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THE BASIS OF NUTRITIVE VALUE — A MODELLING APPROACH

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SUMMARY

Regulation of ruminant digestion is a complex multifactorial process which classical experimental methods have not been able to unravel. This paper describes how modelling and simulation techniques have been used to support a research programme in this area. A model of cellulose digestion in the rumen is detailed and efforts to evaluate the modelling approach are described. Considerable progress has been made in formalizing and integrating ideas in line with current concepts of rumen digestion, evaluating deficiencies in the literature, and identifying many areas where experiments are required.

INTRODUCTION

DESPITE years of work on the prediction of nutritive value of ruminant feeds, nutritionists have been unable to produce a simple reliable index. Many indices have been suggested and tested, but only one, apparent digestibility, has given any degree of reliability. However, it is known that digestibility has deficiencies. There are many instances in the literature where large differences in animal performance have been reported between feeds of the same digestibility (Miles *et al.*, 1969; Ulyatt, 1971). It is unrealistic to expect too much of digestibility as an index, because it only measures the difference between feed consumed and faecal output. It assumes implicitly that the digestive processes are the same for all feeds. It is known that this is not true, because variations in feed composition can result in differences in site of digestion and in the end-products of digestion (*e.g.*, MacRae and Ulyatt, 1974). Much current research emphasizes prediction of digestibility. In the writers' opinion, nutritionists are not addressing the real problem, that is, identification of the mechanisms that control the digestive processes and the subsequent utilization of the end-products of digestion. If these mechanisms can be understood, it will be possible both to devise an index and to manipulate the system to advantage.

The digestion of feed by the ruminant is the result of a very complex interaction among the constituents of the feed, the microorganisms in the digestive tract and the host animal. In addition, this digestion comprises biochemical, physiological and physicochemical processes. A great deal is known about many of the individual processes and reactions. However, the problem is to integrate this mass of data, concepts and hypotheses within a logical framework so that the quantitative importance of each process can be evaluated. Classical intuitive research techniques have clearly failed so far to meet this objective, so modelling and simulation techniques have been applied to see if the computer can be used to help resolve and evaluate the complex interactions and thus guide the present research programme. Clearly, theoretical (or causal) modelling as defined by Baldwin (1976) is required to support the research programme because the objective is to understand the nature of the system.

DEVELOPMENT OF A RUMEN MODEL

Models of various aspects of ruminant digestion have been published. Thus, Blaxter *et al.* (1956) and Grovum and Phillips (1973) mathematically analysed marker excretion curves in faeces, Hungate (1966) and Mertens (1973) estimated digestion parameters from *in vitro* time course digestion studies, and Waldo *et al.* (1972) proposed a model of cellulose digestion. These models all have a common feature; the authors utilized various mathematical procedures to fit experimental data in line with their concepts of ruminant digestion. None of these models is causal because they do not give an insight into the nature of the mechanisms that regulate ruminant digestion. Baldwin *et al.* (1970) described a causal model which was based on fermentation and biosynthetic balance equations. While this model had many desirable features it was still not satisfactory for understanding the basis of nutritive value: the input was potentially digestible substrate, there was no mechanism for feeding, and no account was made of the effect of physical and physiological processes on digestion.

Development of the current model of digestion in the rumen was based on two obvious premises:

(1) Nutritive value is primarily an attribute of the feed and therefore it can be measured on a sample of the feed.

(2) The rumen is the primary site of regulation in the digestive tract. There are several reasons for this:

(a) The rumen is the first organ encountered by the feed.

(b) It is the largest organ in the digestive tract.

(c) It is the site of longest delay in digesta passage (*i.e.*, longest residence time).

(d) The rumen accounts for highest proportion of digestion (60% of digestible organic matter).

(e) Events in the rumen have a large influence on digestion in the post-ruminal tract.

