

## Effect of intraruminal infusion of potassium on the site of magnesium absorption within the digestive tract in sheep

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### SUMMARY

Sixteen 2-year old female sheep were fitted with ruminal and duodenal cannulae at Johnstone Memorial Laboratory, Lincoln University during 1989–90. They were offered, at 2 hourly intervals, a pelleted concentrate diet (900 g/day) and chaffed lucerne hay (100 g/day). In a split-plot experiment they were infused, intraruminally and at four rates, with potassium (providing 16, 26, 36 or 46 g K/kg food DM/day) and magnesium (providing 1.3, 1.8, 2.3 or 3.1 g Mg/kg food DM/day) within a Latin square design and with the liquid and solid phase markers <sup>51</sup>chromium EDTA and <sup>141</sup>cerium chloride. Net absorption of Mg before and after the duodenum was estimated from dietary intake, duodenal flow and urinary and faecal excretion of Mg.

Increasing K intake resulted in a decline in net absorption of Mg from the entire digestive tract, supporting data in the literature. Increasing K intake from 16 to 46 g/kg DM decreased urinary Mg excretion by between 0.14 and 0.30 g/day, the extent of which was independent of the level of Mg intake. At high K intake Mg absorption from the rumen was reduced, the amount absorbed ranging from 0.07 g Mg/day at intakes of 1.3 g Mg/day and 46 g K/kg DM/day to 0.66 g Mg/day at intakes of 3.1 g Mg/day and 16 g K/kg DM/day. However, at high K intake, and when Mg absorption from the rumen was reduced, net Mg absorption from sites distal to the rumen was increased to an extent which suggested compensatory absorption. Increase in K intake was associated with a consistent reduction in plasma Mg concentration which was independent of Mg intake. Increases in Mg intake resulted in increases in Mg absorption and plasma Mg concentration at all rates of K intake in direct proportion to rate of intake. The reduction in Mg absorption from the rumen at high K intake was associated with an increase (0.3 units) in pH of rumen digesta.

### INTRODUCTION

It is well established that dietary potassium (K) decreases magnesium (Mg) absorption in ruminants (Newton *et al.* 1972; Tomas & Potter 1976*a*; Field & Suttle 1979; Greene *et al.* 1983*a, b, c*; Martens & Blume 1986). Quantitative data showing the response surfaces of Mg absorption to changes in dietary Mg and K encountered under grazing conditions, suitable for incorporation into a simulation model of Mg metabolism (Robson 1991) are not, however, available.

Little is known about the effects of high K intake on the partitioning of net Mg absorption between

sites in the gastrointestinal tract. The rumen is considered to be the major site of Mg absorption (Tomas & Potter 1976*a, b*; Field & Munro 1977; Gabel & Martens 1985) but there is evidence that absorption can also occur from the large intestine (Grace & MacRae 1972; Ben-Ghedalia *et al.* 1975; Tomas & Potter 1976*b*; Dalley & Sykes 1989). The role of the large intestine in Mg homeostasis, particularly under conditions of depressed ruminal Mg absorption, is not clear.

This trial was designed first to study the interactions between dietary Mg and K within the range of concentrations encountered in forages and second to measure the partitioning of absorption between the rumen and post-ruminal sites. A further objective was to establish whether increasing Mg intake would overcome the depression in Mg absorption that occurs at high K intake.

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## MATERIALS AND METHODS

Sixteen 2-year-old female Coopworth sheep, average liveweight  $43 \pm 3$  kg, were fitted with a rigid permanent cannula (3 cm i.d.) in the rumen and a T-shaped cannula in the proximal duodenum (c. 50–100 mm distal to the pylorus), at least 2 months prior to experimentation. This surgery was carried out at the Johnstone Memorial Laboratory, Lincoln University during 1989–90. Normal cannulation techniques were used (Hecker 1974).

Animals were housed indoors in metabolism crates designed for the separation and collection of urine and faeces. They were offered 900 g/day of a pelleted diet based on barley grain, barley malt culms and barley straw with a trace element premix and 100 g/day of chaffed lucerne (*Medicago sativa*) hay, both of which were delivered at 2 h intervals, and had free access to fresh tap water.

Animals, ranked hierarchically by weight, were allocated to one of 4 K treatment groups, 0, 8.9, 17.8 and 26.7 g K/day for K treatments 1–4, respectively. Within each K treatment four rates of Mg infusion, 0, 0.5, 1 and 2 g/day, were randomly allocated within a Latin square design.

