Studies on magnesium in ruminant nutrition

8. Effect of increased intakes of potassium and water on the metabolism of magnesium, phosphorus, sodium, potassium and calcium in sheep

By N. F. SUTTLE and A. C. FIELD

Moredun Institute, Edinburgh 9

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1. In Expt 1 daily supplements of 0 or 27–28 g potassium, with 0 or 7.5 l. water, were given to each of eight fistulated wether sheep on a hay and concentrate diet in two 4 x 4 Latin square experiments. Faeces were collected for the last 4 days of, and urine throughout, 10-day treatment periods.

2. Adding K to the diet decreased the urinary output of magnesium by 33 % (P < 0.001) and significantly increased those of phosphorus, sodium and calcium by 98, 76 and 150 %, respectively. Faecal outputs of Mg and K were increased, whereas that of P was decreased. The retentions of P and Na tended to be decreased, whereas that of K was increased (P < 0.001). Mg in serum was decreased by 0.4 mg/100 ml (P < 0.05) and K increased by 4.9 mg/100 ml (P < 0.001).

3. Increasing the water intake increased the urinary outputs of Mg, P, Na and Ca by 33, 165, 47 and 200 %. The faecal output of Ca was increased and the retentions of Mg, P and Ca were decreased (P < 0.01).

4. The effects of water and K were generally independent, but interactions affected the urinary outputs of P and K and the retention of K.

5. The increases in urinary Na output were three- and eight-fold greater during the first 3 days of increased water and K intakes than during the balance study.

6. In Expt 2, mineral balance studies were conducted before and after supplementing the diet with potassium acetate, using five wethers from Expt 1. K intakes were similar to those of Expt 1. The effects of potassium acetate and KCl were generally similar qualitatively but the acetate produced greater decreases in urinary Mg and faecal P outputs and greater increases in urinary Na and K outputs than KCl. K in serum was increased by 28 mg/100 ml but Mg was not affected.

7. The nature of these responses is discussed with particular reference to the aetiology of hypomagnesaemic tetany.

It has been known for many years that the incidence of hypomagnesaemic tetany is associated with a high potassium content in the pasture (Sjollema, 1932). The existence of such an association in the United Kingdom was recently confirmed by the survey conducted by Butler and his associates (Butler et al. 1963). The addition of K salts to the diet of ruminants has been shown to decrease the urinary excretion of dietary magnesium (Meyer & Steinbeck, 1960; Kemp, Deij, Henkes & Van Es, 1961; De Groot, 1961), and cows turned out to graze pasture heavily fertilized with K have developed hypomagnesaemia (Hvidsten, Ødelien, Bærum & Tøllersrud, 1959; Allcroft, 1960). Attempts to produce hypomagnesaemia and tetany by adding K directly to the ruminant’s diet have, however, usually failed (Pearson, Gray & Reiser, 1949; Eaton & Avampato, 1952; Daniel, Hatfield, Shrewsberry, Gibson & MacVicar, 1952; Blaxter, Cowlishaw & Rook, 1960; Hendriks, 1962).

Cases of hypomagnesaemic tetany often occur within a few days of allowing cattle
and sheep to graze lush pasture (see Stewart, 1954). In an earlier paper (Suttle & Field, 1966) we found that the sheep’s metabolism of magnesium, phosphorus, sodium and potassium was considerably affected when water intakes were increased to levels similar to those experienced by sheep grazing lush pasture. The objects of the experiments recorded in this paper were to examine the effect on mineral metabolism of suddenly raising the K content of the diet to 4%, a level commonly found in pastures on which hypomagnesaemic tetany occurs (Butler et al. 1963). The effect of added K was examined with sheep given normal or high water intakes (Expt 1) and with chloride (Expt 1) or acetate (Expt 2) as the accompanying anion. The metabolism of Mg and also of P, Na, K and Ca was greatly influenced by these treatments.

**METHODS**

**Expt 1.** Mineral balance studies were conducted with a group of eight sheep with normal or high intakes of K and water. Four treatments were applied to each sheep at random according to two 4 × 4 latin squares. The treatments were as follows: treatment O, basal diet only, providing 9·5 g K/day (1·1% K in dry matter); treatment KD, K intake was raised to 36 g/day (4·2% K in DM) by adding 7·6% potassium chloride to the concentrate portion of the basal diet; treatment W, water intake was raised by infusing 7·5 l./day into the rumen continuously over 24 h through fistulas; treatment KW, K intake was raised to 37 g/day (4·3% K in DM) by infusing KCl with 7·5 l. water. Each treatment lasted for 10 days and was separated from the next treatment by a rest period of 10 days. Urine was collected daily throughout the treatment period, whereas faeces were collected and pooled over the last 4 days only to allow time for digesta from food consumed in the pretreatment period to be excreted.