Based on the first premise, digestion of ten major feed constituents was considered in the model: soluble carbohydrate, starch, organic acids, pectin, hemicellulose, cellulose, lipid, soluble protein, insoluble protein and non-protein nitrogen. Sub-models were devised to represent the digestion of each of these feed constituents. These sub-models increase in complexity with

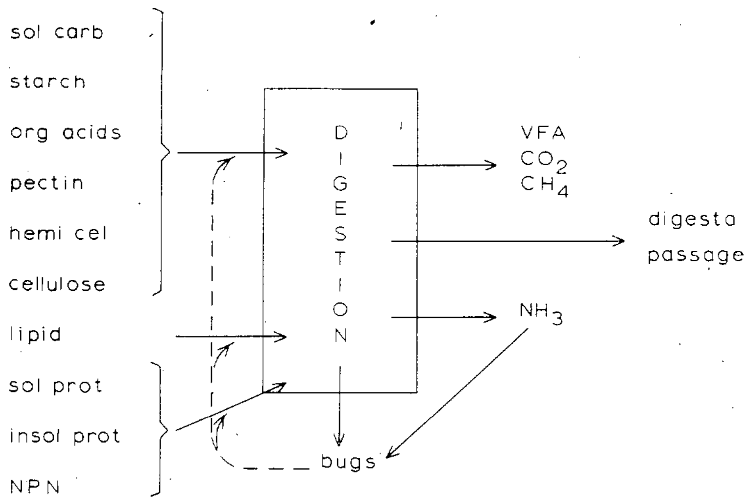

FIG. 1: *A diagrammatical representation of the rumen model showing inter-relationships of major components. Legend: sol carb = soluble carbohydrate; org acids = organic acids; hemi cel = hemicellulose; sol prot = soluble protein; insol prot = insoluble protein; bugs = rumen microbial pool.*

increasing difficulty of digestion of the substrate — *e.g.*, the soluble carbohydrate sub-model was less complicated than the cellulose sub-model. The sub-model for nitrogen digestion was similar to that published by Nolan and Leng (1972).

For model development lucerne chaff of 62% OM apparent digestibility was chosen as a reference diet because there are more data available in the literature from this diet than any other (Hogan and Weston, 1967; Gray *et al.*, 1967, Hungate *et al.*, 1971; Nolan and Leng, 1972; Thomson *et al.*, 1972; Ulyatt, unpublished). Parameter values for each sub-model were either derived from the literature or estimated. The sub-models were then run on the computer using the CSMP73 simulation language. Best fits were obtained by empirically adjusting unknown parameter values until model outputs agreed well with known experimental results. The sub-models were then combined to give a whole rumen model as shown diagrammatically in Fig. 1. Parameter values were again adjusted empirically until the model outputs were close to experimental results. In the rumen model there are two integrating influences: the free microbial pool is common to the digestion of all constituents, and nitrogen (N) metabolism in the rumen is central to microbial growth during fermentation of all substrates. The incorporation of microbial and N metabolism in the model was found essential from use of simpler models (Baldwin *et al.*, 1970).

CELLULOSE SUB-MODEL

Space prohibits detailing the whole rumen model, so the sub-model for cellulose digestion is presented (Fig. 2) to illustrate some of the concepts incorporated. This is one of the more complicated sub-models.

1. Dietary cellulose (DCEL) is consumed and becomes available for digestion (ACEL) in the reticulo-rumen (rumen).

2. ACEL is present in two forms: (a) As long particles (C1) which because of their size are unable to pass out of the rumen, and (b) As particles that are small enough to theoretically pass out of the rumen without further breakdown (C2).

