

Dietary Potassium Bicarbonate and Potassium Citrate Have a Greater Inhibitory Effect than Does Potassium Chloride on Magnesium Absorption in Wethers

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ABSTRACT We addressed the question whether the type of anion in potassium salts affects magnesium absorption and the transmural potential difference by using wethers ($n = 8$) fed a control diet and diets supplemented with equimolar amounts of KHCO_3 , KCl or K-citrate according to a Latin-square design. The control diet contained 10.9 g K/kg dry matter and the high K diets contained 41.3 g K/kg dry matter. Compared with the control diet, KHCO_3 and K-citrate significantly reduced apparent Mg absorption by 9.5 and 6.5%, respectively. Supplemental KCl tended to reduce ($P = 0.070$) group mean magnesium absorption by 5.5%. Consumption of supplemental KHCO_3 and K-citrate produced a significant increase in the transmural potential difference (serosal side = positive) by 17.1 and 20.7 mV, respectively, whereas the addition of KCl to the diet did not. The individual values for the four diets tended to show a negative correlation ($r = -0.336$, $n = 32$, $P = 0.060$) between the transmural potential difference and apparent magnesium absorption. We conclude that different potassium salts have different effects on magnesium absorption in ruminants as caused by different effects on the transmural potential difference. J. Nutr. 129: 2043–2047, 1999.

KEY WORDS: • magnesium absorption • wethers • potassium • potential difference

There is an increased risk of hypomagnesemia in ruminants when they are grazing on pastures rich in potassium (Kemp 1960), which are common in areas with intensive livestock production (Fisher et al. 1994). In controlled feeding trials with sheep and cows, supplemental potassium bicarbonate decreases magnesium absorption (House and Van Campen 1971, Khorasani and Armstrong 1990, Newton et al. 1972, Schonewille et al. 1999). However, the inhibitory effect of potassium was not observed in dry cows fed grass silages with high, but variable potassium concentrations (Schonewille et al. 1997a). The anion of potassium salts in grasses is predominantly in the form of organic acids such as malate, citrate and aconitate (Dijkshoorn 1973, Grunes et al. 1992, Marscher 1986); thus, we hypothesized that potassium intrinsically present in feedstuffs does not impair magnesium absorption due to its anion. In a recent study, we rejected our hypothesis (Schonewille et al. 1999). However, there is evidence to suggest that potassium chloride is less effective in inhibiting magnesium absorption than is potassium bicarbonate (Schonewille et al. 1997a). To prove or disprove the idea that the type of anion in potassium salts affects magnesium absorption in ruminants, this study was conducted. Wethers were fed equimolar amounts of potassium bicarbonate, potassium chloride or potassium citrate, and apparent magnesium absorption was measured.

In ruminants, magnesium absorption takes place essentially in the rumen (Rogers and Van't Klooster 1969, Tomas and Potter 1976) and consists of a potassium-independent, carrier-mediated process and a potassium-dependent, electrogenic transport component (Leonhard et al. 1989). The amounts of magnesium transported by the two mechanisms depend on the concentration of magnesium in the soluble fraction of rumen contents and thus on the ruminal pH, but the potassium-independent, carrier-mediated process can become saturated with magnesium. Magnesium absorption through the potassium-dependent, electrogenic transport component is also determined by the transmural potential difference. We investigated whether different potassium salts would inhibit magnesium absorption to a different extent through different effects on the determinants of the two absorption processes.