**Expt 2.** The K intakes of five sheep from Expt 1 were raised to 37 g/day by adding 10·0% potassium acetate to the concentrate portion of the diet. Mineral balance studies were conducted on each sheep for 7 days before and for 10 days during the period of supplementation with K. Urine was collected for 17 days and faeces for the last 4 days of each period.

**Animals.** Sheep were taken from a group of eight 2-year-old Scottish Blackface wethers, having a mean weight of about 55 kg. Each animal was fitted with a rumen fistula.

**Management.** The sheep were housed individually in wooden pens with slatted floors. The techniques for collecting samples and infusing solutions into the rumen were described in a previous paper (Suttle & Field, 1966). Serum samples were obtained just before the commencement of treatment and on the last day of the treatment period in both experiments. The daily ration consisted of 700 g concentrates and 300 g chopped hay divided equally into two feeds. K salts were incorporated into the concentrate portion of the ration by grinding the cubes in a hammer mill, mixing the supplement with the ground material thoroughly in a 5 cwt auger-mixer and repelleting the mixture using a ½ in. diameter die (Christy Norris Ltd, Essex). Separate batches of concentrates were used in Expts 1 and 2, and although these were made to the same specifications by the compounder, they differed in mineral composition.
The composition of the feedstuffs used and the total daily intakes of minerals which they provided are given in Table 1. The ration of K-supplemented concentrate was adjusted in accordance with changes in the dry-matter content and dilution with K salt so that the intake of nutrients other than K remained constant. K salts were of General Purpose Reagent grade and analyses showed that they contained negligible amounts of the nutrients, other than K, under investigation.

**Analytical techniques.** Details of the techniques used to estimate Mg, K and Ca in serum, urine, faeces and diets were given by Field (1964) and those for Na and P by Suttle & Field (1966) in earlier papers in this series.

Table 1. Concentrations of minerals and protein in hay and concentrates used in Expts 1 and 2 and the total daily intakes (g) of the magnesium, phosphorus, sodium, potassium, calcium, crude protein and dry matter

<table>
<thead>
<tr>
<th>Expt no.</th>
<th>Food</th>
<th>Mg</th>
<th>P</th>
<th>Na</th>
<th>K</th>
<th>Ca</th>
<th>Crude protein</th>
<th>Dry matter (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Concentration (g/100 g DM)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Chopped hay</td>
<td>0.09</td>
<td>0.18</td>
<td>0.29</td>
<td>1.63</td>
<td>0.40</td>
<td>9.0</td>
<td>89.1</td>
</tr>
<tr>
<td></td>
<td>Concentrates</td>
<td>0.22</td>
<td>0.52</td>
<td>0.21</td>
<td>0.87</td>
<td>0.48</td>
<td>18.1</td>
<td>84.0</td>
</tr>
<tr>
<td>2</td>
<td>Chopped hay</td>
<td>0.09</td>
<td>0.14</td>
<td>0.32</td>
<td>1.56</td>
<td>0.40</td>
<td>8.9</td>
<td>87.2</td>
</tr>
<tr>
<td></td>
<td>Concentrates</td>
<td>0.16</td>
<td>0.48</td>
<td>0.48</td>
<td>0.61</td>
<td>1.62</td>
<td>18.0</td>
<td>90.2</td>
</tr>
<tr>
<td></td>
<td>Total intake (g/24 h)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>Mixed ration</td>
<td>1.54</td>
<td>3.50</td>
<td>2.01</td>
<td>9.47*</td>
<td>6.83</td>
<td>130</td>
<td>855</td>
</tr>
<tr>
<td>2</td>
<td>Mixed ration</td>
<td>1.19</td>
<td>3.36</td>
<td>3.77</td>
<td>7.47†</td>
<td>11.10</td>
<td>137</td>
<td>863</td>
</tr>
</tbody>
</table>

* Increased to 36 g/day in treatment KD, and 37 g/day in treatment KW.
† Increased to 37 g/day when potassium acetate was added to diet.