The K and Mg supplements, provided as aqueous solutions of chloride salts, were infused into the rumen through polyvinyl chloride tubing at a rate of 460 ml/day during 12-day periods. Sodium bicarbonate was infused into the rumen, independently of K and Mg, to deliver 0.8 g Na/animal/day in 144 ml water. This was done to protect animals from Na deficiency at high K infusion rates, a situation which occurred in a preliminary trial.

Digesta flow past the duodenal cannula was calculated according to the double marker technique of Faichney (1975) using the  $^{51}\text{Cr}$  ( $^{51}\text{Cr}$ ) complex of ethylenediaminetetraacetic acid ( $^{51}\text{Cr}$  EDTA; Downes & McDonald 1964) and  $^{141}\text{Ce}$  (cerium chloride in 0.1 M hydrochloric acid (HCl)) as liquid and solid phase markers, respectively. Approximately 40  $\mu\text{Ci}$   $^{51}\text{Cr}$  EDTA and 8  $\mu\text{Ci}$   $^{141}\text{Ce}$  were included in the sodium bicarbonate solution during the final 8 days of each infusion period. Samples (50 ml) of duodenal digesta were collected at 4-h intervals and rumen fluid (200 ml) at 8-h intervals during the last 4 days of the infusion period and stored at 4 °C.

Feed offered and refusals were recorded and subsampled daily. Faeces and urine were collected and measured daily throughout the 12-day infusion period. Urine was acidified to pH 2–3 with 1 M HCl and the faeces homogenized before each were subsampled and stored at  $-20$  °C. At 08.30 h throughout the infusion period, 5 ml jugular blood was withdrawn through an indwelling jugular catheter, transferred to blood tubes containing lithium heparin (72 USP

units), centrifuged at 1200 g for 15 min and the plasma stored at  $-20$  °C.

### Laboratory analysis

Samples of rumen and duodenal digesta were centrifuged at 30 000 g for 30 min and the supernatant removed. Further aliquots (10 ml) of rumen and duodenal digesta were suspended in agar (0.5 g) in counting tubes by heating, taking care to maintain a uniform suspension, until the agar set. Radioactivity in both the whole digesta and supernatant fractions was counted in a universal gamma counter (1282 Compugamma, LKB, Wallac).

Feed, faeces and digesta samples were dried to constant weight at 100 °C. Feed and faeces samples were wet-ashed by the technique of Thompson & Blanchflower (1971). Rumen and duodenal digesta samples were ashed at 550 °C for 12 h. All digesta were taken up for subsequent analysis in 5% (v/v) HCl. Magnesium in these samples and in urine, plasma and rumen and duodenal supernatant fractions was determined by atomic absorption spectrophotometry following dilution in 0.1 M HCl containing 2000 ppm strontium. Sodium and potassium in feed, plasma and urine were determined by flame emission spectrophotometry after dilution in a 1000 ppm lithium carbonate solution.

Magnesium solubility was calculated as the proportion of total digesta Mg present in the 30 000 g supernatant fraction.

### Statistical analysis

For ruminal and duodenal flow measurements, the balance period was the last 4 days of the infusion period, whereas for urinary and faecal excretion measurements the balance period was the last 8 days of the infusion period. The basic analysis is that for a split plot of the four K treatments. Within each K treatment there were four animals assigned to each of four Mg treatments (16 animals in total) and these four Mg treatments were repeated over four periods in a 'round robin' manner according to a Latin square design balanced for carry-over effects. Orthogonal polynomials were used to establish if any of the K treatments affected the variates in a non-linear manner. Data for urinary and faecal Mg excretion, plasma Mg concentration and digesta pH were analysed in a balanced Latin square for main effects (K and Mg) and interactions. Data for duodenal Mg flow, rumen Mg solubility and Mg concentration in rumen whole digesta and supernatant were analysed in an incomplete Latin square as these measurements were available only for three periods. Both analyses used the ANOVA procedure of GENSTAT 5, Release 2.2 (Lawes Agricultural Trust 1991) to calculate estimated treatment means.

## RESULTS

The concentrate diet and lucerne hay contained 890 and 920 g DM/kg fresh weight, respectively, and the ration fed had an apparent DM digestibility of 0.72. Individual sheep mean, within-period DM intake ranged from 830 to 893 g/day and was unaffected by treatment. Mineral concentrations in the two feeds are presented in Table 1. Mean dietary Mg, Na and K intakes were 1.3, 0.76 and 15.0 g/day, respectively.

