of transpiration (KILD = 1) or not (KILD = 0) (-)
LE	Leaching efficiency factor (-)
LITTER	Weight of litter (kg DM/ha)
LMF	Threshold fraction of available water below which reduced transpiration occurs (-)
MF	Moisture factor relating rate of decomposition of organic material to moisture content of a soil layer (-)
MFT	Function relating rate of decomposition of organic material to soil moisture content (-)
MSFD	Rate of increase in drought period without transpiration prior to death (d/d)
MSFG	Rate of increase in seed imbibition period for germination (d/d)
MSSTAT	Soil moisture status (if positive then water in root zone is above wilting point)
MSSTD	Duration of drought period without transpiration (d)
MSSTG	Duration of seed imbibition for germination (d)
MXRTD	Maximum rooting depth (mm)
	Number of soil layers simulated
NCBIOM	Nitrogen concentration in shoot (kg N/kg DM)
NCONC	Mineralised nitrogen concentration in water in a soil layer (kg N/mm)
NCR	Nitrogen concentration in rainfall and associated biological nitrogen fixation (bacteria, algae, up to 5% ambient legumes in shoots) (kg/mm)
NDBIOM	Nitrogen concentration in dead shoots (kg N/kg DM)
NFACT	Reduction factor on potential transpiration due to nutrient limitation (-)
NI	Mineralised nitrogen in a soil layer (kg N/ha)
NLEACH	Rate of nitrogen leached from a soil layer (kg N/ha/d)
NUE	Nitrogen uptake efficiency factor (-)
NUPTAK	Rate of nitrogen uptake into shoots from a soil layer (kg N/ha/d)
OGRTD	Potential root growth rate (mm/d)
PDGRT	Potential shoot growth rate (kg DM/ha/d)

PDGRIM	Maximum potential shoot growth rate (kg DM/ha/d)
PROP	Extinction factor for soil moisture withdrawal (-)
PUSHD	Indicator of crop death (PUSHD = 1) or not (PUSHD = 0) (-)
PUSHE	Indicator of germination (PUSHE = 1) or not (PUSHE = 0) (-)
RAIN	Rainfall (mm/d)
RAINTB	Rainfall table (mm/d)
RAVW	Rate of increase in AVW (d/d)
RAVW1	Rate of increase in AVW1 (d/d)
RCLIT	Litter decomposition rate (kg DM/ha/d)
RCN	Rate of change of mineralised nitrogen in a soil layer (kg N/ha/d)
RCSUBS	Rate of dead root organic matter decomposition in a soil layer, negatively signed (kg DM/ha/d)
RCW	Rate of change in water content for a soil layer (mm/d)
RDENF	Normalised root density factor for a soil layer (-)
RDLIT	Relative decomposition rate of litter (/d)
RDR	Relative decomposition rate of dead root organic matter (/d)
RDSUBS	Rate of dead root organic matter decomposition in a soil layer, negatively signed (kg Dm/ha/d)
REDF	Reduction factor for water uptake (-)
RGR	Relative growth rate of shoots (/d)
RGROW	Actual water-or nutrient-limited growth rate (/d)
RNMIN	Rate of nitrogen mineralisation from dead root organic matter in a soil layer (kg N/ha/d)
RNMLIT	Rate of nitrogen mineralisation from litter (kg N/ha/d)
RNOFF	Rate of runoff (mm/d)
RNOFFC	Average long-term fraction of annual rainfall that runs off (-)
RNPAR	Rainfall parity (0 or 1 on rainfree and rainy days, respectively)
ROFINT	Fraction relating fraction of average long-term runoff to individual storm size (-)
RRDENF	Relative root density factor (-)
RTD	Rooting depth (mm)
RTDG	Initial rooting depth after germination (mm)

RTDI	Initial rooting depth (mm)
SCOV	Fraction of soil covered by shoot (-)
SEVAP	Actual soil evaporation rate (mm/d)
SSWTB	Specific shoot weight table (kg DM/ha)
STDAY	Starting day of simulation
STORC	Volumetric available water storage capacity of a soil layer (m^3/m^3)
STRAN	Actual transpiration rate (mm/d)
SUBSTI	Initial weight of dead root organic matter in a soil layer (kg DM/ha)
SUBSTR	Weight dead root organic matter in a soil layer (kg DM/ha)
SUMRRD	Sum of relative root density factors (-)
SUMT	Soil layer thickness weighted sum of VAR factors (mm)
SWPDS	Indicator if soil layer containing root tip is above wilting point (SWPDS = 1) or not (SWPDS = 0)
TAVW	Cumulative sum of AVW (d)
TAVW1	Cumulative sum of AVW1 (d)
TCK	Thickness of a soil layer (mm)
TDBIOM	Weight of dead shoot (kg DM/ha)
TDEPTH	Depth of soil simulated (mm)
TDRAIN	Cumulative sum of water drained below the deepest simulated soil layer (mm)
TEVAP	Cumulative sum of soil evaporation (mm)
TGROWD	Cumulative sum of number of growing days (d)
TIME	Simulated time
TMINL	Cumulative sum of nitrogen mineralised from litter (kg N/ha)
TMINR	Cumulative sum of nitrogen mineralised from dead root organic matter (kg N/ha)
TMINRL	Cumulative sum of nitrogen mineralised from litter and dead root organic matter (kg N/ha)
TNITUP	Cumulative sum of nitrogen taken up in shoots (kg N/ha)
TOTINF	Cumulative sum of infiltrated water (mm)
TOTNI	Mineralised nitrogen in the soil (kg N/ha)

TOTNUP	Rate of nitrogen taken up in shoots (kg N/ha/d)
TOTRAN	Cumulative sum of transpiration (mm)
TRAIN	Cumulative sum of rainfall (mm)
TRAN	Actual transpiration rate from a soil layer (mm/d)
TRANP	Potential transpiration rate (mm/d)
TRNMIN	Rate of nitrogen mineralisation from dead root organic matter (kg N/ha/d)
TRR	Ratio of actual to potential transpiration (-)
TSUBST	Weight of dead root organic matter in the soil (kg DM/ha)
VAR	Soil water content weighted extinction (with depth) factor (-)
W	Water content of a soil layer (mm)
WGER	Water content of a soil layer containing seed and any other layers above the seed (mm)
WI	Initial soil water content of a soil layer (mm)
WIN	Flux of water into a soil layer (mm)
WLTPNT	Volumetric water content of a soil horizon at wilting point (m^3/m^3)
WLTPT	Volumetric water content of a soil layer at wilting point (m^3/m^3)
WTOTR	Water content within the root zone (mm)

Discussion

Question - How does Figure 3, showing higher nitrogen uptake with longer wetting, match with the remark that the more water in a non-fertilized situation, the lower the quality?

Answer - Figure 3 shows that higher rainfall or rather deeper wetting and longer duration of wetting, which are not only a function of the amount of rain but also of its distribution, increases the availability of nitrogen. But it increases dry-matter production more, so that the nitrogen concentration in the material is lower. In a situation where growth is nitrogen-limited, the nitrogen is always diluted to its minimum value, which is not the case where growth is water-limited.

Question - In the model does the amount of available N depend on the amount of biomass from the previous season or is it the amount of N that was in the system last year?

Answer - It is the total amount of nitrogen in the organic material produced last year, i.e. it is assumed that the stable component in the organic material has very little influence on the total nitrogen uptake. The year after a drought year is partly compensated by the fact that the plants in a dry year have not been able to take up all the available nitrogen. There is a carry-over of mineral nitrogen, as has also been shown in Migda (Israel).

Question - Do you assume a constant seed stock?

Answer - No, for each site the biomass at the end of germination is estimated on the basis of specific knowledge about the site, such as seedstock and germination characteristics of the soil type.

Question - The suggestion of a positive correlation between soil wetness and N availability seems contradictory to the information that after the first rain the microbial population increases all of a sudden leading to nitrogen immobilisation followed only later, when those microbes die, by release.

Answer - The discussion about the existence or non-existence of the nitrogen flush is continuing. Experimental work by Birch and others in East Africa suggested a flush of mineral nitrogen after the first rain. The phenomenon was explained by the fact that in the summer, part of the microbial population died. When the soil is rewetted, it forms the substrate for decomposition with a low ratio of carbon to nitrogen, providing the nitrogen flush. The results from work in West Africa point more in the direction of a relationship between total rainfall and accumulated mineral nitrogen.

Statement - A similar problem in the water balance model, as described in the paper, was observed when a model developed in India was applied elsewhere.

Answer - The point is that total evapotranspiration is fairly well predicted as is infiltration. Hence the problem is a completely different distribution in the soil. Such large discrepancies between predicted distribution and that actually measured have never occurred before.

Question - How do you explain the direct relationship between moisture availability and nitrogen concentration? If it is an annual pasture, is there not going to be a change in pasture species towards those which are able to complete their growth and maturation?

Answer - One should distinguish between two processes: the plant can mature and set seed and complete its phenological development but it cannot dilute the nitrogen that it has taken up.

Under conditions where nitrogen is not too limiting the relationship between yield and total nitrogen in vegetation at about flowering will have a slope of about 2 kg N/kg DM. In a situation where water is limiting, dry matter will increase by only a limited amount after flowering. At maturity the concentration will then be 0.015 kg N/kg DM. In a good year on the other hand, dry-matter production after flowering may be substantial and the end result will be a concentration of say 0.0075 kg N/kg DM. It is a matter of how much additional structural material the plant can produce. Thus the variability in dry-matter production as a function of moisture availability is much greater than that in total uptake of nitrogen, and therefore the quality changes from year to year and from site to site.

Question - Are the experimental results based on analysis of the same tissue of the same plant species in different years?

Answer - Yes, that is the case.

Question - Does the nitrogen concentration in the seeds vary?

Answer - The nitrogen concentration in the seed can vary. When growth is nitrogen-limited the concentration may be around 1%, under water-limited conditions much higher. The same phenomenon occurs in wheat grains, which in a dry year may contain 20% protein. The concentration of nitrogen in the seed is usually high shortly after seed set and the nitrogen is diluted with carbohydrates coming into the seed. The rate at which the nitrogen concentration decreases depends on the rate of influx of both carbohydrates and nitrogen coming from tissues that are being depleted. Some plants stay green and hold on to the nitrogen for a long time, so the nitrogen concentration falls sharply; other plants tend to ripen rapidly and lose the nitrogen more quickly and the dilution proceeds more slowly. The final concentration depends on where the dilution process stops.

Behavioural aspects of intake at pasture in ruminants

E.D. Ungar and I. Noy-Meir

Introduction

It is difficult to identify an area of study more fundamental to the dynamics of an agricultural system than the plant-animal interface in pastoral systems. In the main, the agricultural literature dealing with intake at pasture consists of empirical studies related to (1) quantity effects - the relationship between pasture availability and intake rate, or the effect of defoliation on pasture growth and hence subsequent availability or (2) quality effects - the relationship between pasture quality and intake rate/selectivity or the growth response of the sward to selective grazing. The direction of effect most predominantly investigated is the response of the animal to sward characteristics rather than the reverse. The strongly empirical nature of these studies and the relative paucity of hypotheses treating the underpinning theory is reflected in a seeming imbalance in grazing-system models. A large, high-resolution plant model (developed to simulate undisturbed growth) might be placed alongside an equally detailed and complex animal nutrition model whilst the interface consists of a couple of empirical relationships of very low generality.

This paper reports a very preliminary step towards a process-based description of the plant-animal interface. In its broadest sense, the intake process can be defined in terms of three potentially limiting processes - ingestion, digestion, and assimilation. Assimilation rate may limit intake via the nutrient requirement of the animal, which can include the potential for tissue deposition. Digestion rate can limit intake via feed quality, which may have both physical and chemical components. Intake can be limited by the ingestion rate via herbage availability as characterised by quantity and canopy structure or by herbage quality and its relation to selectivity. This study focuses on the relationship between herbage availability and ingestion rate. It is therefore most relevant to early-season dynamics of annual vegetation and to a number of management decisions, such as grazing deferment, that are closely related to the intake - availability function.

The grazing-process model was developed in three stages: models A, B and C. The basic theory should be applicable to all ruminants, though parameterisation of the models is for sheep. Grazing process model B was developed jointly with J. Ketelaars of CABO, Wageningen.

Grazing-process model A

Definitions and assumptions

The sward consists of cylindrical units of biomass (food items) that are randomly distributed in the horizontal plane with a mean density of $\underline{d}$ (/cm^2). This density changes through time as the sward canopy develops and the proportion of cover changes. Proportion of cover is given by $\pi r^2 d$, where $\underline{r}$ is the radius of a food item (cm). Proportion of cover is always less than or equal to unity. Sward height, $\underline{h}$ (cm), and the biomass density of food items, ρ (g/cm^3), are uniform.

Grazing bites are cylindrical and are characterised by surface area, $\underline{a}$ (cm)^2, and depth, $\underline{h}'$ (cm): $\underline{a}$ is less than or equal to πr^2 and $\underline{h}'$ is given by:

$$h' = \min(\max(0, h-h_r), h_x) \qquad (1)$$

Where: h_r = ungrazable residual pasture height (cm),

h_x = maximum bite depth (cm).

There are $\underline{n}$ potential bites in a food item in the horizontal plane, where $\underline{n}$ is defined as $\pi r^2/a$. The animal selects a proportion, $\underline{p}$, of food items it perceives, each bite being of equal size and weight. Bite weight, $\underline{w}$ (g), is given by:

$$w = a\, h' \rho \qquad (2)$$

The grazing process consists of searching, biting, chewing and rechewing. Assuming that these processes do not occur simultaneously, the time taken to ingest a unit weight of food, $\underline{t_i}$ (s/g), is given by:

$$t_i = \frac{t_s + (t_b + t_c + t_r) n\, p}{w\, n\, p} \qquad (3)$$

where: t_s = searching time per food item (s),

t_b, t_c, t_r = biting, chewing, rechewing time/bite (s).

The ingestion rate, $\underline{I}$ (g/s), is the reciprocal of the above expression:

$$I = \frac{w\,n\,p}{t_s + (t_b + t_c + t_r)\,n\,p} \qquad (4)$$

Perception of a food item is by physical contact with the mouth. Thus the effective searching band width is 2r. The animal searches with a walking speed of $\underline{u}$ (cm/s) and requires a recognition and decision time per food item encountered of f (s). Thus the searching time per food item is given by:

$$t_s = \frac{1}{2rdu} + f \qquad (5)$$

Biting time is assumed to be constant. Chewing and rechewing time are both functions of the dry-matter weight per bite, $\underline{w}$:

$$t_c = q\,w \qquad (6)$$

$$t_r = g\,w \qquad (7)$$

where: q, g = chewing and rechewing time per unit weight of ingested food (s/g).

Equation (4) expands to:

$$I = \frac{a\,h'\,\rho\,n\,p}{1/(2rdu) + f + np(t_b + ah'\rho(q+g))} \qquad (8)$$

Multiplying by 2rdu gives:

$$I = \frac{2\,a\,h'\rho\,n\,p\,r\,d\,u}{1 + 2rdu\,(f + np(t_b + ah'\rho(q+g)))} \qquad (9)$$

Pasture biomass, $\underline{V}$ (g/cm^2), is given by:

$$V = h\,a\,n\,d\,\rho \qquad (10)$$

Thus intake rate can be expressed as:

$$I = \frac{2\,(V/h)\,h'\,p\,r\,u}{1 + 2ru(d(f + npt_b) + (V/h)h'p(q+g))} \qquad (11)$$

Results

Table 1 shows a set of standard values for most of the parameters defined thus far.

Table 1. Definition of symbols

Symbol	Definition	Standard value: Model A	Standard value: Model B&C
a	Surface area of bite (cm^2)	10	30
B	Mean biting rate during active (grazing/min)		
c	Fraction of cover of selected biomass		
d	Density of food items in horizontal plane ($/cm^2$)		
E_g	Energy cost of grazing (J/min)		
E_n	Net rate of energy gain (J/min)		
E_p	Energy concentration of pasture (MJ/kg)		11
E_w	Energy cost of walking (J/cm)		2.1
f_h	Fraction of canopy height that is grazed	0.5	0.5
f_v	Fraction of biomass grazed, vertical plane		f_h / f_v: 0 / 0; .25 / .05; .50 / .20; .75 / .50; 1.00 / 1.00
g	Rechewing time/unit weight ingested food (s/g)	2.5	
h_s	Sward height (cm)	10	12
h	Actual biting depth (cm)	5	6
h_r	Ungrazable residual pasture height (cm)	0.5	0.5
h_x	Maximum bite depth (cm)	5	6
I	Rate of pasture intake (g/h)		
i_a	Rate of pasture intake in absence of supps (kg/d)		
i_c	Supplementation rate (kg/d)		

I_e	Energy intake rate (J/min)		
i_p	Actual rate of pasture intake (kg/d)		
l	Intercept of handling time function (s)		0.736
m	Slope of handling time function (s/g)		0.00566
n	number of potential bites in a food item	1	
p	Proportion of food items selected	0.2	
P	Area percentile		
q	Chewing time/unit weight ingested food (s/g)	2.5	
r	Radius of a food item (cm)	1.8	
S	Pasture substitution ratio		
SD	Standard deviation of mean biomass/unit area (g/m^2)		
t_b	Biting time per bite (s)	1	
t_c	Chewing time per bite (s)		
t_h	Handling time per food item selected (s)		
t_i	Time taken to ingest unit weight of food (s/g)		
t_r	Rechewing time per bite (s)		
t_s	Searching time per food item (s)		
u	Searching walking speed (cm/s)	50	50
U	Mean walking speed during active grazing (cm/s)		
V	Mean biomass per unit area (g/m^2)		
V'	Mean normalised biomass		
V_n	Mean normalised selected biomass		
V_s	Mean absolute selected biomass (g/m^2)		
w	Bite weight (g)		
Z	Standard deviations from the mean		
Z_l	Lower bound of selectivity in SD from mean		
	Biomass density of food items (g/cm^3)		
	Recog+decision time/food item encountered (s)	0.3	0

Substituting the appropriate values in Equation (11) yields:

$$I = \frac{18V}{1 + 90d + 90V} \qquad (12)$$

Equation (12) conforms to a saturation functional form that rises asymptotically with increasing V (at constant d) to a maximum intake rate of 720 g/h. Intake is a function of biomass per unit area and the distribution of biomass in the horizontal plane.

Figure 1 shows the intake functional response to biomass at various levels of cover. At low biomass levels, where t_c+t_r is small relative to t_b, handling time increases slowly with biomass and therefore intake rises steeply. At high biomass levels, t_c+t_r is large relative to t_b and handling time increases rapidly with biomass, thereby reducing the rate of increase in intake. Ultimately, for a given increase in biomass, the increase in handling time would exactly offset the increase in intake per food item selected.

At constant biomass, a decrease in cover causes a greater proportionate increase in the intake per food item selected than in the total searching and handling time per food item selected. Thus intake rate increases with decreasing cover. Figure 1 shows that the sensitivity of intake rate to cover is greatest at low levels of cover.

It is important to examine a number of assumptions implicit in the above calculations and discussion. Perhaps the most serious is the premise that pasture height is constant. It follows from Equation (10) that varying $\underline{V}$ at a given level of cover (=f(d)) while $\underline{h}$ and $\underline{a}$ are constant means that the density of the vegetation is changing. It is unlikely that density exceeds about 0.01 g/cm^3, which corresponds to a biomass of about 500 g/m^2 (5000 kg/ha) in Figure 1.

One way of overcoming this problem of enormous variations in ρ is to hold ρ constant and allow pasture height to vary with biomass. For certain pasture types this may be a closer approximation to what actually occurs in the field. To demonstrate the behaviour of the model under this alternative assumption, a value of 0.001 g/cm^3 is taken for ρ. Using the parameter set shown in Table 1 (excluding $\underline{h}$ and $\underline{h}'$), Equation (12) becomes:

$$I = \frac{36 \frac{V}{h} h'}{1 + 180 \left(\frac{d}{2} + \frac{V}{h} h'\right)} \qquad (13)$$

and Equation (10) re-arranges to yield:

$$h = \frac{V}{\text{and}\,\rho} = \frac{V}{0.01d} = \frac{100V}{d} \qquad (14)$$

Substituting into Equation (13) gives:

$$I = \frac{0.36h'd}{1+d(90+1.8h')} \qquad (15)$$

Equation (15) shows that calculating intake rate for various biomass levels at constant cover ($h-h_r \geq h_x$) will now give a constant intake rate in contrast to the results shown in Figure 1. The animal is grazing to its maximum bite depth and the only change occurring in the sward canopy is an increase in biomass by way of increasing height. Furthermore, calculating intake rate as a function of cover at constant biomass will now predict increasing intake rate with increasing cover (see Figure 2).

Equations (12) and (15) represent two extreme caricatures of sward development and intake, one based on constant height and the other on constant density. In reality, sward development involves simultaneous changes in cover, height and density. Both extremes have shown that biomass distribution or spatial heterogeneity is an important factor in determining intake, but the qualitative behaviour of these two models is fundamentally different.

A further limitation of this preliminary grazing process model is the determination of the parameter p - the proportion of perceived food items that are selected. Not only is it unreasonable to assume that p remains constant over a wide range of pasture conditions, but it is also problematic to ascribe any value at all where there is no recognition of heterogeneity within food items. Grazing process model B includes a more realistic description of spatial heterogeneity of the sward and thereby enables the optimisation of the parameter p.

Grazing-process model B

Description of the model

In developing model B, two major changes were made in the description of the sward canopy. Firstly, a distribution function of biomass per unit area at the food-item site is introduced. Secondly, a more realistic function is used to

Figure 1. The functional response of intake to biomass at various levels of cover (grazing-process model A)

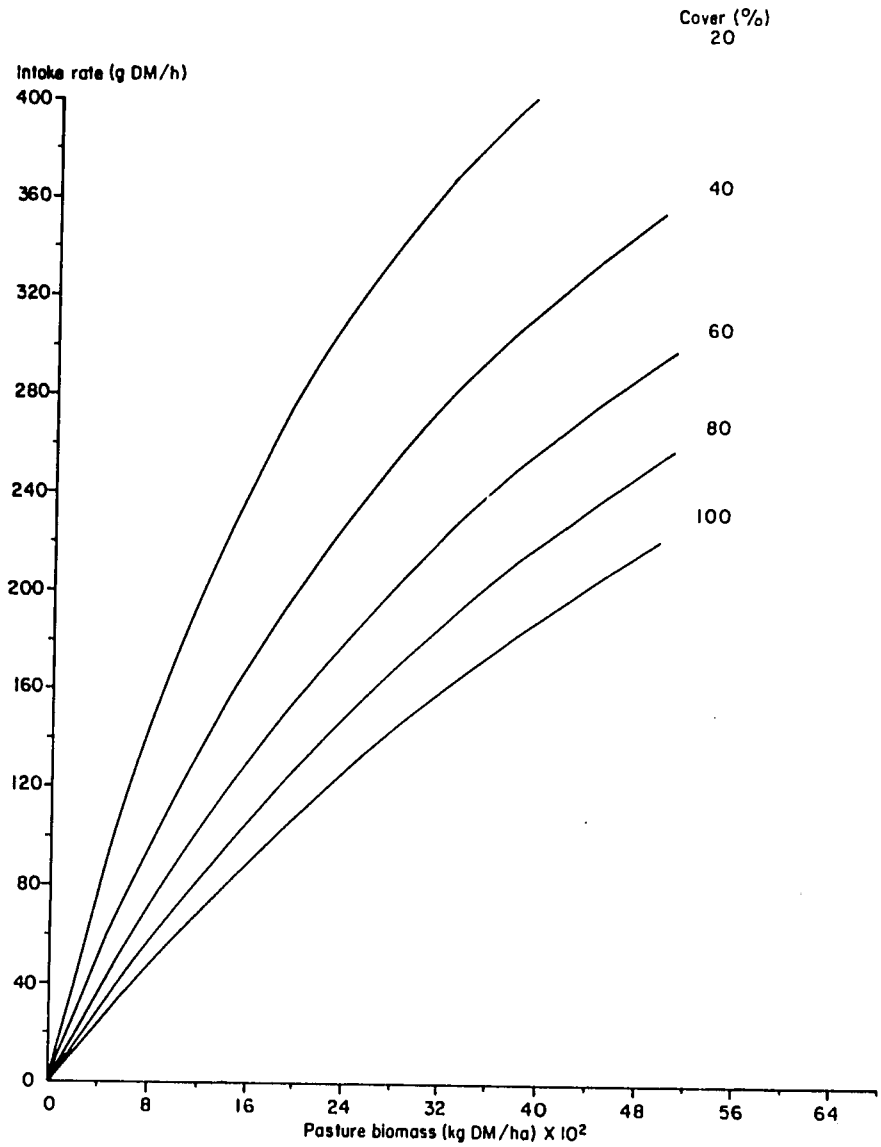
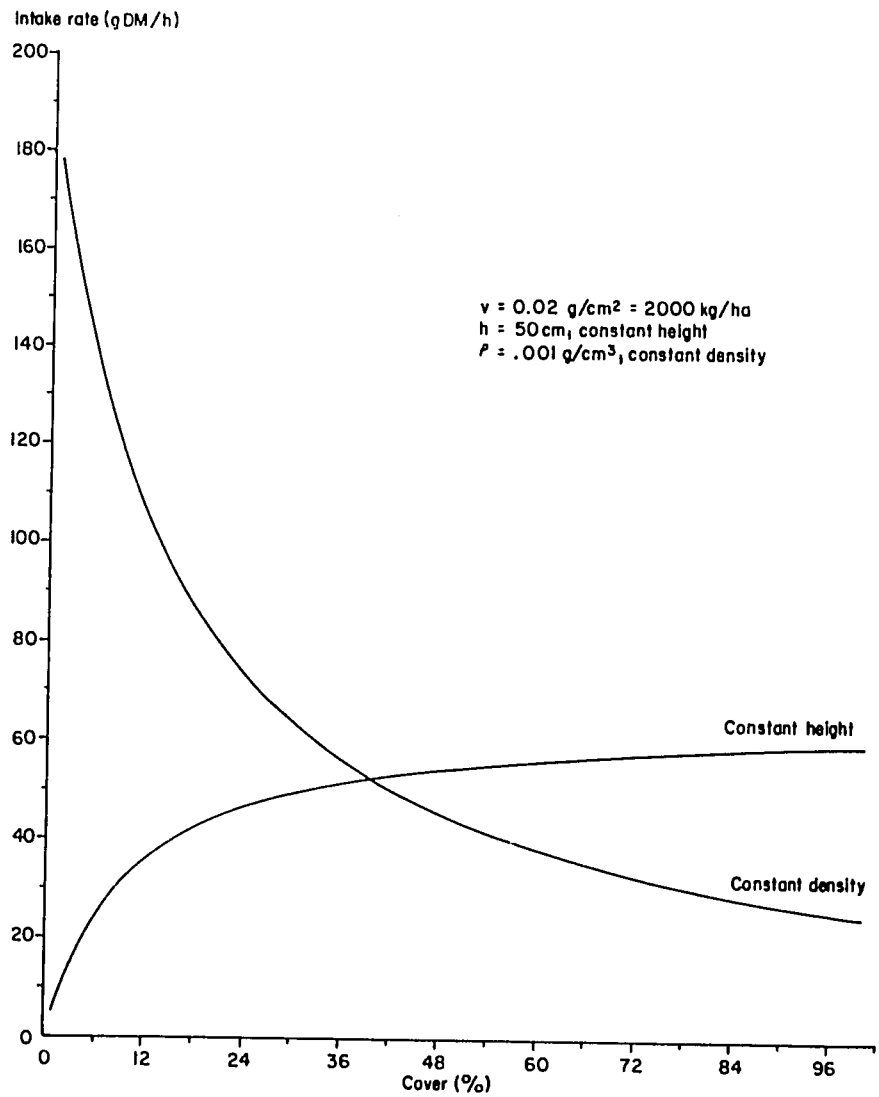


Figure 2. A comparison of hourly intake rate as a function of sward cover assuming constant biomass density or constant biomass height (grazing-process model A)



describe the vertical allocation of biomass within a food-item site (though pasture height remains uniform as in model A).

Inclusion of a distribution function for biomass per unit area at the selection site permits a study of selective foraging and the model can therefore be used as a simple optimal foraging model. The underlying assumption is that the animal selects for biomass concentration in the horizontal plane, which is essentially the same as selecting for bite density and thus bite weight, if the model assumptions are taken as a whole.

The normal distribution function is used to describe spatial heterogeneity of biomass per unit area. A preliminary analysis of biomass data from Migda indicates that the frequency distribution of biomass per unit area of samples based on 100 quadrats of 100 cm^2 approaches a normal distribution approximately mid-way through the growing season. Thus choice of this function does have relevance to the situation in the field albeit at a stage in the season when availability is unlikely to limit intake. A further reason for using this function is the relative ease with which it can be handled mathematically as opposed to skewed functional forms that would be more appropriate for the early stages of the growing season. Characterisation of this aspect of spatial heterogeneity in the model requires the definition of two parameters: mean biomass per unit area and the standard deviation of the mean.

Selectivity is defined in terms of the number of standard deviations from the mean (Z_1) above which the animal selects all food items it encounters. The algorithm calculates intake for Z_1 values of 3 to -3 in steps of 0.1 standard deviation. A value of -3 approximates zero selectivity and a mean selected biomass density equal to that of the field mean.

Vertical biomass distribution is defined in the form of a table giving the cumulative fraction of biomass from the top of the canopy as a function of fraction canopy depth from the top. Values for this function are based on Milne et al (1982) (see Table 1).

Handling time is defined more simply in model B. Rechewing (ruminating) time is no longer incorporated in the calculations since there seems to be little evidence in the literature of ruminating time limiting the time spent in active grazing. Furthermore, excluding rechewing time simplifies the calculation of the daily active-grazing time needed to meet a given intake requirement. Biting and chewing time are no longer differentiated and a

linear function is used to relate total handling time to dry-matter intake per bite. The terms bite and selected food item are synonymous in model B, implying that the animal perceives bite-sized food items as opposed to there being n potential bites in a food item as in model A. (Note, however, that the parameter n was set to 1 for all numerical examples of model A.)

Searching time is a function of the density of food items in the horizontal plane (Equation (5); model B also assumes that food items are randomly distributed i.e. biomass distribution is not clumped). The density of selected food items is the proportion of cover of selected food items divided by the area of the food item. Using the normal distribution curve, the proportion of cover of selected food items is the area under the curve from Z_1 to infinity. This is not soluble analytically but a fifth-order polynomial expression is used to approximate this integral.

The mean selected biomass per unit area is needed in order to calculate both bite weight and handling time. This is not analytically soluble for the normal distribution function and so a set of solutions was calculated numerically and incorporated into the model.

To summarise, the equations used in model B to calculate intake rate are as follows. (Constants for the conversion of area and time units have been omitted for the sake of clarity.)

Bite radius: $r = \sqrt{a/\pi}$ (16)

Biting depth: $h' = \min(h_x, \max(0, h-h_r))$ (17)

Fraction of canopy height that is grazed: $f_h = h'/h$ (18)

Fraction biomass grazed, vertical plane (Table 1) $f_v = f(f_h)$ (19)

Fraction cover of selected biomass (polynomial): $c = f(Z_1)$ (20)

Density of selected items: $d = c/a$ (21)

Searching time: $t_s = 1/(2rdu) + f$ (22)

Mean normalised selected biomass level (table): $V_n = f(Z_1)$ (23)

Mean absolute selected biomass level: $V_s = V_n * SD + V$ (24)

where: SD = standard deviation of mean biomass per unit area,

V = mean biomass per unit area

Mean bite weight: $w = f_v * V_s * a$ (25)

Handling time: $t_h = l + m\,w$ (26)

where: l = intercept of handling time function,

m = slope of handling time function.

Intake rate: $I = w / (t_s + t_h)$

Model B also calculates the mean biting rate and mean walking speed during active grazing, which are both more easily related to grazing behaviour as observed in the field than many of the basic parameters used in the model.

Mean biting rate: $B = 1/(t_s + t_h)$ (28)

Mean walking speed: $\overline{U} = u(1-(B*t_h)) = u(1 - t_h/(t_s+t_h))$ (29)

The energy cost of grazing (E_g) was included in the model to enable calculation of the net rate of energy gain (E_n). The energy cost of grazing is taken to be the energy cost of walking (E_w). No estimate for the energy cost of feed harvesting and chewing could be found in the literature, though these are probably very small relative to the walking cost. An energy concentration (E_p) is ascribed to the pasture dry matter. Thus:

Energy cost of grazing: $E_g = E_w * \overline{U}$ (30)

Energy intake rate: $I_e = I * E_p$ (31)

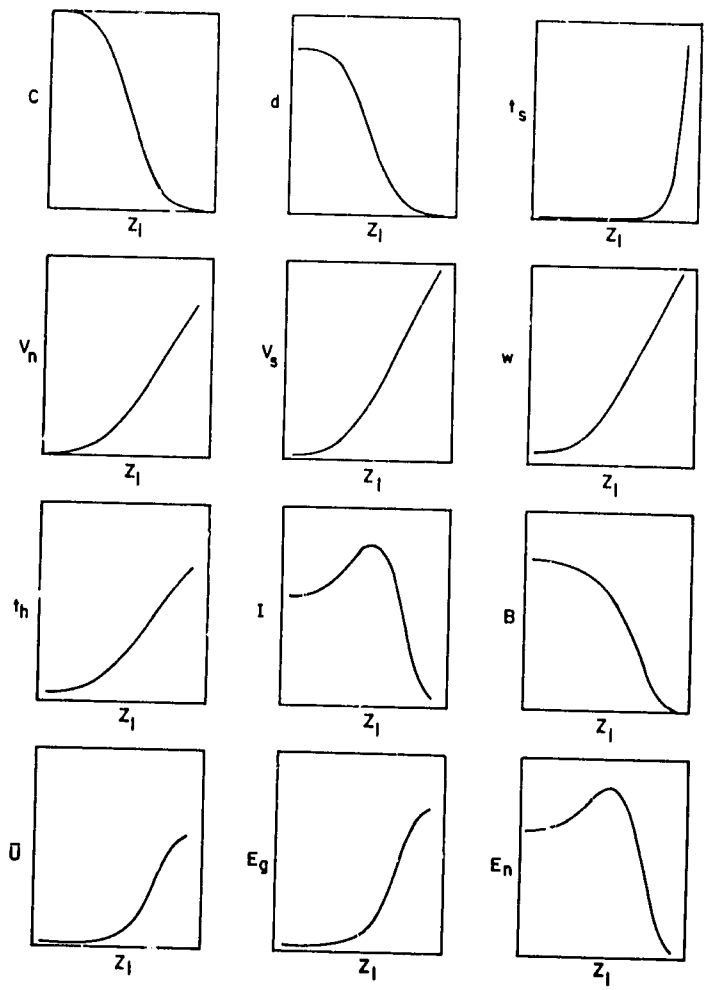
Net rate of energy gain: $E_n = I_e - E_g$ (32)

Results

The standard run uses parameter values shown in Table 1, with a pasture biomass of 50 g/m^2 and standard deviation of 50 g/m^2. A coefficient of variation of 100% (between sampling quadrats of 10x10 cm) is quite typical for pastures at Migda throughout the growing season. Biting depth is the maximum potential of 6 cm, which is 50% of the pasture height and represents 20% of the biomass per unit area. Figure 3 shows the form of relationship between various variables.

As the degree of selectivity declines from the highest values, searching time decreases relatively rapidly compared with the moderate decline in handling time and bite weight. The very rapid decline in searching time more than compensates for the effect of declining bite weight, and the net effect is a sharp increase in intake rate. Searching time declines less rapidly at Z_1 values below about 1.2 whilst handling time and bite weight continue to fall. From the functional form of Equation (27) above, it is clear that the net effect is to reduce intake. At extremely low degrees of selectivity, searching time, handling time and bite weight all remain fairly constant and thus intake rate changes little with further decline in selectivity. The resultant relationship between intake rate and selectivity indicates that the cost to the animal of a small deviation from the optimum selectivity level is greater if the animal is over-selective rather than under-selective.

Figure 3. A selection of relationships between output variables of grazing-process model B under the standard parameter set. (i) Relationships with $\underline{Z}_1$ (all symbols defined in Table 1)



Throughout all runs of the model it was found that the optimum selectivity level (OSL, defined in Z units) is only slightly altered when the optimum is defined in terms of maximising the net rate of energy gain (OSL_g) as opposed to maximisation of intake rate (OSL_i). This is due to the fact that the ratio of energy expenditure rate to energy intake rate rapidly becomes very low as the degree of selectivity declines. At zero selectivity, the energy cost of grazing per unit time (E_g) represents about 3% of the energy intake per unit time (I_e). At OSL_i (Z_1 = 0.5; standard run), E_g/I_e = 4.8%.

For the standard parameter set, OSL_i = 0.5 (standard deviations above the mean). This corresponds to a field cover of selected items (c) of 31% and a mean selected biomass level (V_s) of 105 g/m^2 (2.1 times the mean biomass of the field). At OSL_i the following results were obtained. Searching time, handling time and bite weight are 0.31 s, 1.1 s, and 63 mg, respectively. Intake rate, mean biting rate and mean walking speed are 161 g/h, 43 bites/min, and 11.2 cm/s, respectively.

The effect of biomass heterogeneity (at constant mean biomass) is shown in Table 2. OSL_i and intake rate increase with heterogeneity. At constant heterogeneity, OSL_i is independent of mean biomass level (Table 3). t_s remains constant since it is a function of selected item density which is in turn a function of Z_1. t_h does not increase proportionately with biomass and thus the net effect is for intake rate to increase with biomass. Figure 4 shows various iso-intake contours (at OSL_i) for biomass and heterogeneity.

Table 2. Results of grazing-process model B. Sensitivity analysis to coefficient of variation of biomass. Mean biomass = 50 g/m^2. Other parameter values and symbols defined in Table 1.

CV (%)	OSL_i (-)	V_s (g/m^2)	w (mg)	t_h (s)	t_s (s)	I (g/h)	B (/min)	U (cm/s)
25	-0.2	58	35	0.93	0.17	114	55	7.6
50	0.2	72	43	0.98	0.23	129	49	9.5
75	0.4	89	53	1.04	0.28	145	45	10.7
100	0.5	105	63	1.09	0.31	161	43	11.2
125	0.6	123	74	1.15	0.35	177	40	11.7
150	0.6	138	83	1.20	0.35	191	38	11.4
175	0.6	153	92	1.25	0.35	205	37	11.0
200	0.7	175	105	1.33	0.40	218	35	11.6

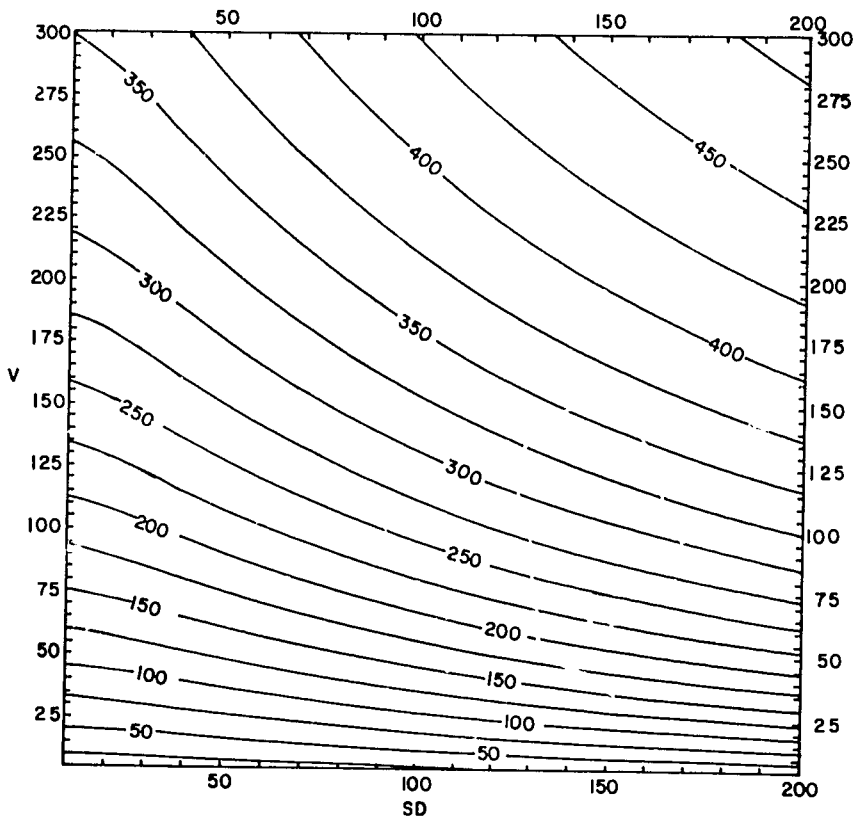
Table 3. Results of grazing process model B. Sensitivity analysis to biomass per unit area. Coefficient of variation = 100%. Other parameter values and symbols defined in Table 1.

V (g/m^2)	OSL_i (-)	V_s (g/m^2)	w (mg)	t_h (s)	t_s (s)	I (g/h)	B (/min)	U (cm/s)
20	0.5	42	25	0.88	0.31	76	50	13.2
30	0.5	63	38	0.95	0.31	108	47	12.4
40	0.5	84	50	1.02	0.31	136	45	11.8
50	0.5	105	63	1.09	0.31	161	43	11.2
60	0.5	126	76	1.16	0.31	184	41	10.6
70	0.5	147	88	1.23	0.31	205	39	10.2
80	0.5	168	101	1.31	0.31	224	37	9.7
90	0.5	189	113	1.38	0.31	241	35	9.3
100	0.5	210	126	1.45	0.31	257	34	8.9

The functional response of intake to biomass is that of a saturation function. Increasing sward heterogeneity steepens the initial ascending section of the function and raises the satiation intake level. On an absolute basis, sensitivity of intake to heterogeneity increases with biomass, but on a relative basis, it decreases. For example, at a biomass of 25 and 250 g/m^2, an increase in the coefficient of variation of biomass from 75% to 100% increases intake rate by 10 and 21 g/h, respectively. On a relative basis, the increases are 12% and 6%, respectively. The result may partly explain the quantitatively very different biomass-intake relationships reported in the literature, even for a given experimental technique carried out using the same animals and plots but in different years.

As noted earlier, the normal distribution function is not an appropriate functional form for describing early-season spatial heterogeneity of natural pasture biomass in environments typified by Migda. Grazing process model C aims primarily to improve the description of heterogeneity.

Figure 4. The response surface of hourly intake rate (g/hour) to mean biomass (V, g/m^2) and biomass heterogeneity (SD,%) at the optimum selectivity level (grazing-process model B)



Grazing-process model C

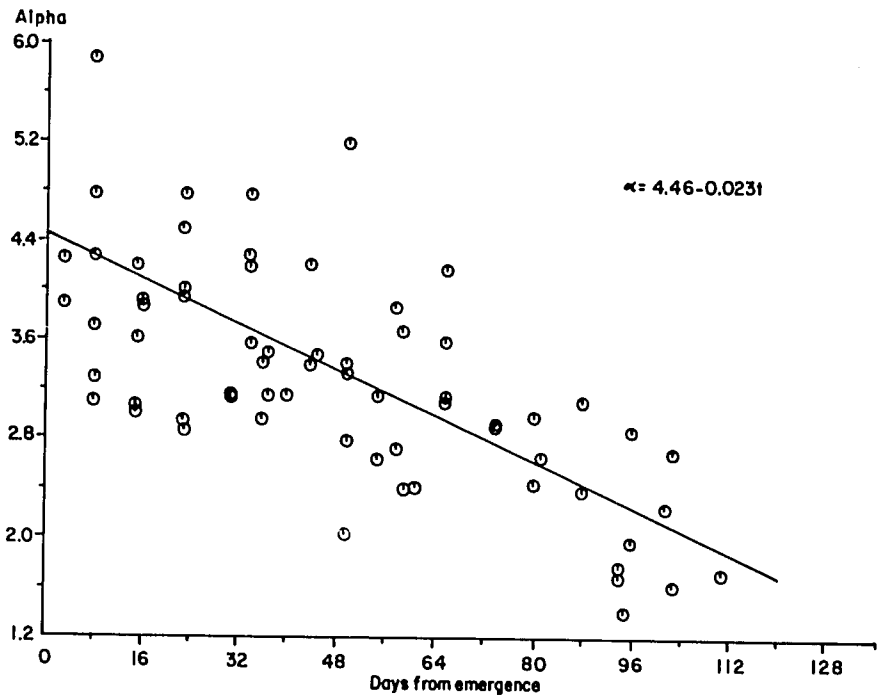
Introduction

Grazing-process model C attempts to improve the description of spatial heterogeneity in the horizontal plane. Figure 5 shows a typical progression of biomass distribution curves for the early-season growth phase of natural pastures as observed at Migda. A conceptually and mathematically simple method was developed to describe this wide range of distribution skewness.

The normalised mean percentile method

Biomass distribution is expressed as a function relating the mean normalised biomass level (V') to the area percentile (P). Assume that a data set consists of 100 biomass estimates for a given field sampling. If these 100 estimates are sorted in descending order, then the first number represents an estimate of the biomass per unit area of the top 1% (area basis) of the field. The mean of the first two numbers represents the mean biomass upto the second area percentile, and so on. The mean of the 100 numbers is the mean biomass level upto the 100th percentile and is therefore the field mean. Since the variability of biomass per unit area is greater than zero, the function of V' against P will always yield a downward-sloping curve. In order to facilitate comparisons of heterogeneity between samplings and fields, the original 100 estimates are normalised by dividing through by the mean. Thus V' = the mean normalised biomass level in multiples of the field mean and V' = 1 at P = 100. Since the distribution functions of biomass are generally skewed to the right, the function of V' against P will be concave with respect to the origin.

Figure 5. Correlation between the alpha heterogeneity parameter and time from pasture emergence (t). (Based on field data from Migda, various fields ungrazed)



The normalised mean percentile functions used in model C were derived as follows:

1. Biomass data for the 1979/80 season at Migda were used. The data consist of 111 biomass sampling sets for a number of fields (grazed and ungrazed) and dates through the season. Each sampling data set contains 100 biomass estimates. Estimates were sorted in descending order and normalised.
2. A series of 20 $\underline{V}'$ - $\underline{p}$ data pairs at 5 percentile intervals was calculated for each sampling set. A third-order polynomial function was fitted to each set of 20 $\underline{V}'$ - $\underline{p}$ data pairs, constrained to ensure that $\underline{V}'=1$ at $\underline{p}=100$.
3. The coefficients of the third-order polynomial functions showed a high degree of linear correlation. Each function can therefore be characterised by one coefficient which would be used in correlation analyses with grazing history. The remaining three coefficients of the polynomial function are predicted from this one. The intercept coefficient (α) was selected as the predictor since it is biologically the most meaningful.

The relationship between grazing history and alpha

In order to establish initial conditions at the commencement of grazing, a linear regression analysis was carried out between $\underline{\alpha}$ and the number of days from emergence ($\underline{t}$, taken as a fixed date for all fields) for ungrazed data sets only (Figure 5). This function simply expresses in terms of $\underline{\alpha}$ the progression of distribution functions shown in Figure 6.

A regression analysis was carried out between $\underline{\alpha}$ and the total number of grazing days (see Figure 7). The correlation is very weak, yielding a decrease in $\underline{\alpha}$ of approximately 0.11 per 100 grazing days. It is unlikely that stocking density and grazing period can be meaningfully reduced to a single factor of grazing days where the stocking density ranges from 3.3 to 15 sheep/ha, as is the case in the data set used. However, this analysis indicates that a larger and well-documented data base would facilitate a useful study of the relationship between grazing history and heterogeneity.

Figure 6. A typical progression of biomass distribution curves for the early-season growth phase of natural pastures under Migda conditions (schematic)

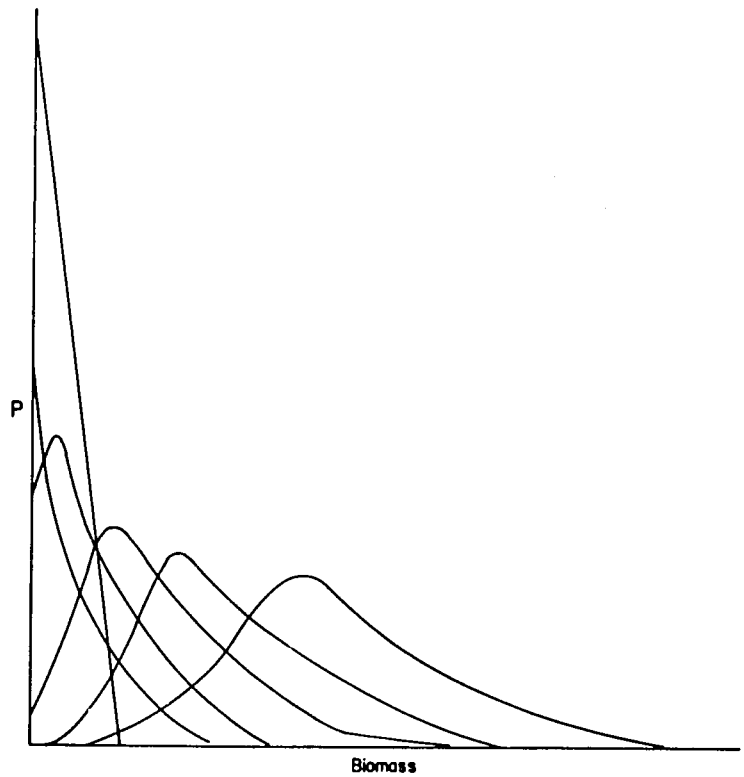
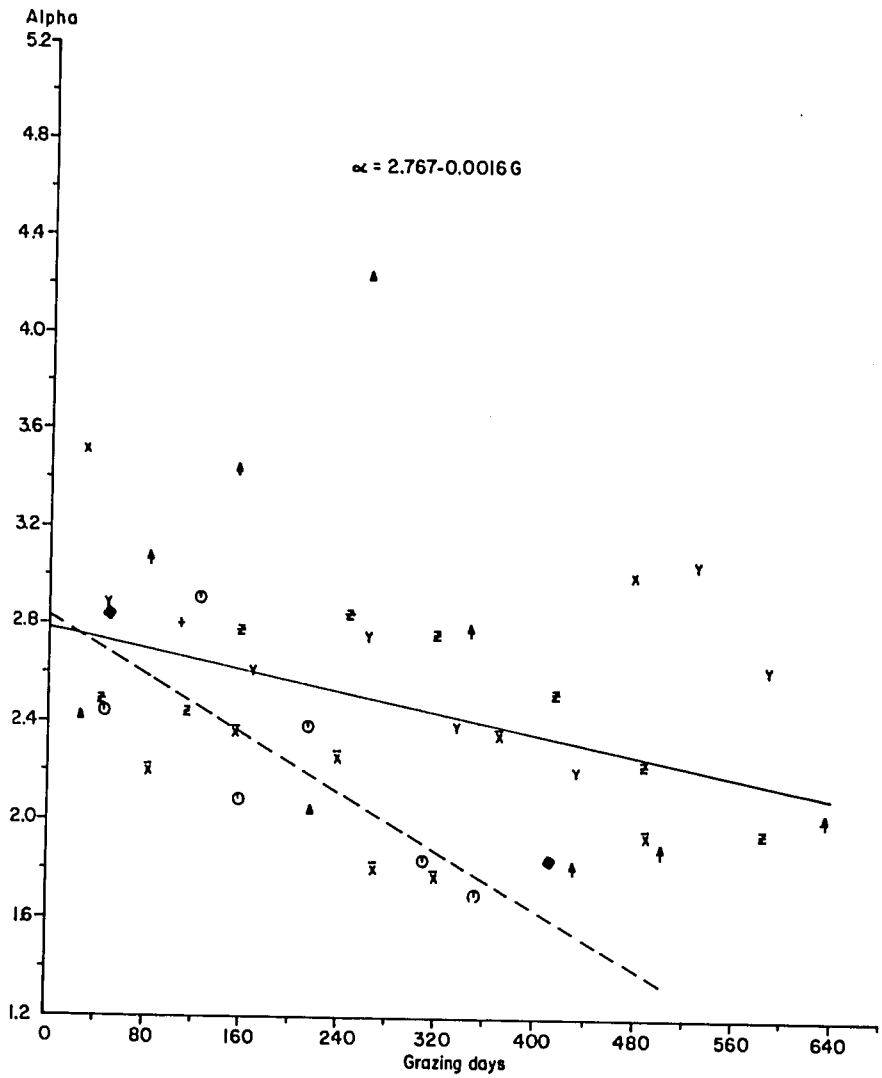


Figure 7. Correlation between the alpha heterogeneity parameter and the total number of grazing days (G). (Based on field data from Migda, 1979/80, various fields)



Description of the model

To summarise, the following changes were made in proceeding from model B to model C:

1. The mean selected biomass level (normalised) ($\underline{V}_n$) is defined by a third-order polynomial expression in which the intercept is defined as a parameter in the program and the remaining three constants are predicted from this parameter by a set of linear regression equations.
2. The mean selected biomass level (absolute) ($\underline{V}_s$) is defined as the product of $\underline{V}_n$ and the mean biomass per unit area.
3. The calculations are made for 100 percentile values that directly provide the selectivity level in terms of percentage area ($\underline{c}$ as defined in model B).

Results

The standard run of model C uses parameter values shown in Table 1. Mean biomass and α were set at 50 g/m^2 and 3, respectively. A number of relationships generated in the standard run of models B and C are compared in Figure 8. On the whole, the shape of response is very similar for the two models. A skewed biomass distribution seems to make the $\underline{I}$ - $\underline{V}$ response more sharply peaked, though the optimum selectivity level is not altered materially. A maximum intake rate of 142 g/h is achieved at a selectivity level equivalent to the top 23% of the area, with a mean selected biomass level of 98 g/m^2. Bite weight and mean biting and walking rates during active grazing are 50 mg, 40 bites/min and 14 cm/s, respectively.

The functional response of intake to biomass for various degrees of distribution skewness is shown in Figure 9. Maximum intake rate increases from 127 to 200 g/h as $\underline{\alpha}$ increases from 2 to 6, at a mean biomass of 50 g/m^2. It should be noted that under early-season grazing conditions, $\underline{\alpha}$ would generally decrease through time, and hence with increasing biomass. Furthermore, the animal can extend grazing time to compensate for a low hourly intake rate. Both these factors will tend to shift the shape of the daily intake-biomass response towards that of a ramp-type function.

Figure 8. A selection of relationships between output variables of grazing process models B (- - -) and C (——) under the respective standard parameter sets

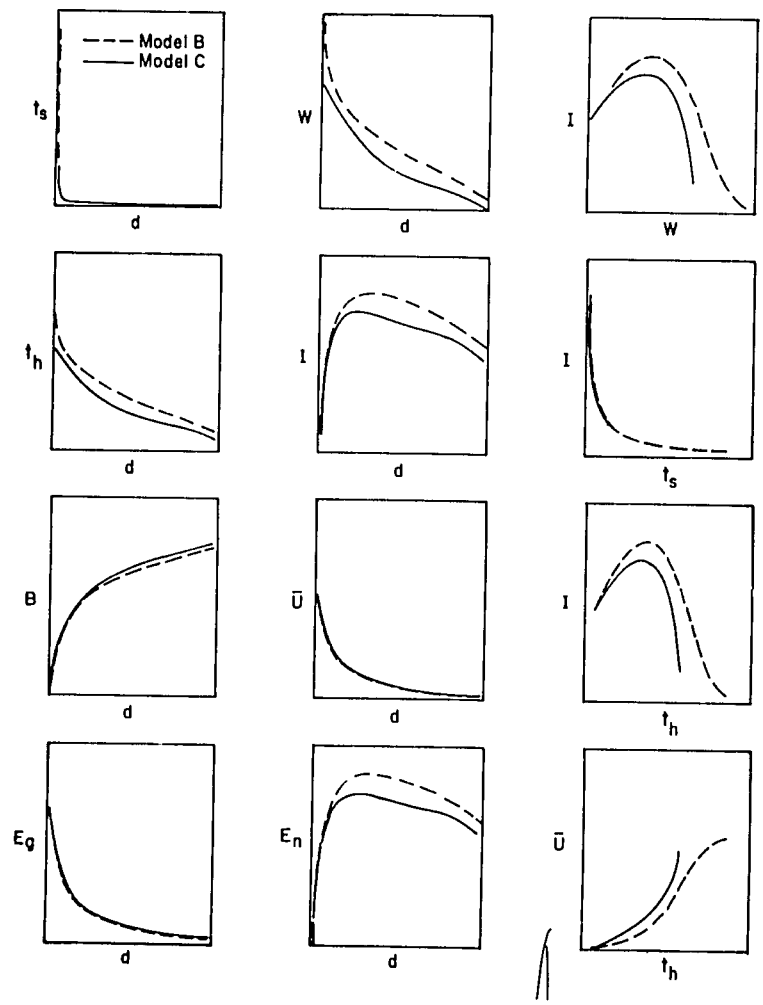
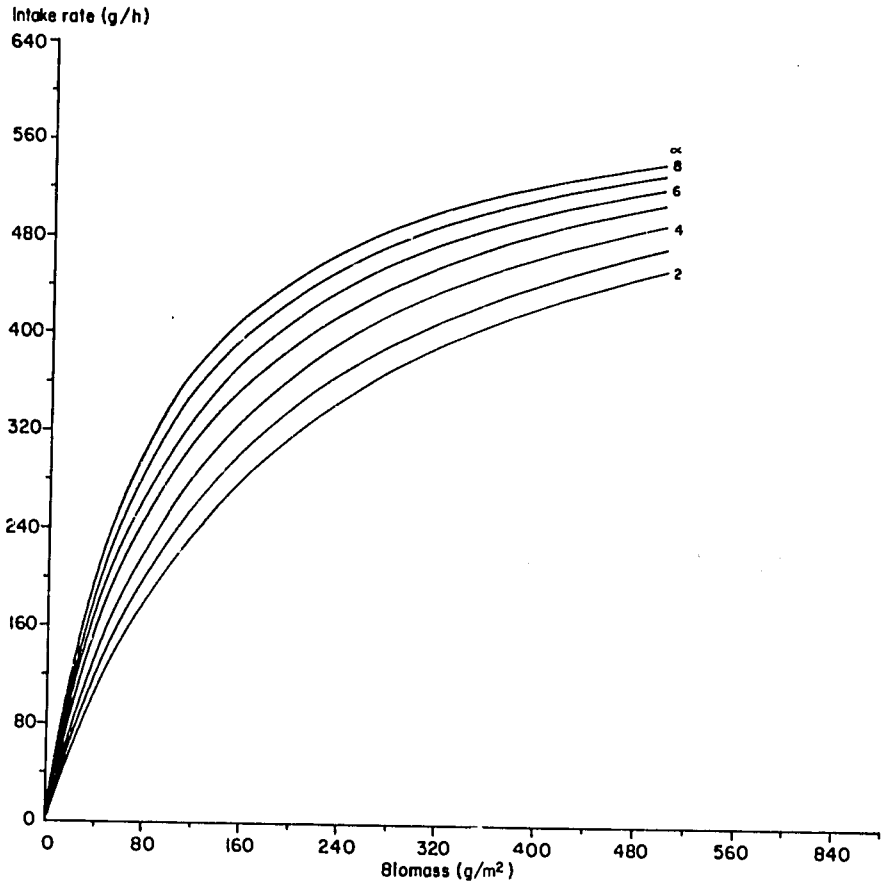


Figure 9. The functional response of intake to biomass for various levels of biomass heterogeneity (grazing-process model C)



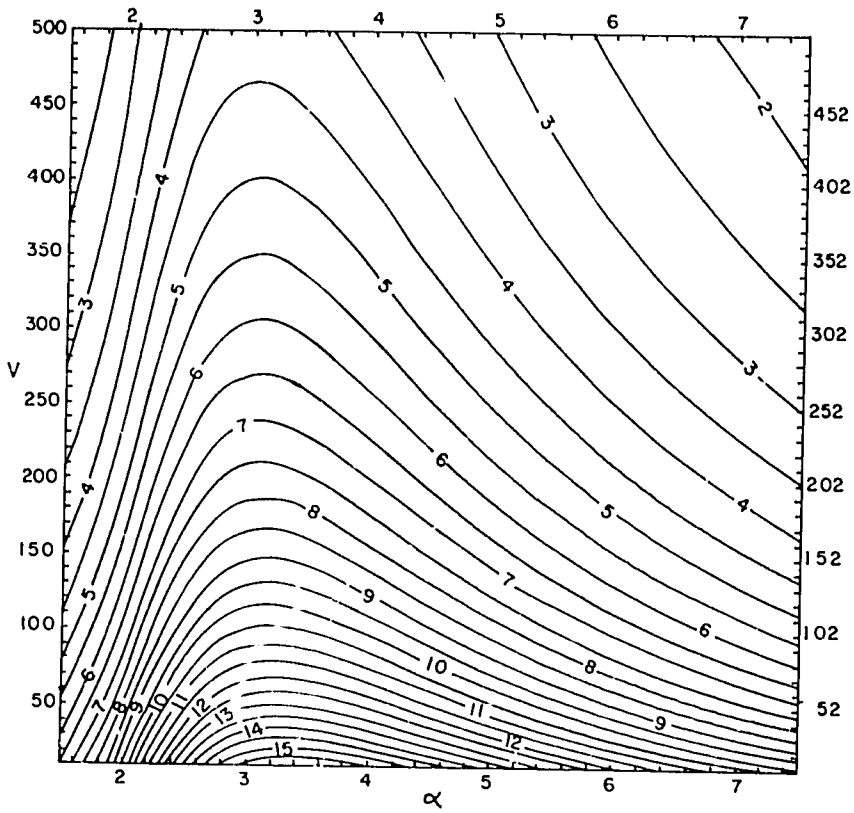
The iso-intake contour map for biomass and heterogeneity is very similar to that obtained with model B, and the sensitivity of intake rate to heterogeneity, $dI/d\alpha$, increases with increasing $\underline{V}$. It may, however, be more useful to look at the sensitivity of $\underline{I}$ to $\underline{\alpha}$ in terms of the relative change in $\underline{I}$. Model C was used to numerically estimate $(dI/d\alpha)/I$ (at the optimum selectivity level), for combinations of $\underline{\alpha}$ and $\underline{V}$. The contour map of this relationship is shown in Figure 10. The percentage increase in hourly intake rate per unit change in $\underline{\alpha}$ decreases with increasing biomass. At a given biomass, the relative change in $\underline{I}$ per unit change in $\underline{\alpha}$ is greatest in the region $\underline{\alpha}$ = 3 to 4. In the context of early-season pasture dynamics, $\underline{V}$ and $\underline{\alpha}$ are generally located in the region of greatest sensitivity to heterogeneity.