MATERIALS AND METHODS

Animals and experimental design. The experimental protocol was approved by the animal experiments committee of the Utrecht Faculty of Veterinary Medicine. Ruminally fistulated, 2-y-old wethers ($n = 8$), weighing 74 kg (SEM 0.84) were used. The wethers had been fistulated for at least 1 mo before the start of the experiment. The trial was conducted in the form of two 4×4 Latin squares with an interval of 2 wk. The four treatments consisted of a control diet low in potassium and three test diets enriched with one of three potassium salts. Within each Latin square, the wethers were randomly assigned to each sequence of feeding of the four experimental diets. Each Latin square was preceded by a 14-d preexperimental period. The experimental periods lasted 28 d. The wethers were weighed just before the

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TABLE 1

Diet components fed to the wethers^{1,2}

	Control	High K diets		
		KHCO ₃	KCl	K-citrate
g/animal · d				
Pelleted concentrate				
Constant components	762.6	762.6	762.6	762.6
KHCO ₃	—	81	—	—
KCl	—	—	60.5	—
K-Citrate	—	—	—	85.8
Hay	219	219	219	219
Pelleted straw	219	219	219	219

¹ The constant components were first prepared, and then divided into four parts, three of which were supplemented with KHCO₃, KCl or K-Citrate.

² The constant components consisted of 220 g sugar beet pulp, 330 g corn, 87.9 g corn gluten meal, 65.9 g fat-extracted soybean meal, 11 g soybean oil, 38.5 g distilled beets, 2.75 g NaCl, 5.46 g MgO and 1.10 g premix. The premix consisted of 0.72 mg CoSO₄ · 7 H₂O, 0.50 mg Na₂SeO₃ · 5H₂O, 0.17 mg KIO₃, 92.3 mg MnSO₄ · 2H₂O, 200.0 mg FeSO₄ · 7 H₂O, 68.6 mg ZnSO₄ · H₂O, 1.21 mg Na₂MoO₄ · 2 H₂O, 11.3 mg vitamin A preparation (1.9 mg retinyl acetate), 6.2 mg vitamin D preparation (0.016 mg cholecalciferol), 80 mg vitamin E preparation (40 mg *dl*- α -tocopheryl acetate), and 639.0 mg CaCO₃.

evening meal on the last day of each dietary period. They were housed individually in pens with a layer of wood shavings or in metabolism cages with slatted floors.

Diets. The experimental diets were formulated by the addition of equimolar amounts of KCl, KHCO₃ or K-citrate to the basal diet. The ingredient composition of the pelleted concentrates (diameter = 3 mm) and the total diets provided are shown in Table 1. During the preexperimental period, all wethers were offered 219 g pelleted straw, 219 g hay and 762.6 g low potassium concentrate. The sheep were then fed one of the three experimental diets and the preexperimental, control diet. The analyzed composition of the experimental diets is shown in Table 2. The control diet contained 10.9 g K/kg dry matter, and the high K diets contained 41.3 g K/kg dry matter, which is equivalent to 2.2 and 8.3 times the potassium requirement of adult sheep (NRC 1985). The sheep were fed a restricted amount of feed to maintain constant intakes of nonvariable nutrients. The diets were offered three times per day in three equal portions at 0030, 0830 and 1630 h.

Collection of samples. The experimental feeds were sampled during each period, dried for 5 d at 60°C, ground and subsequently stored in a sealed jar at room temperature.

On d 17 of each experimental period, rumen liquid samples (~30 mL) were taken at 0900, 1100, 1300 and 1500 h. Immediately after collection, pH was recorded and the samples were centrifuged for 30 min at 30,000 × *g*. The supernatant was stored at -18°C.

From d 19 to 26 of each experimental period, urine and feces were collected quantitatively. The 24-h urine collections were weighed and 10% was stored at -18°C in a bottle that contained 50 mL of 6 mol/L HCl. The 24-h feces collections were stored at -18°C in plastic bags. At the end of each experimental period, the feces collections were pooled per wether and mixed thoroughly. Two samples, each representing 10% of total feces from each wether for each period, were dried for 5 d at 60°C, ground and stored in a sealed jar at room temperature (18°C). Similarly, the urine collections were pooled and two 100-mL samples were stored at -18°C.

