
THE PROCEEDINGS OF THE
NEW ZEALAND SOCIETY
OF
ANIMAL PRODUCTION
VOLUME 62 2002

THE SITES OF DIGESTION OF FRESH PASTURE SPECIES IN THE GASTRO-INTESTINAL TRACTS OF SHEEP

M. J. ULYATT and J. C. MACRAE
DSIR, Applied Biochemistry Division, Palmerston North

SUMMARY

Sheep prepared with re-entrant cannulae in the proximal duodenum and terminal ileum were used to study the sites of digestion in the gastro-intestinal tract of 'Grasslands Ruanui' perennial ryegrass (R), 'Grasslands Manawa', short-rotation ryegrass (M) and 'Grasslands 4700' white clover (C).

The percentage of digestible energy that was digested, respectively, in the stomachs, small intestine, large intestine, was 61, 16, 23 for R, 48, 33, 19 for M, and 60, 35, 5 for C.

Similarly, the percentage of digestible nitrogen that was digested, respectively, in the stomachs, small intestine, large intestine, was 26, 63, 11 for R, 18, 71, 11 for M, and 32, 66, 2 for C.

It was considered that the higher liveweight gain obtained on M than R is due to the greater amount and quality of metabolites absorbed from the small intestine of M. The superiority of C over the grasses was thought to be due to high small intestinal digestion coupled with a high volatile fatty acid production rate in the stomachs.

THE main improved pasture species sown in New Zealand are 'Grasslands Ruanui' perennial ryegrass, 'Grasslands Manawa' short-rotation ryegrass, and 'Grasslands Huia' white clover, and over the past decade much work has demonstrated differences in quality between these species: clover produces greater liveweight gains in sheep than the ryegrasses and of the two ryegrasses Manawa is better than Ruanui (*e.g.*, Butler *et al.*, 1968). Although many suggestions of the causes of these differences have been made, no clearcut evidence of cause has yet been found.

In Palmerston North a number of grazing experiments have been carried out to establish the relative qualities of various pasture species (Butler *et al.*, 1968). Many aspects of plant physical and chemical composition and many qualitative aspects of digestion within the animal have been studied (Johns *et al.*, 1963; Bailey, 1964; Evans, 1964; Ulyatt, 1971). As a result some principles appear to be emerging which may enable the observed differences to be explained.

Ulyatt (1969) suggested that differences in utilization might be caused by differences in the sites of digestion within the animal. Since then a comprehensive series of experiments has been initiated at Applied Biochemistry Division to study quantitative aspects of the digestion of fresh herbage by sheep. In this paper some of the first results of this work are presented.

METHODS

HERBAGE

Three pasture species, 'Grasslands Ruanui' perennial ryegrass (R), 'Grasslands Manawa' short-rotation ryegrass (M) and 'Grasslands 4700' white clover (C) were compared in six experiments conducted in the spring of 1969 (R and M), the autumn of 1970 (C) and the spring of 1970 (R, M and C). Each species was cut when in a vegetative state, at a height between 10 and 15 cm. Purity of the grasses and clover was maintained by spraying with picloram or MCPB. All plots received an annual topdressing of 30% potassic superphosphate (3 cwt/acre) and in addition the grasses received nitrolime (2 cwt/acre/month) applied after harvesting.

SHEEP

Romney wether sheep 1 to 2 years old weighing between 38 and 45 kg were used in all experiments. There were two groups of sheep: (a) one group used for the collection of intestinal contents, was prepared with a rumen cannula and with re-entrant cannulae at the proximal duodenum and terminal ileum (Brown *et al.*, 1968); (b) a second group of sheep, prepared with rumen cannulae only, was used for digestibility and balance trials.

All sheep were housed indoors in metabolism crates and had free access to water.

FEEDING PROCEDURES

The herbage was cut once daily at 0800 hr with an Allan mower. After thorough mixing the following samples were taken:

(a) Rapid dry matter (DM) determination at 190° C for 20 to 30 min, to enable the calculation of daily DM intakes.

(b) True DM determination at 105° C for 24 hr.

