Reviews on the mineral provision in ruminants (V): POTASSIUM METABOLISM AND REQUIREMENTS IN RUMINANTS

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PREFACE

In the Netherlands the ´Handleiding Mineralenonderzoek bij rundvee in de praktijk´[1] is a well-known publication that has been used already for decades as a guide to trace and treat mineral disorders in cattle. The fifth edition of this guidebook was published in 1996. The content of this publication was largely identical to that of the fourth edition (1990). Therefore the (independent) committee that is responsible for the contents of the guidebook (the 'Commissie Onderzoek Minerale Voeding'[2], COMV) decided in 2000 that a thorough revision was desired.
The committee was of the opinion that, if possible, the available scientific literature should be summarized and evaluated once again. Furthermore, attention should be paid to the mineral provision of categories of cattle other than dairy cattle, as well as to that of sheep and goats. Finally, the basic principles for the calculation of the mineral requirements should be described in a transparent way.

The intended revision was made possible as the Dutch 'Ministerie van Landbouw, Natuur en Voedselkwaliteit' (LNV), the 'Productschap Diervoeder' and the 'Productschap Zuivel'[3] were willing to subsidize this extensive and ambitious project.
The COMV decided to execute the project as follows.

- External experts, invited by the COMV, should summarize and evaluate the relevant literature in a so-called 'basal document' (with two exceptions to be written in English).
- Subsequently, these documents should be critically evaluated by the COMV.
- These basal documents should then be used to write and arrange the several chapters of the revised 'Handleiding'.

The revised 'Handleiding' is available (in the Dutch language) since October 2005, under the title 'Handleiding mineralenvoorziening rundvee, schapen en geiten.'[4] This book is published by the 'Centraal Veevoederbureau' (CVB; Central Bureau for Livestock Feeding) in Lelystad, as was also the case for the previous edition.

The COMV was of the opinion that the valuable basal documents, that became available during the course of this project, should be published too. By doing so everyone has the possibility to trace the basis for the text of the revised 'Handleiding'. The CVB was gladly willing to issue these documents as CVB Documentation reports. In connection with this the authors and the members of the COMV have disclaimed all rights and have assigned them to the Productschap Diervoeder, of which the CVB is one of the services.
For an overview of the CVB Documentation Reports that will appear in this context, you are referred to an Annex in the back of this report.

Utrecht/Lelystad, September 2005.

Professor dr. ir. A.C. Beynen	Dr. M.C. Blok
Chair of the COMV	Secretary of the COMV and Head of the CVB

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[1] Guidebook on mineral research for cattle in practice.
[2] Committee for research on mineral nutrition
[3] The Ministry for Agriculture, Nature and Food quality, the Product Board Animal Feed and the Dutch Dairy Board, respectively.
[4] Guidebook mineral provision cattle, sheep and goats.

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CONTENT

LIST OF ABBREVIATIONS

Abbreviation	Unit	Description
ARC		Agricultural Research Council (UK)
BW	kg	Body weight
$BW^{0,75}$ or $BW^{0,67}$		Metabolic body weight
CVB		Centraal Veevoederbureau (NL) (Central Bureau Livestock Feeding)
DLG		Deutsche Landwirtschaft Gesellschaft (G)
DM	kg	Dry matter
DMI	kg/day	Dry matter intake
ECF		Extracellular fluid
ha		Hectare
INRA		Institute National de la Recherche Agronomique (F)
L		Litre
mg		Milligram
MJ		Megajoules (= 10^6 Joules)
mmol		Millimoles
mm		Millimolair
NEl	MJ	Net Energy lactation (G)
NRC		National Research Council (USA)
SD		Standard deviation
Vol	L	Volume
Wt	Kg	Weight

1 PHYSIOLOGICAL FUNCTIONS OF POTASSIUM

In contrast to sodium (Na) and chlorine (Cl), which are the predominant extracellular ions, potassium (K) is the major cation of the intracellular fluid. The typical intra- and extracellular distribution of K (and Na) is regulated by Na/K-pumps which are vital for the generation and maintenance of membrane potentials. Consequently, K is intimately associated with muscle and nerve physiology (51). Furthermore, K is required in protein synthesis and cell growth (51) and also plays an important role in the maintenance of osmotic pressure and acid-base balance (28).

2 DISTRIBUTION OF POTASSIUM BETWEEN TISSUES

According to Houpt (30) 89% of the total body content of K is located within cells but Peterson (51) and Stanton and Koeppen (69) report a higher value, i.e. 98 %. About 75% of intracellular K is found in muscle (51). Small amounts of K are also found in bone and liver (8.8 and 7.3 % of total intracellular K, respectively). In contrast to the liver, K present in bone is not readily exchangeable with fluid compartments. The remaining amount of intracellular K is present in red blood cells (51). Typical K concentrations in extracellular fluid (ECF) are 4-5 mM in plasma and interstitial fluid, while intracellular concentrations are high; i.e. 150 mM (30, 51,60).

3 POTASSIUM METABOLISM

3.1 Absorption

3.1.1 Site of K absorption

From studies with cannulated cows and steers (Table 1) and sheep (Table 2), it can be calculated that in both ruminant species at least 70% of the ingested K is absorbed distal from either the abomasum or proximal duodenum. In contrast, the percentage of K (% of intake) absorbed proximal to either the abomasum or proximal duodenum appears to be different between the two ruminant species; i.e. 8.2 and 23.3 % of K intake in bovine and ovine, respectively. Apart from dietary origin, K also enters the rumen together with saliva. The mean K concentrations of bovine saliva from animals with an adequate provision of Na (salivary Na > 120 mmol/L), observed by Bailey and Balch (3), Kemp and Geurink (38), Rogers and Van't Klooster (58) and Schonewille et al. (64) ranges from 6 to 15 mmol/L, while Cook (8) reported a value of 8 mmol/L for ovine saliva. On the basis of data provided by Rogers and Van't Klooster (58), it was calculated that in dairy cows fed at a moderate level of K, salivary K was responsible for 18 % of the total K entrance into the rumen. Thus, with respect to the total amount of K potentially available for absorption, salivary K is quantitatively of minor importance. Furthermore, these authors (58) also showed that from the total amount of K which entered the rumen (ration and saliva) about 10% was absorbed in the rumen while the remaining K passed to the proximal and distal duodenum, indicating that K absorption from the omasum and duodenum is not important. This observation in dairy cows is substantiated by observations in sheep in that no significant K absorption occurred in the omasum and duodenum (68).
Thus, the main site of K absorption is located distal from either the abomasum or proximal duodenum and it appears that net absorption occurs both in the small and large intestines. Clearly, the small intestine is quantitatively the predominant site of K absorption in both ruminant species (Tables 1 and 2).