Conclusions from the grazing process models

The simple models described above have provided a rudimentary description of the plant-animal interface and have produced results consistent with those of empirical field studies of intake. Qualitatively, hourly intake shows a saturation functional response to herbage availability, which can be explained in terms of the relationship between bite weight, searching time and handling time and the way in which these components change with availability. Quantitatively, the response of hourly intake rate to availability is less steep than that of daily intake rate generally reported in the literature. This indicates the importance of grazing time as a buffer against declining availability, as shown by Allden and Whittaker (1970) and others.

This study confirms the consensus in the literature that biomass alone is not a sufficient predictor of intake rate. However, this is demonstrated by considering spatial heterogeneity of biomass distribution in the horizontal plane rather than in the vertical plane via height. Over a wide range of conditions, the mean selected biomass level (for the optimal foraging strategy) is approximately twice the field mean. This is consistent with results of van Keulen and Benjamin (unpublished data) in a study of the simulation model ARID CROP under grazing. It was found that reasonable simulation of primary

Figure 10. The response surface of the relative change (%) in hourly intake rate per unit change in alpha to mean biomass (V, g/m²) and biomass heterogeneity (α), at the optimum selectivity level (grazing-process model C)



production could only be achieved when defoliation was restricted to the top end of the biomass distribution curve.

Further development of the grazing-process model will need to incorporate heterogeneity of canopy height. This requires an algorithm of considerably greater complexity since a non-linear biomass-height relationship (at the selection site level) results in the uncoupling of bite weight and biomass density in the horizontal plane. Furthermore, even if a reasonable prediction of intake for a given canopy structure can be achieved, dynamic simulation of a growing canopy under defoliation would, at present, be highly speculative.

References

Allden W G and Whittaker I A McD. 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. Aust. J. Agric. Res. 21:755-766.

Milne J A, Hodgson J, Thompson R, Souter W G and Barthram G T. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. Grass and Forage Sci. 37: 209-218.

Discussion

Question - Has this model been validated and if not, would that be the aim?

Answer - No, it hasn't been validated. The approach was that of a theoretical ecologist looking at an agricultural problem, and you would find that it is virtually impossible to observe the relevant parameters in the field. So in terms of coming to a model that can be used in simulation models of grazing systems I am not very optimistic, but it certainly gives insight into what is happening in the field.

Question - If you put a number of reasonable estimates of the parameters in the model, do you get figures of between 1 and 2 kg of intake per sheep per day for an 8-hour grazing day?

Answer - No, not from those tables, but from a simple graph of functional response from grazing. When you look at Figure 9, you will see that the values are quite reasonable.

Question - Is the model suitable to simulate intake of an animal in a given situation or is it rather a means of analysing the interaction between the behaviour of the animal and pasture characteristics?

Answer - This model can help us to understand what is happening in the field, but only on a qualitative level. It will be very difficult to introduce this type of model into an overall model of grazing systems because you also have to simulate the response of the sward to do that.

Question - Is it right that the higher the skewness of dry matter in your pasture the earlier you can put in the animals?

Answer - If the goal is a certain level of intake yes, but from the point of view of stability, the reverse holds, so that you may have to wait a little longer.

Prediction of feed intake in ruminants

J.J.M.H. Ketelaars

Introduction

This paper presents some results from a study of literature on feed intake regulation in ruminants that was made as part of a research project aimed at analysing and predicting ruminant productivity in semi-arid regions.

Feed intake is probably one of the most important constraints on ruminant productivity irrespective of type of production system. Therefore prediction of intake becomes a critical issue in modelling such systems. Under semi-arid conditions the feed intake of ruminants is close to maintenance level for most of the year, resulting in weight stasis, small cumulative weight gain arising from even smaller daily gains, or weight loss. In such a situation small differences between energy intake and energy requirements for maintenance may tip the balance between production and loss. So, our ultimate interest is in the difference between two figures of approximately equal magnitude: total digestible energy intake and digestible energy requirements for maintenance.

Viewed in this way it appears almost impossible to attain any precision in predicting ruminant production from basic processes like feed consumption. However, it is certainly not a useless task, as only such efforts will reveal true limitations on productivity and effective ways to overcome them.

Predicting intake in ruminants requires an understanding of the mechanisms that regulate intake and their sensitivity to particular feed parameters. Over the last three decades much research has been devoted to elucidating intake-regulating mechanisms, with little success. As far as roughages are concerned, the typical diet of ruminants to which this paper will be restricted, emphasis has been on the existence of physical restrictions to intake. To quote Weston and Hogan (1973), it is generally assumed that, 'The ease with which the organic matter of the forage can be removed from the rumen is the most important dietary characteristic determining forage intake. The capacity of the rumen is limited and the rate of entry of feed organic matter into the rumen (rate of feed intake) cannot exceed its rate of removal. Hence the complex structure and function of the rumen, which obviate rapid removal of feed particles, can place a limit on the rate of feed consumption. It follows

that forages with organic matter highly resistant to removal from the rumen are consumed in smaller amounts than those more readily degraded.' This has been repeatedly stated in slightly different forms in many articles dealing with intake regulation. Evidence for such a physical theory of intake control will not be reviewed. Here we will consider the consequences of such a theory for intake prediction given the diversity of roughages available to ruminants.

In order to predict voluntary feed consumption from feed quality two different approaches can be envisaged: either (1) detailed simulation models have to be built of those ruminal processes which are thought to limit intake, or (2) empirical relationships between intake and those feed parameters which should express the rumen filling effect at best must be used.

Currently only the second approach is widely used, although a number of detailed simulation models of ruminal processes have been developed (Mertens, 1973; Baldwin et al, 1977; Black et al, 1980; Beever et al, 1980; France et al, 1982). Simulation studies have yielded one important, though perhaps disappointing, result: if studied at the level of ruminal dynamics, intake appears to be much more sensitive to animal parameters than to feed parameters. For instance, flow rates of water through the rumen and rumen space have a much larger effect on intake estimates than potential digestibility and rate of digestion of the feed (Mertens, 1973; Mertens and Ely, 1979; Poppi et al, 1981a; 1981b; 1981c). As neither variation in water flow rates nor variation in rumen space can be truly explained in current models, these have to be related to the feed which is actually consumed: what was intended as an explanatory model of intake regulation has then become a description of processes related to the ingestion of feed. The finding that intake predictions are more sensitive to animal parameters than to feed parameters confirms what has long been known: animals given the same feed show substantial differences in intake. For instance, lactating animals may eat 1.5 times as much as growing, non-lactating animals. The conclusion that appetite is more important than feed quality would be justified, yet it does not solve the question of intake control. In the absence of truly explanatory models of intake regulation, empirical relations between intake and feed characteristics remain the sole instrument for predictive purposes. How accurate and reliable are they? Do we understand their nature? These aspects are briefly discussed below. The conclusion is that, at present, no simple and accurate formulas exist to predict digestible

energy intake for a given category of animals. In addition, doubt is being expressed as to the usual explanation of intake-feed quality relations, i.e. as an expression of physical restrictions on the ingestion of fibre-rich diets.

A different analysis of the same data set as used for intake-fibre relations is given: instead of relating intake to certain feed parameters, intake of energy (cf. digestible matter) was related to intake of nitrogen for certain groups of feeds. Patterns of energy and nitrogen intake observed were analysed using information on protein metabolism in the rumen and the host animal. From that analysis it was concluded that the role of physical factors in intake control may be over-emphasized and that nutrient relations deserve more attention than has been given hitherto. Although shedding new light on old facts that analysis still leaves important questions unanswered. Having found that ruminants, when confronted with different roughages, appear to regulate both energy and nitrogen intake, the main question is why intake responses to supplementation with nitrogen and true protein are so unpredictable. Concluding this paper possible causes of this discrepancy are discussed.

Relationships between feed intake and feed characteristics

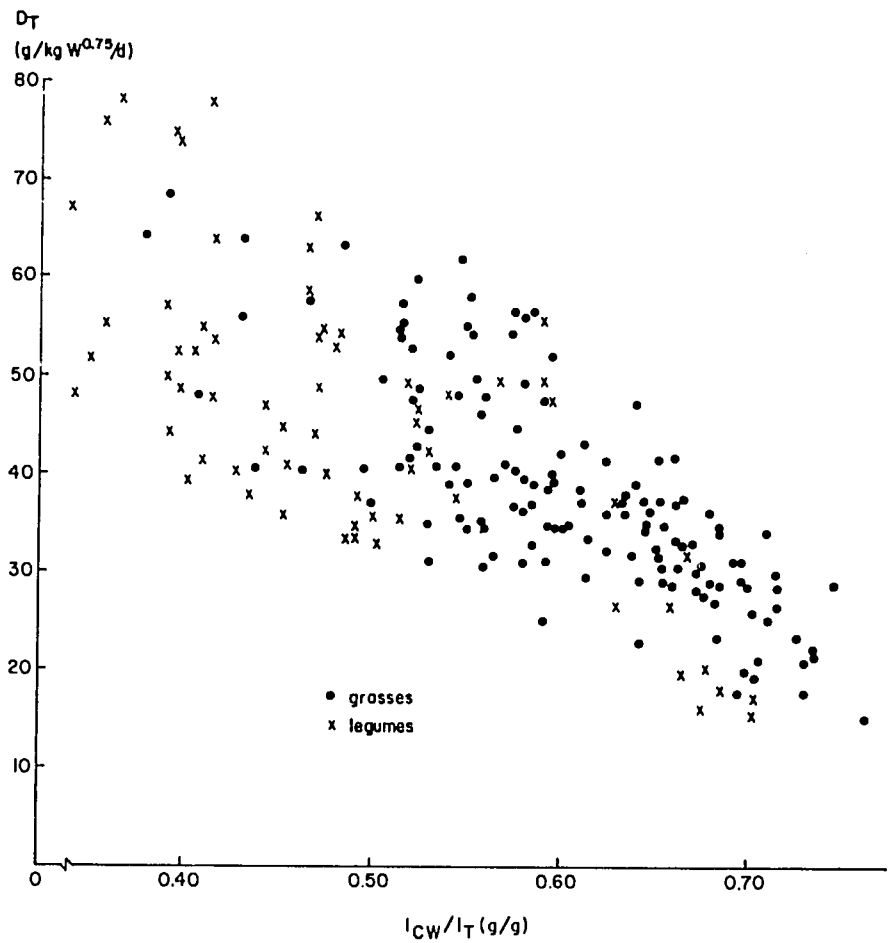
Numerous examples may be found in the literature of studies which correlate voluntary feed consumption of sheep and cattle to single or multiple properties of feeds. These may be of physical, chemical or plant morphological origin. However, most studies have a strong tendency to relate intake in some way to the division of each feed present between soluble, digestible or otherwise readily available or fragmentable components on the one hand and insoluble, indigestible or slowly degradable components on the other hand. Digestibility is perhaps the most frequently used parameter to assess the ingestibility of feeds. Although essentially referring to the absorbable part, the positive association between digestibility and intake has generally been considered as evidence for a physical restriction on intake. In other words digestibility has received the connotation of carrying more or less indigestible matter. The relationship with feed intake would then express a difficulty of ruminants to cope with less digestible feeds. Blaxter and his co-workers (Blaxter et al, 1961; Blaxter and Wilson, 1962) were probably the first to establish such a relationship by comparing different dried forages. Their work formed the basis for the use of

digestibility as an index of feed intake in ARC handbooks (ARC, 1965; 1980). Many other researchers working with both fresh and dried forages have confirmed the positive correlation between intake and digestibility. However, individual regression formulas differ substantially.

Mertens (1973), in a major compilation of intake trials with sheep, used plant cell wall concentration as a predictor of intake (Figure 1). His interpretation of the negative correlation between intake and cell wall concentration is grossly in line with the usually accepted model of feed-intake regulation. High concentrations of cell wall in feeds would create a physical embarrassment to the animal, because they enhance the filling effect of the feed in the rumen: cell walls are slowly and only partially degraded, unlike cell contents which readily and completely disappear from the rumen by digestion and absorption. It was observed, however, that when cell wall intake was regressed upon cell wall concentration, the intake of cell wall material appeared to be lowest at both low and high concentrations and highest at intermediate levels (Figure 2).

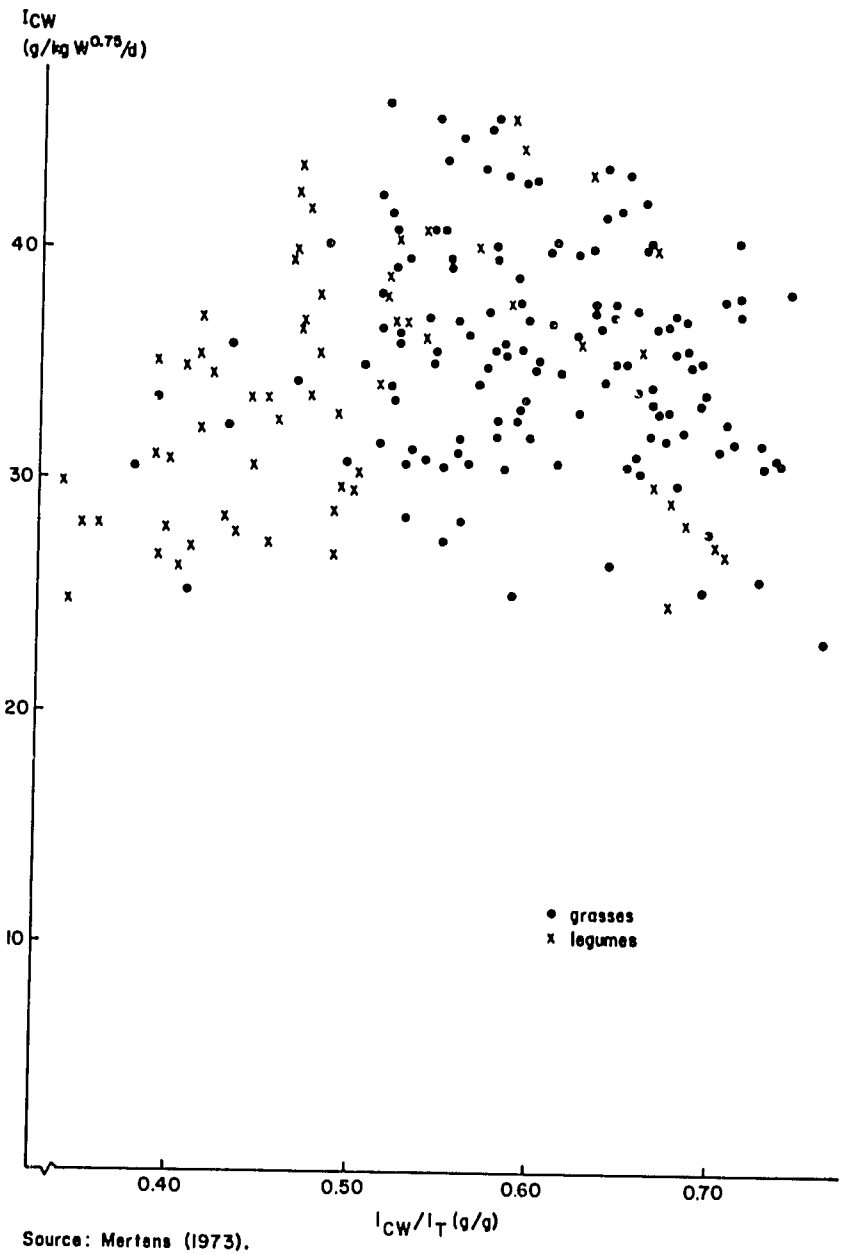
As the bulk density of cell walls increases with age, a similar weight of cell wall material in older plant material would occupy less space. Consequently one would not expect a depression of cell wall intake at higher cell wall concentrations if rumen fill was most affected by volumetric characteristics of a feed. Thus the problem is whether the filling effect of feed and digesta has to be considered on a volumetric or weight basis, which is apparently still unsolved in physical models of intake. It is noteworthy that a similar phenomenon is observed if the intake of indigestible matter is regressed upon digestibility. This is shown in Figure 3, using data from a much larger sample of roughages, which also indicates the amount of ballast (indigestible material) an animal would be willing to consume. This can be used to predict intake if feed digestibility is known. Even in a very homogeneous sample of feeds (Figure 4), all of which were fed in the fresh form to animals of similar age, weight, sex and breed, variation in indigestible matter consumption is considerable and clearly related to feed digestibility. Using a constant faecal output to predict intake from feed digestibility, as in several cattle production models (Sanders and Cartwright, 1979a; 1979b; Konandreas and Anderson, 1982; Kahn, 1982), seems very unsatisfactory in view of these data from sheep.

Figure I. Relationship between intake of digestible dry matter (D_T, g/kg $W^{0.75}$/d) and cell wall concentration of the feed (I_{CW}/I_T, g/g) for sheep fed grasses and legumes ad libitum



Source: Mertens (1973).

Figure 2. Relationship between intake of cell wall material (I_{CW}, g/kgw$^{0.75}$/d) and cell wall concentration of the feed (I_{CW}/I_T, g/g) for sheep fed grasses and legumes ad libitum



Source: Mertens (1973).

Figure 3. Relationship between faecal output of dry matter (F_T, g/kg $W^{0.75}$/d) and dry-matter digestibility of the feed (D_T/I_T, g/g) for sheep fed grasses and legumes ad libitum

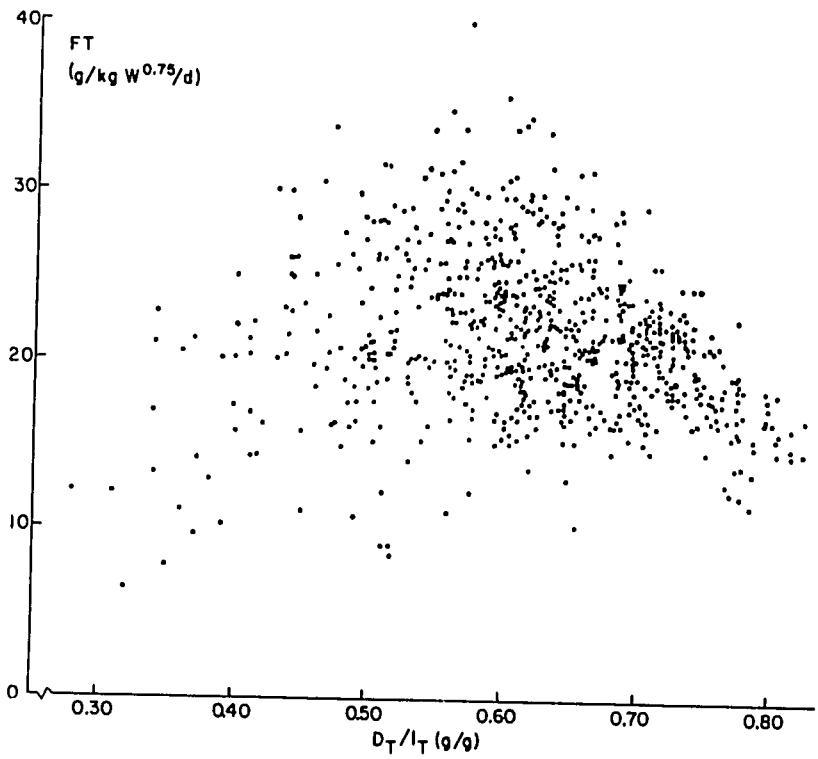
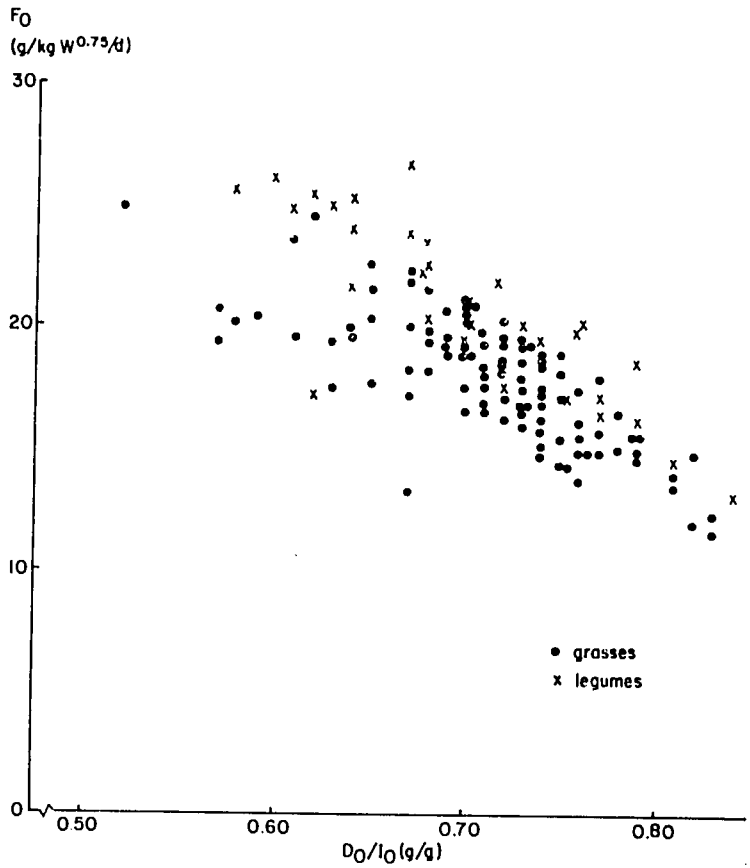


Figure 4. Relationship between faecal output of organic matter (F_O, g/kg $W^{0.75}$/d) and organic-matter digestibility of the feed (D_O/I_O, g/g) for Texel sheep fed fresh grasses and legumes ad libitum



Sources: Demarquilly and Weiss (1970) and INRA (1978).

For this practice of estimating intake reference is usually made to the work of Conrad et al(1964), who fed lactating cows ad libitum rations consisting of all roughage or roughage-grain mixtures. Feed digestibility ranged from 52 to 80%. Digestible dry-matter intake was measured and related to digestibility of the ration. The pattern observed differed from the one presented in Figure 5 for sheep fed all roughage diets that there appeared to be no further increase in digestible dry-matter intake for rations with dry-matter digestibility above about 67%. Statistical analysis revealed that intake of rations with digestibility of less than 67% could be explained from a constant faecal output per kg body weight. With rations with more than 67% digestibility, differences in milk production influenced intake. So they concluded that feed intake regulation changed from physically limited below 67% to metabolically limited above 67% digestibility of rations.

However their conclusions are subject to criticism. As shown by Mertens (1973) their statistical model was inappropriate, essentially in that intake was regressed upon digestibility and faecal output. This yields very little of interest, as intake always is a true mathematical function of the chosen variables: if feed digestibility and faecal output are known, intake can be calculated. The authors do not list individual data of the experiments, so re-analysis by others is not possible, which is unfortunate in view of the efforts invested in such feeding trials. Neither is it possible to check the constancy of faecal output suggested by the authors.

Relationships between intake and feed characteristics will not be further explored. However, two conclusions are particularly relevant. First, it is obvious from Figures 1 and 3 that using single variables like cell wall percentage or digestibility can give only a very crude estimate of digestible energy intake. Real variation in intake of feeds of a given cell wall percentage or digestibility often covers a two-fold range. Such a variation will be unacceptable in many cases, especially if intake changes from below to above maintenance within that range. Second, relationships between intake and feed characteristics invariably have generated the hypothesis that the presence of structural components in feeds (cell wall material, fibre or any other analogue) produces a filling effect in the rumen, which in turn limits voluntary feed consumption in the roughage-fed ruminant. As long as no alternative explanation is available to override the importance of a filling effect, it

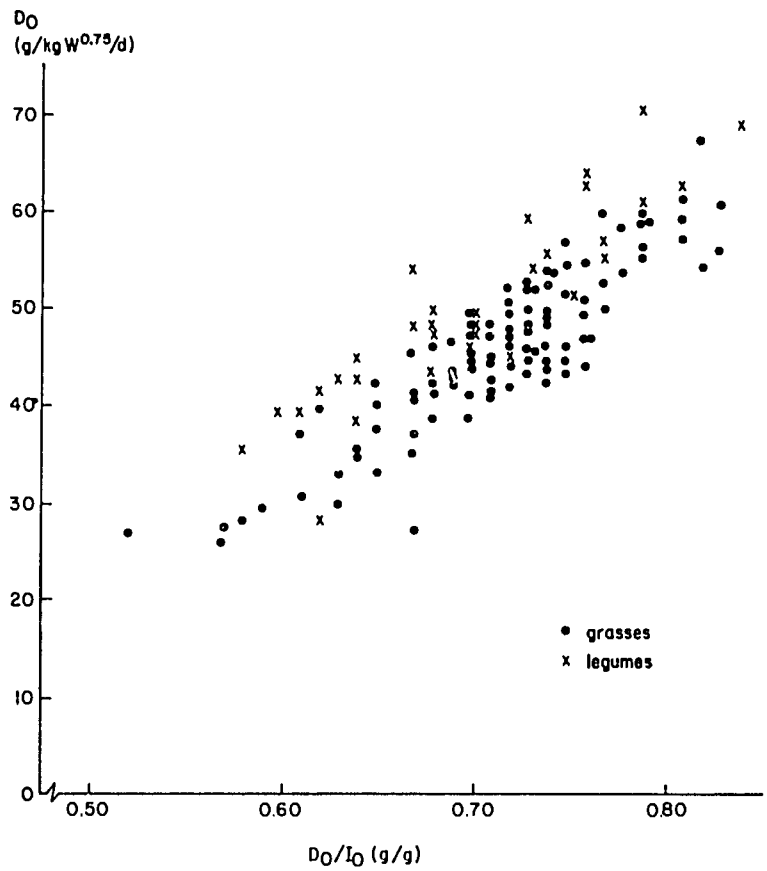
remains a viable hypothesis but nothing more than that: a close correlation between intake and cell wall concentration of feeds is, of course, also a close correlation between intake and cell soluble concentration and the interpretation is left to the biologist. In the meantime some scepticism may be expressed as to the likelihood of such a hypothesis. The interpretation of intake-fibre relations as presented above is unsatisfactory for several reasons:

- As Figures 5 and 6 show, intake of roughages, expressed either as organic-matter intake or as digestible organic matter intake, is a continually rising function of digestibility rather than a satiation function. This suggests that the limitation imposed by digestibility applies equally over the whole range of digestibility values, and that intake of even very immature forages would then be physically restricted although intake of indigestible matter is relatively low with these forages (Figure 4).

- The digestibility of roughages is usually between 40 and 80%. To get the same intake of digestible matter from the lowest-quality feed the animal would have to consume twice as much DM as with the highest-quality feed. Restricting the range to feeds of 60-80% digestibility an increase of only 33% is required. Is this outside the adaptational capacity of ruminants?

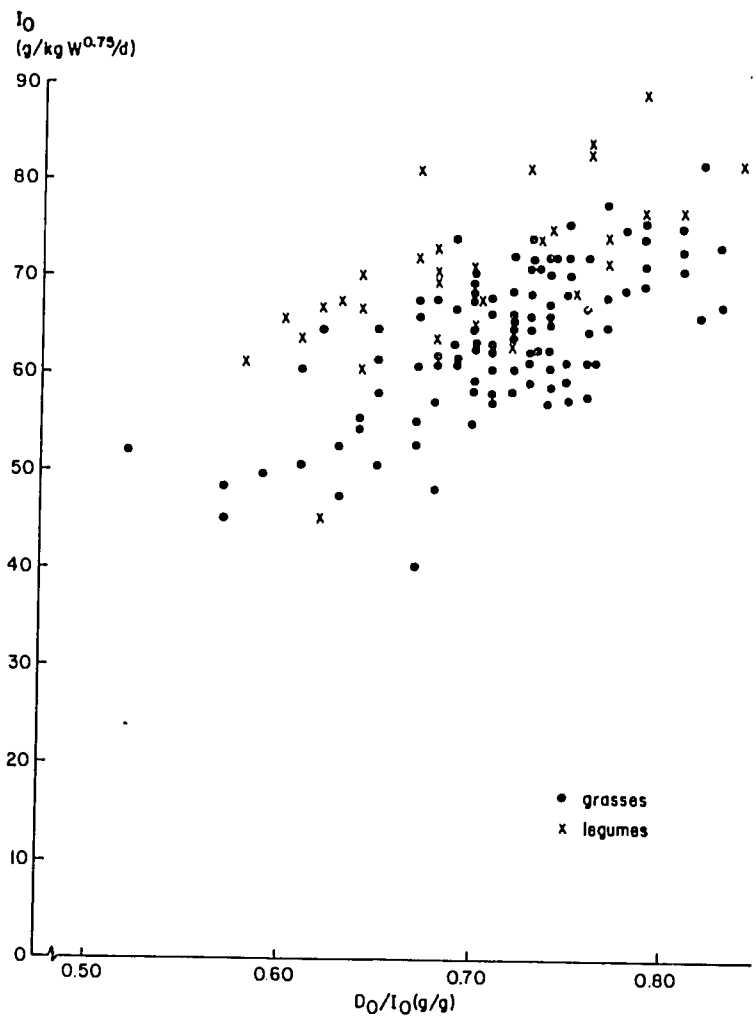
- Under certain conditions animals are able to increase the intake of the same roughage, for instance during cold stress or lactation. In the latter instance, increases of up to 50% have been noted. Intake would then always appear to be a compromise between demand for nutrients and the discomfort (increased rumen distension) associated with intake, a view advocated by many workers (see McClymont, 1967). Thus, production must often be inefficient, both from a biological and an economic point.

Figure 5. Relationship between intake of digestible organic matter (D_O, g/kg $W^{0.75}$/d) and organic-matter digestibility of the feed (D_O/I_O, g/g) for Texel sheep fed fresh grasses and legumes ad libitum



Sources: Demarquilly and Weiss (1970) and INRA (1978).

Figure 6. Relationship between intake of organic matter (I_O, g/kg $W^{0.75}$d) and organic-matter digestibility of the feed (D_O/I_O, g/g) for Texel sheep fed fresh grasses and legumes ad libitum



Sources: Demarquilly and Weiss (1970) and INRA (1978).

- This inefficiency would be greatly decreased if ruminants had bigger stomachs. Especially in natural environments with strong seasonal fluctuations in forage quality and availability, high intakes and rapid growth would improve chances for survival tremendously. Relative to their body weight ruminants apparently do not have a larger gut size than non-ruminant herbivorous species (Demment and van Soest, 1983), from which one is forced to conclude that selection for this trait has not been possible during their evolutionary development, a conclusion which is hardly believable in view of the immense morphological and anatomical diversity between animal species.

Patterns of energy and nitrogen intake in sheep

In addition to parameters like cell wall percentage and digestibility, the use of nitrogen content in estimating intake of digestible matter (which will be considered here a measure of energy intake) has also been suggested. Elliott and Topps (1963), examining a range of feeds of low to medium quality, found dry-matter intake to be more closely correlated with nitrogen concentration than with digestibility of the feed. The same would apply to intake of digestible dry matter. Siebert and Hunter (1977) proposed a regression equation between digestible organic-matter intake of growing cattle fed mixtures of spear grass and lucerne and nitrogen concentration to be used to estimate intake of grazing cattle from oesophageal sample analysis.

Comparing different relationships reveals that important differences exist and that the use of such relationships has to be restricted to the range of forages from which they were obtained. Thus the question arose as to whether, for a given type of stock, some upper limit of intake of digestible matter could be set for any given nitrogen concentration in the feed. From published data on feed intake of growing cattle it became apparent that such an upper limit indeed does exist but that it is of limited use. It was also soon evident that it is more informative to relate intake of digestible matter to nitrogen intake. A first analysis of this relation dealt with data from growing, non-lactating cattle (Ketelaars, 1983). That analysis comprised only a limited number of intake data from a wide range of breeds and weights of animals.

Many more data on intake are available for wether sheep, which are commonly used in trials to compare the ingestibility of a range of feeds. In addition, much experimental work on intake regulation has also been confined to sheep, and wether sheep of 30 - 70 kg body weight are probably the best-studied ruminant animals as far as feed intake and intake regulation are concerned. So it was decided to concentrate on data for sheep to further develop the conceptual model, of which a crude representation was given by Ketelaars (1983).

Sample description

Data on voluntary intake of roughages by wether sheep were collected from the literature. The criteria of selection were that, apart from intake, nitrogen concentration of the feed, in vivo digestibility and weight or metabolic weight of the animals were known. Only data from roughages will be used to present patterns of energy and nitrogen intake. These include grasses and legumes, fed either alone or as mixtures of both. Supplements allowed were minerals and vitamins. Feeds supplemented with protein or nitrogen source were excluded as were ground and pelleted roughages.

Data were obtained from Demarquilly and Journet (1967), Demarquilly and Weiss (1970), Heany et al (1963), INRA (1978), Mertens (1973), Milford (1960; 1967), Milford and Minson (1968a; 1968b), Minson (1967; 1973), Minson and Milford (1967;1968), and Minson et al (1964).

Data were available on 766 different feeds. In reality the number of trials will have been larger as the French data (Demarquilly and Weiss, 1970; INRA, 1978) are averages for a certain feed tested in several trials. Of the total of 766, 32 (less than 5%) were discarded because they did not fit the general pattern of intake shown later. In 21 cases intake of digestible dry matter was substantially less than expected for the digestibility class in question, and for the remaining 11, intake was unusually high.

Of the 734 feeds which were left, 573 were grasses and 161 legumes. Mixtures of grasses and legumes were classified according to the dominant fraction. Rations were fed in the fresh or dried form, long or chopped. Together they comprise a large number of species of temperate, tropical and subtropical origin.

In selecting data no distinction was made as to breed of animal used. Breed was not always recorded but the range spanned typical wool breeds like the Merino and typical meat breeds like the Texel. Exact weights were not always given. Mean weight of the animals used in these trials will probably fall between 40 and 50 kg. Actual weights will have shown wider variation, probably between 30 and 70 kg liveweight.

Special attention must be drawn to the data collected by French workers for fresh pasture grasses and legumes (Demarquilly and Weiss, 1970; INRA, 1978), which have been used in this paper to illustrate various trends in intake. It is the largest homogeneous subsample of the total data available for which essential additional information could be found on protein metabolism in the rumen and the host animal. Therefore these data will be analysed separately but are also included in the analysis of the total sample. Figures 7 and 8 show the relationship between in vivo dry-matter digestibility and nitrogen concentration of the feeds for the total sample, and the relationship between in vivo organic-matter digestibility and nitrogen concentration of the feeds for the subsample. For most of the data digestibility was reported on a dry-matter basis, and digestible dry-matter intake has been chosen as the parameter to be used in the presentation of the total sample data. French workers, however, consistently reported digestibility on an organic-matter basis, and this is preferred as it is a more precise parameter of energy intake. Conversion between organic-matter and dry-matter digestibility is not straight-forward, as it depends on ash concentrations and digestibility of ash and these are often not reported. Where conversion was necessary, e.g. for inclusion of the French data in the total sample, information was used from data given by Troelsen and Campbell (1969). In their trials with 36 hays of temperate grasses and legumes the regression equation between in vivo dry-matter digestibility (D_T/I_T, g/g) and in vivo organic-matter digestibility (D_O/I_O, g/g) appeared to be: $D_T/I_T = 1.00\ D_O/I_O - 0.0146$ with $r = 0.99$. So, if necessary, D_T/I_T has been estimated from D_O/I_O by subtracting 0.015 g/g.

Using the same conversion and assuming a mean ash concentration of 0.10 g/g of dry matter it can be calculated that each gram of digestible dry matter will be roughly comparable to 0.92 gram of digestible organic matter.

Figure 7. Relationship between in vivo dry-matter digestibility (D_T/I_T, g/g) and nitrogen concentration in the dry matter (I_N/I_T, g/g) of grasses and legumes fed to wether sheep of various breeds

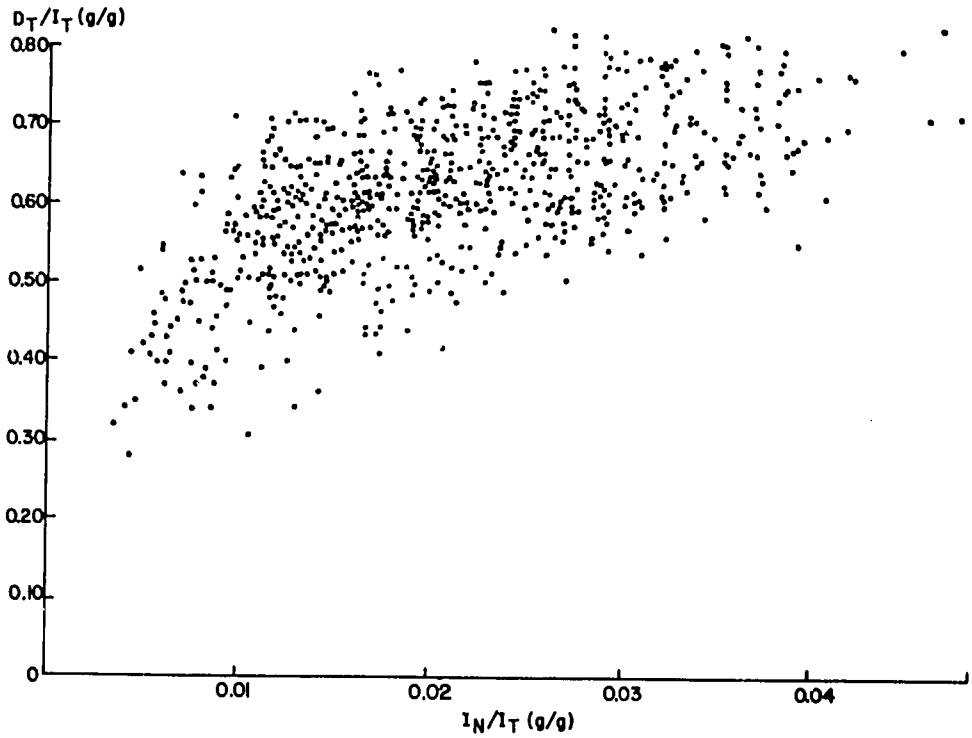
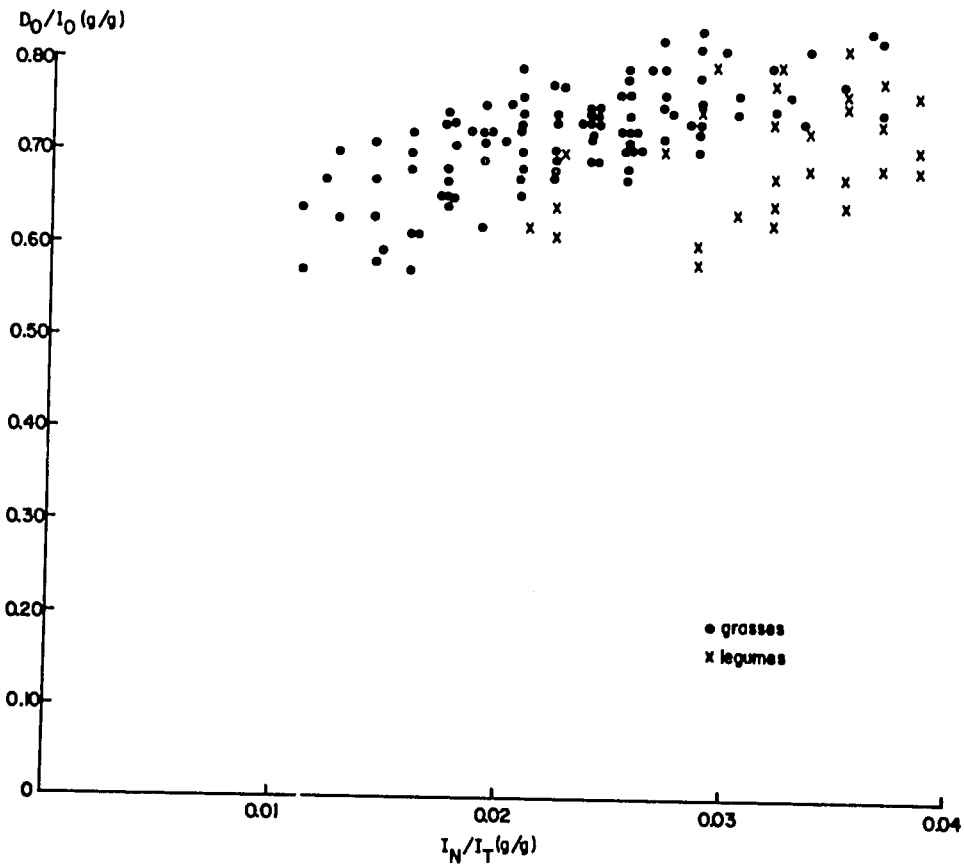


Figure 8. Relationship between *in vivo* organic-matter digestibility (D_O/I_O, g/g) and nitrogen concentration in the dry matter (I_N/I_T, g/g) of fresh pasture grasses and legumes fed *ad libitum* to wether sheep of the Texel breed



Sources: Demarquilly and Weiss (1970) and INRA (1978).

Results of the total sample

Patterns of intake of digestible dry matter and nitrogen for the total sample are presented in Figure 9, 10 and 11. Figure 9 shows all the data. Figure 10 shows data for the 0.59-0.61 g/g digestibility class, which comprised the largest number of feeds, with the linear regression line. Figure 11 shows the regression lines for digestible dry-matter intake as related to nitrogen intake after feeds had been grouped according to digestibility class.

Digestibility classes were first chosen so as to get a reasonable number of data in classes with average dry-matter digestibility of 0.45, 0.50, 0.55, 0.60, 0.65, 0.70, 0.75 and 0.80 g/g, without too much variation in digestibility within classes. In view of the experimental variation in in vivo digestibility measurements, digestibility classes seem sufficiently narrow to relate the results to the mean of the classes. As a consequence digestibility classes in between the first mentioned are narrower. Regression equations are listed in Table 1.

Table 1. Regression equations relating intake of digestible dry-matter (D_T, g/kg $w^{0.75}$/d) to intake of nitrogen (I_N, g/kg $w^{0.75}$/d) for sheep of different breeds fed grasses and legumes of different dry-matter digestibility (D_T/I_T, g/g).

D_T/I_T (g/g)	n*		r
0.44 - 0.46	16	$D_T = 12.45 + 12.23\ I_N$	0.75
0.47 - 0.48	16	$D_T = 13.62 + 9.80\ I_N$	0.72
0.49 - 0.51	47	$D_T = 13.65 + 13.64\ I_N$	0.72
0.52 - 0.53	25	$D_T = 15.52 + 11.75\ I_N$	0.81
0.54 - 0.56	53	$D_T = 21.38 + 8.86\ I_N$	0.80
0.57 - 0.58	51	$D_T = 21.32 + 10.22\ I_N$	0.76
0.59 - 0.61	114	$D_T = 24.29 + 8.75\ I_N$	0.74
0.62 - 0.63	59	$D_T = 27.40 + 8.72\ I_N$	0.77
0.64 - 0.66	92	$D_T = 28.03 + 8.78\ I_N$	0.78
0.67 - 0.68	45	$D_T = 30.85 + 8.89\ I_N$	0.84
0.69 - 0.71	75	$D_T = 36.96 + 7.08\ I_N$	0.71
0.72 - 0.73	35	$D_T = 39.97 + 7.60\ I_N$	0.72
0.74 - 0.76	36	$D_T = 38.80 + 8.20\ I_N$	0.82
0.77 - 0.78	21	$D_T = 36.02 + 9.36\ I_N$	0.50
0.79 - 0.81	13	$D_T = 52.18 + 5.15\ I_N$	0.65

*Number of feeds

Figure 9. Relationship between intake of digestible dry matter (D_T, g/kg $W^{0.75}$/d) and intake of nitrogen (I_N, g/kg $W^{0.75}$/d) for wether sheep of various breeds fed grasses and legumes *ad libitum*

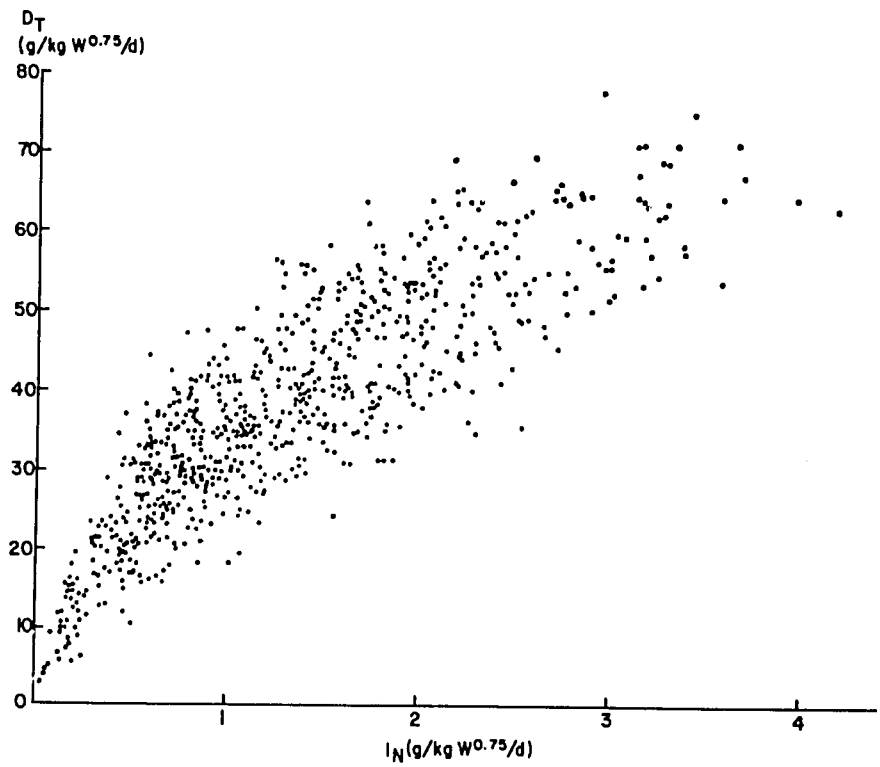


Figure 10. Relationship between intake of digestible dry matter (D_T,g/kg $W^{0.75}$/d) and intake of nitrogen (I_N,g/kg $W^{0.75}$/d) for wether sheep of various breeds fed grasses and legumes with dry-matter digestibilities (D_T/I_T;g/g) in the range of 0.59 to 0.61

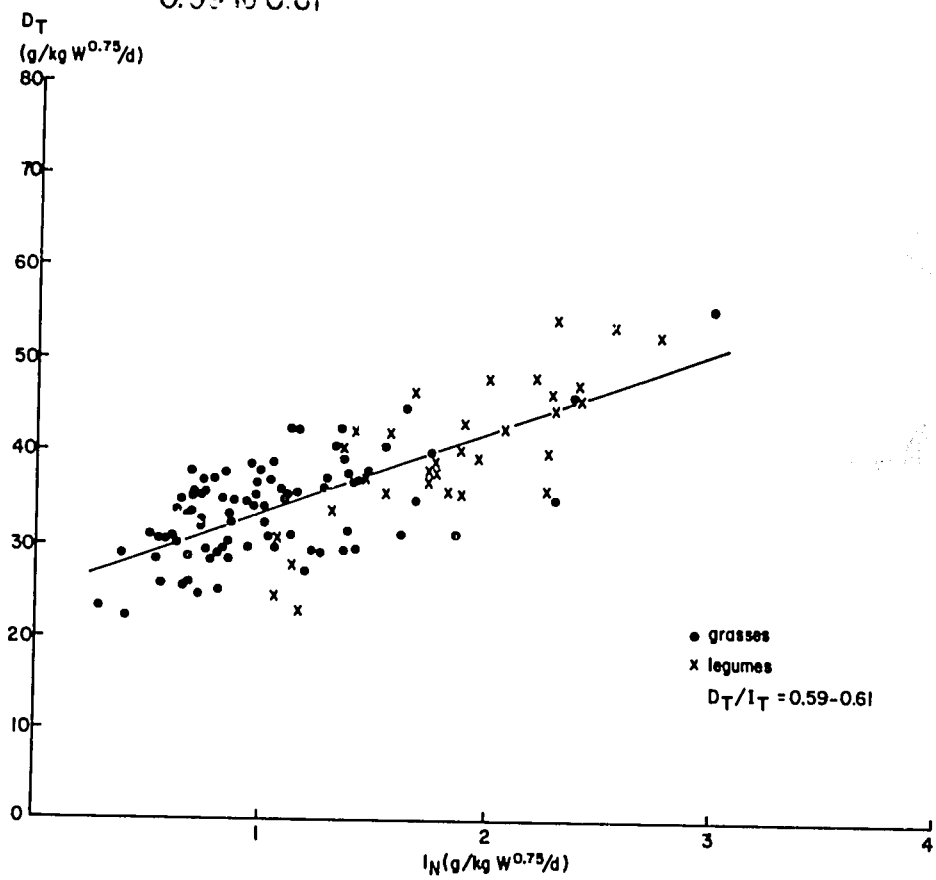
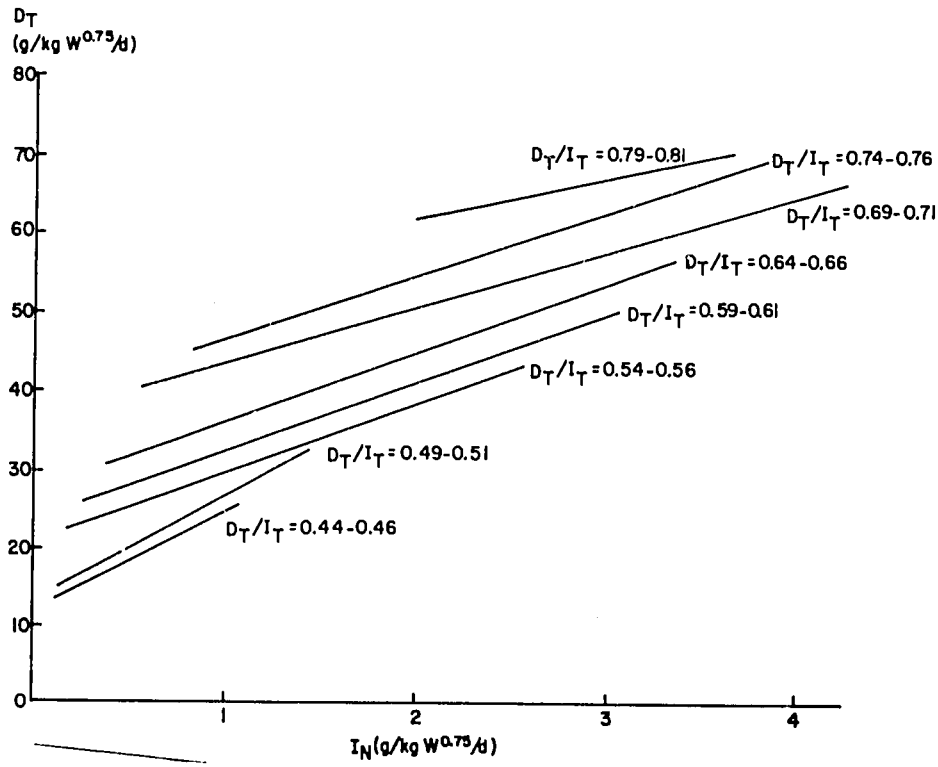


Figure 11. Regression lines relating intake of digestible dry matter (D_T, g/kg $W^{0.75}$/d) to intake of nitrogen (I_N, g/kg $W^{0.75}$/d) at different levels of dry-matter digestibility of the feed (D_T/I_T, g/g)



Discussion

From Figure 7 it is evident that the total sample comprises the entire range of roughage qualities ranging from less than 0.30 g/g dry-matter digestibility and less than 0.005 g/g nitrogen in the dry matter to more than 0.80 g/g dry-matter digestibility and 0.045 g/g nitrogen. A second important observation is that the correlation between *in vivo* dry-matter digestibility and nitrogen concentration of the feed is very weak: in other words, the often rather close association between these parameters observed in aging plant material of the same type and from the same location almost disappears if feeds of widely different origin are studied.

The data from the French subsample shown in Figure 8 are typical for the diet of ruminants during the main grazing season in Western Europe, with immature grasses in spring having up to 0.036 g/g nitrogen (22.5% protein) and over 0.80 g/g organic-matter digestibility. Even when flowering, grasses have nitrogen concentrations above 0.01 g/g and organic-matter digestibility over 0.55 g/g.

At first sight, the nature of the relationship between intake of digestible dry-matter and nitrogen as depicted in Figure 9 is not very clear. Fitting some kind of saturation function curve would have been possible but would give little help in the interpretation. The pattern becomes much clearer if feeds are grouped on the basis of digestibility as shown in Figures 10 and 11. Orderly increases in intake of digestible dry-matter with nitrogen intake become visible at each level of digestibility, although there is still considerable scatter of the data points. Linear relations have been fitted to these increases as they appear, on average, to be the best representation. Only data for feeds of between 0.50 and 0.55 g/g digestibility showed a more curvilinear trend. As slopes of the regression equations for feed intake below maintenance level (approximately 30 g D_T/kg $w^{0.75}$/d) tend to be higher than above it, such curvilinearity might result from the change in feeding level within this data group. If so, a broken line would perhaps be more appropriate.

Individual regression lines for legumes and grasses separately are not shown. Inspection of the data in Figure 10 reveals that the higher intake of legumes as compared with that of grasses of similar digestibility can be attributed to the higher nitrogen concentration of the former. Within both grasses and legumes similar increases in intake of digestible dry matter with nitrogen intake are present.

The main conclusion that can be drawn from the total sample is that if roughages are classified according to digestibility then voluntary intake of digestible dry-matter by sheep increases linearly with nitrogen intake within such classes. For predictive purposes this means that high-protein feeds are eaten in greater amounts than low-protein feeds, irrespective of digestibility level. For our understanding of intake regulation, clearly the most important question is what does digestibility mean to the ruminant animal? This question will be examined with the help of data from the subsample.

Results of the subsample

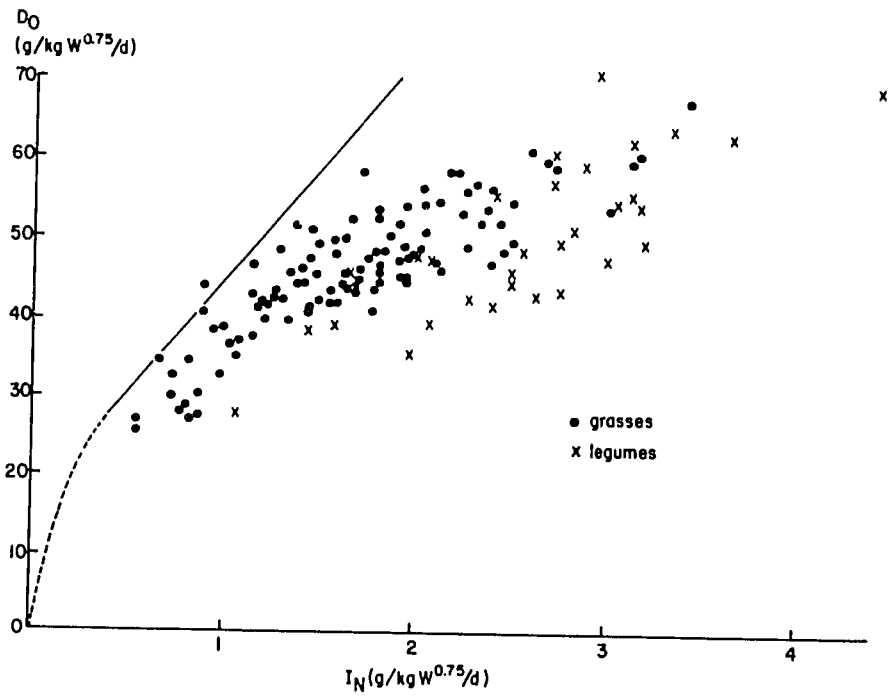
Data from the subsample for sheep or the Texel breed fed fresh pasture grasses and legumes are given in Figures 12, 13 a - g, and 14 and Table 2. Figure 12 shows the complete data set, a total of 137 feeds. Also shown is a curve representing the maximum intake of digestible organic matter for a certain range of nitrogen intakes (abbreviated $D_{0\ max}$-curve). Its derivation is discussed below.