(c) An analysis sample was collected each day, stored at −20° C and later these were bulked on an equal DM basis.

Both the re-entrant and balance groups of sheep were fed at several intake levels between 500 and 1000 g DM per day. After the feed samples were taken the daily allowance for each sheep was weighed and then divided into two equal quantities which were fed at 0900 and 1630 hr.

SAMPLING

The sheep were fed for a minimum of three weeks on the herbage before samples were taken. Samples of faeces and urine were collected over seven-day periods as described by MacRae (1970). Samples of duodenal and ileal digesta were obtained from continuous 24 hr collections, Cr_2O_3-impregnated paper being used as a marker to correct observed digesta flows to an average 24 hr basis as described by MacRae and Armstrong (1969).

ANALYSES

All samples of digesta, feed and faeces were freeze-dried and ground through the 1 mm mesh of a Casella mill. All analyses were by standard methods.

CALCULATION OF RESULTS

The experiments were designed so that a regression approach could be used to express the results. For each herbage constituent, the amounts flowing past the duodenum and ileum and being excreted in the faeces were regressed against the intake of the constituent. An example using nitrogen digestion on Manawa ryegrass is shown in Fig. 1. Each line was fitted by linear regression and in all cases in this paper the relationships were significant ($P < 0.01$). This approach enabled comparisons of flows to be made at any particular intake. In addition, the differences between any two lines at any intake is an estimate of apparent digestion that occurs between the two sites. In the present paper comparisons between herbage species were made at intakes of 4,400 kcal gross energy and 40 g nitrogen. These are approximately equivalent to 1,000 g DM.

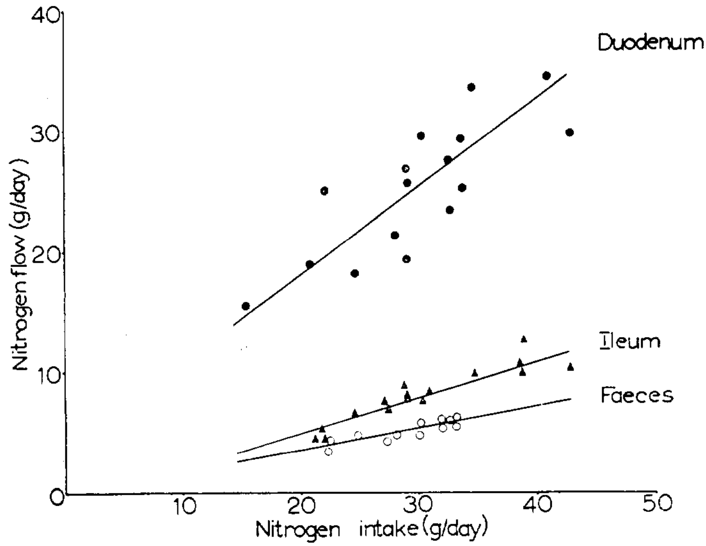

Fig. 1: Relationships between nitrogen intake and nitrogen flows in the duodenum, ileum and faeces in sheep fed Manawa ryegrass.

RESULTS AND DISCUSSION

Herbage Composition

Data on herbage composition are not presented because they were essentially the same as given in previous papers to the Society (Bailey, 1962; Ulyatt, 1969). In summary, R contained less readily fermentable carbohydrate and more structural carbohydrate than M. The ratio of readily fermentable to structural carbohydrate was higher for C than for either ryegrass. The nitrogen content of all three species was similar.

Partition of Digestion

A partition of energy digestion for R, M and C at an intake of 4,400 kcal per day is presented in Table 1. As is common with these high quality pasture species, there was little difference in apparent digestibility. There were, however, distinct differences in the sites of digestion of the energy. With all species the stomach was the site of greatest digestion. R and C had apparent digestibilities in the stomachs of 60 and 61%, respectively, figures which