3.1.2 Mechanisms of K absorption

Currently, it is believed that K is passively absorbed in the rumen (19,50) and it was shown by Scott (65) that the process of K absorption responds in a linear fashion when the ruminal K concentration ranged from 10 to 110 mmol/L. This implicates that the negative influence of the K-induced increase of the transmural potential difference across the rumen wall (blood side positive) (21,43,44) is overruled by the increase of the chemical concentration gradient between rumen contents and blood (65).
With respect to the underlying mechanism(s) of post-ruminal K absorption, there appears to be no specific information available in ruminants. Therefore, the following paragraph contains information primarily obtained from general textbooks on physiology. Most of the ingested K is absorbed from the intestines by flowing down an electrochemical gradient (77). It is assumed that the absorption of K is secondary to the absorption of water which initially increases the K concentration of the chyme, thereby providing the driving force for passive K absorption (41, 51).
In the colon, both active K absorption and K secretion seems to be possible. The uptake of K and Cl from blood is mediated by an Na-2Cl-K co-transporter located in the basolateral membrane, which is followed by extrusion of these ions into the lumen through specific K and Cl channels located in the apical membrane (51). In the distal colon, active K absorption may occur in parallel with the secretion of hydrogen ions through an H/K ATPase exchanger

Table 1: Flow of potassium along the gastro-intestinal tract of bovine

Reference	Species	Body weight (kg)	n	K-intake (g/day)	K-intake + saliva- K (g)	Rumen (g)	Abomasum (g)	Proximal duodenum (g)	Terminal ileum (g)	Faeces (g)
(58)	cow	441	2	224.7	275.6	248.6		253.5	92.2	25.4
(56)	cow	615	5	322.9				291.4		68.6
			5	322.6				285.0		77.3
			5	322.0				275.2		71.5
			5	339.0				311.2		79.6
			5	316.2				273.2		73.3
(40)	cow	648	8	360.3				270.0		40.8
			8	271.2				243.8		46.2
			8	200.0				218.1		34.7
			8	245.7				250.7		64.1
(25)	steers	261	6	18.7			24.5		11.5	4.0
			6	82.5			44.7		15.7	4.5
			6	170.2			94.6		17.9	4.6

Table 2: Flow of potassium along the gastro-intestinal tract of sheep

Reference	Body weight (kg)	n	K-intake (g/day)	K-intake + saliva-K (g)	Rumen (g)	Abomasum (g)	Proximal duodenum (g)	Terminal ileum (g)	Faeces (g)
(52)	adult	2	19.2				16.1	4.1	1.4
		2	19.2				16.8	2.6	1.1
		2	19.2				20.1	2.0	1.7
(55)	42	6	22.8		5.7	6.6		3.4	1.3
		6	59.4		7.7	9.2		5.3	1.1
(26)	36	6	5.5			6.2		1.4	0.8
		6	18.12			10.6		1.4	0.7
		6	35.9			18.1		2.1	1.0
(24)	41	Not given	15.7				12.8	1.4	0.4
			25.2				19.9	3.1	0.8
			19.6				14.6	1.0	0.1
			31.3				35.3	7.1	2.1
			24.8				13.8	1.4	0.9
			39.6				21.1	2.1	1.9
(79)	29	6	4.3			6.5		1.1	0.7

Table 3: Apparent K absorption in bovine species fed various rations

Reference	Species	BW[1]/ Milk (kg) / (kg/day)	n	Ration			K-intake[2] (g/day)	K-content ration (g/kg DM)	Apparent absorption (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[3])			
(56)	cow	615[4] / 20.0	5	40% alfalfa hay(lage), 20% corn silage	grain-based	40%	323	18.6	78.8[5] (grab)
(40)	cow	648[4]/ 27.7	8	alfalfa silage	grain-based	50%	360	18.4	88.7[5] (grab)
			8	barley silage	grain-based	50%	271	14.6	83.0 (grab)
			8	oat silage	grain-based	50%	200	12.0	82.7 (grab)
			8	triticale silage	grain-based	50%	246	14.3	73.9 (grab)
(67)	cow	654 / dry	6	wheat hay		100%	105	14.6	85.3[6] (tot)
		550 / 39.4	6	9.2% vetch hay, 25.6% corn silage	grain-based	35%	126	7.5	81.0 (tot)
		550 / 41.5	6	9.2% vetch hay, 25.6% corn silage	grain-based	35%	186	8.4	74.8 (tot)
(66)	cow	683 / dry	5	wheat silage[8]		100%	145	18.2	89.6 (tot)
		565 / 34.1	5	wheat silage	grain-based + cottonseed	33%	162	11.4	90.8 (tot)
		549 / 31.4	5	wheat silage	grain-based + cottonseed	33%	176	11.6	96.9 (tot)
(58)	cow	440 / 11	2	various rations			225	18.6	88.7 (tot)
(14)	cow	514 / 23.2	18	50% corn silage, 10 % haylage	soybean-based	60%	320	19.1	92.6 (tot)
		518 / 23.4	18	alfalfa hay(lage)	soybean/ear corn-based	55%	356	21.4	81.4 (tot)
(13)	cow	496 / 19.5	18	alfalfa hay(lage)	grain/soybean-based	51%	185	11.4	92.4 (tot)
		477 / 18.3	18	alfalfa hay(lage)	grain/soybean-based	51%	172	11.3	93.1 (tot)
		523 / 18.9	18	alfalfa hay(age)	grain/soybean-based	49%	257	15.1	94.7 (tot)
		514 / 18.2	18	alfalfa hay(lage)	grain/soybean-based	49%	218	14.0	94.3 (tot)
		603 / 15.3	18	alfalfa hay(lage)	grain/soybean-based	56%	302	17.0	94.2 (tot)
		596 / 14.9	18	alfalfa hay(lage)	grain/soybean-based	56%	282	16.8	94.2 (tot)
(12)	cow	723 / dry	11	30% timothy hay, 70% alfalfa hay		100%	280	27.5	95.3 (tot)
		720 / dry	10	30% timothy hay, 70% alfalfa hay		100%	236	23.4	94.0 (tot)

