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STUDIES ON SOME FACTORS INFLUENCING FOOD INTAKE IN SHEEP

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SUMMARY

A review of some factors influencing the intake of food by ruminants is presented. In addition, two sets of experimental results which indicate the complexity of intake control are described:

(1) It was shown that it is possible to produce significant intake depressions in sheep by intraruminal infusions of acetic, propionic and butyric acids. Plane of nutrition of the animal plays a large role in the effect obtained.

(2) A situation where normal intake pattern appeared to be over-ruled by a transient unpalatability is described. Short-rotation ryegrass was rendered unpalatable to sheep by an accumulation of nitrogenous compounds in the grass following unusual environmental conditions.

IN THE LAST five years there has been an increased interest in factors affecting the food intake of ruminants. Some of this work will be briefly reviewed in this paper. In addition two sets of experimental results which indicate the complexity of intake control will be presented.

A REVIEW OF FACTORS DETERMINING RUMINANT INTAKE

Most of the reported work on mammalian food intake regulation has been carried out with monogastric animals. However, there has always been some interest in the factors determining ruminant intake, particularly in relation to the formulation of feeding standards.

Much evidence supports the view that food intake regulation is ultimately mediated through the nervous system. Excellent reviews covering this subject have recently been published by Anand (1961) and Balch and Campling (1962). Anand (1961) has postulated that there are various levels of nervous control over intake, from simple spinal reflexes through to complex activities involving the cerebral cortex, which exercise control of a discriminative nature. One region of the brain, the hypothalamus, has been implicated in the control of intake both in monogastric and ruminant animals (Larssen, 1954). Two areas of the hypothalamus appear to be concerned. Stimulation of the first area, known as the "satiety centre", produces an inhibition of feeding, while stimulation of the other area, which is known as the "feeding centre", facilitates feeding behaviour.

In monogastric animals much interest has focused on elucidating the nature of the stimuli which pass signals to the nervous system in response to the ingestion of food. Several mechanisms have been suggested — *e.g.*, chemostatic; thermostatic; lipostatic; regulation by the gastro-intestinal tract; changes in water balance; hormonal changes.

There is evidence to support each of these possibilities: however, no single mechanism has been shown to give complete control.

When considering ruminant intake regulation, special feasures such as the modification of the stomach into rumen, reticulum, omasum and abomasum, and the magnitude of the microbial fermentation taking place in the rumen must be taken into account.

Previous work on the regulation of ruminant intake has centred on two mechanisms, namely, reduction of rumen load and chemostatic control.

Rumen Load Theory

That ruminants will eat more of a good quality than of a poor quality forage has been recognized for many years.

Lehmann (1941) was the first to recognize that the large bulk of food consumed by ruminants must have some effect on intake when he claimed that they eat to a constant amount of ballast in the rumen. Ballast was defined as non-digestible organic matter and according to this hypothesis animals would eat less of a poor quality forage which contained more ballast. Although Lehmann's idea was criticized by various workers (Mäkelä, 1956), it was accepted that some attribute of rumen distension was of importance in the regulation of forage intake. This, then, was intake regulation in a physical sense: the capacity of the rumen provided an upper limit.

The problem of the regulation of voluntary intake of forages has been the subject of detailed investigation in recent years by three main groups: Blaxter and his associates in Scotland, Campling and co-workers in England, and Crampton's group in Canada. While the approaches of these schools have been different, they have come to essentially the same conclusion, namely, that the amount of forage eaten is closely associated with the rate at which food is broken down in the rumen. The rate at which the rumen load is reduced depends on three variables:

(a) The capacity of the rumen.
(b) The rate of fermentation of the feed.
(c) The rate of passage of indigested food residues through the digestive tract.

According to this scheme, a high quality forage would be broken down and passed through the rumen rapidly compared with a poor quality forage. Thus rumen load would be reduced more rapidly on the high quality forage and the animal would be able to eat more frequently.

It must be emphasized that the above work was carried out with forages such as hay, chaff and dried grass, and there are many situations encountered with ruminants where the rumen load theory does not seem to apply. Depressed intakes have been reported on very high quality diets such as concentrates (Donefer *et al.*, 1963; Freer and Campling, 1963) and also on silages (Thomas *et al.*, 1961).

