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THE USE OF A STEADY STATE FEEDING SYSTEM IN NUTRITION EXPERIMENTS WITH RUMINANTS

M. J. ULYATT

*Plant Chemistry Division, D.S.I.R., Palmerston North**

SUMMARY

A continuous-feeding device was used to produce a continuous fermentation in the rumen of sheep. This should result in a uniform presentation of substrates to the tissues of the whole animal and thus a close approximation to a steady state. Some examples are given to show how the technique can be used in studies of ruminant nutrition.

THIS PAPER describes an experimental feeding system in which continuous feeding was used as a means of producing a steady state in the ruminant. By steady state is meant a situation where the processes taking place in the animal had come to equilibrium and their rates remained constant over a long period of time. In a steady state the concentrations of metabolites in any organ or tissue should be constant. In the case of the ruminant, the aim of continuous feeding was to produce a continuous fermentation in the rumen (Hungate, 1966) so that parameters such as rumen volume, rate of flow of material into and out of the rumen, digestion rate and absorption rate remained constant. If a continuous fermentation could be achieved, then there should be a uniform presentation of substrates to the tissues of the whole animal and a situation which approximates a theoretical steady state might be reached. The idea is demonstrated in Fig. 1 which shows diagrammatically the effect on the concentrations of steam-volatile fatty acids in the rumen of offering the same amount of feed at three different feeding frequencies. In (a) the feed is given as one meal; in (b) as eight meals; and in (c) the animal is fed continuously. As the feeding frequency is increased,

*The work described was carried out at the Hannah Dairy Research Institute and the Rowett Research Institute, Scotland.

the concentration of steam-volatile fatty acids approaches constancy.

The principle of using continuous feeding to produce a steady state in the ruminant was largely conceived by Dr T. M. Sutherland and his colleagues at the Rowett Research Institute.

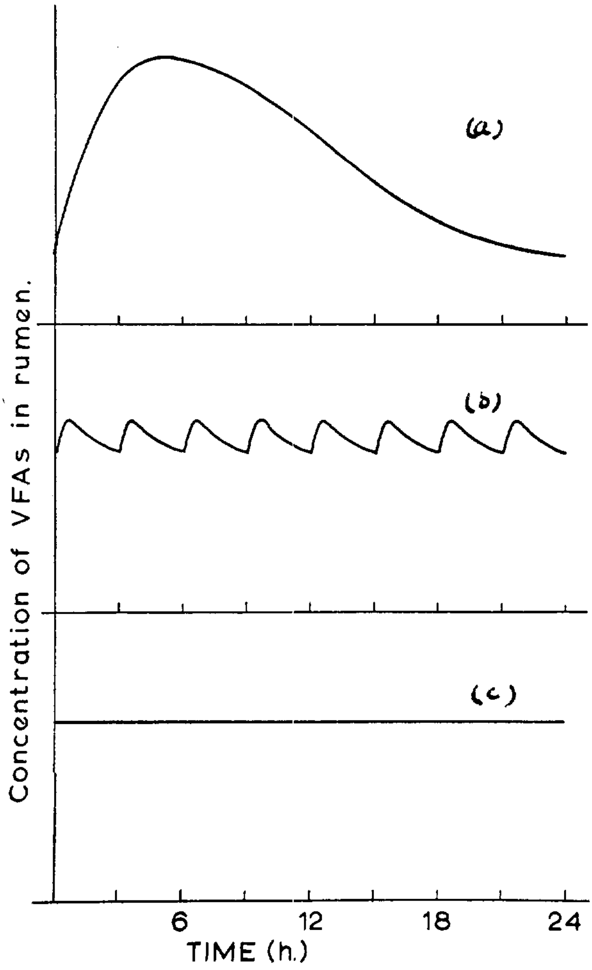

Fig. 1: A diagrammatic representation of the effect on the concentration of steam-volatile fatty acids in the rumen of offering the same amount of feed at three different feeding frequencies: (a) once a day, (b) eight times a day and (c) continuous feeding.