Table 3: (continued)

Reference	Species	BW[1]/ Milk (kg) / (kg/day)	n	Ration			K-intake[2] (g/day)	K-content ration (g/kg DM)	Apparent absorption (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[3])			
(25)	steer	261	6	orchard grass hay	concentrate	40%	15	4.4	74.0 (tot)
			6	orchard grass hay	concentrate + $KHCO_3$	40%	76	21.7	93.7 (tot)
			6	orchard grass hay	concentrate + $KHCO_3$	40%	170	48.4	96.8 (tot)
(63)	cow	671 / dry	6	artificially dried grass	concentrate	86%	168	25.8	94.9 (tot)
			6	artificially dried grass	concentrate	85%	274	42.8	96.0 (tot)
			6	artificially dried grass	concentrate + $KHCO_3$	83%	290	43.2	95.9 (tot)

[1] BW = Body Weight
[2] K intake from total ration.
[3] DM = Dry Matter
[4] Pooled data, data of separate experimental treatments were not given
[5] grab: Calculated on the basis of an indigestible marker (faecal grab samples)
[6] tot : Calculated on the basis of total faeces collection

(41). Whether absorption or secretion of K occurs in the colon is primarily determined by the K concentration of the chyme (41). However, the data listed in Tables 1 and 2 suggest that there is no net K secretion in the large intestines of ruminants because the faecal excretion of K is systematically lower than the flow of K measured in the terminal ileum.

3.1.3 K absorption in relation to K source

Data from balance trials with bovine and ovine species are presented in Table 3 and 4, respectively. The overall apparent K absorption, expressed as a % of intake, was found to be 89.0% (SD $\pm$ 7.4, n = 27) in bovine and 92.8% (SD $\pm$ 5.0, n = 37) in ovine species. Furthermore, on the basis of the presented data, it is difficult to see that there are systematic differences in K absorption between the different rations/feeds. On the basis of the data provided by Schonewille et al. (63), Greene et al. (25,26) the fractional absorption of K from $KHCO_3$ can be calculated; i.e. (Δ apparent K absorption / Δ K intake) x 100% and a mean value of 99.0% was found. Likewise, the fractional absorption of K from KCl and K-acetate was found to be 97.6 % and 96.2%, respectively (71). Since apparent absorption of K is considered to be a valid index of the bioavailability of K, it can be concluded that both intrinsic K present in feedstuffs and that in inorganic K-salts have a high bioavailability (29).

3.2 Excretion

With respect to K, the primary subject of regulation is the K concentration of the extracellular fluid (ECF).

After the ingestion of a K rich ration, K is readily absorbed and the amount absorbed may potentially increase plasma K concentration to life threatening levels. Renal excretion of excessive K is relatively slow, and the short-term increase in plasma K concentration is prevented by K uptake of body cells. Several hormones such as epinephrine, insulin and aldosterone, promote the cellular uptake of K by the liver and muscles, and it is currently believed that insulin, at least in humans, is the most important hormone that shifts extracellular K into cells after the ingestion of K so as to prevent hyperkalemia (69). The underlying mechanism might be that increased levels of insulin activate its receptors, which promote Na/K ATPase activity (51).

Excess of absorbed K is primarily excreted by the kidneys (51) so as to maintain plasma K concentration within a narrow range, despite large variations in K intake (25, 26,79). The amount of nonfilterable K in plasma can be ignored because K is not bound to plasma proteins (69). Thus, nearly all plasma K is filtered in Bowman's capsule (30, 51). Approximately 95% of the filtered load is reabsorbed in the proximal tubule and by the thick ascending limb. Then, K is secreted into the lumen by cells located in the distal tubule and collecting ducts. Thus under normal conditions (K intake > K requirement) urinary K excretion is primarily determined by K secretion into the lumen along the distal tubule and collecting ducts (30, 51, 69). The major physiological regulators of K secretion are the plasma and/or extracellular K concentrations and aldosterone (30,53, 69). An increase of the plasma K concentration stimulates the activity of Na/K ATPase located in the basolateral membrane of tubular cells (30) which increases the flow of K into the tubular cells, thereby providing a powerful driving force for K extrusion into the tubular lumen (30, 51, 69). When animals become hyperkalemic, aldosterone is released from the adrenal cortex, thereby stimulating urinary excretion of K. Thus, the aldosterone mediated stimulation of urinary K excretion may be considered as a "safety valve" so as to control plasma K concentration (53). The aldosterone induced kaliuretic effect is secondary to the stimulation of tubular Na reabsorption (30). Aldosterone increases the Na and K conductance of the luminal membrane by activation of the existing Na and K channels (51). Furthermore, aldosterone increases the activity and amount (69) of basolateral Na/K ATPase pumps. Consequently, the combination of these aldosterone induced actions lead to an increase of K secretion into the tubular lumen. It must be noted that the underlying mechanisms to explain K secretion implicate that this is only possible when Na becomes reabsorbed (51). Apart to secretion, also K reabsorption can occur in the distal tubule and collecting ducts, but in contrast to the mechanism of K secretion the cellular pathways and mechanisms of K reabsorption at this site of the nephron are not completely understood (69). Finally, the mammalian kidney is very efficient in excreting K but rather inefficient in conserving it. Indeed, the kidneys are not able to reduce K excretion to the same extend as Na (69). However, under practical conditions the K conserving capacity of the kidney is of minor importance (30).

