Factors influencing the digestion of dietary carbohydrates between the mouth and abomasum of steers

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1. Six protozoa-free steers with simple rumen and abomasal cannulas were given basal diets consisting of a concentrate mixture of flaked maize and tapioca with either barley straw (BS) or alkali-treated barley straw (BSA). Other diets used were supplemented with urea (BSU and BSAU respectively) or contained fish meal in place of tapioca BSF and BSAF respectively). The diets were given in a 6 × 6 Latin square design. Diets were isoenergetic and provided sufficient metabolizable energy (ME) to support a growth rate of approximately 0·5 kg/d. Basal diets, urea- and fish-meal-supplemented diets had estimated rumen-degradable nitrogen (RDN):ME values (g/MJ) of 0·5, 1·2 and 0·8 respectively. ^{103}Ruthenium and polyethylene glycol were given as flow markers, and flows (g/24 h) at the abomasum of organic matter (OM) and carbohydrate components were calculated.

2. True digestibility coefficients of OM between mouth and abomasum were significantly greater for diets containing alkali-treated straw (approximately 0·63) than for those containing untreated straw (approximately 0·55) but were not significantly affected by N supplementation.

3. Digestibility coefficients of the neutral-sugar components of dietary polysaccharides between mouth and abomasum were 0·28, 0·34, 0·31, 0·23, 0·31 and 0·87 for mannose, galactose arabinose, xylose, cellulose-glucose and starch-glucose respectively for diet BS. Corresponding values were 0·37, 0·42, 0·56, 0·51, 0·40 and 0·88 for diet BSA. All but the mannose and starch-glucose values were significantly greater for the latter diet. N supplementation also led to increases in digestibility of all neutral sugars except mannose and starch-glucose. Fish meal produced a markedly greater effect than urea but only significantly so for cellulose-glucose. Thus, the highest digestibilities were seen for diet BSAF and were 0·68, 0·67, 0·74 and 0·64 for galactose, arabinose, xylose and cellulose-glucose respectively. Of all these sugars xylose consistently showed the greatest response in digestibility to sodium hydroxide treatment or N supplementation.

Sodium hydroxide treatment of straw has been shown to lead to a significant increase in digestibility, in vivo, of organic matter (OM) and, in particular, of the cellulose and hemicullulose fractions of the plant cell walls (Jackson, 1977; Owen, 1978; Evans, 1979). However, these fractions were determined using detergent-extraction procedures (Goering & Van Soest, 1970) and it has been observed by a number of workers (e.g. Evans, 1979) that much of the fraction characterized as 'hemicellulose' by detergent techniques is solubilized by sodium hydroxide treatment. This makes the interpretation of results difficult (Ali *et al.* 1977). No detailed examination of the effects of alkali treatment of straws on the in vivo digestibilities of the component sugars of the structural polysaccharides appears to have been made.

To utilize fully the additional energy made available by alkali treatment, suitable sources of nitrogen are necessary. It has, for example, been reported that the growth rate of lambs receiving diets containing alkali-treated straw was greater in animals receiving soya-bean-meal supplements than in animals receiving urea supplements (Saxena *et al.* 1971). The present experiments were designed to examine in detail the effects of alkali treatment of straw on digestibilities in the rumen of the individual component neutral sugars of the main structural polysaccharides of the straw, and interactions with different levels and kinds of dietary N.

A preliminary report on part of this work has already been published (McAllan & Smith, 1983*a*).

METHODS

Animals, diets and collection of digesta

The experiment was designed as a 6 × 6 Latin square. Six Fresian steers, which remained essentially protozoa-free throughout the experiment, were used, each fitted with simple rumen and abomasal cannulas at approximately 12–16 weeks of age as described by Smith & McAllan (1970). At the beginning and end of the experiment respectively the animals had mean (with SE) weights (kg) of 116(17) and 157(21) and mean (with SE) ages (weeks) of 22·9(4·0) and 39·6(4·0).

They were given six isoenergetic diets providing sufficient metabolizable energy (ME) to support a growth rate of approximately 0·5 kg/d (Ministry of Agriculture, Fisheries & Food, 1975). Two were basal diets (deficient in rumen-degradable N (RDN)) consisting of a concentrate mixture (flaked maize and tapioca) with chopped untreated barley straw (BS) or sodium hydroxide-treated barley straw (BSA). The other diets were similar but two were supplemented with urea (BSU and BSAU respectively) and two had part of the tapioca replaced by fish meal (BSF and BSAF respectively). Straw was chopped to 30–50 mm lengths and alkali treatment was effected by adding 150 ml sodium hydroxide solution (50 g/l)/kg straw (Owen, 1978). Details of the diets are shown in Table 1. Diets were given in equal quantities at 09.00 and 17.00 hours daily.

