Plasma electrolyte concentration in food-deprived goats orally supplemented with potassium chloride

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The aim of the present study was to investigate whether oral potassium supplementation during food deprivation could stimulate rumen electrolyte absorption and maintain plasma electrolyte concentration. Eight goats were subjected to food deprivation in combination with intrarumen loads of potassium chloride or, as a control, mannitol in a change-over design. In addition, four KCl- and four mannitol-treated goats were given an extra KCl load towards the end of the experiment. Food-deprived goats which were given KCl maintained their plasma concentration of Na and Cl, while plasma K concentration increased from 3·6 mM to 4·4 mM. In control goats receiving mannitol during food deprivation, the plasma concentration (mM) decreased from 144 to 140 for Na, 105 to 100 for Cl and from 3·8 to 3·6 for K, but concentrations were restored when these goats were given a load of KCl. The plasma renin activity was suppressed in food-deprived goats receiving KCl, while those given mannitol showed increased activity. It is suggested that the hyponatraemia which occurs in food-deprived ruminants is mainly caused by diminished K intake.

Electrolytes: Potassium chloride supplementation: Goat

Ruminants normally ingest large quantities of potassium with the food, while the sodium intake is smaller. During feeding and rumination, large volumes of saliva containing substantial amounts of Na and K enter the rumen (McDougall, 1948). Re-absorption of Na is necessary in order to maintain the plasma Na concentration and Dobson (1959) estimated that about 50% of the Na in saliva is re-absorbed from the rumen of sheep. It is a matter of controversy whether the rumen fluid concentration of K influences Na absorption. In vivo studies indicate that a high rumen concentration of K stimulates the absorption of Na from rumen to blood (Scott, 1967; Martens & Hammer, 1981). However, in vitro studies indicate that the Na–hydrogen exchange is the predominant system for Na absorption, and that K does not influence the Na absorption through the rumen epithelium (Strozyk, 1987; Martens & Gäbel, 1988).

Food deprivation in small ruminants leads to hyponatraemic hypovolaemia which activates the renin–angiotensin–aldosterone system (RAAS) (Dahlborn & Karlberg, 1986). In a subsequent study it was shown that the Na concentration of the rumen fluid increased, but that the K concentration decreased (Holtenius & Dahlborn, 1990*b*). It was suggested that the Na absorptive capacity of the rumen became impaired during food deprivation, which caused the hyponatraemia and activation of the RAAS.

The aim of the present experiments was to investigate whether plasma and urine electrolytes, plasma volume, and the activity of the RAAS would remain unchanged during food deprivation if the goats were supplemented with K into the rumen in amounts corresponding to that which they normally receive with their food. In control experiments mannitol was given to food-deprived goats. Mannitol is often used to increase the osmotic pressure of rumen fluid in absorption studies (Warner & Stacy, 1977). It was also

decided to study, at the end of the food-deprivation period, the effect of an intrarumen load of potassium chloride given both to goats which had received KCl and to those which had received mannitol during the deprivation period.

MATERIALS AND METHODS

Animals

Eight adult female goats of the Swedish domestic breed (body-weight 38 (SE 2·8) kg) were used. They were kept in metabolism cages and given 500 g hay and 50 g concentrates including 3 g sodium chloride at each meal (08.00 and 16.00 hours) except during the food-deprivation experiments. The hay contained (g/kg): 870 dry matter (DM), 8·7 MJ metabolizable energy (ME)/kg, 70 digestible crude protein (nitrogen × 6·25; DCP), 0·8 Na and 18·4 K. The concentrates contained (g/kg) 900 DM, 11·7 MJ ME/kg, 140 DCP, 0·4 Na and 9·6 K. Water was available *ad lib.*

