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Microbial activity in the omasum

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In a ruminant the omasum forms a relatively small ovoid chamber connecting the reticulum to the abomasum. The two orifices are fairly close together and connected by a channel in the omasal wall. The internal structure has been likened to a loosely-closed book with sheets of tissue forming the leaves and the spine opposite to the channel. 'The omasal leaves are of various sizes; all leaves attach to the wall of the omasum at the "binding" and at the ends, but only part of them extend to the channel at the opposite edge' (Hungate, 1966).

Numerous observations have been made and discussed at length on the very complex processes governing digesta flow into, within and out of the omasum for a variety of conditions (Phillipson & Ash, 1965; Hungate, 1966; Sellers & Stevens, 1966; Bueno & Ruckebusch, 1974; Ehrlein, 1979). Detailed consideration of these is outside the scope of the present review but the net effect appears to be as follows. Digesta enters the omasum intermittently and, in the main, at times when the reticulum is contracting. Much of it is then forced between the omasal leaves where solid material is sequestered. There is some periodic backflow to the reticulum which carries with it any very coarse material trapped near the reticular–omasal orifice. Flow to the abomasum is mainly of two kinds: (a) material of relatively-low dry matter (DM) which appears as a trickle or sometimes as a gush shortly after liquid enters the omasum with a reticular contraction, (b) material of higher DM which appears at irregular intervals as the omasal body contracts. One consequence of this very highly organized sequence of events is that in spite of the inlet and outlet of the omasum being so close together much material, and particularly solid material, is retained for an appreciable period within the organ. Differential flow of solid and liquid is evidenced by findings in several ruminant species that the DM content of total omasal contents is about 19–29% while omasal outflow has a DM content of only 5–7% (Hauffe & Engelhardt, 1975). This characteristic of the omasum will be considered in more detail later.

It is difficult to avoid the conclusion that the omasum is an important component of the gastrointestinal tract of the ruminant but its actual role remains ill-defined. It has been pointed out (Engelhardt & Hauffe, 1975) that earlier conclusions on omasal absorptive function, based on the examination of material from slaughtered animals, greatly overestimated the amounts of water and some other digesta components, absorbed. This was mainly because differential turnover times of solid and liquid components were not recognized. It has now been shown that relatively little water is absorbed in the omasums of sheep or goats (on average approximately 13% (Engelhardt & Hauffe, 1975)), although substantial

amounts (approximately 43% (Edrise & Smith, 1979)) are absorbed in the calf omasum. This species difference corresponds to differences in relative size and complexity between the omasums of sheep and cattle. Edrise (1979), for example, found that in four young lambs omasal tissue formed on average only 0·11% of live weight (approximately 34 kg) and contained only twenty-six leaves with a total surface area (ignoring papillae) of 0·11 m^2. For three calves, on the other hand, omasal tissue formed 0·54% of live weight (approximately 98 kg) and contained seventy-one leaves with a total surface area of 1·23 m^2. Not only water absorption but sodium ions and volatile fatty acid (VFA) absorption and chloride secretion were found to be markedly greater in calves (Edrise & Smith, 1979) than in sheep (Engelhardt & Hauffe, 1975).

Thus recent studies have clarified the absorptive role of the omasum but its importance as a site of microbially-mediated nutritional change is not well understood. This is the subject of the present review.

Suitability of the omasal environment for supporting microbial growth

The composition and properties of the main part of the liquid phase in the omasum can be assessed from the composition of the omasal outflow. Some published values for sheep and young cattle are shown in Table 1. Changes between reticulo-rumen contents and omasal contents were generally greater for young cattle than for sheep (or goats). Nevertheless, even for the former animals Na concentration did not change greatly as both Na and water were absorbed to approximately the same extent but, as there was relatively little absorption of potassium, K:Na approximately doubled during passage of digesta through the omasum. Chloride was secreted in substantial amounts in both calves and sheep and partially replaced bicarbonate but this was not accompanied by any appreciable change in pH (Table 1). Similar pH values, close to neutrality for both reticulum and omasum, were reported also by Prins *et al.* (1972) for both cattle and sheep. The evidence therefore favours the view that the omasum provides an environment that is not inimical to microbial growth, although the possibility that quite different micro-environments exist in the thin layers of digesta found between the omasal leaves cannot be ruled out.