Table 1. *Amounts of main dietary components (kg dry matter/d), nitrogen (g/d) and metabolizable energy (ME; MJ/d) given to steers weighing 110–129 kg**

Diet ... Component	BS	BSU	BSF	BSA	BSAU	BSAF
Flaked maize	1·30	1·30	1·30	1·30	1·30	1·30
Untreated barley straw	1·30	1·30	1·30	—	—	—
Alkali-treated barley straw	—	—	—	1·30	1·30	1·30
Tapioca	0·26	0·24	—	0·26	0·24	—
Fish meal	—	—	0·26	—	—	0·26
Urea	—	0·048	—	—	0·048	—
N	25·2	46·6	57·1	25·5	47·0	57·5
Estimated rumen degradable-N (g/d)†	16·4	36·7	23·8	16·4	36·8	23·9
ME‡	31·5	31·2	31·0	31·5	31·2	31·0

* These amounts were increased by 8% for each succeeding 20 kg weight range.

† Assuming N degradability values of 0·70, 1·00 and 0·25 for the basal diet and urea and fish-meal supplements respectively.

‡ Calculated from energy values for individual components (Ministry of Agriculture, Fisheries and Food, 1975).

Each diet was given for a 20 d period and was then changed. In each period from day 9 onwards, 100 ml of a solution containing 30 g polyethylene glycol (molecular weight 4000; PEG) and approximately 100 μCi ^{103}Ruthenium (as a soluble Ru–phenanthroline complex prepared according to MacRae & Evans, 1974) was introduced directly into the rumen at each feed. On day 18, samples (approximately 150 g) of abomasal digesta were taken immediately before the morning feed and then at three hourly intervals over the next 21 h. Samples were homogenized and subsamples (100 g) were combined and stored for subsequent analysis.

Analytical

Dry matter (DM) and OM were determined as described by Smith *et al.* (1978). Feed or digesta samples were subjected to acid-hydrolysis (McAllan & Smith, 1974) which released

ribose, mannose, galactose, arabinose, xylose and starch-glucose. Amounts of these sugars were measured by ion-exchange chromatography of their borate complexes (McAllan & Smith, 1974). Cellulose-glucose was estimated after more stringent acid-hydrolysis of the residue from the first hydrolysis by automated enzymic analysis (McAllan & Smith, 1974). The specific radioactivity of ^{103}Ru in abomasal digesta was measured in 1 g of sample counted for 1 min in a CG 4000 Gamma Counter (Intertechnique, France).

Daily flows of digesta constituents through the abomasum were calculated using both solid- and liquid-phase markers and a technique similar to that described by Edrise (1979) to assess the flows of partially insoluble minerals out of the rumen. Samples of abomasal digesta were centrifuged at 30000 ***g*** for 15 min. The supernatant fraction was poured off (liquid-rich fraction) and the residue was resuspended in water (solid-rich fraction). Markers and constituents were estimated in the solid- and liquid-rich fractions and in the original untreated digesta. Constituent:PEG values in each digesta fraction were plotted *v.* the

