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FACTORS INFLUENCING THE FLOW OF FLUID, SALIVA AND SOME CATIONS THROUGH THE RETICULO-OMASAL ORIFICE OF THE COW

Selostus:

Tekijöitä, jotka vaikuttavat nesteen, syljen ja eräiden kationien kulkuun lehmän verkkomaha-satakerta-aukosta

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PREFACE

The present study was carried out at the Department of Animal Husbandry of the Agricultural Research Centre in the years 1964—1967. The work was a continuation of the earlier studies on the rumen, as part of the research program of the Department since the year 1952.

The subject of this study was proposed by Mr. Martti Lampila, Dr. Agr. and For. For this initial stimulus as well as for the very valuable advise during all phases of the work I express my sincerest gratitude.

I am very grateful to Professor Orvo Ring, Dr. Agr. and For., who in many ways has helpfully aided this work at the time when he was Head of the Department of Animal Husbandry. To Mrs. Irja Uotila, Dr. Agr. and For., Acting Head of the Department at present, I am thankful for the possibility to continue and finish this work.

I extend my best thanks to Professor Lauri Paloheimo, Ph.D., my highly respected teacher, who with interest has followed my work and given valuable pieces of advice after having read the manuscript.

The fistulation of the experimental animals was done by Mr. Bengt Westerling, Lic. Vet. Med., for which I express my thanks. I wish to thank Miss Lea Sipilä and the whole barn personnel for the feeding and management of the experimental animals. For the help given me in performing the sample analyses I wish to express my best thanks to Mrs. Salli Piispa and Mrs. Kaisu Virri.

In the statistical treatment of the results I have received valuable help from Mr. Tauno Moisio, Mag. Phil., while the computer programming was done by Mr. Seppo Hyvärinen, M. A. I wish to extend my best thanks to them.

I am also grateful to Mr. Ulf Lindström, Agronomist, M. S., who made the translation into English and to Mr. D. R. Homer, M. A., for the linguistic corrections of the translation.

For the financial help given me I am especially indebted to Suomen Kulttuurirahasto, which by granting a 3-year scholarship made it possible for me to concentrate on the investigation. I have also received financial help from August Johannes ja Aino Tiuran Maatalouden Tutkimussäätiö and from Agronomien Yhdistys and wish to express my sincere gratitude for their assistance.

To the Agricultural Research Centre I extend my thanks for including this study in their series of publications.

Tikkurila, March 8, 1968.

Esko Poutiainen

CONTENTS

INTRODUCTION

The most striking feature in ruminal digestion is the microbial digestion of food in the forestomach. Here practically all food constituents are attacked by microbes, chiefly in the reticulo-rumen compartment. The magnitude of microbial digestion is indicated by the fact that 40—80 per cent of the dry matter disappearing from the alimentary tract of the cow disappears in the reticulo-rumen (PALOHEIMO and MÄKELÄ 1960).

The principal products of fermentation are the volatile fatty acids. These acids are considered to be of great importance in ruminant nutrition because they constitute the animal's major source of energy. With regard to the microorganisms, the organic acids formed in fermentations are waste products which, as they accumulate in the living surroundings slow down activity, mainly because of the lowered pH. A continuous ample flow of fluid is the most important stabilizer of the conditions in the reticulo-rumen. The main factor influencing this process in the abundant secretion of saliva, which at the same time is the most important factor maintaining the fluidal state in the rumen. The saliva also introduces great amounts of neutralizing mineral salts into the rumen, preventing the decrease in pH caused by the organic acids (MARKOFF 1913, McDOUGALL 1948, BAILEY 1961 b). Earlier, the prevailing opinion was that the buffering capacity of the saliva is adequate for maintaining the pH of the rumen contents at a level favourable for the microbes (MANGOLD 1929, p. 151, DUKES 1953, p. 330). Nevertheless, already MARKOFF (ibid.) concluded from his calculations that the neutralizing capacity of the alkaline saliva is not sufficient to neutralize all of the acids formed, which means that some other mecanism is also working. In fact McANALLY and PHILLIPSON (1942) were able to show that the volatile fatty acids were absorbed into the blood through the rumen wall, which partly prevents the pH from decreasing. The experiments of DANIELLI et al. (1945) and GRAY (1948) showed that the rate of absorption from the acid solution is much higher than from alkaline solution. The undissociated acid penetrates the membrane more readily than does the anion, which makes the specific absorption rate higher when the rate of acid production increases.