Table 1. *Ion concentrations (mmol/l) and pH in reticular and omasal fluids*

(Mean values are given for four sheep and four calves. The sheep received a concentrate mixture and hay *ad lib.* The calves received mainly flaked maize and dried grass (1:2, w/w))

	Sodium	Potassium	Chloride	Bicarbonate	Total VFA	pH	Source
Sheep:							
Reticulum	65	42	22	21	98	6·4	Engelhardt & Hauffe (1975)
Omasal outflow	57	43	44	17	61	6·6	
Calf:							
Reticulum	110	28	11	—	68	7·1	Edrise (1979)
Omasal outflow	83	42	50	—	50	6·9	

VFA, volatile fatty acids.

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Apart from some observations on protozoal survival there seem to be virtually no direct reports about the composition of the microbial population in the omasum. Oyaert & Bouckaert (1961) stated that, in omasal effluent 'the picture of the bacterial flora more or less resembled that of the rumen fluid' but they gave no further details. These workers recorded the presence of living protozoa in omasal effluent but did not comment on their numbers; other workers have often remarked on the relatively small numbers of viable protozoa in the omasal canal or leaving the omasum (Weller & Pilgrim, 1974; Edrise, 1979). This has sometimes been interpreted as indicating the sequestering of protozoa in the reticulum, a conclusion not entirely compatible with the finding of substantial amounts of 2-amino ethyl phosphonic acid (AEP; generally found only in protozoa) flowing at the duodenum (Hagemeister, 1975). A possible explanation might be that protozoa are destroyed by abnormal conditions, say of pH or osmotic pressure, between the omasal leaves with consequent release of AEP. There is, however, no direct evidence of this.

Evidence of microbial digestion during passage of digesta through the omasum

There appears to be a prima facie case for expecting appreciable microbial activity in the omasum but it is necessary to consider what direct evidence there is of this and what is known of its extent.

Many years ago Weller & Gray (1954) made some interesting observations in sheep given diets containing varying amounts of starch. When starch intakes were quite high with a diet of dried-potato chips and wheaten hay, it was observed that starch:lignin values were persistently much higher in the rumen (mean ratio over 24 h 0·32) than in the abomasum (corresponding mean ratio 0·08). Although firm conclusions must be regarded with caution because of uncertainty as to whether rumen samples were representative of material flowing to the omasum, the results provided evidence of appreciable starch fermentation in the omasum. Other indications of metabolic change in the omasum were provided by Goshtasbpour-Parsi *et al.* (1974) who observed a number of changes in the amounts of particular nitrogen fractions flowing at the omasum and the abomasum. In many instances these were likely to have been influenced by abomasal secretions and are difficult to assess but the finding that free amino acids were much reduced at the latter site may have indicated either absorption of free amino acids in the omasum as postulated by Goshtasbpour-Parsi *et al.* (1974) or perhaps their destruction by microbial attack. Much clearer evidence of substantial fermentation in the omasum was provided by Prins *et al.* (1972) who incubated samples of rumen and omasal digesta from cows and from deer and found for the cows that methane production rates from given amounts of DM were nearly the same for samples from the two sites. Results for deer were similar except that omasal digesta values were a little lower than those for rumen digesta. In studies with sheep, Giesecke *et al.* (1975) measured DNA and diaminopimelic acid in digesta from the reticulum and from the omasal outflow and found that both components were present in appreciably greater amounts in the DM from the latter site. They concluded, however, that the

Table 2. *Amounts (kg) of total digesta (TD) and dry matter (DM) in the stomach compartments of different slaughtered ruminants*

Species	*n*	Mean live wt (kg)	Diet: Main components	Diet: DM intake (kg/d)	Reticulo-rumen contents: TD	Reticulo-rumen contents: DM	Omasal contents: TD	Omasal contents: DM	Source
Sheep	21	58	Hay–concentrates	1·30	7·75	1·10	0·17	0·037	Boyne *et al.* (1956)
Sheep	6	50*	Hay–concentrates	0·82	5·11	0·66	0·11	0·028	Badawy *et al.* (1958)
Calves	5	80	Dried grass	2·55	15·25	2·14*	1·02	0·26*	Hodgson (1973)
Calves	2	100*	Hay–concentrates	2·5*	8·70	1·20	0·83	0·23	Johnston *et al.* (1961)

*Estimated value, not given in the paper.

difference was due primarily to the reticulum samples being unrepresentative of flow to the omasum rather than to production of microbial matter in the omasum. They also measured gas production during in vitro incubation of reticular and omasal samples. Active fermentation was shown in samples from both sites although, on average, the latter produced only about half the gas/unit DM compared with the former. In another study in which samples of omasal outflow from calves were incubated in vitro (Edrise, 1979) it was found that VFA concentrations increased by nearly 25% while the pH dropped from 6·8 to 5·4.