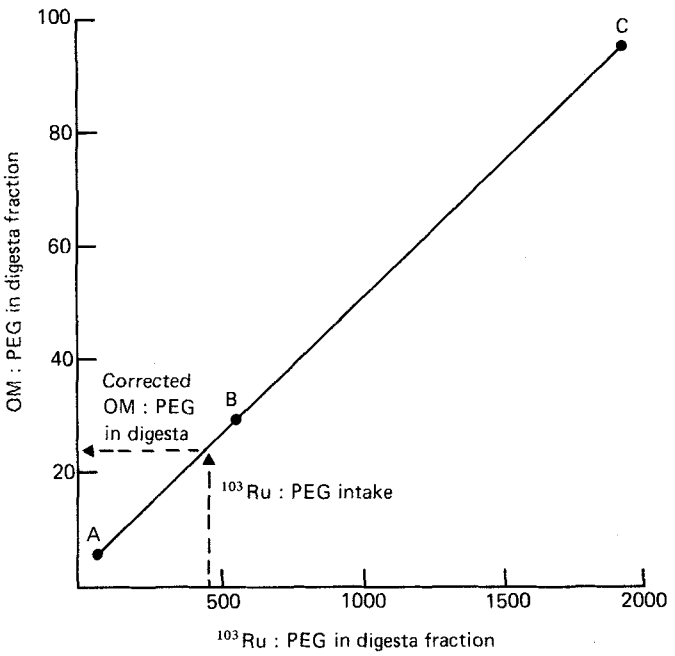

Fig. 1. Example of the use of dual markers (^{103}Ruthenium and polyethylene glycol (molecular weight 4000; PEG)) to assess true flows of digesta constituents. Results are shown for organic matter (OM) flows in one steer receiving the barley straw+fish meal diet (see Table 1). A, Liquid-rich fraction; B, digesta sample as taken; C, solid-rich fraction.

corresponding ^{103}Ru:PEG values. The relationship was nearly always close to linearity (an example is shown in Fig. 1) and it was possible to compensate for possible uneven sampling by reading the component:PEG value at the ^{103}Ru:PEG value introduced in the diet.

Values for RDN used in Table 1 were obtained using estimates of undegraded dietary N derived by difference from measurements of non-ammonia-N and microbial-N at the abomasum (A. B. McAllan and R. H. Smith, unpublished observations) and by assuming endogenous N to be 0·03 g/kg live weight.

Analysis of variance was carried out according to Cochran & Cox (1962).

Table 2. *Carbohydrate composition of feed components (g/kg dry matter)*

(Amounts of neutral sugars released by hydrolysis with 0·5 M-sulphuric acid (ribose, mannose, arabinose, galactose, xylose and α-linked glucose (starch)) and 13 M-sulphuric acid (β-linked glucose (cellulose)). Results are mean values with their standard errors for the nos. of samples shown)

Component*	No. of samples	Ribose		Mannose		Arabinose		Galactose		Xylose		α-linked glucose (starch)		β-linked glucose (cellulose)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Untreated barley straw	15	1·4	0·23	2·6	0·29	25·7	0·84	8·1	0·53	157·8	4·58	31·3	2·34	405·4	3·82
Alkali-treated barley straw	15	1·8	0·35	1·8	0·26	29·5	0·61	9·9	0·85	149·6	3·08	28·5	1·08	361·5	1·53
Flaked maize	17	0·5	0·06	1·7	0·19	19·8	0·69	17·7	1·74	27·1	0·95	708·0	3·3	33·8	1·09
Fish meal	6	1·3	0·09	0·7	0·00	ND		1·0	0·13	ND		5·6	0·09	7·3	1·2
Tapioca	4	ND		ND		ND		ND		ND		937·7	5·3	ND	

ND, not detected.
* See Table 1.

Table 3. *Daily intakes (g/d) abomasal flows (g/d) and apparent rumen digestibilities (g/g intake) of dietary carbohydrates*

(Results are mean values for six animals receiving the diets described in Table 1, except for one missing value for diet BSF)

Carbohydrate diet...	BS	BSU	BSF	BSA	BSAU	BSAF	Pooled SEM	Statistical significance of differences: Treated *v.* untreated straw	Basal *v.* urea	Basal *v.* fish meal	Urea *v.* fish meal
Mannose											
Intake	4·6	4·0	4·8	4·9	5·2	4·4	0·5	NS	NS	NS	NS
Flow at abomasum	3·3	2·6	2·9	3·1	3·2	2·6	0·5	NS	NS	NS	NS
Proportion digested in rumen	0·28	0·35	0·40	0·37	0·38	0·41	0·06	NS	NS	NS	NS
Galactose											
Intake	35	30	31	31	32	34	3	NS	NS	NS	NS
Flow at abomasum	23	20	20	18	16	15	2	**	NS	NS	NS
Proportion digested in rumen	0·34	0·33	0·35	0·42	0·50	0·56	0·07	NS	NS	NS	NS
Arabinose											
Intake	56	51	55	53	54	59	6	NS	NS	NS	NS
Flow at abomasum	38	28	29	23	19	19	3	***	NS	NS	NS
Proportion digested in rumen	0·31	0·44	0·47	0·56	0·65	0·68	0·08	**	NS	NS	NS
Xylose											
Intake	213	199	226	180	185	211	26	†	NS	NS	NS
Flow at abomasum	163	132	132	87	60	53	15	**	*	*	NS
Proportion digested in rumen	0·23	0·33	0·42	0·51	0·68	0·75	0·06	**	†	*	NS
Cellulose-glucose											
Intake	498	469	537	397	401	471	61	***	NS	NS	*
Flow at abomasum	341	307	273	229	197	161	35	**	†	**	NS
Proportion digested in rumen	0·31	0·34	0·49	0·40	0·51	0·65	0·06	**	†	*	**
Starch-glucose											
Intake	1187	1088	890	1115	1120	886	83	NS	NS	***	***
Flow at abomasum	152	106	84	138	112	124	10	NS	NS	NS	NS
Proportion digested in rumen	0·87	0·90	0·91	0·88	0·90	0·86	0·01	NS	NS	NS	NS