The neutralization of the rumen contents were subjected to closer study when some investigations revealed that the pH of the rumen contents may decrease considerably below the optimum range of microbial activity, even with ordinary feeding (BALCH et al. 1955, LAMPILA 1955, SMITH et al. 1956). A harmful decrease of the pH seemed to occur in most cases immediately after feeding and to take place especially in the upper part of the rumen contents (BRYANT 1964, LAMPILA 1964). On diets rich in concentrates low pH-values have been encountered particularly, when roughage has been scarce or lacking altogether (BALCH et al. 1955, EMERY and BROWN 1961). The fine grinding or pelleting of the roughage has also been demonstrated to increase the acidity of the rumen contents (CULLISON 1961, ORTH and KAUFMANN 1964).

Among the cations in the rumen fluid sodium and potassium are the most abundant. A high correlation between the concentration of Na in the saliva and in the rumen fluid is an indication of the great share the saliva has in the transport of this element (McDOUGALL 1948, KAY 1960, BAILEY and BALCH 1961 b). The small amounts of Na introduced with the food seem to have a very slight direct effect on the Na concentration, but the K values rise as a consequence of feeding (Bailey and Balch 1961 b, Lampila 1964). The feeding of neutralizing minerals to the animal in order to increase the neutralizing capacity of the rumen contents has sometimes brought about a slight increase of the pH of the rumen contents, but often the influence of dietary minerals has been rather ineffective (Emery and Brown 1961, Nicholson and Cunningham 1961, Nicholson et al. 1963, Davis et al. 1964, Emery et al. 1964).

With regard to the neutralization aspect of the rumen contents, it seemed important to clarify the effect of dietary factors on the total occurence of mineral elements in the reticulo-rumen at a given time and especially the role of the saliva as a transporter of these. The total amounts of readily soluble minerals such as Na- and K-salts, are obtained as a product of the volume of fluid flowing through the rumen and the concentration of the respective element. Thus a change in either one of these factors causes a change in the total amount of the neutralizing flow within a given period of time.

As far as data on the volume of the flow of fluid through the rumen of the cow are available, they indicate that the volumes are quite large, from about 150 to more than 200 litres per 24 hours (Sperber et al. 1953, Lampila and Poijärvi 1959). This great flow of fluid is made possible only if the saliva makes up the major part of this fluid.

In connection with measurements on the flow of fluid Lampila (1965) has also made calculations on the amounts of certain mineral elements and volatile fatty acid escaping with the rumen fluid. On the basis of these calculations it seemed obvious that the significance of sodium and potassium in the neutralization of the rumen contents is most important and that the secretion of saliva has most profoundly affected the entrance of these minerals into the rumen.

The purpose of the present study was to investigate the effect of certain dietary factors on the following criteria important in the neutralization of the rumen contents:

— the total flow of fluid through the reticulo-omasal orifice.
— the proportion of saliva in the total flow of fluid.
— the concentrations of sodium and potassium in the saliva and in the rumen fluid.
— the removal of sodium and potassium through the reticulo-omasal orifice in the rumen fluid.
— the relative importance of different routes in the sodium and potassium entrance into the rumen.

The following dietary factors were chosen for the investigation of their influence on the above criteria:

— the level of dry matter intake
— the dosage of sodium chloride
— the proportion of coarse fodder in the ration

Some preliminary results of these investigations have already been reported (Poutiainen 1966, Poutiainen and Lampila 1967).

REVIEW OF THE LITERATURE

Amount and distribution of fluid in the reticulo-rumen

The fresh contents of the reticulo-rumen of the mature cow vary, according to different reports, from 40 to 125 kg and the dry matter percentage of the contents from 7 to 17 per cent (Nevens 1928, Mäkelä 1956, 1960, Emery et al. 1958, Paloheimo and Mäkelä 1959, Campling et al. 1961). The disposal of solid substance from the reticulo-omasal orifice takes place by fluid transportation, because the disposed material contains only 5—7 % dry matter (Balch 1959). The amount of dry matter disposed from the reticulo-rumen is regulated by the volume of the flow of fluid and by the dry matter content of the disposed fluid. The fodder particles must undergo a certain decrease in size before their characteristics are such that they remain in the liquid phase and can be transported with the fluid from the reticulo-omasal orifice to the lower parts of the digestive tract.