Apart from urinary and faecal K excretion, K can also be excreted with sweat since K is the most important cation in sweat of ruminant species (74); i.e. approximate values range from 100 to 160 mmol K/L sweat, irrespective of the ruminant species involved (6). Thus, when heat stress occurs, this route of K excretion may be important, but quantitative information is limited.

Table 4: Apparent K absorption in ovine fed various rations

Reference	Species	BW[1] (kg)	n	Ration			K-intake[2] (g/day)	K-content ration[3] (g/kg DM)	Apparent absorption (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[4])			
(55)	wethers	42	6	orchard grass hay		100%	22.8	31.4	94.5 [5](tot)
		42	6	orchard grass hay	100 g $KHCO_3$ in rumen	100%	59.4	31.4	97.9 (tot)
(24)	sheep	41[6]	NG[7]	ryegrass		100%	15.7	28.5	97.5 (tot)
			NG	ryegrass		100%	25.2	28.6	96.8
			NG	short rotation ryegrass		100%	19.6	35.6	99.5
			NG	short rotation ryegrass		100%	31.3	35.6	93.3
			NG	clover		100%	24.8	45.1	96.4
			NG	clover		100%	39.6	45.0	95.2
(52)	sheep	adult	2	hay		100%	19.2	25.8	93.0 [8](grab)
			2	hay	barley + KCl (4.4 g K)	68%	19.2	26.0	94.2
			2	hay	barley + KCl (9.8 g K)	34%	19.2	25.4	91.1
(26)	wethers	36	6		Corn-based, low K	0%	4.7	6.5	91.8 (tot)
			6		Corn-based, +medium $KHCO_3$	0%	16.4	22.9	97.8
			6		Corn-based, + high $KHCO_3$	0%	33.7	47.2	98.5

Table 4: (continued)

Reference	Species	BW[1] (kg)	n	Ration			K-intake[2] (g/day)	K-content ration[3] (g/kg DM)	Apparent absorption (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[4])			
(23)	ewes	39.8	8	Lucerne	oat chaff	12%	4.4	6.1	89 (tot)
			8	Lucerne	oat chaff + 11.5 g Na infused[9]	12%	4.4	6.1	95
			8	Lucerne	oat chaff + 17.3 g Na infused	12%	4.4	6.1	90
			8	Lucerne	oat chaff + 23.0 g Na infused	12%	4.4	6.1	90
			8	Lucerne	oat chaff + 28.8 g Na infused	12%	4.4	6.1	89
			8	Lucerne	oat chaff + 34.5 g Na infused	12%	4.4	6.1	88
			8	Lucerne	oat chaff + 46.0 g Na infused	12%	4.4	6.1	85
(71)	sheep	55	8	Chopped hay	concentrate	30%	9.5	11.1	91.2 (tot)
			8	Chopped hay	concentrate + KCl in diet	30%	36.1	42.2	95.9
			8	Chopped hay	concentrate + water	30%	9.5	11.1	89.8
			8	Chopped hay	concentrate + KCl infused[10]	30%	37.0	43.3	94.9
			5	Chopped hay	concentrate	30%	7.5	8.7	81.5
			5	Chopped hay	concentrate + KAc	30%	37.0	42.9	93.2
(27)	wether	69	4	orchard grass hay		100%	25.0	21.1	98.2 (tot)
			4	orchard grass hay		100%	21.0	16.9	98.3
			4	Brome grass hay		100%	11.3	9.4	95.9

Table 4: (continued)

Reference	Species	BW[1] (kg)	n	Ration			K-intake[2] (g/day)	K-content ration[3] (g/kg DM)	Apparent absorption (% of intake)
				Type of Roughage	Type of Concentrates	Proportion of roughage (% of total DM[4])			
(79)	wethers	29	3	orchard grass hay	Corn-based	10%	4.5	6.4	88.9 (tot)
			3	orchard grass hay	Corn-based + $KHCO_3$, rumen[11]	10%	39.2	6.4	97.7
			3	orchard grass hay	Corn-based + $KHCO_3$, abomasum[11]	10%	16.9	6.4	96.3
			3	orchard grass hay	Corn-based +$KHCO_3$, ileum[11]	10%	16.2	6.4	93.4

[1] BW = Body Weight.
[2] K intake from ration and non-orally supplemented K, if any.
[3] K concentration of ration alone. Thus, without the K supplemented non-oraly.
[4] DM = Dry Matter.
[5] tot : Calculated on the basis of total faeces collection.
[6] Pooled data, data of separate experimental treatments were not given.
[7] NG = Not Given.
[8] grab : Calculated on the basis of an indigestible marker (faecal grab samples).
[9]. Na infused intraruminally in the form of NaCl.
[10] K infused intraruminally in the form of KCl.
[11] K infused into different sites of the gastro-intestinal tract in the form of $KHCO_3$.

4 POTASSIUM REQUIREMENTS

Theoretically, the minimum net requirement of K for maintenance is the amount of K required to compensate the inevitable K losses by the animal; i.e. the inevitable faecal, urinary and dermal (hair, sweat) losses. However, the concept of an inevitable faecal loss of K strictly of endogenous origin is not applicable because under various conditions there might be substantial interchange between K in the gut and that in the body. Indeed, according to the ARC (2) faecal K losses are poorly correlated with K intake. Apart from maintenance, the daily requirement of K is also determined by the amount of K retained by the gravid uterus and/or growth or the amount of K that is associated with milk production. In the following sections, the estimates of the previously mentioned factors used by different councils for dairy cows, beef cattle, sheep and goats are listed and commented when appropriate. Because the Dutch CVB (7) does not provide factorial estimates so as to calculate the K requirements, tentative factorial estimates for dairy cows and other ruminant species are proposed in the following sections.

