Potassium Metabolism of Domestic Ruminants—A Review[1]

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Abstract

Ruminants and other herbivores normally consume amounts of potassium (K) greatly in excess of their dietary requirement, which is probably no more than about 0.5% of the ration, even for rapidly growing sheep or cattle. Ruminants appear to be well adapted to metabolize large amounts of K. The cation concentration in the rumen fluid has an important effect upon ruminal digestion. Under conditions of Na deficiency, K may replace Na as the major cation in saliva.

Large oral doses of K administered rapidly have been fatal to cows. Potassium may be partially responsible for death of calves suffering from diarrhea. Hypomagnesemia grass tetany is the only pathological situation related to high K intakes, and this relationship is not clear.

The K^{40} content of the whole body is being investigated as a means of estimating lean-body mass. This method shows promise of being a rapid and precise method of nondestructive measurement of body composition.

Potassium (K) is unique among the major elements required by man and animals, because dietary deficiencies of this element are very uncommon if not unknown. Any natural diet consumed by ruminants would probably never be deficient in K. For this reason nutritionists, especially those concerned with cattle and sheep, have given little attention to K as a dietary constituent.

Ruminant animals by comparison with other species, particularly the omnivores and carnivores, have an uncommonly large intake of K. The ruminant species are also characterized by a large fluid volume in the gastrointestinal tract, necessary for the digestion of a large mass of low energy feed. One of the purposes of this paper will be to explore the adjustments made by the ruminant to a large K intake.

The literature available does not indicate that the metabolism of K after absorption or at the cellular level is any different in ruminants than in other species. A specialized exception to this general statement is the K content of sheep erythrocytes. Evans (25) has shown that the large differences between breeds in the K content of the red blood cells of sheep which have been observed are under genetic control, and Meyer (49) has confirmed this for German breeds of sheep. Evans and his co-workers have published extensively on this subject and other physiological differences characteristic of the genetically different sheep have been investigated (24). A similar genetic trait has not been detected in cattle (66).

Long et al. (46) found that the blood serum level of K declined slightly with age in sheep, but McSherry and Grinyer (51) found no significant differences in the blood serum potassium of 126 dairy animals of various ages. The potassium concentration of the human body increases until puberty and decreases thereafter (3). A trend in this direction also has been noted in certain organs of sheep (53).

Rubidium and cesium are two other alkali metals which to a degree have chemical and physiological properties similar to potassium (63). The relative behavior of cesium and potassium has received considerable attention since the advent of nuclear weapons testing. One of the fission products, the long-lived, gamma-ray-emitting nuclide, cesium-137, potentially is of quantitative importance in its biological effects. Both Cs^{137} and K^{40} can be determined concurrently by gamma-ray spectrometry and, thus, data for cesium and potassium behavior can be acquired at the same time. It has been postulated that an increase in potassium intake would reduce retention of cesium-137 obtained in the diet. This has been demonstrated with the rat, but quantitatively the effect was not important; a ninefold increase in potassium intake reduced cesium retention by about one-half (83).

The effect of the level of K intake on the retention of cesium-137 or its excretion in milk has obvious significance to radiological health, because milk and beef are the two principal sources of this nuclide in the diet of Western man. However, as pointed out by Stewart et al. (74), it is difficult to distinguish between the effects on cesium metabolism of differences in K and crude fiber intake, because the two are so closely related in common livestock feeds.

Wild ruminants, as well as range-sheep flocks, frequently subsist on diets not only high in K

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but low in Na, and this condition has been considered in detail by Blair-West et al. (10). However, the Na intake of farm animals is nearly always present in adequate or luxury amounts. Therefore, the relation of sodium to K has been given little consideration in the discussion.