Chemostatic Theory

The hypothesis that the rise in metabolites in the blood after a meal could be correlated with intake regulation is of long standing. Mayer (1953) suggested that blood glucose level controlled appetite in monogastric animals by stimulating gluco-receptors in the hypothalamus. In ruminants, chemostatic regulation has been suggested by Freer and Campling (1963) and Donefer *et al.* (1963) to explain depressed intakes on concentrate rations.

Glucose is present in the blood of ruminants but its concentration is relatively stable and is not markedly influenced by feeding (Reid, 1950a). Manning *et al.* (1959) and Dowden and Jacobson (1960) tested whether a glucostatic mechanism was operating in ruminants by infusing varying amounts of glucose intravenously. No effect on intake was observed.

Possible alternative metabolites would be the volatile fatty acids (VFA) which are absorbed from the rumen in large amounts. Only acetic acid is present in significant amounts in peripheral blood, or shows any appreciable post-feeding arterio-venous differences (Reid, 1950b). Trace amounts of propionic and butyric acids are normally present in the blood. Very little work has been carried out to test whether the VFAs do have any influence on food intake. Dowden and Jacobson (1960) studied the effects of intravenous infusions of various metabolites, including the VFAs, on the intakes of identical twin cows. Only acetic and propionic acids depressed intake. The significance of this propionic effect must be questioned because of the low concentration of this acid in peripheral blood. A more physiologically normal experimental procedure would be to infuse the acids into the rumen. This was done by Rook *et al.* (1960) who infused acetic, propionic and butyric acids to heifers on a hay diet, and found that only acetic caused any significant depression of intake.

THE EFFECT OF THE ADDITION OF VFA'S TO THE RUMEN ON INTAKE

In the experiments to be described the effects of intraruminal infusions of acetic, propionic and butyric acids on the intake of sheep on high and low planes of nutrition were studied.

EXPERIMENTAL

Three different rations were used during the experiments. Concentrates I and II were pelleted mixtures of pea meal, barley meal and lucerne meal, while the chaff was a low quality chaffed red clover hay. An indication of the relative nutritional values of the feeds is given in Table 1. On both concentrate diets digestibility, rumen VFA concentration and the proportion of propionic and butyric acids were high, and liveweight gains were always achieved. The chaff was a very poor quality feed: digestibility and VFA production were low. The proportion of acetic acid was high and all animals on this diet lost weight.

TABLE 1: THE RELATIVE NUTRITIONAL VALUES OF THE DIETS USED IN THE INFUSION EXPERIMENTS

	Diet		
	Concentrate I	*Concentrate II*	*Chaff*
Digestibility of D.M. (%)	71.4	81.6	29.4
Total rumen VFA (mM/100 ml)	13.80	18.42	9.96
V.F.A. proportions (%):			
Acetic	50.2	47.3	76.2
Propionic	22.2	25.1	17.7
Butyric	19.3	25.0	6.1
Higher	8.2	2.6	—
Liveweight change	Gain	Gain	Loss

In all experiments there were two sheep per treatment and these were trained to consume their food in six hours. The daily routine was to starve the animals overnight and to feed and carry out infusions for six hours during the day. Infusions were started one hour before the food was offered. For each acid tested, dose rates of 100, 200 and 300 kcal in three litres of water were infused in random order. Each dose rate was used for three days, the procedure being to infuse acid and water on alternate days. The treatment days were then compared statistically with the water days within each dose rate. Three litres of water alone had no effect on intake. It must be remembered that the treatments involved adding extra VFAs to those normally produced by fermentation of the feed.

Results and Discussion

The effect of infusions of acetic acid on daily food intake is shown in Table 2. There were significant depressions in intake at the 300 kcal dose rate on the concentrate diet and at both the 200 and 300 kcal dose rate on the chaff diet.

TABLE 2: EFFECT OF INTRARUMINAL INFUSIONS OF ACETIC ACID (HAc) ON THE FOOD INTAKE OF SHEEP

Diet		*Daily Food Intake (Means and S.E.s) (g D.M.)*
Concentrate II	Water	1,271 ± 37
	100 kcal HAc	1,165 ± 37
	Water	1,276 ± 35
	200 kcal HAc	1,080 ± 35
	Water	1,186 ± 33
	300 kcal HAc	896 ± 33***
Chaff	Water	971 ± 37
	100 kcal HAc	950 ± 37
	Water	1,100 ± 20
	200 kcal HAc	858 ± 20***
	Water	1,100 ± 44
	300 kcal HAc	757 ± 44**