Figures 13 a - g show data for individual classes of digestibility. Only data for grasses were used in the calculation of the regression lines. Figure 14 gives a composite picture of the regression lines together with the $D_{0\ max}$-curve. Finally, Table 2 includes the details of the regression equations.

Discussion

The pattern of linear increases in intake of digestible matter with intake of nitrogen observed in the total sample is confirmed by the subsample. For the grasses, linearity is present at each level of digestibility and scatter of points is reduced. The latter is partly the result of excluding variation due to breed, form of feed, location etc, and partly due to the fact that these data are averages for a certain feed tested in a number of trials. Some sources of variation will be analysed later.

Figure 12. Relationship between intake of digestible organic matter (D_O, g/kg $W^{0.75}$/d) and intake of nitrogen (I_N, g/kg $W^{0.75}$/d) for wether sheep of the Texel breed fed fresh pasture grasses and legumes ad libitum. The solid line shows the calculated maximum intake of digestible organic matter above maintenance as related to nitrogen intake. The broken line shows the estimated maximum intake of digestible organic matter for each level of nitrogen intake below maintenance level



Sources: Demarquilly and Weiss (1970) and INRA (1978).

Figure 13. Relationships between intake of digestible organic matter (D_O, g/kg $W^{0.75}$/d) and intake of nitrogen (I_N, g/kg $W^{0.75}$/d) for Texel wetners fed fresh pasture grasses and legumes with organic-matter digestibilities (D_O/I_O, g/g) of: (a) 0.61-0.63; (b) 0.64-0.66; (c) 0.67-0.69; (d) 0.70-0.72; (e) 0.73-0.75; (f) 0.76-0.78; (g) 0.79-0.81. Regression lines are based only on data for grasses

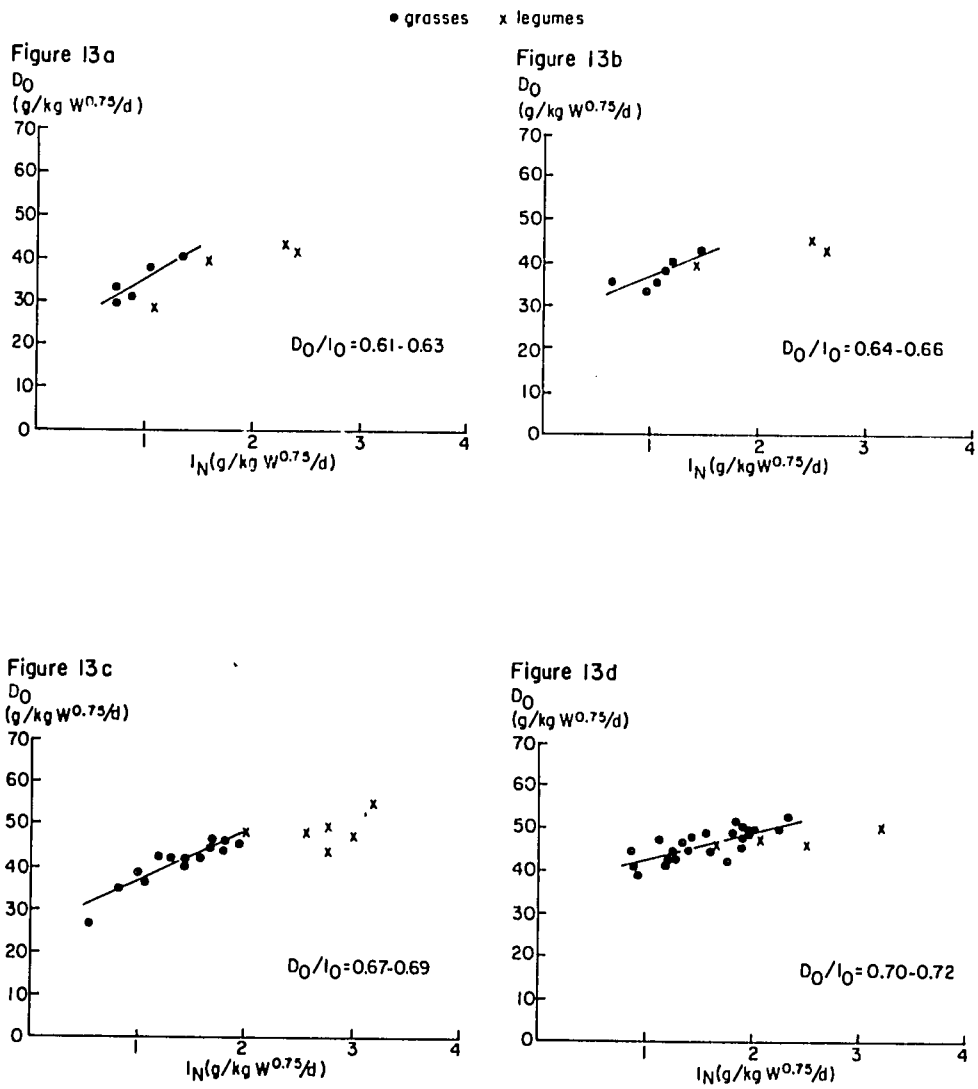


Figure 13e

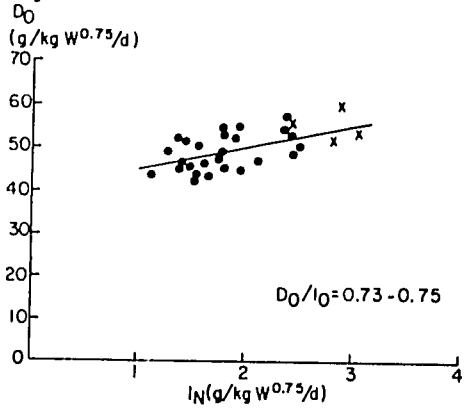


Figure 13f

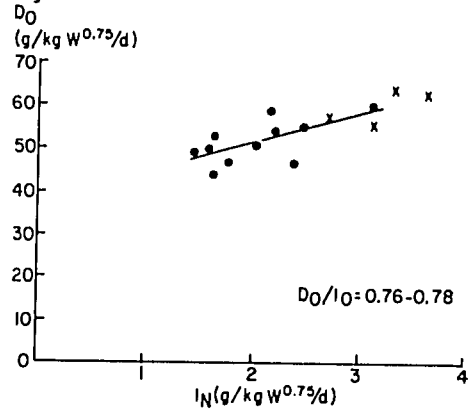
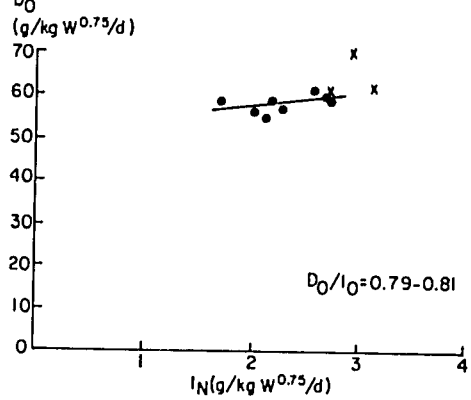


Figure 13g



Sources: Demarquilly and Wesis (1970) and INRA (1978).

Figure 14. Regression lines relating intake of digestible organic matter (D_O, g/kg $W^{0.75}$/d) to intake of nitrogen (I_N, g/kg $W^{0.75}$/d) at different levels of organic-matter digestibility of the feed (D_O/I_O, g/g). This is a composite of the regression lines shown in figures 13 a-g. Also shown is the curve for maximum intake of digestible organic matter from figure 12

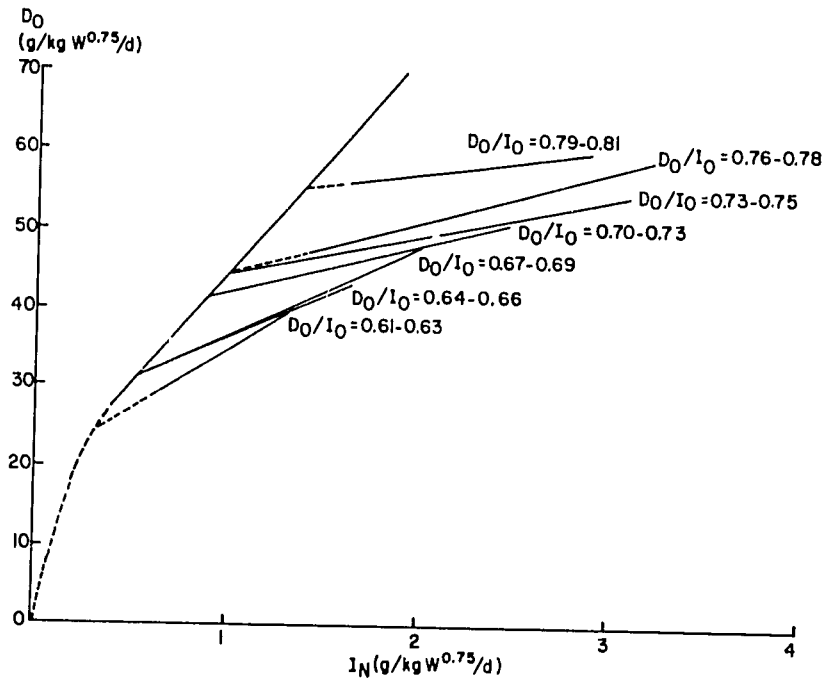


Table 2. Regression equations relating intake of digestible organic matter (D_0, g/kgw$^{0.75}$/d) to intake of nitrogen (I_H, g/kg w$^{0.75}$/d) for sheep of the Texel breed fed fresh grasses of different organic matter digestibility (D_0/I_0, g/g).

D_0/I_0 (g/g)	n*		r
0.61 - 0.63	5	$D_0 = 19.87 + 15.09\ I_N$	0.91
0.64 - 0.66	6	$D_0 = 25.95 + 10.52\ I_N$	0.91
0.67 - 0.69	14	$D_0 = 25.07 + 11.47\ I_N$	0.92
0.70 - 0.72	26	$D_0 = 35.94 + 6.04\ I_N$	0.75
0.73 - 0.75	27	$D_0 = 39.92 + 4.73\ I_N$	0.52
0.76 - 0.78	11	$D_0 = 37.89 + 6.57\ I_N$	0.66
0.79 - 0.81	8	$D_0 = 50.99 + 3.08\ I_N$	0.56

*number of feeds

Another observation is that slopes of the regression lines become smaller at higher digestibility levels. With regard to the difference between legumes and grasses, it now appears that intake of highly digestible legumes (i.e. above 0.72 g/g organic-matter digestibility) can be predicted from intake of grasses taking into account differences in nitrogen concentration, but for lower-quality legumes discrepancies exist: intake of these legumes is less than would have been expected on the basis of intake of grasses and their nitrogen concentration.

The observed pattern of energy and nitrogen intake in sheep resembles similar patterns in young monogastric animals, in which low-protein feeds usually depress energy intake. Analysing a number of feeding trials with rats, dogs and chickens, it was found that if intake of energy is depressed by low protein/energy ratios in the feed, increasing this ratio by adding protein to the feed results in linear increases of both energy intake and nitrogen intake. At the same time liveweight gain and nitrogen retention show similar proportional increases. From these observations it was hypothesised that the intake-depressing effect of low protein/energy rations in monogastric animals

may be functionally explained by an inability of the animal to produce liveweight gain if the diet contains less than a certain concentration of protein. As maintenance requirements are mainly composed of energy and liveweight gain requires relatively more protein, intake of energy above maintenance is dependent on increased protein/energy ratios of the feed. If this hypothesis is correct, maximum allowed intake of energy as a function of protein intake can be calculated from (1) maintenance requirements for protein and energy, (2) the minimum protein energy ratio in liveweight gain and (3) the efficiency of use of feed protein and feed energy by the animal. The intake data for sheep show intake of energy (cf digestible matter) for most feeds, if not for all, below the maximum that can be attained with these animals. Apparently, intake of energy was limited by some factor and for the moment it will be assumed that this factor was availability of true protein. With this assumption, potential energy intake versus nitrogen intake can be calculated according to above mentioned hypothesis, as explained below.

Availability of true protein is taken as the amount of non-ammonia nitrogen which reaches the duodenum. This amount can be quite different from the quantity of protein ingested. For many feeds this will be lower, due to losses of protein in the rumen, while for others it will be more, due to conversion of endogenous nitrogen (mainly ureum in saliva) into bacterial protein. Such changes in availability of protein between mouth and duodenum clearly hamper the interpretation of intake patterns in ruminants. One way to handle this problem is to calculate the $D_{o\ max}$-curve, for which it is assumed that efficiency of conversion of ingested protein into true protein reaching the duodenum is maximal. This is done in the following manner.

- Requirements of energy for maintenance have been set at 425 kJ M_E/kg $W^{0.75}$/d, the value proposed by Orskov (1982). Using an efficiency of 0.81 for conversion of digestible energy to metabolisable energy and an energy value of 19.1 kJ/g digestible organic matter, energy requirements are equivalent to the ingestion of 27.5 g D_O/kg $W^{0.75}$/d. However, energy requirements for maintenance vary between breeds, ages and seasons. Effects of such differences will be analysed later.

The energy value of digestible organic matter is the mean calculated for fresh pasture grasses using data from INRA (1978).

- Requirements of protein for maintenance continue to be a matter of debate as they are difficult to measure in ruminants. Here they have been set at 0.4 g ingested N/kg $W^{0.75}$/day. As Figure 9 shows, this amount is the minimum that allows consumption of 30 g D_T/kg $W^{0.75}$/d, which is equivalent to 27.5 g D_O/kg $W^{0.75}$/d. In addition, a value of 0.4 g on a metabolic-weight basis compares favourably with recent estimates of protein requirements obtained with intragastric infusion techniques. From nitrogen excretion of ruminants on nitrogen-free infusates, Orskov (1982) estimated minimum needs for protein in tissue maintenance to be about 300-400 mg N/kg $W^{0.75}$/d; the higher value would apply to younger animals, the lower value to older animals. Intake of 0.4 g feed nitrogen produces a flow of non-ammonia nitrogen into the duodenum of approximately 0.6 g. Assuming efficiency of nitrogen use to be similar for maintenance and productive processes, i.e. 0.54 (see below) this would provide 324 mg net amino-acid nitrogen to the tissues.

- Efficiency of conversion of ingested nitrogen into animal products has been based on data from infusion experiments with rumen bacterial mass in lambs (data cited by Orskov, 1982). Net efficiency of total microbial nitrogen appeared to be 0.54. Incremental efficiency of ingested nitrogen will, therefore, never be more than 0.54 unless undergraded plant protein has a higher biological value. As there is no evidence for the latter, the value of 0.54 will be retained. The fact that this figure was obtained with lambs may introduce some error. Synthesis of wool protein is more important in older sheep than synthesis of body protein. If efficiency of use of absorbed protein is less for synthesis of wool, overall efficiency would shift to lower values.

It is noteworthy that Boekholt (1976), in N-balance experiments, found a maximum incremental efficiency of 0.75 for retention of digestible nitrogen in lactating dairy cows. As true digestibility of feed nitrogen was 0.83 g/g, maximum incremental efficiency of ingested nitrogen would amount to 0.62, a value 15% higher than the value of 0.54.

- Composition of production above maintenance, i.e. liveweight gain + wool, was not known for the specific animal breed and physiological stage. Instead, data on nitrogen retention were available from a paper of Grenet and Demarquilly (1977). They measured nitrogen retention in the same type of animals (wether sheep of the Texel breed) given 23 different grass samples and 3 lucerne samples ad libitum, all in the fresh form, data from which are

directly compatible with the data on intake. Only information from the grass samples is used here. Grenet and Demarquilly (1977) related nitrogen retention to various parameters in single- and multiple-regression analyses. Using single parameters, intake of digestible organic matter was found to be the best predictor of nitrogen retention. The regression equation between nitrogen retention (R_N,kg/d) and intake of digestible organic matter (D_0,kg/d) was:

$$R_N = 0.01875\ D_0 - 0.0104\ (r = 0.86.)$$

Multiple regression with other parameters (digestibility of organic matter, concentration of crude-fibre and soluble carbohydrates in the feed and nitrogen intake) could not improve this prediction equation substantially.

From this finding it is concluded that, irrespective of level of ad libitum intake of digestible organic matter, animals produced a product which required a fixed ratio of digestible energy and net protein. As Tolkamp (personal communication) showed, utilisation of metabolisable energy for net energy is constant in ad libitum fed animals (i.e. 0.60) and metabolisable energy is a fairly constant proportion of digestible energy (i.e. 0.81), and it is concluded that composition of total product had a constant ratio of protein to energy. It should be noted that exactly the same conclusion was reached for monogastric animals under conditions of protein-limited intake of energy.

The regression equation cited above is expressed on a per animal basis. Assuming 55 kg as the mean weight of the animals, R_N equals zero at an intake of digestible organic matter of 27.5 g/kg $W^{0.75}$/d which coincides with the proposed maintenance requirements for energy.

The slope of the regression line gives the increase of retained nitrogen per gram of extra digestible organic matter ingested. Conversely, it also incorporates the maximum incremental increase in intake of digestible organic matter as related to nitrogen intake: 28.8 g D_0/g R_N. The latter value is obtained by dividing the maximum efficiency of conversion of ingested nitrogen into retained nitrogen (0.54) by the incremental increase of retained nitrogen per gram of digestible organic matter intake (0.01875 g/g).

Summarising, the function giving maximum intake of digestible organic matter for intakes of nitrogen equal to or more than 0.4 g/kg $W^{0.75}$/d can be written as:

$$D_0\ max = 16.0 + 28.8\ I_N,\ I_N \geq 0.4$$

with $D_{0\ max}$ as maximum intake of digestible organic matter in g/kg $W^{0.75}$/d and I_N as intake of nitrogen in g/kg $W^{0.75}$/d. This would apply up to the satiation level for intake of digestible organic matter.

The course of the $D_{0\ max}$-curve below maintenance level could not be established in a similar way as for above maintenance: the concept of a fixed composition of weight gain cannot be readily interpreted for a situation of increasing weight losses. It is also evident that, below maintenance, intake measurements are more time dependent: intake of feeds which do not sustain maintenance often declines with time. Extrapolation of the $D_{0\ max}$-curve below maintenance level has therefore been based on information from Figures 9 and 15. Figure 9 suggests that intake of digestible organic matter and nitrogen both converge towards zero with decreasing feed quality. The outer border of the scatter of points in Figure 15, which relate intake of dry matter to nitrogen concentration of the feed, would also indicate that animals refuse feeds with nitrogen concentrations below 0.003 g/g. The fact that feeding nitrogen-free diets usually results in cessation of eating within one week (Orskov, 1982) was another reason to extrapolate the curve $D_{0\ max}$ towards the origin. In view of the functional meaning of this curve it would mean that sheep voluntarily stop consumption of feed energy in the absence of feed protein, not because of disturbance of digestive processes.

The $D_{0\ max}$-curve has been included in Figures 12 and 14. From Figure 12 it is clear that intake of digestible organic matter is close to this curve for only a few feeds and that the majority of intake data are to the right of it. From the assumptions made above the most likely cause is that efficiency of conversion of ingested nitrogen into retained nitrogen is less than maximal for most feeds. This explanation is supported by data on levels of ruminal ammonia in the animals that supplied the nitrogen retention data. These are shown in Figure 16 with the voluntary intakes of digestible organic matter for the respective feeds. Information in this graph is extremely useful as it allows a large number of conclusions:

- Lowest values for ruminal ammonia concentrations are found close to the $D_{0\ max}$-curve, almost approaching zero for data on the curve itself. As the presence of ammonia in the rumen inevitably is accompanied by losses of nitrogen from the ruminal system, due to the rapid passage of ammonia across the ruminal wall, feeds with intake on the $D_{0\ max}$-curve are obviously those with maximal efficiency of nitrogen conversion.

Figure 15. Relationship between dry-matter intake (I_T, g/kg $W^{0.75}$/d) and nitrogen concentration of the feed (I_N/I_T, g/g) for wether sheep of various breeds fed grasses and legumes ad libitum

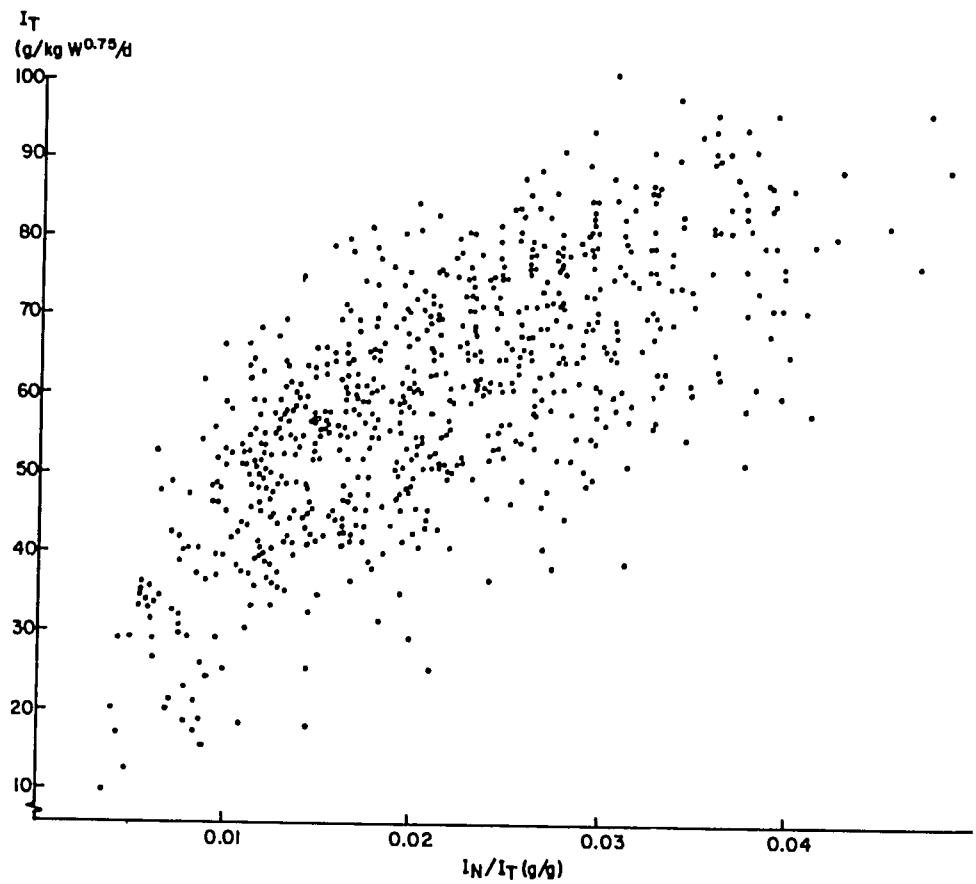
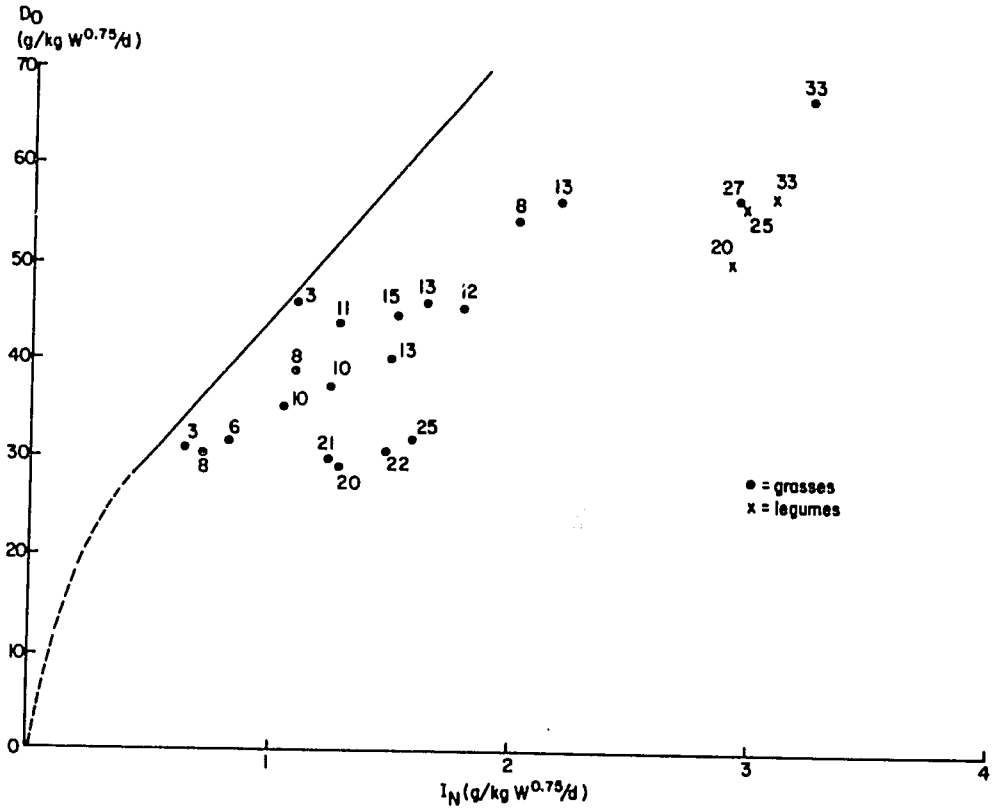


Figure 16. Rumen ammonia levels (mg NH_3-N/100 ml rumen fluid) of wether sheep of the Texel breed fed fresh pasture grasses and legumes ad libitum. Ammonia levels are shown next to data points. Compare figure 14 with figure 16 for interpretation of nitrogen metabolism in the rumen and related intake patterns



Source : Grenet and Demarquilly (1977).

- Intake of nitrogen for most feeds will overestimate true protein availability for the host animal due to variable losses of feed protein as ammonia in the rumen.

- The $D_{0\ max}$-curve was constructed assuming that intake is protein-limited in a similar fashion as was observed in growing monogastric animals, not hindered by bulk limitations to intake. Consumption of feeds with measured intake of digestible organic matter close to this curve can therefore be considered protein-limited. However these are also the feeds for which availability of ruminal nitrogen has been generally considered the limiting factor on rates of digestion and hence on feed intake. From this presentation of data there appears to be sufficient evidence to state that the limitation to intake of such feeds is a true protein limitation of the host animal and not a physical limitation on the through-put of feed across the rumen.

- Increases in intake of digestible organic matter along the $D_{0\ max}$-curve are made possible by changes in the ratio in which digestible organic matter and true protein are absorbed by the host animal. For ruminant animals this ratio will also reflect the ratio in which organic matter is digested and microbial protein concurrently synthesised. The latter is usually referred to as the efficiency of microbial protein synthesis, being the amount of microbial protein synthesised per gram of apparently digested or ruminally-fermented organic matter. The expression based on ruminally-fermented organic matter is the most common and will be used here also.

- The organic matter apparently fermented in the rumen is a constant fraction of the total digested organic matter(Ulyatt and Egan, 1979). For roughages ranging between 0.45 and 0.85 g/g digestibility of organic matter it appeared to be on average 0.61 g/g of total digested matter.

Assuming a certain fraction of feed protein to be rumen-degradable (i.e. available for microbial protein synthesis) for the feeds with intake at the $D_{0\ max}$-curve then the increased intake of digestible organic matter along this curve must be accompanied by an increase in efficiency of microbial protein synthesis; in other words more feed nitrogen is converted to microbial protein flowing from the rumen per gram of fermented organic matter. This is illustrated by data in Table 3 which shows the concentration of nitrogen in feed

at which rumen ammonia starts to accumulate. Concentrations were estimated for feeds with assumed intakes at the intersection points of the regression lines with the $D_{O\ max}$ -curve (for instance points B_1 and C_1 in Figure 17). The nitrogen concentration at which ammonia starts to accumulate shows a two-fold increase for feeds between 0.62 and 0.80 g/g organic matter digestibility.

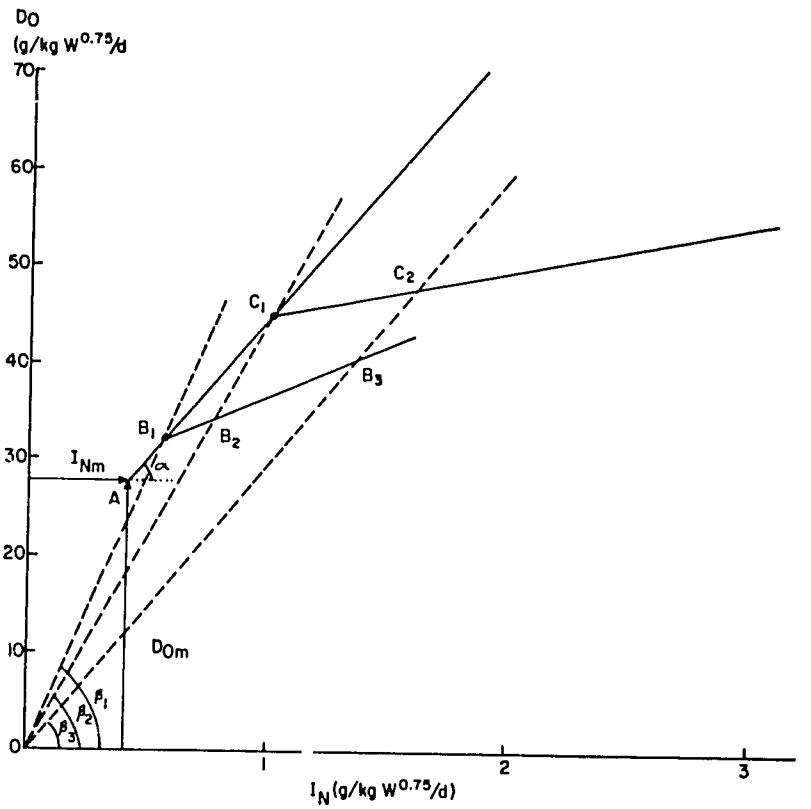
Table 3. Nitrogen concentration of feed and intake of nitrogen (I_N, g/kg $W^{0.75}$/d) and digestible organic matter (D_O, g/kg $W^{0.75}$/d) at point of ammonia accumulation for increasing organic matter digestibility (D_O/I_O, g/g).

D_O/I_O (g/g)	D_O (g/kg $W^{0.75}$/d)	I_N	Nitrogen concentration of feed $100 \times I_N/D_O$[a] %	$100 \times I_N/I_O$[b] %
0.61 - 0.63	24.2-	0.28	1.16	0.72
0.64 - 0.66	31.7	0.55	1.74	1.13
0.67 - 0.69	31.0	0.52	1.68	1.14
0.70 - 0.72	41.2	0.88	2.13	1.52
0.73 - 0.75	44.6	0.99	2.22	1.64
0.76 - 0.78	44.4	0.99	2.23	1.72
0.79 - 0.81	55.2	1.36	2.46	1.97

[a]per cent nitrogen in the digestible organic matter.
[b]per cent nitrogen in the organic matter.

- Feeds with intake at the $D_{O\ max}$-curve belong to a group differing in digestibility and nitrogen concentration. In addition they are characterised by differences in efficiency in synthesis of microbial protein in the rumen. The interrelationship between these parameters will now be examined.

Figure 17. Graphical representation of intake patterns of Texel wethers fed fresh pasture grasses ad libitum



Point A = Maintenance level, with digestible organic matter intake (D_{om}) of 27.5g D_o/kg $W^{0.75}$/d and nitrogen intake (I_{Nm}) of 0.4g I_N/kg $W^{0.75}$/d.

Line A B_1 C_1 (D_o max curve) = Calculated intake of digestible organic matter from nitrogen retention data assuming maximum efficiency of conversion of ingested nitrogen to retained nitrogen (0.54 R_N/g I_N).

Tangent α = The maximum incremental increase of digestible organic matter increase per gram of ingested nitrogen (28.8g D_o/g I_N).

Line B_1 B_2 B_3 = Regression line from figure 13b.

Line C_1 C_2 = Regression line from figure 13c.

Tangents β_1, β_2 and β_3 refer to feeds with different ratios of digestible organic matter and nitrogen in the dry matter.

- Figure 16 shows that rumen ammonia levels increase parallel to the $D_{0\ max}$ -curve. As far as synthesis of rumen microbial protein is concerned, values between 2 and 5 mg NH_3-N/100 ml appear to be critical. According to the work of Satter and Roffler (1981) efficiency of microbial protein synthesis does not increase further once this critical level is attained. For non-roughage feeds higher values may apply. Comparing Figures 16 and 14 it can now be concluded that, within each group of feeds with similar digestibility, there is one particular feed nitrogen concentration which allows maximum efficiency of microbial synthesis. Higher concentrations of feed nitrogen show immediate increases in levels of ruminal ammonia above this critical level. Therefore they do not induce higher efficiency of synthesis of microbial protein within this group of feeds.

The final conclusion is that increased feed digestibility is associated with increased efficiency of microbial protein synthesis. This is important as the classification of feeds previously made on the basis of digestibility is no longer arbitrary but has received a firm basis in rumen nitrogen metabolism.

- The fact that intake of digestible organic matter continues to increase for higher concentrations of feed protein within the same class of digestibility must mean that availability of true protein to the host animal also increases along this axis: only changes in the ratio of digestible organic matter and true protein availability would allow such increases in energy intake. If microbial protein synthesis in the rumen does not contribute to this greater availability of true protein then the only source which remains is undegraded feed protein. As feed protein is never completely degradable the undegraded part can provide the animal with relatively more duodenal non-ammonia nitrogen once the capacity for microbial protein synthesis is saturated. The slope of the regression lines relating intake of digestible organic matter to intake of nitrogen for feeds of similar digestibility will therefore in some way reflect the response of sheep to an increased availability of undegraded plant protein.

Among these conclusions two elements are clearly of great interest: the relationship between efficiency of microbial protein synthesis and feed digestibility, and the response of animals to undegraded plant protein as compared with bacterial protein. Both aspects have been quantified. In principle, efficiency of microbial protein synthesis could be directly

calculated from the $D_{0\ max}$-curve if it was known what proportion of feed protein is rumen-degradable. Only this and some endogenous nitrogen may contribute to microbial protein synthesis. However, degradability of plant protein and microbial protein synthesis are still little understood. Therefore, instead of assuming some average value for protein degradability another approach was chosen: it was assumed that irrespective of source of protein, whether of microbial origin or of plant origin, both would have a similar effect on the intake of digestible organic matter. In other words it was assumed that at the duodenal level a unique relationship exists between intake of digestible organic matter and non-ammonia nitrogen flow, each increment of non-ammonia nitrogen provoking the same increment in intake of digestible organic matter. This allowed estimates to be made of both efficiency of microbial protein synthesis and protein degradability. The way these have been derived will be shown elsewhere. Here only the results are given, summarized in Table 4.

The data in Table 4 clearly show an increase in efficiency of microbial protein synthesis with higher feed digestibility: for highly digestible roughages relatively more microbial protein per gram digested organic matter becomes available to the host animal. Degradability of feed protein also appears to increase from low to high digestibility feeds, which means relatively greater losses of feed protein.

The theoretical calculations in Table 4 could not be adequately checked against values reported in the literature. According to a comparison made by Orskov (1982), most protein evaluation systems currently available use average values for microbial protein synthesis. Values range between 1.25 and 1.38 g N/MJ M_E or approximately 19-21 grams of protein per 100 grams of ruminally-fermented organic matter. Such values are in the middle of the range estimated here. A major cause of this lack of differentiation between feeds is the absence of sufficient reliable measurements. Data for any well-defined category of feeds, such as fresh forages fed ad libitum, are few and obtained by different techniques. The latter prevents any real comparison, as different methods in the same situation yield widely diverging results. However, it is noteworthy that Hagemeister et al (1981), working with lactating dairy cows, reported consistently lower values for microbial protein synthesis with high than with low-roughage rations.

Table 4. Microbial protein synthesis (g/100g FOM[a]) and protein degradability (g/g) calculated for feeds of increasing organic matter digestibility (D_0/I_0, g/g).

D_0/I_0 (g/g)	Microbial protein synthesis (g/100g FOM)	Protein degradability (g/g)
0.61 - 0.63	12.1	0.66
0.64 - 0.66	17.6	0.81
0.67 - 0.69	16.9	0.79
0.70 - 0.72	22.6	0.92
0.73 - 0.75	23.9	0.95
0.76 - 0.78	23.3	0.92
0.79 - 0.81	26.4	0.97

[a] FOM: organic matter apparently fermented in the rumen.

A similar situation applies to the values calculated for protein degradability. Although protein degradability of fresh forages is generally assumed to be high, techniques to measure this parameter independently from the contribution of microbial protein in total duodenal protein flow are not available.

Despite this lack of validation it seems unlikely that the trend in efficiency of microbial protein synthesis is very different from that shown in Table 4. On theoretical grounds one also may expect a lower efficiency with increased concentration of indigestible matter in the rumen. As indigestible feed particles serve as the major carrier of microbial mass in the rumen, retention times of microbes in the rumen will tend to increase with less-digestible feeds, resulting in increased turnover of microbial matter within the rumen and lower efficiency of microbial protein synthesis. Therefore, to return to our basic question, 'what does digestibility mean to the ruminant animal?', perhaps a more important aspect than its physical meaning may be the

close association between digestibility and relative availability of microbial protein. That would also explain why animals which produce a product containing less protein - for instance, lactating dairy cows - may eat more of a given feed per kg of metabolic weight than animals producing a high-protein product, e.g. wether sheep.

Reasoning along this line it is tempting to suggest that the opportunities to utilise a certain protein energy ratio will set the limit for intake of roughages. If so, one would expect that supplemental protein should induce consistent changes in intake. But, although intake responses to protein supplementation have been found, they are not consistent. For example, Egan (1977) experimented with infusions of casein into the duodenum of sheep fed a range of different feeds. For some feeds moderate increases in intake were found as a consequence of casein infusion, but these were generally feeds which did not support maintenance without supplementation. Above maintenance, responses were almost negligible.

A similar situation exists with regard to additions of protein to the diet. Although more difficult to analyse, because of the uncertain effects on true protein availability in the duodenum, responses are inconsistent, ranging from nil to substantial.

So, the question clearly is: why are energy intake patterns so easily interpreted as responses to protein availability, whereas in practice such responses cannot be satisfactorily reproduced by manipulating true protein availability?

No clear answer has yet been found. One could hypothesise that the effect of protein availability on intake of digestible dry matter is determined by other factors. As ruminants receive a large proportion of their protein in bacterial mass, a whole array of substances will present themselves at the duodenum along with the protein. Also, plant protein which reaches the duodenum undegraded will certainly be mixed with non-protein or even non-nitrogen substances. Many of these substances may have very different nutritive properties to proteins or amino-acid mixtures. Thus, any relationship between digestible dry matter intake and nitrogen intake in ruminant nutrition is inevitably very unclear and potentially misleading.

Summarising, the following conclusions can be drawn. Intake data which are usually presented in a form to support the idea of physical regulation of intake fit equally well into a picture of a metabolic regulation. The latter would imply that ruminants, like monogastric animals, regulate both energy and nitrogen intake when given a range of feeds. Such a regulation, of course, must be reflected in the composition of animal products. It is tempting to suggest that the requirements of the animal for a certain balance of nutrients set limits to the intake of most roughage rations. That animals are sensitive to the balance, or imbalance, of nutrients absorbed from the gut is evident from intake responses to supplementation with various nutrients. However, such responses do not follow a pattern to be expected from nutrient relations in the intake of roughages. Thus, further research is needed to clarify the nature of nutrient relations in roughage feeding and supplementation trials. It would be extremely valuable to understand where, when and to what extent intake and thus production can be increased with definite inputs of essential nutrients, especially for many extensive livestock-production systems in semi-arid regions. To be able to predict such increases in productivity would make modelling livestock production systems much more meaningful.

Summary

Feed intake is a major determinant of ruminant productivity. Accurate prediction of intake is therefore important in modelling ruminant livestock production systems. Prediction of intake of roughages by ruminants has usually been based on a concept of physical restrictions to the ingestion of fibre-rich diets. However, explanatory models of intake incorporating this concept are not available. Use of empirically-based equations to predict intake from feed characteristics is inaccurate.

Re-analysis of numerous intake trials reported in the literature, both with sheep and with cattle, suggests that physical factors in intake regulation have been overemphasised. An important finding is that ruminants, given a wide range of roughages *ad libitum*, appear to regulate both energy and nitrogen intake. Above maintenance level this results in a proportional excess of energy and true protein available to the host animal, which, in turn, leads to a

relatively constant composition of animal products under such feeding conditions. This suggests that intake is a response to relative nutrient availability from the gut and therefore can be manipulated by dietary nutrient additions. However, a consistent framework of intake responses to supplementation with essential nutrients is lacking. Possible causes of this discrepancy are discussed.

References

ARC (Agricultural Research Council). 1965. The nutrient requirements of farm livestock, No. 2. Ruminants. HMSO, London

ARC (Agricultural Research Council). 1980. The nutrient requirements of ruminant livestock. HMSO, London. 351 pp.

Baldwin R L, Koong L J and Ulyatt M J. 1977. A dynamic model of ruminant digestion for evaluation of factors affecting nutritive value. Agric. Systems 2:255-288.

Beever D E, Black J L and Faichney G J. 1980. Simulation of the effects of rumen function on the flow of nutrients from the stomach of sheep. Part 2. Assessment of computer predictions. Agric. Systems 6:221-241.

Black J L, Beever D E, Faichney G J, Howarth B R and Graham N McC. 1980. Simulation of the effects of rumen function on the flow of nutrients from the stomach of sheep. Part 1. Description of a computer program. Agric. Systems. 6:195-219.

Blaxter K L, Wainman F W and Wilson R S. 1961. The regulation of food intake by sheep. Anim. Prod. 3:51-61.

Blaxter K L and Wilson R S. 1962. The voluntary intake of roughages by steers. Anim. Prod. 4:351-358.

Boekholt H A. 1976. De stikstofhuishouding van het melkrund en de betekenis van de gluconeogenese uit aminozuren. Mededelingen Landbouwhogeschool Wageningen 10. 206 pp.

Conrad H R, Pratt A D and Hibbs J W. 1964. Regulation of feed intake in dairy cows. I. Change in importance of physical and physiological factors with increasing digestibility. J. Dairy Sci. 47:54-62.

Demment M W and van Soest P J. 1983. Body size, digestive capacity, and feeding strategies for herbivores. Winrock International, Morrilton, Arkansas, USA. 66 pp.

Demarquilly C and Journet M. 1967. Valeur alimentaire des foins condensés. 1. Influence de la nature du foin et de la finesse de broyage sur la digestibilité et la quantite ingerées. Ann. Zootech. 16:123-150.

Demarquilly C and Weiss Ph. 1970. Tableaux de la valeur alimentaire des fourrages. Etude no. 42. S.E.I., Versailles. 65 pp.

Egan A R. 1977. Nutritional status and intake regulation in sheep. VIII. Relationships between the voluntary intake of herbage by sheep and the protein/energy ratio in the digestion products. Aust. J. Agric. Res. 28:907-915.

Elliot R C and Topps J H. 1963. Voluntary intake of low protein diets by sheep. Anim. Prod. 5:269-276.

France J, Thornley J H M and Beever D E. 1982. A mathematical model of the rumen. J. Agric. Sci., Camb. 99:343-353.

Grenet E and Demarquilly C. 1977. Utilisation de l'azote des fourrages verts par le mouton en croissance: influence de stade de végétation, de l'espèce fourragere, de la fertilisation azotée et de l'addition d'orge. Ann. Zootech. 26:481-501.

Hagemeister H, Lupping W and Kaufmann W. 1981. Microbial protein synthesis and digestion in the high-yielding dairy cow. In: W Haresign and D J A Cole, eds. Recent developments in ruminant nutrition. Butterworths, London. pp. 41-48.

Heany D P, Pigden W J, Minson D J and Pritchard G I. 1963. Effect of pelleting on energy intake of sheep from forages cut at three stages of maturity. J. Anim. Sci. 22:752-757.

INRA (Institut National de la Recherche Agronomique). 1978. Alimentation des ruminants. INRA Publications, 78000 Versailles, France. 597 pp.

Kahn H E. 1982. The development of a simulation model and its use in the evaluation of cattle production systems. Ph.D. thesis, Univ. of Reading, UK.

Ketelaars J J M H. 1984. Evaluating rangeland as feed resource for livestock production. In: W Siderius, ed. Proceedings of the workshop on land evaluation for extensive grazing, ILRI, Wageningen. pp. 165-181.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: an integer and stochastic model for evaluating production alternatives. ILCA Research Report No. 2. ILCA, Addis Ababa. 95 pp.

McClymont G L. 1967. Selectivity and intake in the ruminant. In: C F Cole, ed. Handbook of physiology. Section 6. Alimentary canal I. American Physiological Society. Washington D C. pp.129-137.

Mertens D R. 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. thesis, Cornell Univ., Ithaca, New York. 217 pp.

Mertens D R and Ely L O. 1979. A dynamic model of fiber digestion and passage in the ruminant for evaluating forage quality. J. Anim. Sci. 49:1085-1095.

Milford R. 1960. Nutritional values for 17 sub-tropical grasses. Aust. J. Agric. Res. 11:138-148.

Milford R. 1967. Nutritive values and chemical composition of seven tropical legumes and lucerne grown in subtropical south-eastern Queensland. Aust. J. Exp. Agric. Anim. Husb. 7:540-545.

Milford R and Minson D J. 1968a. The digestibility and intake of six varieties of rhodes grass (Chloris gayana Kunth). Aust. J. Exp. Agric. Anim. Husb. 8:413-418.

Milford R and Minson D J. 1968b. The effect of age and the method of haymaking on the digestibility and voluntary intake of the forage legumes Dolichos lablab and Vigna sinensis. Aust. J. Exp. Agric. Anim. Husb. 8:409-412.

Minson D J. 1967. The voluntary intake and digestibility, in sheep, of chopped and pelleted Digitaria decumbens (pangola grass) following a late application of fertilizer nitrogen. Brit. J. Nutr. 21:587-597.

Minson D J. 1973. Effect of fertilizer nitrogen on digestibility and voluntary intake of Chloris gayana, Digitaria decumbens and Pennisetum clandestinum. Aust. J. Exp. Agric. Anim. Husb. 13:153-157.

Minson D J and Milford R. 1967. The voluntary intake and digestibility of diets containing different proportions of legume and mature pangola grass (Digitaria decumbens). Aust. J. Exp. Agric. Anim. Husb. 7:545-551.

Minson D J and Milford R. 1968. The nutritional value of four tropical grasses when fed as chaff and pellets to sheep. Aust. J. Exp. Agric. Anim. Husb. 8:270-276.

Minson D J, Harris C E, Raymond W F and Milford R. 1964. The digestibility and voluntary intake of S_{22} and H_1 ryegrass, S_{170} tall fescue, S_{48} timothy, S_{215} meadow fescue and germinal cocksfoot. J. Brit. Grassl. Soc. 19:298-305.

Orskov E R. 1982. Protein nutrition in ruminants. Academic Press, London. 160 pp.

Poppi D P, Minson D J and Ternouth J H. 1981a. Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. Aust. J. Agric. Res. 32:99-108.

Poppi D P, Minson D J and Ternouth J H. 1981b. Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of feed in the reticulo-rumen. Aust. J. Agric. Res. 32:109-121.

Poppi D P, Minson D J and Ternouth J H. 1981c. Studies of cattle and sheep eating leaf and stem fractions of grasses. III. The retention time in the rumen of large feed practices. Aust. J. Agric. Res. 32:123-137.

Sanders J O and Cartwright T C. 1979a. A general cattle production systems model. 1. Structure of the model. Agric. Systems 4:217-227.

Sanders J O and Cartwright T C. 1979b. A general cattle production systems model. 2. Procedures used for simulating animal performance. Agric. Systems 4:289-309.

Satter L D and Roffler R E. 1981. Influence of nitrogen and carbohydrate inputs on rumen fermentation. In: W Haresign and D J A Cole, eds. Recent developments in ruminant nutrition. Butterworths, London. pp. 115-139.

Siebert B D and Hunter R A. 1977. Prediction of herbage intake and liveweight gain of cattle grazing tropical pastures from the composition of the diet. Agric. Systems 2:199-207.

Troelsen J E and Campbell J B. 1969. The effect of maturity and leafiness on the intake and digestibility of alfalfas and grasses fed to sheep. J. Agric. Sci., Camb. 73:145-154.

Ulyatt M J and Egan A R. 1979. Quantitative digestion of fresh herbage by sheep. V. The digestion of four herbages and prediction of sites of digestion. J. Agric. Sci., Camb. 92:605-616.

Weston R H and Hogan J P. 1973. Nutrition of herbage-fed ruminants. In: G Alexander and O B Williams, eds. Practice and technology of sheep and cattle production. Sydney Univ. Press, Australia. pp. 233-268.

Discussion

Statement - When you turn your graph around, you have the biological relationship of nitrogen retention as a function of TDN intake.

Reply - That's the usual way we present such a relationship, but I think that the animal reacts to the availability of protein. The energy intake is a function of protein intake, and that leads to a relationship between energy intake and nitrogen balance.

Question - For predictive purposes, would it not be better to correlate dry matter, digestible energy intake, or digestible dry matter with N% of the feed?

Answer - It would only be a trick. This relationship shows that if you characterise a feed by the ratio of digestibility and nitrogen content, the intake of such a feed will always develop along an almost straight line from the origin. If you hold digestibility constant, the intake of digestible material is a function of nitrogen percentage.

Question - Do you assume the same digestibility of protein as of total organic matter, or do you check the digestibility of protein independently? The two are not always the same.

Answer - I did not use digestibility figures for protein at all, because digestible protein is very difficult to interpret. You can use true protein concentrations, in combination with some measurement of rumen ammonia concentration, rather than digestible nitrogen because it is quite uncertain how much of the digestible nitrogen is indeed digested by the animal.

Statement - Deficiency of amino acids can reduce digestibility. For instance, ground-nuts are not a good source of protein.

Reply - The effective amino acid profile supplied to the animal and the possible deficiencies could be a factor that explains differences in results of protein supplementation trials.

Questions - 1. Have you any particular reason for using metabolic weight, rather than liveweight in your measurements? It is used for maintenance but should it be used for intake?

2. You said that you found no experiments that showed faecal output was constant at different digestibilities. We have found that the faecal output at dry pasture and green pasture was identical, even though the intake was almost double in the green pasture.

3. How would you then predict intake, when you have ad lib availability of straw and poultry litter?

Answer - To start with your first question, there is no particular reason to use the exponent of 0.75. I use it to put animals of different weights on a similar scale.

If you stick to an explanation of requirements for production and maintenance, then intake should be related to the same exponent as maintenance requirements.

The second question regarding faecal output: I do not deny that you can find similar figures for faecal output in some cases, but I have looked at a wide range of data from sheep trials. There is a large variation and also a certain trend.

Your third question: At the moment we are not able to predict possible increases in intake due to non-protein N supplementation. Some people suggest using measurements of rumen ammonia as an indicator of the possible benefits, including non-protein nitrogen, but even if you know that the rumen ammonia concentrations are very low, say below 5 mg/100 ml, you can not say anything about the possible increases in intake that could be expected by including non-protein nitrogen.

Question - Would you expect the animal to obtain its requirements if it had ad lib access to these two feeds?

Answer - Yes, but the problem is to decide how much extra nitrogen can be effectively converted to bacterial protein. That depends on other characteristics of the ration, mainly on the potential digestibility of the

total ration. The higher the digestibility the greater the quantity of nitrogen in the ration that can be effectively converted to microbial protein.

Question - The ILCA model usually over-estimates growth by about 100 - 250 kg. Would you predict that we would reduce the output if we put in your type of protein relationship?

Answer - I have not tried that so I can not specifically answer your question, but I have tried to convert the figures from sheep trials into intake figures for growing cattle using the idea that you construct the intake curve by looking at specific requirements for maintenance in terms of nitrogen and energy, and then by looking at the conversion of liveweight gain. The problem is that you have to find the intersection points, where the regression equation for a certain class of digestibility intersects this curve. It is also the point where rumen ammonia starts to accumulate. For every digestibility class there is one specific concentration of nitrogen below which feed nitrogen is converted to bacterial protein, and above which nitrogen is lost. The problem is that predictions are very sensitive to the slope of that curve and to assumptions about that critical protein content.

Question - It would seem reasonable to assume that some physical limit to processing rate must exist in ruminants. Would a combination of the traditional theory of some physical processing rate together with your energy/protein ratio theory explain the data that do not fit this hypothesis alone?

Answer - It is very difficult to combine both concepts. I cannot see any way to do that.

Statement - Even if the feed has the correct protein/energy ratio for a given animal product and physiological state of the animal, and if you have a very low quality feed with a very low digestibility, an intake limit would be imposed by the physical processing potential of the animal.

Reply - It is very difficult to prove that such a limit exists. If you look at trials with monogastric animals, they have an enormous capacity to adjust for

ballast in the ration. For instance you can feed rats with 50% indigestible matter as long as you can keep the protein/energy ratio in the digestible part at an appropriate level.

Comment - In the case of the ruminant, I think that there is quite good evidence (from Minson's lab, for example) that for the same level of digestibility and for the same nitrogen content, the feeds which are more easily and more rapidly broken down are in fact eaten in greater quantity. So I think the analogy of the ruminant and the non-ruminant is not a fair way to answer that last question.

Reply - It's true that feeds that are more rapidly comminuted are also eaten in greater quantities, but if you look at the work of Minson et al, their conclusion is that the rate of particle breakdown can not be a very severe limit to intake. That is illustrated by the fact that if you look at the particle size distribution in the rumen, there are many more small particles, even with low-quality rations. The water passage through the rumen could have a much more profound effect on intake than the rate of particle breakdown. In principle, the animal should have a larger capacity to increase its intake by simply increasing the water flow through the rumen. Whatever the reason, some animals eat much more of a given feed than other animals, so the physical limit must be very flexible.

Comment - Salt bushes for instance, have a high nitrogen content, but dry matter intake of these is low. The reason seems to be the low digestibility of the dry matter, which is something below 60%. True digestibility of protein is something like 90% so it seems that nitrogen is being used as an energy source by the microbes that need the correct proportionality between the available nitrogen and available carbon.

Reply - Yes, that is true, but the fact that an animal eats more of high- protein feeds than of low-protein feeds is ultimately due to an action of the animal itself. It is true that the microbes also need a certain ratio of protein and energy, but if you have feeds which supply sufficient nitrogen to the microbes, but not enough energy, the intake of such feed still increases. That can be

explained by the fact that only a certain fraction of the total feed protein is degradable in the rumen by microbial action and there is always a certain undegradable fraction. That is the fraction that will raise the true protein availability to the host animal.

Comment - These bushes have a very high crude-protein content, which is highly degradable in the rumen, and is used as an energy source. Because the energy is not readily available, intake is low.

Reply - The true protein available to the host animal is mainly a function of the amount of microbial protein. Where you have, like in the salt bush, relatively low dry matter digestibility, then the contribution of microbial protein will also be small, because there seems to be some functional relationship between the efficiency of microbial protein synthesis and the digestibility of the feeds. The lower the digestibility of the feeds, the smaller the amount of microbial protein which becomes available per gram of digestible organic matter. To say something about the additional value of increased protein in salt bushes, you have to compare salt-bush material of different protein concentrations. Then I suppose you will find some increase in intake with higher N content because not all the protein will be rumen degradable.

Relationships between chemical composition and voluntary intake of feeds by sheep and cattle

L.J. Lambourne, A.K. Mosi and M.H. Butterworth

Introduction

The Texas A&M University (TAMU) herd model (Sanders and Cartwright, 1979) and its derivatives, such as the ILCA model (Konandreas and Anderson, 1982; Konandreas et al 1983) estimate voluntary dry matter (DM) intake as being primarily a function of DM digestibility, down to the point at which protein content falls below 6%, when it becomes a function of feed protein percentage.

Predicted intake is subject also to either a physiological upper limit depending mainly on energy requirements at high values of digestibility (Conrad, 1966), an availability limit or a physical limit, the last being imposed on low-quality feeds by the apparent limitation to daily throughput of faecal DM of cattle. This has been estimated variously as about 1.07 kg/100 kg liveweight (Conrad et al, 1964) for dairy breeds in USA, or from 4.2 to 4.5 kg/100 kg metabolic weight for dry cows up to 4.9 kg/100 kg metabolic weight for lactating beef cows in Southern Africa (Elliott et al, 1961, as cited by Konandreas and Anderson, 1982).

Recent work by ILCA, using Ethiopian highland sheep and both highland Zebu and Friesian/Zebu cross cattle fed on local forages and crop residues, suggests that there is much variation in these relationships and that they may need to be re-examined.

Methods

Sheep experiments

Sheep were fed in metabolism cages to measure voluntary intake and digestibility of four cereal-crop residues fed in conjunction with different proportions of a clover hay (*Trifolium tembense*) (Mosi and Butterworth, 1985).

Cattle experiments

Zebu oxen and Friesian/Zebu cross cows, four animals per subgroup, were fed individually ad libitum (approximately 20% rejection), on a range of local hays and experimental forages for 10 days, after preperiods of 5-7 days. Digestibility was determined by total faecal collection.

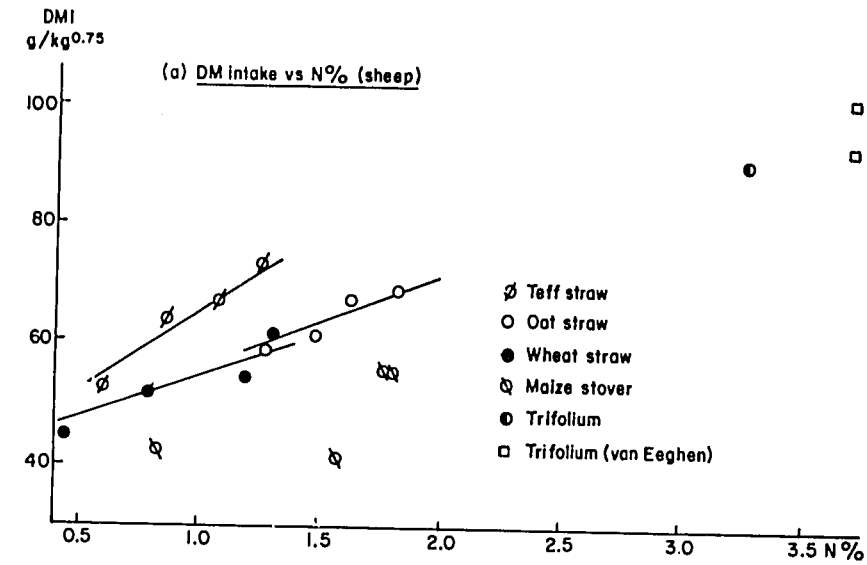
Results and discussion

Sheep experiments

Feed DM intake expressed as $g/kg^{0.75}$ or as g/head/d generally showed positive correlations with crude protein (CP) content and with DM digestibility, and negative correlations with neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) content of the feed mixtures. Figure 1 illustrates the relationship between DM intake and the nitrogen (N) percentage (Figure 1 a) and the digestibility (Figure 1 b) of the feeds based on the four crop residues fed alone (left-hand points), with increasing proportions of clover hay, and the clover hay itself (right-hand point). Each data point is the mean for five sheep per feed over two periods of 10 days. Two extra points are shown, for similar sheep fed T. tembense harvested on different dates in earlier work (van Eeghen, 1984).