METHODS

The sheep used in the experiments described here were fed from the continuous belt feeder designed by Sutherland *et al.* (1963). This can be seen in Fig. 2. A slow-speed electric motor moved the belt a set distance in 24 hr and the day's feed was spread evenly on the belt over this distance. Pelleted feeds were used because of their ease of handling: the apparatus delivered a pellet into the sheep's feed bin every 2 to 3 min. In all experiments the sheep were fed at approximately the maintenance level of nutrition. It was considered important to administer the animals' drinking water continuously so as to avoid sudden influxes of water into the rumen owing to drinking. Accordingly, the water intake of approximately 3 litres per day was given as a continuous infusion through a rumen cannula. A period of 2 to 3 months was allowed for adjustment when the sheep were first introduced to the feeding system and a shorter period of at least 3 weeks was allowed when diets were changed.

It was considered necessary, if a steady state was to be approximated, to eliminate diurnal variations by controlling the animals' external environment as closely as

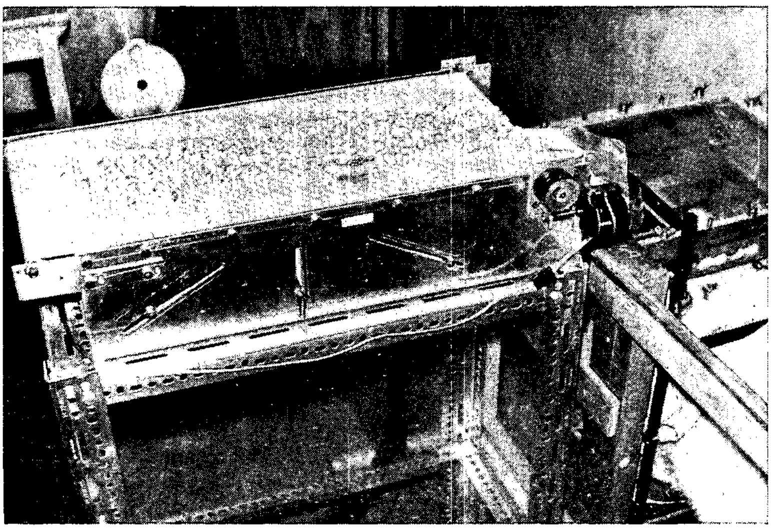

Fig. 2: The continuous belt feeder.

possible. The animals were kept under continuous artificial lighting, constant ventilation and at a temperature of 18 ± 1°C. The ventilation system also contributed a constant low background noise. Some people (*e.g.*, Minson and Cowper, 1966) consider that background noise is very important and they provide taped music or a radio tuned to a 24 hr "pop" station.

CAN A STEADY STATE BE ACHIEVED?

Several workers have used continuous feeding in an attempt to produce a steady state in the sheep. Ulyatt, Blaxter and Czerkawski (unpubl.) collected samples of digesta from sheep prepared with both rumen and abomasal cannulae at 4 hr intervals over 24 hr. Lignin in the feed and polyethylene glycol (PEG) administered with the water infusion were used as markers. The results of this experiment are shown in Table 1. There were

TABLE 1: CONCENTRATIONS OF MARKERS IN SAMPLES OF RUMEN AND ABOMASAL CONTENTS COLLECTED AT 4 HR INTERVALS OVER 24 HR FROM CONTINUOUSLY FED SHEEP

(Mean ± SE)

Sheep	Lignin (g/100 g D.M.)		PEG (mg/ml liquor)	
	Rumen	Abomasum	Rumen	Abomasum
J	8.65 ± 0.16	7.28 ± 0.10	2.80 ± 0.06	1.85 ± 0.06
H	8.42 ± 0.16	8.48 ± 0.19	2.25 ± 0.03	1.89 ± 0.09
B	8.23 ± 0.19	7.00 ± 0.12	7.18 ± 0.22	4.37 ± 0.10