In the disposal of dry matter and fluid from the reticulo-rumen a difference which seems to increase with increasing dissolubility of the foodstuff has been observed (CORBETT et al. 1959, WELLER et al. 1962). Apparently the finely divided material, being easily dispersed in the fluid, is transported from the reticulo-rumen at approximately the same rate as the fluid (CASTLE 1956).

As the fluid serves as a transporter of dry matter from the reticulo-rumen the disposal of both of these products is connected. The entrance of fluid into the reticulo-rumen is on the other hand influenced by the amount and nature of the rumen contents which thus also affect the amount and flow of fluid.

Factors affecting the amount and physical character of rumen ingesta.

E f f e c t o f f o o d a n d w a t e r i n t a k e. — The quantity of food eaten has only a slight influence on the amount of fresh contents in the reticulo-rumen of the cow (NEVENS 1928, MÄKELÄ 1956, 1960, PALOHEIMO and MÄKELÄ 1959). In the investigation of MÄKELÄ (1956) the correlation coefficient between the amount of the reticulo-rumen contents (y) and the dry matter intake per 100 kg reduced net weight (x) of cows receiving from 2.4 to 12.0 kg dry matter of hay per day was $r = +0.31 \pm 0.18$ and the regression equation $y = 1.41x + 14.1$. The correlation between the dry matter percentage of the rumen (y) and the dry matter of the fodder eaten (x) was observed to be considerable closer, the correlation coefficient in this case being $r = +0.72 \pm 0.10$ and the regression equation $y = 2.67x + 7.92$. With decreasing dry matter consumption the contents of the rumen get a more watery consistency, which slows down the rate of decrease of the total amount of rumen contents.

However CAMPLING et al. (1961) have observed that the level of feeding caused marked differences in the weight of digesta and of digesta dry matter in the reticulo-rumen of cows receiving 10 lb, 15 lb or *ad libitum* hay. On the same level of hay intake there were quite large differences in the weight of the digesta and of the digesta dry matter in different cows. Small amounts of dry matter in the reticulo-rumen were associated with short retention times of food residues in the digestive tract.

BATH et al. (1966) restricted the food intake of two heifers, reducing the total digestible nutrient allowance to 65 per cent of the minimum requirement. The mean weight of the rumen contents of the heifers increased however during the first week of restriction, due to the increased water content of the rumen ingesta. HYDÉN (1961 a) found little or no reduction in the volume of rumen fluid in sheep fasted up to five days. Similar results for cattle were presented by GROUVEN (1865 ref. RITZMAN and BENEDICT 1938) and NEVENS (1928). Results somewhat contradictory to the above were reported by HECKER et al. (1964). They found that the volume of rumen fluid in sheep deprived of food or of both food and water decreased rapidly during the first 2—3 days of deprivation and after that slowly approached an approximately constant value.

An increase in the quantity of food consumed has in general been observed to have an increasing effect on the rate of transfer of food residues in cattle (BALCH 1950, MÄKELÄ 1956, 1960, PALOHEIMO and MÄKELÄ 1959, CAMPLING et al. 1961, THOMAS et al. 1961, FREER and CAMPLING 1963), in sheep (POIJÄRVI 1952, BLAXTER and GRAHAM 1956, GRAHAM and WILLIAMS 1962) and in goats (CASTLE 1956).

Quality of food consumed influences the amount and fluidity of the rumen contents and on the transfer of digesta. The dry matter percentage in the rumen of sheep which on hay diets was about 10 per cent (GRAY et al. 1954), was higher when concentrates were fed and approached 20 per cent on diets supplemented with maize (BOYNE et al. 1956). The amount of the rumen contents of sheep on a hay diet has been observed to be significantly greater than for sheep on a diet rich in concentrates (NICHOLSON et al. 1961). Similarly BALCH et al. (1955) observed that a reduction of the proportion of hay in a hay-plus-concentrates diet caused a pronounced drop in the total weight of digesta and in the weight of the dry matter in the reticulo-rumen of the cow.