4.1 Dairy cows

4.1.1 Maintenance

According to the ARC faecal K losses are related to dry matter intake and they were estimated to be 2.6 g K for each kg dry matter ingested (Table 5), which is the overall weighted mean from 6 studies (estimates ranged from 1.2 to 3.4 g K/kg dry matter) (2). A value of 4.1 g K/kg faecal water was adapted by the DLG as an estimate for the faecal K losses (Table 5). Unfortunately, the DLG (18) does not provide any information about minimum K concentrations of faecal water, but a value of 4.1 g K/L faecal water seems to overestimate the faecal K losses because the mean K concentrations in faecal water reported by Van' Klooster (75), Van Weerden (76), and Renkema et al. (57), were about 3 times lower; i.e. 1.5, 1.3 and 1.0 g K/L respectively. Indeed, when a digestibility of the dry matter of 65% is assumed (a value corresponding to a NEl of 5.2 MJ/kg DM (=equivalent to 750 VEM) and a dry matter content of faeces of 15%, each kg of dry matter ingested yields 2 kg of fecal water. Consequently, the faecal K losses are calculated to be 8.2 g K/kg DM ingested when a value of 4.1 g K/L faecal water is used. This value is about three times higher than the estimate set by the ARC. Thus, it seems that a faecal water content of about 1.3 g K/L corresponds with a faecal output of 2.6 g K for each kg dry matter ingested.
A value of 2.6 g K/kg DMI to estimate the maintenance requirement for K has also been adapted by the NRC for non-lactating cows (Table 5) and they refer for this value to the INRA (33). However, the INRA does not mention a value of 2.6 g K/kg DMI but they estimate that total K loss is equal to 70 mg/kg BW (Table 5) and surprisingly, they cite the ARC (2). On the basis of observational studies (15,16,20,62), the NRC stated that 2.6 g/kg DMI as the maintenance requirement for K is too low for optimum feed intake and milk yield. Therefore, an empirical value of 6.1 g/kg DMI was set as the net maintenance requirement of K for lactating cows (Table 5). Thus, the difference in maintenance requirement of K between lactating and non-lactating cows as suggested by the NRC (Table 5) is based on empirical rather than scientific grounds. Therefore, it seems without doubt that more research is needed so as to properly estimate the maintenance requirement of K under various physiological conditions (49). With respect to the inevitable urinary losses of K, the ARC and NRC adapted a similar value; i.e. 37.5 and 38 mg/kg BW, respectively. Furthermore, the estimates of inevitable dermal K losses (sweat, skin) set by the ARC and

Table 5: Summary of estimates of endogenous K losses expressed in mg/kg BW, unless otherwise noted.

	Endogenous/inevitable losses			
	Dermal/Sweat	**Faecal**	**Urine**	**Total**
Dairy cows				
CVB (7)	not given	not given	not given	not given
ARC (2)	0.4[1]	2.6 g/kg DMI[2]	37.5	37.9 + 2.6 g/kg DMI
DLG (18)	not given	not given	not given	4.1 g/kg faecal water[3]
NRC (49)				
non-lactating	0.4- 4.0[4]	2.6 g/kg DMI	38	42 + 2.6 g/kg DMI
lactating	0.4- 4.0	6.1 g/kg DMI	38	42 + 6.1 g/kg DMI
INRA (33)	not given	not given	not given	70
Beef cattle				
CVB (7)	not given	not given	not given	not given
ARC (2)	0.40[1]	2.6 g/kg DMI	37.5	37.9 + 2.6 g/kg DMI
DLG (17)	not given	not given	not given	not given
NRC (48)	not given	not given	not given	not given
INRA (33)	not given	not given	not given	70
Sheep				
CVB (7)	not given	not given	not given	not given
ARC (2)	negligible	1.0 g/kg DMI	37.5	37.5 + 1.0 g/kg DMI
NRC (47)	not given	not given	not given	not given
INRA (33)	not given	not given	not given	50
Goats				
CVB (7)	not given	not given	not given	not given
ARC (2)	not given	not given	not given	not given
NRC (46)	not given	not given	not given	not given
INRA (33)	not given	not given	not given	not given
Kessler (39)	not given	not given	not given	50

[1] Temperate conditions (no further specifications).
[2] DMI = Dry Matter Intake
[3] Calculated on the assumption that faecal water contains 105 mmol K/L.
[4] At temperatures between 25-30 °C, 0.4 mg K/kg BW is considered as part of maintenance while a value of 4.0 mg/kg BW was taken when temperatures are > 30 °C. The latter value is used so as to calculate K requirement for maintenance.

NRC are the same for temperate conditions (Table 5), i.e 0.4 mg/kg BW. The ARC (2) does not specify "temperate conditions", but the NRC (49) mentions that additional K should be provided when environmental temperatures are higher than 30 °C so as to compensate for the increased K losses by sweat. Mallonee et al. (42), measured the rate of K excretion with sweat during three, 2 h intervals, and they reported values of 16.7 (9:00-11:00 h, 45 °C), 46.7 (13:00-15:00 h, 50 °C) and 8.1 mg K/m^2 per h (20:00-22:00 h, 24 °C) (relative humidity was not reported). Cows exposed to maximum environmental temperatures of 37 °C had a maximum rate of K excretion of 9.6 mg K/m^2 per h. Assuming that the surface area of cows with a BW of 650 kg, is about 6.9 m^2 (Surface area = 0.09 x $BW^{0.67}$; (59)) maximum K excretion rates are 1.0 mg/kg BW (2 h at 50 °C) and 0.2 mg/kg BW (2 h at 37 °C). Thus, when environmental temperatures do not exceed 37 °C, we arbitrarily suggest to adapt the ARC (2) values for estimating the maintenance requirements for K in dairy cows; i.e. 2.6 g K/kg DMI (faecal losses) + 38 mg/kg BW (inevitable urinary losses together with dermal losses).