DM intake was generally more closely correlated with N% than with digestibility and the negative correlations with NDF% were generally closer than with ADF% (Table 1). None of the correlations was significant with the oat/trifolium mixtures despite the apparently good agreement of the means in Figure 1. In the case of the maize stover/trifolium feeds, too, the correlation between intake and DM digestibility was not significant. Intakes of all the maize stover diets were significantly lower than the intakes of the other diets.

Figure I. Relationships between (a) dry matter intake (DMI, g/k$^{0.75}$) and nitrogen concentration (N%) and (b) dry matter intake and dry matter digestibility (DM D%), for sheep fed different rations



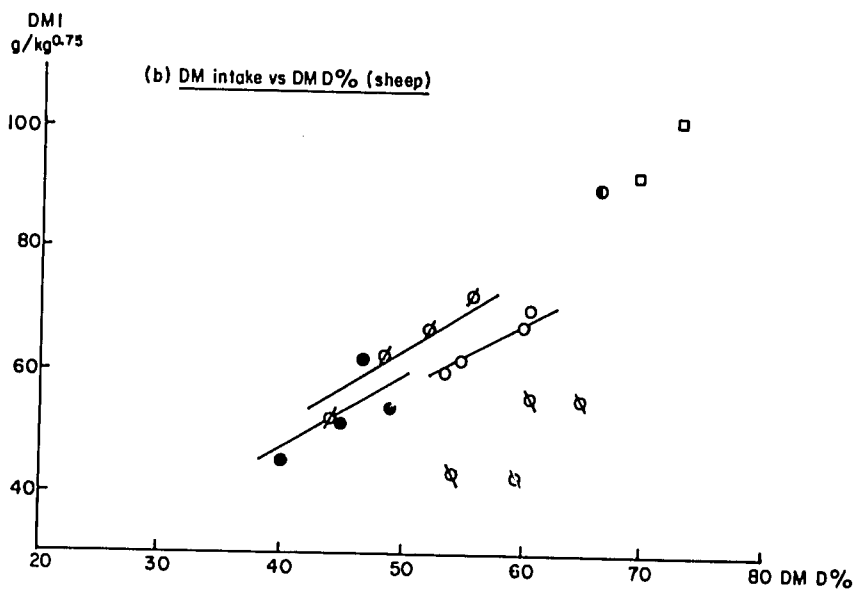


Table 1. Relationships between dry-matter intake (DMI) and nitrogen percentage (N%), neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and dry-matter digestibility (DMD%) for diets containing cereal crop residues and Trifolium tembense.

Cereal		r	r^2	Significance
Wheat	DMI x N%	0.77	0.59	0.01
	DMI x NDF	-0.73	0.53	0.01
	DMI x ADF	-0.66	0.44	0.01
	DMI x DMD%	0.50	0.25	0.01
Oats	DMI x N%	-	-	NS
	DMI x NDF	-	-	NS
	DMI x ADF	-	-	NS
	DMI x DMD%	-	-	NS
Maize	DMI x N%	0.26	0.07	0.1
	DMI x NDF	-0.63	0.40	0.01
	DMI x ADF	0.57	0.26	0.01
	DMI x DMD%	0.15	0.02	NS
Teff	DMI x N%	0.77	0.60	0.01
	DMI x NDF	-0.58	0.34	0.01
	DMI x ADF	-0.24	0.06	NS
	DMI x DMD%	0.69	0.48	0.01

The results over all diets were in general agreement with the theory of Mertens (1973) as developed by Bywater (1984) that intake of NDF tends to be constant at about $40g/kg^{0.75}$ regardless of the NDF% in the feed. In this case

NDF intake was more nearly constant within feeds than was faecal DM output, although there were also significant differences in NDF intake among the crop residues. Recent research in this laboratory (Reed, unpublished) indicates that in vitro digestibility is influenced considerably by the concentration of tannins in different parts of the sorghum plant, and it is possible that similar effects may account for the differences among other cereals reported here.

Cattle experiments

1. Figure 2 shows the results of an initial comparison of voluntary intake of four grass hays of diminishing quality fed to Zebu oxen and dry crossbred cows.

Expressed as g/ $kg^{0.75}$, DM intake of the smaller (275-350 kg) Zebus was similar to that of the heavier (400-450 kg) crossbreds for each of the four hays. However, the Zebus gave 5-10% higher digestion coefficients on the poorer hays, so that the relationship in Figure 2 b indicates that their DM intake was lower in relation to DM digestibility than that of the crossbreds. This is misleading, since on a given feed DM intake by both Zebus and crossbreds was the same. The relationship between DM intake and N% of the hays over the range 0.5-1.25% N was more consistent between breeds than was its relationships to DM digestibility and would provide a better basis for prediction of feed intake.

2. Figure 3 shows the linear regressions for the crossbreds from Figure 2, without data points, and the means (each again for four cows over 10 days) from another experiment comparing a good grass hay with a Trifolium tembense/grass hay of much higher N% but similar (64-68%) digestibility (van Eeghen, 1984).

Dry matter intake in relation to N% conformed very closely to the relationship for crossbreds from Figure 2, but DM intake of the trifolium hay was excessively high in relation to its modest digestibility. Thus, in both cases and over a range of N% from 1.0 to 1.75%, N% proved a better predictor of intake than did digestibility.

Figure 2. Dry matter intake (DMI) as a function of (a) nitrogen concentration (N%) and (b) dry matter digestibility (DM D%), for Friesian/Zebu crosses and Zebus

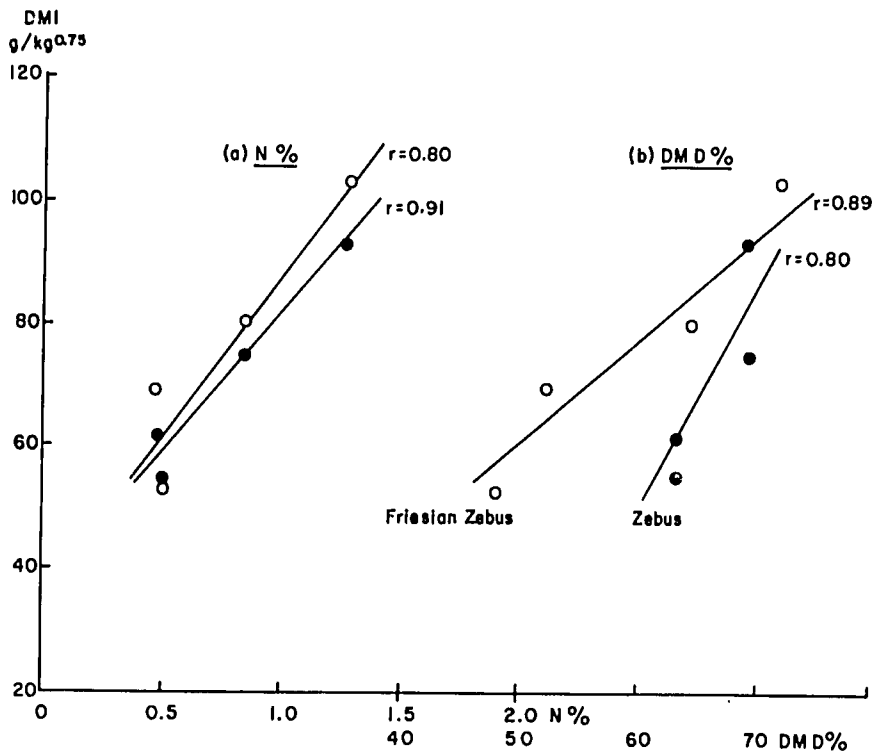
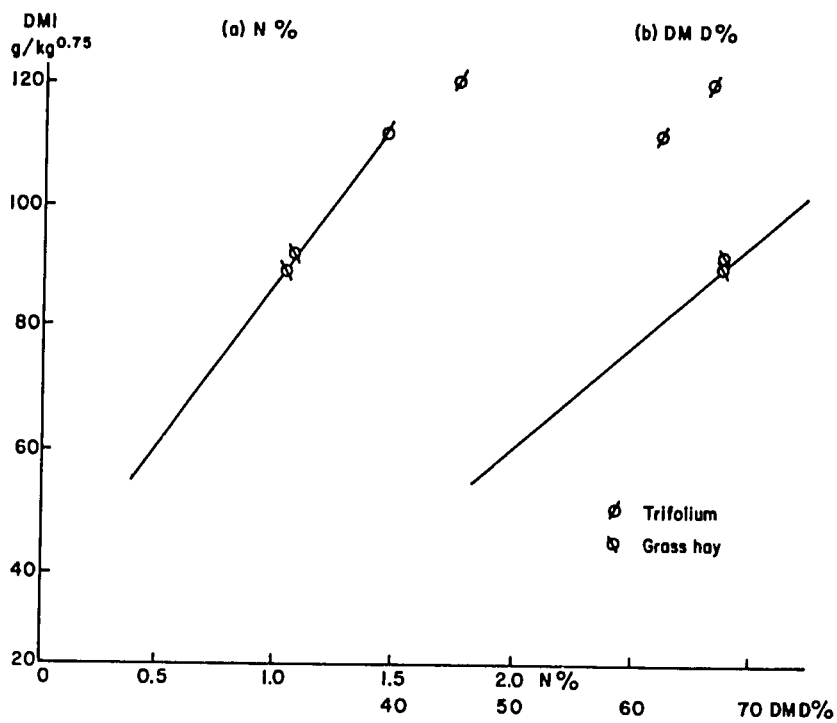


Figure 3. Dry matter intake (DM) as a function of (a) nitrogen concentration (N%) and (b) dry matter digestibility (DM D%) for cows fed Trifolium or grass hay (van Eeghen,1984). Reqression lines from Figure 2



3. The results of experiments with crossbred cows fed oat hay cut early, oat/vetch hay and a tall, fast-growing grass common in wetter parts of the Ethiopian highlands - Snowdenia polystacha - are shown in Figure 4, superimposed on the linear regressions from Figure 2 for crossbreds (Lambourne and Askabe, unpublished data). The digestibility of all these feeds was about 68 to 75%, but they contained only 1.0 to 1.2% N.

In contrast to the data in Figure 3, DM intakes were very close to the original regression for crossbreds of intake on digestibility but the intakes of oat hay and S. polystacha were nearly 10 $g/kg^{0.75}$ higher than the original regression of intake on N%. The oat/vetch mixture, which had somewhat higher N%, fell 5 $g/kg^{0.75}$ below this line.

4. The data in Table 2 show the mean daily faecal DM output of each group of cattle on each of the nine feeds used in the trials mentioned above.

There were significant differences ($P < 0.05$) in daily faecal DM output between the Zebus (0.55% Lwt.) and the crossbreds (0.65% Lwt.) over the four grass hays and among the hays within the Zebus (0.48-0.72% Lwt., Table 2a). The difference between the daily faecal DM output of crossbreds fed Trifolium tembense (0.93% Lwt.) and those fed the other feeds (0.65% Lwt.) was highly significant ($P < 0.01$, Table 2b). The values found in this study are lower than that found by Conrad et al (1964) of 1.07% Lwt. and that found by Kahn and Spedding (1984) for non-lactating cattle of 0.8-0.9%. The values for the Zebus are significantly lower for all the feeds studied than even the lowest of these values, which suggests that faecal DM output varies so much between closely related breeds and among a small sample of forages fed without supplements that its use as a constant to set limits to predicted DM intake should perhaps be re-examined.

General discussion

When a general simulation model is to be applied to local livestock breeds in a particular pastoral setting, it is desirable to check that the more important of the model's basic algorithms really apply in these new conditions. The results of this study suggest that for some native African livestock, and for at least one of the exotic/indigenous crosses being studied as a possible means of

Figure 4. Dry matter intake (DMI) as a function of (a) nitrogen concentration (N%) and (b) dry matter digestibility (DM D%) for crossbred cows fed three feeds. Regression lines are from figure 2

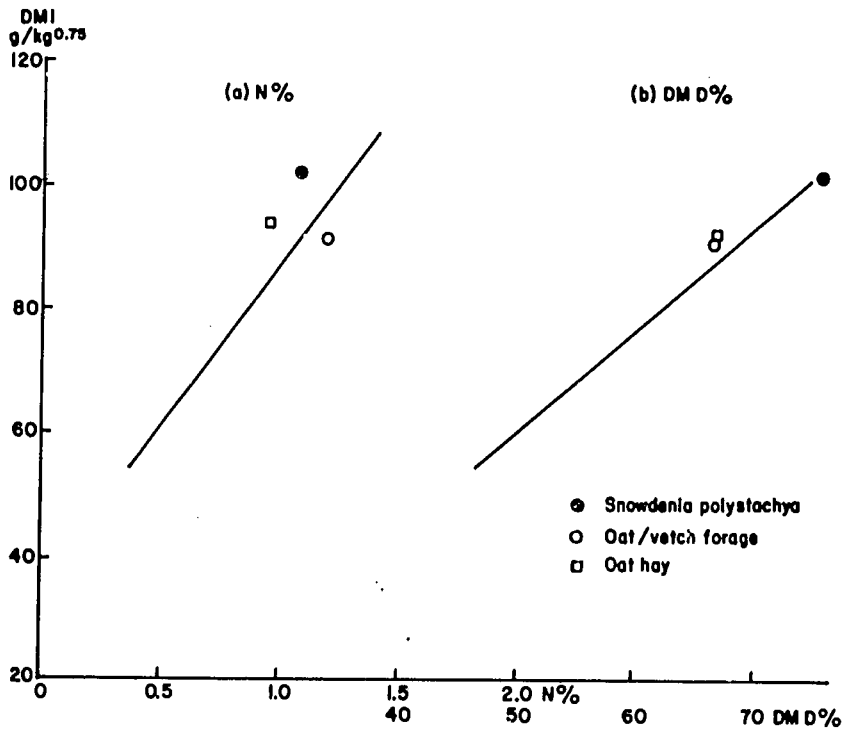


Table 2. Faecal DM output (% Lwt.) of Zebu and Friesian/Zebu crosses given a range of feeds.

Zebu and Friesian crosses		Faecal DM output (% Lwt.)				
	Feed:	1	2	3	4	all
Zebu		0.54	0.48	0.53	0.72	0.55
Friesian crosses		0.63	0.60	0.70	0.67	0.65*
Friesian crosses						
Feed:						
Snowdenia		0.57				
Oats/vetch		0.68				
Oat hay		0.69	0.65			
Grass hay		0.66		**		
T. tembense	(a)	0.90				
	(b)	0.96	0.93			

Feeds 1-4 were grass hays of diminishing quality.

* = significant at $P < 0.05$.

** = significant at $P < 0.01$.

increasing production, the relationships derived from experiments in temperate production systems may need modification before they can be used with confidence (Wagenaar and Kontrohr, 1986). This is doubly important if the results of simulation modelling may be used as a guide for development and investment plans, rather than for purely academic purposes.

Specifically, it may be wise to reconsider present algorithms which place prime emphasis on feed digestibility, and to include feed protein (N) content as an equally-ranked second predictor over the full range of feed

protein (N) values, rather than just at their lower end. This will become particularly important as forage legumes become more widely used to improve productivity of pastoral livestock systems, since intake of legume forage appears to be a function of their higher N content rather than of their normal DM digestibility.

It seems sensible also to study further the possibility of replacing daily faecal DM output by NDF intake in $g/kg^{0.75}$ or some similar unit, as an upper limiting factor. Sanders and Cartwright (1979) considered using intake of indigestible DM in this way. Use of NDF would have the merit also of providing a third predictor based on chemical analysis of the feed, but inversely related to N% and digestibility. These last two factors both reflect the content of soluble, largely digestible, cell contents, and are often closely correlated. The NDF content, on the other hand, measures the generally indigestible structural carbohydrate material of the plant. The compensating nature of their relationships might well make the joint use of N%, digestibility and NDF intake a fairly robust approach.

Several authors have suggested that animal production is more closely related to the amount of green material available than to chemical composition of a whole pasture sample, and changes in nutritive value and voluntary intake with senescence of the green and dry fractions of a sward have been described and modelled (see Lambourne, 1986). The broader approach argued from the present results might help to embrace these ideas also - perhaps in time it may seem worthwhile to determine, say, chlorophyll content as a proxy for greenness and for carotene content and vitamin A adequacy. The widespread availability of oesophagal fistulation means that analyses can be carried out on samples of feed on offer or of feed eaten.

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References

Bywater A C. 1984. A generalized model of feed intake and digestion in dairy cows. Agric. Systems 13:167.

Conrad H R. 1966. Physiological and physical factors limiting feed intake. J. Anim. Sci. 25:226.

Conrad H R, Pratt A D and Hibbs J W. 1964. Regulation of feed intake in dairy cows. 1. Change in importance of physical and physiological factors with increasing digestibility. J. Dairy Sci. 47:54.

van Eeghen M. 1984. Trifolium tembense: an exploratory study on its value as a fodder crop. Dissertation submitted to the Agricultural University of Wageningen in Tropical Animal Husbandry and Grassland Science. August 1984.

Elliott R C, Fokkema K and French C H. 1961. Herbage consumption studies on beef cattle. Rhodesian Agric. J. 58:124.

Kahn H E and Spedding C R W. 1984. A dynamic model for the simulation of cattle herd production systems. 2. An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. Agric. Systems 13:63-82.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: an integer and stochastic model for evaluating production alternatives. ILCA Research Report No.2 ILCA, Addis Ababa.

Konandreas P A, Anderson F M and Trail, J C M. 1983. Economic trade-offs between milk and meat production under various supplementation levels in Botswana. ILCA Research Report No. 10. ILCA, Addis Ababa.

Lambourne L J. 1986. ILCA's policy towards modelling in the framework of livestock systems research. In: N de Ridder, H van Keulen, N G Seligman and P J H Neate, eds. Modelling of extensive livestock production systems. Proceedings of the ILCA/ARO/CABO workshop, 5-9 Feb 1985. Bet Dagan, Israel. ILCA, Addis Ababa.

Mertens D R. 1973. Application of theoretical mathematical models to cell wall digestion and forage intake in ruminants. Ph.D. thesis, Cornell Univ., Ithaca, USA.

Mosi A K and Butterworth M H. 1985. The voluntary intake and digestibility of combinations of cereal crop residues and legume hay for sheep. Anim. Feed Sci. Technol. (in press).

Sanders J O and Cartwright T C. 1979. A general cattle production systems model. Part II - Procedures used for simulating animal performance. Agric. Systems 4:289.

Wagenaar K T and Kautrohr E. 1986. Appraisal of the ILCA cattle herd dynamics model using data from pastoral systems in Mali and Kenya. In: N de Ridder, H van Keulen, N G Seligman and P J H Neate, eds. Modelling of extensive livestock production systems. Proceedings of the ILCA/ARO/CABO workshop, 5-9 Feb 1985, Bet Dagan, Israel. ILCA, Addis Ababa.

Discussion

Comment - The digestive capacity of the Zebus is, I understand, about 15% higher than that of the Friesian crosses.

Reply - The difference between them was more noticeable on feed of lower quality; on feed of 70% digestibility, the digestion coefficient was the same for the two breeds. But where the Zebu consistently gave figures of around 60 or 62%, the digestibility with Friesians dropped back to the low fifties.

Question - That would be of advantage to the Zebus, but on the otherhand, with equal intake and limited faecal output, would the two factors cancel each other out?

Answer - On those same feeds, the intake of the Zebu was a little lower than that of the Friesians. Here we have two confounded effects; was the digestibility higher because the intake was lower, or did they digest it better and therefore need to take in less? We think that one of the reasons that the correlation between dry-matter intake and dry-matter digestibility was not as close as expected was the way the experiment was done. The animals were fed a fixed amount of Trifolium and then fed teff, wheat, oats, or maize ad libitum. Having eaten a fixed amount of Trifolium, an animal which eats more teff straw has a higher intake, which will automatically have a slightly lower digestion coefficient, because of the smaller proportion of highly digestible Trifolium in its intake. So that among the animals in the trial a negative relationship is obtained between dry-matter intake and digestibility. Between means there is undoubtedly a positive relation: higher digestibility, higher intake.

Question - What were the weights of the cattle used in those experiments?

Answer - There was quite a difference between them. The Zebu weighed on average between 270 and about 330 kg and the Friesian crosses were normally 350 to 450 kg.

Comment - My impression from the literature is that differences in digestive capacity between Zebus and Friesians, or rather between *Bos indicus* and *Bos taurus* are not very large, unless you compare animals which differ substantially in weight. The heavier animals have, in general, higher digestive capacity.

Comment - What strikes me in the discussion we have just heard is its statistical naivete. Not only are the two variables, digestibility and nitrogen content, highly correlated, which makes it very difficult to use one as a predictor of the other, but there are probably block effects and interactions between other independent variables and the experimental animals. With a very small sample size, you would rapidly reduce the confidence with which you can make inferences from this kind of data.

You are attempting to use some variables to predict intake, digestibility and nitrogen. Now, it does not make too much difference which is more important. What you are really interested in is the prediction of the dependent variable, intake, and you are not so much interested in assigning it to the one or the other. The question is then, how much better is the prediction of the dependent variable? The methods presented here do not tell you that.

Reply - Well, there is a difference of course, between statistical regression models and what Jan Ketelaars has been trying to explain, which is why differences in intake take place, rather than actually using those relations for intake predictions. That is the ultimate goal of course.

At the moment the weakness in the intake formulation of the ILCA model and the TAMU model is that nitrogen percentage comes in only at a lower limit, when in fact it is closely correlated with dry-matter intake over the whole range of nitrogen contents. I think, therefore, that it should not come in simply as a lower limit. We should use both digestibility and nitrogen content, and perhaps NDF content, over the full range of intake. Your criticism is perfectly valid, but I do not have enough data for a sophisticated analysis. It does seem to me that there are at least three or four variables which influence dry-matter intake over the full range of each variable, and that it is not a hierarchy in which we have one variable over a certain range and others over a different range.

Comment - A strong correlation between digestibility and protein only exists if you look at a range of feeds at a given location. But if you extend the sample to more feeds, from different sites, then the correlation is very low, as you can see in some of the grasses.

Reply - That probably just means you have to exclude variables, because the data are based on research from experiments done in different countries and different years. The fact that the correlation breaks down when you use data from different countries, different breeds, different experimenters, and different years, is not surprising. There are differences in the ways the experiments were conducted and one has to be very careful when making such inferences using data collected in different ways.

Comment - Yes, but even if you look at a very homogeneous sample like the experiments done by French workers, you will find a large range of protein concentrations within each digestibility level.

Reply - From our rather narrow view point, which is restricted to animals on the range of pastures in African grazing systems, there is probably a very close correlation between nitrogen content and digestibility. Granted, this relationship breaks down when you look at cattle fed on straw, citrus waste, brewers' grains, and chicken manure, but we don't have that many options in Africa. For the broad class of forages, I think the relationship is pretty close. My example shows that you can get some feeds which have an abnormally high intake in relation to either their protein content or their digestibility. I would therefore prefer to have a predictor which includes both those variables, and a fibre component as well, because if we rely only on one of them in an individual feed we can be out by 20 - 30%. I think a mixture of the three would give us a greater robustness.

Comment - I tried to see if, within a given digestibility class, there were species characteristics related to high or low intake. I couldn't find any species characteristic or any species differences which lead to higher or lower intakes that could not already be derived from digestibility and nitrogen content alone.

Comment - Could I just suggest that the problem is not necessarily just a question of running a multiple regression package? The objective of Ketelaars' paper is to arrive at a new structural model. That should be the first step, and then the statistical analysis should be used to test whether that new structural model gives better fit than the simpler models.

Comment - You can expect that including protein concentration in addition to digestibility will certainly improve predictive power.

Comment - I still feel that digestibility *per se* is a very poor independent variable because of the inherent errors in its determination.

Dr Amos Goldman of ARO, Bet Degan, received about 450 feed samples from all over the world for which there were data for *in vivo* digestibility. He did a detailed multiple regression analysis of the data and concluded that *in vitro* digestibility gave a more reliable estimate than *in vivo* determination, because a very large part of the variation was animal variation. If you really want to know the digestibility of a feed, do not put it into an animal, because it will just make a mess of it!

Reply - What we need to know, for predictive purposes, is the digestibility of the feed which the animal is given. So I think we have to rely on some sort of *in vitro* procedure or a chemical determination, or a bio-assay of the intrinsic features of the pasture. We use a double enzyme assay, because it is quick and easy. It is not as precise as the nitrogen, but it is probably better than an *in vivo* assay with all of its inherent errors.

The effect of breeding season duration on production and feed consumption in grazing beef cattle in the south of Israel

Hava E. Kahn

Introduction

In Amatzia, a cooperative village in the south of Israel, the beef cattle production cycle is planned to take advantage of the limited green-pasture season for pre-weaning calf growth and for the lactating dam. The calves are weaned at the end of the green-pasture season, irrespective of age. It follows, therefore, that weaning weights will be greatly influenced by time of calving.

In grazing cattle, a 12-month reproduction cycle is considered optimal in order to coincide with the pasture production cycle. A spread of calvings will eventually ensue, even if, initially, calvings took place within a limited period. Nevertheless, calvings can be restricted to a specified period by curtailing the breeding season.

In Amatzia, the breeding season has been reduced over the past three years, from 6 months (November to April, inclusive) to 4.5 months (November to mid-February), resulting in higher conception rates, higher weaning weights, shorter calving intervals (non-pregnant cows are culled) and a concentration of calvings (85%) in the first two months of the season. The aim is to reduce the season further, to 2.5 months, by eliminating the stragglers.

A simulation study of the system was made, using the model developed by Kahn (1982), in order to examine the long-term effects of this policy and its repercussions on other factors.

Methods

The model developed by Kahn (1982) was revised in accordance with the findings of Kahn and Spedding (1984) and Kahn and Lehrer (1984). Other modifications made recently are:

1. The death routines for both calves and adults were completely revised.
2. The optimal lactation curve no longer decreases after plateauing at the age of 7 years.

The model was run to investigate the long-term effects of 2-, 4- and 6-month breeding periods (beginning in November in each case) on the overall performance of the system. The 10-year runs were replicated five times. Annual averages were calculated for only the last five years of each run in order to eliminate the effects of the initial state of the system. The integration time interval was set at 30 days (10 days for calves); the run-year was 360 days.

The run-year was set to commence after weaning on 1 May. At weaning, performed after integration for April but before the next integration time-step, all non-pregnant cows were culled and replaced by heifer calves from the weaned calf crop. Any cows which died during the run-year were similarly replaced. This method resulted in an almost constant herd size throughout the run period.

Herd size was set at 30 head. The initial weights and approximate pregnancy status of the cows were derived from a sample of the May 1983 weight and autumn 1983 calving data in the Amatzia herd. Accordingly, 12 cows calved in August, 12 in September, 2 in October and 4 in November, in the first run-year. In trial runs it was found that different initial pregnancy settings (2, 16, 6 and 6 calvings in August, September, October, November, respectively) had no significant effects on subsequent yearly (year 6 to year 10) averages in the 4- and 6-month treatments but did affect runs with a shorter season (3-month).

An attempt was made to simulate average conditions in Amatzia as far as possible. Green pasture was therefore set for three months - February, March and April - with 0.75, 0.7 and 0.65 digestibility values, respectively. May, an intermediate month, was set at 0.55; the remaining months were set at 0.45 (until November), 0.4 (December) and 0.35 (January).

Supplementation, per head and quality-wise, was as given in Amatzia, from June 1983 to January 1984, inclusive. However, replacement heifer calves were given 1 kg of concentrate supplement per day over and above the recycled feed (if and when the latter was allocated) until half-way through their second

lactation. Calves were given an allowance of concentrate feed in accordance with their weight, amounting to about 175 g/day in October and rising to 950 g/day in January. These amounts are similar to those given in Amatzia. Only the calves and heifers were given concentrate feed; cow supplementation consisted of recycled feed only (average energy concentration of 9.74 MJ ME/kg DM).

No economic analysis of the system was attempted at this stage. However, supplementary feeds and calf/cow sales were represented by averaged values to enable an overall appreciation of the differences between the systems. The prices were:

Recycled feed	$0.06/kg DM
Concentrate feed	$0.22/kg DM
Weaned calves	$2.25/kg liveweight
Culled cows	$1.25/kg liveweight.

Results

The key values of the simulation runs, representing the biological performance of the system, are presented in Table 1.

Discussion

The simulated long-term effects of length of breeding season on production variables showed that concentrating calvings in November-December significantly increased average calf age and weaning weight (7%), compared with the two longer-season treatments. However, as a result of the lower conception rates in the 2-month treatment (84 vs. 90 and 93% in the other two treatments), the number of calves weaned was reduced by 12%. Despite higher weaning weights, calf sales in this treatment were 13.5% lower than in the other two treatments, since those heifer calves reared as replacements (5.5 calves per year, almost twice as many as in the other treatments) are not included in the sales figure. The high replacement rate also accounts for the considerably higher concentrate consumption figures (39 and 56% higher than in the 4- and 6-month treatments,

Table 1. Various consumption and production variable values for model runs simulating 2-,4- and 6-month breeding seasons. (All values are for a 30-cow herd plus unweaned calf crop.)

Variable	Breeding season		
	2-month	4-month	6-months
Pasture consumption (t DM/year)	72.3*	73.3	74.1
Green pasture consumption (t DM/year)	34.7[b]	35.8[a]	35.9[a]
Recycled supplements (t DM/year)	43.1	43.0	42.7
Concentrate supplements (t DM/year)	6.1[a]	4.4[b]	3.9[c]
ME (from supplements) (1000 MJ/year)	512[a]	486[b]	473[c]
Cost of recycled feed ($1000/year)	2.6	2.6	2.6
Cost of concentrate feed ($1000/year)	1.3[a]	1.0[b]	0.9[c]
ME supps/kg cow+calf sold (MJ)	70	67	66
Annual conception rate (%)	84[c]	90[b]	93[a]
No. weaned (N/year)	21.8[b]	24.6[a]	24.6[a]
Ave. wean. wt. (kg)	288[a]	274[b]	269[b]
Ave. wean. age (years)	0.73[a]	0.69[b]	0.67[c]
Ave. cow age (years)	6.3[b]	9.0[a]	9.5[a]
No. replaced (N/5 years)	27.2[a]	16.8[b]	14.4[b]
Cow mortality (N/5 years)	3.8	2.2	3.4
Calf mortality (N/5 years)	10.8	8.4	9.6
Calf sales (t/year)	4.9[b]	5.9[a]	6.0[a]
Culled cow sales (t/year)	2.5[a]	1.5[b]	1.1[c]
Cow+calf sales ($1000/year)	1.5	1.5	1.5
Feed cost: sales (ratio)	0.28[a]	0.24[b]	0.23[b]

*Within row, values with different superscripts differ significantly at the 5% level.

respectively), since heifers receive 1 kg concentrate/day during two 9-month periods. These simulated long-term effects are in contrast to the short-term (2-year) records in Amatzia, as well as in Kubbutz Sha'alvim (Lehrer and Schindler, 1984), in which reducing the spread of calvings was associated with an increase in the annual conception rate.

Nevertheless, the overall picture is less clear. The proceeds from culled cows in Treatment 1 are 1.7 and 2.3 higher than in the other treatments so that there are no differences at all between the treatments in total income from livestock sold. Consequently, the feed-cost:livestock-sales ratio was only 17 and 22% higher than in the 4- and 6-month treatments, respectively. The difference between the latter treatments is not significant, in keeping with most of the other differences between these treatments.

These results suggest that, mainly as a result of the progressively lower conception rate associated with the shorter breeding seasons, concentrating calvings in a short season entails some loss of profit, which may be significant when the season is reduced to as little as two months. Interpretation of the simulation results therefore hinges largely on the credence placed on the simulated, long-term reproduction performance.

Kahn and Lehrer (1984) critically examined the reproduction probability equations, adopted by Kahn (1982) from Sanders and Cartwright (1979), and suggested several major modifications. These were validated with field data from Israel. The data used related to herds with 6-month breeding seasons, i.e no attempt had been made to systematically improve the reproductive performance of the herd. On the assumption that curtailing the breeding season weeds out the stragglers, viz. those cows with long or irregular calving intervals, herd conception rate should rise with the more stringent culling policy, a phenomenon observed during the past two seasons in Amatzia. The reproduction probability equations used in the model do not allow for an improvement in overall herd performance; their upper limits under optimal conditions are p=0.85 for post-partum oestrus and p=0.75 for conception, given oestrus, values obtained by Sanders (1974) from extensively-managed beef-cattle herds. If a reduction in the breeding season and associated culling substantially increase herd reproductive performance, as was shown by Warnick and Fields (1976) in Florida, the threshold values for the probabilities should be modified accordingly.

The 2-year data from Amatzia show prima facie that reproductive performance does improve with reduced length of breeding season. However, considerably more data are required before this can be conclusively established, if the variance of the simulation results are any indication of the actual variance of the system. For instance, in the 2-month treatment, November conceptions ranged between 50 and 90% between years and had SD's of 1.2 to 12.2 (ave. for 10 years and 5 replications = 73%). The Amatzia records may represent erratic results which are not repeatable over the years, especially if the effect of cow age is taken into account (see Kahn and Lehrer, 1984).

Another attribute of the probability equations, as expressed in the present model runs, may have distorted the results, especially those for the 2-month treatment. The original Sanders and Cartwright (1979) equations were quantified and adjusted for a 30-day integration step, while taking into account the 21-day reproductive cycle of cows. This device may be inappropriate when the breeding season is reduced to two months, a hypothesis which can be tested by running the model under different time steps (Kahn and Lehrer, 1984).

Concentrating calvings in a short season allows a more specifically production-targeted supplementation policy. For instance, the January supplementation could be reduced to a point where lactation level is not severely jeopardised, if January is no longer in the breeding season. In the model runs, allocations of recycled feed supplements were identical in all treatments. However, the potential saving would not be large since the January allocation is about one sixth of the annual total and probably could not be reduced by more than 40%.

Despite the potential sources of error in the model, enumerated above, and perhaps others still undiscovered, the model results do indicate that pushing the herd to ever-shorter breeding seasons may have its dangers. However, as long as reproductive performance of the herd is not impaired, the process can be continued, provided that the system is monitored closely.

References

Kahn, Hava E. 1982. The development of a simulation model and its use in the evaluation of cattle production systems. Ph.D. thesis, Univ. of Reading, UK.

Kahn, Hava E and Spedding C R W. 1984. A dynamic model for the simulation of cattle herd production systems: II. An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. Agric. Systems 13:63-82.

Kahn, Hava E and Lehrer A R. 1984. A dynamic model for the simulation of cattle herd production systems: III. Reproductive performance of beef cows. Agric. Systems 13:143-159.

Lehrer A R and Schindler H. 1984. Adjustment of the breeding cycle of beef herds to the vegetational cycle of the range in Israel. In: The reproductive potential of cattle and sheep. INRA, Paris, France.

Sanders J O. 1974. A model of reproductive performance in the bovine female. M.Sc. dissertation, Texas A & M Univ., USA

Sanders J O and Cartwright T C. 1979. A general cattle production systems model: II. Procedures used for simulating animal performance. Agric. Systems 4:289-309.

Warnick A C and Fields M J. 1976. Reproduction and fertility in beef cattle. In: Beef Cattle in Florida. Institute of Food and Agricultural Sciences, Gainesville, Florida, USA.

Discussion

Question - Since this is a 10-year model and since you have benefits which accrue, have you worked out the present value of the costs and sales?

Answer - No, this is not an economic model. The cost calculation is done just to give a rough idea of the costs of inputs and value of output.

Question - Is the incorporation of stochastic elements really worth the effort? Could not one carry out much simpler calculations just using average conception rates and average costs etc. and arrive at as good an answer?

Answer - The TAMU model was built on class averages, and so it needed a hundred or a thousand classes in order to account for cows of different age and different conception status and so on. Cows would move from class to class but you could not follow cow performance throughout its life.

Comment - But in fact, from a management point of view, it is the herd that one is concerned with, not with individual cows.

Reply - It would be difficult, if not impossible to analyse the reproduction and mortality aspects of the herd with a deterministic model. It is also much simpler to write and to conceptualise the model as composed of individual cows. It makes it easier to communicate with non-modellers. That is a very important aspect of the modelling process.

Comment - If you are interested in keeping the herd as individual animals, then you must deal with stochastic analysis. But if you are interested in management problems, then you do not use the results of individual cows, but need estimates of the mean value.

Comment - The purpose of this exercise is to provide some practical advice on management regimes. It would help to do a cost-benefit analysis on a stochastic versus a deterministic model. It would be interesting to see whether in fact, after a run of years, the model came up with any different final conclusion after eliminating the stochastic element and just using the average conception

and mortality rates for a particular age class of animals. When you get a result which is counter-intuitive, then you want to figure out why you got it. It is very difficult to do so with a stochastic model.

Comment - I would say that the importance of a stochastic element in a pastoral model becomes very small, because there are so many other factors that restrict conception rate.

Reply - I tend to agree with you, because where there are all sorts of stress factors that reduce the conception rate, then they will be dominant. Where stress factors are excluded the only factor that remains is the time since calving. Then you get more random variation, rather than less variation.

Comment - The discussion seems to be confusing two issues, the source of the variation and the size of the variation. There is less variation in this kind of system than in a pastoral model. Therefore, to use the stochastic model in this type of system would have less effect, because the coefficient of variation on a calving rate of 90% is probably less than 10%. In the pastoral system with a mean calving rate of 50% and a much higher coefficient of variation, and probably a highly positive skewed distribution a stochastic model might have a much larger effect irrespective of what causes the calving rate to vary so much.

Comment - My question rose from the fact that if at the end of the day you just want to end up with average results, the average cost per calf, the average economic performance, then is it worth tracking out all of this stochastic variation? It may well be that one ought to be using a more sophisticated analysis for decision-making which takes account of this variability. But if you are not interested in measuring the variability, then a priori it would seem wasteful to model it. Whether it is large or small is irrelevant.

As far as reproductive performance is concerned, working with distribution rather than averages is essential if you want to learn about the situation of the herd.

If you take the average probability of performance on a herd basis it would be the same as taking the stochastic probability for the individual animal performance, adding them up and getting the same expected value. The advantage of working on individual animals would be in studying dynamics of a herd that is

undergoing major changes in structure. In a stable herd, the expected value should be the same in both cases, whether the model is stochastic or deterministic.

Question - Have you used independent input data to validate your equations?

Answer - I used one set of data, which was collected by a colleague, M. Weitz, and I changed the functions of the TAMU model accordingly. Then I validated on a different set of data also from Israel and from a quite different herd. In the present model I am using the revised, not the original, equations. The biggest difference between the equations was that there was very little effect of weight change on conception if condition score was above 0.9.

Cows start the breeding season in fairly good condition, above 0.9 and then even if they lose weight throughout the breeding season, they attain a very high conception rate. This is in contrast to the widely held view that for high conception rates the cows should be either in weight balance or gaining weight.

Adaptation of the Kahn model for a mixed farming system in southeastern Asia

C. Hermans

Introduction

The Centre for World Food Studies (CWFS) conducts research related to food policies and hunger. The core of this work is the formulation of national models which describe food production, the functioning of markets and government interventions. The models are multidisciplinary in that they pertain to the physical factors and economic causalities that, together, determine a country's food system. The purpose of the models is to help in formulating national food policies (CWFS, 1984).

The physical factors that determine production are studied by CWFS-Wageningen (CWFS-W). A crop production model simulates crop yields, taking into account soil type, climate and soil moisture content. The effects of fertilizers, weed, pest and disease control measures and harvest losses are also analysed.

The Department of Tropical Animal Husbandry of the Agricultural University of Wageningen and CWFS-W work together on modelling of livestock in mixed farming systems in South and Southeast Asia, where both institutions are involved in research projects. This model (SOWIV) quantitatively describes and identifies the different components of the livestock system and their interrelationships, and their interactions with factors outside the system.

The livestock model is used to investigate the consequences of different interventions on the production of the livestock system. Interventions considered include changes in animal husbandry practices, i.e. changes in feed quality or quantity, kinds of feed, animal breed and animal type; changes in marketing conditions, i.e. supply and demand, prices, and imports; and changes in development strategies, such as the development of the livestock sector *vis-a-vis* the crop production sector.

It was decided to model at the farm level, which requires treatment and monitoring of each animal, the study of the production processes, the investigation of the interactions between livestock and other farm enterprises

and the study of the consequences of the farmer's decisions on the livestock enterprise. Once the processes and interrelationships are understood at the farm level, the farm-level knowledge can be aggregated to the regional or national level.

The model is linked to the crop production model of CWFS-W to analyse interrelationships between primary and secondary production, but can also function as a separate entity.

This paper describes a model of the livestock component of a mixed farming system that has been developed by the Department of Tropical Animal Husbandry and CWFS-W. The characteristics of the Southeast Asian livestock system are given. The boundaries of the model are explained, and the Kahn model, which was used as a basis for this model, is introduced. Finally, the different modules of the model are discussed.

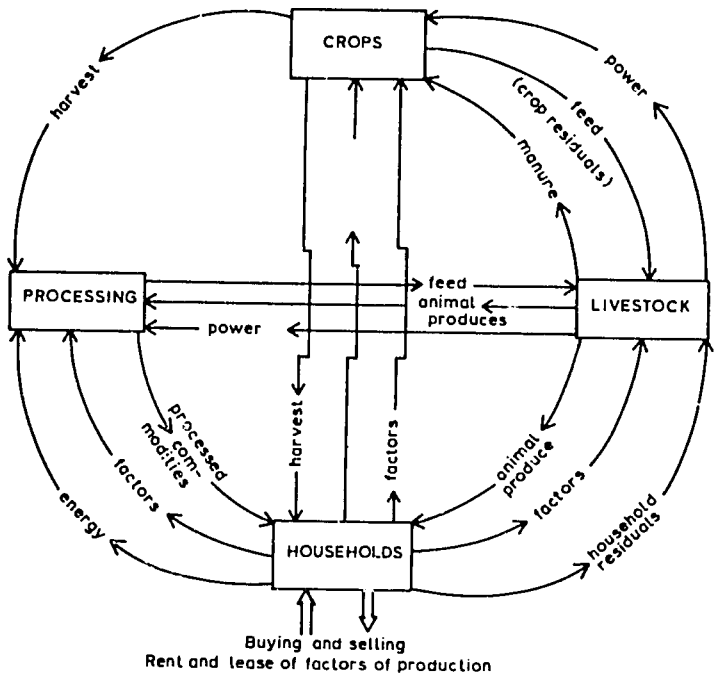
Characteristics of the livestock system in Southeast Asia

Crop and animal production are closely interrelated in the farming system of Southeast Asia. Animal traction and manure play essential roles in land preparation and maintenance of soil fertility, while agricultural products and wastes from the farm constitute the main constituents of the animals' diets. Thus, the animals complement and support crop production.

The system also comprises a wide variety of species: cattle and buffaloes, sheep, goats and poultry. Figure 1 illustrates the most important components of the integrated farming system: crops and their products and byproducts, animal husbandry with livestock products and byproducts, the family and the market.

The land use in a country gives a first indication of the type of livestock system. India, Bangladesh and Thailand grow annual or perennial crops on a large part of the land (57, 69 and 35%, respectively), while not more than 5% of the land is available for pasture (FAO, 1983). Most of animals' rations will consist of crop byproducts, mainly low-quality crop residues. Most of these byproducts are consumed by cattle and buffaloes. Crop residues such as straw are not readily eaten by sheep and goats (Table 1) (Dolberg, 1983), which consume better quality resources and thus graze pasture land and road sides. From the distribution of land to pasture and crops, and the demands

Figure I. Schematic representation of interactions within the agricultural sector



made by the different species on feed, it is obvious that the number of cattle and buffaloes greatly exceeds the number of sheep and goats in these countries.

Table 1. Comparative performance of small and large ruminants on a roughage[1] diet in Egypt.

Animal species	Body weight kg	Intake of dry matter kg/day	Intake of dry matter g/kg $W^{0.75}$/day	Change in body weight[2] g/day
Cattle	259	7.8	121	+0.58
Buffaloes	230	8.9	151	+0.65
Sheep	40	0.6	38	-0.03
Goats	24	0.4	38	-0.04

Source: El-Naga, not dated (reproduced from Dolberg, 1983)

[1] The diet DM was composed of 50% corn stover (ammonia treated) plus rice and faba bean straws (not clear whether they were treated). In addition the animals received minerals.

[2] Change in body weight was recorded over the week in which the intake of the animals was recorded, which followed two weeks of adjustment to the diet.

The same holds for Java, although in Indonesia as a whole the situation is quite different (FAO, 1983). Pasture land is relatively more abundant, reflected in the relatively larger sheep and goat population compared with the cattle and buffalo population. Moreover, the relatively small number of cattle and buffaloes in Thailand and Indonesia can be explained partly by the lactose intolerance of the population. Milk is generally an unwanted and unimportant product. The limited feed resources are used to produce draught power and meat (Crotty, 1980).

Between 1974 and 1982 the livestock population in the Far East increased by between 6 and 31% for cattle, buffaloes, pigs, sheep, goats, chickens and ducks (FAO, 1983) (Table 2). Small ruminants and poultry showed the largest increase during this period.

Table 2. Increases (%) in population number of the animals from 1974-1976 to 1982 in some Southeast Asian countries.

Animal	Far East	Thailand	Indonesia	India	Bangladesh
Cattle	6	7	4	1	38
Buffaloes	7	8	5	4	49
Pigs	21	3	21	30	
Sheep	25	22	29	4	8
Goats	22	1	10	4	54
Chicken	31	16	23	6	53
Ducks	30	16	38		39

Calculated from data in FAO (1983).

The changing emphasis on particular types of livestock may partly be explained by social factors:

a. There is, generally speaking, a positive relationship between the size of the holding and the animal species kept. Smaller farms keep mostly goats and poultry, while larger farms keep draught animals.

b. The increasing population causes increased fragmentation of holdings, and thus favours an increase in the number of small animals. The number of cattle and buffaloes decreases when population pressure increases.

c. The growing human population and higher incomes increase the demand for livestock products. This increased demand can only be met by an increased animal population.

As explained above, considerable differences in feed production potential, animal species and animal numbers exist within the integrated farming system among the different countries. Considerable variation also exists in production potential of the different animal species, distribution of the animals over the farms, seasonal variation in the feed production, etc.

Boundaries of the modelled system

Not all the components of the integrated farming system - crops and their products and byproducts, animal species and their products and byproducts, the family and the market - are included in the SOWIV model. Research is focused on the animal components and the relationships between feed supply and livestock performance. The family, the market, crop production and policy decisions outside the farm unit are considered as exogenous factors. The interactions between the components of the farming system are strongly reduced. Until now, only one species, cattle, has been considered, but other species will be included later. Buffaloes probably do not differ from cattle and will overlap in use of feed resources, feed intake and animal production. Sheep, goats and poultry only partly utilise the same feed resources as cattle and buffaloes.

The supply of crop byproducts for feed is considered as a fixed input, and effects of draught power and dung on crop production are not yet described in the model. These products are available output. Similarly, the interactions between the livestock and the family are not taken into account. It is taken for granted that enough human labour is available to do the work involved in keeping the animals. Also the effect of the availability of animal products - meat, milk, draught, manure - on the family's behaviour are not considered. The animal products are the technical output of the system without an economic evaluation. The same holds for non-farm inputs. All products, except the animal feed, are considered to be available in non-limiting amounts. These simplifications obviously affect the assumptions of the integrated farming system. However, they allow us to concentrate on the livestock aspects with their most simple link to crop production: available feed.

The subjects that are included in the model are:

a. Feed aspects, including availability (quantity and quality), intake and conversion of feed energy into animal products (meat, milk, traction, manure).

b. Herd dynamics, including mortality, reproduction and purchase or sale.

c. Feedback between herd dynamics and feed availability.

Necessary changes in Kahn's model

The model of Kahn (1982) was used as a starting point. This model is a version of the Texas A & M University (TAMU) model (Sanders and Cartwright, 1979a; 1979b) that has been adapted to African conditions. The model calculates animal performance on the basis of specific feed resources and genetic potentials for animal production. Animal performance is calculated on an individual basis. The randomly occurring discrete events - mortality, conception and calf sex - are treated stochastically, and for every time step, the biological status of the animals (growth, reproduction, mortality) is recalculated according to the intake of energy and its utilisation (Kahn and Spedding, 1983).

However, the Kahn model had to be modified for various reasons.

- The Kahn model describes a grazing system for cattle. Because of the need to describe a mixed farming system - including a number of different animal species and a variety of feeds - the model had to be adapted to allow a flexible combination of different feeds into animal rations in the course of the year. These adaptations consisted mainly of extensions to the feed-offer module. As mentioned above, only cattle are included in the SOWIV model so far. When different species are included, competition between species for feeds will have to be taken into account.

- Other changes are included in the model as a consequence of further development of scientific theories, especially with regard to the regulation of feed intake. In the Kahn model only energy (digestibility) is considered as a factor determining intake with an empirical correction factor for feeds containing less than 6% crude protein. The SOWTV model follows the suggestions of Ketelaars (1983; 1984), who found that at all levels of energy (digestibility) and crude protein content both factors interact in the regulation of intake. This has immediate consequences for the calculation of the animal requirements, because both energy and protein requirements have to be defined for the different animal functions.

- Lack of data forced us to include some simplifications. In modelling, the interactions between factors have to be quantified, and often this information is not available. This problem has been encountered in the quantification of herd dynamics. Reproduction and mortality probabilities in Kahn's model are quantitatively related to factors such as age, weight index, weight change, stage of maturity and lactation stage. However, it has not been possible to quantify the various relationships from literature studies or available data, and therefore simplifications were introduced.

In the remainder of this paper, the different modules of the Kahn model, the modifications implemented and the problems encountered during the modelling exercises are discussed.

General structure of the model

In essence, the general structure of the Kahn model is maintained. The state-variable approach is employed. At each time step each state variable is recalculated from the situation at the beginning of the time step and the energy exchanges and production during the time step. Where Kahn uses a single animal, or, in the case of suckler cows, the cow-calf entity as the calculation unit, the SOWTV model uses a single animal in all cases.

The time step in the SOWIV model is 30 days, but, as in the Kahn model, any time step from one day upwards can be used.

A random number generator is used to preserve the integer quality of the herd. Discrete events, such as mortality or reproduction, occur with an exogenously-defined probability. A random number is generated and compared with that probability. If the generated random number is less than or equal to the probability, the event will occur. Otherwise, it will not. Indeed, the simplicity of the integer approach is achieved at the expense of random variation between replicate model runs (Kahn and Spedding, 1983). In the case of small herds, the variation between replicate runs is too large to be useful for mean herd composition calculations. However, replicate runs have a value in risk assessment.

Within the replication loop in the SOWIV model, the various calculation modules are treated separately. For all animals, the following modules are successively passed through: allocation of a feed ration to each animal, calculation of the animal's energy and nitrogen requirements, calculation of the theoretically possible intake, calculation of the real intake, and calculation of the animal's production in terms of meat, milk, manure and offspring. The herd-dynamics module then generates pregnancy and mortality probabilities.

Discussion of the modules of the SOWIV model

Feed allocation

The Kahn model describes a grazing herd of female cattle. In addition to a seasonally-dependent pasture component, provisions are made for a seasonal allocation of supplementary feed to heifer-replacers and calves. An option is also included to supplement according to physiological group (calf, lactating cow, pregnant cow).

The climate of Southeast Asia is suitable for year-round production of various crops. Crop residues are the main animal feed in this region. Different residues are available during different seasons, and the feed allocation module in the SOWIV model has been made more flexible to allow for this.

Nine animal classes are distinguished:

1. Calves, male and female, only consuming milk, until 1 month old;
2. Calves, male and female, from 1 month old to weaning age;
3. Young stock, male and female, from weaning to 1.5 years old;
4. Young stock, male, from 1.5 to 3 years old, and female animals from 1.5 years old to the fifth month of the first pregnancy;
5. Dry cows, not in the last 4 months of pregnancy;
6. Lactating cows, not in the last 4 months of pregnancy;
7. Pregnant cows in the last 4 months of pregnancy;
8. Male animals, older than 3 years, not working; and
9. Working male animals, older than 3 years.

Fifteen different feeds can be allocated. A distinction is made between farm-produced feeds (mainly roughages and crop byproducts) and purchased feed. In the model, available roughage is given in total amount per month per farm. This amount is distributed over the different animal classes, according to a distribution factor defined for each class. Purchased feeds are given in absolute amounts per animal per day. In addition, for every feed, an indication is given as to whether it can be saved for the following time-step, what percentage is wasted while eating, and the sequence in which it is fed.

To allow calculation of feed intake, the crude protein content, the digestibility of the dry matter and the energy content of the digestible dry matter are given for the different feeds. These values are given as monthly averages.

These structural modifications allow greater flexibility in the combination of feed sources, their availability during the year and their allocation over the different animal categories than the original Kahn model. The module is valid in a mixed farming system, but can also be used in any system in which the amount of feed available to the animal is known, i.e. intensive or extensive production systems, including grazing systems.

The output of the feed allocation module, i.e. the amounts of different feeds available to each individual animal from which it can select, is used as input for the feed intake module.

Feed intake

The feed intake regulation in Kahn's model is based on two concepts: the existence of a physical control operating on most roughages, and the existence of a physiological control associated with highly digestible diets.

The idea underlying physical control of feed intake is the assumption that undigested material in the digestive tract (ballast) restricts the rate of passage of feed through the digestive tract and thus restricts feed consumption. Following this theory, dry-matter intake per kg liveweight is inversely proportional to the non-digestible fraction when digestibility is less than 67%, while the faecal dry matter output per kg liveweight remains constant (Conrad et al, 1974). Kahn (1982) uses a value for faecal dry matter output of 0.0093 kg/kg liveweight per day, but this value gradually increases in the case of lactating cows to a maximum value of 0.0116 in the fifth month of lactation, and decreases gradually to the basic value at the end of lactation.

Analysis of data on sheep by Ketelaars (1984), however, showed considerable variation in faecal dry matter output as shown in Table 3. Therefore, using a constant faecal dry matter output to predict the feed intake, as done by Kahn (1982) and also by Sanders and Cartwright (1979a; 1979b) and Konandreas and Anderson (1982) seems very inaccurate.

Table 3. Digestibility (%) of the dry matter and corresponding minimum and maximum values of faecal dry matter output (kg DM/kg LWT/day) for sheep.

DM digestibility %	Faecal DM output kg DM/kg LWT/day	
	Minimum	Maximum
70	0.00590	0.01079
60	0.00572	0.01343
50	0.00425	0.01177
40	0.00440	0.00914

According to Conrad et al (1974) and Kahn (1982) physiological control becomes important when the feed is highly digestible (more than 67%). Feed intake will then be restricted by the animal's potential to absorb and utilise digestible nutrients, or, stated differently, intake is regulated by energy requirements. Kahn (1982) calculated the physiological limit for dry-matter intake as 2.5% above the calculated requirements for maintenance, traction, lactation, gestation, growth or weight gain. However, she also found that intake predictions obtained in this way were not very accurate.

It may be concluded that intake predictions based on a combination of physical and physiological control can be criticised on different points, and, therefore, remain questionable.

An alternative system was developed by Ketelaars (1983). According to his analysis, feed intake of growing cattle can be explained from the relative availability of energy and protein in the feed, and the capacity of the animal to utilise energy and protein in a certain ratio. The data used to develop that theory pertained to both temperate and tropical cattle fed temperate as well as tropical grasses and legumes. This conceptual model has been developed further for sheep (Ketelaars, 1984). At any level of intake of nitrogen the maximum amount of energy the animal can consume - given the feed digestibility - and convert into animal product (meat, milk, draught) can be calculated from:

- the energy and protein content of the animal product;
- the minimum protein concentration in the product; and
- requirements of energy and protein for maintenance.

In this calculation assumptions have to be made about the efficiency of conversion of metabolisable energy into net energy, of digestible energy into metabolisable energy, and of ingested nitrogen into animal product. Also the energy content of the digestible dry or organic matter has to be estimated. The nitrogen/energy ratio or the animal product (g N/MJ NE, NE = net energy) defines the slope (b) or the maximum intake versus nitrogen intake line. The intercept (a) of the maximum intake curve with the energy intake axis is defined by this slope and the maintenance requirements. The maximum intake curve can be visualised as:

$$D_{O\ max}\ (g\ DOM/kg^{0.75}) = a + b * I_N\ (g\ N/kg^{0.75})$$

where $D_{O\ max}$ = maximum digestible organic matter intake
I_N = nitrogen intake

The maximum intake is very sensitive to the maintenance requirements and the composition of the animal product (Ketelaars, 1984).

Whether the animal will eat this maximum possible amount of energy is co-determined by feed availability. If the animal has less feed available than it can consume, feed intake will equal feed availability. In the SOWTV model the animal selects the ration it will ingest, according to predefined criteria (nitrogen content of the feed), from the feeds available. For these calculations the animal's energy and nitrogen requirements have to be known. How these requirements for the different products are defined is explained below.

Requirements

The TAMU (Sanders and Cartwright, 1979a; 1979b), ILCA (Konandreas and Anderson, 1982) and Kahn (1982) models use energy availability and requirements to explain animal performance. For these calculations ARC (1980) standards are used, with some slight modifications if necessary; if model predictions are unsatisfactory, they can often be brought into line by exchanging one or more functions for others that are equally-well documented.

The SOWTV model uses the method of Ketelaars (1984) to calculate feed intake; thus, animal production is predicted not only from energy, but from both energy and protein availability.

One reason for not applying the ARC standards for tropical breeds is that an analysis of data from Bangladesh showed that if ARC feed requirements are used to explain animal production, predicted feed intake is below even the maintenance requirements. In reality, the animals did grow and produce.

In the following paragraph, the requirements applied in the model for the different animal functions are discussed.

Maintenance: Accurate estimates of the maintenance requirements of animals are crucial in the calculation of their maximum voluntary feed intake. In the literature no consensus exists on the value or the method of calculation of these requirements. Wallach et al (1984) compared 14 methods for calculating energy requirements for maintenance in grazing sheep and found that widely differing approaches are used. One approach independently evaluates fasting energy loss and the efficiency of utilisation of feed energy for maintenance. A second approach determines maintenance requirements from indoor feeding trials. Short-term or short- and long-term trials were often performed on mature and non-producing animals.

In calculating maintenance requirements, some authors include the heat production associated with muscular activity, in addition to the fasting heat production. Some also include the loss of energy in the urine.

Calculations of the fasting heat production almost always include a term proportional to metabolic weight (animal weight raised to the power 0.73 or 0.75). However the animal weight used is not always the same. Some authors use empty body weight, others use weight including gut fill. Sometimes, an age factor is included, a distinction is made between suckling or ruminant animals of the same weight, or an effect of sex or a lactation factor is included.

The calculations of the energy costs of muscular activity are also not unequivocal. Sometimes it is assumed that the cost of activity is included in the fasting heat production, sometimes a fixed level of activity is added, or the level of activity varies. Factors that are included separately or in combination are: standing, changing position, walking, climbing, ruminating and eating. As a result, estimates of the maintenance requirements differ according to the system used.

A first rough comparison has been made of six different methods for calculating maintenance energy requirements of cattle: ARC (1980), Sanders & Cartwright (1979a; 1979b), Siebert and Hunter (1977), Levine et al (1981), Levine and Hohenboken (1981), Konandreas and Anderson (1982) and Kahn (1982). The equations are given in Table 4, and the results obtained with these equations are given in Table 5. The differences between the lowest and the highest values in each column range from 28 to 64% for the different animals.

Table 4. Equation for calculating maintenance energy requirements for cattle.