PALOHEIMO and MÄKELÄ (1959) investigated the effect of different combinations of foodstuffs on the cow's rumen contents and dry matter percentage and on the retention time in different parts of the digestive tract. The experimental groups were fed hay only or hay and concentrates in the ratio 1:0.5 or 1:1. It was observed that the fresh contents of the reticulo-rumen were much the same for all feeding regimes. The dry matter percentage tended to be greater with the 1:1 hay: concentrate diet than with the other feeding regimes.

MÄKELÄ (1960) observed that replacing part of the hay with sugarbeet pulp, swedes and concentrates had no consistent effect on the mean retention time of dry matter in the reticulo-rumen.

According to CAMPLING (1966) the addition of concentrates to a given amount of hay increased the amount of reticulo-rumen contents due to the prolonged retention time of hay. The addition of different amounts of concentrates (2.5, 5.0 and 7.5 kg per day) to the *ad libitum* hay diet did not significantly affect the total amount of digesta and of digesta dry matter in the reticulo-rumen immediately following feeding. Just before feeding, the amount of digesta was significantly lower ($P < 0.05$) for the diets containing 5 or 7.5 kg concentrates compared with the other diets, but there were no significant differences between the four diets with respect to the amount of dry matter.

FREER and CAMPLING (1963) noted that physical character of food consumed influences the amount of the digesta and of the dry matter: liquid ratio. Cows were fed with hay, dried grass or concentrates in one meal under a 5 hour period *ad libitum*. Immediately before feeding the reticulo-rumen contained 40 % more digesta and 84 % more dry matter when the diet consisted of hay than when it consisted of dried grass. Immediately after feeding these differences were much smaller. When the diet consisted of concentrates the reticulo-rumen contained about two-thirds the amount of dry matter found for diets of dried grass, both before and after feeding. The differences could not be explained by the amount of dry matter consumed.

The frequency of feeding is also one of the factors affecting changes in the rumen contents and the character and disposal of the ruminal contents. In the investigation of BALCH (1958 a) food was given either once or twice daily. The decline in the total content between meals was 4.3 lb/100 min. for cows fed once and 3.5 lb for cows fed twice a day. The losses in the total content during meals were 29.5 and 26.7 lb/100 min. respectively. It was established that the rate of decline in the total content as well as in the content of dry matter was constant and the same after both morning and evening meals. The decline in the total content was less rapid than the decline in the dry matter content — consequently the amout of fluid decreased more slowly than that of the dry matter or of the total content.

PALMQUIST and RONNING (1963) investigated the effect of a 12 hour and a 6 hour feeding interval on the amount of dry matter in the rumen and on the retention time. These proved to be very similar for both feeding intervals. The rate of removal during the last two thirds of the time after feeding was constant, whereas during the first third of the time after feeding it was considerably faster. WALDO et al. (1965) have made calculations for obtaining regression equations between the wet or dry rumen contents and the dry matter percentage and the time elapsed from the beginning of feeding. When cows were fed on a ration of hay, pellets, hay-plus-grain or silage, the decrease in the dry matter percentage with time (on a 12 hour feeding interval) after feeding was expressed by a polynomial of the first degree ($P < 0.05$) and the change in wet content by a polynomial of the third degree ($P < 0.05$).

Water intake by cattle is proportional to the amount of dry matter consumed, but it depends also on a number of factors such as the kind of diet, the environmental temperature and the physiological state of the animal (LEITCH and THOMPSON 1944). The water consumption of animals is dependent on how much of their requirements they receive with the food. WALDO et al. (1965) observed, however, that the total water consumption was greater for animals receiving silage (45 % DM) than for those receiving hay. The increase in the total water intake was not reflected as a difference in the dry matter or moisture content of the rumen. Restriction of the water intake to 50—70 % of the amount consumed *ad libitum* decreased the amount of food eaten but had little or no influence on the dry matter content of the rumen ingesta. The retention time was not prolonged above that which could be attributed to the depression of food intake (BALCH et al. 1953, PHILLIPS 1961).

A fasting animal consumes little water (RITZMAN and BENEDICT 1938, p. 40).