*$P < 0.05$ **$P < 0.01$ ***$P < 0.001$

The effect of propionic acid infusions on food intake is shown in Table 3. In the case of the concentrate diet there was no significant depression when the treatment days were compared with the water controls. However, there seemed to be a cumulative effect: a progressive decline in both treatment and control intakes occurred as the dose of propionic acid was increased. When the treatment ceased, the intake returned to the pre-treatment level over a period of 4 to 5 days. Infusions of 300 kcal of propionic

TABLE 3: EFFECT OF INTRARUMINAL INFUSIONS OF PROPIONIC ACID (HPr) ON THE FOOD INTAKE OF SHEEP

Diet	*Infusion*	*Daily Food Intake (Mean and S.E.s) (g D.M.)*
Concentrate I	Water	1,512±30
	100 kcal HPr	1,440±30
	Water	1,272±45
	200 kcal HPr	1,257±45
	Water	1,130±52
	300 kcal HPr	1,047±52
Chaff	Water	847±25
	100 kcal HPr	797±25
	Water	874±35
	200 kcal HPr	894±35
	Water	850±28
	300 kcal HPr	597±28***

***$P < 0.001$

acid caused a significant intake depression in sheep on the chaff diet and no cumulative effect was noticed.

Some infusions were carried out with butyric acid at a dose rate of 300 kcal. There was little effect on the chaff diet and a small depression of intake on the concentrate diets. Because the pathways of butyric acid metabolism are not fully understood and because the infusion of butyric acid results in high blood ketone levels, no attempt was made to study the effect of this acid on intake in detail.

Of all the VFAs, it would seem that acetic acid comes closest to fulfilling the requirements of an intake regulatory metabolite because:

(a) It is the only VFA present in significant amounts in blood leaving the liver.

(b) It is the only VFA that shows appreciable arterio-venous differences after feeding.

(c) It is the largest single energy source in ruminants: the sheep derives at least 35 to 45% of its energy from the oxidation of acetic acid.

(d) Acetic acid is the main precursor of acetyl co-enzyme A, a substance that occupies a key position in the energy metabolism of the VFAs.

The main argument against acetic acid as a regulatory metabolite has been that it is non-glucogenic and cannot supply the glucogenic substances that are essential to its own metabolism (Manning *et al.*, 1959). However, the rate of acetate metabolism in the sheep is dependent on nutritional status, being much faster on a high than a low plane of nutrition. Acetate metabolism has also been shown to be closely related to carbohydrate metabolism and increased levels of blood glucogenic substances increase the rate of removal of acetate from the blood. Hence the objection to acetic acid as a satiety stimulant may be overcome by the evidence that acetate metabolism is rapid as long as an adequate supply of blood carbohydrate is available.

Returning now to the results presented in this paper. Ruminal fermentation of the high plane concentrate diet produced large amounts of the glucogenic propionic acid and presumably resulted in a high glucose turnover in the animal. Conversely, fermentation of the low quality chaff diet produced large amounts of acetic acid and a low concentration of propionic acid, which would indicate a low glucose turnover in the chaff-fed animals. Therefore animals on the concentrate ration should have been able to deal with an acetate load more efficiently than those on chaff diet. This is apparently what happened: the effect of acetic acid infusions on food intake was more pronounced on the chaff than on the concentrate ration (Table 2).

Explanation of the propionic acid effect in terms of an interaction of carbohydrate and acetate metabolism does not satisfy the results. Evidence is available to suggest that the liver can only deal with a certain load of propionate (Leng and Annison, 1963) and above this level the excess escapes to general circulation. This would ascribe the propionic acid effect to an abnormal physiological situation, and would also explain the depression of intake observed by Dowden and Jacobson (1960) when propionic acid was infused intravenously.

It seems, therefore, that chemostatic regulation of food intake in ruminants is possible. No more than this can be said at the moment: the results described cannot be regarded as providing unequivocal proof. If the VFAs are involved in the regulation of food intake, it appears that their effect is not a major one. Further, it seems unlikely that any single mechanism would be responsible for food intake regulation in ruminants: an interaction of many factors as suggested for monogastric animals by Brobeck (1955) would seem more reasonable.

PALATABILITY AS A FACTOR DETERMINING THE INTAKE OF RYEGRASS

In this section a situation where short-rotation ryegrass was rendered unpalatable by unusual environmental conditions will be described.