**RESULTS**

**Expt 1**

*Water balance.* The voluntary intake of water ceased within 48 h of infusing 7.5 l. water/day into the rumen during treatments W and KW, but the mean daily consumption increased by 0.97 l. during treatment KD (Table 2). The net increases in total water intake caused by these treatments were accompanied by quantitatively similar increases in urine output. A small portion of the infused water was, however, excreted in the faeces and the resultant increase in faecal water output during treatments W and KW, 0.11 l./day, was significant (P < 0.05). The mean daily changes in body-weight on treatments O, KD, W and KW were -0.01, -0.05, -0.08 and +0.04 kg/day and they did not differ significantly from zero. Changes in the water content of the sheep would therefore have been very small and the difference between total water input and measured water output can largely be attributed to insensible water losses through perspiration and respiration; these losses tended to be greater in sheep on treatments W and KW.

*Urinary excretion of Mg, P, Na, K and Ca.* The urinary outputs of each element were relatively constant during the last 4 days of each treatment period and the mean daily excretions during that time are given in Table 3. With Mg and P the effects of each
Table 2. Expt 1. Mean intakes and excretions (l./day) of water by a group of eight sheep given no treatment (O), 27 g K/day as KCl in diet (KD), 7.5 l. water/day by intraruminal infusion (W), or 28 g K/day in 7.5 l. water by infusion (KW), each for a period of 10 days.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Free water intake</th>
<th>Free + combined* + metabolic† water intake</th>
<th>Excretion of water</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>±SE of mean</td>
<td>In faeces</td>
<td>In urine</td>
</tr>
<tr>
<td>O</td>
<td>1.08 ± 0.11</td>
<td>0.26</td>
<td>0.72</td>
</tr>
<tr>
<td>KD</td>
<td>2.05 ± 0.10</td>
<td>2.50</td>
<td>0.31</td>
</tr>
<tr>
<td>W</td>
<td>7.5 ± 0</td>
<td>7.95</td>
<td>0.36</td>
</tr>
<tr>
<td>KW</td>
<td>7.5 ± 0</td>
<td>7.95</td>
<td>0.38</td>
</tr>
<tr>
<td></td>
<td>Residual SD ± 0.02</td>
<td>± 0.75</td>
<td>± 0.19</td>
</tr>
</tbody>
</table>

* From determination of dry matter of food.
† Derived from probable contents of digestible carbohydrate, protein and fat in food multiplied by the factors 0.6, 0.41 and 1.07 respectively.
‡ Since body-weights were relatively constant, insensible loss is approximately equivalent to water input minus measured water output.

**Fig. 1.** Expt 1. Mean urinary excretion of Na and K by eight sheep given no treatment (O—O), 27 g K/day, as KCl, in diet (Δ—Δ), 7.5 l. water/day by intraruminal infusion (○—○) or 28 g K/day in 7.5 l. water by infusion (▲—▲).**

treatment, evident in this table, were present after only 2 days of treatment but this was not so with Na and K. It can be seen from Fig. 1 that the urinary excretion of Na reached a peak after 1–2 days of treatments KD and KW, when values were some 3–4 g/day higher than those recorded during treatment O. There were also large
Table 3. Expt I. Mean urinary and faecal outputs and retentions (g/day) of magnesium, phosphorus, sodium, potassium and calcium in a group of eight sheep given no treatment (O), 27 g K/day as KCl in diet (KD), 7·5 l. water/day by intraruminal infusion (W), or 28 g K with 7·5 l. water by infusion (KW)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mg In urine</th>
<th>Mg In faeces</th>
<th>Retained</th>
<th>P In urine</th>
<th>P In faeces</th>
<th>Retained</th>
<th>Na In urine</th>
<th>Na In faeces</th>
<th>Retained</th>
<th>K In urine</th>
<th>K In faeces</th>
<th>Retained</th>
<th>Ca In urine</th>
<th>Ca In faeces</th>
<th>Retained</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>0·30</td>
<td>0·89</td>
<td>0·35</td>
<td>0·49</td>
<td>2·45</td>
<td>0·56</td>
<td>0·66</td>
<td>0·84</td>
<td>0·52</td>
<td>7·42</td>
<td>0·83</td>
<td>1·41</td>
<td>0·02</td>
<td>5·97</td>
<td>0·84</td>
</tr>
<tr>
<td>KD</td>
<td>0·20</td>
<td>1·00</td>
<td>0·34</td>
<td>0·97</td>
<td>2·07</td>
<td>0·45</td>
<td>1·16</td>
<td>0·71</td>
<td>0·14</td>
<td>3·06</td>
<td>1·48</td>
<td>4·41</td>
<td>0·05</td>
<td>5·83</td>
<td>0·95</td>
</tr>
<tr>
<td>W</td>
<td>0·40</td>
<td>0·89</td>
<td>0·24</td>
<td>1·30</td>
<td>1·97</td>
<td>0·23</td>
<td>0·97</td>
<td>0·84</td>
<td>0·21</td>
<td>8·24</td>
<td>0·97</td>
<td>0·26</td>
<td>0·06</td>
<td>6·49</td>
<td>0·28</td>
</tr>
<tr>
<td>KW</td>
<td>0·27</td>
<td>1·23</td>
<td>0·05</td>
<td>1·35</td>
<td>2·22</td>
<td>0·06</td>
<td>1·11</td>
<td>0·79</td>
<td>0·12</td>
<td>3·67</td>
<td>1·87</td>
<td>1·62</td>
<td>0·06</td>
<td>6·31</td>
<td>0·46</td>
</tr>
</tbody>
</table>