P r e - t r e a t m e n t s a n d f o o d s u p p l e m e n t s. — With regard to the rumen contents, their character and transfer, the most effective pretreatments are those in which the coarseness of the fodder is modified. Of these one can mention primarily grinding of roughage, pelleting and briquetting.

The digesta in the reticulo-rumen of cows having ground hay as their only food source is a dry, thick and homogenous mass containing little free liquid (BLAXTER and GRAHAM 1956, CAMPLING et al. 1961). An increase in the dry matter content of the rumen juice amounting to 2—3 per cent units is reported in the investigation of ORTH and KAUFMANN (1964) when ground hay was fed. O'DELL et al. (1963) did not find significant differences in the dry matter percentage of the rumen contents in dairy heifers fed baled hay, ground hay (1/4 inch screen) and ground pelleted (3/8 inch) hay. On the other hand the amounts of dry matter in the reticulo-rumen were clearly different: 9.3 kg for baled hay, 5.9 kg for ground hay and 4.1 kg for pelleted hay. When feeding only ground hay or pellets it has been observed that the rumen contents assume a frothy consistency (OLTJEN et al. 1965, COLVIN and DANIELS 1966).

According to several investigations ground or pelleted roughage is transported more rapidly from the reticulo-rumen than the respective amount of untreated hay (BALCH 1950, BLAXTER and GRAHAM 1956, RODRIGUE and ALLEN 1956, 1960, KING et al. 1962, CAMPLING et al. 1963, O'DELL et al. 1963). The passage of finely-cut hay from the reticulo-rumen seems to be particularly accelerated during and immediately following eating, but the final excretion is distinctly prolonged (BALCH 1950, RODRIGUE and ALLEN 1960, CAMPLING et al. 1963, BALCH and CAMPLING 1965).

Concerning supplementary foodstuffs, the addition of minerals has generally been observed to exert a decreasing effect upon the dry matter percentage of the rumen contents (NICHOLSON and GUNNINGHAM 1961, NICHOLSON et al. 1963, OLTJEN et al. 1962 a), an increasing effect upon the total amount of rumen contents, and to accelerate the passage of the rumen contents (MURRAY et al. 1962, ELAM 1961).

C h e w i n g a n d r u m i n a t i o n. — BAILEY (1961 a) observed that the rate of eating varied markedly, being usually under 100 g/min. for hay or dried grass, about 350 g/min. for fresh grass and dairy cubes, and was 457 g/min. for one cow fed mangolds. For fodders consumed more slowly, the swallowing of boluses took place at longer intervals and the size of the boluses was smaller. According to SCHALK and AMADON (1928), cows on dry food rations consisting of ground grain, alfalfa and corn silage spent 6—7 hours daily eating, the same time ruminating and 10—11 hours resting.

BALCH et al. (1955) noted a marked reduction in the time spent eating on diets low in hay and high in concentrates compared with a pure hay diet. The same was observed for sheep by GORDON (1965).

CAMPLING (1966) observed that the cow spent 12 min. chewing a kilogram of hay when the diet contained 4.5 kg hay, but 18 min./kg hay when the cow in addition to the same amount of hay was fed 6 kg of concentrates; the time spent ruminating was 49 min./kg and 69 min./kg hay respectively. KICK et al. (1937) found that steers required 153, 130, 90 and 78 min. for the prehension of equal amounts of whole hay, 2 in. cut, 1/4 in. cut and ground hay respectively. Rumination time was 402, 437, 414 and 277 min. respectively. The rate of jaw movements was observed to be 75—80 per minute for hay and about 90 for concentrates. The number of jaw movements during rumination was 58 per minute on an average (BALCH 1958 a).

Stratification of rumen ingesta

The digesta in the reticulo-rumen are roughly separated into two layers; an upper layer of dry fibrous material and a lower layer of a more fluid consistency (SCHALK and AMADON 1928, BALCH 1950, 1958 a and b). BALCH and KELLY (1950) observed that the difference in dry matter percentage of the upper and lower layer of the rumen contents can be as much as 10 per cent. The distinctness of the stratification depends mainly on the character of the food consumed. With diets rich in roughage the borderline between the fluid and the cruder material is distinct whereas with diets containing much ground food this borderline is indistinct (BALCH 1950, BALCH et al. 1955, FREER and CAMPLING 1963). The crude hay particles collect into a »mat» in the top of the rumen whereas grain and other foodstuffs with a smaller particle size sink more rapidly in the fluidal layer (SCHALK and AMADON 1928, SMITH et al. 1956, BALCH 1958 b, 1961). This phenomenon depends partly on the character of the individual food particles and partly on the contractions of the walls of the reticulum and the rumen causing a mixing of the contents and maintaining the interval ruminal flow of the contents and the fluid.