Earlier experiments have suggested that higher liveweight gains can be expected from sheep grazing short-rotation ryegrass (S) than those grazing perennial ryegrass (P) (Rae *et al.*, 1963; Barton and Ulyatt, 1963; Johns *et al.*, 1963). Results of such experiments are summarized in Table 4. Although liveweight gains of sheep on S were greater, rumen size was smaller than that of the P sheep. Further, the rumens of the S-fed sheep had a greater development of the rumen papillae and contained a higher concentration of VFAs than rumens from the P-fed sheep. There was a lower proportion of acetic and higher proportions of propionic and butyric acids in the rumen liquor from the S-fed sheep.

TABLE 4: SUMMARY OF PREVIOUS RESULTS COMPARING SHEEP GRAZING PERENNIAL AND SHORT-ROTATION RYEGRASSES

Short-rotation Ryegrass		*Perennial Ryegrass*
Higher	GROWTH RATE	Lower
Higher	CARCASS WEIGHT	Lower
Small	RUMEN SIZE	Large
Large	RUMEN PAPILLAE DEVELOPMENT	Small
Higher	RUMEN VFA CONCENTRATION	Lower
Lower	ACETIC	Higher
Higher	PROPIONIC	Lower
Higher	BUTYRIC	Lower

Several possibilities have been suggested to account for the observed differences between the P- and S-fed sheep. Bailey (1964) has shown in ryegrass samples collected over several seasons, that there was a consistent and significantly higher cellulose content in P than S. There was a trend towards higher soluble sugars in S but this was not as marked as the cellulose difference. In the rumen, cellulose is degraded mainly to acetic acid while the fermentation of soluble carbohydrates produces predominantly the higher molecular weight propionic and butyric acids (Bailey, 1962). This evidence provides a logical explanation for the observed differences in VFAs in the rumens of sheep grazing S and P. Blaxter (1960) has shown that propionic and butyric acids are utilized more efficiently for productive purposes in sheep than is acetic acid. It was possible that a rumen fermentation producing more butyric and propionic acids was the cause of the superior weight gains on S. Another possibility was that the S sheep had a higher food intake than those grazing P. As the S sheep had smaller rumen volumes, the above suggestion would imply a faster rate of passage of the undigested food residues through the rumens of the S sheep.

Experiments were set up to test the various factors which could be giving rise to the differences in weight gains.

EXPERIMENTAL

In March, 1962, an area of one acre at D.S.I.R., Palmerston North, was divided into six plots, of which three were sown with P, and three with S. These plots were grazed or mown when necessary and by September, 1962, thick even swards had been established. Throughout the experimental period, nitrogenous fertilizers, either Nitrolime or sulphate of ammonia, were applied at the rate of one cwt per acre per month. On August 27, 1962, six two-year-old Romney Marsh wethers fitted with permanent rumen fistulas were introduced to a mixed ryegrass-white clover pasture for a period of common grazing. From September 10 to 12, these animals were dosed with a polyethylene glycol (PEG) marker for rumen volume and flow rate measurements. The animals were then divided into two groups of three and introduced to the S and P plots of the experimental area where they were grazed for seven weeks. Each plot of the experimental area was subdivided and one half was grazed in rotation by the experimental sheep while the other half was mown to grazing height. Over the last three weeks of the experimental period, an indoor digestibility trial was conducted and faecal collection made from the fistulated sheep. The digestibility trial, which consisted of seven days prefeeding and ten days collection, was conducted with three non-fistulated wethers per treatment. They were fed on grass cut from the non-grazed portions of the experimental area. Immediately after the outdoor faecal collection, samples of rumen contents were obtained for VFA determinations and following this the animals were dosed with PEG for three days for rumen volume and flow rate measurements.

Throughout the experimental period the animals were weighed regularly and samples of herbage were collected and freeze-dried for chemical analysis.

In the experiments to be discussed, rumen fluid volume and the flow rate of fluid from the rumen were estimated with the PEG marker technique introduced by Sperber *et al.* (1953) and developed by Hydén (1961).