Standard error of difference between means

± 0·03 ± 0·08 ± 0·09 ± 0·13 ± 0·19 ± 0·13 ± 0·15 ± 0·11 ± 0·18 ± 1·29 ± 0·18 ± 1·24 ± 0·01 ± 0·21 ± 0·21

Significance:

K effect:
P < 0·001 P < 0·01 NS P < 0·05 NS ↑ P < 0·05 NS ↑ P < 0·001 P < 0·01 NS ↑ NS NS

W effect:
P < 0·001 NS P < 0·01 P < 0·001 NS P < 0·001 NS NS P < 0·01 ↑ P < 0·01 P < 0·05 P < 0·01 P < 0·01

Interaction:
NS NS NS P < 0·05 NS NS NS NS P < 0·01 NS P < 0·01 ↑ NS NS NS

NS, not significant. ↑ 0·1 > P > 0·05.
differences between individual sheep in the pattern of urinary Na excretion. During treatment KD five of the eight sheep excreted most Na on the 1st day of treatment when values ranged from 1.39 to 6.36 g/day. With treatment KW, maximal values were obtained on the 2nd day in six sheep; one animal, however, excreted 9.18 g Na on the 1st day of treatment KW. Treatment W also caused an increase in urinary Na output which reached a peak of 2.3 g/day on the 2nd day. By the 5th day, however, the increase due to each treatment was only about 0.5 g/day and these effects remained for the last 5 days of the treatment period. The output of K in urine increased daily after the initial increase in K intake until a plateau was reached after 3–6 days (Fig. 1).

During the balance study, conducted between days 7 and 10, the following effects were obtained (Table 3). Treatment KD decreased the urinary output of Mg by 33% and increased those of P, Na and Ca by 98, 76 and 150% respectively. Less than 1% of the ingested Ca was, however, excreted in the urine. Treatment W increased the urinary outputs of Mg, P, Na and Ca by 33, 165, 47 and 200%, respectively, but the effect on Na was not significant. The responses in the urinary outputs of Mg, Na and Ca to treatment KW were similar to those obtained by summatng the responses to treatments KD and W. The urinary outputs of both K and P were, however, affected by interactions between the two treatments. Thus, whereas the infusion of water alone increased urinary K excretion by 1 g/day, at high K intakes it increased excretion by 6.6 g/day. Increasing the intakes of water and K, separately, produced increases in urinary P output of 0.81 and 0.48 g/day respectively; together they produced an increase of only 0.86 g/day.

Faecal excretion of Mg, P, Na, K and Ca. The daily faecal outputs of these elements are also given in Table 3. Since there was no interaction between the K and water treatments the separate effects of increasing the K and water intakes can be calculated from the mean response to treatments KD and KW, and W and KW, respectively. K significantly increased the faecal excretion of Mg and K by 26 and 88% respectively but was without effect on the faecal excretion of Na and Ca. The infusion of water increased the faecal output of Ca by 8% (P < 0.01) but did not affect the faecal excretion of the other elements studied.

Retentions of Mg, P, Na, K and Ca. The retentions of these elements, measured as the difference between intake and faecal + urinary excretions, were not affected by interactions between the K and water treatments with the exception of K (P < 0.01; Table 3). The retention of K was increased by 3.0 g/day by treatment KD, decreased by 1.2 g/day by treatment W and decreased by 3.0 g/day by treatment KW. Increasing the K intake did not significantly affect the retentions of Mg, P or Na but the decreases of 0.20 and 0.24 g/day in the retentions of P and Na were almost significant. The infusion of water significantly reduced the retentions of Mg, P and Ca by 0.20 (P < 0.01), 0.43 (P < 0.001) and 0.53 (P < 0.01) g/day, respectively.