Experimental procedures

The eight goats were randomly divided into two groups. Both groups were subjected to two treatments in a change-over design: food deprivation either in combination with intrarumen loads of KCl (KCl goats), or, as a control, food deprivation in combination with intrarumen loads of mannitol (mannitol goats). Mannitol was given in order to raise the osmotic pressure of the rumen fluid to the same level as the KCl goats. There was an interval of 1 week between experiments. Between experiments all goats were fed according to normal routines. The experimental routine is described in Fig. 1. Water intake and urinary excretion were measured during two periods each of 24 h. On day 1 the goats were fed normally. On day 2 at 08.00 hours food residues, if any, were removed and no food was offered until 16.00 hours the following day (day 3), when the goats were given 500 g hay and 50 g concentrates. At normal feeding times (08.00 hours and 16.00 hours) when no feed was offered, 17 g KCl (K 9 g) or 87 g mannitol dissolved in 350 ml water were introduced into the rumen via a stomach tube. The osmolality of both solutions was 1·3 osmol/kg. The calculated increase of the rumen fluid osmolality was about 70 mosmol/kg immediately after dosing, assuming a rumen fluid volume of 6 litres (Holtenius & Björnhag, 1989). On day 3 at 10.00 hours a blood sample was taken from all animals and immediately thereafter an intrarumen load of 3 litres water at 39°, mixed with 50 μCi tritiated water (TOH), were given by stomach tube to two KCl goats and two mannitol goats from each group. After administration of the water load, blood samples for analysis of TOH activity in plasma were withdrawn every 10 min for 60 min. At 11.00 hours all four goats were given an intrarumen load of KCl as described previously. Additional blood samples were collected according to Fig. 1.

Analysis

The TOH activity in plasma was measured in a scintillation counter (LKB 1217, Wallac Oy. Turku, Finland), and values were corrected for quenching. Na and K were determined by the ion-selective method (System E2A electrolyte analyser, Beckman Instruments Inc. Glenrothes, Scotland) and the Cl concentration was determined colorimetrically (CMT 10; Radiometer, Copenhagen, Denmark). The osmolality was determined by molar freezing-point depression (VAO 1 osmometer; Roebeling, Berlin, Germany). Total plasma protein concentration (PP) was measured by refractometry. For determination of plasma renin activity (PRA) and plasma aldosterone concentration (PAC), blood was collected in pre-chilled tubes containing K_3EDTA and centrifuged at 4°. The plasma was separated and

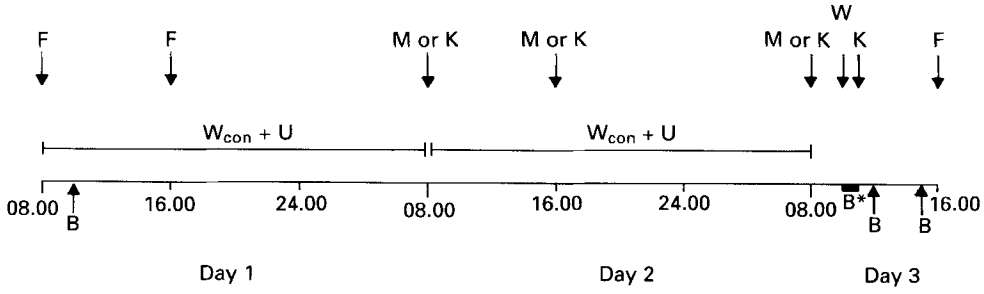

Fig. 1. Experimental procedure. F, feeding; U, urine collection; W_{con}, water consumption measurements; B, blood sampling; B*, blood sampling every 10 min; M, K and W, intrarumen loads of mannitol, potassium chloride and water respectively.

stored at −20°. PRA was determined by radioimmunoassay using an assay kit (Phadebas Angiotensin I test; Pharmacia Diagnostics, Uppsala). PAC was determined according to McKenzie & Clements (1974).