*Potassium and magnesium infusion rates*

The four K treatments provided total daily K supplies of 15, 24, 33 and 42 g/day, or the equivalent of 16, 26, 36 and 46 g K/kg DM for K treatments 1-4, respectively.

Magnesium infusions supplied between 0 and 1.86 g Mg/day which resulted in total daily Mg supplies of 1.3, 1.8, 2.3 and 3.1 g/day, or the equivalent of 1.5, 2.0, 2.5 and 3.5 g Mg/kg DM for Mg treatments 1-4, respectively.

Table 1. *Dry matter (DM; g/day) intake and mineral concentration (g/kg DM) of the concentrate diet and lucerne hay*

	Intake	Mineral concentration				
		Mg	K	Na	Ca	P
Concentrate	801	1.35	12.14	0.91	5.57	2.68
Lucerne hay	92	2.32	57.56	0.29	9.95	2.67

*Main treatment effects*

There were significant effects of K treatment on four of the eight variable means, viz. a reduction in urinary Mg excretion ( $P < 0.001$ ) and plasma Mg concentration ( $P < 0.001$ ) and an increase in duodenal Mg flow ( $P < 0.05$ ) and rumen digesta pH ( $P < 0.05$ ). There was no effect of K on faecal Mg excretion, rumen Mg solubility or Mg concentration in either rumen supernatant or whole digesta.

Magnesium treatment, however, had significant effects ( $P = 0.001$  or below) on all variable means except digesta pH and rumen Mg solubility.

*Urinary magnesium excretion*

A significant linear relationship ( $P < 0.001$ ) was observed between the rate of Mg intake and urinary Mg excretion (Table 2). Increasing the K supply from 16 to 46 g/kg DM reduced urinary Mg excretion ( $P < 0.001$ ) linearly across all Mg treatments (Table 2). In absolute terms the reduction in urinary Mg excretion was similar for all K infusion rates. However, as a proportion of total urinary excretion, the reduction was greatest at low Mg supplies.

*Urinary potassium excretion*

A significant linear increase in mean urinary K excretion ( $P < 0.001$ ) was observed as K supply increased. Mean urinary K excretion values ranged from 5.8 for K1 to 25.4 g/day for K4 (S.E. 0.68).

Table 2. *Effect of potassium (K) and magnesium (Mg) infusion on mean urinary and faecal magnesium excretion (g/day), plasma magnesium concentration (mmol/l) and duodenal magnesium flow (g/day) during the balance period*

Treatment	Urinary Mg	Faecal Mg	Plasma Mg	Duodenal Mg flow
	(g/day)	(g/day)	(mmol/l)	(g/day)
K1	0.61	1.34	0.94	1.65
K2	0.55	1.38	0.87	1.86
K3	0.47	1.47	0.81	2.08
K4	0.42	1.43	0.79	2.02
S.E.	0.022	0.094	0.023	0.110
D.F.	12	12	12	8
Mg1	0.28	0.85	0.81	1.17
Mg2	0.42	1.18	0.84	1.52
Mg3	0.60	1.45	0.88	2.04
Mg4	0.74	2.14	0.88	2.88
S.E.	0.030	0.069	0.014	0.052
D.F.	24	24	24	12

Table 3. *Effect of potassium and magnesium infusion on rumen digesta pH, rumen Mg solubility and rumen whole digesta and supernatant Mg concentration*

Treatment	Digesta pH	Rumen Mg solubility	Mg concentration whole rumen digesta	Mg concentration in supernatant
		(%)	(mg/100 g DM)	(mg/100 ml)
K1	5.83	37	224	26.8
K2	5.71	35	246	27.8
K3	6.02	34	256	24.8
K4	5.91	33	265	23.7
S.E.	0.085	5.3	14.3	3.55
D.F.	12	8	8	8
Mg1	5.88	34	162	19
Mg2	5.85	33	211	21
Mg3	5.90	36	264	26
Mg4	5.84	36	353	37
S.E.	0.044	1.4	8.1	1.2
D.F.	24	12	12	12

Overall, urinary K excretion values, irrespective of Mg supply, represented 38, 55, 58 and 60% of total daily K supply for K treatments 1–4, respectively. Magnesium supply had no significant effect ( $P > 0.05$ ) on urinary K excretion.