Concentrations of Mg, P, Na, K and Ca in serum. The mean serum concentrations of Mg, P, Na, K and Ca at the beginning and end of the treatment periods are given in Table 4. Effects were assessed statistically by comparing initial and final values within sheep for each treatment, using the paired t test. On average, treatment KD increased the serum concentration of K by 4.9 mg/100 ml (P < 0.001) and decreased that of Mg
Table 4. Expt 1. Mean serum concentrations (mg/100 ml) of magnesium, phosphorus, sodium, potassium and calcium in a group of eight sheep before and after 10-day periods during which they were given no treatment (O), 27 g K/day as KCl in diet (KD), 7.5 l. water/day by intraruminal infusion (W), or 28 g K/day as 7.5 l. KCl solution by infusion (KW)

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Mg Before</th>
<th>After</th>
<th>P Before</th>
<th>After</th>
<th>Na Before</th>
<th>After</th>
<th>K Before</th>
<th>After</th>
<th>Ca Before</th>
<th>After</th>
</tr>
</thead>
<tbody>
<tr>
<td>O</td>
<td>2.39</td>
<td>2.35</td>
<td>7.78</td>
<td>7.64</td>
<td>351</td>
<td>331</td>
<td>222</td>
<td>24.4</td>
<td>8.26</td>
<td>8.73</td>
</tr>
<tr>
<td>KD</td>
<td>2.38</td>
<td>1.98</td>
<td>8.24</td>
<td>6.95</td>
<td>352</td>
<td>326</td>
<td>21.6</td>
<td>26.5</td>
<td>8.45</td>
<td>9.03</td>
</tr>
<tr>
<td>W</td>
<td>2.45</td>
<td>2.38</td>
<td>8.01</td>
<td>6.82</td>
<td>361</td>
<td>307</td>
<td>21.6</td>
<td>25.3</td>
<td>8.39</td>
<td>8.81</td>
</tr>
<tr>
<td>KW</td>
<td>2.42</td>
<td>2.20</td>
<td>7.77</td>
<td>7.08</td>
<td>326</td>
<td>319</td>
<td>21.0</td>
<td>24.9</td>
<td>8.26</td>
<td>8.73</td>
</tr>
</tbody>
</table>

* One final value of 85 mg/100 ml omitted as atypical.

Table 5. Expt 2. Mean urinary and faecal outputs and retentions (g/day) of magnesium, phosphorus, sodium, potassium and calcium by five sheep, before and during a 10-day period when K intake was increased from 7.5 to 37 g/day by adding potassium acetate to the diet

<table>
<thead>
<tr>
<th>Mg</th>
<th>P</th>
<th>Na</th>
<th>K</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td>In urine</td>
<td>In faeces</td>
<td>Retained</td>
<td>In urine</td>
<td>In faeces</td>
</tr>
<tr>
<td>Basal K intake</td>
<td>0.27</td>
<td>0.87</td>
<td>0.05</td>
<td>1.21</td>
</tr>
<tr>
<td>High K intake</td>
<td>0.10</td>
<td>1.07</td>
<td>0.02</td>
<td>1.95</td>
</tr>
<tr>
<td>Effect of raising K intake</td>
<td>-0.17</td>
<td>+0.26</td>
<td>-0.03</td>
<td>+0.03</td>
</tr>
<tr>
<td>SE of mean difference between treatments</td>
<td>±0.03</td>
<td>±0.06</td>
<td>±0.08</td>
<td>±0.29</td>
</tr>
<tr>
<td>Significance of paired t test</td>
<td>P&lt;0.01</td>
<td>P&lt;0.05</td>
<td>NS</td>
<td>P&lt;0.01</td>
</tr>
</tbody>
</table>

NS, not significant.
by 0.40 mg/100 ml ($P < 0.05$). The final concentrations ranged from 22.0 to 31.0 and from 1.47 to 2.43 mg/100 ml for K and Mg, respectively. The effects of treatment KW on serum K and Mg concentrations were smaller and not significant. Serum P levels tended to decrease ($0.05 < P < 0.1$) under the influence of treatments W, KD and KW. The concentration of Na in serum tended to decrease during each treatment period, but serum Ca concentrations were constant throughout.