Blood samples were taken on the last day of each experimental period, between 1500 and 1530 h. Blood was sampled from the jugular vein into evacuated heparinized tubes. The samples were centrifuged for 15 min at 2700 × *g* and the plasma was collected and stored in plastic tubes at -18°C.

Chemical analyses. Nitrogen contents were determined by the macro-Kjeldahl method (International Dairy Federation 1986); a

factor of 6.25 was used to convert grams of N into crude protein. Ether extracts of the feedstuffs were prepared according to the Association of Official Analytical Chemists (1984); the solvent was evaporated and the crude-fat residue weighed. The crude fiber contents of the feedstuffs were estimated using the Fibertec System M2 (Tecator, Stockholm, Sweden). Before the determination of the selected minerals in feedstuffs and feces, the samples were ashed (480°C for 12 h) and dissolved in 15 mL of 4 mol/L HCl. Magnesium, Ca and K were estimated by atomic absorption spectroscopy and Na by atomic emission spectroscopy (Perkin Elmer 3110, Perkin-Elmer, Norwalk, CT). Total P in feedstuffs was determined by the method of Quinlan and DeSesa (1955). The accuracy of each assay run was monitored using a commercial reference sample (hay powder, CRM 129, Community Bureau of Reference, Brussels, Belgium) and in-house reference samples; it was found to be within 5% deviation from the target values. Magnesium in plasma and urine was measured directly by atomic absorption spectroscopy. Sodium, K and Cl in the supernatants of ultracentrifuged rumen liquid samples were estimated using an ion-selective electrode (Beckman Instruments, Mijdrecht, The Netherlands). Magnesium in the supernatants was estimated directly by atomic absorption spectroscopy. The combined within- and between-run precision of the determinations (CV) was ≤ 3.0%.

Potential difference. The potential difference between rumen liquid and blood (jugular vein) was measured as described by Dobson and Phillipson (1958). Measurements were done on the last day of each experimental period for 7 h (0900–1600 h). The transmural potential difference of four sheep was measured four times per second using an analog-to-digital (A/D) converter (Data Acquisition Board, PCI 20428W-1, Intelligent Instrumentation, Tucson, AZ) built into a computer. The A/D converter was connected with two separate reference electrodes (Radiometer REF201, Copenhagen, Denmark) and each electrode was dipped into a saturated KCl solution (3.5 mol/L). Saturated KCl-agar bridges (1 g agar/20 mL saturated KCl solution) connected the saturated KCl solutions to the sheep. The bridge to the rumen was made by filling a polyethylene tube with saturated KCl-agar. Contact with the rumen content was made by inserting the bridge through the rumen fistula. The bridge to the blood was made by filling a nylon tube with saturated KCl-agar and inserting it through a polyethylene tube that was placed into the jugular vein. To prevent air bubbles from being trapped at the tip of the catheter, ~1 L of saline (154 mmol/L NaCl) was infused through the catheter during the 7 h. Before statistical analysis, data for each animal were pooled for periods of 1 h.

Statistical analyses. All data were checked for normal distribution using the Kolmogorov-Smirnov test (Wilkinson 1990). Data were not significantly different between the two Latin squares (*F*-test); thus all data were pooled before statistical analysis of treatment

TABLE 2

Analyzed composition of the experimental diets¹

	Control	High K diets		
		KHCO ₃	KCl	K-citrate
g/kg				
Dry matter	864.4	864.1	863.2	870.4
g/kg dry matter				
Crude protein	139.6	133.1	132.3	132.2
Crude fiber	194.8	184.7	187.9	184.0
Crude fat	21.9	22.5	19.3	21.0
Mg	4.31	4.31	4.30	4.35
K	10.9	41.7	41.8	40.4
Na	4.04	4.22	4.08	4.19
Ca	4.06	3.87	4.00	4.00
P	2.23	2.19	2.21	2.19

¹ Values are means; *n* = 8.