Calculations

If the transfer of TOH from rumen to plasma follows first-order kinetics, the rate constant for the TOH transfer can be calculated according to the equation:

$$A_{p300} - A_{pt} = A_{p300} \times e^{-kt},$$

where A_{pt} is the plasma TOH activity at time t (samples were taken 10, 20, 30, 40, 50, 60 and 300 min after the fluid load), A_{p300} is the equilibrated plasma TOH activity 300 min after the fluid load and k is the rate constant for TOH transfer from rumen to plasma.

The back flow of TOH from plasma to rumen was not compensated for since the rumen TOH concentration was much higher than the plasma TOH concentration during the 60 min measurement period (K. Holtenius, unpublished results). The model was fitted to data with a microcomputer program (PCNONLIN, Statistical Consultants Inc. Edgewood, USA). Values are presented as means with their standard errors. The tests for significance were done by analysis of variance (general linear model; SAS Institute Inc., Cary, USA).

RESULTS

Effects of KCl or mannitol treatment during food deprivation

Water intake decreased from 2·6 litres/d and 2·2 litres/d (SE 0·19) to 0·9 litres/d and 0·8 litres/d (SE 0·22) for KCl goats and mannitol goats respectively, during food deprivation ($P < 0·01$ *v.* control in each group). The urine excretion was 1·4 (SE 0·21) litres/d for both treatments before food was withdrawn, and during food deprivation KCl goats excreted 1·7 litres/d and mannitol goats 1·0 litre/d (SE 0·34; the differences were not significant). Urinary Na and Cl excretions increased when the goats received the KCl solution. When mannitol was given neither Na nor Cl excretion changed significantly (Table 1). The K excretion did not change significantly when KCl was given, but decreased when the goats received mannitol (Table 1).

When the goats received KCl solutions the plasma Na and Cl, osmolality and PP remained unchanged, while plasma K increased. In mannitol goats the plasma concentrations of Na, K and Cl, and the osmolality decreased while PP was not significantly affected (Table 2).

Table 1. *Effects of food deprivation in combination with intrarumen loads of mannitol or potassium chloride on urinary excretion of sodium, potassium and chloride (mmol/d) in goats*†

(Mean values with their standard errors of least square means for eight goats)

	Control			Food deprivation		
Component	KCl goats	Mannitol goats	SE	KCl goats	Mannitol goats	SE
Na	27	22	13·6	110**	45	9·7
K	390	355	31·1	299	118**	30·1
Cl	80	74	18·4	290**	32	16·7

Mean values (day 2, 08.00 hours – day 3, 08.00 hours) were significantly different from the corresponding control values (day 1, 08.00 hours – day 2, 08.00 hours): ** $P < 0{\cdot}01$.

† For details of procedures, see Fig. 1 and p. 212.

Table 2. *Effects of food deprivation in combination with intrarumen loads of mannitol or potassium chloride on plasma concentrations of sodium (mM), potassium (mM) and chloride (mM), plasma osmolality (mosmol/kg) and total plasma protein (PP; g/l) in goats*†

(Mean values with their standard errors of least square means for eight goats)

	Control			Food deprivation		
Component	KCl goats	Mannitol goats	SE	KCl goats	Mannitol goats	SE
Na	145	144	0·4	144	140***	0·3
K	3·6	3·8	0·10	4·4*	3·6*	0·14
Cl	107	105	1·0	107	100***	0·4
Osmolality	299	298	1·9	298	292**	0·4
PP	64	65	0·7	66	65	1·3

Mean values after 26 h food deprivation (day 3, 10.00 hours) were significantly different from corresponding control values (day 3, 10.00 hours): * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$, *** $P < 0{\cdot}001$.

† For details of procedures, see Fig. 1. and p. 212.

The PRA on day 1 (control values) were 0·09 and 0·07 pkat/l for KCl goats and mannitol goats respectively (SE 0·050). On day 3 at 10.00 hours, PRA had decreased to 0·01 pkat/l for KCl goats ($P < 0{\cdot}01$, KCl *v.* control values), whereas it had increased to 0·11 pkat/l for mannitol goats ($P < 0{\cdot}05$; mannitol *v.* control values) (SE 0·011).