Expt 2

Urinary and faecal excretions and retentions of Mg, P, Na, K and Ca. The mean effects on the excretion and retention of these elements of raising the K intake of five sheep by adding potassium acetate to the diet are given in Table 5. The K supplement decreased the urinary outputs of Mg and Ca by 63 and 67%, respectively, and increased those of P and Na by 38 and 186%, respectively, and the only non-significant effect was that on urinary P excretion. The initial effects on urinary Na excretion were similar to those obtained during K supplementation in Expt 1, with output reaching a maximum of 3.7 g on the 1st day of treatment. The urinary output of K reached 34 g/day after only 2 days' treatment and remained around that level thereafter. The faecal outputs of Mg and K were significantly increased and those of Na and P were significantly decreased by K supplementation. The faecal excretion of Ca and the retentions of all elements studied were not affected by the treatment.

Concentrations of Mg, P, Na, K and Ca in serum. Serum K concentrations had increased from 22 to 50 (range 45-58) mg/100 ml after 10 days supplementation with potassium acetate. Values for Mg, P, Na and Ca at that time were, however, all within the normal range.

DISCUSSION

Most cases of hypomagnesaemic tetany occur within a few days of allowing lactating sheep and cows to graze lush spring pasture, and it is possible that the sudden change of diet causes disturbances of mineral metabolism which contribute to the development of this disorder. In the experiments we have described, a balance technique was used to examine the effects on mineral metabolism of sudden increases of both water and K intakes to levels commonly encountered by sheep grazing lush spring herbage. The nature of our investigation made it necessary to depart slightly from the ideal conditions for conducting balance experiments. For instance, the balance studies were conducted only 6 days after the commencement of treatment and it is possible that both the residual effects of the pretreatment diet and adaptation to the dietary treatments influenced the results obtained. Although the urinary output of each element studied was relatively constant during the balance studies, we would emphasize that the effects recorded after 7–10 days of the respective treatments are not necessarily those obtainable from a longer period of treatment.

The addition of KCl and potassium acetate to the diet caused a marked decrease in the urinary excretion of Mg and this is in accordance with the findings of Meyer & Steinbeck (1960), Kemp et al. (1961) and De Groot (1961) for cattle; there was also a significant increase in faecal Mg output. In contrast, the addition of K increased the
Potassium intake and mineral metabolism

urinary and decreased the faecal excretion of P. A similar response has been recorded in K-supplemented rats (Miller, 1926) and Hendriks (1962) has reported an increased urinary P excretion in two lactating cows given a KCl supplement. Although he states that the excretion of P in faeces was not affected, it appears from his results that, after allowing 3–4 days for the carry-over of digesta from the pretreatment period, a marked decrease in P excretion occurred.

Since the retentions of Mg and P were not affected by K supplementation, K clearly altered the partition of ingested Mg and P between the urine and faeces. This altered partition could arise from changes in the secretion into and reabsorption of these elements from the gut or from changes in their true absorption. It can be calculated that the endogenous losses of Mg would have to be increased by about 100% and those of P decreased by 40% to account for the changes of 110–200 mg and 380–550 mg in the daily faecal outputs of Mg and P, respectively (Suttle & Field, 1966). Alternatively, the true absorption of Mg might be decreased and that of P increased. This could arise, for example, if the potential difference across the wall of the small intestine is increased, as that across the rumen wall is increased (Harrison, Keynes & Nauss, 1964), following an increase in the K concentration of the digesta.

The marked natiuresis which promptly followed an increase in K intake (Fig. 2) has been found under different experimental conditions by other workers. Hix, Evans & Underbjerg (1953) produced a similar response in lambs given 32 g potassium bicarbonate/day after a prolonged period of high Na intake. Sellers, Gitis & Roepke (1951) also found a marked increase in urinary Na output of cows in the 2 h following a single large oral dose of KCl. Oyaert (1962) has recorded a relatively small effect following the infusion of KCl into the rumen, but the relationship, in time, of collection period to treatment is not given.