TABLE 3

Magnesium balance and absorption in wethers fed the control diet and diets supplemented with equimolar amounts of KHCO_3 , KCl or K-citrate¹

	Control	High K diets			Pooled SEM	ANOVA <i>P</i> -value for treatment
		KHCO_3	KCl	K-citrate		
Mg Intake, g/d	4.65	4.65	4.64	4.70		ND ²
Fecal Mg, g/d	2.92 ^b	3.36 ^a	3.17 ^{ab}	3.25 ^a	0.069	0.002
Urinary Mg, g/d	1.74 ^a	1.19 ^c	1.55 ^{ab}	1.24 ^{bc}	0.084	0.001
Mg Absorption g/d	1.73 ^a	1.29 ^b	1.47 ^{ab}	1.45 ^b	0.068	0.002
% of intake	37.2 ^a	27.7 ^b	31.7 ^{ab}	30.7 ^b	1.463	0.002
Mg Balance, g/d	-0.01	0.09	-0.08	0.20	0.094	0.195

¹ Values are means; *n* = 8. a,b,c Values in a row with different superscripts differ significantly (*P* < 0.05, Tukey's *t* test).

² ND, not determined because the wethers were given a restricted amount of feed.

effects. It was reasoned that each day had three identical postfeeding periods and that ruminal variables averaged for the entire postfeeding period would be the correlates, if any, of apparent magnesium absorption, i.e., magnesium intake minus fecal excretion of magnesium. Thus, postfeeding ruminal variables were averaged for each sheep and each period before statistical analysis. All data were subjected to ANOVA with animal, experimental period and dietary treatment as factors (Wilkinson 1990). When the influence of treatment was significant, Tukey's *t* test was used to identify diets with different effects on the variable involved. For the data from each sheep (*n* = 8) and for each diet (*n* = 4), linear correlations were calculated between ruminal variables and magnesium absorption. The calculations were done under the assumption that the 32 data points could be considered independently. To detect rumen variables that were related to magnesium absorption, multiple regression analysis was performed (Wilkinson 1990) with sheep as factor, magnesium absorption as dependent variable and rumen liquid concentrations of magnesium and potassium, ruminal pH and transmural potential difference as independent variables. Forward, stepwise regression was performed by incorporating into the model the rumen variable showing the highest significant, partial correlation coefficient for its relation to the residual variance in magnesium absorption. Throughout, the level of significance was preset at *P* < 0.05.

RESULTS

Feed intake and body weight. The wethers consumed all feed supplied. Mean body weight, across all treatments, was 76 kg (SEM 0.79, *n* = 8). There was no significant influence of dietary treatment on body weight.

Magnesium absorption and plasma magnesium. Intake of magnesium did not differ for all treatments (Table 3). The addition of KHCO_3 or K-citrate to the diet significantly increased fecal magnesium excretion. Potassium chloride did not significantly raise fecal magnesium excretion. Consequently apparent magnesium absorption was significantly decreased after supplementation of the diet with either KHCO_3 or K-citrate, but not with KCl. The decrease in magnesium absorption seen after feeding KHCO_3 or K-citrate was accompanied by a significant decrease in urinary magnesium excretion. In contrast, the diet with KCl did not affect urinary magnesium excretion.

The dietary treatments did not significantly affect plasma magnesium concentrations. For all treatments combined plasma Mg concentration was 0.96 mmol/L (SEM 0.011, *n* = 8).

Minerals in rumen liquid and pH. Magnesium concentrations in rumen liquid were not affected by dietary treatment (Table 4). Addition of potassium to the diet increased the potassium concentrations in rumen liquid, irrespective of the type of salt. Rumen concentrations of sodium and chloride were not significantly affected by dietary treatment.

Ruminal pH was significantly increased after feeding the diet with KHCO_3 instead of the control diet. The diet containing K-citrate vs. the control diet tended (*P* = 0.166) to raise the pH, but KCl had no effect (Table 4).