The PAC on day 1 (control value) was 149 pM for KCl goats and 111 pM for mannitol goats (SE 58·1). The corresponding values on day 3 at 10.00 hours were 184 and 127 pM (SE 75·6; not significant when compared with control values).

Effects of an intrarumen load of water

In KCl goats the plasma K concentration was significantly elevated both before and after the water load, while none of the other variables was significantly altered (Fig. 2). In the mannitol goats the plasma Na, Cl and K concentrations and plasma osmolality which were reduced by food deprivation, remained at a lowered level 60 min after the water load (Fig. 2). The PP was not affected by the water load in either of the two treatments. The rate of TOH transfer from rumen to plasma after the water load was 2·3 (SE 0·3)%/min in mannitol goats, and 1·7 (SE 0·3)%/min in KCl goats. The difference between treatments was not significant.

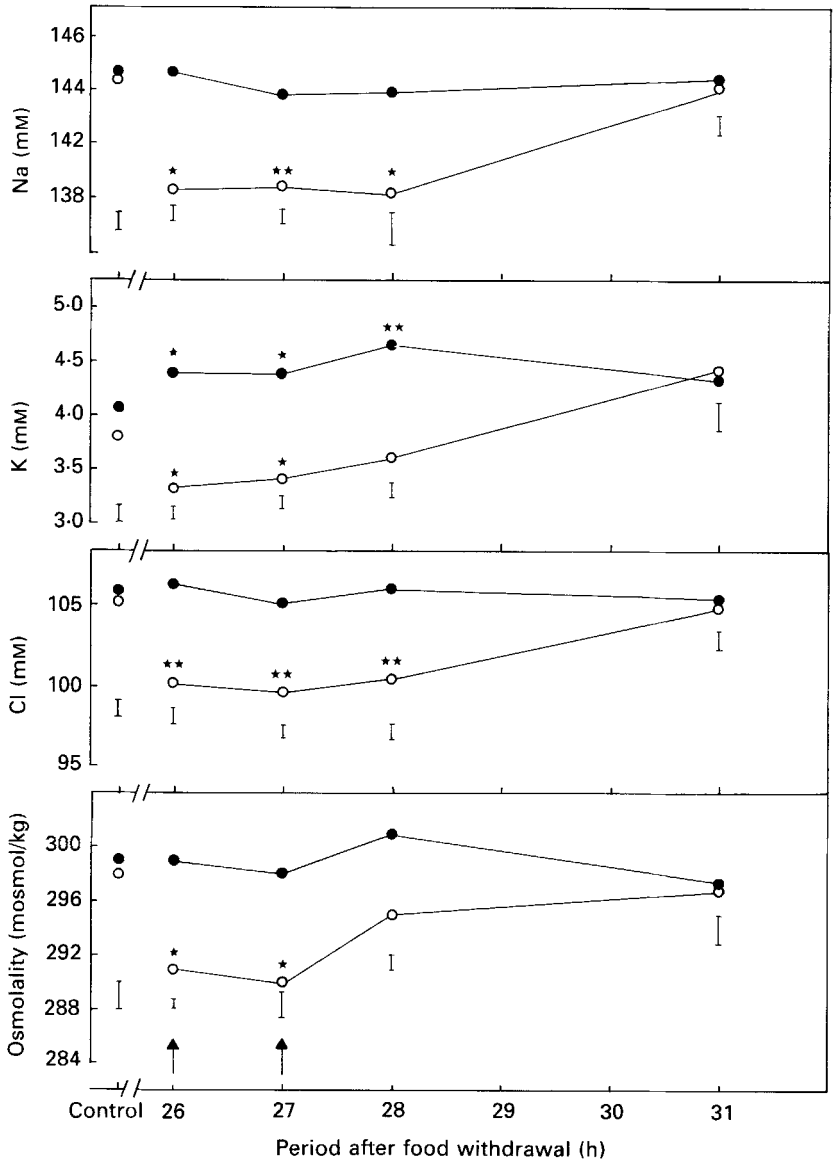

Fig. 2. The plasma concentration of sodium, potassium and chloride, and osmolality in fed goats (control), and in food-deprived goats which had been given either KCl (●) or mannitol (○) at their regular feeding times. First arrow indicates an intrarumen load of water; second arrow indicates an intrarumen load of KCl. Mean values were significantly different from control values by analysis of variance (n 4): * $P < 0{\cdot}05$, ** $P < 0{\cdot}01$.

Effects of the extra KCl load

In KCl goats the extra KCl load did not affect the plasma Na and Cl concentrations, the osmolality or the PP, but the plasma K concentration increased. In mannitol goats given a KCl load the plasma Na and Cl concentrations remained lowered, compared with control values 60 min after the load, while the plasma K concentration and osmolality increased towards the control values (Fig. 2). The PP dropped from 65 to 61 g/l (SE 1·1; $P < 0{\cdot}05$).

Plasma Na, Cl and K concentrations, and the plasma osmolality were all close to the

control values 4 h after the extra KCl load with both treatments (Fig. 2). By then PP still did not significantly deviate from the control level in KCl goats, but had decreased to 59 g/l (SE 1·5; $P < 0·05$ mannitol *v.* control values) in mannitol goats.

DISCUSSION

The results of the present study indicate that the concentration of plasma electrolytes and the plasma osmolality decreased in mannitol goats in a similar way to that reported with food-deprived goats and sheep receiving no treatment (Dahlborn & Karlberg, 1986; Holtenius & Dahlborn, 1990*a*, *b*). Mannitol has been used extensively to raise the osmolality of rumen fluid in absorption studies (Warner & Stacy, 1977; Gäbel *et al.