It is inevitable that the organic matter (OM) entering the omasum would contain a higher proportion of totally indigestible material than would the dietary OM and this may account, in part, for the finding that in some experiments DM from the omasum was fermented more slowly than DM from the reticulo-rumen. Most digestible OM surviving passage through the reticulo-rumen is likely to be cellulose and hemicellulose and there is little reason to suppose that these substances would be degraded any less rapidly in the omasum than in the reticulo-rumen. If similar degradation rates are accepted, it is possible to assess in general terms how much fibre is fermented in the omasum if it is known how long it remains there.

Although there will be variations between animals and between diets, the results in Table 2 indicate in broad terms the distribution of digesta between the reticulo-rumen and omasum in sheep. It is apparent that the ratio, total digesta (TD) (omasum):TD (reticulo-rumen) is only about 0·02 while the corresponding value for DM (omasum):DM (reticulo-rumen) is about 0·035–0·045.

If it is assumed that approximately 50% of the DM consumed in these experiments flowed consistently out of the reticulum it can be calculated that DM turnover times (mean retention times) and the corresponding turnover rate-constants for sheep were 1·37–1·60/h and 0·63–0·73/h respectively. The former

values would slightly underestimate the turnover times for particulate fibrous matter as a small part of the DM would be in solution but the estimate is reasonably consistent with the mean value of 2·5 h (range 1·0–4·5 h) put forward by Giesecke *et al.* (1975) on the basis of the rate of passage of ^{144}Cerium-labelled hay particles through the sheep omasum. From these values the only reasonable conclusion is that of Giesecke *et al.* (1975) that fermentation in the omasum of the sheep would make a negligible contribution to the total fermentation in the alimentary tract.

The situation is, however, much less clear for the bovine. There is relatively little information available for this species but it is apparent from the values given in Table 2 that the omasum, in at least the young bovine, has a substantially greater capacity than that in the ovine both as a proportion of total body-weight and in relation to the reticulo-rumen. This finding has a good deal of general support in the literature (Church, 1979). One consequence is that DM turns over much more slowly in the calf omasum than in the sheep omasum. Thus, making the same assumptions as for sheep, turnover times of DM for the calves included in Table 2 can be calculated to be 4·4–5·0 h corresponding to turnover rate-constants of 0·20–0·23/h. If, for the sake of argument, it is assumed (a) that the turnover rate-constant for fibre fermentation in the omasum is the same as that observed for cellulose in the reticulo-rumen of a cow by Maeng & Baldwin (1976) (i.e. 0·02/h) and (b) that the over-all turnover rate-constant for digestible fibre in the omasum is 0·20/h, then it follows that 10% of the digestible fibre would be fermented in the omasum.

The simplifications and assumptions required to reach this conclusion must be recognized but it is suggested that, in the absence of more firm evidence, the possibility that fermentation in the omasum makes a significant contribution to total fibre digestion in the bovine should be taken seriously. This view is contrary to the usual tacit assumption that microbially-mediated changes between the mouth and abomasum occur only in the rumen.

There is virtually no unequivocal direct evidence in the literature on the extent of omasal involvement of this kind but some recent observations of J. N. Banks (unpublished results) may be relevant. Four calves (live weights 100–120 kg) equipped with rumen and abomasal cannulas and a flexible sleeve sutured at the reticular–omasal orifice (for details, see Edrise, 1979) were given, at 3 h intervals, diets mainly of flaked maize and dried lucerne (*Medicago sativa*) (2:1, w/w) providing DM intakes of 1·55–1·85 kg/d. Both polyethylene glycol and ^{103}Ruthenium-phenanthroline were added to the diets as markers and flows of DM out of the reticulum and out of the omasum were estimated in the manner described by McAllan & Smith (1983). These flows, expressed as proportions of DM intakes, were 0·71 (SEM 0·027) and 0·59 (SEM 0·023) respectively. There was a significant difference between them ($P<0·01$) of about 17% but approximately one-quarter to half the change must have been due to absorption of minerals and of other solutes already present in the reticulum outflow. The use of this value to predict OM or fibre disappearance therefore contains an amount of uncertainty and

further studies to examine, for example, the disappearance of specific fibre components would be desirable.

Conclusions

The omasum appears to be of much greater importance in cattle than in sheep or goats both in terms of its absorptive function and as a site of microbial activity. Although fermentation undoubtedly occurs in the omasum in all these species, the relatively small capacity of the organ in sheep and goats indicates a much more rapid turnover of omasal DM in these animals than in the young bovine. Making certain reasonable assumptions it may be calculated that, on average, the amount of fibre digested between the mouth and abomasum of the calf which is digested in the omasum may be as much as 10%. The corresponding value for sheep or goats seems unlikely to exceed 3–4%.

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