Transmural potential difference. The three diets supplemented with potassium raised the group mean transmural

TABLE 4

Rumen liquid mineral concentrations, pH and potential difference across ruminal wall in wethers fed the control diet and diets supplemented with equimolar amounts of KHCO_3 , KCl or K-citrate¹

	Control	High K diets			Pooled SEM	ANOVA <i>P</i> -value for treatment
		KHCO_3	KCl	K-Citrate		
Magnesium, ² mmol/L	8.17	7.68	8.68	8.80	0.955	0.832
Potassium, ² mmol/L	44.5 ^b	78.2 ^a	82.9 ^a	79.1 ^a	7.058	0.021
Sodium, ² mmol/L	90.6	72.3	72.1	76.6	7.358	0.274
Chloride, ² mmol/L	20.2	19.5	29.5	18.5	3.513	0.135
pH ²	6.09 ^{bc}	6.31 ^a	6.04 ^c	6.25 ^{ab}	0.054	0.006
Potential difference ³	39.6 ^b	56.7 ^a	49.3 ^{ab}	60.3 ^a	3.010	0.001

¹ Values are means; *n* = 8. a,b,c Values in a row with different superscripts differ significantly (*P* < 0.05, Tukey's *t* test).

² Values are means for 0900, 1100, 1300 and 1500 h.

³ Values are means for 0900–1000, 1000–1100, 1100–1200, 1200–1300, 1300–1400, 1400–1500 and 1500–1600 h.

TABLE 5

Multiple regression model accounting for 42.2% of the observed variance in magnesium absorption¹

Constant or independent variable	Unit	Regression coefficient \pm SEM	P
Constant	Mg absorption (% of intake)	45.7 \pm 4.84	0.007
Animal	Rank order (2-8)	NG ³	0.010
Transmural potential difference	mV	-0.21 \pm 0.080	0.016

¹ $P = 0.005$; $n = 32$.² The regression coefficient equals the change in average response of magnesium absorption (% of intake) if the independent variable increases by one unit.³ NG, not given, because the values are not of interest and because there were seven regression coefficients for the factor sheep.

potential difference (serosal side = positive), with KCl producing the smallest rise (Table 4). The effects of KHCO_3 and K-citrate were significant, i.e., $P = 0.004$ and $P = 0.001$, respectively.

Correlations for individual values. Apparent magnesium absorption did not correlate with rumen liquid concentrations of magnesium ($P = 0.491$), potassium ($P = 0.311$) or rumen liquid pH ($P = 0.976$), but there was tendency ($P = 0.060$) toward a negative association with the potential difference across the ruminal wall. The multiple regression model with a constant, the factor sheep animal and rumen liquid concentrations of magnesium and potassium, rumen liquid pH and transmural potential difference explained 31.5% of the observed variance in magnesium absorption ($P = 0.082$). After forward, stepwise regression it appeared that only the factor animal ($P = 0.010$) and the transmural potential difference contributed significantly ($P = 0.016$) to the explained variance in magnesium absorption (Table 5).

DISCUSSION

This study confirms earlier work (House and Van Campen 1971, Khorasani and Armstrong 1990, Newton et al. 1972, Schonewille et al. 1999), showing that the addition of KHCO_3 to the diet of ruminants lowers magnesium absorption. The KHCO_3 -induced decrease in magnesium absorption was 9.5%, which agrees with a previous experiment using wethers fed a similar amount of KHCO_3 (Ram et al. 1998). On the basis of a comparison of different studies, we predicted earlier that KHCO_3 would reduce magnesium absorption more effectively than an equimolar amount of KCl (Schonewille et al. 1997a). By direct comparison within one study, we have now substantiated our prediction. The difference in magnesium absorption for the diets containing either KHCO_3 or KCl reached significance only with respect to urinary magnesium excretion, which can be considered an index of magnesium absorption under maintenance conditions (Ram et al. 1998, Schonewille et al. 1997b). Compared with the control diet, the intake of supplemental KCl did not significantly reduce magnesium absorption. K-citrate, on the other hand, significantly lowered magnesium absorption by 6.5%. This appears to be the first feeding trial demonstrating that the lowering effect of potassium on magnesium absorption is dependent on the type of anion in the potassium salt ingested. Even though magnesium absorption was depressed by supplemental KHCO_3 and K-citrate, hypomagnesemia did not occur. Thus, in this study, the wethers absorbed sufficient magnesium to maintain magnesium balance as indicated by Table 3.