Potassium requirement. Rations containing some roughage would probably always be adequate in K, but the possibility of a deficiency does exist for cattle and sheep fed high-concentrate rations. Greater interest has been evident in the K requirements of cattle and sheep with the advent of high-concentrate rations as a common feeding practice. Du Toit et al. (22) were the first to investigate potassium requirements for cattle. They found that a ration providing K as 0.32% of the dry matter was adequate to maintain milk production of 2 gal per day over a period of two lactations. Telle et al. (77) found that 0.34% K in the ration was the minimum for growing finishing lambs and that the optimum intake was 0.55% of the ration. Roberts and St. Omer (65) found that a K level of 0.5 to 0.6% of ration dry matter was adequate for rapid weight gains in fattening steers. The percentage of K found in most common grains is only slightly less than the required levels, as suggested by the studies just described. Telle et al. (77) made the interesting observation that the length of rumen papillae was directly related to the K content of the diet and that the amount of K on the skin increased with supplemental K supplied to deficient sheep. The K content of rumen epithelium has been reported to be higher for sheep with genetically high red blood cell K than for the genetically low K animals (53).

Potassium absorption. The K of the diet is readily absorbed, as indicated by the high percentage of the intake excreted in urine and in the milk of lactating cows. From the data of Ward (80) it was calculated that urinary K as a percentage of total K output for nonlactating cows was 86% and for lactating cows urine represented 75, feces 13, and milk 12% of the total. The contribution of endogenous K to the fecal fraction is uncertain, but the ready absorption of K would indicate that fecal K arises principally from endogenous sources.

Although the evidence indicates that Na is removed from fluid throughout the entire length of the G.I. tract by a mechanism of active absorption, it appears that K enters blood plasma only by flowing down a concentration or electrochemical gradient (37, 59). Potassium is absorbed from the rumen (37, 59) and from the omasum (58), although in both organs the rate of absorption is greater for sodium than potassium. The K concentration of the fluid fraction throughout the gastrointestinal tract is consistently several times higher than plasma levels. On the other hand, the content of the tract are generally electro-negative. Thus, the concentration gradient must be sufficiently great to overcome an adverse electrical gradient.

The fluid of the G.I. tract tends toward isotonicity with blood; however, rapid increases in ionic concentration are produced by the end products of digestion in the rumen and the small intestine. According to Brouwer (12) the intestinal contents change from a hypertonic condition in the small intestine to a hypotonic condition in the colon and fecal water. The hypotonic condition results from absorption of Na and some organic ions. At the same time the K concentration becomes progressively greater, reaching a maximum in the fecal water (12). Despite the relatively increased concentration of K, the feces is not an important avenue of potassium excretion for the ruminant since, as pointed out, it represents only about 13% of the total K excretion. However, the percentage of total K output excreted in the feces is higher for herbivores than carnivores (1, 2). Brouwer (12) suggests that K excretion is higher in cattle because this species has the highest fecal water excretion. It has been observed that Zebu cattle excreted less K in their feces and more in the urine than Hereford cattle when both breeds consumed the same ration (35). It has frequently been suggested that loss of electrolytes and body water occurs in cattle recently turned to pasture. Rook and Balch (67) showed that this was not the case and that the attendant diarrhea was merely a reflection of less dry matter in the feces as a result of higher digestibility of fresh pasture forage. The loss of Na, K, and water by this route was no greater than occurred when the cattle were fed dry feed.

The ruminant is not only capable of very effective recovery of large amounts of Na from the digestive tract but, like other species, is capable of conserving body Na by action of the kidney. The combination of the two processes can reduce Na excretion to nearly zero. On the other hand, there is an obligatory excretion by cattle of K, both in the feces and urine (14). Some K excretion is probably necessary to prevent severe alkalosis, because K ions are exchanged in the kidney for hydrogen ions and vice versa (62). Stacey and Brook (73) observed that the urine volume of pen-fed sheep was reduced as well as the total output of Na and K when their daily feed was given. At the same time the hydrogen ion output in the urine increased. This was interpreted to mean that the secretion of large quantities of saliva created a drain on the Na and bicarbonate of the blood plasma, which initiated an aldosterone response to conserve Na and eliminate K. Kay (40) reviewed the subject of salt concentration and its effect on the osmotic pressure of rumen fluid and made the point that little attention has been given to this relationship.

