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Sulfur and Methionine Metabolism in Sheep. IV.* Metabolism and Absorption in the Intestines

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Abstract

Twelve 18-month-old Merino wethers were fed a ground and pelleted diet of equal parts oaten chaff and lucerne chaff. Sulfur flows at the ileum and faecal excretion of sulfur were estimated for two levels of dry matter intake (500 and 1000 g/day) in sheep receiving intraruminal infusions of water or 4·5 g DL-methionine per day.

Increasing dry matter intake from 500 to 1000 g/day resulted in greater flows of total sulfur from 660 to 1183 mg/day in the ileum; protein sulfur increased correspondingly from 312 to 585 mg and non-protein organic sulfur rose from 324 to 497 mg; DL-methionine infusions had no effect. The 1000-g level of intake increased the excretion of all faecal sulfur components compared to those of sheep receiving 500 g dry matter; the amino acid supplement increased total, neutral and total reducible sulfur excretion only at the 500-g level of dry matter intake.

The apparent digestibility of sulfur in the small intestine ranged from 36 to 44%, while apparent digestibility between the proximal duodenum and anus ranged from 59 to 66%. Most of this digestion was due to a reduction in organic sulfur in digesta during flow through the intestines.

Introduction

There is little information, by comparison with that available for nitrogen, on the digestion of sulfur in the intestines, or on its flows and uptake. Non-sulfate sulfur is of the order of 90–95% of the sulfur flowing from the abomasum (Bray and Till 1975; Doyle and Moir 1979*b*).

The apparent digestibility of sulfur in the total digesta and that associated with the bacterial fraction in the post-ruminal gastrointestinal tract has been measured in a series of experiments reported by Bird and co-workers. Of the total sulfur reaching the omasum, *c.* 40% was apparently digested in the remainder of the tract (Bird and Moir 1972). But, when bacteria labelled with ^{35}S were injected into the abomasum or caecum the apparent digestibilities of the microbial sulfur were 71% (Bird 1972*a*) and 31% (Judson *et al.* 1975) respectively.

This paper reports the apparent digestibility of total sulfur in the small and large intestines, and looks at the disappearance of sulfur from chemically defined fractions. No attempt was made to differentiate between sulfur associated with feed or microbial fractions within the digesta, nor to determine the nature of non-protein organic sulfur compounds.

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Materials and Methods

Twelve Merino wethers, each weighing *c*. 38 kg and fitted with a permanent ruminal cannula and simple T-piece cannulae in the proximal duodenum and terminal ileum, were used. They were fed rations supplying either 500 or 1000 g dry matter per day of a ground and pelleted diet comprising chopped oaten hay (49%), chopped lucerne hay (49%) and minerals (2%). The sheep received continuous infusions into the rumen of water or a solution providing DL-methionine at the rate of 4·5 g/day. Digesta flows through the gastrointestinal tract were estimated using [^{103}Ru]tris(1,10-phenanthroline)ruthenium(II)chloride (^{103}Ru-phen) and ^{51}Cr-EDTA as markers. Detailed information on the experimental animals; composition, preparation and feeding of the diet; administration of the supplement and markers; as well as analytical methods; methods of calculating digesta flows and the design of the experiment is presented by Doyle and Moir (1979*a*, experiment 2).

Ileal digesta was fractionated into particulate and fluid fractions by centrifuging at 100 *g* (refer to Doyle and Moir 1979*a* for the procedure) and the flows of sulfur at the ileum were estimated. Total sulfur, reducible sulfur (inorganic sulfate sulfur, ester sulfate sulfur, and any trace of thiosulfate, thiosulfite and sulfide) and protein sulfur (total sulfur content of trichloroacetic acid precipitates) were determined by the methods of Bird and Fountain (1970). Neutral sulfur (sulfur in compounds with C—S linkages) was estimated by difference between total sulfur and reducible sulfur. The flow of sulfur at the ileum was partitioned into these fractions, and the excretion of sulfur in faeces was measured as total sulfur and total reducible sulfur, neutral sulfur excretion being obtained by difference.

Results

Treatment means for flows at the ileum and faecal excretion of sulfur are presented in Table 1. Greater ($P<0·05$–$P<0·001$) total, neutral and protein sulfur flows from the ileum occurred when intake was increased, but not when infusions of DL-methionine were given. There was a tendency for a greater flow of ester sulfate sulfur from the ileum on the higher level of intake, while sheep receiving DL-methionine had lower ($P<0·001$) flows of inorganic sulfate sulfur from the ileum.

The excretion of all sulfur components in the faeces was greater ($P<0·05$–$P<0·001$) for sheep fed 1000 g dry matter than for those fed 500 g dry matter. DL-Methionine supplementation increased total ($P<0·01$), neutral ($P<0·05$) and total reducible ($P<0·05$) sulfur excretion only at the lower level of intake.

Apparent digestibility of total sulfur in the small intestine varied from 36 to 44%, while apparent digestibility post abomasum ranged from 59 to 66%. There was no significant effect of treatment on apparent digestibility of total sulfur in the intestines.

Discussion

The apparent digestibility of total sulfur in the small intestine was 36–44% and that of protein sulfur 26–41%. Ben-Ghedalia *et al.* (1974) found similar apparent digestibilities for nitrogen (48% for total nitrogen; 43% for protein nitrogen) in sheep fed a hay-concentrate diet. These values are of particular relevance to total sulfur digestion in the sheep if protein sulfur absorption in the small intestines is of similar importance to protein nitrogen absorption. Ulyatt and Egan (1979) state that 'the most meaningful measure of nitrogen digestion in terms of protein availability to the animal is the amount of protein absorbed from the small intestine'. In addition to protein absorption, the present experiment and that of Ben-Ghedalia *et al.* (1974) indicate that digestion of non-protein organic compounds may also occur in the small intestine.