NS, not significant.

† $P < 0·10$, * $P < 0·05$, ** $P < 0·01$, *** $P < 0·001$.

BS, straw + flaked maize; BSU, straw + flaked maize + urea; BSF, straw + flaked maize + fish meal: BSA, alkali-treated straw + flaked maize; BSAU, alkali-treated straw + flaked maize + urea; BSAF, alkali-treated straw + flaked maize + fish meal.

RESULTS

The carbohydrate contents of the main dietary components are presented in Table 2. Alkali treatment of the barley straw resulted in small (6–10%) but significant ($P < 0.05$) losses of both xylose and cellulose-glucose as proportions of DM. This led to significantly lower intakes of these components when treated straw was given to the steers (Table 3). Intakes of starch-glucose were markedly lower on diets BSF and BSAF compared with the other diets because tapioca was replaced by fish meal. Daily abomasal flows of bound galactose, arabinose, xylose and cellulose-glucose (Table 3) were all significantly lower ($P < 0.05$–0.001) on corresponding diets containing treated rather than untreated straw, but flows of mannose and starch-glucose were similar for both kinds of straw.

Amounts of dietary carbohydrates apparently digested between mouth and abomasum, expressed as proportions of intakes, are also given in Table 3. Alkali treatment of straw significantly improved the digestibilities of the main structural carbohydrate component sugars arabinose ($P < 0.001$), xylose ($P < 0.001$) and cellulose-glucose ($P < 0.01$). N supplementation of the basal diets also improved digestibilities of these sugars, and effects of alkali treatment and N supplementation were additive. Thus the greatest fibre digestibility was observed with the diet containing alkali-treated straw and fish meal (BSAF). Improvements in digestibilities of the components of the main fibre polysaccharides were, in descending order of magnitude, xylose, cellulose-glucose, arabinose and galactose. No difference between diets was observed for the proportions of starch-glucose or mannose digested in the rumen.

There was a significantly higher ($P < 0.01$) apparent digestibility of OM between the mouth and abomasum for animals receiving diets containing alkali-treated rather than untreated straw (Table 4), but supplementation of either basal diet (BS or BSA) with N did not significantly increase OM digestibility. Table 4 also shows estimates of the amounts and proportions of OM truly digested in the rumen. Proportions were significantly different ($P < 0.01$) between untreated and corresponding alkali-treated straw diets but there was no significant effect of N supplementation.

Table 4. *Amounts (kg/d) of organic matter (OM) consumed and apparently (ADOM) and truly (TDOM) digested in the rumen*

(Proportions represented by different components of TDOM are also shown. Results are mean values for six animals each given the six diets described in Table 1 (except for one missing value for diet BSF))

Diet...	BS	BSU	BSF	BSA	BSAU	BSAF	SEM
OM intake	2·67	2·42	2·54	2·27	2·39	2·42	0·28
ADOM	1·15	1·04	1·08	1·19	1·26	1·16	0·18
TDOM*	1·43	1·38	1·43	1·43	1·56	1·47	0·23
TDOM:OM intake	0·537	0·561	0·562	0·633	0·654	0·608	0·043
Proportion of TDOM contributed by							
Starch-glucose	0·792	0·786	0·600	0·765	0·715	0·588	0·063
Cellulose-glucose	0·104	0·107	0·164	0·110	0·127	0·208	0·024
Arabinose+xylose	0·045	0·059	0·085	0·078	0·099	0·138	0·012
Fish-meal protein	—	—	0·053	—	—	0·055	0·004

* ADOM in the rumen plus estimated microbial OM synthesized in the rumen (A. B. McAllan and R. H. Smith, unpublished results).