The concentration of Na in the rumen fluid exceeds K by a factor of 1.5 to 3.0. Whereas the major source of ruminal K is the diet, Na is introduced into the rumen primarily by saliva. Bailey (6) investigated a variety of diets and found K values in saliva of 4-70 and in rumen fluid of 24-85 meq/liter. Comparable values for Na were 74-166 and 83-147 meq/liter. The ionic composition of rumen fluid is closely related to the rate of salivary secretion, and the chemical composition of saliva can vary, particularly in K concentration. Both flow rate and chemical composition vary with the diet. The sodium status of the animal has a profound effect on the composition of saliva. A Na deficiency stimulates increased production of aldosterone, with the consequence that K largely replaces Na in saliva. This subject has been studied intensively and reviewed in detail recently by Blair-West et al. (10) and Dobson (20).

Dobson (20) reports an interesting situation in which a change from a high to a low K intake resulted in an apparent Na deficiency. He found that in sheep a change from grass providing an intake of 0.7 mole of K to hay and meal providing 0.25 mole of K per day produced an aldosterone-like response. Sodium retention was greatly increased and the concentration of potassium in saliva increased and Na decreased. Sodium concentration in the rumen at the same time increased from 55 to 90 mmoles per liter. The author (20) postulates that this sequence of events is due to removal of sodium from extracellular water to the gut, to maintain the ionic concentration of the fluid which otherwise would be markedly reduced because of the lower potassium intake. This exchange reduces the concentration of sodium in extracellular water, which serves as the stimulus for increased aldosterone output. Increasing aldosterone output has the effect of increasing potassium output in saliva as a mechanism for conserving Na (10). This may explain the sodium diuresis found by Hix et al. (34) when potassium bicarbonate was added to the diet of sheep.

Potassium, representing an important fraction of cation contents of the rumen fluid, is important in maintaining a desirable medium for bacterial fermentation. Hubbert et al. (36) have shown that K is essential for cellulose digestion in an in vitro system. Maintenance of osmolarity with plasma is important to maintain a desirable moisture content of the rumen fluid (7, 54). Balch and Johnson (7) have shown that a higher moisture content favors cellulose digestion by the cow. They found that the contents of the ventral part of the reticulorumen had a dry matter content of 5-6% on a long-hay diet and about 10% for ground hay. A similar moisture requirement may exist for cellulose digestion in the colon. It has been suggested that bicarbonate and water are secreted in the ileum to provide a medium for fermentation in the colon (5).

In recent years there has been much interest in high-concentrate rations for beef and dairy cattle, as well as for sheep. Differences in physiological and biochemical responses to these diets have been extensively investigated in terms of physical form and crude fiber content of the feed, rate of digestion, and rate of passage. However, one of the most striking differences between high-roughage and high-concentrate rations is that the K intake may be as much as fourfold higher for animals consuming mostly forage. Although a strict nutritional deficiency of K probably is seldom a factor, an osmotic deficiency in rumen fluid may be responsible for results attributed to these more commonly considered factors just mentioned.

Sodium and K added as bicarbonates to high-grain rations of dairy cows under experimental conditions have generally tended to change the rumen pH, molar ratios of short-chain fatty acids, and milk fat percentage to values obtained when diets containing larger amounts of hay are fed (18, 23). However, two recent papers indicate no advantage in feeding Na or K as bicarbonates to fattening steers fed an all-grain ration (46, 85). The usual rationale for feeding bicarbonates is that it will increase the buffering capacity of rumen fluid, which has been lowered because of the decreased salivary secretion associated with consumption of high-grain rations. Perhaps of equal importance to the bicarbonate is the addition of the cation, which increases the osmotic pressure of rumen fluid and tends to maintain a more nearly optimum moisture content in the rumen. If this is the case, then K might be somewhat more effective than Na, because it is more slowly absorbed from the rumen. By the same logic the divalent cations which are poorly absorbed (59) should be even more effective. A recent report by Emery et al. (23), that magnesium oxide is at least as effective as sodium bicarbonate, lends some support to this speculation.