4.1.2 Pregnancy

The net requirement for pregnancy set by the ARC (Table 6) was calculated on the basis of following formula :

K content of foetus and adnexa (g) = 0.025 x Birth weight x $10^{4.441 - 5.687*(EXP(-0.00312*D))}$

D = days from conception in the range of 141 to 281 (=parturition)

Assuming a birth weight of 44 kg, K retention in foetus and adnexa was calculated to be 1.1 and 1.8 g/day during the 8th and 9th month of gestation, respectively. The net requirement for pregnancy set by the NRC (Table 6) is derived from slaughter experiments of House and Bell (31). They reported a K accretion rate of 1.0 g/day between 190 and 270 days after conception, which is almost the same value obtained on the basis of the formula provided by the ARC (2), i.e. 1.07 g/day. Thus, the formula provided by the ARC (2) appears to accurately predict K accretion rate of the gravid uterus. The net requirements for pregnancy set by the DLG (18) are lower than those estimated by the ARC (2) which may be explained by the fact that the German estimates for K accretion rate in foetus and adnexa are based on beef cattle delivering calves with a lower birth weight (18). The net K requirement for pregnancy provided by INRA (33) is somewhat lower than that estimated on the basis of the formula provided by the ARC for the last 12 weeks of pregnancy. This discrepancy cannot easily be explained since the value provided by INRA (33) seems to be arbitrarily adapted. The accretion rate of K during pregnancy seems to be properly predicted by the formula provided by the ARC (2). Thus, it is decided to use the formula of the ARC to calculate the K requirement of the gravid uterus during the dry period.

4.1.3 Growth

The value adapted by the NRC (49) as the K requirement for growth is in the range from 150 to 500 kg BW, and has been taken from INRA (33), although the latter indicates a range in BW from 150 to 600 kg (Table 6). Both councils (33, 49) do not provide any further information. The K requirement for growth was set on 2.0 g/kg growth by the ARC (2) and is based on the body K content of castrated beef Shorthorn and Hereford males or German black pied steers. The latter value corresponds well with the estimated K requirement for growth provided by the DLG (18), who based their estimate also on whole body K contents of young steers (no further information). Thus, it is suggested to adapt a value of 2.0 g/kg growth as the estimate for K requirement for growth for replacement heifers ranging from 100 to 500 kg of BW. According to the ARC (2) this value is probably too high for animals with a BW greater than 500 kg and it is has been suggested by the NRC and INRA (33, 49) to adopt the value of 1.6 g K/kg growth for the heavier animals.

Table 6: Summary of estimates of net K requirements for fetal retention, growth and milk.

	Gravid uterus (g/d)	Growth (g/kg gain)	Milk (g/L)
Dairy Cows			
CVB (7)	not given	not given	not given
ARC (2)	1.8[1] (8-4 weeks ante partum) 1.1[1] (4-0 weeks ante partum)	2.0 (75-500 kg BW)[2]	1.58[3]
DLG (18)	0.6 (6-4 weeks ante partum) 0.8 (3-0 weeks ante partum)	1.9	1.5
NRC (49)	1.0 (190-270 days of gestation)	1.6 (150-500 kg BW)	1.5
INRA (33)	1.0 (12 weeks ante partum)	1.6 (150-600 kg BW)	1.6-2.0
Beef Cattle			
CVB (7)	not given	not given	not given
ARC (2)	not given	2.0[2]	not given
DLG (17)	not given	not given	not given
NRC (48)	not given	not given	1.5
INRA (33)	not given	1.6 (150-600 kg BW)	not given
Sheep[4]			
CVB (7)	not given	not given	not given
ARC (2)	0.24 (9-5 weeks ante partum)[5] 0.21 (4-0 weeks ante partum)[5]	1.8 (4-45 kg BW)	1.4
NRC (47)	not given	not given	1.5
INRA (33)	0.2 (6 weeks ante partum)	1.8 (10-50 kg)	not given
Goats			
CVB (7)	not given	not given	not given
ARC (2)	not given	not given	not given
NRC (46)	not given	not given	not given
INRA (33)	0.2 (6 weeks ante partum)	not given	not given
Kessler (39)	[6]	2.4 (birth-31 kg) 0.4 (32 - 39 kg)	2.1 (Saanen/Alpine breeds) 1.7 (African/Asian breeds)

[1] Calf with birth weight of 44 kg.
[2] Values obtained from castrated Beef-Shorthorn/Hereford steers and German Black Pied steers
[3] British Friesian cows
[4] K accretion due to wool production range from 50 to 200 mg/day at growing rates from 2.7-11.0 g/day (2).
[5] Total birth weight of 8 kg
[6] Accretion of K during pregnancy is not given, but the K content of goat foetus is estimated to be 2.1 g K/kg foetus at term.

4.1.4 Milk production

The estimated K concentration in milk as provided by the several councils, varies from 1.5 to 2.0 g/L (Table 6). Furthermore, the combined overall mean K content of milk, taken from 10 studies (1,9,13,14, 15,22, 58,61,66,67), was 1.6 g K/L. The mean of all values referring to the K content of milk, reported in this section is 1.5 g K/L, and it is suggested to adapt this value for calculating the K requirement due to milk production.