no systematic trends in marker concentrations and the standard errors were very low. Portugal (1963) showed that the concentrations of total nitrogen, precipitatible nitrogen and ammonia stayed constant in the rumen during continuous feeding and cited the unpublished work of Sutherland which showed that rumen steam-volatile fatty acids also remained constant. Continuous feeding has also been found to produce stable concentrations of sodium and potassium ions in the rumen (Scott, pers. comm.), plasma steam-volatile fatty acids (Whitelaw, pers. comm.) and plasma glucose (Ulyatt, unpubl.), while Minson and Cowper (1966) have shown that hourly feeding can eliminate diurnal patterns in urine and faeces excretion. All these observations would indicate that steady state conditions can be closely approached by continuous feeding. There are obvious exceptions, with respect to the whole animal, where the steady state would not hold if a short time interval were considered, such as those organs which store secretions or excretions and which require discrete emptying. However, these problems can be overcome if a longer time interval is considered, or by use of suitable cannulation techniques.

ADVANTAGES OF A STEADY STATE

The steady state technique has several advantages to the experimenter over the normal practice of offering feed in one or more discrete meals.

1. The Measurement of Body Pools and their Turnover Rates.

In order to measure accurately the size and rate of turnover (or rate of utilization) of body pools, it is necessary that two criteria be fulfilled during the period of measurement:

(a) Pool size should remain constant.

(b) The rates of turnover of metabolites in the pool should be constant.

The system of continuous feeding to produce a steady state was designed primarily to meet these requirements. In the past it has been the practice either to fast the animals or to remove the feed shortly before an experiment (*e.g.*, Annison and White, 1961; Ford, 1963). In many cases it is unsatisfactory to use starved animals because the supply of a metabolite to the tissues may affect its rate and mode of utilization. Fasting is particularly unsatisfactory when several diets are being compared. However in recent studies such as those on the rate of production of steam-volatile fatty acids in the rumen (Bergman *et al.*, 1965; Leng and Brett, 1966) continuous feeding methods have been employed with considerable success. The technique has been used at the Rowett Research Institute in a comparison of the rates of glucose utilization in sheep fed at maintenance on three different diets (Ulyatt, Whitelaw, Watson and Reid, unpubl.). In-dwelling catheters were placed in each jugular vein the day before an experiment, one for infusing and one for sampling. On the day of an experiment, a trained sheep was placed with its head in a hood so that respired carbon dioxide could be collected, but at the same time the sheep could be fed continuously. A priming dose of glucose-^{14}C was then injected to equilibrate the plasma glucose pool to a chosen specific activity, followed by a continuous infusion of glucose-^{14}C at a rate calculated to maintain constant plasma glucose specific activity. The result of a typical experiment is shown in Fig. 3. Plasma glucose concentration and plasma glucose specific activity remained constant. In contrast, the

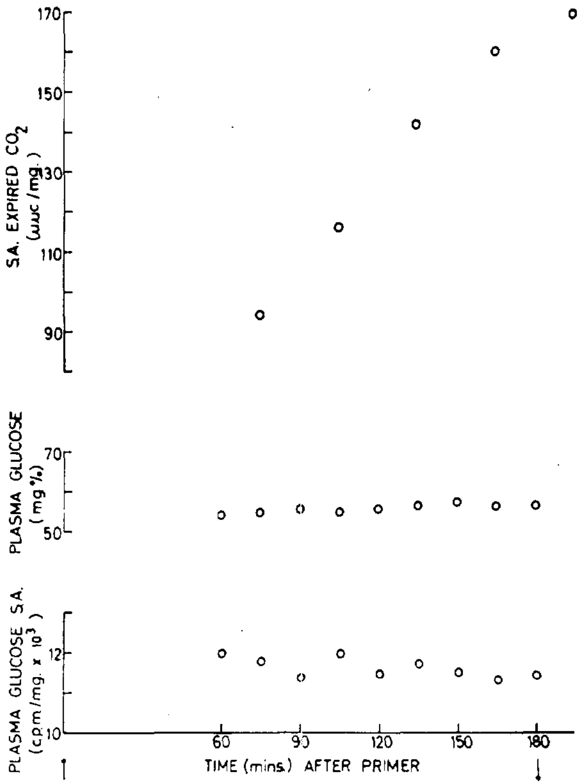

Fig. 3: Results of a typical experiment using a continuous infusion of glucose-^{14}C to estimate parameters of glucose utilization in the sheep.