The excessive appetite for salt and bone meal observed by Hinders et al. (33) in cows fed pelleted alfalfa or those fed a highly concentrated ration may represent an attempt to increase the osmotic pressure of the rumen contents. A number of trials with cattle and sheep fed high-grain rations or rations containing corn cobs as the roughage have shown that improvements in digestibility and weight gains could be produced by adding alfalfa or alfalfa ash to the rations. These data were summarized by Chappell et al. (15), who showed that a mineral mix corresponding to the chemical composition of alfalfa was adequate, whereas a mineral mix which met the known mineral requirements of sheep was not. A striking difference between the two mineral supplements was the much higher concentration of potassium in the former.

It would appear that the ionic composition of rumen fluid does have an influence on fermentation in the rumen and that this factor should receive more consideration in comparisons involving feeds of widely different cation content.

Milk. The concentration of K, like most mineral elements in milk, probably is not influenced appreciably by diet. The concentration of K in milk is five to ten times that in blood plasma, whereas the reverse is true for sodium. In this respect milk has the ionic composition characteristic of intracellular substances and, since milk is an aprocrine secretion, its composition would be expected to resemble intracellular constituents. Rook and Wood (68) have found that the K content of milk is characteristic of individual cows and may vary by 50% between cows, but remains amazingly constant for the same cow. Ward (81) found significant differences in K concentration in dried milk from different areas of the United States, and Nickerson (55) reported differences between locations within the state of California. No explanations have been offered for these differences. One report indicates that high environmental temperatures resulted in a slight decline in the potassium content of milk (39). The data of Forbes et al. (29) indicate a decline in the concentration as the lactation period progresses. Colostrum has a lower concentration of K, which gradually increases as the milk becomes normal (30). Potassium was shown to be absorbed through the mammary epithelium more slowly than Na and chloride, when the elements were introduced via the teat as radioactive isotopes (43).

Potassium toxicity. The possible toxic effects of excessive intake of K by ruminants has received more attention than K requirements. This is a realistic approach because the ruminant animals, subsisting as they do on a high-roughage diet, may have a K intake throughout their lifespan which is many times their dietary requirement. Potassium, unlike other less available minerals (i.e., calcium), is almost completely absorbed by animals, and the excess excreted principally in the urine. Pickering (62) says, "That the cow normally does not suffer from a permanent hyperkalaemic acidosis seems to be the result of a fortunate coincidence, that in the herbivorous diet the large amounts of K are part of an excess of inorganic cations which necessitates the excretion of an alkaline urine in order to avoid metabolic alkalosis." About 200-400 g per day of K would be an average intake for a 500-kg cow fed alfalfa hay and 500 g or more are probably regularly consumed by cows on fresh pasture or cows fed green-cut alfalfa. The latter intake would represent over 1 kg per day of KCl.

The toxicity of K administered intravenously is well known and widely appreciated. What is not commonly recognized is that K has about equal toxicity, whether administered orally or intravenously, because of its rapid and probably nearly complete equilibration with extracellular water. Talbot and Pichie (76) have made the point quite clearly that there is no difference in effect whether potassium is administered orally or intravenously. One cow was killed by an oral dose of 238 g of K (82). Dennis and Harbaugh (19) administered 648 g of KCl orally to two cows. One died and the other recovered after treatment with calcium gluconate. Two animals received 300 and 400 g, respectively, and manifested no clinical symptoms, whereas a third cow receiving 350 g developed milk fever symptoms and recovered after treatment with calcium gluconate.

Anderson and Pickering (4) administered two liters of one normal KCl by slow intravenous infusion to cows and found no cardiac abnormalities. Plasma K levels increased by 1 to 2 meq/liter (from 4-5 to 6-7 meq/liter) and remained at that level. Urinary excretion of K rapidly increased to equal rate of infusion. In the dog, on the other hand, K infusion results in elevated plasma levels unless the dog has been conditioned by feeding additional K salts (62). Rats were able to develop a tolerance to oral K when the dose was progressively increased (78), but rabbits were progressively less able to tolerate intraperitoneal injections of K salts (79).