As well as the sulfur flowing to the small intestine of which over 94% was organic sulfur (Doyle and Moir 1979*b*), there are considerable additions of organic and inorganic sulfur into the intestinal tract. Some estimates are available for daily sulfur inputs in the combined bile–pancreatic secretions (Bird 1972*b*), as plasma protein (Campbell *et al.* 1961) and from plasma sulfate (Kennedy *et al.* 1976). A substantial input may also occur from the turnover of mucosal cells. Clarke *et al.* (1966) and Bird and Thornton (1972) noted the secretion of organic sulfur into the small intestine and suggested that 30% of sulfur flow to the ileum was mucoprotein. Applying this value to our data indicates that net sulfur absorption underestimates actual absorption by at least 200 mg sulfur per day.

Table 1. Digesta flow, flow of sulfur from the ileum, sulfur excretion in faeces, and apparent digestibility of sulfur in the intestines of sheep fed daily at two levels of dry matter intake and also receiving methionine infusions

Dry matter intake 500 or 1000 g per day; methionine infusions 4·5 g per day. Significant differences between treatment means are indicated by dissimilar superscripts: *a*, *b*, *c*, $P<0\cdot05$; *x*, *y*, *z*, $P<0\cdot001$

Parameter	Daily treatment			
	500 g	500 g+Met	1000 g	1000 g+Met
Ileal digesta flow (kg/day):	$2\cdot986^{byz}$	$2\cdot436^{bz}$	$5\cdot806^{ax}$	$5\cdot091^{axy}$
Ileal sulfur (mg/day):				
Total	677^{by}	643^{by}	1252^{ax}	1114^{axy}
Neutral	699^{byz}	603^{bz}	1127^{ax}	1039^{axy}
Protein	322^{b}	302^{b}	569^{a}	602^{a}
Total reducible	69^{ab}	40^{b}	125^{a}	75^{ab}
Inorganic sulfate	37^{x}	15^{y}	73^{x}	27^{y}
Ester sulfate	29^{bc}	25^{c}	51^{a}	48^{ab}
Apparent digestibility of sulfur in the small intestine (%):				
Total	36·1	43·9	40·0	40·4
Neutral	33·0	44·5	42·9	40·9
Protein	33·2	37·3	41·3	26·3
Total reducible	−9·5	34·4	−12·6	31·2
Faecal dry matter output (g/day):	174^{y}	179^{y}	391^{x}	380^{x}
Faecal sulfur (mg/day):				
Total	366^{cy}	428^{by}	740^{ax}	766^{ax}
Neutral	328^{cy}	380^{by}	663^{ax}	693^{ax}
Total reducible	37^{cy}	48^{by}	77^{ax}	74^{ax}
Inorganic sulfate	15^{b}	27^{ab}	35^{a}	33^{a}
Ester sulfate	23^{y}	20^{y}	42^{x}	40^{x}
Apparent digestibility of sulfur in the intestines (%):				
Total	65·5	62·7	64·5	59·0
Neutral	67·2	65·9	66·4	60·6
Total reducible	41·3	21·3	30·6	32·1

Net changes in the reducible sulfur fraction during passage through the small intestine are small in comparison to changes in neutral sulfur fractions. These small net changes may be associated with considerable exchange of reducible sulfur between the tissues and gut in bile and pancreatic secretions (Bird 1972*b*), in the transport of plasma sulfate across the wall of the small intestine (Kennedy *et al.* 1976), and in sulfate absorption from the intestines (Bird and Moir 1971).

Further digestion of sulfur occurred between the terminal ileum and anus; again the disappearance of sulfur was largely accounted for by a reduction in the neutral sulfur fraction. The disappearance of neutral sulfur between the ileum and anus is probably due to fermentation of organic sulfur compounds in the hindgut and subsequent absorption of the end products of fermentation. Ørskov *et al.* (1970) suggest that extensive breakdown of protein may occur during caecal fermentation on the basis of the high proportions of isobutyric and isovaleric acids detected. Judson *et al.* (1975) found that ^{35}S appearing in the urine from ^{35}S-labelled bacteria injected into the caecum of sheep accounted for 21% of the dose, and as negligible amounts of sulfur amino acids are absorbed from the ovine large intestine (Judson *et al.* 1975; Elliott and Little 1977), the sulfur was presumably absorbed as sulfide. The disappearance of organic sulfur in the present experiment accounted for 33–51% of the sulfur flowing from the terminal ileum. As with the small intestine, estimates of net absorption from the large intestine differ substantially from true absorption, as there may be considerable inputs of inorganic sulfate into the large intestine (Kennedy *et al.* 1976).

Of the sulfur flowing from the duodenum, 59–65% was apparently absorbed in the intestines. These estimates of net absorption, indicating the minimum sulfur uptake from the intestines, could differ widely from actual absorption values due to the considerable additions of sulfur into the post-ruminal digestive tract. Further data on the digestion in the intestines of dietary and microbial sulfur components and on the quantitative pathways of hindgut fermentation are necessary to establish the amount and form in which sulfur is absorbed, and its availability for production processes.

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