Size and specific gravity of the particles. — Size is probably the main factor of importance in determining how rapidly particles of the digesta will leave the reticulo-rumen, but the specific gravity can also be assumed to exert an influence on the chances of individual particles being carried through the reticulo-omasal orifice (BALCH and CAMPLING 1965, p. 119).

BALCH and KELLY (1950) did not observe any marked differences in specific gravity between the digesta particles of the dorsal and ventral sacs of the rumen. The average for the dorsal sac was 1.038 and for the ventral sac 1.039. KING and MOORE (1957) observed a maximum passage rate for plastic particles with a density of approximately 1.2 gm/cm^3 and a size of 20—30 mm^3. CAMPLING and FREER (1962), using rubber or plastic particles, showed that in the specific gravity range of 1.0—1.4 the shortest retention time in the reticulo-rumen was obtained with a specific gravity of 1.2.

Small particles absorb water more easily than larger ones and consequently more rapidly attain a specific gravity suitable for their retention in the fluid and their transport in it. Gas bubbles become attached to the larger particles and lift them to the upper part of the rumen contents (BALCH and KELLY 1950, SMITH et al. 1956). Thus the copious formation of gases in rumen fermentation tend to stratify the rumen contents.

Contractions of the reticulo-rumen. — The cyclic contractions of the rumen and the reticulum exert an essential influence upon the stratification of the food particles and upon the passage of the ingesta from the reticulo-rumen to the omasum.

The basic processes of the contractions of the rumen and the reticulum were demonstrated already in the 1920-s in the classical work of WESTER (1926 ref. by SELLERS and STEVEN 1966) and SCHALK and AMADON (1928). The views on the motor functions of the ruminant forestomachs, based on these and later investigations, have recently been reviewed by SELLERS and STEVEN (1966).

The mixing movements of the reticulum and the rumen appear to be insufficient to counteract the factors causing heterogeneity of the digesta. HYDÉN (1961 a) reported significant differences in polyethylene glycol (PEG) concentration between samples drawn from five different parts of the sheep's rumen. LAMPILA and POUTIAINEN (1966) observed that the PEG-concentration of the fluid of the upper part of the cow's rumen contents was maintained at a level 8 % higher than that demonstrated at the same time in the lower or forepart of the lower portion of the rumen contents. The authors attributed the chief cause of this difference as being due to the saliva, which when continuously flowing into the lower parts of the rumen maintains a lower concentration of the reference substance here than in the contents of the upper part.

The contractions of the rumen and the reticulum maintain an organization between the crude material and the fluid similar in direction to the one provided by the size and specific gravity of the particles, i.e. the cruder material rises to the upper part of the rumen and the fine material sinks to the bottom. The free fluid deposit is located as the bottom of the ventral sac, and due to the contractions the free fluid continuously washes the mass of food in the rumen.

The separation of the crude material from the fine material takes place at the reticulo-omasal orifice. The fine material is transported with the fluid to the omasum, but the cruder material is ruminated and is mixed by the contractions with the contents once more (BALCH 1958 b).

The reticulo-rumen orifice is almost continuoulsly below the fluidal level (BALCH 1958 b). BALCH et al. (1951) noted that the reticulo-omasal orifice was open 60—70 % of the observed time. At other times, according SELLERS and STEVEN (1966), the sphincter surrounding the orifice closes it completely. It is generally accepted that during the second reticular contraction the omasal canal exhibits a negative pressure and that at the height of this contraction the reticulo-omasal orifice opens and reticular contents are forcefully ejected into the omasal canal (WESTER 1926, SCHALK and AMADON 1928, BALCH et al. 1951, STEVEN et al. 1960).