TABLE 2: DIGESTIBLE ENERGY INTAKE, GLUCOSE PRECURSOR INTAKE AND SOME PARAMETERS OF GLUCOSE UTILIZATION IN SHEEP FED CONTINUOUSLY AT THE MAINTENANCE LEVEL OF NUTRITION ($n = 3$)

	Barley	Dried-grass	Hay	S.E.
Digestible energy intake (kcal/24 hr)	2,520	2,402	2,286	
α-linked glucose polymer intake (g/24 hr)	297	38	53	
Glucose utilization rate (mg/min/kg)	1.24	1.49	1.37	0.11
% Carbon dioxide derived from glucose	3.6	4.1	3.9	0.20

specific activity of expired carbon dioxide rose at first and then tended towards an equilibrium plateau. The overall results of the experiment are shown in Table 2. Despite large differences in glucose precursor intake, there were no significant differences between diets or between animals in either glucose utilization rate or the percentage of carbon dioxide derived from glucose at equilibrium. Thus, by use of the continuous feeding technique, it was demonstrated that when sheep were fed at maintenance there appeared to be no dietary influences on glucose utilization.

2. REDUCTION IN THE NUMBER OF SAMPLES

Fewer samples are required to describe fully the pattern of events occurring during 24 hr when a steady state system is used. This is evident if Fig. 1 is referred to; it is clear that many more samples are required to describe (a) than (c). It follows that with a steady state there should be no difficulty in extrapolating from one sampling period to the whole 24 hr; in fact, it should be possible to describe (c) with only one sample. In practice, several samples were taken over a time period and then bulked. This can be illustrated by an experiment conducted at the Hannah Dairy Research Institute where the continuous feeding technique was utilized to measure quantatative digestion in the stomachs of the sheep (Ulyatt, Blaxter, and Czerkawski, unpubl.). Sheep prepared with

TABLE 3: TOTAL AMOUNTS OF VARIOUS FOOD CONSTITUENTS PASSING THE PYLORUS AND APPARENTLY DIGESTED IN THE STOMACHS OF TWO SHEEP FED 700 G D.M. OF DRIED-GRASS PELLETS PER 24 HR.

	Sheep	α-linked Glucose Polymer	Total Reducing Sugars	Cellulose	Crude Lipid	Total Nitrogen	Non-protein Nitrogen
Pyloric flow (g/24 hr)	J	6.5	75.3	97.4	49.9	30.6	15.9
	B	5.6	61.3	100.3	45.6	27.3	13.9
Apparent digestibility in stomachs (%)	J	86.7	64.3	64.3	28.6	2.6	—195.7
	B	88.2	70.0	62.0	32.5	10.2	—167.3

rumen and pyloric cannulae were fed continuously on a maintenance diet of ground and pelleted dried grass. Weller *et al.* (1962) and Reid (1965) had demonstrated that the liquid phase of digesta passes out of the rumen at a faster rate than the solid phase. This principle was utilized together with continuous feeding: lignin in the feed was used to mark the solid phase of the digesta and PEG was administered as a continuous intraruminal infusion to mark the liquid phase. Under steady state conditions it should be possible to sample digesta at any level of the digestive tract and, by reference to the markers, estimate the amount of digestion occurring anterior to the sampling site. In this experiment samples were taken from near the pylorus and thus estimates could be made of quantitative digestion in the stomachs of the sheep. Two samples of digesta were collected each day for 6 days and then bulked on an equal weight basis to give one sample. The solid and liquid phases of this bulked sample were separated by centrifuging at 20,000 × *g* for 30 min. By this means most particulate plant debris and micro-organisms were included arbitrarily in the solid phase. The rate of flow of each phase past the pylorus was calculated from the relationship:

$$\text{Flow} = \frac{\text{Amount of marker administered per unit of time}}{\text{Marker concentration}}$$