The experiences of Bergman and Sellers (8) indicate that the calf responds more like the dog than the mature cow. The toxicity level of K for calves was reached at a blood plasma level of less than 8 meq/liter. At this level calves were irritable and urinated every few minutes. Death from cardiac failure resulted at a plasma level of 12.7 meq/liter (8). Roy et al. (69) reported death by cardiac arrest in calves which had localized *E. coli* infections of the intestinal tract. They observed increased plasma potassium levels, attributed to cellular breakdown associated with loss of weight and consequent release of K from cells. Fisher (27) more recently has reported death attributed to primary cardiac failure of calves with diarrhea. He observed increased plasma K levels as well as increases in blood urea in calves not losing weight. The increased plasma levels were attributed to renal inefficiency in removal of K via urine. Another explanation for the source of increased plasma K might be that the abnormal intestinal epithelium allowed absorption of K from the lower intestinal tract, where the concentration is much higher than in plasma. Such calves are severely acidotic, and this may indicate H^+ going into cells and K^+ moving out. This could result in an increase in plasma K sufficient to produce cardiac arrest.

It would appear from the studies described that the calf, because of renal insufficiency, is less efficient in excreting K than the cow, and the increased levels of blood urea (27) observed in calves add support to this conclusion. In the cow, severe diuresis did not increase the absolute amount of K excreted in the urine but, on the other hand, the total loss of Ca^+, Na^+, Cl^-, and PO_4^{-3} was increased (71). The water demands for urinary excretion of K may be a factor in the water turnover rate, but this has not been investigated. The water intake and urine excretion volume are directly related to the K intake, but increases in K intake are also related in most cases to a variety of other factors, such as increases in crude fiber intake (42, 45). The relation between K intake and water turnover rates would seem worthy of investigation.

Grass tetany. Consideration of the detrimental effects of K has usually centered on its relation to the disorder of sheep and cattle associated with a hypomagnesemia and referred to in the western United States as wheat poisoning and in Europe as grass tetany. Hypomagnesemia is the common symptom of the disease and usually is associated with hypocalcemia. Potassium should be considered in any investigations of the etiology of this syndrome, because those cases associated with lush pastures involve K concentrations much higher than found in stored feed. The influence of high dietary K intake on blood magnesium levels has been considered by a number of workers. Daniels et al. (17), Dennis and Harbaugh (19), Pearson et al. (60), and Storry (75) did not find a depression in blood magnesium associated with increased K intakes. On the other hand, Kunkel et al. (44) and Fontenot et al. (28) found with increases in K intake a reduction in blood magnesium, and the latter showed an increased fecal excretion of magnesium. Curme et al. (16) found a reduced calcium retention associated with increased potassium intake, but magnesium analyses were not included. De Groot (32) found that increases in K intake decreased blood magnesium levels and also increased plasma and red cell levels of K. He reviewed a number of experiments performed with cattle and, although the results were conflicting, he concluded that K intake was very important in explaining hypomagnesemia.

An hypothesis to explain certain aspects of the pasture-induced hypomagnesemia is suggested by the above data and much of the evidence has been discussed by De Groot (32). The hypothesis assigns two basic actions to K, the first that increased K intake is responsible through mass action for reducing the absorption of calcium and magnesium from the gut. Thus, if the animal is temporarily unable to mobilize sufficient amounts of these elements from body stores, then a hypocalcemia and hypomagnesemia would result. In support of this idea it is of interest that blood serum magnesium levels increased in sheep fed low K diets (77). The other key role assigned to K in the hypothesis is that a rapid change to a much greater dietary intake of K per se could result in tetany or death. The inference for this is from the discussion above of toxicity. On the other hand, it must be considered that Pearson et al. (60) fed up to 5% K and Daniels et al. (17) fed 7.7% KCl in rations with little or no effect on sheep. It is possible that the sheep in these experiments were slowly introduced to these high levels of K, in which case the kidneys could probably accommodate to the increased K load (62). This is not the situation, however, in grass tetany and wheat poisoning cases, which usually occur when an animal on winter feed is suddenly changed to grass on high K content.