In quantitative terms K supplementation in Expts 1 and 2 resulted in an increase of 8–10 g in the daily urinary output of Na after 3 days. A negative balance of a similar order must have resulted, since unsupplemented sheep retained only 0·5 g Na/day and excreted only 0·84 g Na/day in the faeces, giving little scope for Na conservation. Since the concentration of Na in serum was not decreased, Na must have been lost from one or both of the two other principal pools of Na in the body, namely the rumen contents and the skeleton. At normal Na concentrations of 100 m-equiv./l., the rumen contains about 10 g Na. Denton (1957) has shown that, when the sheep is depleted of Na, K+ rapidly replaces Na+ as the dominant ion in both saliva and the rumen contents. Furthermore, increases in the ratio of K to Na in saliva and rumen contents have been recorded in sheep after a change of diet from hay with concentrates to K-rich herbage (Sellers & Dobson, 1960). It is conceivable that a similar replacement occurs under conditions of K loading, facilitated by the rapid turnover of Na through its copious secretion in saliva and its rapid absorption from the rumen. The skeleton of the adult sheep contains about 25 g Na (Field & Suttle, unpublished), but studies with other species during Na depletion suggest that only 3–15% of this can be mobilized (Forbes, 1962).

The urinary excretion of Na in K-supplemented sheep decreased rapidly after 3 days, and during the balance study the effect of K was to increase the urinary
excretion by 0.47 g Na/day and to decrease the retention by only 0.39 g Na/day. This reduction of Na excretion could have arisen simply through the exhaustion of the supply of Na. Conservation of Na through the secretion of adrenocortical hormones and the subsequent increase in tubular reabsorption of Na in the kidney (Barger, Berlin & Tulenko, 1958) seems unlikely since the urinary losses of Na remained greater than those of untreated sheep.

The effects of water infusion on mineral metabolism in Expt 1 were generally similar to those recorded in our earlier studies (Suttle & Field, 1966). The decreases in Mg and Ca retention during water infusion were, however, not found previously. The finding that the increase in urinary Na excretion was maximal on the 2nd day of infusion was also at variance with the previous studies in which a pronounced peak was not observed. The changes in the urinary excretion of Na following a large increase in water intake may be related to decreases in the salivary secretion rate leading to a reduction in the pool of Na in the rumen.

The responses to increases in K and water intakes were generally independent. For example K and water, when administered separately, exerted approximately equal but opposite effects on urinary Mg output and output was not affected when they were administered together. Different effects may be produced by altering the ratio of supplementary K to water, and Oyaert (1962), using 45% more K and 20% less water than we used, found that intraruminal infusions of KCl into sheep can decrease the urinary Mg excretion.

There was a marked interaction evident in the effects of our treatments on the urinary excretion and retention of K. Of the supplementary K added to the diet and given by infusion, 85 and 105% respectively were excreted in the urine, and 12.6 and –8.0%, respectively were retained. There was a considerable lag in K excretion, however, and in the 6 days preceding the balance study about 54 g (33%) of the dietary K and 20 g (12%) of the infused K supplement were retained, assuming that faecal K excretion was never more than 2 g/day. It should be noted that no account has been taken of K lost from the body as suint, but it is unlikely that these losses differ widely between treatments or that they could affect the interpretation of our results.

The concentration of K in soft tissues is relatively constant and this factor is used in certain methods for determining body composition (Hansard, 1963). Since the total K content of the soft tissues of adult sheep is only 60–70 g (Field & Suttle, unpublished) it is inconceivable that appreciable quantities of supplementary K could be retained in these tissues without measurable increases in tissue mass. On the other hand, substitution for Na in the rumen on a chemical equivalent basis would account for about 20 g of the retained K. Increases in K concentration lower down the alimentary tract would account for a further small fraction of the retained K. Substitution of K for Na in the skeleton is possible although there is no experimental evidence for this. The fact that K, administered intravenously to cows, is rapidly and quantitatively excreted in the urine (Vogel, 1959; Anderson & Pickering, 1962) gives indirect support to the hypothesis that the supplementary K not excreted was retained largely in the gut.

The nature of the K salt used affected the metabolism of each element that was
Potassium intake and mineral metabolism

studied but the differences were quantitative rather than qualitative. The decreased faecal excretions of P and Na obtained with potassium acetate and the increased urinary P excretion obtained with KCl were significant effects, whereas those with the alternative salt were not. Since the intakes of most elements differed in the two experiments (see Table 1) some comparisons of the effects of the K salts have been made in terms of the percentage of the ingested mineral excreted in the urine and faeces before and after K supplementation in the same five sheep in Expts 1 and 2 (Table 6). It can be seen that potassium acetate produced a greater decrease in the urinary excretion of Mg and greater increases in the urinary excretions of Na and K and in the faecal excretion of Mg than did KCl \( (P < 0.05) \). Qualitative differences were found in that the two salts had opposite effects on urinary Ca excretion and whereas potassium acetate was without effect on mineral retention, KCl tended to reduce the retentions of P and Na and significantly increased K retention. Oyaert (1962) compared the effects of these two salts in a single sheep and found that potassium acetate produced a greater fall in urinary Mg output and a smaller increase in urinary Na output than KCl. The different effects of the two K salts on mineral metabolism may be due to the direct effects of the anions or to indirect effects, for example, through their influence on K metabolism or through changes in acid–base status, but little can be said about the possible nature of the anionic effect until more information is available.