In the present experiment, diurnal variations in rumen dry matter (D.M.) percentage were found, with the highest values being obtained in late afternoon. Accordingly, during every rumen volume determination a rumen D.M. sample was obtained at 4.00 p.m. and maximum rumen D.M. calculated by simple proportion as below:

$$\frac{\text{Rumen D.M. \%}}{\text{Rumen Fluid \%}} = \frac{\text{Maximum Rumen D.M. (g)}}{\text{Rumen Fluid Volume (ml)}}$$

Results and Discussion

A chemical analysis of the herbage at the time of the digestibility trial is shown in Table 5. Although only soluble sugar and cellulose fractions of the carbohydrate are shown, the water-soluble polysaccharide, pectin and hemicellulose fractions were also measured but showed no differences between grasses. There was no difference between the grasses in soluble sugars but there was a significant difference in cellulose in favour of the P.

TABLE 5: CHEMICAL COMPOSITION OF SHORT-ROTATION AND PERENNIAL RYEGRASSES IN OCTOBER 1962

Sample	*SRE*	*SRL*	*P*
Carbohydrates (% D.M.):			
Soluble Sugars	10.50	10.50	9.75
Cellulose	15.20	15.00	18.30
Lignin (% D.M.)	3.30	4.10	2.20
Nitrogenous Fractions:			
NPN (mg/100 g)	556	758	498
NO_3-N (mg/100 g)	232	378	177
Protein N (% D.M.)	3.58	3.67	3.59
Total N (% D.M.)	4.24	4.43	4.09

SRE=A random sample from all short-rotation plots.
SRL=A sample from the long unpalatable areas.

The nitrogenous fractions will be referred to below.

Animal production results from the experiment are given in Table 6. Although mean liveweight gain was greater for the P animals, organic matter (O.M.) digestibility of both grasses was the same. One of the aims of the digestibility trial was to allow an estimate of the intake of the grazing animals to be made. Digestibility was assumed to be the same both indoors and outdoors and the intake of the grazing sheep was calculated as the product of their daily faecal output and feed to faeces ratio. On this basis the O.M. intakes of the P sheep were 16% higher than the S animals. The VFA situation was similar to previous work, the S sheep having a higher concentration of acids, a higher proportion of propionic and butyric acids, and less acetic acid in their rumens than the P sheep. Rumen volume and flow rate data for the experimental sheep are shown in Fig. 1. After the P sheep had been on their treatments for seven weeks they had developed significantly larger rumen fluid and maximum D.M. contents than the S sheep. Fluid flow rate rose for animals grazing P, and fell for those grazing S, and by the end of October the two groups were significantly different.

TABLE 6: ANIMAL PRODUCTION DATA FOR SHEEP GRAZING SHORT-ROTATION AND PERENNIAL RYEGRASSES

	Perennial Ryegrass	*Short-rotation Ryegrass*
Liveweight gain (lb)	15.8	5.5
Organic matter digestibility (%)	81.7	81.6
Organic matter intake (g/day)	1,184	1,014
Rumen VFA concentration (mM/100 ml)	12.50	13.61
VFA proportions:		
Acetic	60.5	57.1
Propionic	24.4	26.5
Butyric	15.1	16.4

There was thus a situation where VFA and rumen volume data were similar to earlier work yet liveweight gain was in the reverse order, with the P sheep gaining more. The conclusion was that the S sheep ate less, as is indicated by data on O.M. intake and flow rate.

The question must be asked: Why did the S animals have a reduced intake? A palatability problem was encountered on the S in October and large areas of this pasture, distinct from urine patches, were not eaten. The S sample designated SRE in Table 5 was a random sample from all plots, while SRL was collected solely from the unpalatable patches. These samples differed in the nitrogenous fractions, SRL being noticeably higher in non-protein-nitrogen (NPN) and nitrate. Both S samples were higher than P in NPN and nitrate. At the time of the unpalatability on the experimental area, samples of P and S from adjacent mixed ryegrass and white clover swards were collected and analysed for nitrate. They contained 100 and 36 mg/100 g D.M. for S and P, respectively. This indicated that the experimental grass was extremely high in nitrate.