Other metabolic disorders. In studies of parturient paresis (milk fever) and bovine or ovine ketosis, two other metabolic disorders which are unique to ruminants, K determinations on blood and urine have frequently been recorded, but little causal relationship has been established with these disorders. Ward (80) found negative potassium balances which paralleled a negative calcium balance during the prepartum period for cows which subsequently succumbed to milk fever. Forbes et al. (29), on the other hand, found small negative balances for K in most cases with lactating cows and generally positive balances for nonlactating cows. Urinary calculi problems are common in ruminants and mineral interrelationships have been explored extensively in an attempt to clarify the etiology of this disorder. It has been reported recently that increased K in the diet was associated with a decrease in the incidence of urinary calculi in lambs (64).

Potassium and body composition. Potassium, because of its predominantly intracellular location, is indicative of the metabolically active tissue of the body and of the muscle or lean-body mass (13). Potassium concentrations are low in the other major compartments of the body: extracellular water, fat, and bone. The K content of the whole body or any fraction is highly correlated with the lean and water content and shows a negative correlation with the fat content. Potassium has been determined for individual muscles of the pig recently in two laboratories. One reports no difference in the K concentration between muscles when expressed on a water-free, fat-free basis (61); whereas, the other reports significant differences, expressed on the same basis (31). Mounib and Evans (53) found small but significant differences between the K content of some of the organs of sheep with a genetically determined low K content of the erythrocytes and sheep with a high K content.

Potassium has a naturally occurring isotope, K^{40}, with a very long half-life (1.5×10^9 yr), which exists in equilibrium with all K as 0.012% of the total. K^{40} is a strong gamma-ray emitter and is uniquely suited for determination of lean-body mass of the live animal, because the nuclide can be determined with precision in whole-body counters.

This technique has been widely used to determine K^{40} and to estimate body composition of humans. The present status of this technique in human research has been described recently (52). Estimation of body composition by whole-body counting of ruminant animals was first reported by Kirton et al. (41), who found generally low correlations between K^{40} and lean meat in sheep. More recently, at least three whole-body counting facilities have been designed for sheep or cattle. The installation at Purdue University has been used for counting sheep, calves, and pigs (48). Breidenstein (11) has described the equipment used at the University of Illinois and has shown that high correlations between K^{40} and lean-muscle mass can be obtained in pigs and sheep. The large mass of rumen ingesta, containing interfering gamma-emitting radionuclides, limited the precision of the K^{40} determination in the animal body. This is particularly true of liquid scintillation counting systems. Colorado State University has developed a unit capable of counting mature cattle or other animals of comparable size or smaller, which uses a solid sodium iodide crystal as the detector (38, 83). Because of much greater resolution this device eliminates many of the problems of interfering radionuclides. The solid crystal system, however, requires longer counting times, e.g., 30 min as compared to 2 or 3 min.

At present K^{40} counting appears the most promising technique for nondestructive carcass evaluation which will produce precise estimates of lean-muscle mass, but it cannot as yet be considered a routine method. Whole-body counting installations are very expensive, but operation and maintenance are relatively inexpensive and once the equipment is calibrated and automated it can be operated by unskilled technical help.

Conclusions

A review of the literature on potassium metabolism by ruminant animals suggests that further investigation in the following areas would be of value in understanding the physiological importance of the cation:

The importance of the K cation in the maintenance of an optimum ionic concentration in rumen fluid and particularly with relation to feeding low-forage rations.

Further work is needed on the relation of the K level in the gastrointestinal tract to the absorption of Ca and Mg. This is closely related to the function of dietary K in the etiology of grass tetany.

The implications of excessive K intake on the general health and longevity of ruminants, as well as interspecies comparisons of mechanisms for K excretion.

The relation of potassium intake to water requirements and water turnover rate.

If K^{40} is to be used to estimate lean-body mass, it is important to know the influence on the K content of muscles and organs of age, sex, and nutritive status.

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