The frequency and amplitude of the contractions influence the rate of passage of the fluid as well as of the whole ingesta. The contraction cycles of the rumen and the reticulum are subjected to a control by the central nervous system (SELLERS and STEVEN 1966, p. 645) and cease to function if the vagus nerve is cut. The movements of the stomach are affected by the sensori stimuli delivered by the mouth, the oesophagus, and all regions of the stomach (SELLERS and TITCHEN 1959, TITCHEN and REID 1965).

The rate of contractions is highest during eating. BALCH (1958 a) obtained the following values for the number of contractions (per hour) of the reticulum during different phases of activity of the animal: eating 87, standing resting 63, lying resting 57, standing ruminating 66, and lying ruminating 63. Feeding affects the frequency as well as the amplitude of the contractions and the duration of the contraction of the individual parts of the rumen (TITCHEN and REID 1965).

WESTER 1926 (ref. SELLERS and STEVEN 1966) found that the frequency of rumino-reticular contractions was increased with increased rumen content. It has been observed that the contractions continue even in a fasting animal, but with decreased strength and frequency (TITCHEN and REID 1965). The replacement of the normal rumen contents with a completely liquid substance does not noticeably influence the frequency of contractions of the rumen and the reticulum (SELLERS and STEVEN 1966).

Scabrous material in the diet may maintain or reinforce the tonic activity of the motor neurons responsible for ruminal motility. Significant differences ($P < 0.01$) in rumen contraction amplitude were found when steers were fed diets of oats hay fed unchopped and ground through a 1/4 in. or 3/32 in. screen. The difference in rumen contraction frequency of steers on diets of long and 1/4 in. hay was not statistically significant, but both of these diets produced rumen contractions significantly ($P < 0.05$) more rapid than for steers on a 3/32 in. hay diet (COLVIN et al. 1958, COLVIN and DANIELS 1966). CAMPLING (1966) reported that the frequency of reticular contractions was higher during consumption of concentrates than it was when hay was fed.

CLARK and LOMBARD (1951) found that the rumen contractions of sheep were depressed in amplitude or completely inhibited by the induction of alkali into the rumen. ASH (1959) observed no threshold pH value of the contents of the reticulo-rumen for the acid inhibition. The pH value at which inhibition occurred depended to a large extent upon the type and concentration of the acid.

Factors contributing to the flow of fluid through the reticulo-rumen

Secretion of saliva

Saliva has been estimated to supply some 70—90 per cent of the total fluid entering the reticulo-rumen of the cow (BAILEY 1961 a, POUTIAINEN 1966). The abundant secretion of saliva and the factors influencing it also control the total flow of fluid through the reticulo-rumen. Investigations concerning the secretion and composition of ruminant saliva have been reviewed e.g. by SOMMERS (1957) and KAY (1963 and 1966).

The saliva flowing into the reticulo-rumen is a mixture of secretions from several glands, each functioning at specific times. KAY (1960 a) divided the salivary glands of sheep and cows into three groups according to their histological and physiological characteristics and the composition of their secretions. The first group, the serous glands, consisting of paired parotid and inferior molar glands, secrete continually. The basal secretion of these glands does not seem to be under nervous control (COATS et al. 1956, 1958, KAY 1958). They may be stimulated by reflexes from the mouth, oesophagus and rumen (CLARK and WEISS 1952, ASH and KAY 1959). An increased flow of saliva has also been observed with tactile stimulation of the reticulo-rumen fold and nearby structures in the reticulo-rumen (COMLINE and KAY 1955, KAY 1958).

The second group, called mucous glands, consists of unpaired palatine, buccal and pharyngeal glands. They secrete mucous saliva mostly during the time of stimulation. The paired submaxillary, sublingual and labial glands, which secrete mucous and serous saliva are called mixed glands. They respond fairly weakly to stimulation of the oesophagus and reticulo-rumen (KAY and PHILLIPSON 1959, KAY 1960 a).

The flow of saliva from the cannulated parotid glands has been observed to be equal to the flow of saliva from the rest of the salivary glands (PHILLIPSON and REID 1958, KAY and PHILLIPSON 1959, TRIBE and PEEL 1963).