#### *Faecal magnesium excretion*

Mean faecal Mg excretion was positively linearly related to Mg ( $P < 0.001$ ) but not K ( $P > 0.05$ ) supply (Table 2). However, a significant carry-over effect was observed, which was still present in further analysis when the data were pooled over the last 3 days of the balance period.

#### *Plasma magnesium*

Significant positive linear relationships ( $P = 0.001$ ) were observed between Mg supply and plasma Mg concentration and linear negative relationships ( $P < 0.001$ ) with K supply (Table 2). In general, the effect of K in depressing plasma Mg concentration was least at the lowest rate of supply of Mg, although the effects of high K and low Mg supply on plasma Mg were independent but additive in effect.

#### *Plasma potassium*

A significant ( $P < 0.01$ ) linear increase in plasma K concentration was observed as K supply increased from 16 to 46 g/kg DM on all Mg treatments. Mean plasma K concentration was 4.35 ( $\pm 0.058$ ) and 4.73 ( $\pm 0.063$ ) mmol/l for K1 and K4, respectively. Magnesium supply had no significant effect on plasma K concentration.

#### *Rumen digesta*

There was no effect of Mg supply on rumen pH or Mg solubility in rumen digesta and the data have been combined within K treatments and are given in Table 3. There was a significant cubic effect of K supply on digesta pH ( $P < 0.05$ ), with the two highest K treatments having the highest pH. The concentration of Mg in whole rumen contents increased linearly with increase in Mg supply ( $P < 0.001$ ) but not with an increase in K supply ( $P > 0.05$ ). Magnesium concentration in the supernatant fraction of rumen digesta increased with increase in Mg supply ( $P < 0.001$ ), and tended to decrease with increase in K supply.

#### *Duodenal digesta flow*

Duodenal digesta flow increased ( $P < 0.005$ ) with increasing K supply from 10.2 during K treatment 1 to 12.3 litres/day during K treatment 4 (S.E. 0.46) and was associated with a non-significant increase in rumen volume from 3.1 to 3.7 litres for K treatments 1 and 4, respectively. There was a tendency for digesta flow rate to increase with Mg supply, but this increase was not significant.

The flow of Mg in whole duodenal digesta (Table 2) increased linearly with both K ( $P < 0.05$ ) and Mg ( $P < 0.001$ ) supply, although the effect of Mg was greater than that of K.

## DISCUSSION

The amount of Mg disappearing before the duodenum at the low K intake increased with increasing Mg supply, as would be expected from the work of Martens *et al.* (1978) and McLean *et al.* (1984) which

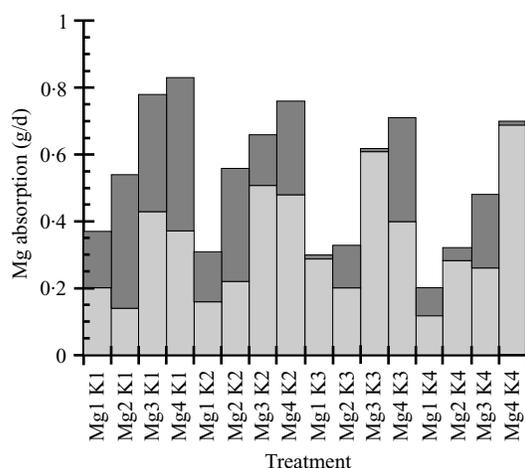


Fig. 1. Effect of potassium and magnesium infusions on the partitioning of magnesium absorption between the rumen (■) and a post-ruminal site (▨).

showed a direct relationship between rumen Mg concentration and rate of Mg absorption. In addition, at this level of K supply the rumen appeared to be the major site of Mg absorption, as would be anticipated from the studies of Grace & MacRae (1972), Tomas & Potter (1976*b*) and Field & Munro (1977). The increase in duodenal Mg flow with increasing K supply (Table 2) further confirms the findings of Tomas & Potter (1976*c*) which have demonstrated impairment of Mg absorption from the rumen with increasing rumen fluid K concentration.