Source	Requirement	Unit
ARC (1980)	$(COF*(LWT/1.08)^{0.67} + 0.0043*LWT)/KM$	MJ ME/day
Sanders and Cartwright (1979)	$0.465*LWT^{0.75}$ (no activity included) (quoted by Kahn, 1982)	MJ ME/day
Konandreas and Anderson (1982)	$(0.376*LWT^{0.73} + 0.0021*LWT*D)/KM$	MJ ME/day
Siebert and Hunter (1977)	$((12150-8.8*AGE + 0.0045*AGE^2)*4.2*LWT^{0.75} + 200*LWT)/(61.6 + (6.75*ME/DM))$ (activity included)	kJ ME/day
Levine et al (1981)	$C*ELAC2*LLAC2*LGEST*((12150-(8.8*AGE) + (0.0045*AGE^2))*LWT^{0.75} + 200*LWT)/(61.6 + (6.75*ME/DM))$	kcal ME/day
Kahn (1982)	$COF*(LWT/1.08)^{0.67}/KM + ACI*0.012*LWT$	MJ ME/day

LWT liveweight (kg).
KM efficiency of conversion of ME to NE.
D walking distance (km/day).
AGE age in days.
ME/DM metabolisable energy concentration in the dry matter (MJ/kg).
COF coefficient, 0.53 for female animals, 0.67 for male animals.
C 0.955 to modify maintenance requirements during early rainy season on native savanna or to early and/or late rainy season on molasses.
ELAC2 1.4 to modify maintenance requirements of cows during the first 100 days of lactation.
LLAC2 1.32 to modify maintenance requirements of cows during the remainder of the lactation period after the first 100 days.
LGEST 1.05 to modify maintenance requirements of cows during the last trimester of pregnancy.
ACI activity factor 0: no activity;
1: moderate activity;
2: high activity.

Table 5. Maintenance energy requirements (MJ ME) of cows, calculated with the equations of Table 4.

Source	LWT (kg) / Age (days)	25 / 109	50 / 365	100 / 730	100 / 1095	200 / 1095
		Maintenance energy (MJ ME)				
ARC (1980)[1,6]		6.56	10.49	16.83	16.83	27.03
Sanders and Cartwright (1979)		5.20	8.74	14.70	14.70	24.73
Konandreas and Anderson (1982)[2,6]		5.95	9.32	16.56	16.56	27.69
Siebert and Hunter (1977)[3]		5.13	7.34	10.57	10.30	17.38
Levine et al (1981)[3,5]		5.26	7.62	11.14	10.87	16.93
Kahn (1982)[4]		6.55	10.48	16.79	16.79	26.96
Orskov (1981)[7]		4.47	7.52	12.65	12.65	21.27

[1] COF = 0.53

[2] D = 2 km/hour

[3] ME/DE = 1.50 Mcal/kg

[4] ACI = 0.5

[5] C = ELAC2 = LLAC2 = LGEST = 1

[6] KM = 0.68

[7] Estimates for Bengali cattle

Although further study is necessary, no reason was found to prefer one of the calculation methods in our model. Therefore, the maintenance energy value given for Bengali cattle (0.4 MJ ME/kg$^{0.75}$) by Orskov (1981) is used. It can be seen in Table 5 that this value is within the range of the other estimates. This value is used for female animals: For male animals, it is increased by 26%, as proposed by ARC (1980).

For the time being, the value given by Preston (1972) for protein requirements is adopted: 0.5 g N/kg$^{0.75}$. No comparison was made with other estimates reported in the literature.

Traction: Few data on nutrient requirements for animal traction are reported in the literature, and little attention is paid to this subject in the different models. In Kahn's model the animals can perform 'light' work for 2 hours per day or no work at all. Two hours of 'light'work per day requires 10 MJ ME. Only animals older than 4 years, lactating for more than 60 days, or during the first 180 days of pregnancy are allowed to work. Because animal traction is one of the important production goals in Southeast Asia, it was felt that this subject should be investigated more thoroughly.

Mainly cattle and buffaloes are used for traction in Southeast Asia. Buffaloes have a lower heat tolerance than cattle, and can be used only during cool morning hours if no bathing facility is available. Cattle are stronger than buffaloes in the dry season, i.e they can be used for longer periods and travel faster (Rufener, 1971).

Immature cattle (less than 3 years old) and pregnant cows are unsuitable for work (Gill, 1981). In villages around Noakhali (Bangladesh), cattle less than 100 kg are never used for work (Hermans, 1984). Fertility and lactation problems arise if cows are used for draught (Gill, 1981; Groenewold, 1983; Jabbar, 1983). Lactation is more severely affected by draught work than is fertility. On working days milk production losses amount to 20-30%. Fertility is 6-7% lower in working animals (Goe, 1983).

Training for work starts when the animals are between 2.5 and 4 years old (Goe, 1983; Howard, 1980; Starkey, 1982; Nourrissat, 1965; FAO, 1972). In Senegal animals are used for work until they are 14 to 15 years old (Nourrissat, 1965).

The number of hours per day an animal works depends on its sex and physiological status. The literature does not show much variation. Bullocks work for 5-6 hours per day (Gill, 1981; FAO, 1972) in one single session, interrupted by reasonable rest periods, or half in the morning, half at the end of the day. Female animals work for 2-4 hours per day (Goe, 1983). Our survey in Bangladesh showed that bullocks did not work for more than 5 hours per day, cows work at most for 3.9 hours per day, while lactating animals never work more than 2.8 hours per day. N'Dama cattle in Sierra Leone are used for 4 hours per day (Starkey, 1982). The number of days animals are used during the year varies between 50 and 200 (Sarker, 1981). Nourrissat (1965) stated that the animals are used for 350 hours per year. Assuming a working day of 5 hours, this means that the animals are used for 70 days. Rough calculations on the Noakhali data

(Hermans, 1984) show that the bullocks are used for 520 hours per year or about 100 days per year.

The number of hours needed to plough one hectare is also variable and depends on the type of plough and the type of soil. With a traditional plough, between 22.2 and 33.3 hours would be necessary to plough 1 hectare (Sarker, 1981; Sarker & Farouk, 1982), while 14.3 to 28.6 hours are needed with an improved plough.

The walking rate of the animals differs according to species and category. Buffaloes walk at 2.5 to 3.2 km/h (Goe, 1983), or 2.9 to 3.2 km/h (Smith, 1980). Generally they are known to walk slower than cattle. Bullocks work at a walking speed of 2.2 to 3.1 km/h (Smith, 1980; Howard, 1980), 2.5 to 4.0 km/h (Goe, 1983) or 2.2 to 3.6 km/h (Lawrence, 1984). Howard (1980) makes a distinction between the speed for ploughing (2.5 km/h) and the speed for the roundabout (2.2 km/h). Cows walk about 2.5 km/h (Smith, 1980; Howard, 1980) or 2.5 to 3.5 km/h (Goe, 1983). Other authors do not differentiate between animal categories and give walking rates between 2.5 km/h and 5 - 6 km/h for draught animals (Sarker, 1981; Sarker and Farouk, 1982; FAO, 1972).

The tractive effort cattle can produce is directly proportional to body weight up to 500 kg (Hussain, 1981). An effort of 10% of the animals' bodyweight is frequently given (Rivière, 1978; Howard, 1980). However, other sources show more variation: 18 - 22% of body weight for animals of 200 to 275 kg (Sarker, 1981); 10 - 13% of body weight for cows of 400 to 600 kg (Howard, 1980); 9 - 12% of body weight for bullocks of 500 to 900 kg (Howard, 1980). An increace in tractive effort reduces the speed of the animals (Goe, 1983).

The power developed by the animals is the result of the tractive effort and the walking rate. According to Singh and Chancellor (1975), small bullocks develop 224 watts (W) and large buffaloes 746 W, while most bullocks develop between 373 and 522 W. Information for cattle in Bangladesh gives 128 W for bullocks and 124 W for cows (Hussain, 1981).

The power necessary to pull the plough varies between 256 and 336 W for traditional ploughs and between 240 and 331 W for improved ploughs (Sarker and Farouk, 1982). Two animals would thus be necessary to deliver the power, resulting in less power developed per animal, since animals hitched as a team incur a loss of energetic efficiency (Goe, 1983).

The nutrient requirements of draught animals vary according to age, sex, breed, species, tractive effort and duration of work. The tractive effort depends on species and rate and type of work. Age, sex and breed are known variables of the animal. Estimates have to be made of the tractive efforts of the different animal categories and the duration of work.

Feed requirements given in the different references are calculated according to different principles. Rivière (1978) and FAO (1972) make a distinction between light, medium and sustained work. For these types of work, the animals need a surplus of 0.5, 1 and 1.5 times maintenance needs above maintenance requirements. However, no definition is given of light, medium and sustained work. Hrabovszky (1983) states that working animals need 30% feed above maintenace.

ARC (1980) and Mathers (1980) estimate the energy needed for walking at 2 Joules (J)/meter walked per kg liveweight. Mathers (1980) defined the energy requirements for pulling a plough at 33 J/kg pulled per meter for Brahman cattle, and at 26 J/kg pulled per meter for buffaloes.

The literature gives conflicting information for the protein requirements of draught animals. Most sources suggest that no excess protein is needed provided the maintenance requirements are met (Smith, 1980; Rivière, 1978; Goe, 1983). Other references suggest an additional 13.6 g digestible crude protein per hour worked (Smith, 1981), or 250 g digestible crude protein daily for maintenance and traction for a 300 kg working bullock (FAO, 1972).

The following assumptions are incorporated in the model. The model calculates the required metabolisable energy for draught work, depending on the force delivered by the animals its walking speed, the working time, a factor for soil characteristics, plough characteristics, and an efficiency factor for traction.

Fixed parameters in the model are:

1. Tractive efforts produced by cattle:
   - 12% of body weight for males
   - 9% of body weight for females
2. Maximum time animals are used for traction:
   - 5 hours per day for males
   - 4 hours per day for non-pregnant, non-lactating cows
   - 2 hours per day for lactating cows
3. Walking speed: 3 km/hour

4. Time needed to plough 1 hectare: 22 hours
5. Efficiency factor for traction: 0.30.

Variation is brought into the model via:

1. The number of hectares that have to be ploughed seasonally;
2. The number and category of animals (bulls, lactating cows or dry cows) that can be used for work;
3. A soil- and plough-specific parameter; and
4. Choice between single or team work.

In the model, preference is given to male animals to do the work. Only in case of shortage of tractive power, dry cows are used, and ultimately lactating cows. If these categories are not able to execute the work, it is assumed that farmers hire animals. No feed requirements are included for hired animals.

Because it is assumed that no supplementary protein above maintenance is required for draught work, maximum feed intake calculations do not take into account a possible increased intake due to draught work. This is in accordance with the calculation procedure of Ketelaars (1984), which needs a protein to energy ratio of the product.

Growth: In the model of Kahn (1982), weight gain and weight loss are the result of a positive or negative balance between energy intake and energy expenditure. Kahn uses two equations for the translation of the energy balance into a weight change:

- the efficiency of conversion of metabolisable energy into net energy for body tissue or the reverse, and
- the energy content of 1 kg liveweight gain.

The equations used are modified ARC (1980) equations.

Because of the feed intake calculation method used, energy and protein requirements for body-weight gain or loss are needed in the SOWTV model. These are calculated from data in ARC (1980), which give the protein and fat content per kg body-weight gain for animals of 50 - 500 kg. These protein and fat contents have been modified, according to breed (small - large), sex (female - male) and daily gain. Because 1 kg of protein contains 23.6 MJ NE, and 1 kg of fat 39.3 MJ NE, the energy content of 1 kg liveweight gain can be calculated.

Using linear regression, a straight line is derived, giving the composition of the liveweight gain, at any given liveweight, for small breeds with a mean daily growth rate of about 50 g:

- For female animals, BODYCF (g N/MJ NE) = 2.84 - 0.01 * LWT (kg); and
- For male animals, BODYCM (g N/MJ NE) = 4.68 - 0.01 * LWT (kg)

where BODYCF is the composition of 1 kg liveweight gain of a female;
BODYCM is the composition of 1 kg liveweight gain of a male; and
LWT is liveweight

These equations define the slope of the maximum energy intake as a function of the nitrogen intake.

Pregnancy: To calculate energy requirements for pregnancy, Kahn (1982) uses the ARC (1980) equations, modified for birth weight and for the difference between actual and simulated gestation period. A correction factor is also introduced to minimise errors due to large time-steps. The requirements depend on the number of days of pregnancy.

In the SOWTV model, energy and protein requirements are derived from data given by ARC (1980). The protein and fat content per kg liveweight gain due to pregnancy is calculated from the composition of the body weight of a new-born calf, the deposition of nutrients in the foetus at full term, the time course of nutrient deposition in the foetus and the gravid uterus during pregnancy and the weight of the foetus and the gravid uterus. The protein and fat content allow calculation of the energy and nitrogen content of 1 kg of liveweight gain, and also the ratio of nitrogen to energy during pregnancy (Table 6). The ratio of nitrogen to energy determines the slope of the maximum energy intake line as a function of the nitrogen intake (Ketelaars, 1983; 1984).

Table 6. Composition of the foetus and gravid uterus during different stages of pregnancy.

	Days from conception					
	141	169	197	225	253	281
Weight of foetus + gravid uterus (kg)	5.50	8.88	13.36	19.33	26.97	36.40
Protein content (kg/kg gain)	0.051	0.059	0.072	0.087	0.107	0.124
Fat content (kg/kg gain)	0.007	0.007	0.009	0.012	0.016	0.021
Energy (MJ NE/kg gain)	1.479	1.668	2.289	2.525	3.154	3.752
Nitrogen (kg/kg gain)	0.008	0.009	0.012	0.014	0.017	0.020
g N/MJ NE	5.41	5.4	5.24	5.54	5.39	5.33

Lactation: According to ARC (1980), the energy required for lactation equals the energy content of the milk yield, divided by a conversion efficiency coefficient. The lactation potential, defined by Kahn (1982) is a function of the genetically defined maximum potential daily milk yield, the number of days to peak yield, the lactation stage and the age of the animal. The potential for mobilising body tissue to meet lactation requirements in case of energy deficit is also included.

Kahn's calculation of the lactation potential and tissue mobilisation is adopted in our model. These subjects still need further verification. Energy and protein requirements for lactation are defined in a similar way to

requirements for pregnancy and growth. Milk composition, in terms of protein and energy value, tends to be constant for a given breed (Ketelaars, 1984). From the fat content of the milk the energy content can be deduced through the formula of Tyrell and Reid, given by ARC (1980): E (kJ/kg) = 40.6 * F (g/kg) + 1509.0. Finally, the nitrogen/energy ratio can be calculated and this ratio is again used to define the slope of the line giving the maximum energy intake as a function of the nitrogen intake.

Production

To estimate an animal's production - traction delivered, milk, growth and offspring - a comparison is made between its intake and its requirements as specified in terms of nitrogen and energy. Although the ultimate intention is to define production as a function of the limiting factor - either energy or nitrogen - until now only energy availability is used to determine production.

Priorities for the various production alternatives as defined by Kahn (1982) have been retained in this model. This implies that maintenance requirements have to be met before draught-work requirements and they in turn have to be met before growth requirements are considered. In addition, pregnancy and lactation requirements have priority over growth requirements. If an animal is pregnant and lactating, pregnancy requirements are considered more important.

Herd Dynamics

The dynamics of a herd are basically determined by its mortality rate and its reproduction rate. Consequently, expulsion (culling or sale) or purchase can be practiced to restore the balance in the herd size.

Kahn's model (1982), as well as the TAMU model (Sanders and Cartwright, 1979a; 1979b), deal with herd dynamics. In these models the effects of nutrition on reproduction and mortality are defined separately fro; the effects of other environmental and internal factors.

The reproduction equations in Kahn's model (1982) are based on results of Wiltbank et al (1962; 1964) and Dunn et al (1969), who investigated the

effects of pre- and post-partum energy intake on reproductive performance of different breeds of different ages. The equations calculate:

- the probability of oestrus in previously non-cycling females
  $PEST = 0.85 * CFT * CFW * CFDW * CFM * CFL * CFA;$
- the probability of continuous cycling in previously cycling females which had not conceived
  $CCYC = CFW^{0.1} * CFDW^{0.1} * CFA^{0.5}$; and
- the probability of conception following oestrus
  $PCON = 0.75 * CFT^{0.75} * CFW^{0.2} * CFDW^{0.3} * CFA^{0.5}$

where CFT is a correction factor for time since calving, CFW a correction factor for body condition, CFDW for daily weight loss, CFM for immaturity, CFL for lactation stage and CFA for age.

Two of the equations were again validated using results of Wiltbank et al (1962; 1964) and Dunn et al (1969) and one was validated with the results of Kahn and Lehrer (1984).

No evidence is found in the literature to substantiate these equations. Wiltbank et al (1962; 1964) and Dunn et al (1969) used Hereford and Angus and Hereford cattle, respectively, of different ages and found indications that energy intake before calving determines the onset of oestrus following calving: a low energy intake causes a delay in the onset of oestrus. Holness et al (1980) also found a significant effect of the level of nutrition on the duration of post-partum anoestrus for Afrikaner and Mashona cattle. In the latter case the animals were fed from early pregnancy to mid-breeding season on either a high or low level of nutrition, and it could not be confirmed whether just the feeding level before parturition was important. Some authors mention breed differences under given experimental conditions (Dunn et al, 1969; Holness et al, 1980). However, comparison of the results of various authors for one breed shows that considerable differences also exist within a breed (Table 7).

Table 7. Days from calving to first oestrus.

Breeds	Days (mean±S.E.)	Source
Afrikaner	102.2 ± 6.2	Holness et al (1980)
Mashona	69.7 ± 6.8	Holness et al (1980)
Friesian	63.8	Donkin (1980)
Hereford	70.8 ±11.7	Wiltbank et al (1964)
Hereford	51.7 ± 8.2	Wiltbank et al (1962)
Experimental conditions		
Hereford		
low nutrition before calving, high post partum	65	Wiltbank et al (1962)
post partum	49	Wiltbank et al (1964)
Mashona & Afrikaner		
high nutrition	77.6 ± 5.4	Holness et al (1980)
low nutrition	98.4 ± 6.8	Holness et al (1980)

According to Wiltbank et al (1962; 1964) and Dunn et al (1969), the post-partum level of energy intake influences the conception rate, i.e. a low energy intake results in a low conception rate. The authors are not sure whether this response is a result of energy intake per se or of body condition. Holness et al (1980) conclude that the level of nutrition does have a significant effect on calving rate and thus on conception rate, but it must be noted that the feeding level in their experiments did not differ before and

after calving. They also deduced from their data that total conception rate increased with increasing post-partum body-mass, indicating that the ability to conceive is a function of body weight. Richardson et al (1975) came to the same conclusion in their experiments with Nkone and Afrikaner cattle. Ward (1968) observed the existence of a critical weight for Mashona cattle below which conception did not take place. Again, there were breed differences in conception rate and subsequent calving rate under given environmental conditions (Table 8).

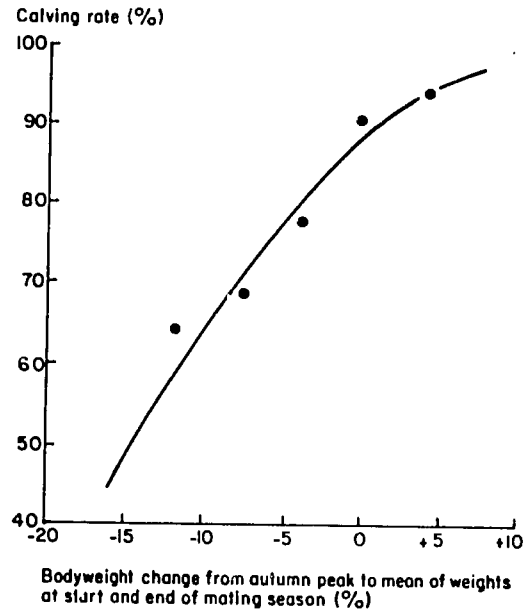
Table 8. Mean calving rate of different breeds under different environmental conditions.

Breed	Calving rate (%)	Source
Afrikaner & Mashona	89	Holness et al (1980)
Nkone & Afrikaner	94	Richardson et al (1975)
Afrikaner & Mashona	44	Holness et al (1980)
Nkone & Afrikaner	78	Richardson et al (1975)
Nkone & Afrikaner	69	Richardson et al (1975)

There is conflicting evidence about the effect of weight changes prior to the breeding season on fertility. Richardson et al (1975) found a relationship between body-weight change and fertility as measured by calving rate (Figure 2), and suggest that this effect may be explained by the effect of a critical weight. Some cows may have been so heavy relative to the critical weight that they could suffer severe weight losses and still be above the critical weight during the mating season, while other cows of a very low weight would be below the critical weight for conception even without any additional losses.

Although we do not deny that the various factors discussed above influence fertility, insufficient data are available about the additional effects of the various factors to allow their quantification. Therefore it was

Figure 2. Relationship between bodyweight change from autumn peak to mid-mating and subsequent calving rate



decided to simplify the fertility module of Kahn (1982). In a first approximation a minimum value is introduced for age, post-partum interval and weight at which conception can occur. At the same time the probability of conception is estimated from the literature, and this determines the calving rate.

These simplifications restrict the applicability of the model. The Kahn (1982) model investigates the effects of the feed situation on the reproduction rate of the herd via animal characteristics. The SOWTV model can not do this, because, in this model, reproduction is independent of animal characteristics, except for those mentioned above.

The mortality module suffers from problems similar to those of the reproduction module. In the model of Kahn (1982), mortality is described by a basic mortality rate, modified by a factor for weight index, an age factor, a post-partum interval factor and a seasonality factor. It is even more difficult to validate the separate effects for mortality because 'experiments generally are not designed to elucidate mortality thresholds' (Kahn, 1982).

De Vaccaro (1974) states that mortality is influenced by breed, season of birth, birth weight and management practices. The data presented in her article represent the combined effect of the various factors. In an experiment with Brahman Shorthorn crossbred heifers, Taylor et al (1982) found that feed supplementation significantly reduced death rate. It appeared impossible to deduce the influence of individual factors from these data.

Because quantification of the individual factors influencing mortality was not possible, a simplified description was introduced. In the model mortality rates are related to age and only a minimum critical value for weight is introduced to eliminate very thin and weak animals.

Figure 3 and Table 9 show the evolution in herd size resulting from the simplified calculation method. Variation in the conception rate causes small differences in animal numbers. A 5% lower or higher conception rate increases or reduces the time necessary to double the herd number by one year (from 9 to 10 years, and from 9 to 8 years respectively). A variation in mortality rate causes considerable variation in herd size. The doubling time of the herd size increases by more than 200% when mortality rate increase by 5%. This means that mortality data are crucial in animal production models since they influence the ultimate model output decisively, i.e. other animal characteristics and even feed characteristics become of minor importance. The same conclusion holds for the age at first calving.

Figure 3. Evolution of the herd size under different experimental conditions

(Treatment details given in Table 9)

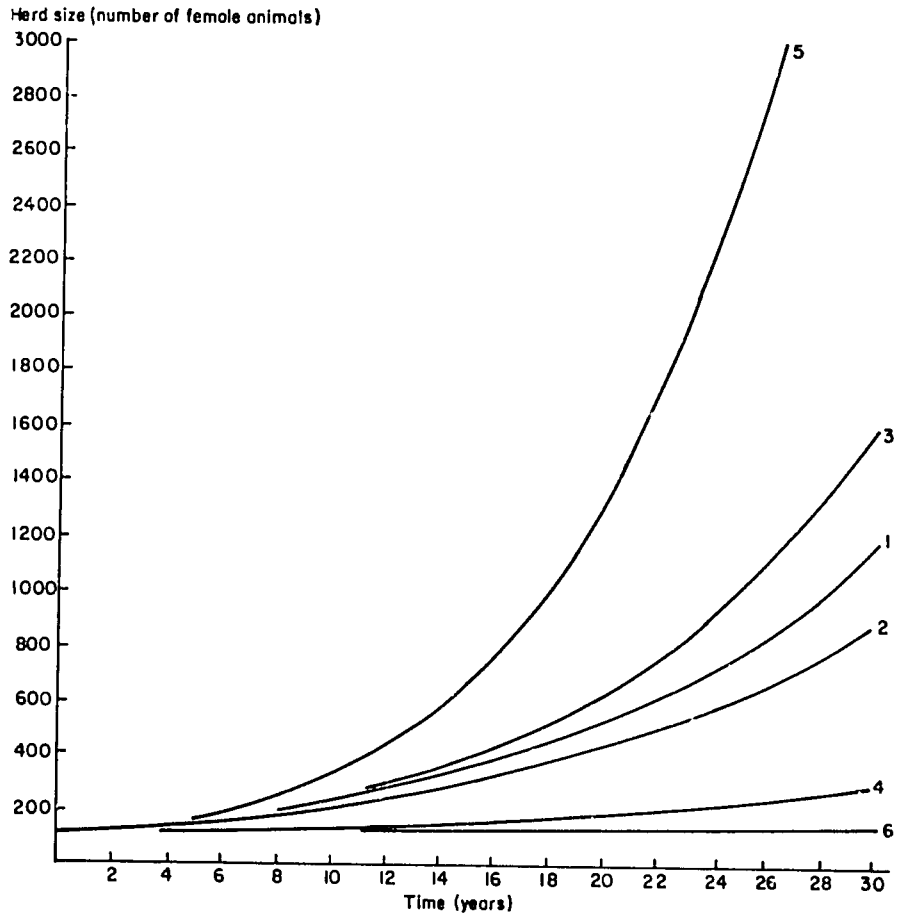


Table 9. Annual herd growth (%) and doubling time (years) as affected by different fertility (PPREG) and mortality (PMORT) rates and age at first calving.

	PPREG (%)	PMORT (%)	Age at first calving (yr)	Doubling time (yr)	Herd growth (%/yr)
SOWTV	72	standard[1]	≥3	9	8.5
Low reprod.	67	standard	≥3	10	7.4
High reprod.	77	standard	≥3	8	9.6
High mortality	72	+ 5%	≥3	12	3.4
Low mortality	72	- 5%	≥3	6	13.7

[1] Standard mortality rates.

Age (yr)	0	1	2	3	4	5	6	7	8	9	10	11	12
PMORT	14.4	7	7	7	5	5	5	10	10	20	33	49	90

In Table 10 the annual herd growth (%) and the doubling time (years) are given for ages at first calving varying between 2 and 5 years old. The annual herd growth varies between 3.3 and 12.3%, and the doubling time varies between 7 and 22 years.

Management

Farmers' decisions on feeding, breeding and management practices influence livestock production. In the SOWTV model, feeding practices are explicitly described in the feed allocation module. Breeding practices are partly included in the herd dynamics module.

Table 10. Annual herd growth (%) and doubling time (years) of a herd for various ages at first calving.

PPREG (%)	PMORT (%)	Age at first calving (yr)	Doubling time (yr)	Herd growth (%/yr)
72	standard[1]	≥3	9	8.5
72	standard	≥2	7	12.3
72	standard	≥4	12	5.7
72	standard	≥5	22	3.3

[1] Standard mortality rates

Age (yr)	0	1	2	3	4	5	6	7	8	9	10	11	12
PMORT	14.4	7	7	7	5	5	5	10	10	20	33	49	90

In a separate management module, decisions with respect to weaning, culling and buying of animals and the period during which lactating animals are hand-milked can be imposed. In the SOWIV model, weaning takes place according to two criteria, adopted from Kahn (1982): the age and/or the weight of the calf. Culling and buying decisions differ for different countries, regions or populations. Social factors (e.g. wedding, status of the farmer), religious factors (e.g. an Islamic holiday, such as Eid El Adha, on which people are obliged to sacrifice an animal) and economic factors (income) influence culling and buying practices. For every modelling effort, culling and buying practices have to be studied, quantified and introduced in the model.

A final option included in the SOWIV management module is the farmer's decision to stop milking a cow if a specified lactation period is exceeded, if milk production is less than a specified level, or if pregnancy is advanced beyond a specified period.

Conclusion

The model generates data on the animal's feed intake, requirements, actual production, reproduction and mortality events and herd composition. These calculations require input data on feed characteristics (type, amount and quality of the feed) and animal characteristics (genetic potential for growth and milk production of the breed, traction characteristics).

One of the future steps in the SOWIV livestock modelling research will comprise a sensitivity analysis of the model for the various parameters and estimates used. There is considerable quantitative variation documented in the literature for some of the parameters used, while no criteria are available with which to judge the accuracy of the chosen value. In this respect, the influence of the estimated mortality rates and the age at first calving on herd composition and herd number has already been mentioned. Other parameters that may be considered are the nitrogen/energy ratio of the various animal products, the estimates of maintenance requirements, the values for weaning age, stopping of hand milking, walking rate and tractive effort of the animals, etc. The results of such a sensitivity analysis are essential for correct interpretation of the model output. Another topic in the development of the SOWIV model is the validation of the different modules of the model, and the validation of the model as a whole. This requires a detailed set of input and output data for the different modules as well as for the entire model. Quite often it is difficult to get access to these data. Presently an attempt is being made to validate the intake and production module of the model with data from Bangladesh. These data comprise daily records on the animal's ration, its milk production, traction produced and reproductive status, and weekly information on the animal's growth. The first results of this validation will be discussed at the workshop.

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References

ARC (Agricultural Research Council). 1980. The nutrient requirements of ruminant livestock. HMSO, London. 351 pp.

CWFS (Centre for World Food Studies). 1984. A science approach to present-day hunger and food policies. Internal publication.

Conrad H R, Pratt A D and Hibbs J W. 1974. Regulation of feed intake in dairy cows. I. Change in the importance of physical and physiological factors with increasing digestibility. J. Dairy Sci. 47: 54-162.

Crotty R. 1980. Cattle, economics and development. Commonwealth Agricultural Bureaux, Farnham Royal, London. 253 pp.

Dolberg F. 1983. An analytical framework for livestock strategy in Bangladesh. In: Preston et al. eds. Maximum livestock production from minimum land. Proceedings of the fourth seminar held in Bangladesh, May 2-5, 1983. Bangladesh Agr. Univ., Mymensingh.

Donkin E F. 1980. Reproductive activity in dairy cows post-partum 2. Ovarian and sexual activity. Zimbabwe J. Agric. Res. 18: 71-80.

Dunn T G, Ingalis J E, Zimmerman D R and Wiltbank J N. 1969. Reproductive performance of 2-year-old Hereford and Angus heifers as influenced by pre- and post-calving energy intake. J. Anim. Sci. 29:719-726.

FAO (Food and Agriculture Organization). 1972. The employment of draught animals in agriculture. FAO, Rome. 249 pp.

FAO (Food and Agriculture Organization). 1983. 1982 FAO production yearbook. Volume 36. FAO statistics series no. 37. 320 pp.

Gill G J. 1981. Choice of cultivation technique in Bangladesh. In: Jackson et al. eds. Maximum livestock production from minimum land. Proceedings of a seminar held in Bangladesh, 2-5 Feb 1981. Bangladesh Agr. Univ., Mymensing: pp. 311-341.

Goe M R. 1983. Current status of research on animal traction. World Anim. Rev. 45: 2-17.

Groenewold H H. 1983. Some observations on livestock in Asia. FAO - World Bank Cooperative Programme Investment Centre, Rome.

Hermans C. 1984. Pattern of seasonality in livestock production and cattle rations. Unpublished.

Holness D H, Hale D H and Hopley J D H. 1980. Ovarian activity and conception during the post-partum period in Afrikaner and Mashona cows. Zimbabwe J. Agric. Res. 18: 3-11.

Howard C R. 1980. The draft ox - Management and uses. Zimbabwe Rhodesia Agric. J. 77: 19-34.

Hrabovszky J P. 1983. Feeding of draught animals. World Anim. Rev. 46: 47-48.

Hussain A A M. 1981. Draught power requirements in Bangladesh. In: Jackson et al. eds. Maximum livestock production from minimum land. Proceedings of a seminar held in Bangladesh, 2-5 Feb 1981. Bangladesh Agr. Univ., Mymensingh: pp. 342-347.

Jabbar M A. 1983. Effect of draught use of cows on fertility, milk production and consumption. Extract of a report 'The status and potential of livestock within the context of agricultural development policy in Bangladesh' by Jabbar M A and Green D A G., Department of Agricultural Economics, The University College of Wales, Aberystwyth.

Kahn, Hava E. 1982. The development of a simulation model and its use in the evaluation of cattle production systems. Ph.D. thesis, Univ. of Reading.

Ketelaars J J M H. 1983. Evaluating rangeland as feed resource for livestock production. In: W Siderius, ed. Proceedings of a Workshop on Land Evaluation for Extensive Grazing. ILRI publication 36: 165-181.

Ketelaars J J M H. 1984. Patterns of nitrogen and energy intake and their relation to the control of voluntary feed consumption in ruminants and monogastric animals. CABO internal publication.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: an integer and stochastic model for evaluating production alternatives. ILCA Research Report No. 2. 95 pp.

Lawrence P R. 1984. The energy cost of pulling loads. Draught Animal News No. 1. CTVM, Univ. of Edinburgh.

Levine J M and Hohenboken W. 1981. Simulation of beef cattle production systems in the Llanos of Colombia - Part 2. Results of the modelling. Agric. Systems 7:83-93.

Levine J M, Hohenboken W and Nelson A G. 1981. Simulation of beef cattle production systems in the Ilanos of Colombia - Part 1. Methodology: an alternative technology for the tropics. Agric. Systems 7:37-48.

Mathers J C. 1980. Work output and nutrient needs of draught animals. Paper presented at the first conference on 'Recent developments in animal nutrition and their application to tropical countries.' Centre for Industrial Consultancy and Liaison, Edinburgh.

Nourrissat P. 1965. Draft cattle in Senegal. Abstract in The role of animals in draught and transport. Commonwealth Agricultural Bureaux, UK.

Orskov E R. 1981. Nutritional evaluation of poor quality roughage. In: Jackson et al. eds. Maximum livestock production from minimum land. Proceedings of a seminar held in Bangladesh, 2-5 Feb 1981. Bangladesh Agr. Univ., Mymensingh: pp. 263-270.

Preston, R.L. 1972. Cited by L.D. Satter and R.E. Roffler, 1981. In: W Haresign, and D J A Cole eds. Recent developments in ruminant nutrition. Butterworths, London.

Rivière R. 1978. Manuels et précis d'elevage. 9. Manuel d'alimentation des ruminants domestiques en milieu tropical. Institut d'élevage et de médecine vétérinaire des pays tropicaux, Ministère de la cooperation, Paris, France.

Richardson F D, Oliver J and Clarke G P Y. 1975. Analyses of some factors which affect the productivity of beef cows and of their calves in a marginal rainfall area of Rhodesia. 1. Factors affecting calving rate. Anim. Prod. 21: 41-49.

Rufener W H. 1971. Cattle and water buffalo production in villages of northeast Thailand. Ph.D. thesis. Urbana, Illinois. 201 pp.

Sanders J O and Cartwright T C. 1979a. A general cattle production systems model. I: Structure of the model. Agric. Systems 4: 217-227.

Sanders J O and Cartwright T C. 1979b. A general cattle production systems model. II: Procedures used for simulating animal performance. Agric. Systems 4: 289-309.

Sarker R I. 1981. Improved utilisation of animal draught power in Bangladesh. In: Jackson et al. eds. Maximum livestock production from minimum land. Proceedings of a seminar held in Bangladesh, 2-5 Feb 1981. Bangladesh Agr. Univ., Mymensingh: pp. 70-78.

Sarker R I and Farouk S M. 1982. Animal-drawn mouldboard ploughs: an improvement over the existing ones. In: Preston et al. eds. Maximum livestock production from minimum land. Proceedings of the third seminar held in Bangladesh, 13-18 February 1982. Bangladesh Agr. Univ., Mymensingh.

Siebert B D and Hunter R A. 1977. Prediction of herbage intake and live-weight gain of cattle grazing tropical pastures from the composition of the diet. Agric. Systems 2: 199-208.

Singh G and Chancellor W. 1975. Energy inputs and agricultural production under various regimes of mechanisation in northern India. Transact. ASAE 18: 252-259.

Smith A J. 1980. The role of draught animals in agricultural systems in developing countries. In: Vegetables for feeding r live-stock. Institute of Biology, London.

Smith A J. 1981. Draught animal research - A neglected subject. rld Anim. Rev. 40: 43-48.

Starkey P H. 1982. N'dama cattle as draught animals in Sierra Leone. World Anim. Rev. 42: 19-26.

Taylor W J, Holroyd R G and Rebgetz J G. 1982. Influences of nitrogen based supplements on live-weight, fertility and mortality of heifers grazing dry season native pasture. Proc. Aust. Soc. Anim. Prod. 14: 277-280.

de Vaccaro L P. 1974. Some aspects of the performance of European pure-bred and crossbred dairy cattle in the tropics. Part 2. Mortality and culling rates. Anim. Breeding Abstr. 42: 93-103.

Wallach D, Elsen J M and Charpenteau J L. 1984. Maintenance energy requirements of grazing sheep: A detailed comparison between models. Agric. Systems 15: 1-22.

Ward H K. 1968. Supplementation of beef cows grazing on veld. Rhodesian J. Agric. Res. 6: 93-101.

Wiltbank J N, Rowden W W, Ingalis J E, Gregory K E and Koch R M. 1962. Effect of energy level on reproductive phenomena of mature Hereford cows. J. Anim. Sci. 21: 219-225.

Wiltbank J N, Rowden W W, Ingalis J E and Zimmerman D R. 1964. Influence of post-partum energy level on reproductive performance of Hereford cows restricted in energy intake prior to calving. J. Anim. Sci. 23: 1049-1053.

Discussion

Question - Are you assuming that food supplies will increase proportionally to maintain the herd?

Answer - We assume that the animal gets the same amount of feed every day, so the feed supply is unlimited. But the number of animals in the region is determined by the available feed resources as determined by a regional planning model.

Question - You said that the probability equations for fertility and mortality are not sufficiently scientifically-based and are not applicable to your situation. Did you try to run your model and compare the results with actual data? I feel that you probably would get a more representative picture of the situation if you did take into consideration the effects of weight changes and condition on reproduction and mortality.

Answer - I don't think so. We tried to quantify the information that was available and we found that it was not possible. For instance, regarding mortality rate, everybody agrees that weaker animals are more likely to die than stronger animals, but how do you quantify this? In certain experiments you find a mortality or reproduction rate for a particular animal or breed and a particular feeding system. But when we used the same equation or the same quantification for another set of data or another set of experiments in the literature, there was no consensus at all, except that the absolute weight is more important than weight change. So we have a fixed critical weight index that determines performance, but it is not related to weight change or condition.

Question - Do you use the same level of production throughout the year?

Answer - The production level does not change with the season but if we use the model for another situation or another region, we try to find experimental results in the literature for that particular situation. If there are no new data we can run the model with the available information but also with other mortality or reproduction rates to make it clear that the results are just estimates and that they are closely related to the input data.

Question - What is the range in liveweight change within one year in mature cows?

Answer - In Bangladesh the weight change is about 20-25 kg, but the maximum weight of the animals is not more than 150 kilos.

Question - So, the animals may be within the range of liveweights at which neither reproduction nor mortality are affected?

Answer - I do not know. We have not been able to find a relation or an influence, but there may be one.

Question - Do you fix the reproduction and mortality rates in advance, independently of the feeding situation?

Answer - When dealing with a different feeding situation, we put a higher or a lower reproduction rate into the model, instead of the model producing that figure.

Question.- But then are you not defeating the whole purpose of the model? Must not the model tell you which parametres are going to change if you change the feeding system?

Answer - We cannot investigate that with the model as it is constructed now. That is one of the limitations of the model, but we prefer not to say something, rather than say something about that which we do not know.

Question - So you only model growth and milk production?

Answer - We also model the herd dynamics.

Statement - But herd dynamics is a result of those fixed variables. So you have got two separate models, a feed model and a herd dynamics model, and you use them side by side.

Reply - If you mean that the two of them do not interact, you are right. The two fit together in one model and we run them together.

Question - Is the main purpose of the model to get an estimate of herd increase when there are no limitations to feed production? If so, how will you use the information that you generate?

Answer - The reason that we included herd dynamics in the model is that we then have an idea of how many animals a farmer can sell, how many he can buy. In Bangladesh animal traction is important. A farmer needs two male animals. We can look up the herd dynamics file, and see how many male animals we have at any moment. If we have too few, we have to buy, or if there are too many, we can sell. We just try to imitate the situation on the farm and adjust the herd size of the farmer. The model is not meant to be used to study effects of management interventions.

The model must be able to provide activity tables for the economists of CWFS in Amsterdam. The ultimate goal of the model is to get predictions on management and farming practices, but until now these possibilities are very limited.

Question - If the main purpose is to get activity tables for the economic model, would it not be better to get them directly from the farm statistics in Bangladesh?

Answer - This model is able to generate input/output data for livestock systems, which are used in regional LP programmes by CWFS.

If an animal is meant to grow by 1 kilogram a day, or if it is being used for traction for two hours a day, you need a set of inputs, including feed resources. Another set of activity tables is generated for cropping activities, such as for growing rice, maize, wheat. Those also go into a linear programming model, together with the regional resources. This generates a feasible development pattern over a number of years. The link between cropping and animal husbandry is in the linear programming model which is used to calculate the amount of rice, maize etc. that is grown each year. This determines the amount of crop byproducts produced which influences the number of animals that can be kept, and whether the herd can be allowed to increase.

By linking up with other interest groups, the model has assumed a multipurpose function, not only generating data for this linear programming model, but also analysing effects of management changes on a typical farm. I do not know whether this is the optimum way of developing and using such a model.

Comment - It probably would be if there was more certainty about the parameters that have been discussed here today. Most of the discussion seems to add more uncertainty to the parameter values, so that one wonders how much precision one can get with that sort of model.

Reply - I agree completely. When we use these herd or animal production models, some of the parameters are so critical that the results have to be checked in the region itself.

Comment - Mr J. Gartner of FAO is doing this sort of work in the Agriculture Towards 2,000 project, but uses a much simpler estimate of food requirements. It starts with an estimate of the future demand for animal products and then determines the prospects for the necessary increase in animal population.

Reply - We are cooperating with FAO in crop production modelling and on the problems of animal husbandry in Thailand. All the statistics on crops, crop residues and pastures indicate that it is impossible to feed the animals that are reported to be there. So, we do not know what they are living on or whether they are there at all. That is a common problem with rural statistics.

Appraisal of the ILCA cattle herd dynamics model using data from pastoral systems in Mali and Kenya

K.T. Wagenaar and E. Kontrohr

Introduction

ILCA's initial modelling efforts were based on the use of existing models. The beef cattle production model of Texas A&M University (TAMU) was applied to commercial ranching and traditional cattle systems in Botswana by ILCA, TAMU and the Animal Production Research Unit (ILCA/APRU, 1978).

This work highlighted the need for a model with stochastic feature, particularly for the primary production component. An operational model was developed in which animals in the simulated herd are treated as individuals (Konandreas and Anderson, 1982) and was applied in Botswana (Konandreas et al, 1983). A users' guide to the model is in press.

Recent analysis of data from long-term animal productivity studies in Mali and Kenya provided new material for further appraisal of the ILCA model, particularly with respect to the representations of biological processes. When this data was used, the predicted patterns of productivity were significantly different from those actually observed. This prompted a closer examination of the steps by which the model operated, the basic system parameters that are provided as data and the algorithms that are used to predict animal productivity.

This paper reports on the problems encountered during the appraisal and changes to some of the subroutines of the model are proposed that should improve the simulation of the performance of range cattle ine extensive pastoral production systems.

The forage intake subroutine

Like the TAMU model, the ILCA model simulates the response of beef cattle to specific primary production conditions. The model deals only with the animal; the primary production system is not modelled. Thus, plant production is

exogenous to the model and there is no feedback of the effects of its exploitation on primary production systems.

This limitation, which has been the subject of vigorous debate in Agricultural Systems (Whelan et al, 1984 versus Cartwright and Doren, 1984), is legitimate but restricts the use of the model.

Animal productivity is simulated for individual animals on the basis of forage intake, which is calculated from the following equation derived from the work of Conrad et al (196.):

$$I = f(p).W^{0.73}/(1-d)$$

where I = forage intake (kg/day)

W = liveweight (kg)

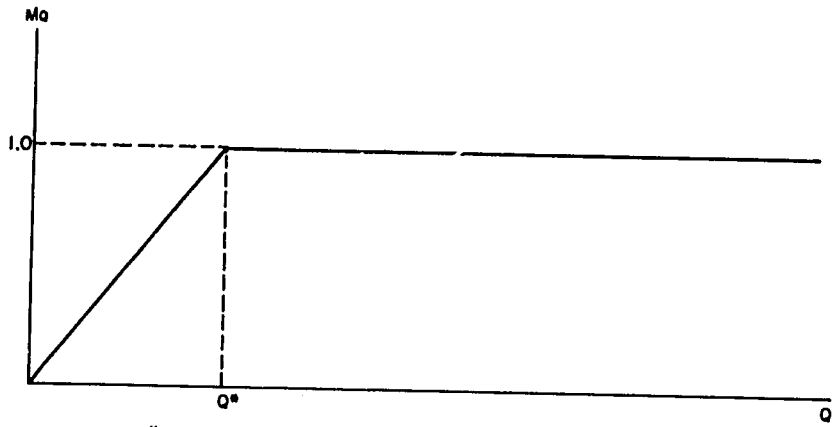
d = digestibility of forage consumed (fraction)

f(p) = the rate of passage through the digestive tract (kg/kg metabolic weight/day) which is, in general, a function of the animal's physiological status.

The animal's age, weight and physiological status are used to determine the use of the energy supplied by the feed, plus energy from catabolism of body tissues if necessary.

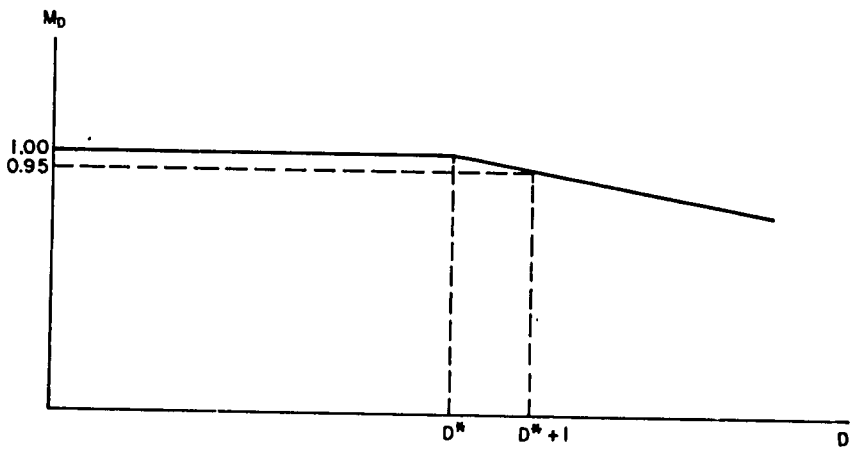
Statistical descriptions of the quantity (t/ha) and quality (digestibility and crude protein) of the forage on offer, based on field observations, plus the distance walked (km/day), which is used to check whether there is a limitation on grazing time, are the driving forces of the model. They are each vectors with 12 values, corresponding to the months of the year, and are provided to the model as data. There is a discrepancy between the input of digestibility of feed on offer and its use in the model as if it were digestible feed consumed. In a draft paper, Konandreas (unpublished) tried to develop a simple model of the grazing selectivity of animals with emphasis on transhumant cattle in Mali. In this he subdivided the available biomass into quality classes. In the original TAMU model the digestibility of the forage consumed was required as input data (Sanders and Cartwright, 1979). The forage subroutine of the ILCA model requires threshhold values for DM availability per hectare and distance walked, below which intake is reduced. These are used to quantify two multipliers, M_Q and M_D (Figures 1 and 2).

Figure I. Multiplicative effect (Mq) of quantity of acceptable[1] forage on offer (q) on voluntary intake



1. The word "acceptable" is used in the description of the model and suggests a quality criterion which is, however, not considered in the Mq-calculation

Figure 2. Multiplicative effect (M_D) of daily distance walked (D) on voluntary intake



These multipliers adjust the ad libitum intake of the individual animal if the threshholds are passed. Other multipliers adjust the voluntary intake of the animals:

m(d,t) corrects for digestibility of the fodder above 65% and below 40%;
m(t) corrects for the age of the animal, less than 2 months and more than 8 years old;
m(x,t) corrects for the greater appetite of young males; and
m(p,t) corrects for the physiological status of an animal (pregnant, lactating, etc.).

Thus, equation 1.1 can be restated as:

$$I = a.Wt^{0.73}.m(d,t).M_Q,M_D,m(t).m(x,t).m(p,t)/(1-d) \qquad (1.2)$$

where a is the intake coefficient for the reference class of animals (7-year-old dry female, less than 7-months pregnant) and equals the rate of passage through the digestive tract.

In any production system there is a calendar month (in the most probable year type) during which the liveweight of the reference class of animals is in equilibrium, i.e. the animals are neither gaining nor losing weight. This implies that during this month the daily dry-matter intake is just sufficient to maintain the body weight of the reference animal at the level of activity for that month. The a factor is calculated from equation 1.2 at this equilibrium, for which the reference month(s) has to be specified. An adjustment is made when the reference digestibility of the feed falls outside the range of 40-65%. The a factor is also corrected for sex, age and physiological status for each category of animal.

Two major problems were encountered when the model was applied to transhumant cattle in Mali. Firstly, stocking rate is not taken into account in the model. Whether the quantity of forage available per hectare is grazed by one animal or 200 is not considered[1], because there is no feedback between secondary and primary production processes in the model.

[1]Under controlled (fenced) conditions the stocking rate can be simulated by a smaller or larger decrease in DM availability from one month to the next.

As explained, the intake of the individual animal is adjusted if the availability of good-quality fodder drops below a certain quantity per hectare (M_Q in equation 1.2). In the model, the quantity of fodder on offer is neglected in the calculation of the intake of the animal as long as the threshhold is met ($M_Q = 1$). This means that, via the a factor, digestibility is the sole determinant of forage intake.

In Mali feed digestibility during the dry season was high, due to regrowth of forage after burning and the stepwise accessibility of the bourgoutieres[1]. As a result the model predicted that the normal growth of the animals would occur during the dry season, whereas, in reality, the small quantities of forage available per hectare are a constraint to growth during the dry season. Table 1 presents data on the availability of dry matter and digestibility values for the most probable year type, and the measured and simulated body weights of adult female cattle.

Table 1. Monthly values of dry-matter availability (t/ha) and its digestibility (%) for the most probable year type as used in the Mali validation, complete with the simulated and measured average monthly body weights (kg) for adult females.

Month	DM (t/ha)	Dig. (%)	Average LW adult females simulated (kg)	measured (kg)
January	2.5	50	184	
February	2.5	50	171	
March	1.4	55	172	215
April	1.0	62	193	
May	1.1	65	216	
June	1.5	66	234	205
July	1.1	68	238	
August	0.3	70	254	
September	0.8	67	266	
October	1.0	46	225	
November	2.5	53	210	233
December	3.5	52	196	
Threshold value	0.6			
Reference dig.		55		

Source: Breman (unpublished data); Diallo (1978); Traore (1978)

[1] Wet season inundated pastures consisting of high-quality grasses such as Echinochloa stagnina, Oryza longistaminata, etc, which dry out during the dry season.

Some adaptation of the model is needed for its application to extensive production systems such as in Mali. It is suggested that the input data, DM availability in t/ha, should be modified to DM availability per individual animal/day, as in the GRO subroutine of the original TAMU model (Sanders and Cartwright, 1979). The M_Q multiplier should be changed in a similar way.

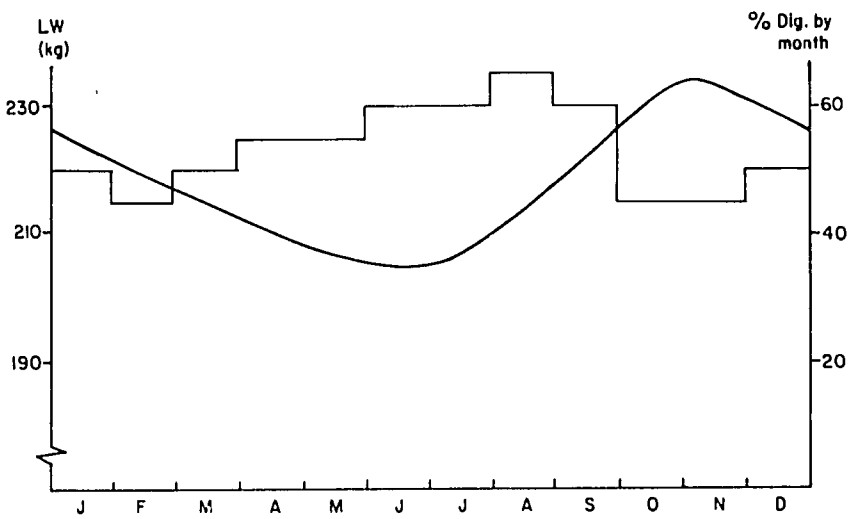
The second problem is related to the a factor through which the intake of each animal is calculated. When all six multipliers are equal to unity the a factor is defined as:

$$a = I\ ref.\ (1-d\ ref)/Wt^{0.73} \qquad (1.3)$$

where I ref. = intake of reference animals in the reference month(s)
d ref. = average digestibility in the reference month(s)
Wt = liveweight (kg)

Consequently the intake of the reference animal increases when the digestibility is greater than d ref (within the limits of 40 to 65%), resulting in an energy surplus for growth. With lower digestibilities the animal will lose weight. This formulation has important consequences, which are illustrated in Figure 3.

Figure 3. The measured weight change in adult females over the year and the fluctuation in digestibility



Source: Wagenaar et al (in press)

A user might choose June-July as the reference months while another user chooses October-November. In the first case the simulation output will tell the user that his herd died out, predicting that the animals will lose weight on all digestibilities lower than the reference 60% (Table 2). In the second case all the animals achieve a condition score of 100 corresponding to the maximum weight allowed by the model. Thus the choice of the reference months is crucial for the outcome of the simulation (Table 2). Data in Table 2 indicate that a should be about 0.045 to approach a normal outcome. Using data reported by Elliot et al (1961), Konandreas and Anderson (1982) calculated an a factor for dry cows of 0.042. It is proposed to replace the existing forage intake algorithm using the a factor by the original TAMU GRO subroutine. If the intake subroutine as it stands in the ILCA model is preferred, an alternative to the current model is to focus on the reference digestibility instead of the reference months as an input requirement.

Table 2. Results after 5 years simulation for different reference months with the same initial data set.

Ref. months	Ref[a] digest. %	Ref. C.P.	"a" factor	Herd size after 5 yrs	Fertility rate %	Weaning wt (kg)	Adult female wt(kg)	Calf mortality % 0-1 yrs	Calf mortality % 1-2 yrs
10+11	45	5.25[b]	0.0676	75	64	87	260	24	26
12+1	50	4.85	0.0527	71	62	82	228	31	33
3+4	53	5.85	0.0442	70	57	66	196	40	43
4+5	55	6.65	0.0400	60	54	46	175	36	55
6+7	60	10.05	0.0322	12	13	20	147	100	100
Base-line data entry				67	53	70	210	34	40

[a] Digestibilities as in Figure 3.

[b] The "a" factor is corrected for CP less than 6%.

The reproduction subroutine

As specified, the model requires the minimum age in months at first parturition for heifers in best, average or poor condition. This information, together with liveweight boundary data provided elsewhere to the model, is used to calculate the moment at which a heifer becomes a breeding female (Figure 4).

The Mali appraisal, in which excessive liveweight gains were simulated, also had most females entering the breeding herd at an age close to t_1. After an animal has been identified as a potential breeding female it will have a stochastic chance to conceive in accordance with the age-specific calving rates (R_t) which are provided to the model. These are net calving rates, so abortions are excluded. With this information the model establishes the effect of age on cow fertility in the case of Mali as shown in Figure 5.

Together with the length of the breeding season, the expected probability of conception ($\bar{P}_t$) is calculated. In the validation year-round breeding is assumed, so there is no seasonal restriction of the chance to conceive.

Subsequently, two multipliers are introduced to translate the influence of the liveweight condition (c) of the animal and of the number of months post-partum(n) on the probability $\bar{P}_t$.

The way these multipliers are described in the model is now believed not to be appropriate for application to Zebu cows in extensive production systems. Reasons for this conclusion are given below.

The post-partum period multiplier (m_n) is assigned a constant value of 1.0 for cows more than one month post-partum.

In general, post-partum anoestrus lasts for more than one month when African Zebu cows are subject to nutritional stress (Moore, 1984) as is the case in Mali and Kenya. Under these conditions the females also suffer from lactational stress. About 70% of the cows in the Mali sample did not conceive during lactation, which is in agreement with data from Kenya (Semenye, 1982). Those cows which conceived while lactating were in their 7th month or later post-partum (Wagenaar et al, in press). Therefore, it is suggested that for application in extensive systems, the post-partum period multiplier could be modelled as in Figure 6.

Figure 4. Age and liveweight combinations for heifer reproductive maturity

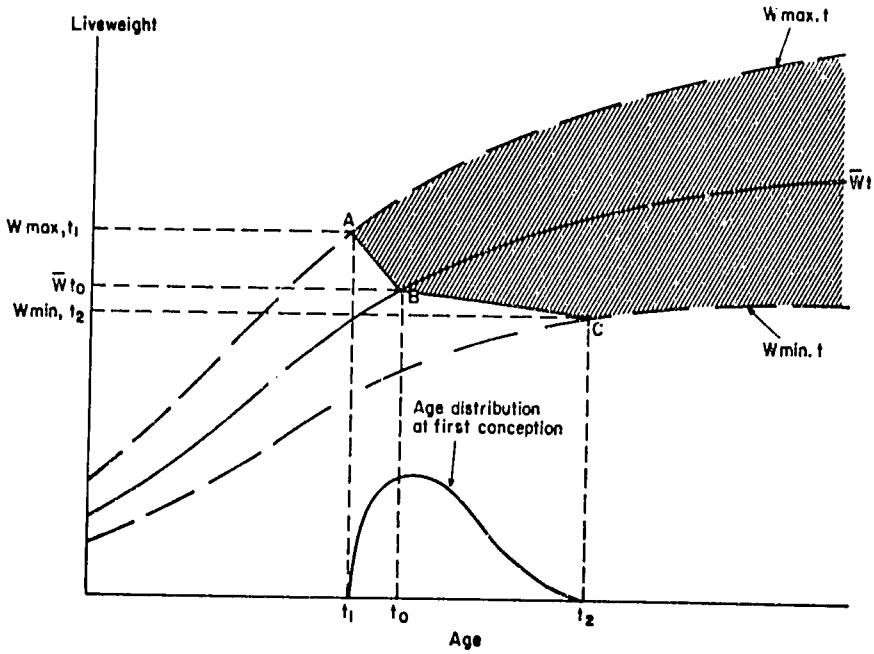
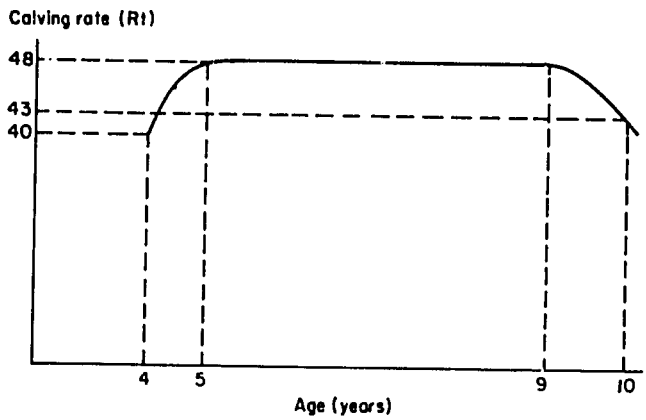


Figure 5. Effect of age on cow fertility



The condition multiplier (m_c) adjusts the probability of conception according to condition score (Figure 7).