BS, straw+flaked maize; BSU, straw+flaked maize+urea; BSF, straw+flaked maize+fish meal; BSA, alkali-treated straw+flaked maize; BSAU, alkali-treated straw+flaked maize+urea; BSAF, alkali-treated straw +flaked maize+fish meal.

The proportions of OM intakes contributed by cellulose (β-linked glucose) and hemicellulose (as represented by arabinose + xylose) respectively were similar for all diets (mean values (with SE) were 0·185(0·011) and 0·120(0·005)). The proportion of OM intake contributed by starch-glucose was significantly ($P < 0·001$) lower on the diets containing fish meal than on the basal diets (0·36 and 0·47 respectively), The difference being made up mainly by fish-meal protein.

Alkali treatment led to increases in the contribution made to OM truly digested in the rumen by cellulose and hemicellulose (Table 4). These were, in most case, significant to at least $P < 0·05$. There was no significant difference between basal (BS and BSA) diets and corresponding urea-supplemented diets. Fish-meal-supplemented diets, relative both to basal and urea-supplemented diets, showed marked and significantly greater (P at least $< 0·05$) proportions of total true OM digestion contributed by cellulose and hemicellulose.

DISCUSSION

Appreciable increases in the amounts of structural sugars digested between mouth and abomasum in the present experiments after supplementing the flaked maize and straw diet with protein confirm earlier findings in which low-N diets for steers (approximately 10 g N/kg DM) containing flaked maize as the main concentrate component were similarly supplemented (McAllan *et al.* 1982). In other earlier experiments when basal diets of similar low-N content (approximately 13 g N/kg DM), but consisting of approximately equal amounts of barley and roughage, were supplemented with protein, no such increase in structural carbohydrate digestion between mouth and abomasum was observed (McAllan & Smith, 1983*b*). It was earlier suggested that the different responses may have been due to marked differences in the rumen degradabilities of the protein in barley and maize (McAllan & Smith, 1983*b*) so that RDN was deficient for the maize diet but adequate for the barley diet.

Treatment of the straw with sodium hydroxide resulted in improved OM digestion between mouth and abomasum of approximately 10%. This is similar to the values reported, in vivo, by other workers (Ali *et al.* 1977; Jentsch *et al.* 1978) but considerably less than might be predicted from in vitro studies (Jackson, 1977). However, these in vitro studies involved incubation for at least 48 h and most fibre components would not remain in the rumen for that length of time under in vivo conditions. Furthermore, when alkali-treated straw is used its rapid breakdown and the possible effects of increased intakes of sodium on rumen fractional outflow rates (Berger *et al.* 1980) may result in appreciably shorter residence times of the particles in the rumen and, therefore, reduced times for digestion. It must also be recognized that the steers used in the present experiment were essentially protozoa-free, and this may have resulted in depressed fibre digestion if the contention of Demeyer *et al.* (1981), that protozoa play an important role in such digestion, is correct. Digestibilities of the different component neutral sugars of hemicellulose and cellulose did not increase equally with alkali treatment of straw and N supplementation. Greatest responses were for xylose followed, in descending order, by arabinose, cellulose-glucose and galactose. No comparative in vivo work has apparently been published but Bacon *et al.* (1981) studied the degradation of the component sugars of structural carbohydrates in alkali-treated barley straw in the sheep rumen using a polyester-bag technique. They found that the xylose and cellulose composition of the undigested fraction remaining in the bags after 72 h incubation in the rumen was essentially the same as that of the original material. However, for feed entering the rumen unconstricted by a polyester bag, little or no material would be likely to remain in the rumen for that length of time, and at the early stages of digestion of the structural carbohydrates differential breakdown may have occurred. Bailey (1967) reported that the arabinose and galactose components of dietary hemicelluloses were degraded in the rumen more rapidly than the xylose component and, in examining the effects

of alkali treatment of cotton straw on in vitro carbohydrate digestibilities, Shefet & Ben-Ghedelia (1982) found a greater increase in xylose compared with cellulose-glucose digestibility.