As the technique is dependent upon the markers being indigestibile, faecal recoveries were made. In three experiments the recovery of PEG was 101.8 ± 3.2% and in eight experiments the recovery of lignin was 98.7 ± 2.3%. The quantitative flow of any digesta constituent past the pylorus was calculated from the relationship:

$$\text{Quantitative flow of constituent past the pylorus} = F_l\ C_l + F_s\ C_s$$

Where F_l = Rate of flow of liquid phase past pylorus.
C_l = Concentration of constituent in liquid phase.
F_s = Rate of flow of solid phase past pylorus.
C_s = Concentration of constituent in solid phase.

Results from two sheep that were fed 700 g D.M./day were averaged and are given in Table 3. Various food fractions were chosen to be representative of the major nutrients available to the sheep—*i.e.*, soluble carbohydrates (α-linked glucose polymer and reducing sugars), insoluble carbohydrates (cellulose), crude lipid and nitrogenous compounds. The flow figures are in line with what one might expect from published figures (Armstrong, 1965; Gray *et al.*, 1958; Phillipson and Ash, 1965).

It should be emphasized that these results were obtained from the analysis of one bulked sample of digesta from each sheep.

3. The Collection of Samples Over a Long Period of Time

The third main advantage of the steady state system is that it makes it possible to collect similar samples of body fluids over a long period of time. This is very desirable in many biochemical and microbiological studies where large quantities are required.

LIMITATIONS OF THE TECHNIQUE

The continuous feeding method, used as above, has certain limitations.

(1) The animals must be fed at less than *ad lib.* food intake. If food is offered *ad lib.*, refusals will occur, the animal will follow behavioural patterns in its rate of eating and the steady state approximation will break down. In the present experiments the sheep were fed at maintenance and although they were often observed through the 24 hr they were never allowed pellets to accumulate in their feed bins.

(2) Continuous feeding does not overcome the problem of obtaining a representative sample of digesta from the rumen. Bergman *et al.* (1965) used the pump designed by Sutherland *et al.* (1962) in addition to the continuous feeder to obtain samples of rumen digesta. However, this pump can be used with only a limited range of ground and pelleted diets. The technique of emptying the entire rumen contents to obtain a representative sample of digesta (Reid, 1965; Minson and Cowper, 1966) might be a useful addition to the continuous feeding method.

(3) Some animals do not adapt readily to the continuous feeding system and exhibit various neuroses. One

way of reducing this is to place the feed bin low so that the sheep can lie down and eat.

(4) In the present experiments only ground and pelleted rations were used because of their ease in handling. This type of ration is not necessarily desirable for all types of work on ruminant digestion—*e.g.*, rumen movements are often irregular when sheep are fed ground and pelleted diets (Reid, 1963). However, there is no reason why long and chopped forages cannot be fed from a continuous feeder—*e.g.*, Minson and Cowper (1966) fed hay with their hourly feeder.

THE EFFECT OF FEEDING FREQUENCY ON ANIMAL PRODUCTION

A detailed discussion of the effects of changing feeding frequency on animal production is outside the scope of this paper, although some comment is required. In a review article, Mochrie (1964) concluded that increased liveweight gains often occurred when feeding frequency was increased. The reasons for this are not clear but it has been suggested that a more uniform presentation of metabolites to the tissues might result in a less wasteful oxidation, lower heat loss, and improved efficiency. There is biochemical evidence to suggest that certain enzymic pathways are rate limiting and cannot cope with an excessive load of substrate (Krebs and Kornberg, 1957). For this reason, a uniform presentation of substrate might result in a higher efficiency of feed utilization.

It must be stressed that continuous feeding has been considered in this paper only as an experimental technique. If any practical justification is required, it might be that continuous feeding is closer to the grazing situation than is once or twice a day feeding. Properly used, the technique can be a valuable tool in the study of ruminant nutrition.

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