In vitro studies with rumen epithelium (Leonhard-Marek and Martens 1996) have indicated that the inhibitory action of potassium on magnesium absorption can be explained by

the depolarizing action of potassium on the apical membrane potential of rumen epithelial cells, which reduces the driving force for magnesium uptake by these cells. The reduced apical membrane potential difference results in an increased transmural potential difference associated with depressed magnesium absorption (Martens and Blume 1986, Martens et al. 1987). This feeding trial supports the mechanism proposed on the basis of studies with isolated rumen models. The feeding of KHCO_3 significantly elevated the transmural potential difference. K-citrate administration also significantly lowered magnesium absorption associated with a marked increase in the potential difference. The elevating effect of KCl on the potential difference was intermediate as was its lowering influence on the percentage of magnesium absorption. Multiple regression analysis showed that there was a significant, negative correlation between the potential difference and the percentage of magnesium absorption (Table 5).

It can be concluded that the different effects of KHCO_3 and KCl on magnesium absorption are secondary to the different effects of these salts on the potential difference. The different effects of the salts were unrelated to the potassium concentration in the rumen fluid (Table 4), supporting the theory that the type of anion affects the potential difference. Indeed, the potassium concentration in rumen liquid alone was weakly associated with the potential difference across the ruminal wall ($r = 0.323$, $n = 32$, $P = 0.093$), but when the chloride concentration in rumen liquid was added to the model, both potassium and chloride contributed significantly ($P = 0.015$ and $P = 0.026$, respectively) to the explained variance in the transmural potential difference ($R^2_{\text{adj}} = 21\%$, $P = 0.020$). Furthermore, in vitro studies have shown that chloride vs. sulfate lowers the potential difference (Ferreira et al. 1966, Martens and Blume 1986). Thus, potassium and chloride appear to have opposite effects on the transmural potential difference.

In addition to diffusion, ruminal magnesium absorption also involves a carrier-mediated process that is based on exchanging a magnesium ion for two hydrogen ions (Martens et al. 1991, Scharrer and Lutz 1990). The two transport mechanisms are dependent on the magnesium concentration in the rumen fluid, even though the carrier-mediated mechanism can become saturated (Brown et al. 1978, Care et al. 1984, Martens and Harmeyer 1978, Martens 1979). Thus, it could be suggested that dietary potassium also reduces magnesium absorption by lowering the concentration of magnesium in the rumen liquid. The soluble-magnesium concentration, in turn, depends on the ruminal pH. At pH values >6.0 , there is a sharp fall in the concentration of soluble magnesium (Dalley et al. 1997). There was no relation between either ruminal pH or magnesium concentration and magnesium absorption. The data in Table 4 indicate that only KHCO_3 feeding raised the

ruminal pH and lowered magnesium concentrations. K-citrate also raised the group mean ruminal pH but did not lower magnesium concentrations. It seems that a pH-induced change in magnesium concentration was not an important determinant of magnesium absorption in our wethers fed different potassium salts.

In conclusion, this study shows that the type of anion in potassium salts has an effect on magnesium absorption in addition to the inhibitory effect of potassium itself. Compared with the control diet, supplemental KHCO_3 and K-citrate significantly lowered the percentage of magnesium absorption, whereas KCl did not. On the basis of this study, the salt effect relates to the transmural potential difference. Compared with the control diet, supplemental KHCO_3 and K-citrate significantly raised the potential difference, whereas KCl did not.

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