TABLE 1: THE SITES OF ENERGY DIGESTION IN SHEEP FED MANAWA RYEGRASS, RUANUI RYEGRASS AND WHITE CLOVER

	Ruanui Ryegrass	*Manawa Ryegrass*	*White Clover*
Intake (kcal/day)	4400	4400	4400
Apparent digestibility (%)	75.9	78.2	76.0
% digestible energy digested in:			
stomachs	61	48	60
small intestine	16	33	35
large intestine	23	19	5

agree very well with values obtained on dried feeds (*e.g.*, Harris and Phillipson, 1962; Weston and Hogan, 1968). In contrast, M had the very low stomach digestibility of 48%. In the small intestine, the amount of energy digested from M and C was twice that of R. The situation in the large intestine was different again: a small amount of digestion of C occurred compared with the two ryegrasses. R was the only species studied which had a higher apparent digestibility in the large than in the small intestine.

The small intestine is the most important site of nitrogen digestion in the ruminant, because this is the main site of absorption of amino acids. Nitrogen apparently digested at the other two sites, the stomachs and large intestine, will mainly be absorbed as ammonia (McDonald, 1962) and this results in wastage by the animal because this ammonia is largely converted to urea in the liver and excreted in the urine.

The partition of nitrogen digestion in the three pasture species is given in Table 2. The greatest apparent digestion in the small intestine was obtained on M, probably because less nitrogen was lost from the stomach region with

TABLE 2: THE SITES OF NITROGEN DIGESTION IN SHEEP FED MANAWA RYEGRASS, RUANUI RYEGRASS AND WHITE CLOVER

	Ruanui Ryegrass	*Manawa Ryegrass*	*White Clover*
Intake (g/day)	40.0	40.0	40.0
Apparent digestibility (%)	79.3	82.2	79.2
% digestible nitrogen digested in:			
stomachs	26	18	32
small intestine	63	71	66
large intestine	11	11	2

this species. C in comparison, had the greatest nitrogen loss in the stomachs, but the digestible nitrogen leaving this region was nearly all digested in the small intestine, only 2% being apparently digested beyond the ileum. The greatest wastage of digestible nitrogen appeared to occur with R where 26% was lost in the stomachs and a further 11% in the large intestine.

The Significance of Different Sites of Digestion

To appreciate the significance of these results it is necessary to consider briefly the processes of digestion in the ruminant digestive tract.

Digestion in the rumen is a combination of microbial fermentation and physical breakdown by mastication and rumen movements, the major metabolizable end-products of this fermentation being the volatile fatty acids (VFA). It can be calculated (*e.g.*, Hungate, 1966) that VFAs account for 65 to 75% of the organic matter (OM) that is digested in the stomachs. Thus approximately 25 to 35% of the OM that is digested in the stomachs is lost to the animal as methane, ammonia and heat of fermentation.

Feed residues, micro-organisms and unabsorbed metabolites pass out of the stomachs and are available for digestion in the small intestine by the host animal's enzymes. The major end-products of this digestion are amino acids, fatty acids and small amounts of sugars. In contrast to the stomachs, there is virtually no wastage of OM from this type of digestion: all of the end-products can be utilized by the animal.

When the residues from small intestinal digestion pass to the large intestine they are subjected to a secondary fermentation, and the main end-products, as with the stomachs, appear to be VFAs, with losses of methane, ammonia and heat of fermentation. No reliable estimates of VFA production in the caecum are available but they are likely to be of the same proportion of digestible energy as in the rumen, *i.e.*, 70% of the digested OM.

Two main points emerge from these considerations:

(1) The OM apparently digested in the gastro-intestinal tract is not all of equal nutritive value to the animal. Because of the wastage involved a unit of OM digested in the stomachs or large intestine is of less value than a unit digested in the small intestine.

(2) There are differences in the quality of the end-products formed at the various sites of digestion. The VFAs are

used by the animal mainly as an energy source or for fat synthesis, while the end-products of small intestinal digestion are predominantly amino acids which can be used as an energy source, but whose primary use is in a host of metabolic pathways, notably protein synthesis.

Causes of the Differences in Utilization between Species

Differences between R, M and C in efficiency of utilization for liveweight gain in the order C > M > R, have been reported by Grimes *et al.* (1967), Joyce and Newth (1967), Rattray and Joyce (1969) and Ulyatt (1969). It is possible from the present data to suggest causes of these differences.