The increase or reduction in $\bar{P}_t$ due to a higher or lower condition index, respectively, is based on the assumption that $\bar{P}_t$ is optimal for the breed and weight involved. It is, however, doubtful whether the 48% calving rate for Malian Zebu cows of 215 kg average weight is the maximum calving rate for this breed. An increase in weight of 83 kg is expected to have a much greater effect than the model estimate of 13% increase in calving rate. A calving rate of about 75-80% might be expected for animals in such a good condition. Cows of the same Fulani breed on the research ranch in Niono with an average body weight of 302 kg are reported to have a calving rate of about 70% (ILCA/IER, 1978, corrected for abortions).

The reproductive physiology of Zebu cows under extensive, suboptimal conditions seems much more complex than in the ILCA model. In order to test, for example, the effect of supplementation under these conditions, it is felt that the multiplicative effect (m_c) of the liveweight condition index should give more room for increase in the probability of conception than the present 13%, as suggested in Figure 8. An m_c of 1.45 is obviously only applicable for initially low fertility rates.

Calving rate in the model is defined as:

$$\frac{\text{The number of calves produced in the herd}}{\text{The number of breeding females in the herd}} \times 100(\%)$$

The numerator, as explained above, is directly related to the mean calving rates provided as data and the condition of the herd (via m_c). Because of the model's restriction on m_c this calving rate is too low under good conditions (some more calves and many more breeding females) and too high under moderate conditions.

The mortality subroutine

The model is structured so that deaths can occur due directly to nutritional stress if harsh production environments are being simulated. Additionally, the model allows for normal losses caused by a complex set of factors not directly related to nutritional status.

Figure 6. Proposed multiplicative effect (m_n) on $\bar{P}_t$ of the period in months post-partum

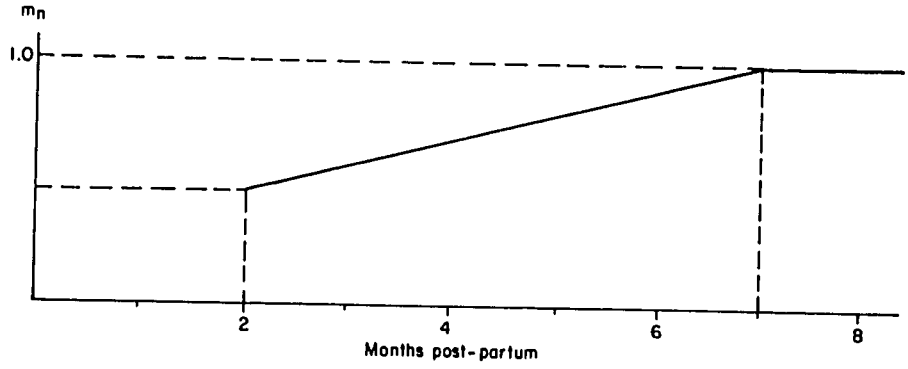


Figure 7. Assumed multiplicative effect (m_c) of liveweight condition index on the probability of conception

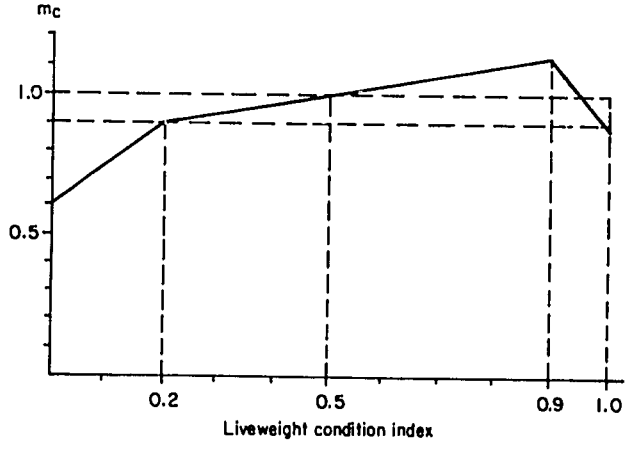
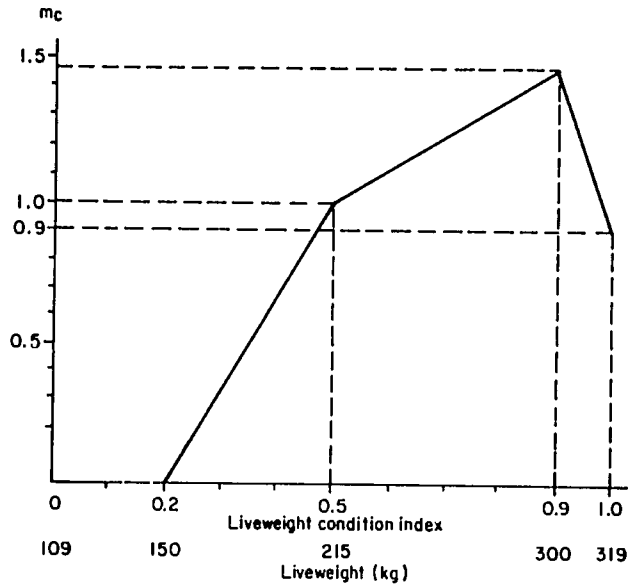


Figure 8. Proposed multiplicative effect (m_c) of liveweight condition index on $\bar{P}_t$



Mortality due to starvation[1] occurs when the liveweight of an animal falls below the lower liveweight limit, as shown in Figure 9, and is a function of the liveweight data and the forage data provided to the model.

The mortality rates provided to the model are used to simulate the non-nutritional losses. The average annual mortality rate (M_t) as a function of age is shown in Figure 10. These M_t values are used to calculate monthly rates, such that when compounded over 12 months they give the annual rates.

For calves less than one year old, the probability of death is calculated by month, based on the entered survival rates. These monthly rates for both adults and calves are the test values in binomial trials, where a random number between 0 and 1 is drawn for each animal from a uniform distribution. Death due to non-nutritional reasons occurs if the number drawn is less than the test value. As already mentioned at the 1983 workshop (van Keulen et al, 1984) the mortality from causes other than malnutrition is completely descriptive, so the model does not adequately simulate differential mortality losses arising as a result of changes in management.

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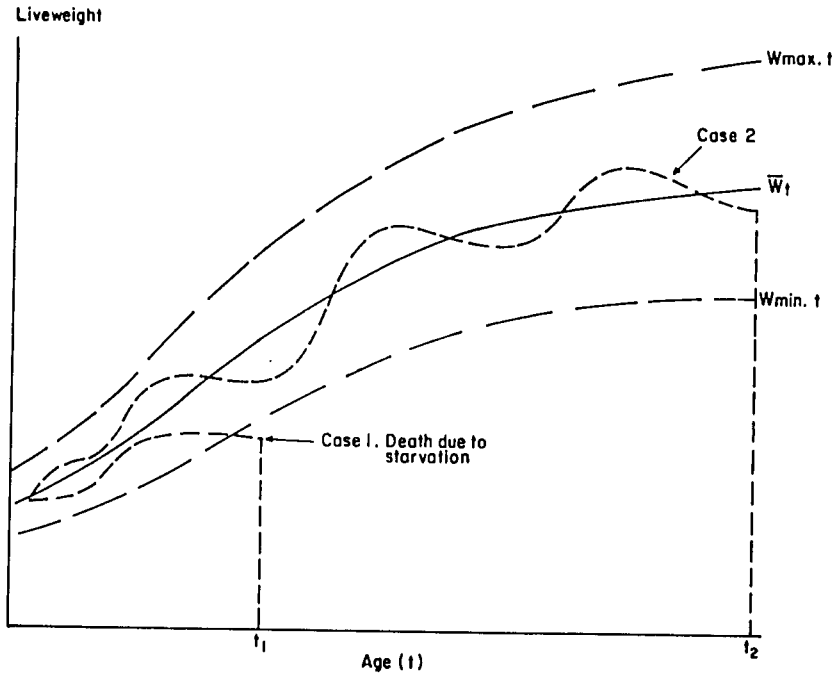
[1]Starvation mortality is not printed out in the monthly output option.

Figure 9. General shape of the average liveweight evolution curve and associated boundary curves, and illustration of two simulated liveweight paths

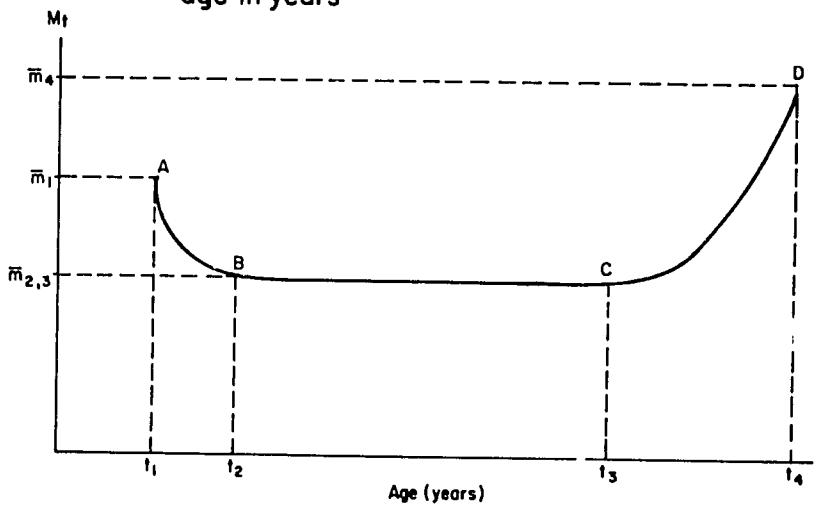


No distinction in the input data is made between starvation and normal death. If the model is running for a system under harsh conditions, as in Mali, the mortality due to starvation is added to the stochastic mortality (input data) of which it was already a part.

The model assumes that all conceptions result in a birth 9 months later. Abortions are not considered in calf mortality to 3 months of age nor in the calving rate. In the Mali studies, however (ILCA/IER, 1978; Wagenaar et al, in press), the average percentage of abortions was found to be 10 and 6.7 with calving percentages of 70 and 48, repectively. Thus in both cases, 14% of the conceptions did not result in parturition. Improvement of disease control (not considered as a policy in the model) or in nutritional level could well decrease this pre-partum mortality, immediately resulting in an increase in productivity.

It is suggested that the abortion rate should be included in the calving rate as data to the model, i.e. to ask for the fertility rate. Parallel to the calculation of the probability of conception ($\overline{P}_t$), a stochastic probability of abortion could be built into the model.

Figure 10. Average annual mortality rate (M_t) as a function of age in years



Conclusions

The appraisal of the ILCA secondary production model with data from extensive semi-arid production systems in Mali and Kenya has revealed that, for such systems, the model needs some adaptations.

The forage intake of uncontrolled grazing animals is calculated by using almost solely the digestibility of the forage on offer. Availability and crude protein content of the forage and the time available for grazing are only used for possible adjustments. It is suggested that the forage availability per animal per day should play a more important role in the forage intake algorithm.

Due to its definition, the a factor used as a calibration factor for intake causes considerable variation in the outcome of the simulation processes. The functioning of this a factor in the model needs close examination.

Emphasis is given to the complicated reproductive physiology of Zebu cows under extensive range conditions. Some proposals are advanced to make the assumed multiplicative effects match more closely to Zebu cow physiology.

Finally the mortality subroutine has been discussed, and some modifications are proposed.

Acknowledgements

The authors wish to thank Dr F.M. Anderson for his fruitful comments and Dr H. Breman and Mr P.N. de Leeuw for their supply of material for this appraisal.

References

Cartwright T C and Doren P E. 1984. Letter to the editor. Agric. Systems 15:249-251.

Conrad H R, Pratt A D and Hibbs J W. 1964. Regulation of feed intake of herbage by ruminants: Physiological and physical factors limiting feed intake. J. Anim. Sci. 25:227-235.

Diallo A. 1978. Transhumance: comportement, nutrition et productivité d'un troupeau zébus de Diafarabé. Thesis CPS, Bamako, Mali.

Elliot R C, Fokkema K and French C H. 1961. Herbage consumption studies on beef cattle. Rhodesian Agric. J. 58:124-130.

ILCA/APRU (International Livestock Centre for Africa/Animal Production Research Unit, Botswana). 1978. Mathematical modelling of livestock production systems: Application of the Texas A & M University beef cattle production model to Botswana. ILCA Systems Study No. 1. ILCA, Addis Ababa.

ILCA/IER (International Livestock Centre for Africa/L'Institut d'Economie Rurale du Mali). 1978. Evaluation of the productivities of Maure and Peul cattle breeds at the Sahelian station, Niono, Mali. ILCA Monograph No.1. ILCA, Addis Ababa.

van Keulen H, Ketelaars J J M, Butterworth M H and Anderson F M. 1984. Modelling activities in the framework of livestock research: considerations of a workshop held at Addis Ababa, 1983. CABO Report No. 53. CABO, Wageningen, the Netherlands.

Konandreas P A. (Unpublished). Modelling forage intake and animal performance when the quality of forage on offer is highly variable: the case of transhumance in Mali. Draft paper, ILCA.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: an integer and stochastic model for evaluating production alternatives. ILCA Research Report No. 2. ILCA, Addis Ababa.

Konandreas P A, Anderson F M and Trail J C M. 1983. Economic tradeoffs between milk and meat production under various supplementation levels in Botswana. ILCA Research Report No. 10. ILCA, Addis Ababa.

Moore C P. 1984. Early weaning for increased reproduction rates in tropical beef cattle. World Anim. Rev. 49:39-50.

Sanders J O and Cartwright T C. 1979. A general cattle production systems model. II. Procedures used for simulating animal performance. Agric. Systems 4:289-309.

Semenye P P. 1982. Preliminary report of cattle productivity in Olkarkar, Merueshi and Mbirikani group ranches. Documents prepared for the Program Committee. ILCA, Kenya.

Traoré G. 1978. Evaluation de la disponibilité et de la qualite de fourrage au cours de la transhumance de Diafarabé. Thesis CPS, Bamako, Mali.

Wagenaar K T, Diallo A and Sayers A R. (in press). The productivity of transhumant Sudanese Fulani cattle in the Niger Inner Delta in Mali. ILCA Research Report.

Whelan M B, Spath E J A and Morley F H W. 1984. A critique of the Texas A & M model when used to simulate beef cattle grazing pasture. Agric. Systems 14:81-84.

Discussion

Comment - In the TAMU model the equation from Conrad is used. He had a coefficient which related the amount of dry faecal output per day to liveweight, and assumed a constant faecal output. Conrad referred to lactating cows. With feed digestibilities at which the digestive tract is not limiting, then of course the intake normalising factor should be metabolic weight. It is suggested that faecal output may be higher in animals grazing poor-quality pasture because they may have a higher inner capacity.

Comment - There is real variation in faecal output. It is not so constant and not within such a small variation as is often assumed. You have to deal with a factor of 2 or even 3 in faecal output.

Comment - In the way you use reference intake, it is assumed that digestibility is the determining factor of that intake, so in fact any possibility of detecting other possibly limiting factors is lost. Therefore it is not an objective reference intake, but, in my opinion, simply a way to adjust model output to observed output. A whole range of factors, such as mineral deficiencies and disease conditions, may explain the reference intake.

Reply - I concluded that digestibility is the only forcing factor at the moment. The program has possibilities to use quantity of feed as a limiting factor, as well as nitrogen percentage or distance walked per day. I agree with you entirely that there are more factors determining intake, which are not operational in the model at the moment. There is obviously a certain level of accuracy which you can reach when you want to apply a model. There are factors that are neglected because they are, for the moment, too dificult to model, or they are not yet fully understood, but there is no reason not to try to build a model based on the actual state of knowledge and possibilities.

Comment - We could say that the modelling problem lies between the ground and the animal's mouth, in that nobody is challenging the partition of energy or protein within the animal. We do understand quite well those factors that affect the handling of the food after it gets into the rumen at least.

Comment - But if an animal is sick, it will certainly have a lower intake, as with mineral deficiencies. The supply of animal drinking water is also important for intake. You should try to estimate the level of production in a system given the quality of the feeds available and subsequently compare it with the observed levels of production. If there is a difference between them, then we should look for the factors which explain it.

Comment - You give the impression that you are trying to simulate observed data. You are getting a set of data from Mali, and then you are changing the model to make it fit the data.

Reply - I believe that the use of models in general is limited to the kind of situation for which you have created it. If we apply the ILCA model as developed for ranches in Botswana to a ranch in Kenya, we will have no major problems. But if we use it for a significantly different set of data, i.e. data from pastoral systems under suboptimal conditions, like in Mali, we have to change some of the assumptions in the model. With the data from Mali, we can at least approach the mortality or fertility subroutine more realistically, and then use this modified model for pastoral systems in Kenya. I will not say that one model will be applicable everywhere, neither will I say that the model is only applicable for the situation in which you validate it. There must be something in between.

Modelling pastoral livestock production: Problems and prospects

P.N. de Leeuw

Introduction

One of the principal tasks of the International Livestock Centre for Africa (ILCA) is to identify opportunities for improving livestock productivity in sub-Saharan Africa. Therefore, the underlying causes of the variable and usually low output levels of livestock production systems need to be understood and quantified. From the beginning, ILCA staff believed that modelling should be complementary to other research activities as it would help to analyse the multiple interactions that exist between herd productivity, forage resources and management regimes. ILCA chose to develop further the Texas A & M model because of its high level of generalisation and flexibility, and its proven ability to simulate production systems in tropical environments. As described by Konandreas and Anderson (1982) several modifications have been built into the ILCA model to make it more suitable for modelling pastoral systems.

In this paper the focus is on the key determinant of pastoral herd productivity, i.e. the quantity and quality of available forage, which in turn generates the daily intake of metabolisable energy as the driving input of the model. It is argued that the model seeks to simulate the input and output of well-defined and location-specific production systems for which field data are available to validate and fine-tune the model. This leads to the contention that there is little merit in using a model in which the input component inadequately resembles the real world. Several shortcomings in the quantification of the required inputs were identified when the output of the model was validated for a number of West African pastoral production systems (de Leeuw and Konandreas, 1982), while further modifications to the output side have been proposed by Wagenaar and Kontrohr (1986).

The main premise of this paper is that a more realistic approach to the prediction of daily intake of forage is desirable. To identify the major problems and suggest solutions a stepwise scenario is proposed. Firstly, the general characteristics of the system that is to be modelled should be identified. Since by definition, each system is location-specific, the second step is to define its boundaries and assess its resource base. This requires

delimiting the expected levels of primary productivity taking into account the environment, inter-annual variation and rates of exploitation. The third step involves the development of realistic profiles of the quantity and quality of forage on offer and the interactions of these variables with daily feed intake. To better identify and quantify the limitations to intake, the model should take into account the two primary determinants of intake: the amount of forage on offer daily, and the harvesting activities of the grazing animal.

Input requirements for predicting intake

The general structure of the model and the data needed to run it have been described in detail by Konandreas and Anderson (1982). For this paper, it suffices to discuss briefly the data needed for simulating intake: i.e. the driving force of the model.

Although it is recognised that voluntary intake of feed by grazing cattle is influenced by the quantity and quality of forage and by climatic and management factors, it is mainly forage quality that determines the prediction of intake. Forage on offer is simulated based on monthly data for an annual cycle of 12 months. Several year types are required to provide an adequate representation of the long-term resource variability. For each year type, monthly digestibility and crude protein content of forage on offer are identified. Year types are drawn randomly based on a given probability of the forage supply situation for each production system.

Intake is reduced when CP content is less than 6%, but given the close relationship between CP% and digestibility, the reduction of intake is defined in terms of digestibility alone as $(d/0.4)^{0.6}$. Thus, intake begins to decrease when forage digestibility is less than 40%. Similarly, when digestibility of the forage rises above 65%, intake is constrained by the physiological limit of the animal and is reduced to maintain metabolisable energy intake equal to that at 55% digestibility. Forage intake is reduced when standing biomass is less than 0.8 t/ha and when the distance grazing animals walk exceeds 14 km/day (or c. 4 hours of non-grazing activity).

In summary, the model requirements indicate that, in addition to climate and management, other factors such as forage palatability, species preference and regularity and quantity of water intake are not considered in the prediction of intake.

Forage resources in pastoral systems

Before discussing the monthly input of forage data required for the model, attention is focused first on the characteristics of three location-specific pastoralist production systems as examples of their complexity. These are: (1) transhumant Fulani in Mali; (2) semi-sedentary Fulani in the subhumid zone in Nigeria; and (3) semi-sedentary Maasai in Kenya. Their general features are summarised in Table 1 with regard to climate, degree of mobility and the importance of cropping, while components of the seasonal fodder supply are illustrated in Table 2. From these tables it is clear that pastoralists need to employ a wide range of management and movement strategies to exploit fully the different forages available and to minimise the effects of fluctuating supply between seasons and years.

For example, in the rainy season transhumant herds in Mali mainly graze annual grasslands several hundred kilometres away from their home area, while during the dry season they gradually move across the floodplain of the Niger following the recession of the floods. Due to different levels and durations of flooding, plant cover on the floodplain is extremely variable and consequently stock have access, simultaneously, to tall-standing Andropogon gayanus stands, inundated Echinochloa stagnina grassland and regrowth on rice fields after harvest, some of which are burnt (de Leeuw and Diallo, 1983; Breman et al, 1978).

In Nigeria the resource base of pastoralists in the subhumid zone is less diverse, since they rely on upland savanna for over 80% of their total grazing. Nevertheless, crop residues, browse and regrowth after burning are important grazing resources during the dry season (van Raay and de Leeuw, 1974; Bayer, 1984). The fluctuation in quality and quantity of the potential components of the diet of grazing cattle is shown in Table 3 for grazable residues of sorghum and millet and in Table 4 for a tall stand of perennial grass at the end of the growing season.

Table 1. Major characteristics of three livestock production systems in Mali, Nigeria and Kenya.

Country	Mali	Nigeria	Kenya
Tribe	Fulani	Fulani	Maasai
Zone	Semi-arid (Sahel)	Subhumid (Guinea)	Semi-arid
Annual rainfall (mm)	400-600	1100-1300	400-700
No. of rainy seasons/year	One	One	Two
Mobility	High	Low	Low
Grazing orbit (km)	200-400 km	20-50 km	10-20 km
Importance of farming	Medium	High	Almost nil
Crops	Rice Sorghum Millet	Sorghum Millet Grain legumes	

Derived from de Leeuw (1984).

Table 2. Seasonal fodder utilisation of three livestock production systems in Mali, Nigeria and Kenya.

Country	Mali		Nigeria		Kenya	
Season	Wet	Dry	Wet	Dry	Wet	Dry
Period	July-Sept	Oct-June	May-Oct	Nov-Apr	Oct-Dec Mar-May	Jan-Feb June-Sept
Annual grasses	xxx	x	x	x	xx	x
Perennial grasses	x	x	xxx	xx	xx	xxx
Floodplain grasses	-	xxx	-	x	-	x
Browse	x	-	x	x	-	x
Crop residues	-	xx	-	xx	-	-

xxx = highly important; xx = important; x = low importance.

Table 3. Components and quality characteristics of forage from sorghum and millet fields at the start of grazing in the subhumid zone of Nigeria.

Component	Sorghum			Millet		
	D%	CP%	% yield	D%	CP%	% yield
Immature panicles	60	7.8	1	65	12.6	2
Upper leaves	60	7.3	6	60	11.4	7
Lower leaves	54	3.3	8	59	7.6	10
Upper stalk	49	1.4	16	48	2.4	23
Lower stalk	45	1.3	35	46	2.5	38
Total cereal	48	2.8	66	50	4.1	8.0
Grasses and weeds	55	7.0	34	55	7.0	20
Total	50	4.2	3.3[a]	51	4.7	2.1[a]

Derived from Powell (1984).

d% = digestibility;

CP% = Crude Protein Content.

a = t/ha

Table 4. Crude protein content (CP%) and *in vitro* digestibility (IVDMD%) of young and old leaves of *Andropogon gayanus* at the end of the growing season, Nigeria.

Date	CP%		IVDMD%	
	Young	Old	Young	Old
12 September	6.8	2.1	66.0	49.5
3 October	8.7	3.1	56.6	29.2
26 October	6.6	3.4	54.4	39.4

Derived from Haggar (1970).

The least complex of the examples chosen, as regards forage resources and management options, is that of the Maasai in semi-arid Kenya. They rely on cattle and small-stock husbandry for most of their subsistence and cash income, exploit a rather uniform and limited orbit mainly of perennial grasslands and rarely engage in cropping. However, their resource base is subject to tremendous variability in time and space, giving rise to unpredictable cycles of boom and bust periods (de Leeuw et al, 1984).

Range resources and primary productivity

For modelling specific range livestock production systems a prediction of the geographical and temporal distribution of range resources is required. As a first step, grazing resources are derived from secondary sources such as natural resource and vegetation surveys, which provide maps and descriptions of the major land uses and vegetation types of the area within which the livestock production system operates. Often, those regional surveys include estimates of end-of-season biomass, from which assessments of potential carrying capacity can be made. Furthermore, analysis of demand for and supply of forage resources can lead to identification of regional imbalances in utilisation (e.g. de Leeuw and Milligan, 1983; de Leeuw, 1976).

Equations linking annual or seasonal rainfall to end-of-season biomass are used to assess the grazing capacity of the land. Linear regressions were developed by Le Houerou and Hoste (1977) for West Africa and by Deshmukh (1984) for East Africa. Although the limitations of this approach are well recognised (cf Breman et al, 1984), these relationships appear to hold even when applied to smaller areas like the Tsavo National Park in semi-arid Kenya (Figure 1). Long-term weather variables have been used to explain past boom and bust periods for Maasai pastoralists in Kenya (de Leeuw, unpublished), and famine conditions in maize-growing regions in Kenya and Ethiopia (Stewart and Faught, 1984; Henricksen and Durkin, 1984). Fluctuations in carrying capacities are shown by the data in Table 5, which were generated to identify probable sequences of year types for modelling the Maasai system (see Figure 3).

Figure I. Linear regressions of annual or seasonal rainfall on primary productivity of herbaceous cover in sub-Saharan Africa

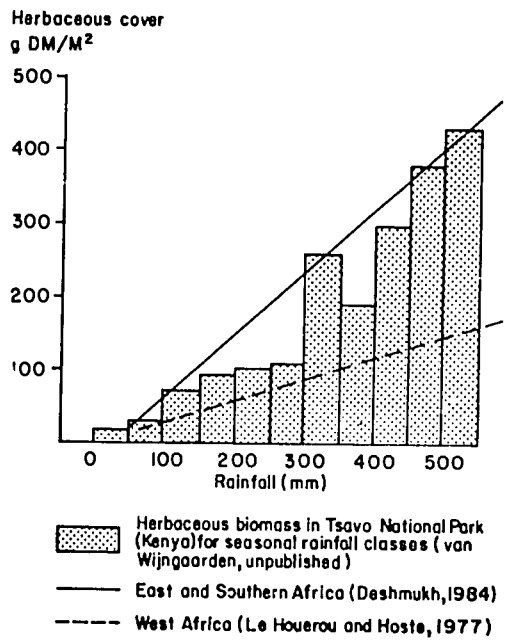


Table 5. Annual carrying capacity based on biomass yield for different combinations of rainfall seasons in semi-arid Kenya (ha/TLU/annum).

First rains	Good ----------> Bad				
Second rains[1]	Biomass t/DM/ha	3.0	2.0	1.0	0.5
Good	3.0	1.2	1.5	2.0	4.2[a]
	2.0		1.8	2.2	4.5
	1.0			2.7	5.0
Bad	0.5				7.2

[1]First rains: October-December; second rains: March-May.
[a] Based on the assumption that 50% of standing biomass is consumed, and daily DM disappearance rate is 10 kg/day for a TLU of 250 kg.

After defining the overall demand and supply situation of the system to be modelled, the monthly average data on quantity and quality of forage on offer are required. For modelling African systems, mostly secondary data were used: e.g. Sullivan et al (1981) in Tanzania, de Leeuw and Konandreas (1982) for West Africa, and Konandreas et al (1981) for Botswana. The problems with this approach when applied to pastoral production systems have been discussed above.

There have been many efforts to simulate the forage supply available to grazing animals. These range from a simple pasture growth model using the length of the growing season (derived from a soil water balance model, e.g. McCown, 1981) to complex models that aim at simulating the entire soil-plant-animal complex (e.g. Wight, 1983). Although the ultimate aim of these models is to simulate animal productivity, the majority treat plant productivity as a separate subroutine and use plant production as an input for simulating the animal production component.

In Australia, McKeon et al (1980) developed an index of daily pasture growth from the product of separate soil, moisture, temperature and radiation indices. Daily indices were transformed into a mean seasonal growth index which was then multiplied with the potential pasture growth rate (McKeon et al, 1982).

Thus plant growth was related to the amount of green material capable of transpiring at a rate predicted by the daily soil moisture balance. Cornet (1984) used a similar model for predicting annual forage growth in the Sahel in Senegal, while Sullivan et al (1981) simulated changes in composition of perennial swards in subhumid Tanzania by partitioning biomass in standing green and dry material on a daily basis. The daily amount of green herbage (available to livestock) was a function of green forage at the beginning of the day, accounting for additional new growth and for losses of green growth to the dry biomass pool. Daily growth rate was influenced by soil moisture balance, the starting date of the growing season, the leaf-area index and stocking rate. The principal concept of these models is to relate transpiration to dry-matter yield and appears well suited to generating the input for simulating animal productivity. The approach is flexible enough to model both annual and perennial species and their inter-annual variation as well as defoliation and grazing effects.

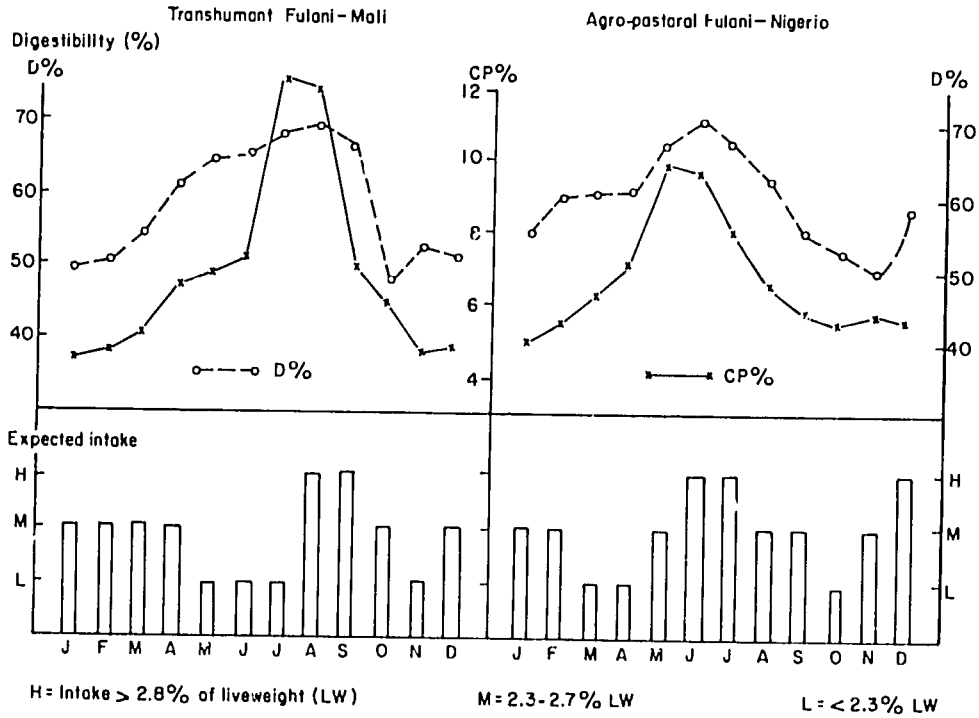
An alternative approach to modelling plant growth uses the same abiotic variables to drive the CO_2 assimulation rate and to simulate the flow of plant biomass and nitrogen in daily time steps (Hansons et al. In: Wight, 1983). These models were originally developed for the Grassland Biome Study and were modified to simulate the Serengeti grasslands in East Africa (Coughenour et al, 1984), monsoonal grassland in India (Parton and Singh, 1984), and the annual Sahel grassland (Penning de Vries and Djitèye, 1982).

It is not within the scope of this paper to indicate which of these primary production models is most appropriate for simulating plant-animal systems, but it seems that for this purpose, models are needed that combine "increased generality, less unnecessary complexity, easier data demand and greater validity" (van Keulen et al, 1981).

Forage quality profiles

Monthly values of forage quality for the two West African systems are shown in Figure 2. As already shown in Table 2, the forage resources are extremely variable and it is unlikely that these averages approximate the real world, even if between-year variations are accounted for by inserting year types into the model.

Figure 2. Average monthly quality values of biomass on offer and expected intake levels for two pastoral production systems in West Africa



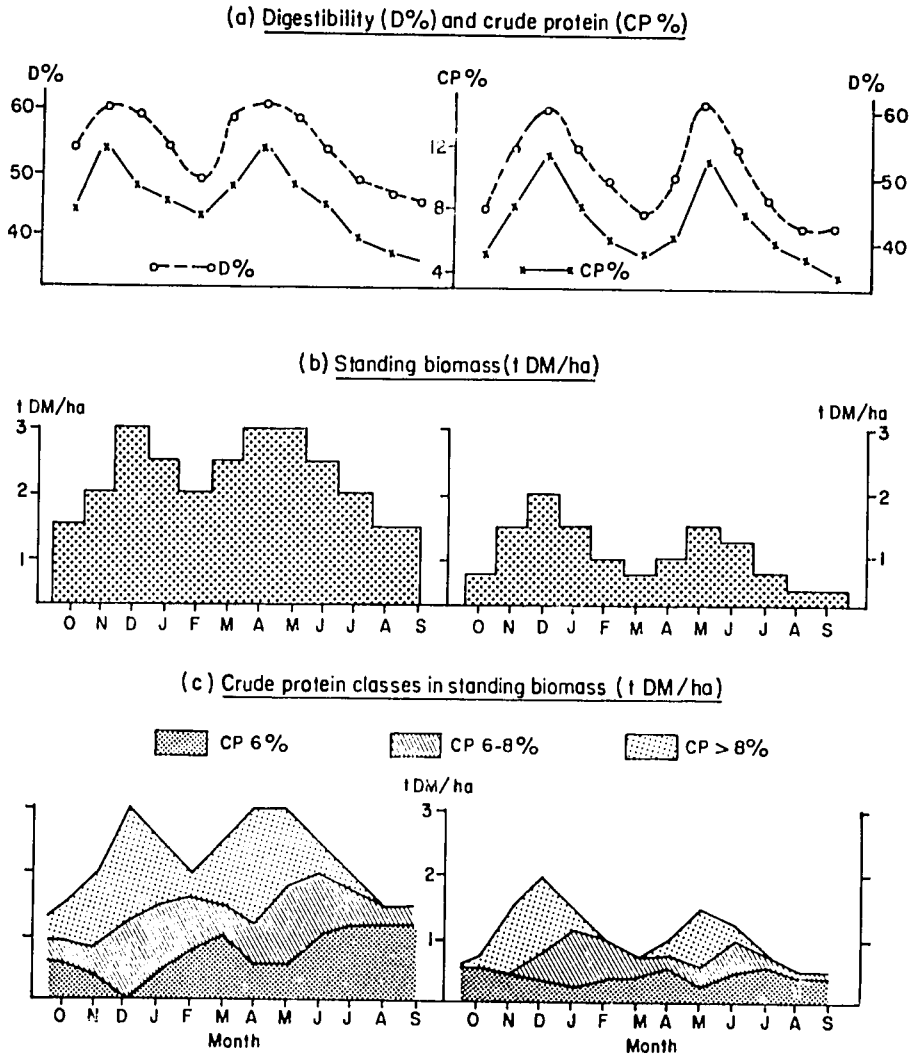
Therefore, it is proposed to construct monthly forage profiles which provide ideally a combined assessment of the quantity of forage on offer by quality class based on digestibility and/or crude protein content. This approach was tried for the Maasai system in Kenya, where fodder supplies are less diverse because rangelands with perennial grasses are the major grazing resource. Also, herd mobility is relatively low, implying that forage quality classes can be linked to known grazing pressure and expressed in kg/ha. Hence the monthly forage available in each quality class can be calculated (Figure 3).

To analyse the grazing resource situation, three data sets were compiled. The first provided monthly averages of digestibility and crude protein content. To illustrate the variability between year-types, the parameters are given for an above- and below-average rainfall (Figure 3a). Although differences between years are pronounced the annual curves follow similar trends. In a good year, average crude protein content is at 8% or more during 8 months, in constrast to 5-6 months in a poor year.

The second set provides estimates of monthly averages of standing biomass derived from relationships between seasonal rainfall and biomass (Figure 3b) and supplemented by field measurements. The yield data in Figure 3 represent monthly estimates of standing biomass under a moderate level of stocking of 3-4 ha/TLU. It is shown that in a good year standing biomass rarely drops below 1.5 t DM/ha whereas in a bad year, standing crop is less than that level for most of the year.

The third data set divides the standing biomass into three quality classes using CP% as a proxy for quality. At the onset of the rains there is a rapid increase in high-quality biomass concomitant with a rapid disappearance of old standing crop left from the previous season (Figure 3c). With continued herbage growth, CP content in current growth declines together with further reduction in old standing forage, so that at the end of the rains only medium- and poor-quality forage are still available for grazing. Comparing the two year-types, it is evident that differences in CP supply become very pronounced; while in a good year there is 1 t of good-quality forage per hectare for 6 months in a poor year this period lasts only for 2-3 months. Hence for 9-10 months only poor- and medium-quality feed is available.

Figure 3. Grazing resource profile by month in semi-arid Kenya



Grazing behaviour of pastoral cattle

The concepts governing grazing behaviour and the search strategies which herbivores use when preferred species or the quantity of acceptable forage are limiting have not been well defined experimentally (Rice et al, 1983).

In pastoral systems, where livestock are herded, insufficient time to graze has been recognised as a factor limiting daily intake of forage. In the ILCA model, this limitation is simulated through reducing intake when the daily distance travelled by the herd exceeds 14 km (Konandreas and Anderson, 1982). Although distance travelled reduces time for grazing (14 km equates to approximately 4 hours of walking at 3.5 km/h), the actual duration and intensity of foraging may be more directly related to forage intake than the distance walked.

Most herded cattle walk less than 14 km per day. Exceptionally, longer distances (20-30 km) were covered by pastoral herds in northern Nigeria during the latter part of the dry season (van Raay and de Leeuw, 1974). In Mali, Dicko et al (1981) reported an average daily distance walked of 12.7 km, which consisted of 5.1 ± 0.5 km of walking and 7.6 ± 0.1 km of searching for forage. In Nigeria, semi-settled pastoralists rarely cover more than 10 km daily (Bayer, 1984; van Raay and de Leeuw, 1974), while Maasai herds walk 10-14 km during the dry season and less during wet periods.

There is a general trend for herders to extend the grazing orbit and the length of grazing day when grazing resources become scarce and of poorer quality. The grazing day may increase from 6-7 hours in the wet season to 9-12 hours in the dry season. Bayer (1984) recorded very short grazing days in the subhumid zone of Nigeria during the rainy season and concluded that this may contribute to the low productivity of this production system.

Another variable that may affect forage intake is grazing intensity. Van Raay and de Leeuw (1974) found that the proportion of high-intensity grazing was inversely related to total grazing time, indicating a self-adjusting mechanism in grazing behaviour. Using number of bites per minute as a measure of grazing intensity, de Leeuw and Peacock (1982) found that grazing intensity was negatively correlated with walking speed. Almost all grazing (93-96%) was done at walking speeds of less than 1.5 km/h. Consequently, daily 'speed profiles' were used to determine actual hours of grazing per day. Therefore, it seems necessary to adapt the model so that, in addition to the intake restriction due to distance walked, a second restriction is inserted that takes account of situations where grazing time is limiting.

Forage on offer and intake

Although Konandreas and Anderson (1982) included a correction factor to adjust voluntary intake for limitations in the quantity of acceptable forage on offer, this was never validated. Sanders and Cartwright (1979) incorporated the monthly forage dry matter available per animal per day and stated that forage consumption per unit time may be affected by forage density and several other factors, such as distance from water. However, no minimum quantity was given for acceptable forage per unit area below which intake is restricted. In a further development, Sullivan et al (1981) interfaced livestock productivity with forage quantity and quality, but in the application for Tanzania, available forage was assumed to be non-limiting. However, they used two levels of stocking which resulted in lower simulated growth rates at the higher level due to lower CP content and digestibility.

The SPUR model is probably the most comprehensive, since annual preferences for grazing sites and locations as well as for up to nine forage species or species groups were included together with a factor for physical availability of forage (Rice et al, 1983). This factor was defined as the proportion of the total above-ground biomass of a plant species group which is readily consumed by a single grazing event. Availability is therefore primarily a function of the growth form of the plant, rather than its quantity per unit area. From these, a plant supply matrix for grazing was developed. Supply and demand matrices for all sites were calculated on a daily basis, yielding daily intake of digestible dry matter. This daily removal was discounted in subsequent supply matrices.

Hendricksen et al (1982) in Australia related intake to dietary CP content, which was generated from a herbage growth model. This model estimated green herbage by age class and assumed that grazing progressed preferentially from young to old herbage[1]. Intake was reduced when standing biomass was less than 230 kg/ha and also when the amount of herbage removed was greater than 30% of the standing dry matter.

Several validations of these simulation procedures have been published. Kothman and Smith (1983) used the Texas A & M model to evaluate management alternatives in cow-calf operations and stated that the model was adequate when forage quality and availability were available for different alternatives, but emphasised that there is a critical need to develop plant/animal interface models that will accurately predict availability and quality for forage and

[1] Konandreas (1980) outlined a similar procedure in the early phase of the development of the ILCA model.

nutrient intake of grazing animals for different range and livestock management schemes. Validations of interfaced plant/animal models in Australia were satisfactory for sown grass/legume pasture. However, growth predictions of livestock grazing native pastures was poor, partially because the modelling of the quality of dead material on offer during winter periods was considered inadequate (McKeon et al, 1980).

To what extent the inclusion of other intake-limiting factors will improve simulations of pastoral systems remains to be seen. If the opinion expressed by Cordova et al (1978) that 'no method has been devised by which intake of grazing livestock can be quantified' remains valid, validation of modelled intake will continue to be difficult. Variable levels of intake by pastoral cattle were recorded by Dicko et al (1983) using total faecal collection. Daily intake ranged from 1.9 to 3.9% of liveweight and from 0.5 to 1.2 kg per hour of actual grazing. These values are comparable to those given by Cordova et al (1978).

Few data are available on the effect of low biomass yield on intake. Allison et al (1982), in comparing a wide range of short-term grazing pressures, showed that intake did not decrease even when daily forage availability was close to daily intake (± 10 kg/day) and there was very little standing biomass. It may be advantageous to consider the forage availability per grazing event, as proposed by Rice et al (1983), to define relationships between available forage and intake. If such events are equivalent to bites, it can be postulated that for freely ranging cattle, daily available forage is related to the area covered. If average number of bites/day equals 16 000 and the bite area is approximately 0.01 m^2, a mature animal can cover 160 m^2/day. If 10 kg DM/day is assumed to be the minimum quantity required, standing acceptable forage should be more than 625 kg/ha. This is close to the 800 kg/ha mentioned by Konandreas and Anderson (1982) as the quantity below which intake is reduced.

Model validation

To date, few African pastoralist production systems have been modelled, due to the complexity of this mode of production coupled with the difficulties and costs involved in monitoring the long-term production parameters of traditional livestock enterprises.

De Leeuw and Konandreas (1982) validated the ILCA model for four West African pastoralist systems and found good correspondence between model output and the real world when productivity parameters were aggregated in a production index, but stated that simulated animal growth rates were over-estimated, and that mortality and monthly conception rates were difficult to simulate. Improvements to the simulation of these parameters have been proposed by Wagenaar and Kontrohr (1985) using the data from a 4-year study of transhumant herds in Mali (Wagenaar et al, 1984). Therefore, in this section comparison between simulated and actual productivity will be confined to animal growth rates. This parameter has received more attention, because weight changes are easier to monitor than reproductive rates, mortality and milk output (Wilson and Semenye, 1983).

As shown in Table 6, simulated and actual weights of one-year-old calves and animals close to maturity are well matched, whereas the model over-estimated the growth of immature animals. Possible causes of these discrepancies have been given by Wagenaar and Kontrohr (1985). Also monthly weight changes usually showed a good fit both in West Africa (Table 7) and in Botswana (Kahn and Spedding, 1984). Unfortunately, none of the field data were for pastoralist cattle but were derived from grazing trials on experimental stations. The same applies to the growth data used by Sullivan et al (1981) to validate their model in Tanzania.

Table 6. Actual and simulated liveweights at four ages for female cattle in production systems in Mali and Nigeria.

System	Year 1	2	3	4	Reference
	Liveweight (kg)				
Transhumant, Mali					
Actual	80	125	170	198	Wagenaar et al (1984)
Simulated	71	153	226	237	de Leeuw and Konandreas (1982)
Agropastoral, Nigeria					
Actual	80	145	190	245	Pullan (1980)
Simulated: 1.	80	164	262	280	Konandreas and
2.	98	192	277	280	Milligan (1981.)

1. Born in December (mid dry season).
2. Born in May (early wet season).

Table 7. Actual and simulated liveweight changes of growing cattle in semi-arid West Africa.

Actual changes	Initial weight (kg)	Dry season loss (kg)	Wet season gain (kg)	Total annual gain (kg)
Mali[1]	255	35	90	55
	344	65	95	35
Niger[2]	150	15	75	60
Simulated changes				
Mali[3]	250	40	104	64
Mauritania[4]	133	+10	82	92
	225	43	58	13

[1] Derived from grazing trials on the Niono Ranch with steers during 1978/79 (de Leeuw and Hiernaux, 1980).

[2] Summarized from grazing trials on four ranches in the Sahel zone of Niger (Wylie et al, 1983).

[3] Simulation of the agropastoral livestock system in the 'Office du Niger' area in Mali (de Leeuw and Konandreas, 1982).

[4] From Greenwood (1985) based on livestock nutrition and grazing trials in Southern Mauritania.

The sensitivity of the Texas A & M model to changes in the nutritive value of forage on animal performance was tested by Kahn and Spedding (1984) in Botswana and by Sullivan et al (1981) in Tanzania. In Botswana, by lowering monthly digestibility by 5%, annual weight gain dropped from 105 kg to 90 kg per head, while weight losses (3 kg vs 23 kg) and subsequent growth rates were pronounced. In Tanzania, nutritive value of forage was influenced by stocking rate and annual rainfall; simulated annual growth in a good year at low stocking rate was 110 kg, dropping to 50 kg in a poor year at high stocking rate.

Simulated weight changes in adult female cattle in the subhumid zone in Nigeria were given by Konandreas and Milligan (1981). Season and parturition time interacted strongly, resulting in seasonal weight ranging from 350 to 260 kg. These weight changes seem in excess of those reported by Wilson (1983) for Mali.

In an attempt to predict animal performance across a climatic gradient in West Africa, Ketelaars (1984) used the length of the growing season and dietary N content as driving forces. For the 600-800 mm rainfall zone (southern Sahel and Sudan zone) his predictions are close to those presented in Tables 6 and 7. In contrast, annual weight gain in the subhumid zone reached 147 kg, because dietary N% was assumed to be more than 1% for 9 months, whereas in reality this period lasts only for 5-6 months. As a consequence, actual liveweight gains in long-term grazing trials are in the range of 60-80 kg per annum or fairly similar to those in the drier areas further north (de Leeuw, 1971).

From this review, it appears that growth rates and seasonal liveweight changes can be simulated satisfactorily whenever data on forage quality and availability adequately resemble the real world (Kothman and Smith, 1983; Kahn and Spedding, 1984). It also implies that the simulated output is as good as the input data that generate the driving force of the model.

References

Allison, C D, Kothman M M and Rittenhouse L R. 1982. Efficiency of forage harvest by grazing cattle. J. Range Manage. 35:351-354.

Bayer W. 1985. Agropastoral herding practices and grazing behaviour of cattle. In: Livestock systems research in Nigeria's subhumid zone. Proceedings of the 2nd ILCA/NAPRI symposium, Kaduna, Nigeria, 29 Oct - 2 Nov 1984. ILCA, Addis Ababa.

Breman H, Diallo A, Traore G and Djiteye M A. 1978. The ecology of the annual migrations of cattle in the Sahel. In: Proceedings of the 1st International Rangeland Congress. Denver, Colorado, USA.

Breman H, van Keulen H and Ketelaars J J M H. 1984. Land evaluation for semi-arid rangeland: a critical review. In: W Siderius, ed. Proceedings of the workshop on land evaluation for extensive grazing. ILRI, Wageningen. pp. 229-244.

Cordova F J, Wallace J D and Pieper R D. 1978. Forage intake by grazing livestock: a review. J. Range Manage. 31:430-438.

Cornet A. 1984. Utilisation de modèles simples de bilan hydrique et de production de biomasse pour déterminer les potentialités de production de parcours en zone sahélienne sénégalaise. In: W Siderius, ed. Proceedings of the workshop on land evaluation for extensive grazing. ILRI, Wageningen. pp. 207-228.

Coughenour M B, McNaughton S J and Wallace L L. 1984. Modelling primary production of perennial graminoids - uniting physiological processes and morphometric traits. Ecol. Model. 23:101-134.

Deshmukh I K. 1984. A common relationship between precipitation and grassland peak biomass for East and southern Africa. Afr. J. Ecol. 22:181-186.

Dicko M S, Lambourne J L, de Leeuw P N and de Haan C. 1981. Voluntary intake and livestock productivity in the Sahel zone of Mali. In: Proceedings of the 32nd annual meeting of EAAP. August 1981, Zagreb, Yugoslavia.

Dicko M S, Lambourne L J, de Leeuw P N and de Haan C. 1983. Nutrition animale, les bovins. In: R T Wilson, P N de Leeuw and C de Haan, eds. Recherche sur les systèmes des zones arides du Mali: résultats préliminaires. ILCA Research Report No. 5. ILCA, Addis Ababa, Ethiopia.

Greenwood G. 1985. Evaluation of Sahelian livestock strategies using regression models of cattle performance. (submitted for publication.)

Haggar R J. 1970. Seasonal production of Andropogon gayanus. J. Agric. Sci. Camb. 74:487-494.

Henricksen B L and Durkin J W. 1984. Moisture availability and prospects for early warning of famine in Ethiopia. Internal report, ILCA, Addis Ababa, Ethiopia.

Hendricksen R, Rickert K G, Ash A J and McKeon G M. 1982. Beef production model. Proc. Aust. Soc. Anim. Prod. 14:204-208.

Kahn, Hava E and Spedding C R W. 1984. A dynamic model for the simulation of cattle herd production systems. Agric. Systems 13:63-83.

Ketelaars J J M H. 1984. Evaluating rangeland as feed resource for livestock production. In: W Siderius, ed. Proceedings of the workshop on land evaluation for extensive grazing. ILRI, Wageningen. pp. 165-181.

van Keulen H, Seligman N G and Benjamin R W. 1981. Simulation of water use and herbage growth in arid regions. Agric. Systems 6:159-193.

Konandreas P A. 1980. Modelling forage intake and animal performance when the quality of forage on offer is highly variable: The case of transhumance in Mali. Unpublished report, ILCA, Addis Ababa, Ethiopia.

Konandreas P A and Anderson F M. 1982. Cattle herd dynamics: An integer and stochastic model for evaluating production alternatives. ILCA Research Report No. 2. ILCA, Addis Ababa, Ethiopia.

Konandreas P A and Milligan K. 1981. Evaluation of alternative production strategies within sedentary Fulani systems in northern Nigeria. Draft report. ILCA, Addis Ababa, Ethiopia.

Konandreas P A, Anderson F M and Trail J C M. 1981. Economic trade-offs between milk and meat production under various supplementation levels in Botswana. In: Proceedings of the IASTED conference. Cairo, September 1981.

Kothman M M and Smith G M. 1983. Evaluating management alternatives with a beef production systems model. J. Range Manage. 36:733-740.

de Leeuw P N. 1971. The prospect of livestock production in the northern Guinea zone. Samaru Agric. Newsl. 13:124-133.

de Leeuw P N. 1976. Fodder resources and livestock development in northeastern Nigeria. Savanna 5:61-74.

de Leeuw P N. 1984. Pastoral production systems and land utilization types. In: W Siderius, ed. Proceedings of the workshop on land evaluation for extensive grazing. ILRI, Wageningen. pp. 119-132.

de Leeuw P N and Diallo A. 1983. Conditions de pâturage et nutrition. In: R T Wilson, P N de Leeuw and C de Haan, eds. Recherches sur les systèmes des zones arides du Mali: résultats préliminaires. ILCA Research Report No. 5. ILCA, Addis Ababa, Ethiopia.

de Leeuw P N and Hiernaux P. 1980. The secondary productivity of Sahelian rangelands. Internal report. ILCA/Mali, Bamako.

de Leeuw P N and Konandreas P A. 1982. The use of an integer and stochastic model to estimate the productivity of four pastoral production systems in West Africa. In: Proceedings of the National Beef Conference. Kaduna, Nigeria, July 1982. pp. 184-212.

de Leeuw P N and Milligan K. 1983. Resources animales. In: R T Wilson, P N de Leeuw and C de Haan, eds. Recherches sur les systèmes des zones arides du Mali: résultats préliminaires. ILCA Research Report No. 5. ILCA, Addis Ababa, Ethiopia.

de Leeuw P N and Peacock C P. 1982. The productivity of small ruminants in the Maasai Pastoral System, Kajiado district, Kenya. In: Proceedings of the SR-CRSP workshop on small ruminants. pp. 118-138.

de Leeuw P N, Bekure S and Grandin B E. 1984. Some aspects of livestock productivity in Maasai group ranches in Kenya. In: Proceedings of the International Savanna Symposium. Brisbane, Australia. (in press.)

Le Houerou H N and Hoste C H. 1977. Rangeland production and annual rainfall relations in the Mediterranean basin and in the African Sahelo-sudanian zone. J. Range Manage. 30:181-189.

McCown R L. 1981. The climatic potential for beef cattle production in tropical Australia. Part III. Agric. Systems 7:163-178.

McKeon G M, Rickert K G, Robbins G B, Scatini W J and Ivory D A. 1980. Prediction of animal performance from simple environmental variables. In: Proceedings of the 4th biennial conference of the Simulation Society of Australia. Brisbane, Australia. pp. 9-16.

McKeon G M, Rickert K G, Ash A J, Cooksley D and Scatini W J. 1982. Pastoral production model. Proc. Aust. Soc. Anim. Prod. 14:201-204.

Parton W J and Singh J S. 1984. Adapting a biomass simulation model to a tropical grassland. Ecol. Model. 23:151-163.

Penning de Vries F W T and Djiteye M A (Eds). 1982. La productivité des pâturages sahéliens: Une étude des sols, des végétations et de l'exploitation de cette ressource naturelle. Agric. Res. Reports 918. PUDOC, Wageningen. 525 pp.

Powell M. 1984. Cropping and crop-livestock interactions. In: Livestock systems research in Nigeria's subhumid zone. Proceedings of the 2nd ILCA/NAPRI symposium, Kaduna, Nigeria. 29 Oct - 2 Nov 1984. ILCA, Addis Ababa.

Pullan N B. 1980. Productivity of White Fulani cattle on the Jos Plateau, Nigeria. II: Nutritional factors. Trop. Anim. Health Prod. 12:17-24.

van Raay H G T and de Leeuw P N. 1974. Fodder resources and grazing management in a savanna environment. Occasional paper No. 45, Institute of Social Studies, The Hague, The Netherlands.

Rice R W, MacNeil M D, Jenkins T G and Koong L J. 1983. SPUR livestock component. In: J R Wight, ed. SPUR simulation of production and utilization of rangeland: a rangeland model for management and research. Misc. Publ. 1431, USDA.

Sanders J O and Cartwright T V. 1979. A general cattle production systems model. II. Procedures used for simulating animal performance. Agric. Systems 4:289-309.

Stewart J I and Faught W A. 1984. Response farming of maize and beans at Katumani, Machakos district, Kenya. East Afr. Agric. For. J. 44:29-51.

Sullivan G M, Cartwright T C and Farris D E. 1981. Simulation of production systems in East Africa by use of interfaced forage and cattle models. Agric. Systems 7:245-265.

Wagenaar K T and Kontrohr E. 1986. Validation of the ILCA model on cattle herd dynamics with data from pastoral systems in Mali and Kenya. In: N de Ridder, H van Keulen, N G Seligman and P J H Neate, eds. Modelling of extensive livestock production systems. Proceedings of the ILCA/ARO/CABO workshop, 5-9 Feb 1985, Bet Dagan, Israel. ILCA, Addis Ababa.

Wagenaar K T, Diallo A and Sayers A R. 1984. The productivity of transhumant Sudanese Fulani cattle in the Niger Inner Delta. Internal report, ILCA, Addis Ababa, Ethiopia.

Wilson R T. 1983. Production animale. In: R T Wilson, P N de Leeuw and C de Haan, eds. Recherches sur les systèmes des zones arides du Mali: résultats préliminaires. ILCA Research Report No. 5. ILCA, Addis Ababa, Ethiopia.

Wilson R T and Semenye P P. 1983. Livestock productivity and management. In: Proceedings of a workshop on 'Pastoral systems research in sub-Saharan Africa.' ILCA, Addis Ababa, Ethiopia. pp.151-180.

Wight J R. (Ed.). 1983. SPUR simulation of production and utilization of rangeland: a rangeland model for management and research. Misc. Publ. 1431, USDA.

Wylie B R, Sencock L, Snyder B, Roentgen B and Porter B. 1983. Range research and results. USAID/NRL preliminary report, Niamey, Niger.

Discussion

Question - The upper line in Figure 1 is based on data from enclosed areas. All the plotted data from van Wyngaarden seem to fall below this line. Are those data collected from grazed areas?

Answer - I am not sure.

Question - Is your poor year in Figure 3 a really poor year? You measured 3.5 t/DM/ha with 450 mm of rainfall. In a really poor year I would expect higher CP%.

Answer - It was below average. We did not have enough data to compare standing crop of the same age with low and high rainfall, but we did look at the correlation between quality and quantity.

Quality should be higher in a bad year than in a good year, but my figures do not show that, because the sampling system was not designed to prove that particular point.

Question - What do you mean by boom and bust periods?

Answer - That is the long term fluctuation of good and bad periods of about 5 years each.

Question - Bad and good years in rainfall or also in productivity?

Answer - Difficult to say, since we only collected data for two years. But calculations of productivity indices for systems in Mali, Nigeria, Kenya and Sudan did indicate much similarity.

Question - Would you say that there is a strong stabilising factor in the system which maintains a fairly constant reproduction rate, and that all of the variations that we are looking at in detail are in fact elements of one system?

Answer - It is a very interesting hypothesis to test.