Results in the present study were consistent with earlier findings for steers (McAllan & Smith, 1983*b*) and sheep (Elliott & Armstrong, 1982) in showing that supplementation of either of the basal diets with urea led to a significant increase in microbial growth efficiency. However, only small and non-significant increases in fibre digestion were observed in the earlier studies. In the present work, urea supplementation led to only small increases in fibre digestion although these were significant at the $P < 0{\cdot}1$ level for xylose and cellulose-glucose. These observations were in marked contrast to the finding in the present study that a similar increase in N intake achieved by replacing tapioca in the diet with amounts of fish meal of similar ME content led to marked and significant improvements in digestibilities of xylose, arabinose and cellulose-glucose (Table 3) for both treated- and untreated-straw diets. Cellulose digestibility with fish-meal supplements was significantly greater ($P < 0{\cdot}01$) than with urea supplements. The better result with fish meal occurred in spite of the fact that the unexpectedly low degradability of the fish meal used (Table 1) meant that RDN:ME (g/MJ) was considerably lower for the BSF and BSAF diets ($\simeq 0{\cdot}8$) than for the BSU and BSAU diets ($\simeq 1{\cdot}2$). These ratios should be compared with the value of 1·25 suggested as optimal by the Agricultural Research Council (1980).

It could perhaps be argued that stimulation with fish meal occurred as a result of a reduction in dietary starch intake leading to a change in the microbial population to one that favoured cellulolytic and hemicellulolytic activity. This was not directly tested in the present work but the change in fibre:starch was not great (approximately 1·4:1–1·1:1) and there is little or no evidence in the literature to support the possibility of such an effect. Thus, although Stewart *et al.* (1979) observed, in vitro, that there appeared to be a small (approximately 15%) depression of roughage digestibility when starch supplementation was increased so as to alter straw:starch values from 4:1 to 1:1, Mackie *et al.* (1978) found little or no change in the types and numbers of cellulolytic bacteria during stepwise adaptation of sheep from a high-roughage to a high-concentrate diet. It should perhaps also be borne in mind that, on fermentation, protein yields less ATP than carbohydrate (Demeyer & Van Nevel, 1979). This, however, would if anything be expected to lead to a depression in fibre digestion.

A likely explanation of the stimulating effect of fish meal on fibre digestion may be provided by reports in the literature that microbial activity in vitro and in vivo may be stimulated by the presence of preformed amino acids (Hume, 1970; Maeng *et al.* 1976). However, unpublished results (A. B. McAllan and R. H. Smith) showed that there was no substantial difference between efficiencies of microbial protein synthesis with urea- or fish-meal-supplemented diets. It is tacitly assumed in the Agricultural Research Council (1980) rationing scheme and elsewhere that if sufficient N in a suitably available form (RDN) is supplied to achieve an optimum efficiency of microbial growth – as determined by the relationship between flow of microbial protein at the duodenum and energy digestion up to that point (a value of approximately 30 g N incorporated/kg apparently digested OM is proposed (Agricultural Research Council, 1980) – then microbial activity in the rumen will also be optimal. The present results do not support this contention and, in interpreting them, it is necessary to consider how fish meal addition led to increased fibre digestion without any apparent increase in microbial growth efficiency. An explanation may rest in the heterogeneous nature of the rumen microbial population. It has been pointed out that there are several different microbial compartments in the rumen (Smith *et al.* 1975; Czerkawski, 1979; Cheng & Costerton, 1980). These include organisms that are (1) free-floating, (2) adhering to food particles, (3) adhering to the rumen wall. Digesta flowing

to the abomasum and duodenum undoubtedly contains a higher proportion of free-floating organisms than are present in the total rumen, and effects on these would therefore dominate changes in microbial growth efficiency between mouth and abomasum. On the other hand it seems likely that stimulation of cellulose and hemicellulose digestion would affect mainly organisms associated with feed particles. It is not necessary, therefore, to suppose that these two manifestations of changes in microbial activity would act in parallel. Further support for the view that optimum N supply may differ depending upon what response is being studied is provided by reports that optimal ammonia concentration for continuous liquid cultures of free-floating rumen micro-organisms was about 4 mM (Satter & Slyter, 1974), while optimum ammonia concentration for maximum OM digestion in the rumen was much greater at approximately 14 mM (Mehrez *et al.* 1977). These considerations may have considerable consequences when N-rationing schemes to predict the most suitable dietary N intakes are being developed, particularly for high-forage diets.

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