3. C1 is colonized by free rumen micro-organisms (FBUG) via pathway K2 to form a microbial-cellulose complex BC1. This

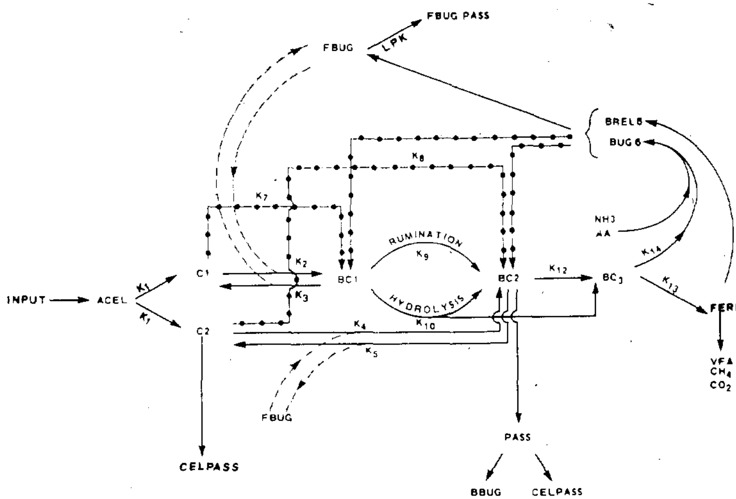

FIG. 2: *A model of cellulose digestion in the rumen. The coding is explained in the text.*

mechanism provides for an initial lag phase in digestion during colonization, which has been suggested in the literature (Dehority, 1961). The rumen micro-organisms are treated as one pool, with no attempt made to divide them into bacteria, protozoa or individual species. However, by definition the cellulolytics in the free pool are those micro-organisms that colonize cellulose. As micro-organisms are bound to the cellulose particles they become part of the bound microbial pool (BBUG).

4. Diminution of long cellulose particles (BC1 to BC2) proceeds via two routes: (a) Rumination (K9) and (b) Hydrolysis by the micro-organisms (K10). As a consequence the hydrolytic breakdown, a certain amount of the cellulose is fermented (BC1 to BC3 direct).

5. BC2 is the microbial-cellulose complex that has been reduced to a particle size that can pass from the rumen (K11). The micro-organisms bound in BC2 can also pass out of the rumen via pathway K11.

6. Small dietary cellulose particles (C2) either pass directly out of the rumen (K6) or they can be colonized by FBUG (K4) and can pass directly to BC2.

7. The pathway BC2 to BC3 (K12) allows for the final reduction of small cellulose particles to readily fermentable substrate (presumably glucose) (BC3).

8. BC3 is then fermented (K13) to produce volatile fatty acids (VFA), methane (CH_4) and carbon dioxide (CO_2), via published stoichiometric relationships (Baldwin *et al.,* 1970). ATP formed during fermentation is used for microbial growth (K14).

9. Micro-organisms grown during the digestion of cellulose (BUG6) and colonizing micro-organisms released after fermentation (BREL6) can proceed two ways: (a) They can recolonize both C1 and C2 directly (K7, K8). This mechanism is important because it allows an accelerating phase of cellulose digestion under the stimulus of positive feedback. (b) They can return to the FBUG pool where they can either recolonize more cellulose (K2, K4) or they can pass out of the rumen with liquid passage (LPK).

Thus the model incorporates experimental data, current concepts of cellulose digestion, and estimates of unknown parameter values obtained by successive approximation. These latter values can later be determined experimentally if they are found to be essential to model validation.

TABLE 1: A COMPARISON OF SOME MODEL PREDICTED VALUES WITH PERTINENT DATA FROM THE LITERATURE FOR SHEEP FED DRIED LUCERNE OF APPROXIMATELY 62% OM DIGESTIBILITY

	Model	*Hungate* et al. (*1971*)	*Hogan and Weston* (*1967*)	*Thomson* et al. (*1972*)	*Gray* et al. (*1967*)
OM intake (g/day)	836	904	930	834	806
OM digestibility (%)		62.4	62.4	60.6	
Entering duodenum (g/day):					
OM	383		549	595	
Cellulose	156		152	138	
Hemicellulose	64			69	
Microbial-N	6.1	15.8		13.9	
Rumen products (moles/day):					
VFA	3.60	4.94			4.12
CO_2	2.13	2.76			
CH_4	0.94	0.83			

EVALUATION OF THE RUMEN MODEL

By adjusting parameter values empirically the stage has been reached where the rumen model responds realistically in a qualitative manner, but has some significant quantitative limitations. An example of this is given in Table 1 where some model-predicted results are compared with pertinent data from the literature. This table demonstrates two main points, (a) the paucity and variability of literature values, and (b) the model output agrees well with literature values except for duodenal flows of OM and microbial-N. The duodenal OM and microbial-N flows are low because the model at this stage does not simulate the growth of microbial cells correctly. The current failure of the microbial growth element within the model is being investigated, with emphasis on factors which determine microbial growth rates and yields.