4.2 Beef cattle

4.2.1 Maintenance

The maintenance requirements set by the ARC and INRA for beef cattle are similar to those of dairy cattle (Table 5). The other councils (Table 5) do not provide estimates with respect to the maintenance requirement of K in beef cattle. Because both the ARC (2) and INRA (33) do not distinguish between dairy cows and beef cattle in their approach for estimating the K requirement for maintenance, we consider it opportune to do the same. Thus, we suggest to adapt the following values in order to calculate the maintenance requirement of K in beef cattle; i.e. 2.6 g K/kg DMI (faecal losses) + 38 mg/kg BW (inevitable urinary losses together with dermal losses).

4.2.2 Pregnancy, growth and milk production

Specific factorial estimates with respect to pregnancy and growth are not given by any of the listed councils (Table 6). However, the K requirements for growth provided by the ARC are based on observations in beef cattle (see section about dairy cows). Therefore, we suggest to apply the values used for dairy cows also in beef cattle; i.e. 2.0 and 1.6 g K/kg growth for beef cattle ranging from 75 to 500 and > 500 kg BW, respectively. According to the NRC (48) the K content of milk (suckling cows) is 1.5 g/L. The other councils do not mention a specific K content of milk from suckling cows. In contrast to Na, the NRC (48) does not provide a recommendation with respect to the dietary K concentration in rations for beef cattle.

4.3 Sheep

4.3.1 Maintenance

The estimates for the faecal losses of K set by the ARC (2) are estimated to be 1.0 g/kg DMI (Table 5), which is based on the observations from 2 studies. The inevitable dermal and urinary losses are estimated to be similar to cattle; i.e. 0.4 and 37.5 mg/kg BW, respectively. The total net maintenance requirement for K set by INRA is calculated to be 50 mg/kg BW, which is based on the observation from 1 study (Table 5). The estimate of the inevitable urinary K losses set by the ARC (2) is derived from balance studies with bullocks. However, it can be estimated on the basis of data provided by Cowen and Philips (10) that the obligatory urinary K losses are 10.4 mg/kg BW, which suggests that the ARC (2) estimate may be too high. However, in contrast to a similar overestimation of the inevitable urinary Na losses by the ARC (2), both Todd (72) and Underwood and Suttle (74) do not mention that obligatory urinary K losses are overestimated by the ARC (2). Therefore, we considered it opportune to adapt a value of 37.5 mg K/kg BW as the estimate of the endogenous urinary K losses. Thus, we suggest that the K requirement for maintenance of sheep can be estimated as follows: 1.0 g K/kg DMI (faecal losses) + 37.5 mg/kg BW (inevitable urinary K loss).

4.3.2 Pregnancy

The net requirement for pregnancy set by the ARC (Table 6) was calculated on the basis of following formula :

$$\text{K content of foetus and adnexa (g)} = 0.25 \times \text{Birth weight} \times 10^{1.143 - 5.255*(EXP(-0.0245*D))}$$

D = days from conception in the range of 63 to 147 (=parturition)

Assuming a total birth weight of 8 kg, K retention in foetus and adnexa was calculated to be 0.24 and 0.21 g/day during 9 to 5 weeks and 4-0 weeks before parturition respectively. The net K requirement for pregnancy provided by INRA (33) is similar to the value that can be estimated on the basis of the formula provided by the ARC for the last 6 weeks of pregnancy; i.e. 0.22 g/day. Thus, we suggest to adapt the formula provided by the ARC (2) to estimate the K requirement of the gravid uterus during gestation.

4.3.3 Growth and milk production

With respect to the net requirement of K for growth and milk production, there are no remarkable differences between the ARC and INRA (Table 6). Therefore, we suggest to adapt a value of 1.8 g/kg growth for sheep with BW ranging from 4 to 50 kg and a value of 1.5 g K/kg of milk. The NRC (47) gives no factorial estimates with respect to the net K requirement of sheep but recommend a dietary K concentration of 5-8 g/kg dm for sheep.

4.4 Goats

4.4.1 Maintenance

Estimates about the inevitable K losses in goats are not known/provided (Table 5), but a value of 50 mg/kg BW was adapted by Kessler (39). However, since goats resemble cattle in terms of their digestive physiology, we suggest that the approach to calculate the net maintenance requirements of K in goats can be similar to that of cattle. Thus, the following values are suggested in order to calculate the maintenance requirement of K in goats; i.e. 2.6 g K/kg DMI (faecal losses) + 38 mg/kg BW (inevitable urinary losses together with dermal losses).

4.4.2 Pregnancy, growth and milk production

A specific factorial estimate for goats with respect to the requirement for growth is only provided by Kessler (39) but the origin of this, relative high, value is not clear. Therefore, it was arbitrarily decided to adapt a value similar to that of cattle; i.e. 2 g of K/kg growth. Furthermore, Kessler (39) uses a value of 2.1 g K/kg foetus as the net requirement for pregnancy. However, it appears that this value represents the K content of newborn goat kids (39), which is obviously not the same as the K accretion rate (g/d) during pregnancy. According to the INRA (33), K accretion rate during pregnancy in goats is similar to that of sheep (Table 6). Therefore, we suggest to use the formula for sheep set by the ARC (section 4.3.2.) to calculate the net K requirement for pregnancy. For Saanen/Alpine breeds, the K content of milk was estimated by Kessler (39) to be 2.1 g/L, which is similar to value reported by Jenness (34); i.e. a mean value of 1.9 for Saanen, Toggenburg and Alpine goats (reported range was 1.6-2.4 g K/L). Stelwagen et al. (70) reported K concentrations ranging from 2.0 to 2.3 g/L in Saanen goats. Thus, we suggest to adapt a value of 2.1 g K/L so as to calculate the K requirement for milk production in dairy goats. The NRC (46) does not provide factorial estimates with respect to the net K requirements of goats (Angora, dairy- and meat goats) but they consider 5 and 8 g K/kg DM as a minimum dietary requirement for growing and lactating goats, respectively.