Comment - I do not agree with your conclusion that there is little difference in productivity of livestock systems in semi-arid Africa. Your hypothesis is very dangerous, because it doesn't show whether the system is in a steady state or not, whether herds are growing or dying out. You should first check if your parameters of reproduction and mortality can create a viable herd or not.

Comment - I agree that we have to take into account good and bad situations. I calculated a productivity index for four or five systems in Africa and they all seem to have the same ratio, but I want to make the point that this index will not discriminate between a higher productivity of milk in one system and higher calving rates and lower calf mortality in another system, because of the relationship between calving rates, calf mortality and milk offtake.

Reply - The final productivity index obscures the difference in values among its various factors. It is only useful as a broad comparison of productivity. Despite the uniformity over systems, you will find big differences between individual flocks and herds in the area, associated with some aspect of management or health. This indicates that the system can be manipulated.

Question - Are you sure that the difference between herds is not a matter of inequitable distribution of resources: some are doing well because others are doing badly?

Answer - As soon as someone loses 50% of his herd, flock productivity index is low as compared with those who did not lose stock, but productivity per animal is not so depressed.

Comment - I would like to add something to that question of large differences between the individual flocks. It is irrelevant to all systems which are close to maintenance because under such circumstances small improvements in feed conditions can have a tremendous effect on productivity. A 12% increase in energy could double the liveweight gain or make the difference between weight gain and weight loss.

Analysis of management impact in semi-arid agropastoral systems

Eugene D. Ungar

Introduction

The integration of wheat and sheep production has been examined in the field over a number of years at the Migda experimental station in the northern Negev. Research at Migda has aimed at determining the potential primary and secondary production in such an environment and in designing farming systems that could be implemented widely in the region. These systems would aim to provide a more stable income than the pure wheat production system that currently predominates.

In conjunction with research at Migda, a modelling study was conducted to examine the management problems involved in operating intensive agropastoral systems in a semi-arid environment. The aim was to develop a procedure for improving decision making, with an emphasis on management options created by integration with wheat production.

The system studied is lamb production from a flock of sheep, of constant animal number from year to year, reproducing once a year at fixed dates. The flock is sedentary, grazing a rain-fed area (individual use) consisting of annual vegetation (all species of similar growth and palatability) in a semi-arid, winter-rainfall zone with mild to cool winters. The pasture is fertilized and the animals are supplemented to 'optimal' production. The economic environment is characterised by a high meat: grain price ratio. There is no drinking water limitation. Most importantly, the pastoral component is integrated with small grain production (wheat).

Approach

The approach adopted was to develop a series of optimisation algorithms for individual management decisions that can be usefully examined in isolation. The system model is built around these algorithms, rather than constructing a single biological simulator for the entire system with a large set of management control parameters. In this problem-oriented approach, the algorithms were developed independently with little emphasis on consistency of resolution or precision between them. Each optimisation algorithm is based on relatively simple biological formulations that seek to incorporate the essential dynamics of the relevant subsystem.

Emphasis was placed on using the models (1) to derive practical guidelines and rules for optimal management that would obviate the need for a model by the decision-maker and (2) to indicate not only the optimal management decision but also the cost of poor decision-making resulting from indifferent management, inadequate model formulation or poor field monitoring for parameterisation purposes.

By linking the individual decision algorithms to a relatively detailed biological simulation framework, system response to structural management decisions, such as stocking rate and land allocation, can be examined. In addition, using a higher-resolution whole-system simulation framework enables the optimality of solutions derived from simpler models to be evaluated.

Decision algorithms

Early-season grazing of green wheat

Under deferred-grazing management, the flock is generally maintained in a holding paddock or supplementary feeds. The cost of feeding can be high since this period usually coincides with pregnancy or early lactation. A significant reduction in these feed costs can be achieved by grazing green wheat during some part of the deferment period. Experiments at Migda indicate that there is a period of at least six weeks after emergence of wheat during which defoliation does not cause a significant reduction in grain yield. Beyond this period, defoliation reduces grain yield, the effect on yield increasing with lateness and severity of defoliation. Thus, if grazing is restricted to the no-damage period, the problem can be formulated as minimising supplementation costs over the possible wheat grazing period. In a target-oriented approach to animal (ewe) feeding, this is equivalent to maximising herbage utilisation over the same period. The problem is therefore to determine the day of flock entry to the wheat that will maximise cumulative herbage consumption.

The problem has been defined in terms that are closely related to the management decision itself rather than in terms of maximising overall system profitability. In the latter case, an optimal solution may well have been found using a total-system simulator. However, the solution would most probably have appeared arbitrary in the sense that the underlying reasoning or principle that determines the solution may have remained obscured in the sheer impenetrability

so characteristic of total-system models. It is suggested that the insight into the essential dynamics of a problem that can be gained from analysis with simple models is more important than any claim to increased accuracy of solution that the 'big' model can provide. Perhaps the view should be added that simpler does not necessarily mean less explanatory or mechanistic.

The simple model used to locate the optimal day for stock entry is based on an exponential growth function (realistic for the early growth stage) and a ramp consumption function. All sections of the study connected with grazing dynamics were strongly based on the analyses of Noy-Meir (1975a; 1975b; 1978a; 1978b). Table 1 briefly describes the model and lists the parameters required and a guess at the ease of monitoring them on-farm. Clearly, if the algorithm were to be applied at a specific location, a number of parameters would have to be based on other, possibly very different, locations. The relative growth rate (g) and stocking rate (H) are two parameters most likely to vary between locations and so these were chosen as criteria for exploring the response space. Figure 1 shows the response surface of mean daily intake rate per animal during the grazing period (for the optimal entry day) to stocking rate and relative growth rate. A sensitivity analysis was carried out in which the mean daily intake rate per animal was calculated for a fixed entry day of 25 days after emergence for the same H-g space. The shaded area in Figure 1 represents zones of this space for which an entry day of 25 days after emergence yields an intake rate with 10% of the optimised value.

On the basis of this analysis one might tentatively conclude that, for a specific site, a single robust solution for stock entry day can be derived given reasonable parameter estimation. The robustness, or otherwise, of the system as a whole to this management decision will be discussed later.

Green pasture grazing deferment

The management decision of when to commence grazing of green pasture is a major determinant of pasture dynamics. The optimal deferment period is that which enables maximum herbage utilisation. Utilisation can be defined in terms of green-herbage consumption and dry-herbage consumption weighted according to their relative nutritive values. In addition, in the integrated agropastoral system, the lower requirement for dry-pasture herbage due to the availability of wheat aftermath can be taken into account.

Table 1. Model to optimise early-season grazing of wheat: description, assumptions and required parameters.

Problem: Find entry day to wheat (a) such that cumulative herbage consumption between decision time and final wheat grazing day is maximised.

Model: Maximise $\int_{t=a}^{x} C \, dt$

Herbage growth rate (exponential): $\frac{dV}{dt} = g\,v$

Herbage consumption rate (ramp): $C = H \min(s(V-V_r),\ c_s)$

Important auxiliary assumptions: Constant animal performance (=target-oriented approach), therefore constant energy requirements which must be met, therefore cost of deferment does not effect solution.

Required parameters	Ease of on-farm monitoring*
Number of ewes/hectare wheat (H)	1
Number of days since emergence	2
Final wheat grazing day (x)	2
Residual ungrazable biomass (V_r)	5
Current biomass (V)	3
Relative growth rate (g)	4
Grazing efficiency parameter (s)	5
Satiation intake rate of wheat (c_s)	5

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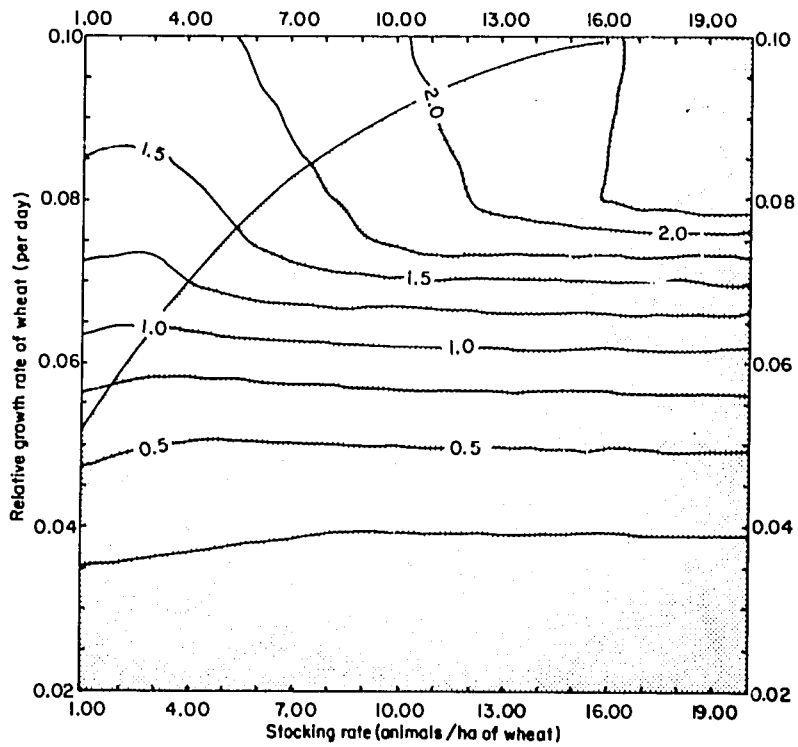
* 0 = easy/readily available information, 5 = extremely difficult.

The simple model used to determine the optimal stock-entry biomass or day is based on a logistic growth function and a negative exponential consumption function. Table 2 briefly describes the model and required parameters.

Figure I. Results of the early-season wheat grazing algorithm. Contour map of the mean daily herbage intake rate (kg/animal/day) as a function of relative growth rate of wheat per day and stocking rate (animals/ha wheat) for the period from the optimal stock entry day to the end of the early-season grazing period



It seems reasonable to venture, as a crude generalisation, that the number of parameters in a model stands in inverse relation to the experimental or analytic effort invested in establishing their values. In this study, it was possible to devote considerable effort to establishing the intake function and long-term average parameter values for the logistic pasture growth function. In the latter case, a relatively high resolution model was used to simulate 20 growing seasons and the simulated results were analysed statistically. Sometimes, though, the simple model becomes so succinct and abstract that the parameters become meta-parameters and not directly measurable. This objection can be countered by the fact that this implied distinction between theoretical construct and observable data has yet to be successfully argued by philosophers of language.

Figure 2 shows the relationship between the herbage consumption objective function and length of deferment for various stocking rates. Note the increasing sensitivity to decision-making with increasing stocking rate. One way of analysing the cost of poor parameter estimation is to map out the response surface of the decrease in objective function to actual and estimated parameter values. An example is shown in Figure 3 for the relative growth rate parameter. To construct this response surface, the optimal entry day is calculated using an estimated g value in the optimisation algorithm. This deferment period is then implemented in the deferment model using a wide range of actual g values. The consumption objective function is calculated for each actual value taken and the reduction in cumulative consumption caused by a suboptimal deferment period is computed. The response surface of forfeited utilisation is not exactly intuitively obvious. However, with a model of such simplicity, it is not a major undertaking to 'take it apart' and find out why such surfaces are obtained.

Lamb feeding

The management decision regarding supplementary and complete ration feeding of lambs essentially consists of whether or not to provide feed and at what rate. The choice of feed is not considered here; it is assumed that a high-energy and high-protein concentrate feed is available. Since only the maintenance and liveweight change functions are involved in the growing lamb, the problem of lamb feeding is amenable to optimisation.

Table 2. Model to optimise green-pasture grazing deferment: description, assumptions and required parameters.

Problem: Find entry day (a) to green pasture such that cumulative herbage utilisation between decision time and expected start of next green season is maximised.

Model: Maximise $\int_{t=a}^{x} C\, dt + \min(V_1+V_m(1-I)R,\ n\,H\,c_s)F$

Herbage growth rate (logistic): $\frac{dV}{dt} = gV(1 - \frac{V}{V_m})$

Green herbage consumption rate (negative exponential):

$$C = c_s\ (1 - \exp(-(V-V_r)/(V_s-V_r)\ )$$

Important auxiliary assumptions: Constant animal performance (= target-oriented approach) therefore constant energy requirement which must be met, therefore cost of deferment does not effect solution. Interactions between time of stock entry, sward canopy structure and herbage quality are ignored.

Required parameters	Ease of on-farm monitoring
Cumulative green pasture consumption (C)	computed
Time of end of green season (long-term average) (x)	2
Dry pasture biomass remaining at the end of the green season (V_1)	computed
Peak undisturbed pasture/wheat biomass (long-term average) (V_m)	5
Fraction of peak wheat biomass that remains available for grazing after harvest (long-term average) (1-I)	4
Ratio of wheat to pasture area (R)	1
No. days from end of green season to start of the next (long-term average)	2
No. of ewes/hectare pasture (H)	1
Satiation intake rate at green/dry pasture (c_s)	5
Relative value of dry: green pasture (F)	5
Relative growth rate (long-term average) (g)	5
Current biomass (V)	3
Residual ungrazable biomass (V_r)	5
Biomass for intake satiation (V_s)	5

* 0 = easy or readily available information, 5 = extremely difficult

The system, as defined in the introduction, is limited in the amount of product rather than by the production rate. The product of the number of lambs born, the maximum saleweight and the price of meat constitutes an income ceiling that cannot be exceeded. Hence, annual profit is maximised by maximising profit per unit output rather than per unit time and the optimal feeding level is that which minimises the cost per unit liveweight gain. The fact that time itself may represent a cost in terms of interest and risk does not alter the underlying approach. Such factors can be incorporated into the computation of cost per unit liveweight gain.

Figure 2. Results of the green pasture grazing deferment algorithm: the relationship between normalised herbage consumption and the length of the grazing deferment period, for various stocking rates

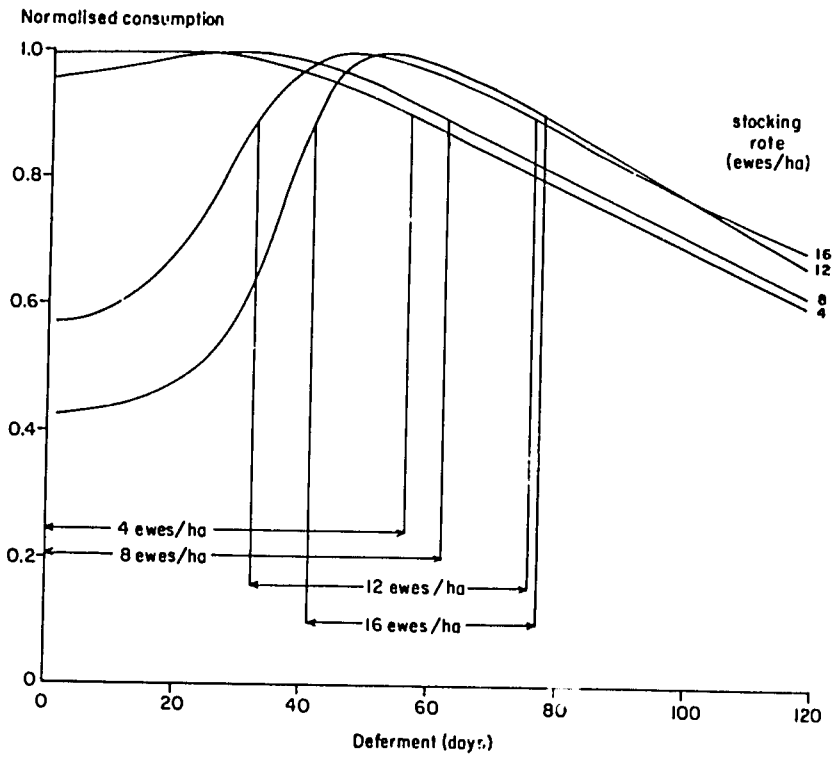


Figure 3. Results of the green pasture grazing deferment algorithm: the response surface of forfeited intake (kg/ha) resulting from poor parameter estimation to actual and estimated relative growth rate (g), at a stocking rate of 5 ewes/ha of pasture

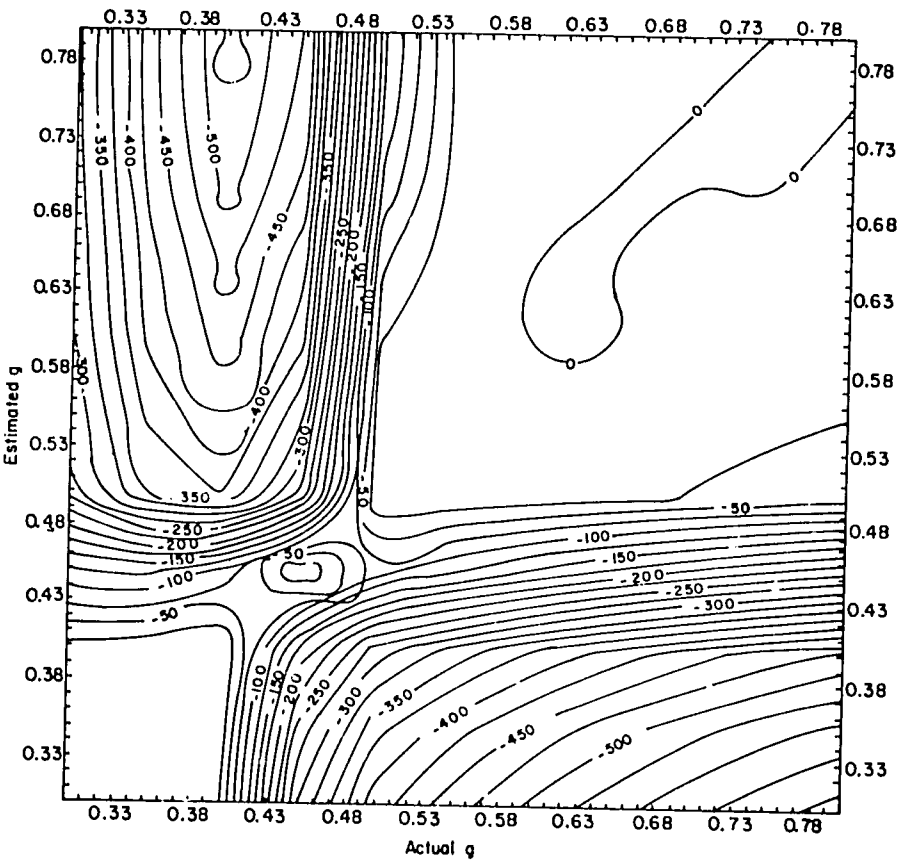


Figure 4 outlines the main elements of the feeding optimisation algorithm. Analytic treatment of the problem can yield useful formulae for certain restricted cases only.

The general relationship between cost per unit liveweight gain and supplementation rate is for the cost to decline rapidly with increasing supplementation rate down to the minimum point, and to subsequently increase relatively slowly. If the animal can put on weight at a reasonable rate in the absence of supplementation, then the function is at the minimum at zero supplementation and the cost per unit gain increases over the entire supplementation range.

The problem of monitoring for parameterisation purposes is severe, though perhaps it is misleading to apply the term 'monitoring' to parameters that are (wishfully) treated as universal constants. Even so, there remain items such as lamb liveweight and pasture intake. An appealing solution to that problem is to simulate what you cannot measure, which has the additional advantage of greatly simplifying model validation. Given these limitations, it becomes even more imperative to extract rules of operation which can be implemented relatively easily. Towards this end, the following conclusions were drawn on the basis of extensive runs of the feed optimisation algorithm.

a. The optimal supplementation level is virtually independent of the meat price; as long as the cost per unit gain is less than the meat price, it is optimal to continue lamb rearing according to the solution provided by the algorithm.

b. At pasture, if some minimal growth rate can be supported in the absence of supplementation, then no supplements should be provided. If pasture intake in the absence of supplementation is insufficient to support growth, the optimal supplementation level tends to be ad lib.

c. The response space of optimal supplementation level to a number of parameters shows large regions of zero and ad lib supplementation mediated by a fairly narrow zone of intermediate supplementation levels. It is reasonable to assume that, under field conditions, the system will traverse this boundary region fairly rapidly and the management problem of lamb supplementation reduces to a choice between two extreme, easily implemented, actions.

Figure 4. Main elements of the lamb feeding optimisation algorithm

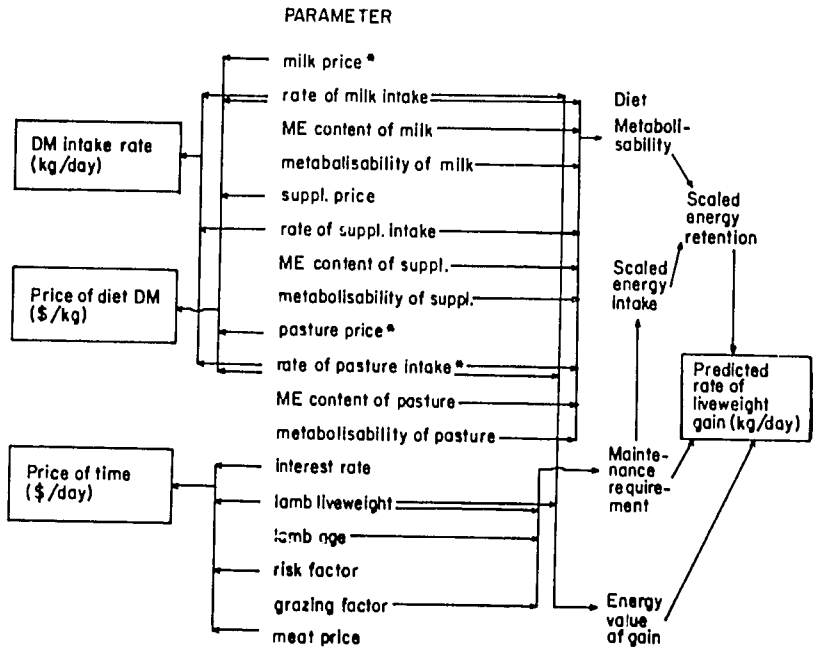
Problem: Find the supplementation rate for a lamb at pasture or in a fattening unit, sucking or weaned, that minimises the cost per unit liveweight gain

Model: Based on standard ARC equations

$$\text{Cost per unit gain } (\$/kg) = \frac{\text{Price of diet DM} * \text{DM intake rate} + \text{price of time}}{\text{Predicted rate of liveweight gain}}$$

Minimum found numerically.

Important auxiliary assumptions : Constant prices



* Computed variables dependent on a number of other parameters

d. Time-based costs only begin to take on importance at extremely high leves (much higher than the interest cost on the value of the lamb liveweight).

Lamb rearing

The management problem of lamb rearing consists of selecting a rearing pathway that maximises profits. The rearing pathway is a nutritional time course where nutrition is determined by the physical location of the lamb in the system, whether or not the lamb is sucking, and the supplementary feeding regime. In an agropastoral system, seven nutritional locations can be defined: holding paddock, pasture, wheat (each sucking or weaned), and fattening unit (weaners only). In the expanded system, there may also be a special-purpose pasture for lamb fattening, as a forward creep or for weaners. (The fattening unit and holding paddock are nutritionally equivalent.)

The rearing options can be defined in a lamb-movement matrix which specifies the possible flow links between each of the rearing locations. A standard configuration is shown in Table 3. Having defined the optimal supplementation level for any given location on the basis of minimum cost per unit liveweight gain, the same principle can be extended to selecting between locations. The optimal location at any point in time is the one that provides the lowest cost per unit liveweight gain. Thus the lamb-movement algorithm predicts lamb performance for each possible alternative, as defined by the movement matrix, and does so at the optimal supplementation level for each one. Lambs are moved to the location that provides the lowest cost per unit gain. Using this approach, it is not necessary to arbitrarily set criteria for weaning, supplementation or lamb sale.

This crude short-term optimisation approach is inadequate if the response surface of profit to rearing pathway has local optima that represent a significantly lower total income to the global optimum. This would mean that there are circumstances in which it might be more profitable to suffer poor economic performance in the short term in order to follow a pathway of high income accumulation later. Such a possibility is not taken into account in this approach. However, the lamb-movement matrix enables the optimality of the solution under the standard matrix setting to be checked by simply using the matrix to force alternative rearing pathways. Testing of the algorithm requires a total system model with the necessary interfacing with pasture production and ewe performance. Results from the algorithm will be discussed later.

Table 3. The standard configuration of the lamb-movement matrix — a definition of the possible flow links between nutritional locations of a lamb in an agro-pastoral system.

	To					
From	Holding paddock Sucking	Holding paddock Weaned	Pasture/wheat Sucking	Pasture/wheat Weaned	Spec.-purpose pasture Weaners	Fattening unit Weaners
Holding paddock						
- sucking	1	1	1	1	1	1
- weaned	0	1	0	1	1	1
Pasture or wheat						
- sucking	1	0	1	1	1	1
- weaned	0	0	0	1	1	1
Special purpose pasture	0	0	0	0	1	1
Fattening unit	0	0	0	1	1	1

1 = possible flow.

0 = non-feasible or restricted flow

The agropastoral system model

The various short-term decision algorithms, including a number not described above, were incorporated as subroutines into an overall biological simulation framework. Primary production (pasture, wheat, special-purpose pasture) was based on ARID CROP (van Keulen, 1975). Secondary production of ewes and lambs was based on ARC equations (ARC, 1980), some functions based on Migda data and a few speculative hypotheses regarding the response of ewe lactation to level of nutrition. The primary and secondary production sections were interfaced by a low-resolution intake subroutine. (A detailed description of the model is given in Ungar, 1984.) The model was implemented using 21 years of climatic data for Migda in the northern Negev. The standard run refers to a land

allocation of 50% natural pasture, 50% wheat (no special-purpose pasture), a stocking rate of 10 ewes/ha of pasture and a meat grain price ratio of 10:1. Ewe prolificacy is low-to-medium relative to the potential in the field.

Response to management at the system level

The following results were obtained at the system level regarding the short-term management decisions discussed earlier.

Early-season grazing of green wheat: Despite the seemingly significant saving in feed costs that should derive from utilising early-season green wheat, there are compensatory effects operating at the system level that reduce the opportunity cost of this management option (Table 4). Firstly, by not grazing the wheat the ewe spends more time in the holding paddock but the total seasonal energy requirements of the ewe are thereby reduced. Secondly, early-season grazing reduces the peak biomass and hence quantity of wheat aftermath for dry-season grazing. Though the straw baling decision algorithm was not described above, Table 4 shows the response of the system to various management options regarding aftermath utilisation. The 'normal' straw-baling criterion is simply to bale everything in excess of the expected requirement until ploughing time, while the remainder is left in the field to be grazed. Unless the manager makes obviously stupid decisions, he is generally operating in an insensitive zone of response space.

Green-pasture grazing deferment: The optimality of the optimisation algorithm for grazing deferment was examined using the relatively complex system model. The optimal entry biomass (OEV) supplied by the deferment algorithm was multiplied by a factor ranging from zero (no deferment) to 1.2, and the adjusted value used to determine stock entry in the system model. The results for 21-year runs are summarised in Table 5. The gross margin (GM) response to deferment is quite flat over a broad range at the standard stocking rate. Factors such as the relative timing of lambing and break of season, changes in the lamb-rearing pathway with changes in OEV and even the length of the management decision time step can contribute to the buffering capacity of the system.

Table 4. Comparison of alternative strategies of wheat utilisation in feeding the ewe. Alternatives are arranged in descending order of profitability.

Early wheat grazing	Wheat aftermath grazing	Straw baling*	Gross margin
No	Yes	Max	109.9
Yes	Yes	Max	106.6
No	No	Reg[a]	105.2
Yes	No	Reg[b]	103.0
Yes	Yes	Reg[c]	97.7
No	Yes	Reg	93.1
Yes	Yes	No	82.1
No	Yes	No	71.6
Yes	No	No	68.1
No	No	No	56.3

* Max = always bale if biomass > 1000 kg/ha,
Reg = normal straw baling criterion.

a. Equivalent to No No Max.

b. Equivalent to Yes No Max.

c. Standard run.

Gross margin is mean for 21 years, in $/ha.

The mean GM for the non-adjusted OEV was only 8% below the maximum value obtained. However, there is really no justification to assume that the system-model optimum is necessarily more accurate than that generated by the deferment algorithm. Rather, such a test of optimality lends confidence to the aproach of utilising a low-resolution algorithm for decision making.

Lamb feeding and rearing: The approach taken to lamb rearing via use of the lamb-movement matrix opens up a large range of rearing permutations. Despite this, the algorithm almost always selected fairly conventional patterns and, in so doing, offerred a straightforward explanation as to why such pathways are indeed preferable.

Table 5. Analysis of sensitivity to the length of the grazing deferment period. Deferment is defined in terms of the optimal entry biomass (OEV) as determined by the simple grazing deferment model.

OEV multiplication factor	Gross margin
0	86.3
0.1	92.8
0.2	98.3
0.3	103.0
0.4	104.8
0.5	106.0
0.6	106.7
0.7	103.3
0.8	102.0
0.9	99.5
1.0*	97.7
1.1	96.8
1.2	95.3

Gross margin is mean for 21 years, in $/ha.
*Standard run.

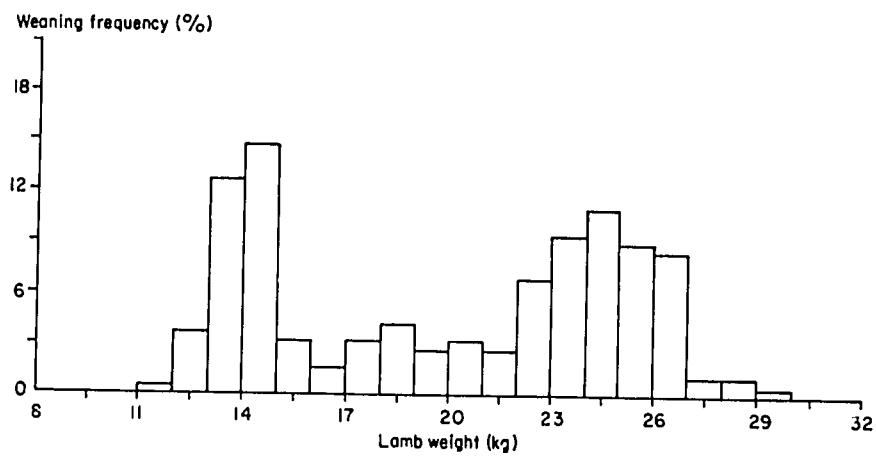
The overall performance of the rearing algorithm can be summarised as follows:

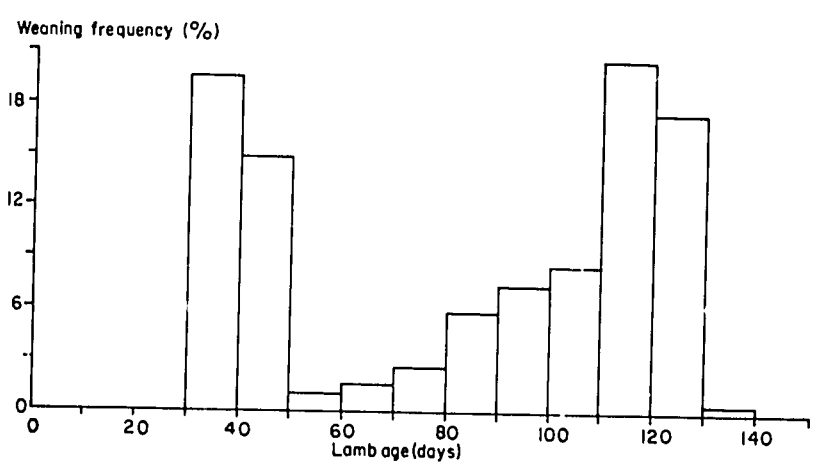
- At a meat:grain price ratio of 10:1, lambs are always reared to the saleweight limit of 45 kg. Lambs would be sold at lower weights in the absence of a fattening unit.
- Weaning tends to occur either early (30-50 days of age) or late (110-130 days of age) and relatively less in the intermediate period (Figure 5). The main determinant of weaning is season, though there is a tendency for weaning age to decline with stocking rate. In a number of seasons an increase in stocking rate caused a switch from late to early weaning.

- Lambs are almost always moved to the fattening unit at weaning. In only a few instances are weaners kept at pasture for any period of time.
- Lamb supplementation tended to switch rapidly from zero to ad lib shortly before transfer from pasture to fattening unit.

By forcing the selection of alternative pathways, the lamb-movement matrix can be used to evaluate the optimality of a given pathway. An example of such an exercise is shown in Figure 6 in which four alternative rearing pathways

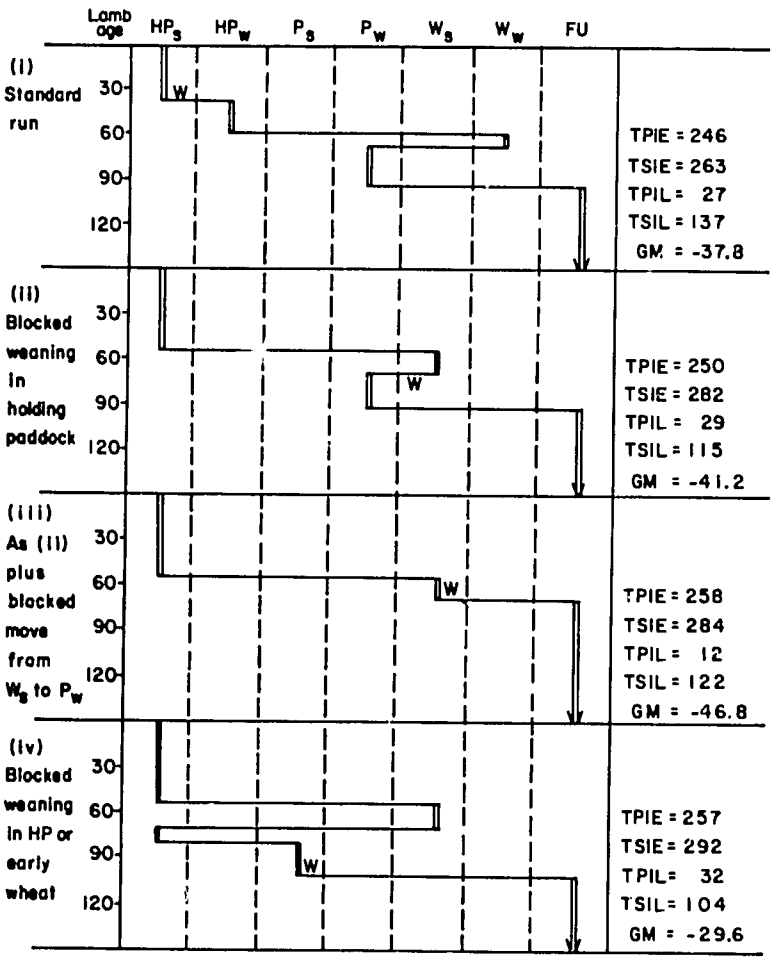
Figure 5. Bar chart of weaning frequency according to lamb weight and age, based on 189 seasons (nine sets of 21-year runs) using various combinations of stocking rate and land allocation





were examined for the 1976/77 (poor rainfall distribution) season, at a stocking rate of 7.5 ewes/ha of pasture. Clearly, the principle of short-term optimisation in lamb rearing does not always lead to a global optimum. However, in all cases examined, the default-matrix setting yielded solutions close to the 'after-the-fact' global optimum (found by trial-and-error). Here again, there are compensatory effects inherent in the biology of the system that tend to reduce the opportunity cost of suboptimal lamb rearing. This is evident to some extent in the supplementation values shown in Figure 6.

Figure 6. Comparison of four alternative lamb rearing pathways for the 1976/77 season



HP_s, HP_w - holding paddock; sucking, weaned.
P_s, P_w - pasture; sucking, weaned. W_s, W_w - wheat; sucking, weaned.
FU - fattening unit (weaned). W - weaning.

TPIE, TSIE - total herbage, supplements intake/ewe (kg)
TPIL, TSIL - total herbage, supplements intake/lamb (kg)
GM - gross margin ($/ha)

Concluding remarks

Is the agropastoral system robust, insensitive, sluggish to respond to management? (Can such assertions be extended to complex agricultural systems generally?) Does management matter or is the multi-dimensional response space characterised by gently undulating plains? Perhaps looked at from a sufficient distance, any surface appears flat, and the perspective of the observer is what really counts. For the farmer, a small 'pot-hole' might mean a discernable difference in his income - and sensitivities are generally high to reductions in income. For the planner, such variation may simply be noise.

In one sense, the economic performance of agropastoral systems must be robust by the mere fact that (a) they are practiced at all in one form or another under conditions of weather unpredictability, price uncertainty, and total absence of quantitative monitoring, and (b) if managers were confronted by precipitous cliffs on all sides, many of the questions examined in this study would have been solved (at least empirically) long ago and there would have been no need for the model.

On the other hand, there are clearly dangers in operating such systems. Firstly, the higher the system intensity (e.g. stocking rate, prolificacy) the less leeway does the manager have in decision making. Careful monitoring becomes more important and a greater responsiveness in management is called for. Secondly, it should be noted that the management model is very much self-correcting in that all short-term decisions are based on the state of the system at the decision time (as opposed to fixed strategies) and therefore respond to errors in previous decisions. Operating according to fixed strategies is likely to exhaust the compensation capacity of the system very quickly.

So the answer for the farmer might be, if management standards are low performance might be very erratic. If management standards are good, a high degree of robustness can be expected. Nevertheless, the difference in income between excellent and good management would seem to be very significant.

References

ARC (Agricultural Research Council). 1980. The nutrient requirements of ruminant livestock. HMSO, London, UK. 351 pp.

van Keulen H. 1975. Simulation of water use and herbage growth in arid regions. Simulation Monographs. PUDOC, Wageningen, The Netherlands. 176 pp.

Noy-Meir I. 1975a. Primary and secondary production in sedentary and nomadic grazing systems in the semi-arid region: Analysis and modelling. Research report to the Ford Foundation, Project 7/E-3. Department of Botany, the Hebrew University, Jerusalem, Israel.

Noy-Meir I. 1975b. Stability of grazing systems: an application of predator-prey graphs. J. Ecol. 63: 459-481.

Noy-Meir I. 1978a. Stability in simple grazing models: effects of explicit functions. J. Theor. Biol. 71:347-380.

Noy-Meir I. 1978b. Grazing and production in seasonal pastures: analysis of a simple model. J. Appl. Ecol. 15: 809-835.

Ungar E D. 1984. Simulation of grazing systems in semi-arid regions. Ph.D. thesis, The Hebrew University of Jerusalem, Israel.

Discussion

Question - In the model constant prices are assumed. In a situation with fluctuating sales prices it could be profitable to alter the fattening period: take longer for the growing period, and supply less costly feed. Could you optimise under that assumption?

Answer - Not yet, because the assumption of constant prices is critical to this whole approach. With fluctuating prices adjustments must be made using common sense. I started working on this, trying to solve it analytically, but it is tricky.

Comment - You could check the effect of a different feed with a different price and feed value as long as it was constant for the period.

Reply - Yes, and the results did not change, except for a different level at the end. I also want to point out that the interest rate does not matter, i.e.the point of transfer from pasture to fattening units shifted by at most a few days, when ridiculously high interest rates were assumed. So these time- based costs, in a reasonable range, are not important.

Question - Is there a minimum sale weight target for those systems?

Answer - The target weight used is 45 kilograms. In the model the lambs are always sold at the upper sale weight limit, rather than as a result of the cost per unit liveweight gain exceeding the price of meat.

Comment - If there is some minimum sale weight, then in moving a lamb through a certain pathway several options will disappear in time because they would not produce that minimum weight.

Reply - That is not relevant as long as the animals grow. I work with minimum cost per unit liveweight gain. If time has a cost to it, that cost is included in the equation and converted to the cost per unit liveweight gain. So, as long as the animals grow they do so at minimum cost until they reach the upper weight limit. An interesting result of the model is that if there is no fattening unit then the lambs are sold earlier, at about 30 kg of liveweight, which is what

happened in the Bedouin systems before they started using large amounts of supplementary feed. The reason is that it is not profitable to supplement at pasture due to the higher maintenance requirements of the animal, leading to a cost per unit liveweight gain exceeding the price of meat. In a fattening unit the cost per unit liveweight gain, at the optimal supplementation level, is less than the price of meat and the profits increase by selling at a high liveweight. Having a fattening unit is thus critical to the profitability of the system.

Question - Is the cost per unit liveweight gain not time-dependent because of the maintenance requirements? Higher maintenance costs lead to longer fattening periods and hence to higher costs per unit liveweight gain.

Answer - Yes, therefore at growth rates close to zero the cost per unit liveweight gain increases dramatically. If the growth rate is 1 g/day the costs per kilo are tremendous. But if the system operates continuously at the minimum cost per unit liveweight gain while the animals are growing, it will lead to the maximum profit at the end.

Comment - But the total cost is changing, because both the average cost per unit liveweight gain and the number of days required to reach the target weight are changing.

Reply - That is right, but as long as at each point the gain is produced at minimum costs, the total costs will also be at a minimum. This was substantiated by, for example, forcing early weaning and transfer to the fattening unit onto the model. The target weight was reached much earlier then, but because of the high cost the profit was lower.

Question - Would your conclusion be that such agropastoral systems are more robust than pastures only because they allow the farmer to do almost anything?

Answer - Within limits yes, but the higher the system intensity, i.e. the higher the stocking rate, the more the cliff-edge syndrome is operating. Its position with respect to pastures only very much depends on the meat/grain price ratio. In the present agropastoral system there is a pastoral component and a wheat component. The presence of the wheat aftermath is a very important slack in the

system. In the model all kinds of decision algorithms are included that help in deciding whether to bale that straw and feed it indoors or graze it. Again it appears that the trade-offs are very finely balanced, and that the result is insensitive to the decision.

Comment - You have missed a very important point: the inference is that the agropastoral system is more robust because its performance is less sensitive to the decisions of the manager.

Reply - Yes. However, the optimal allocation between wheat and pasture is very dependent on the meat/grain price ratio, as is the optimal strategic set up of the system in terms of prolificacy, stocking rate and land allocation. But all the response surfaces have very flat zones and usually the area of operation is exactly there. If, as a farmer, you take all the wrong decisions you are going to lose money and you are really swimming against the flow of the river. The model should point out which way the river is flowing, where the rapids are, where the cliff edges are. Subsequently the behaviour of the manager depends on what he wants: if he is willing to take high risks, there is a chance of making high profits. Generally it is better to operate in the safe zone, at a reasonable intensity.

Question - Is the greater biological stability not simply due to an overall reduction in stocking rates, due to the presence of that wheat area and to the use of concentrates?

Answer - No; on the contrary, the stocking rate per unit area of pasture at the optimal level would be higher in an integrated system than in a true pastoral system. For the sake of comparison it should be expressed per unit area pasture. The concentrate serves as an important buffer in this system.

Comment - The system may be robust but in some years the situation will be bad and in others it may be pretty good. As a manager, it is about the best you can do, but it does not mean that because the system is robust in management it is that stable from year to year.

Answer - No, it is definitely not. On the contrary, the higher the system intensity, the higher the variability in income. An interesting result from the model was that, for the 20 years used in the study, an almost linear relation was found between rainfall and income. Repeating the analysis for a higher stocking rate resulted in a relation with a steeper slope, crossing the first one at about average rainfall. Hence, at a higher stocking rate in years with good rainfall income will be higher and in bad rainfall years, the losses will be greater, i.e. the variability is greater, with higher system intensity.

Comment - The same holds for biological productivity: increased system intensity increases variability.

Modelling economic outcomes of livestock production systems

Martin Upton

"A good model is one that abstracts from all the details that are unnecessary for the purpose of solving the problem at hand."

(Walsh and Gram, 1980)

"Farming systems research rests on two central propositions: (i) that effective research in agricultural technology starts and finishes with the farmer; (ii) that integration of the perceptions of biological and social scientists is an essential element in such research."

(CIMMYT, 1980)

The purpose of model building

Objectives and values

The purpose of model building is to improve our understanding of systems in order (i) to operate them, (ii) to repair them, (iii) to improve them and (iv) to construct new ones (Spedding, 1975). Applied to livestock production these aims amount to either better management of an existing system or the design of improvements. In either case some criteria are needed for evaluating performance. We can only judge whether a system is operating effectively if the objectives have been defined. Similarly, we can only judge whether an improvement has been achieved in relation to specified objectives.

It is now widely recognised that the producer's objectives are critical in this respect. There is no point in developing systems which maximise meat offtake per hectare if this is not the pastoralist's main objective; the new

system simply will not be adopted. Hence, effort is needed to elicit the livestock producer's aims, often no easy task, before evaluation can be attempted. Sometimes the producer's aims conflict with declared national objectives or the public interest, for instance where overstocking occurs. The solution then is to develop new institutions, which eliminate the conflict: New techniques of production on their own will not eliminate the conflict. It is assumed for the remainder of this paper that systems are operated and designed to meet the producer's objectives, insofar as they can be ascertained.

Closely linked with the formulation of objectives is the measurement of value. If we can evaluate inputs and outputs in the producer's terms, then system performance might be measured in terms of net increase in value (value added) or productivity (value of output divided by value of input). It may be noted that the two measures do not necessarily result in the same ranking. Thus, the productivity of small ruminants per kg liveweight of the dam is probably higher than for cattle, but the net liveweight production per dam per year is probably lower.

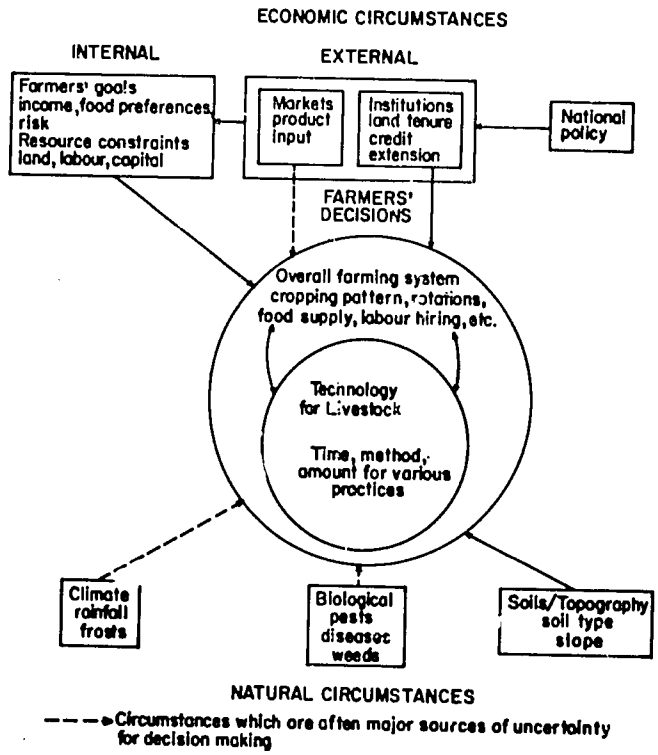
Within a system, inputs may be evaluated in terms of their contribution to output or value added, the measures being known as the 'shadow prices.' For instance, the shadow price of pasture might be measured in terms of livestock production from that land. Problems of valuing inputs only really arise where inputs cross the boundaries of the system. This consideration may influence where we draw the boundaries.

Boundaries of the system

The treatment of a very small part of the universe as a separate system is arbitrary in order to limit the scale and complexity of the modelling task. Generally, farming systems research is limited to those items which are under the producer's managerial control; his crops, his livestock and his family (Figure 1). However, there are various external relationships with the natural environment and the economic and social environment. Inputs and outputs must be evaluated at these boundaries.

The farming system may be subdivided into three main subsystems: crops, livestock and the household. Some livestock enterprises, such as pigs and poultry or small ruminants in West Africa, do not compete directly with crop production for the use of land. If there is division of labour within the

Figure I. Various circumstances affecting farmers' choice of a livestock technology (Based on: CIMMYT, *Planning Technologies Appropriate to Farmers: Concepts and Procedures* (Mexico: 1980))



household, the enterprises may not compete for labour. In these circumstances the livestock form a supplementary enterprise and may be considered independently of the rest of the farm.

For pastoral systems the three subsystems of rangeland, animals and household are clearly linked in both directions (Figure 2). Nonetheless, for purposes of analysis it may be necessary to model the subsystems independently and then to link the models together.

Time-dependence

Much farming systems analysis and model building is essentially static in nature. It is concerned only with inputs and outputs over a single production period, often taken to be one year. This may be appropriate in the case of annual crops, but represents an arbitrary curtailment of a time-dependent process when dealing with permanent crops or livestock. A breeding flock or herd of livestock, at any point in time, is the outcome of reproduction and growth in the past, and may be expected to survive into the future. In economic terms it is capital.

All populations of livestock, or anything else, develop over time according to what Boulding (1978) calls 'the bathtub principle,' namely that change in population over a given time interval is equal to inflows minus outflows. For a herd of livestock we have the simple difference equation:

$$P_t - P_{t-1} = B(t) - D(t) \qquad (1)$$

where P_t = herd population at date t

$B(t)$ = inflows in t-th time period (births and immigration)

$D(t)$ = outflows in t-th time period (mortality and offtake)

In practice, net immigration, through receipt of gifts or purchases from outside the herd, is often unimportant and may be ignored. Also, it may be convenient to separate offtake, a control variable directly under the producer's influence, from mortality, a parameter largely influenced by environmental factors (Figure 3). However, for simplicity, in the following remarks, the two are combined.

Figure 2. The Borana system

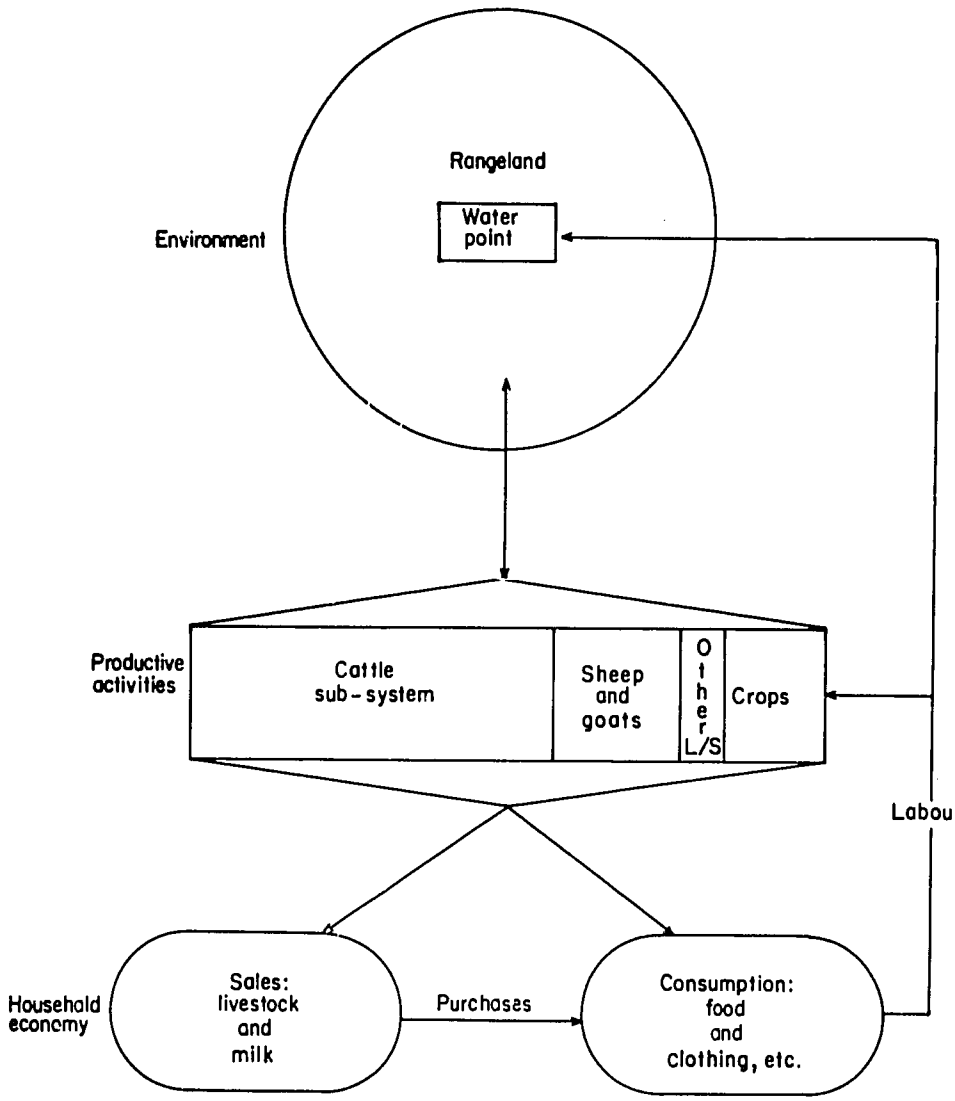
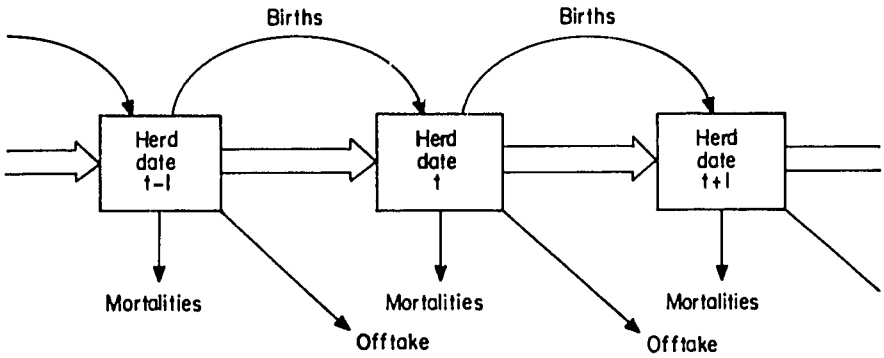


Figure 3. The dynamics of herd development



Generally, inflows and outflows are measured as proportions of the existing stock and are assumed to remain constant, on average, over time so that equation (1) becomes:

$$P_t = (b + 1 - d) \cdot P_{t-1} \qquad (2)$$

where b = rate of inflow (birthrate)

and d = rate of outflow (mortality and offtake)

$1-d$ = survival rate

If the herd is changing in size and perhaps ageing, there are problems in estimating the change in value; that is, the herd appreciation or depreciation. Most accounting methods are rather arbitrary. There are two ways of avoiding the problem. One is to consider the whole lifetime of a herd over many years and to use discounting methods for evaluation. The other, simpler, approach is to assume that herd size and structure remain constant, this being achieved by adjusting offtake so that inflows equal outflows. Thus the herd structure remains in a steady state or, more strictly, a stationary state.

In order to analyse the implications for herd structure, the herd should be subdivided into sex and age cohorts and reproductive rates and survival rates made age specific.[1] Equation (2) is then replaced by a set of simultaneous equations relating herd structure at date t to structure at date t-1. Thus, for instance,

Number of calves 0-6 months at date t

= net calving rate x number of cows at date t-1

Number of calves 6-12 months at date t

= survival rate 0-6 months x number of calves 0-6 months at date t-1

Choice of the number of age cohorts and the time interval between one date and the next involves a trade-off between complexity and precision, but also depends upon data availability. The whole simultaneous equation system may be represented in matrix vector form as

$$\underline{P}_t = [\ T\ ] \cdot \underline{P}_{t-1}$$

where $\underline{P}_t$ is a vector of populations at date t for each sex-age cohort and [T] is a transition matrix, based on reproductive and survival rates (see Hallam, 1983, or Murdie, 1976).

Cohort analysis shows that achievement of a stationary state or steady state growth (without fluctuations) requires the establishment of a particular herd structure in terms of the relative numbers in each cohort. This herd-growth model may be used in various ways. For instance, we could calculate for a given matrix [T] (i.e. given reproductive, mortality and offtake rates) and the existing herd structure, what will be the pattern of herd development over time, whether it is likely to achieve a steady state and if so, when. Alternatively, and this is the approach used in the remainder of this paper, we can calculate, for given reproductive and mortality rates, (i) what offtake rate and (ii) what herd structure is appropriate to maintain a stationary state. In short, the only empirical data used in the evaluation are productivity and mortality data. The existing herd structure is irrelevant.

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[1] Note that the adult breeding female is the central unit in flock structure. Numbers of males are simply linked through the required ratio of breeding males to females.

Before leaving the question of time, it should be noted that the interaction of the pastoralist with his environment may be a very long-term process. This may pose serious problems for economic evaluation, and is not attempted here. The problems are exacerbated by shorter term environmental variations, which are a major cause of risk.

Sensitivity analysis

The incorporation of risk greatly complicates model building. There are problems both of measuring risk and of evaluating the producer's attitude to it. Thus risk has an important effect on choice of objectives; the pastoralist may be more concerned with maintaining an adequate output for survival in all conditions than with maximising average value added. Much work remains to be done on attitudes of livestock producers to risk, but no attempt is made here. The sensitivity analysis carried out is aimed simply at measuring risk or variability of outcomes.

Sensitivity analysis is a fairly crude means of measuring risk. It consists of selecting certain key parameters that affect performance, such as reproductive rates, growth rates and mortalities, and repeating the analysis for different values of these key parameters by substituting these alternative values in the model. The parameters may be varied individually or in combination, and may be changed in a direction likely to improve performance or in an adverse direction. In order to limit the number of repeat analyses, and for simplicity, a case can be made for only varying the parameters individually and in an adverse direction. Thus, separate analyses may be made to estimate performance with low reproductive rates, or with low growth rates or with high mortalities.

The question then arises as to how low or high these parameters should be set. Ideally the choice should be based on objective measures of the range or variability of the key variables. Where standard errors have been estimated from empirical data, these may be used to determine a lower (or upper) limit for the appropriate confidence interval. However, this approach may mislead if the data series on which the estimated standard errors are based is too short to cover all possible environmental variations.

Sensitivity analysis may also be used to test the effect of purposive variation of control variables, such as varying the offtake rate or nutritional levels of the animals.

Small ruminants in southwest Nigeria

The model

Dwarf sheep and goats are kept as a supplementary enterprise on many arable and tree-crop farms of southwest Nigeria. The system has been studied extensively by the ILCA Humid Zone Programme based in Ibadan and described by ILCA (1979), Matthewman (1980) and Upton (1985). Since the enterprise, consisting of only three or four animals, represents a small part of the whole household economy and, according to the farmers themselves, is operated mainly for financial gain, the use of market prices to evaluate output seemed appropriate. For goats the market price of a yearling in 1983 was ₦20 while that of a breeding doe was ₦36. (Note ₦1 was worth approximately $1 US in 1983).

Goats, in particular, are left to scavenge on scraps found in the centre of the village, so they do not compete with crops for land. Labour and other inputs are minimal. For these reasons it seemed appropriate to treat the breeding flock as an independent system, with virtually no input costs other than those of the animals themselves. Goats were analysed separately from sheep.

The goat flock was divided into five age cohorts:

1. Female kids less than 1 year old;
2. Replacement does;
3. Breeding does;
4. Male kids less than 1 year old; and
5. Adult males.

Productivity data, derived from more than 400 individual records by the ILCA Ibadan team (Mack, 1983) were used to predict the steady-state flock structure and annual offtake. The results all related to a single breeding doe are as follows:

Flock structure		Offtake	
Female kids less than 1 year old	1.2	Female yearlings	0.37
Replacement does	0.25	Male yearlings	0.61
Breeding does	1		
Male kids less than 1 year old	1.2	Total	0.98
Adult males	0.08		

Evaluating the offtake figures at market prices gives a net value added per doe per year of ₦17.27, and a rate of return on the value of the stock of 34%.