* 1987), and there appears to be no evidence of a direct influence of mannitol on electrolyte absorption. When the goats were supplemented with KCl during the food-deprivation period they maintained their plasma osmolality and plasma concentration of Na and K at the control level, and the plasma K concentration increased. These results suggest that the absorption of Na, K and Cl from the rumen of food-deprived goats is increased by intrarumen loads of KCl. In contrast to our findings, Rabinowitz *et al.* (1988) did not find any increased plasma K concentration in sheep in which one meal was replaced by an intrarumen infusion of KCl. One explanation for the different results may be that three meals were replaced by KCl solutions in the present study.

The transport of Na and Cl across the rumen epithelium appears to be coupled over a wide range of physiological Na concentrations (Martens & Blume, 1987). Thus, it is difficult to distinguish the roles of K and Cl in maintaining the electrolyte concentration during food deprivation in the present study. It has previously been observed that oral NaCl supplementation cannot maintain the plasma osmolality and plasma Na concentration of food-deprived goats (Dahlborn, 1987). Suttle & Field (1967) have shown that fed sheep supplemented with 27 g K given as KCl or potassium acetate increased the urinary Na excretion. A similar increase in the urinary Na excretion due to intrarumen KCl loading has been observed in fed dik-dik antelopes (*Rhynchotragus kirkii*) (Rugangazi & Maloiy, 1988). This could be explained by the fact that intrarumen K supplementation stimulates absorption of Na from the rumen (Scott, 1967; Martens & Hammer, 1981), and the enhanced absorption in turn increases the renal Na excretion. This, together with the results presented here, suggest that the rumen fluid K concentration is one important factor for the maintenance of plasma osmolality and plasma Na concentration during fasting. However, these in vivo studies do not agree with in vitro work in which increased K concentration on the lumen side of the rumen epithelium did not enhance Na absorption (Strozyk, 1987; Martens & Gäbel, 1988). Therefore, Martens & Gäbel (1988) suggested that lumen K could have an effect in vivo on blood flow or nervous activity, or both, with secondary effects on Na transport. However, the present results do not give support for changes in subepithelial blood flow as a cause for changes in Na transport since there was no significant difference in TOH clearance from the rumen between KCl goats and mannitol goats. The TOH clearance is correlated to rumen subepithelial blood flow (Dobson, 1979). It is thus not likely that the higher plasma Na concentration in KCl-treated animals in the present study could be explained by enhanced rumen subepithelial blood flow.