4.5 Coefficient of absorption

As far as we know, no data are available on the basis of the radio-isotope technique with K to asses the efficiency of true absorption of K. Indications about the coefficient of K absorption are provided by the DLG, NRC, INRA and Kessler (Table 7) and only the NRC (49) value is based on experimental data in which apparent K absorption was measured. A value of 80% as the true absorption coefficient of K, as suggested by INRA (33), seems too low in the light of the data presented in Tables 3 and 4. Overall apparent K absorption (% of intake) was calculated to be 89.0 % and 93.5% in bovine and ovine, respectively (Tables 3 and 4). However, it was already mentioned that the concept of an inevitable faecal loss of K strictly of endogenous origin is not applicable because there may be substantial interchange between K in the gut contents and that in the body. Therefore, the total faecal K excretion was estimated in the previous section, in relation to dry matter intake. This approach implicates that the maintenance requirement of K is equal to the amount of K excreted with faeces and the minimum amounts excreted with urine and sweat. In pregnant, growing and lactating animals, K-intake is calculated by raising the maintenance requirement of K with appropriate amounts of K; i.e. the amount retained due to pregnancy or growth and/or associated with milk production. It is clear that with this method of calculation, neither the apparent nor the true absorption coefficient K is necessary so as to calculate K requirements.
Finally, the current proposal with respect to the faecal K losses is probably higher than the minimum faecal K loss estimated on the basis of minimum K loss with faecal water. However, it seems that there are not enough data available in literature to establish a reliable quantitative relationship between dry matter intake, K- and Na intake and the amount of K excreted in faeces.

Table 7: Summary of estimates for the coefficient of K absorption (% of intake)

	apparent absorption	**true absorption**	**nature of absorption not specified**
CVB (7)	not given		
ARC (2)	not given		
DLG (18)		95	
DLG (17)	not given		
NRC (49)	90		
INRA (33)		80	
Kessler (39)		90	

4.6 K allowances

In was already mentioned (sections 4.1.4 and 4.4.2) that the reported K contents in milk varies considerably. Therefore, it was considered opportune to incorporate a safety margin of 1.3 in order to calculate the K allowance for lactating animals so as to ensure sufficient K supply in lactating cows, sheep and goats with a high K concentration in milk.

5 POTASSIUM DEFICIENCY

The clinical signs of K deficiency are not well documented, but reduced appetite, poor growth, muscular weakness, stiffness paralysis and intracellular acidosis are reported (74). In lactating cows fed rations containing < 1.5 versus 8 g K/kg of DM, severe anorexia developed together with a drop in milk yield, pica and a loss of coat condition (less pliable) (74). Dennis and Hemken (15) fed mid-lactation HF-cows rations containing 4.6, 6.9 and 9.7 g K/kg of DM and it was found that 6.9 versus 4.6 g K/kg of DM improved feed intake and milk yield. In another feeding trial from the same group (15) early lactating cows were fed rations containing either 5.1, 7.5 or 9.9 g K/kg of DM and only feed intake was significantly affected when the dietary K content was increased from 5.1 to 7.5 g/kg of DM. In both the early- and mid-lactation cows plasma K was unaffected (15). The observations of Dennis and Hemken (15) are corroborated by that of Daniels et al. (11) in that a dietary K content of 8 g/kg DM appears to sustain milk production. In both steers and sheep, the feeding of rations containing 6 g K/kg of DM was associated with an urinary K excretion of at least 50% of K intake (25, 26) which implies that K intake was adequate in both animal species. Finally, on the basis of feeding trials with dairy calves fed rations with varying K contents (73,78), it was concluded that the dietary requirement of K apparently lies in the range of 3.4 to 5.5 g/kg of DM. Apart from the reference cited in Underwood and Suttle (74), no specific signs of K deficiency were reported in any of the above mentioned feeding trials. In practice, K deficiency is unlikely to occur because of the ample supply of K from most feedstuffs (74). Therefore, it is not meaningful to discuss dietary interventions so as to prevent K deficiency.

6 POTASSIUM INTOXICATION

Potassium intoxication is unlikely to occur under practical feeding conditions (49) and it is illustrative that K intoxication is not even mentioned both by the ARC (2) and by Humphreys (32) in a review on animal poisoning. However, excess supplementation of K produced signs of intoxication such as salivation, muscular tremors of legs and excitability and even death when levels of 1.73 g K/kg BW and higher were directly infused into the reticulorumen of 6 month old calves (45). Excess K was associated with hyperkalemia and plasma K values ranging from 5.5 to 12.5 mmol/L were reported. The highest value was observed just prior to the death of the animal. Furthermore, blood acid-base balance was perturbed and acidosis occurred at infusion rates of 1.15 g K/kg BW and higher (45). Under the assumption that these animals (300 kg live weight) would consume 6 kg of DM, conversion of 1.73 g K/kg BW yields a value of 86 g supplemental K/kg of DM but such high values are not commonly encountered in practice. Interestingly, both dry cows and sheep fed rations containing 75 g K/kg of DM, did not show any signs of K intoxication and were apparently healthy during the four weeks of such a high K load, but Mg absorption was significantly reduced by such a high dietary K content (35,36). Indeed, chronic exposure to high K intakes may lead indirectly to Mg deficiency (37, 49, 72, 74, 77).

7 POTASSIUM STATUS

Although excess K above requirement is primarily excreted with urine, the urinary K concentration appears to be a poor predictor of K intake under field conditions (5). However, Underwood and Suttle (74) report that urinary K concentrations < 20 mmol/L may be indicative for K deficiency. Furthermore, plasma K may be used to asses K status and values < 2.5 mmol/L and > 6 mmol/L are associated with K deficiency and excess K, respectively (74). In several studies with sheep, plasma K concentrations of 8 mmol/L were observed after intravenous K loading, and it appeared that such high values were tolerated because health problems were not reported (4, 53,54). However, these high plasma K values were observed for a relatively short period of time (hour) and it is not known whether chronic high plasma K levels up to 8 mmol/L, would negatively affect health.

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