A significant finding, however, was that despite negligible absorption of Mg from the rumen at high K supply, between 0.2 and 0.7 g/day of Mg was excreted in urine. This must suggest that compensatory absorption was occurring from some site distal to the rumen (Fig. 1) particularly since this could not be furnished by the depression in plasma concentration and skeletal Mg cannot be rapidly mobilized in mature sheep (Terashima *et al.* 1987). The data in Fig. 1 clearly show that not only was less Mg absorbed from the entire digestive tract as K supply increased but the site of net absorption also changed, the amount absorbed from the hindgut increasing significantly. Tomas & Potter (1976*b*) showed the large intestine to be capable of absorption of substantial quantities of Mg when Mg was supplied by infusion into the ileum rather than the rumen and McLean *et al.* (1984) showed that with increasing rate of Mg infusion increasing proportions of the Mg absorbed were absorbed distal to the pylorus. Furthermore, Grace & MacRae (1972) observed that while only 2% of net Mg absorption occurred distal to the pylorus in continuously fed sheep, 50% was absorbed at this site in sheep fed once daily, which they interpreted as resulting from a pulse of Mg which overloaded the

rumen capacity for transport and became available for absorption distally. The present work suggests that distal sites become more important in K induced reduction in absorption from the rumen (Fig. 1) and could well be the sites from which orally administered Mg supplements are absorbed. Interestingly, Robson *et al.* (1997) found it necessary to assume hindgut absorption of Mg in order to satisfactorily explain experimental observations from balance trials in the development of a computer simulation model of Mg absorption.

The distal site of Mg absorption in the present experiment is most likely to be the large intestine, as net secretion of Mg from the small intestine has been reported in many experiments (Ben-Ghedalia *et al.* 1975; Tomas & Potter 1976*a*; Bown *et al.* 1989) and there are several reports of net Mg absorption from the large intestine (Tomas & Potter 1976*a*; McLean *et al.* 1984; Dalley & Sykes 1989). Little is known, however, about the mechanism of absorption from the hindgut. The increase in Mg absorption from the large intestine observed by Tomas & Potter (1976*b*) was associated with a 20–25% increase in Mg entering the large intestine, and in the present work a greater Mg flow and concentration was probably responsible for the observed increase in Mg absorption. Although McLean *et al.* (1984) demonstrated a much lower potential difference between the duodenum and plasma than between rumen and plasma (13.30 and 36.67 mV, respectively), which would facilitate diffusional transport, nothing is known about conditions and transport mechanisms in the hindgut. Clearly it is either not subject to the same depression by digesta K concentration or K concentration in that part of the tract is not significantly affected by K intake. The former might be the more likely since we had indirect evidence, in urinary K excretion, that K content in hindgut digesta would have increased with K supplementation.

The effect of K and Mg on retention of Mg in the body was estimated by multiplying plasma Mg concentration by the estimated volume of the extracellular fluid (ECF) pool ( $0.15 \times \text{weight}$ ; Storry 1961), assuming ECF Mg was in equilibrium with plasma Mg. Despite significant increases in plasma Mg concentration with increasing Mg supply and decreases with increasing K supply, actual quantities of Mg amounted to only 0.1–0.3 g, indicating that retention of Mg was small relative to daily throughput of Mg.

Coefficients of absorption for Mg ranged from 0.13 at low Mg and high K intakes to 0.35 at high Mg and low K intakes and span the range anticipated in mature ruminants (ARC 1980). The very low coefficient of absorption observed at high K supplies when combined with a low Mg supply was less than the conservative value of 0.17 used in most calculations of Mg requirement (ARC 1980). The K concentrations

used in the present work (16–46 g K/kg DM) represent the range experienced by pastoral ruminants. It may be that the magnitude of the depression in net Mg absorption at high K and low Mg intake is greater than previously thought.

The decrease in Mg absorption from the rumen with increasing K supply was associated with a small increase in rumen digesta pH which depressed Mg concentrations in the liquid phase of digesta. Smith & Horn (1976) demonstrated *in vitro*, using rumen fluid, a decline in Mg solubility with increasing pH, the critical pH for change in solubility being 6.5–7.0. Although rumen digesta pH at the low K supply in the present experiment was *c.* 5.8, at high K supplies

it increased to 6.0 and was associated with a decline in Mg solubility from *c.* 0.37 to 0.33. The greatest effect of K supply on Mg solubility was observed at low Mg supply where it was 0.42 and 0.29 on treatments with K1 and K4, respectively. Similar effects of K were observed by Greene *et al.* (1983*c*) and Wylie *et al.* (1985), although these workers used potassium bicarbonate as the K source and change in pH may have been due to the increase in bicarbonate ion concentration.

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