Table 6. Percentage excretion of ingested minerals in urine and faeces by sheep given unsupplemented rations \((-K)\) or rations supplemented with potassium acetate \((\text{Expt 2})\) or potassium chloride \((\text{Expt 1, treatment KD}) \((+K)\)

<table>
<thead>
<tr>
<th>Excretory route</th>
<th>Mg</th>
<th>P</th>
<th>Na</th>
<th>K</th>
<th>Ca</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(\text{K salt} -K)</td>
<td>+K</td>
<td>-K</td>
<td>+K</td>
<td>-K</td>
</tr>
<tr>
<td>Urine</td>
<td>Acetate</td>
<td>22.7</td>
<td>8.4</td>
<td>36.0</td>
<td>49.7</td>
</tr>
<tr>
<td></td>
<td>Chloride</td>
<td>18.8</td>
<td>13.6</td>
<td>20.3</td>
<td>31.4</td>
</tr>
<tr>
<td>Faeces</td>
<td>Acetate</td>
<td>73.2</td>
<td>90.0</td>
<td>59.5</td>
<td>43.2</td>
</tr>
<tr>
<td></td>
<td>Chloride</td>
<td>58.4</td>
<td>65.0</td>
<td>63.7</td>
<td>54.8</td>
</tr>
</tbody>
</table>

The urinary excretion of K added to the diet as the acetate was similar to that of KCl given with water but was much greater than that of KCl added to the diet, with the result that the retention of K was much lower. These differences in urinary excretion and retention are almost certainly the result of temporary differences in the amounts of K retained in the gut. We have no explanation for the high plasma K concentrations recorded in sheep given potassium acetate. The increase of 28 mg/100 ml would, if true also for the extracellular fluids, represent a retention of 3 g K over the entire experimental period.

Kunkel, Burns & Camp (1953) and De Groot (1961) have found decreases in the concentrations of Mg in the serum of ruminants given K supplements, but the majority of workers have found no effect (Pearson et al. 1949; Eaton & Avampato, 1952; Daniel et al. 1952; Blaxter et al. 1960; Hendriks, 1962). We found a small decrease only with KCl added to the diet in Expt 1. Since Mg absorbed in excess of requirements is excreted rather than accumulated by mature ruminants, it follows that decreases in
the intake or absorption of Mg will be followed by decreases in Mg excretion rather than decreases in serum or tissue Mg concentrations. Effects of dietary K on serum Mg levels are most likely to be found when the absorbed Mg is approximately equal to or less than the requirement for Mg before supplementation. In our experiments the diets should have contained adequate Mg.

The treatments employed in these studies increased the intakes of K and water to levels similar to those experienced by sheep grazing lush spring pasture. It is interesting to compare the responses obtained with those recorded when the diet is changed from hay or hay plus concentrates to spring grass; this has been shown to decrease the urinary excretion (Field, 1961) and increase the faecal excretion (L'Estrange & Axford, 1966) of Mg, lower the serum Mg concentration (Care & Ross, 1963; Dobson, Scott & Bruce, 1966) and increase the excretion of Na (Dobson et al. 1966; L'Estrange & Axford, 1966). These responses are similar to those found when K was added to the diet. When K was given with 7.5 l. water, however, the urinary output of Mg was not affected. This discrepancy may be due to differences in the relative amounts or effectiveness of the K and water ingested in herbage or given as supplements. Alternatively, there may be further factors in spring herbage, such as the relatively low Mg and high nitrogen contents, which contribute to the lowering of the Mg contents of both the urine and the serum.

There are several aspects of the response to K supplementation which warrant further study, including the mechanisms by which K alters the partition of Mg and P between urine and faeces and by which a large temporary negative Na balance is produced. The effects of K loading in lactating ruminants might also yield useful information about the aetiology of hypomagnesaemic tetany.

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REFERENCES


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