Sensitivity analysis

For purposes of sensitivity analysis, standard error estimates for productivity parameters from the ILCA survey were used to determine the corresponding standard error for a flock of four goats. Each key variable was adjusted in an adverse direction by one standard error to test the impact. The results (Table 1) show that variation in mortality has the greatest impact on economic performance, followed next by reproductive performance. Variation in prices had the least effect. Similar results were obtained for dwarf sheep though generally at a higher level. These results, therefore, suggest directions for research policy, in that the first aim should be to reduce or stabilise mortalities if this can be achieved relatively cheaply. Secondly, emphasis should be given to stabilising reproductive performance. Improved marketing to reduce price variation may produce few benefits and, since it would require seasonal production to meet peak demand, is difficult to achieve.

Table 1. Sensitivity analysis of returns to Dwarf goat production (average rate of return 34%).

Parameters changed	Change	Net output per doe	Rate of return %
1. Reproductive -			
(a) Mean litter size	Reduced		
(b) Parturition interval	Increased	8.27	18
2. Mortality -			
(a) Survival to 3 months	Reduced		
(b) Survival to 12 months	Reduced		
(c) Breeding stock mortality	Increased	-0.31	-0.6
3. Growth -			
Liveweight at 12 months	Reduced	12.05	24
4. Price per kg.	Reduced	14.00	29

Southern Ethiopian rangelands

Objectives and the household economy

The Borana pastoralist system of the southern Ethiopian rangelands is much more complicated than the small ruminant system discussed above. Here the cattle and supplementary sheep and goats form the basis of the household economy. The Borana are almost entirely dependent on livestock for their survival. However, this is a semi-subsistence system. A substantial portion of the diet is made up of home-produced milk and dairy products and some, particularly fallen, meat. However, animals are also sold, together with some milk. Indeed, it is estimated (Cossins and Upton, 1984) that at the present ratio of livestock to human populations the Borana could not survive without trading some livestock produce for grain, which is a much cheaper source of metabolisable energy.

Thus, there is a problem of how best to evaluate inputs and outputs. For traded items, money values are appropriate, but for subsistence produce, nutritional values such as the metabolisable energy content are more relevant.

In cases such as this, some form of multi-objective programming may be appropriate, incorporating both nutritional and cash-income goals. However, since it is not clear how these goals should be specified or weighted, and to avoid undue complexity, both methods of evaluation were used.

Of course, the nutritional value of a foodstuff does not depend solely upon the metabolisable energy content. Indeed, livestock products are particularly important as a source of protein. However, given that energy deficiency is the most prevalent form of malnutrition, and that protein malnutrition is unlikely to occur among pastoralists, it seemed reasonable to concentrate only on energy values as a measure of nutritional contribution.

As mentioned earlier, the study of pastoralist systems should involve the rangeland, the herd and the household (Figure 2), but rather than attempting to build a comprehensive model of the entire system, the three subsystems may be modelled separately, for greater simplicity and flexibility in analysis. This separation requires some means of evaluating the output of each subsystem as it contributes inputs to another. We have already considered how the output of the livestock herd can be evaluated in terms of its contribution to the household economy. Given the ratio of livestock to human population and the allocation of offtake between subsistence consumption and sales, energy and financial budgets can be used to model the household economy. Estimates of the total energy value of subsistence consumption, when compared with total household food energy requirements, show what deficits must be made up from purchased food. Estimates of the cash value of sales provide measures of the disposable income available to meet additional food and other needs. These measures are the ultimate test of the viability of the system.

The rangeland system

Various models are available for estimating primary productivity of rangeland, generally based on vegetation type and length of growing season. In order to relate the livestock subsystems to the rangeland system, it is necessary to arrive at the carrying capacity in terms of hectares per grazing livestock unit (ha : LSU, or its reciprocal). This may be based on estimates of primary productivity and the assumption of a minimum 'offer requirement' per livestock unit of between 7 and 8 tonnes, as was done in the southern rangelands study (Cossins and Upton, op. cit.) or directly from environmental and climatic data

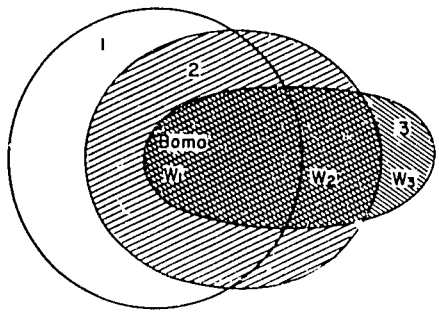
as suggested by Gartner (1981). Although the definition of livestock units and the conversion factors for different classes and age groups of livestock are arbitrary and inaccurate, they are necessary to allow sufficient flexibility for comparing alternative livestock and pasture management policies. Thus value added per LSU is a useful measure of the livestock production in relation to a limited carrying capacity of the rangeland.

It is important that the variability in carrying capacity over time should be determined both between wet and dry seasons within the year and between years of good rain and of drought. According to the general principle that the most limiting constraint actually determines what is feasible, the primary productivity in dry or drought seasons is effective in determining carrying capacity. Availability of surplus dry matter in good seasons is irrelevant unless policies can be devised to make use of these surpluses. However, in many cases, and probably in the southern rangelands of Ethiopia, water is the most limiting factor. Again, a distinction must be drawn between wet- and dry-season water; normally the latter is the effective constraint. That being so, improvement in dry-season water supply is the key to increased rangeland productivity. Naturally if too much water is provided then primary productivity becomes the limiting constraint and overgrazing will occur. Generally speaking, accurate estimation of rangeland dry-matter production and attempts to improve primary productivity or to increase wet-season water supply are of little value if these are not effective constraints.

Modelling dry-season water supply is a challenging problem in location theory since wells and ponds represent spatially distributed key centres. With a relatively sparse distribution of water points, overgrazing (i.e. dry matter being the effective constraint) in the vicinity of these points and under-utilisation of the pasture (i.e. water being the effective constraint) elsewhere is inevitable. A denser scatter of low-yielding[1] water points would result in more even and better utilisation of the rangeland, but would be more costly. The transhumance or settlement patter of the pastoralists also affects the utilisation of water and rangeland (Figure 4). Some exploratory analysis of the effects of location of water points has been done (Andreae, 1966; Helland, 1977; Cossins, 1983), but no comprehensive model exists to take account of such complexities as separate management of dry and milking herds and variations in the frequency of watering.

[1]Low-yielding water points have the advantage that fewer animals can be watered so that less overgrazing occurs in their vicinity.

Figure 4. The size of the grazing area, showing its dependence on the distance from the watering place to the homestead
(1) Watering place at the boma: large pasture area.
(2) Watering place removed: smaller pasture area.
(3) Watering place far removed: small pasture area



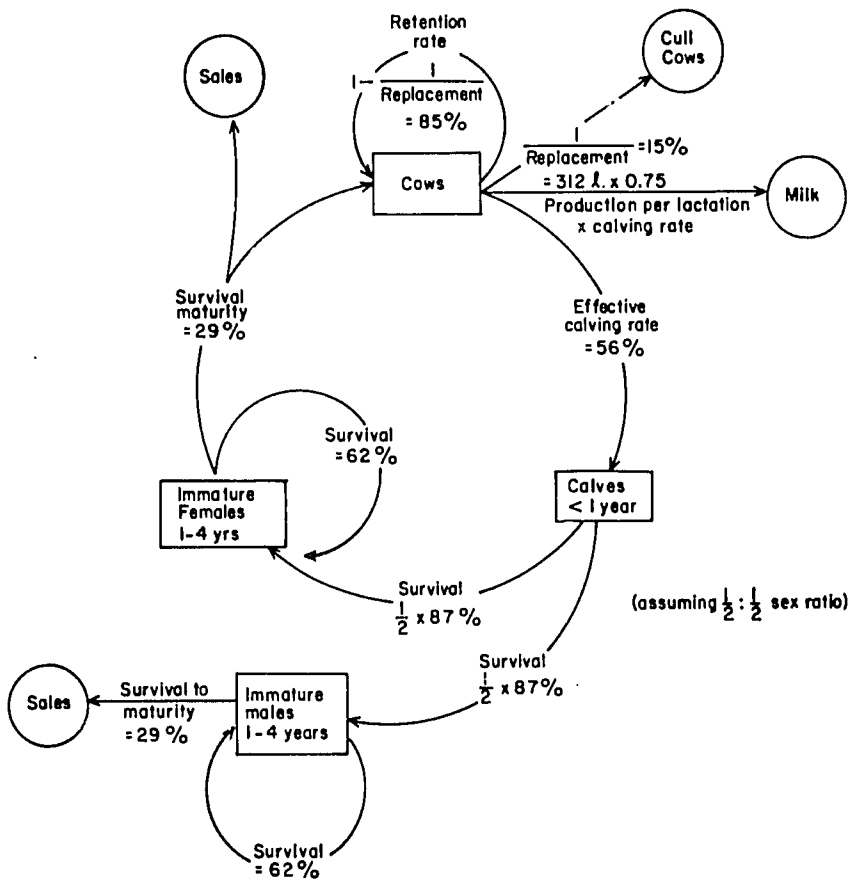
For the southern rangelands study, a crude analysis based on mapping of grazing areas accessible from dry-season water points suggests that dry-season water supply limits rangeland utilisation, particularly in the northern and western parts of the area. An increase in the number of strategically-sited wells could raise the average livestock support capacity by 100 000 LSUs or 25% of the existing average.

The cattle subsystem

Production parameters for Boran cattle have been collected in the southern rangelands by the ILCA team (Nicholson, 1984) and these were used to construct a herd-growth model, as outlined above. The main parameters and their effects are illustrated in Figure 5. Under the existing traditional system, Boran cattle do not reach maturity until 4 years old, although faster growth rates are achieved on ranches. This slow growth is due, at least in part, to the human consumption of milk which competes with supplies to the calf. On average 312 litres, or more than a third of the total yield, is taken per lactation for household consumption. Therefore, in the first analysis it was assumed that animals are slaughtered, sold, or drafted into the breeding/milking herd at 4 years of age.

Figure 5. Cattle sub-model (annual model)

Use: For any given number of Cows N
To calculate 1. Number of animals in other age/sex classes hence total herd size
2. Total milk production/year
3. Total offtake/year



The resultant stationary-state herd structure differed significantly from that recorded in a large number of observations at watering points (Table 2). In particular, the observed herds included fewer immature animals, which suggests that offtake occurs at an earlier age in practice, even at less than 1 year of age. Further evidence of this was obtained from market surveys, where sales of calves were recorded.

Table 2. Borana herd structure.

	Modelled	Observed
Cows	1	1
Female calves	0.28	0.28
Male calves	0.28	0.25
Heifers	0.63	0.31
Young males	0.63	0.35

A comparison was, therefore, made between the system with offtake at 4 years of age and that with offtake mainly at 1 year, when animals have much lower cash and energy values. In both cases an average milk offtake of 312 litres per lactation was assumed. Cash and energy values of the offtake per livestock unit, with the energy value of home-consumed fallen meat added in the latter case, and the rate of return on the value of stock were all used as criteria for comparison (see first two lines of Table 3). These results suggest that early offtake of calves is sound policy for maximising both cash and energy production per livestock unit. The reason for this somewhat surprising result is the high value of milk offtake in both cash and energy terms. Milk is the most valuable product for the Borana pastoralist. Hence, a system which reduces the proportion of immature followers and increases the proportion of milking cows in the herd raises total returns per livestock unit.

Table 3. Sensitivity analysis of Borana cattle performance.

	Cash value of offtake	Energy value of offtake	Plus energy value of fallen meat	Rate of return
	Birr	MJ ME	MJ ME	%
Offtake at maturity	88	673	779	35
Early offtake	112	739	819	45
Early maturity at 3 years	109	802	900	43
Early maturity and reduced mortality	113	805	872	44
Milk offtake increased to 470 litres	111	886	991	44
Milk offtake increased with increased mortality	110	900	1033	44

Sensitivity analysis in this case was aimed at exploring the potential for improved performance under alternative management practices rather than evaluating risk. Two main alternatives were considered; first, increased growth rates and earlier maturity which might be achieved through improved calf nutrition and second, increased milk offtake. The former policy might require reduced milk offtake and/or supplementary feeding of concentrates. Improved nutrition should reduce mortality besides increasing growth rates and this prospect was also considered. In either case there is a clear improvement over the system of offtake at 4 years maturity, as might be expected. However, the advantage over the early offtake of calves is less clear when evaluated in cash terms.

Increasing milk offtake by 50% brings about substantial increases in the energy output per livestock unit, even though it may increase calf mortality. This is perhaps to be expected since milk represents nearly two-thirds of the total energy offtake even at the average level of consumption. However, in practice there is a limit on the quantity required for domestic

consumption, whilst clearly the required offtake per cow decreases with increasing cow ownership per person. Milk is a highly priced commodity at Birr 0.11 per MJ of metabolisable energy, compared with Birr 0.03 per MJ for maize. However, the market is strictly limited, except for the few pastoralist households within easy access of a town. Hence, improved dairy processing and market facilities would be needed to allow the Borana pastoralists to benefit from the milk-production potential of their cattle.

Conclusions

This paper illustrates the use of simple herd growth models in the evaluation of livestock production systems. Such models take account of the time dependency of livestock production and are suitable for use in sensitivity analyses to test the effects of random biological variation or of alternative management policies. Useful insights are obtained. However, it is necessary to separate the production relationships within the breeding herd from the rangeland or fodder subsystem. It would be exceedingly difficult to incorporate complex physiological relationships, and this would undoubtedly reduce the flexibility of the model.

The model also has other uses which have not been explored here. For instance, it could be used to test alternative culling policies in the face of drought and to map the changes in flock structure during the period of recovery. In assessing the producer's objectives, it is not really adequate to assume that he maximises value in some sense. This does not explain, for instance, why small ruminant producers in southwest Nigeria generally restrict the number of animals kept per household to four or five, or how pastoralists decide on their flock sizes. Much work remains to be done in modelling the application of alternative objectives, alternative policies to minimise risk and alternative flock and herd growth patterns.

References

Andreae. 1966. Weude wirtschaft im Sudlichen Afrika. Geog. Z. 15.

Boulding K. 1978. Ecodynamics. Sage Publications.

CIMMYT (International Wheat and Maize Improvement Center). 1980. Planning technologies appropriate to farmers: concepts and procedures. CIMMYT, Mexico.

Cossins N J. 1983. The crucial centres: water production and well efficiency in Borana. Joint Ethiopian Pastoral Systems Study Research Report No. 12.

Cossins N J and Upton M. 1984. The productivity and potential of the southern rangelands of Ethiopia. Unpublished manuscript, ILCA.

Gartner J A. 1981. Evaluation of feed supply from grassland and other sources. Paper presented at the informal meeting on modelling livestock production in developing countries, 8-12 September 1981, Winrock International, Arkansas.

Hallam D. 1983. Livestock development planning: a quantitative framework. Centre for Agricultural Strategy, University of Reading, UK. Paper No. 12.

Helland J. 1977. Social organisation and water control among the Borana of southern Ethiopia. In: S B Westley, ed. East African pastoralism: Anthropological perspectives and development needs. ILCA, Addis Ababa.

ILCA (International Livestock Centre for Africa). 1979. Small ruminant production in the humid tropics. Systems Study No. 3. ILCA, Addis Ababa.

Mack S D. 1983. Evaluation of the productivities of West African dwarf sheep and goats in south-west Africa. ILCA programme document No. 7.

Matthewman R W. 1980. Small ruminant production in the humid tropical zone of southern Nigeria. Trop. Anim. Health Prod. 12:234.

Murdie G. 1976. Population models. In: J G Andrews and R R McLone, eds. Mathematical modelling. Butterworths, London, UK.

Nicholson M J. 1984. Calf growth, milk offtake and estimated lactation yields of Borana cattle in the southern rangelands of Ethiopia. Joint Ethiopian Pastoral Systems Study Research Report No. 6.

Spedding C R W. 1975. The study of agricultural systems. In: G E Dalton, ed. Study of agricultural systems. Applied Science Publishers.

Upton M. 1985. Returns from small-ruminant production in south-west Nigeria. Agric. Systems (in press).

Walsh V and Gram H. 1980. Classical and neoclassical theories of general equilibrium. Oxford University Press.

Discussion

Question - Do the results presented in Table 2 mean that the modelled herd size is much bigger than observed?

Answer - Well, it is all expressed per milk cow.

Question - So, my statement is not necessarily true but, if you have the same number of cows in the model as observed, then presumably the model gives a much bigger herd size?

Answer - The observed data refer to a series of observations at wells, reduced to proportions of the total number of animals observed, and then related to one cow. So they do not refer to individual herds. However, these model figures assume the steady state, unchanging herd structure, and the herd structure in reality could be changing.

Question - Are young female animals also sold?

Answer - In the market data, sales of young animals were observed and the low proportion of heifers worries us. They would allow only a very low replacement rate of about 8 or 9%. Possibly these figures represent a decreasing herd size due to the high mortality.

Question - Could the observations have been biased, because young animals are in the dry herds and not watered at the wells?

Answer - They are watered at the homestead, but these figures were adjusted accordingly.

Question - Is cash value of offtake calculated at a fixed price per kilo for meat, so that it equals biomass?

Answer - Market prices for animals in specific age groups were used.

Question - Could you explain what you mean by livestock unit?

Answer - It is the weight of the cow, plus the necessary replacement. Expressing the results per livestock urit implies that, with early offtake, cows represent a higher proportion of the stock and since cows produce milk and calves, that higher proportion gives a larger return from early offtake. So, on the basis of these calculations, it looks as if it is sound policy to get rid of calves before maturity.

Question - Is not the difference in rate of return entirely determined by the price ratio between mature and immature animals?

Answer - The situation would be different if prices were different, but these are based on the prices that have been collected in local markets.

Question - Do the data in Table 3 show that the mortality rate for these cattle is not important, while for goats (Table 1) it seems to have a big effect?

Answer - Mortality was adjusted for age, so the increased mortality means higher mortality of young stock. Early offtake reduces the proportion of the young stock, which increased the productivity of the system per livestock unit.

Question - Could it be that early offtake is increasing the productivity because it decreases the number of non-productive animals?

Answer - That could be the biological reason.

Statement - Herd productivity is increased by earlier offtake but in fact the herd will die out.

Reply - No, the basic assumption is a steady-state herd that is replacing itself.

Question - Can you explain why increased milk offtake gave a better result?

Answer - Because it is high-priced. It was assumed that all the extra milk offtake is sold.

Question - If an animal dies under the extra milk offtake, that would increase mortality. Is the value of that included in the rate of return?

Answer - The value of fallen meat is not included in the cash offtake but only in energy offtake, so the similarity in return in the last two lines of Table 3 is somewhat surprising.

Statement - If it is considered that the second line in Table 3 in fact represents current practice in the region, it seems there is very little scope for improvement, which again shows that the farmers are exploiting the resources optimally.

Reply - That would indeed appear to be the case.

Selection of sheep husbandry technologies under single and multiple goal constraints.

I. Spharim and N. G. Seligman

Introduction

Agricultural development involves the introduction of new technology that, at least potentially, should increase production and profits. The development process itself creates new conditions which affect the choice of technology. As development usually affects a whole region with all its interactions between land, labour, capital and climate the course of technology diffusion can be very difficult to predict. This is so when one goal, e.g. profit maximi[illegible] is dominant. It is even more difficult when different participants development process have different goals that sometimes conflict wi[illegible] other. A single participant can also have a number of goals that may con[illegible] e.g. income stability and income maximisation. A method that could ind[illegible]te likely paths of development with the complementary technology selection would be useful in formulating both development and research policy. In this paper we will deal first with the single goal situation. The multiple goal approach will then be discussed.

In the single goal situation, development is seen as a series of technologies that are selected in order to maximise regional consumption over an extended period. The approach adopted includes the use of a multi-period linear-programming model that allows comparisons of many technological options and considers the economic and natural factors that determine the rate of technology adoption. The existing options open to the farmer and the resources of the region have to be defined. The abundance of specific plant and animal genetic resources is of particular importance to agricultural production, which may be limited by biological reproduction rates, especially in the early stages of introduction.

The analysis can be conducted for a number of future scenarios. The questions of interest would include the following: What mix of agricultural technologies, new and old, would tend to be selected under given regional conditions, prices and policies, over a period of time? What is the marginal

benefit of a particular new technology? Which technologies have no significant value in the regional context and need not be considered in a research or development scheme?

Definitions

The following definitions have been used in this study.

A production system is a set of components organised and operated to convert inputs into useful outputs (Salter, 1966). The components of the system are units of hardware (e.g. machinery, fertilizers, genetic stock) with appropriate software (operating instructions). These components incorporate information (know-how) that has been obtained by experience or by research and development (R and D). Technology is the science that deals with the information on which the system and its components are based. In the present paper, and elsewhere, technology is used in a narrower sense and refers to the specific information content of a given system. A 'new' technology is derived from an existing one by changing at least one unit of information. Similarly, a new system is derived from an existing one by changing at least one component. An activity is a description of a production system in terms of its input:output ratios expressed in physical or money units.

A region is defined by its borders, resources and distance from major trade centres. Theoretically, any product can be transferred through regional borders; in reality, what can be transferred is determined by political and economic considerations and sometimes by veterinary and similar restrictions. In our study, it is assumed that concentrate feed, fertilizers and mutton can be freely transferred but there is a restriction on the transfer of labour, capital, land, ewes and roughage produced locally as a byproduct of the cultivation of wheat or other crops.

Regional resources (or constraints) are the amount of available labour; cultivable land area and range are, which with their specific climate determine primary production potential; initial number of ewes of different breeds and crossbreeds; and the initial amount of physical capital.

Agricultural system inputs include hardware (physical inanimate inputs, e.g. sheds, equipment, fertilizers, concentrate feed), software (a set of operating instructions, e.g. feeding and grazing regimes), and genetic stock (animal and plant material) which is a category of hardware specific to

agricultural (and other biological) production systems. Slow rates of reproduction can be an effective constraint to the adoption of any technological changes dependent on new genetic stock.

A physical, inanimate input can have a long technical life (e.g. sheds and fences) or a short technical life, i.e. it is consumed within the production year (e.g. medicines or concentrates). It can become economically obsolete before it becomes technically obsolete (i.e. physically unusable). Software does not become technically obsolete, in the sense that it does not wear out, but it can become economically obsolete. The genetic stock also does not necessarily become obsolete as it can replace itself by reproduction. Individual sheep or flocks of a given breed can, of course, become economically obsolete. The single goal of this analysis is to maximise regional consumption. Other possible goals include maximum production, improvement of regional balance of payments and maximum employment. The goals can be treated as constraints or can be used as target functions in an iterative procedure (Nijkamp and Spronk, 1978).

System management is understood as the choice and timing of alternative paths of action available for operating a system or a set of systems. It can be divided into strategic and tactical choices. Strategic management involves choice between systems; tactical management involves choice within systems. The present study simulates strategic management within a region. It does not deal with each farmer separately, but assumes that economic opportunities that are created in a developing region will be exploited by one farmer or another.

Approach

Information on activities and regional constraints can be set up as a linear-programming (LP) model in which an optimum mix of activities over time is determined (Beneke and Winterboer, 1973). The LP routine can be applied in a multi-period format or recursively (Cocks, 1965; Storck and Shurmer, 1970; Porat, 1972). The recursive approach can be used in an interactive manner that does not assume prior knowledge of prices, constraints or climatic changes. In that sense it probably simulates farmers' behaviour fairly accurately (Day, 1963; Heides, 1966). In the multi-period approach (MPLP) the target function can be optimised over the whole planning horizon. It uses average input/output values and so does not confront directly the problems of climatic uncertainty

and risk that characterise most agricultural regions. It assumes prior knowledge of prices, constraints and climatic changes.

In the present study, only the multi-period approach has been developed as it is more appropriate to problems related to the time-span of technology selection and to long-term policy assessment, in which problems of year-to-year management can be neglected. MPLP can simulate many of the important features of strategic farm management in the following manner:

1. System selection is based on long-term optimisation and is calculated for the whole planning horizon.

2. The target function can be adapted to the characteristics of a specific region. It could be maximum meat production if the development goal was to increase food supplies, maximum return on investment if the study was conducted for an investment agency, or maximum consumption if regional welfare is the major goal. We chose maximum consumption as the most appropriate target function for our specific region. Other objectives, like a minimum return on investment or social security, can be defined as constraints.

3. System selection can be implemented by transfers of various sorts from one period to the next. These transfers include investment (financial capital to physical capital), young female stock to breeding ewes or to mutton, hardware from one system to another, and transfer or sale of breeding stock from one system to another.

4. Consumption and investment: The choice between consumption and investment is made endogenously (Kislev et al, 1971). A subjective discount rate (or capitalisation rate), S, provides a common denominator for consumption over different periods. An objective discount rate, R, represents the investment opportunities outside the agricultural sector. The two discount rates, as well as the opportunities for on-farm investment, govern management decisions concerned with the amount and timing of investment and consumption.

5. The economically justifiable price that can be paid for additional resources (e.g. imported sheep or straw) at any time is given in the model by the shadow prices of the various constraints throughout the planning horizon.

6. When implementing a new technology the farm manager will try to use as much of the existing capital assets as possible until they become technically or economically obsolete. The model simulates manager behaviour by optimising the choice among the following options: use of existing assets if the new technology allows it; postponing the acquisition of assets specific to the new technology until the old assets become obsolete; and investment in new assets to exploit new technology.

7. It is possible to adjust the herd (and breed) size and composition according to the demands of the selected technologies by retaining animals for breeding or selling them. The periodic decision to cull and sell hoggets depends on the alternative uses of annual income for consumption and investment outside the agropastoral sector as well as on the revenues expected from the larger herd. Thus, the herd population dynamics are a result of both biological and economic factors.

The model can be used to analyse different development policies as well as to assess the short- and long-term impacts of a wide variety of technologies under different socioeconomic scenarios. The information generated can also be used for regional planning purposes as it optimises the mix of technologies required during each period along the course of development. However, one would then have to be sure that all the technologies in the R and D pipeline will indeed be available for implementation at the appropriate time.

Case Study

General

This analysis is applied to the specific case of agropastoral development in a semi-arid Mediterranean region in Israel where the traditional activities of sheep husbandry and dryland agriculture are now undergoing extensive change. This is due not only to research and technology transfer but also, if not mainly, to the parallel development of input industries (equipment, concentrate feeds, recycled agricultural wastes, veterinary services, etc.). These inputs increase the range of optimal systems but also increase the alternative values of labour and capital. In the present study, wheat cultivation is introduced as representative of alternative agricultural activities to sheep husbandry. Activities outside agriculture can be assessed by comparing shadow prices for labour calculated by the model with salaries in industrial and commercial activities. The agropastoral systems in this region have been surveyed and studied fairly extensively (Noy-Meir, 1975; van Keulen, 1975; Noy-Meir and Seligman, 1979; Zaban, 1981; Benjamin et al, 1982). Detailed information on the regional characteristics, existing and potential technologies and the method of system definition is given by Spharim and Seligman (1983). The sheep husbandry systems are summarised in Table 1. The coefficients for the linear-programming matrix were generated by a special program (Seligman et al, 1982).

Technology selection

From the large number of technologies available, the most appropriate must be selected and ordered over time. The multi-period linear-programming approach (MPLP) is used to select an optimum mix of technologies in order to maximise consumption over a whole planning horizon subjects to a set of constraints. The constraints are the regional resources, e.g. land, capital, labour and genetic stock. A social constraint was included by stipulating a minimum sum of money ('social security' or unemployment allowance) for each labour unit available. The set of technologies includes those that exist in the region, those that are available but not yet applied ('on the shelf') and those that are still in the R and D pipeline. A planning horizon of 15 years was adopted, as preliminary studies showed little change in the solutions between 15 and 20 years. The technical aspects of the optimisation matrix for the specific purpose of the present study are given by Spharim and Seligman (1979).

Table 1. Sheep husbandry systems used in the model.

Serial no.	Code (4)	Description
1.	AYN05	Awassi, year-round grazing, normal weaning. 50% lambing rate.
2.	AGN05	As above with green-season grazing only: straw and concentrates in dry season.
3.	AYN06	As above with year-round grazing and 60% lambing rate.
4.	IYN07	Improved-Awassi, year-round grazing, normal weaning, 70% lambing rates.
5.	IGN07	As above with green-season grazing only: straw and concentrates in dry season.
6.	IYN09	As above, with year-round grazing and 90% lambing rate.
7.	IGN10	As above, with green-season grazing only and 100% lambing rate.
8.	MDN10	German Mutton Merino (GMM), deferred early-season grazing, normal weanning, 100% lambing rate.
9.	MDN12	As above, with 120% lambing rate.
10.	MDN14	As above, with 140% lambing rate.
11.	MDE16	As above, with early weaning and 160% lambing rate.
12.	MGN17	GMM, green-season grazing, normal weaning, 170% lambing rate.
13.	MGE19	As above, with early weaning and 190% lambing rate.
14.	MGH19	As above, with labour-saving artificial weaner.
15.	FGN20	Finn-cross, green-season grazing only, normal weaning, 200% lambing rate.
16.	FGE22	As above, with early weaning and 220% lambing rate.
17.	FGE24	As above, with 240% lambing rate.
18.	FGH24	As above, with labour-saving artificial weaner.

Notes 1. Weaning weights: 20-40 kg in Awassi systems; 40 kg in extensive GMM systems. 15-30 kg in intensive GMM systems; 15-20 kg in Finn-cross systems.

2. Sale weight of lambs: 20-45 kg in Awassi systems; 45-50 kg in GMM systems and 50 kg in Finn-cross systems.

3. Pasture fertilization: in systems with less than 90% lambing rates (systems 1-5) no fertilizer is applied to pasture. In the more intensive systems, nitrogen is applied at the rate of 50 kg N/ha; P is applied to the limited extent that annual legumes are grown.

4. Systems code is a mnemonic for breed (A,I,M,F); grazing system (Y,D,G); weaning and lamb-rearing system (N,E,H); and effective lambing rate (50-240%).

Results

One hundred and eight technologies were analysed in terms of 17 different scenarios (Table 2). These scenarios varied with regard to available labour and land, breed and prices of lamb, concentrate feed and wheat. The standard run was chosen rather arbitrarily but is meant to approximate to the current resource situation in the region.

Table 2. Description of development scenarios used in the model.

Run*		Labour (man-years)	Price (meat: grain)	Wheat price	Awassi (head)	Merino (head)	Finn x (head)	Cultivable area (ha)	Range (ha)
Standard	1	400	10:1	Subsid.	100 000	2 000	200	25 000	25 000
	2	700	10:1	Subsid.	100 000	2 000	200	25 000	25 000
	3	850	10:1	Subsid.	100 000	2 000	200	25 000	25 000
	4	1000	10:1	Subsid.	100 000	2 000	200	25 000	25 000
	5	400	10:1	Subsid.	100 000	2 000	0	25 000	25 000
	6	700	10:1	Subsid.	100 000	2 000	0	25 000	25 000
	7	1000	10:1	Subsid.	100 000	2 000	0	25 000	25 000
	8	400	10:1	Subsid.	100 000	0	200	25 000	25 000
	9	400	10:1	Subsid.	100 000	0	0	25 000	25 000
	10	400	10:1	Subsid.	100 000	2 000	200	25 000	0
	11	400	10:1	Subsid.	100 000	2 000	200	0	25 000
	12	400	6:1	Subsid.	100 000	2 000	200	25 000	25 000
	13	400	8:1	Subsid.	100 000	2 000	200	25 000	25 000
	14	400	12:1	Subsid.	100 000	2 000	200	25 000	25 000
	15	400	14:1	Subsid.	100 000	2 000	200	25 000	25 000
	16	400	10:1	Low	100 000	2 000	200	25 000	25 000
	17	400	10:1	High	100 000	2 000	200	25 000	25 000

*Additional characteristics that apply to all scenarios: 15-year run; 3% capital interest rate; 4% discount rate for consumption(s); 4% population growth rate; 7 years' technical obsolescence; 1 year software elasticity, i.e. systems need not be maintained for more than 1 year.

Rejected technologies

Activities that were not selected (or selected only occasionally) are listed in Table 3. The most extensive system - Awassi sheep, year-round grazing, normal weaning, 50% net lambing rate (AYN05) - was not consistently rejected, but the other extensive systems, which were based on only slightly higher outputs and moderate increases of feed inputs per ewe, were rejected in all scenarios tested. The more productive improved-Awassi systems on the other hand, were selected frequently over their whole range of management intensities. The only system based on this breed that was rejected involved green-season grazing combined with the lower productivity level (IGN07). Green-season grazing was selected only when the breed was managed at the limit of its productive capacity (IGN10).

Table 3. Selection of the technologies used in the model under different management systems.

System (1)		Range		Cultivable land				Feedlot only	
				Unfenced		Fenced			
No.	Code	Unfenced minimum straw (OS)	Fenced min. conc. (RC)	Min. straw (US)	Min. conc. (UC)	Min. straw (FS)	Min. conc. (FC)	Min. straw (NS)	Min. conc. (NC)
1	AYN05	x	x			*		Not defined	
2	AGN05	x	x	*	x	0	x	Not defined	
3	AYN06	x	x	0	0	0	0	Not defined	
4	IYN07		*	*		0	0	Not defined	
5	IGN07	*	x	*	0	0	0	Not defined	
6	IYN09							Not defined	
7	IGN10		x		*		x	Not defined	
8	MDN10	0	x	*	0	x	x	Not defined	
9	MDN12	x	x	x	x	x	x	Not defined	
10	MDN14							Not defined	
11	MDE16			0				Not defined	
12	MGN17	Not defined		0	0		*	0	0
13	MGE19	Not defined						*	
14	MGH19	Not defined		0	0	*	*	0	0
15	FGN20	Not defined		*	0	*	0	*	0
16	FGE22	Not defined		0	0	0	0	0	0
17	FGE24	Not defined			*			*	
18	FGH24	Not defined		*	*			0	

Key: x = screened as inefficient.
0 = consistently rejected.
* = occasionally selected.
Blank = consistently selected.
(1) = See Table (1)

The two least productive (and most extensive) systems based on the German Mutton Merino (MDN10, MDN12) were consistently rejected. The most intensive system, based on the labour-saving artificial weaner (MGH19) was also consistently rejected; only the most intensive Finn-cross systems (FGE24, FGH24) were selected.

A pattern of rejection emerges when the systems are arranged in order of a dominant aspect of production performance, which, in the present study, is ewe fecundity. Each breed has a maximum fecundity dependent on its genetic characteristics. Below this maximum, fecundity is determined by management factors. As a result, the fecundity ranges of the breeds overlap. The technologies rejected tend to be those based on the highest and lowest fecundity levels of a given breed. At the highest levels, a more fecund breed tends to be selected, and at the lowest fecundity levels of a given breed, another less fecund breed tends to be selected. These less fecund breeds are often hardier and thrive under less favourable conditions.

Selected technologies

The degree to which a system was selected over the whole 15-year test period can be expressed as the number of ewes that were managed or the number of lambs sold in that system totalled over the whole planning horizon. Another criterion is the number of times a system was selected over the period analysed. A summary of the systems selected is given in Table 4.

Two basic technologies were consistently selected in all combinations: the improved Awassi, year-round grazing, normal weaning, 90% net lambing rate (IYN09) and the German Mutton Merino (GMM), deferred grazing, normal weaning, 140% net lambing rate (MDN14). Two other technologies (MDE16, MGE19) were selected in all but one of the combinations tested and one (FGE24) in all but two; four (AYN05, IYN07, MGN17, FGH24) were selected, but not consistently and not heavily, and one system (IGN10) was occasionally selected, sometimes with many sheep involved.

Table 4. Technologies most frequently and heavily selected in the model under different management systems.

System(1)		Range		Cultivable land				Feedlot only	
				Unfenced		Fenced			
No.	Code	Unfenced minimum straw (OS)	Fenced min. conc. (RC)	Min. straw (US)	Min. conc. (UC)	Min. straw (FS)	Min. conc. (FC)	Min. straw (NS)	Min. cons. (NC)
1	AYN05			+	*		*	Not defined	
4	IYN07	*			*			Not defined	
6	IYN09	**	**	***	*	***	***	Not defined	
7	IGN10	*		**		+		Not defined	
10	MDN14	**	**	+	*	*	***	Not defined	
11	MDE16	*	*		*	*	***	Not defined	
12	MGN17	Not defined				+			
13	MGE19	Not defined		*	**	*	*		*
17	FGE24	Not defined		+		*	*		**
18	FGH24	Not defined				+	*		+

Key: Blank = consistently rejected.
+ = selected occasionally to a moderate degree.
* = selected often to a moderate degree.
** = selected often, sometimes heavily.
*** = often selected heavily.
(1) = See Table 1.

The most heavily selected group was of the intermediate breeds, the improved Awassi and the GMM, both at a production level below the breed potential. The highly productive systems based on the Finn-cross were selected less regularly and, as will be seen below, only under special conditions. The systems that were selected only occasionally range from the most extensive to the most intensive systems defined.

Dynamic aspects of technology selection

The choice of breed and production level varied over the period analysed. In the standard run (see Table 2), the Awassi was predominant initially (the present situation in the region) but its numbers declined as GMM increased in numbers (Figure 1). The highly productive Finn-cross was selected to the limit of its availability up to year 9, but was then phased out. It was selected during the early period as an interim solution for increasing the more productive systems as quickly as possible, but when there were sufficient number of the preferred GMM for optimal use of the resources the more productive Finn-cross lost its relative advantage of high fecundity. A different result is also possible as this pattern is dependent on the regional constraints. If the standard-run scenario changes, and the labour available increases from 400 to 1000 man-years, then the labour-intensive Finn-cross is selected to the limit of its availability throughout the test period (Figure 1). However, this is accompanied by a drastic reduction in income per man-year.

Effect of price change on technology selection

An increase in the meat:grain price ratio produced a sharp increase (from 5 to 73%) in the area of cultivable land used for pasture (Figure 2) and in the herd size, all breeds increasing as a rule. The systems based on the Awassi breed that were selected are the efficient group of land-intensive technologies, and the selected systems based on the GMM breed are the efficient group of concentrate-intensive technologies. When prices of meat rise (and prices of wheat are left unchanged) it becomes more profitable to produce meat from pasture by means of Awassi-based technologies, and also from concentrates via the GMM systems. As a result, the Awassi herd increases at the expense of land under wheat, which is put down to pasture, and the GMM increases by using more concentrates. On the other hand, as the wheat price rises, the area under wheat increases and the area of cultivable land under pasture decreases, from 61% to 29%. As a consequence, the number of Awassi sheep is reduced, but the GMM and Finn-cross numbers remain more or less constant.

The increasing meat:grain price ratio has a somewhat unexpected effect on the grazing systems that are selected: year-round grazing increases, deferred and green-season-only grazing decrease, while confinement to feed lots increases only slightly, even when the ratio is 14:1 (Figure 2). Under these

Figure 1. Predictions of breed selection over a 15-year period

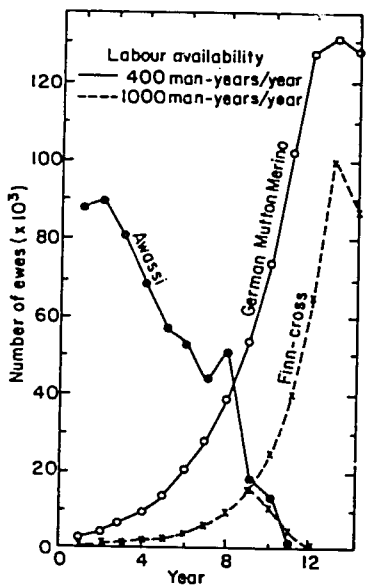
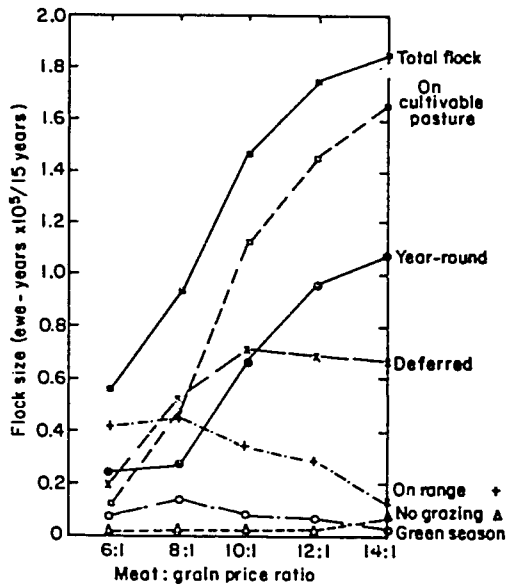


Figure 2. Effect of meat: grain price ratio on grazing system, land use for grazing and total flock size



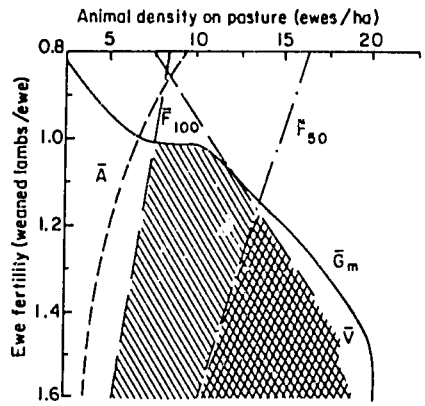
circumstances it may seem surprising that range use decreases. These trends in pasture use are also related to the relative profitability of wheat in the region. When the area under wheat is reduced by higher meat prices, cultivable land that can produce good pasture becomes available for sheep husbandry, thus providing an apparently more profitable alternative to raising sheep on either concentrate feed or on range. This is an interesting result for those who deal with future trends in sheep husbandry, as even under scenarios with a meat:grain price ratio of 14:1, most sheep are raised on improved grassland rather than under feedlot confinement. However, extensive rangelands tend to be neglected as meat production from improved pasture becomes more profitale per labour unit. The shift from open to fenced range and pasture occurs for apparently the same reason.

With regard to the specific technologies selected, the general trend was to select more productive systems (higher lambing rates) as the price ratio increased, but there are many exceptions: GMM at 140% lambing rate, grazing unfenced range for 9-10 months of the year, was heavily selected when the meat:grain price ratio was 6:1, while improved-Awassi grazing year-round on sown pasture with a lambing rate of only 90% was heavily selected when the price ratio was 14:1. However, this is very much dependent on the initial conditions, which stipulated a herd containing 97.8% Awassi in the first years of the analysis. In the long run, the more extensive systems, with their associated breed (Awassi), tend to be phased out.

Multiple-goal analysis

The present model is now being developed into a multiple-goal model in the manner presented by Nijkamp and Spronk (1978). Legume pastures have been added as an additional option. Preliminary results are available but a detailed study is in preparation. A different approach to multiple-goal analysis of a non-dynamic situation has also been developed (Spharim and Seligman, 1984). This is based on an input/output model of agropastoral systems and the definition of a number of relevant regional goals. The model does not attempt to find a single optimum solution. Instead, it defines a feasible set of technologies that meet minimum threshold standards for each defined goal (Figure 3). The choice of technology within the feasible set is then dependent on other factors that vary from farmer to farmer and depend also on the relative strength of interest

Figure 3. The feasible technology space, S, bounded by threshold isolines of the multiple-goal indices



$\bar{A}$ = \$ 350/ha

$\bar{V}'$ = 1.1

$\bar{G}_m$ = 12 000/man-year

$\bar{F}_{50}$ = 50 ha

$\bar{F}_{100}$ = 100 ha

S_{100}, bounded by F_{100}

S_{50}, bounded by F_{50}

Goal thresholds

$\bar{A}$ = contribution to regional balance of payments

$\bar{V}'$ = relative cost of added foreign currency

$\bar{G}_m$ = gross margin per man-year

$\bar{F}$ = farm size

groups that influence the development situation. Some farmers may even practice technologies outside the 'feasible' set because of resources or goals that are not covered by the model. Consequently the model solution can be used mainly to focus on the main issues between technology and development policy.

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References

Beneke R R and Winterboer R. 1973. Linear programming applications to agriculture. Iowa State University Press, Ames, Iowa, USA.

Benjamin R W, Eyal E, Noy-Meir I and Seligman N G. 1982. Intensive ley-farming systems in the Migda Experiment Farm, northern Negev, Israel. Internal report, ARO, Bet Dagan, Israel. (Hebrew, mimeo.)

Cocks K D. 1965. Capital accumulation and Hicksian models. Farm Econ. 10:458-465.

Day R H. 1963. Recursive programming and production response. North Holland Publishers, Amsterdam.

Heides T. 1966. A recursive programming model of farm growth in northern Germany. J. Farm Econ. 48:668-684.

van Keulen H. 1975. Simulation of water use and herbage growth in arid regions. PUDOC, Wageningen, The Netherlands. 176 pp.

Kislev Y, Plasner Y and Prahia A. 1971. Multi-period linear programming with consumption functions. Center for Agricultural Research, Revohot, Israel. 38 pp. (Hebrew)

Nijkamp P and Spronk J. 1978. Interactive multiple goal programming. Reports Nos. 7803/A and 7812/F. Center for Research in Business Economics, Erasmus University, Rotterdam, The Netherlands.

Noy-Meir I. 1975. Primary and secondary production in sedentary and nomadic grazing systems in the semi-arid region: Analysis and modelling. Research report to the Ford Foundation, Grant 7/E-3, Dept. of Botany, The Hebrew University of Jerusalem, Israel.

Noy-Meir I and Seligman N G, 1979. Management of semi-arid ecosystems in Israel. In: B Walker, ed. Management of semi-arid ecosystems. Elsevier Scientific Publishers, Amsterdam, The Netherlands. pp. 113-160.

Porat Y. 1972. Perspective planning of a kibbutz farming operation with a multiple period LP model, Agricultural Settlement Planning Authority, Ministry of Agriculture, Tel Aviv, Israel. 61 pp. (Hebrew)

Salter W E G. 1966. Productivity and technical change. Cambridge University Press, London, UK. 220 pp.

Seligman N G, Eyal E, Benjamin R, Noy-Meir I and Spharim I. 1982. A pasture system generator. Internal report. ARO, Division of Range and Forage Crops, Bet Dagan, Israel (Mimeo).

Spharim I and Seligman N G. 1979. Long-range agricultural planning of agro-pastoral systems in a semi-arid region. Paper presented at the Conference on Operation Research in Agriculture and Water Resources (ORAGWA), Jerusalem (Mimeo).

Spharim I and Seligman N G. 1983. Identification and selection of technology for a specific agricultural region. Agric. Systems 10:99-125.

Spharim I and Seligman N G. 1984. A graphical model for relating multiple socio-economic goals to research and development objectives in agriculture. Res. Policy (in press).

Storck H and Shurmer E. 1970. Experiences with multi-periodic investment models for planning the growth of a vegetable holding. Acta Hort. 40:497-515.

Zaban H. 1981. A study to determine the optimal rainfed land-use systems in a semi-arid region of Israel. Ph.D. thesis, Univ. of Reading, UK.

Discussion

Question - Your conclusion is that fecundity is the main characteristic determining selection or rejection of certain breeds at a certain moment. Since the prolificacy figures of the various breeds overlap, there must be other technical coefficients in the input/output relations that determine which breed is actually selected. What are those other technical coefficients?

Answer - The other technical coefficients varying among breeds are the veterinary costs and the labour requirements.

Question - An important conclusion derived from the model is that restrictions on land allocation should be lifted to improve the prospects for the development of agro-pastoral systems. Did I understand that correctly?

Answer - Yes, in some scenarios the model allocated substantial parts of cultivable land to pasture.

Question - How much does that change if you use an unsubsidised wheat price?

Answer - In that scenario the wheat acreage is reduced to almost zero.

Question - Can you please clarify what the objective function is, i.e. to maximise consumption? You are using the word consumption because you are discounting future consumption, but in fact you mean the money value of output minus operating costs.

Answer - The objective function, as defined in the paper, is maximising the amount of cash available for consumption after deductions for operating costs, investments and savings. I mentioned that this model has another version that is not covered here, in which various goals are defined. These goals are defined in accordance with the aims of various interest groups, such as regional industry, regional consumers, regional environmentalists, the settlement agency, the national government or international money lending agencies.

Question - In the agropastoral systems there is an opportunity to select between sheep breeds. Do you have a similar choice for wheat production, allowing application of different technologies? For instance, instead of ploughing and discing to use only discing or to combine the disc and the drill or to grow wheat with or without fertilizer.

Answer - In the present model most attention was paid to sheep husbandry technologies, because that was the difficult test. The arable systems were treated rather superficially. Arable technologies in the model were continuous wheat and wheat on fallow. If the input-output relations of other technologies can be defined, however, they can be easily accommodated in the model.

General discussion

Types, purposes and users of models

Benjamin - It might be advisable to call upon different disciplines (researcher, manager, planner) in determining the use of models. It is obvious that models have a different meaning, purpose and use for each of these, and that they can be separated in some way.

Few complex models have been used by managers. Simple models have been of more use: in these, some day-to-day management decisions are reduced to a simple yes or no answer. Another type of model is that with a fundamental approach, e.g. Ketelaars' approach towards intake based on energy and protein ratios. These can be extremely useful to farmers, although energy and crude protein do not mean very much to them. What they really want to know is what they get with small inputs of supplements.

Seligman - Benjamin raised two good points. One is the complexity of the models, and the other was the question of how to deal with quality and intake. The latter will be discussed in the second part of this session. Regarding the first, I would like to say that we should be careful with terms like complex and simple. Many of the 'complex' models are conceptually quite simple, while some of the 'simple' models are conceptually very sophisticated.

The usefulness of a model depends on the system, on the way the model has been conceptualised and on the way in which one goes about the modelling process: some complex models are well conceptualised and are very useful, while some of the simple ones do not mean much. It is important that the final answer from the model should be in a form which can be easily understood by the people who will apply the results.

Lambourne - I think that Benjamin has brought up a very important point that is of considerable interest to ILCA. The ILCA model is a modification of the TAMU model. I am beginning to wonder if the ILCA model is not a sort of hybrid, because ILCA's requirements are likely to diverge from those of TAMU. One direction is the use of decision-type management models and practical models. These do not give a great deal of resolution, but they do give an idea of the actual output of a system: figures for herd dynamics and production which give a broad indication of the productivity of different systems. ILCA also needs

models that go into greater detail of the physiological basis of plant growth or the reproductive performance of the animals. I do not see that one model, e.g. the ILCA model, can serve both purposes.

Spharim - I would like to raise a related subject. It was mentioned that the ILCA model, which is applicable to the conditions in Botswana, does not fit well in a different environment. If the biological basis of the system was well understood, it would be possible to find a factor within the model that would be widely applicable to different environments. Furthermore, if the mechanism was understood, less data would have to be collected in a given place, but the model would still be applicable to that environment.

Upton - Possibly one could distinguish between models by the degree of their mathematical complexity. Conversely, complexity can be determined by the number of relatively simple relationships that you are trying to investigate simultaneously. A common notion is that there is a particular constraint that limits the achievement of the objective. If you can pinpoint that constraint, your efforts can be focused on overcoming it.

Seligman - That is true. When you want to find the limiting factor in a particular situation, you have to investigate the situation itself. A comprehensive model will define lots of processes, but not necessarily those that deal with the limiting factors. The problem in modelling production systems is to combine these two approaches: the identification of the limiting factors and the elaboration of the model so that it expresses them correctly.

de Ridder - I want to go back to the choice of the type of model. The matter is not of choosing a particular type of model, but to choose the one best suited to the defined problem. Starting with a general, low-resolution model, you can try to determine the possibilities for improving production from a system. Much of the input for the model will be data collected from the system itself, but some guesses will have to be made about how the system will react to proposed interventions. A biological simulation model is needed to quantify these guesses, e.g. the effect of increased forage availability on overall production of the system.

Lambourne - I agree. One of the justifications for the scientific type of model is that they produce reliable units which can then be used to assess research and development priorities or to assess management decisions in the decision-type models.

Orshan - One has to distinguish between problem-oriented and system-simulation models. The first is a deducive and the latter an indicative approach. There is no advantage to using one alone. Both have to be used, but one must distinguish between aims and techniques -- that is the point.

van Keulen - In Wageningen we have been modelling biological systems for many years, with the aim of gaining a basic understanding of the biological systems. Some of these models go from a plant to an organ or even cellular level, while others go in the opposite direction, from the plant to the whole canopy level. With both types of model disatisfaction creeps in. One begins to wonder how the models are to be used. In this there are two approaches that can be adopted. First, you can sit and wait until someone comes along with a specific problem which needs to be solved. This will probably not work, since most people are not very enthusiastic about models. The second approach is to ask yourself how you can use the knowledge you have gained. An example of this approach has been developed in the Netherlands. The same people who developed the detailed crop growth and population dynamics models, with a view to increasing insight into these systems, developed simplified equations from these models which could be of direct use to the farmer, e.g. rules on whether or not to spray a wheat crop.

These rules have been tried out by farmers for several years now. Last year there were 9 000 fields of wheat that were being served by this advisory service.

In our experience, one has to develop fairly detailed and fundamental models, and then bring them down to a level at which they can be used to solve practical problems.

Seligman - The success of the Wageningen group in modelling is clear, but I was under the impression that the amount of modelling used in the advisory services is almost nil.

van Keulen - Both the population dynamics model and the crop growth model have been reduced to a few lines of FORTRAN dealing with factors relevant to the development of a particular disease on a particular crop at a particular physiological growth stage. This could not have been done unless the detailed models had been developed first.

Ungar - I see that some important methodological points have been touched upon. I think that linguistics is important. The problem defines the way in which the reality is conceptualised.

The language that is used depends upon one's outlook. Thus the concept of relative growth rate in the ARID crop model has no meaning, because ARID crop is not concerned with grazing-systems dynamics, but grazing-systems dynamics cannot be explained without that concept. The problem is that model builders do not have a single level on which they wish to provide an explanation, but many. They try to explain not only foreign income, but changes in animal liveweight, herbage growth and moisture in the soil. They are forced to take the lowest common denominator, and end-up explaining soil moisture but not explaining farm income, only simulating it. In order to develop explanatory power, we need appropriate concepts and language. That is why Noy-Meir's models, which used the correct language and concepts to deal with the problem in hand, are so successful. A model that is more detailed might be more precise and more realistic, but it would lose the explanatory power of the simpler conception.

Upton - In a sense the mandate of ILCA is to develop new technologies. But new technologies developed by research institutes need testing through expensive field trials and extensive pilot projects before they can be presented to the farmers. Another application of modelling is to speedup this testing and substitute for field work. It is a means to test a technology, but can never be a complete substitute for field trials.

Spharim - There is no difference between the wind tunnel that an engineer uses to check wings and the models that we are talking of now. Even in a wind tunnel an engineer only simulates the real world. The final test of the wing is in the air, but a good engineer will know what is being tested in the wind tunnel and what is not.

Ungar - There is a temporal as well as a philosophical sequence to be followed in modelling. Do we need a good scientific animal model before we can build a managerial-type model? Must we have ARID CROP before we can model the management of lambs? Or can we approach the problem from a different point of view?

van Keulen - If you are interested in the potential yield of a wheat crop in a Mediterranean environment with 250 mm rainfall, you can cut out a lot of detail, use fairly simple descriptions, and come up with results that are extremely relevant to the given situation. But you should also realise that the model is descriptive rather than explanatory.

de Leeuw - So the question is, are we just going to use the observations from the Borana system or do we need to know the details of the competitive elements, e.g. between milk offtake and calf growth?

van Keulen - When you are interested only in what will happen in that particular region or system, then you can formulate a site-specific hypothesis, either on the back of an envelope or with a computer. That hypothesis can be used in analysing what will happen if you change certain elements in that system. But if you want to be able to predict what will happen elsewhere on the basis of these data, then you need something a lot more sophisticated.

de Leeuw - Let me pose another question. We know that milk is a limiting resource during the dry season. I could modify the system by feeding certain proportions of urea. What I want to know is whether this is economically feasible in the long- or short-term. I want to know the effects of this intervention on the herd development and on overall productivity, both in good and bad years. Do I need the ILCA model to do this, or can I calculate this on the back of an envelope?

van Keulen - The relevant question is, can you describe the effect of urea supplementation in order to predict its effects on animal performance over a number of years? If you can, then there is no harm in using the ILCA model. But if you cannot quantify the effects of urea supplementation then you would be fooling yourself by using the model, because the results would be spurious.

Ketelaars - I think that, with regard to changes in nutritional conditions, the ILCA model is not an explanatory one, and, as far as I know, there are no explanatory models that can judge the possible effects of such changes. Thus, I think that there are many possible interventions the effects of which cannot be predicted, and these should be investigated in field trials.

Problems related to intake

Seligman - We will leave this topic, and go on to the problem of intake, which is central in interfacing primary and secondary production models.

Lambourne - Again, it seems to me that we can probably skip the interface stage altogether, and simply relate animal performance to characteristics of the resource which we are using. We do not want to predict pasture intake, we want to predict animal performance, and to relate this to characteristics of the area. I think that more needs to be done on how to incorporate the ideas of Ketelaars and others and to assess their importance, but we have to do this at a scientific level. I do not see why that should hold up the practical use of models that simply relate resources to animal performance.

de Leeuw - If you are asking these questions in relation to the ILCA model, we can put in a number of reasonably realistic limitations to intake with slight modification to the model. If we want to use the ILCA model for all purposes, we have to look at the intake side of the model.

van Keulen - In Holland we are confronting problems that mean that we cannot leave the intake side to experimental and theoretical control. We have pastures that are fertilized with high levels of nitrogen; dairy farmers want their cows to produce 40-50 litres of milk per day, while the government does not want the ground water and the soil to be polluted, and the environmentalists do not want acid rain. In that situation we have to describe in clear, quantitative terms what the properties of the forage offered to the animals should be in order to meet all these requirements. What little experience we have in Africa indicates that the performance of animals in extensive systems is limited by the fact that they cannot eat enough. If that is the case, then one would like to know whether the limitation is the amount or the quality of the forage available.

Lambourne - Am I right in thinking that this is an important field, particularly at the scientific level, and that there are a number of things that we do not understand about it? This probably calls for more careful research, and may be built into a model in the long run. In the meantime, we need to do research to understand the processes of intake and digestion and the factors that are involved.

van Keulen - That may be true to some extent, but you need that information in the short-term. For example, with the data that ILCA is collecting in their country programmes, you need to know if the poor performance of those herds is due to a problem in the interface between the feed resources and the animal or if the animals are sick. There is little you can do in the way of giving advice or making recommendations until this is clarified.

Wagenaar - I do not agree that models should not be used at present. They should be used as much as possible, keeping in mind that there are gaps in the knowledge on which they are based. These gaps are not a reason to avoid using the model. Meanwhile work should continue to fill in these gaps in the knowledge. If the knowledge is available, it should be incorporated into the model. For instance, Ketelaars' approach could be introduced into the model without knowing much about water intake or mineral requirements.

van Keulen - That is true, but individual modules of the model have to be tested just as in the primary production situation. At a certain stage in our model, the prediction of dry-matter accumulation did not agree with measured data. It is a long way from CO_2 molecules in the air to the grain at the top of a wheat crop. A deliberate decision was made to change the boundary of the system in this model and to first make sure that the part that models the pathway from the CO_2 molecule to the glucose molecule in the plant could be tested. This led to the development of a method for measuring carbon dioxide exchange in the field using a mobile laboratory. On the basis of this, I would suggest that you take out the intake module of the ILCA model and try to validate it on the basis of any data that are available.