An example of the good qualitative behaviour of the model is given in Table 2, where some N digestion values from the model are compared with some experimental data using a lucerne chaff diet (Ulyatt, unpublished). Given that rumen microbial protein synthesis in the model was inadequate (Table 1), one would expect as a consequence elevated rumen ammonia and blood urea concentrations, together with increased urinary-N excretion. This is what happened in the model.

TABLE 2: COMPARISON OF SOME PARAMETERS OF N DIGESTION PREDICTED FROM THE RUMEN MODEL WITH VALUES OBSERVED EXPERIMENTALLY FROM SHEEP FED DRIED LUCERNE

	Predicted	*Observed*
N intake (g/day)	25.2	31.5
Rumen NH_3-N (mg/100 ml)	34.3	16.0
Plasma urea-N (mg/100 ml)	32.9	21.2
Urinary-N output (g/day)	22.4	15.8

Detailed examination of the microbial growth aspect of the model should either detect numerical or representational errors, or indicate that further experimental work is required because there is insufficient knowledge of the process. This is a valid outcome of research modelling.

A further example of how modelling can identify pertinent experiments is given in Table 3. In the rumen model the importance of reduction of particle size was recognized as a factor

TABLE 3: PARTICLE SIZE DISTRIBUTIONS (% DM RETAINED ON SIEVE) DETERMINED FROM WET SIEVING OF LUCERNE CHAFF AND RUMEN AND ABOMASAL DIGESTA FROM SHEEP FED LUCERNE CHAFF

Sieve Size (mm)	*Feed*	*Rumen*	*Abomasum*
4.0	91.8		
2.0	1.7	27.0	0.0
1.0	1.4	6.4	0.0
0.5	0.4	15.6	14.1
0.25		12.1	24.8
< 0.25	0.4	38.9	61.1

controlling the rate of digestion. However, no data were available in the literature so some measurements have been made by slaughtering sheep that had been fed at hourly intervals on a lucerne chaff diet of 62% OM digestibility. Particle size distributions in the feed (suspended in artificial saliva), the rumen, and the abomasum were measured using the wet sieving technique of Evans *et al.* (1973).

The results in Table 3 show that:

(a) 92% of the feed but none of the rumen DM was retained on the 4.0 mm sieve, suggesting that there is appreciable reduction in particle size by chewing.

(b) No particles greater than 1.0 mm reached the abomasum, suggesting a very sharp demarcation in the size of material that can leave the rumen.

(c) 66.6% of the DM in the rumen was of a particle size that could pass. Therefore reduction of particles to less than 1.0 mm only increases their probability of passing.

Initiation of this work was directly attributable to the modelling programme. It has led to these very interesting findings which will allow the analysis of control of digestion to be taken further.

CONCLUSION

This paper has given an example of the use of theoretical or causal modelling techniques (Baldwin, 1976) by the research scientist. This approach is adopted because the usual objective of a research scientist is to understand the nature of the system being studied. This is not necessarily the same type of modelling useful to the manager, administrator, adviser or farmer, because their objective is usually prediction and thus a more empirical approach may be justified.

The modelling process is not an end in itself, because in the final analysis the model is only as good as the data on which it is based. Modelling thus complements experimentation in a similar manner to statistics, and should lead to a more efficient choice of experiment. The model is regarded as a dynamic working hypothesis.

The modelling work on nutritive evaluation has just started but it is considered that progress has already been made in the following ways:

(a) It has helped in formalizing and integrating ideas in line with current concepts of rumen digestion.

(b) It has pointed to inadequacies in the literature.

(c) It has identified many areas where experiments are required.

The writers have found that the modelling process itself, independent of progress made in model development, is beneficial in forcing more rigorous and quantitative thinking, destroying preconceived notions, and aiding greatly in the identification of critical experiments.

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