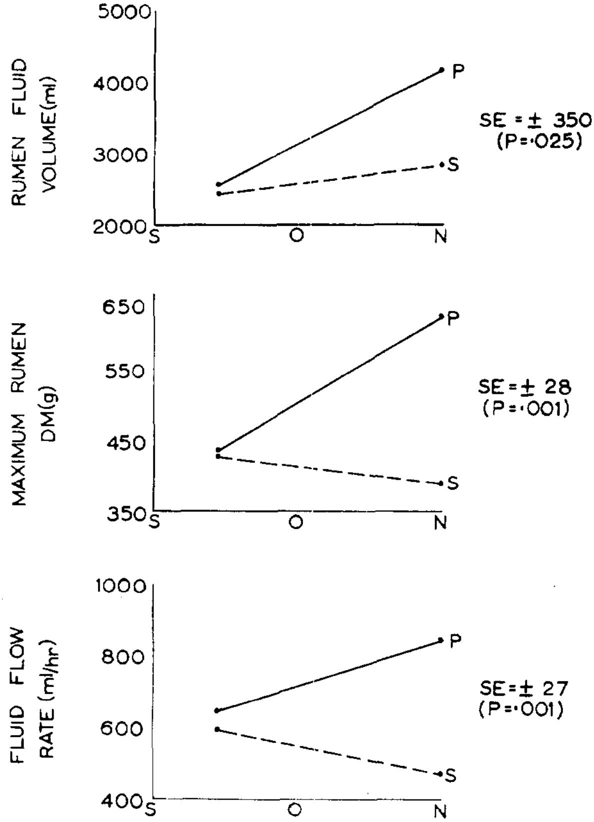

Fig. 1: Effect of short-rotation and perennial ryegrasses on rumen fluid volume, rumen D.M. content, and rumen fluid flow rate.

Unusual environmental conditions were experienced in this experiment, with a warm, dry September followed by an abnormally wet October. A similar situation was reported in Palmerston North in 1957 by Butler (1959) who indicated that sheep grazing this "spring flush" pasture showed checks in liveweight gain. Another point of interest was that, at the same time as the present experiment, animals grazing S and P pastures on paddock 16 of the Massey University farm, showed no treatment differences in liveweight gain. The animals on S subsequently grew faster once the spring period had been passed (Rae, pers. comm.). Under New Zealand conditions, ryegrass varieties have shown a tendency to accumulate nitrate (Butler, 1959). The safe limit of nitrate for ruminants is generally recognized as 200 mg of nitrate nitrogen per 100 g of dry feed (Garner, 1963) and any ration containing excess of this must be considered a potential source of nitrate intoxication. In the present experiment, where there were high applications of nitrogenous fertilizers as well as a season favouring the accumulation of nitrogenous compounds in the ryegrass, the S, particularly the unpalatable sample, was above the safe nitrate level. While factors such as the concentration of soluble carbohydrate in the grass will determine the course of nitrate metabolism in the rumen, the possibility of subclinical nitrate intoxication cannot be excluded. However, as none of the symptoms of nitrate poisoning described by Garner (1963) were observed, it is thought more likely that some other nitrogenous fraction of the feed, such as an organic nitro compound suggested by Butler (1959), could have caused the unpalatability. This possibility is strengthened by the observation that, during the period of unpalatability, the animals were reluctant to eat S and sniffed at the grass when selecting their feed. It seemed likely, therefore, that the lower intake of S could have been due to an unpalatability caused by the accumulation of unusually high amounts of nitrogenous substances during abnormal environmental conditions. It is of interest that these environmental conditions are similar to those associated with outbreaks of hogget ill-thrift.

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DISCUSSION

DR N. M. TULLOH: *Was Mr Ulyatt able to depress total calorie intake* (i.e., *food calories + acetic acid calories*) *with acetic acid infusions?*

M. J. ULYATT: Food intake was measured in grams of D.M. not calories. I would expect the chaff diet to be of lower calorific value than the concentrate diet. On this basis total calorie intake would be depressed by less acetic acid on the chaff diet than on concentrates. It is the nature of the diet to which the acid is being infused, and thus the plane of nutrition of the animal, that is of importance.

Q: *Has Mr Ulyatt any data on the recently developed Ariki ryegrass, and if not, would he expect the nitrate levels and growth rates to be intermediate between the two ryegrasses he has tested?*

MR ULYATT: I have not used Ariki ryegrass in any experiments. Ariki is a cross between short-rotation and perennial ryegrasses and I would expect nitrate levels and growth rates to be intermediate between these two grasses.

Q: *Since both acetic acid and high nitrogen intake are associated with reduced intake or lowered weight gain, is there any postulated relationship between them?*

MR ULYATT: No. It was not suggested that the lower intake of short-rotation ryegrass was due to a high nitrogen intake but rather to an unpalatability that may be associated with the NPN fraction of the grass.