In the present study the KCl goats increased both their Na and Cl excretions during food deprivation, although they did not receive any Na during the deprivation period. The result could scarcely be explained by increased K intake, since the amount given corresponded to the regular intake of K. Therefore it appears more likely that in the present study renal excretion of Cl in the KCl-treated animals brought about the increased Na excretion observed.

The PP did not change during food deprivation in the present study, indicating that the plasma volume was unchanged. Previous studies have shown that food deprivation in goats leads to decreased plasma volume (Dahlborn & Karlberg, 1986). Thus, it seems that water absorption from the gastrointestinal tract was maintained during food deprivation by intrarumen loads of both mannitol and KCl. Intrarumen addition of K seems to stimulate rumen Na absorption in food-deprived goats, and water is mainly absorbed from the gastrointestinal tract secondary to Na absorption (Stevens, 1988). Thus, the unchanged plasma volume in KCl goats during food deprivation could be explained by the stimulation of Na absorption. In support of this explanation is the fact that when the mannitol goats were given an intrarumen load of KCl, the plasma volume increased in combination with increasing plasma Na concentration. However, mannitol goats also maintained their plasma volume during food deprivation. This effect of the intrarumen loads of mannitol is difficult to explain.

The lowered PRA in KCl-supplemented goats is interesting. Goats drinking a NaCl solution during food deprivation also seem to react with decreased PRA, although the effect has not been statistically tested (Dahlborn, 1987). Kirchner *et al.* (1978) proposed that inhibition of the renin release in NaCl-loaded rats is related to Cl transport in the thick ascending loop of Henle. A similar conclusion was drawn from studies with human subjects (Julian *et al.* 1982). The results obtained in the present study indirectly indicate that an intrarenal Cl load could be an effective suppressor of the renin release also in ruminants.

Increasing plasma K concentration, decreasing plasma Na concentration and activation of the renin-angiotensin system are important factors stimulating the plasma aldosterone secretion in ruminants (for review, see Denton, 1982). The increased plasma K concentration in KCl goats in the present study could thus be expected to give rise to elevated secretion of aldosterone. However, in the goats the PRA was suppressed which in turn could be expected to decrease the PAC. Thus, the net effect on the PAC was probably small.

In mannitol goats PRA increased, and the plasma Na concentration was lowered, but PAC was unaffected. This might be explained by the fact that the plasma concentration of K decreased.

When the mannitol goats were given an intrarumen dose of KCl the plasma concentrations of Na, K and Cl as well as the plasma osmolality rose, and had returned to prestarvation levels within 4 h. Food-deprived goats receiving 3 litres water, and then subjected to a similar blood sampling procedure as in the present study, did not restore their plasma Na concentration to prestarvation levels after the load (Holtenius & Dahlborn, 1990*a*). Neither the plasma K concentration nor plasma osmolality returned to their prestarvation values (K. Holtenius and K. Dahlborn, unpublished results). It is therefore reasonable to assume that intrarumen loads of KCl can not only maintain plasma electrolyte concentration during food deprivation but can also restore the plasma electrolyte concentration in goats that had been food deprived for 27 h.

In conclusion, the results presented here indicate that dietary K is an important factor in the rumen absorption of Na, and that the hyponatraemia which develops during food deprivation in ruminants could be explained by diminished K intake. Further investigations are needed in order to clarify the mechanism of K-stimulated Na absorption from the rumen.

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