It is thought that the difference between R and M lies in the greater amount and quality of metabolites absorbed from the small intestine of M (Tables 1 and 2).

The superiority of C over the grasses is thought to be a combination of high small intestinal digestion coupled with a high rumen VFA production rate. Indeed clover would appear to be particularly suited to the ruminant mode of digestion because there is little digestible substrate left by the time digesta reaches the large intestine.

Differences in the intakes of the herbage species, which tend to follow the same order as liveweight gain (Ulyatt, 1971), possibly act through the same mechanisms and emphasize quantitatively the differences in sites of digestion.

What Controls Partition of Digestion?

The present study would appear to support the hypothesis, advanced by Ulyatt (1969), on possible causes of the differences in herbage quality. R has a different morphology, a greater leaf strength and a lower ratio of readily fermentable to structural carbohydrate than M. This means it takes longer to breakdown R in the rumen and thus leads to a longer retention time in the rumen for R than M. Conversely, M passes through the rumen quicker and has a lower rumen and higher small intestinal digestibility than R. With C the situation is different. Leaf strength cannot be considered because of morphological differences from the ryegrasses, but C has a much higher ratio of readily fermentable to structural carbohydrate than the grasses and is broken down in the rumen more rapidly than the ryegrasses. C appears to have a high rate of VFA production and the material passing from the stomachs appears to be suitable for small intestinal digestion.

It is not suggested that the differences in partition of digestion demonstrated in this paper provide the final solution of the causes of differences in liveweight gain between R, M and C. Indeed, only events occurring within the digestive tract have been considered. One obvious field for investigation is the utilization by the animal of the end-products of digestion, particularly the utilization of the end-products of small intestinal digestion.

ACKNOWLEDGEMENTS

The help of Dr N. D. Grace is gratefully acknowledged. The skilled technical assistance of Mrs E. Davies, I. D. Shelton, S. E. Pickmere, J. Kook, B. S. Henderson, B. Karl, A. S. D. King, W. D. Holdsworth and the Applied Biochemistry Division analytical group, was greatly appreciated.

REFERENCES

Bailey, R. W., 1962: *Proc. N.Z. Soc. Anim. Prod., 22:* 99.
——— 1964: *N.Z. Jl agric. Res., 7:* 496.
Brown, G. F.; Armstrong, D. G.; MacRae, J. C., 1968: *Br. vet. J., 124:* 78.
Butler, G. W.; Rae, A. L.; Bailey, R. W., 1968: *N.Z. agric. Sci., 3:* 8.
Evans, P. S., 1964: *N.Z. Jl agric. Res., 7:* 508.
Grimes, R. C.; Watkin, B. R.; Gallagher, J. R., 1967: *J. agric. Sci. Camb., 68:* 11.
Harris, L. E.; Phillipson, A. T., 1962: *Anim. Prod., 4:* 97.
Hungate, R. E., 1966: *The Rumen and its Microbes,* Academic Press, London and New York.
Johns, A. T.; Ulyatt, M. J.; Glenday, A. C., 1963: *J. agric. Sci. Camb., 61:* 201.
Joyce, J. P.; Newth, R. P., 1967: *Proc. N.Z. Soc. Anim. Prod., 27:* 166.
McDonald, I. W., 1962: *Proc. N.Z. Soc. Anim. Prod., 22:* 79.
MacRae, J. C., 1970: *Proc. N.Z. Soc. Anim. Prod., 30:* 218.
MacRae, J. C.; Armstrong, D. G., 1969: *Br. J. Nutr., 23:* 15.
Rattray, P. V.; Joyce, J. P., 1969: *Proc. N.Z. Soc. Anim. Prod., 29:* 102.
Ulyatt, M. J., 1969: *Proc. N.Z. Soc. Anim. Prod., 29:* 114.
——— 1971: *N.Z. Jl agric. Res. 14:* 352.
Weston, R. H.; Hogan, J. P., 1968: *Aust. J. agric. Res., 19:* 567