The secretion of saliva occurs at different rates during different functions (rest, eating and rumination) of the animal. In the experiments of WILSON (1963) of the total secretion of parotid saliva in sheep on a hay diet, 36 % was secreted during the resting period, 27 % during the eating period and 37 % during the rumination period. The proportion of basal secretions rose on diets where the hay was finely ground. BAILEY (1961 a) showed that in cattle on diets of hay, silage or grass the amount of mixed saliva secreted during the resting period made up 40—45 % of the total daily secretion. For diets consisting of hay and concentrates in the ratio 0.6:1 or 0.1:1 the proportion of basal secretion was 52 % and 72 % respectively.

It has been observed that the secretion of saliva changes during the intervals between feeding so that the secretion is lowest immediately after feeding and then gradually increases. This phenomenon was observed regarding the secretion of parotid saliva by BAILEY and BALCH

(1961 b) and by MEYER et al. (1964), PUTNAM et al. (1966 a) in cattle and WILSON and TRIBE (1963) in sheep. A similar change takes place also with regard to the secretion of mixed saliva (BAILEY and BALCH 1961 b). These authors observed that the lower secretion of saliva after feeding was not associated with the degree of fullness of the rumen, and concluded that the inhibition effect is connected with the act of eating itself. In contract, WILSON (1963 a) in his experiments with sheep observed that the parotid secretion was diminished in all cases where the volume of the rumen contents was increased. Similarly the rate of secretion of parotid saliva was increased when the volume of the rumen contents was decreased. It has also been observed that liquid or gas passed into the rumen exerts a decreasing influence upon the secretion of parotid saliva (PHILLIPSON and REID 1958, KAY and PHILLIPSON 1959). WILSON and TRIBE (1963) found that the infusion of saliva or a 1 % saline solution into the reticulo-rumen of sheep decreased the parotid secretion whereas the infusion of water did not.

The amount of parotid or mixed saliva secreted on a particular diet is dependent mainly on the amount and nature of food consumed. BAILEY and BALCH (1961 b) found that when the intake of hay was increased, the rate of mixed salivary secretion during resting was decreased. WILSON (1963 a) observed a marked increase in parotid saliva secretion in resting sheep as the food intake was increased. From the experiments of BAILEY and BALCH (1961 a) and MEYER et al. (1965) it can be noted that the high secretion rate on a given diet during eating is associated with a high rate of secretion during resting. The rate of salivary secretion is most rapid during eating and rumination. The rate of secretion rises during these activities to a level 2—5 times higher than the rate during resting (BAILEY and BALCH 1961 a, BAILEY 1961 b, STEWART and DOUGHERTY 1958). The total amount of secretion on a given diet during each of the activities depends not only on the rate of secretion but also on the duration of the activity (BALCH 1958 a, BAILEY 1961 a).

A positive linear relationship has been observed between the amount of dry matter consumed and the secretion of parotid saliva. This was shown by WILSON and TRIBE (1963) with sheep, as well as by HAWKINS et al. (1965) and PUTNAM et al. (1966 a, b) with cattle. The tendency for more saliva to be secreted per kg dry matter eaten at a lower level of food intake than on a higher level was observed in the investigation of WILSON and TRIBE (l.c). The association between the amount of dry matter eaten (x) and the volume of parotid saliva secreted (y) was $y = 1.42+2.01x$ ($r = 0.73$) in an investigation with steers on a diet of corn silage and ground snapped corn fed at the ratio of 3.0 and 1.0 kg/100 kg body weight respectively (HAWKINS et al. 1965). On the other hand KAY (1960 a) and LAWLOR et al. (1966) did not observe correlations between the daily food consumption and the quantity of parotid saliva secreted by sheep.

The amount of saliva secreted has been observed to vary greatly depending on the nature of food eaten. BALCH (1958 a) observed that for every 10 lb dry matter of hay consumed, 43—57 lb of saliva was added during eating but for every 10 lb of concentrates, only 12—15 lb of saliva was secreted; similarly the amount of saliva secreted per 10 lb dry matter of fodder beet was 30 lb and for every 10 lb dry matter of grass 53 lb. BAILEY (1961 a) in his experiments with dairy cows obtained a mean rate of secretion of mixed saliva of 229 ml/min. during eating. The rate of secretion varied from 108 ml/min. for mangolds to 250 ml/min. for dairy cubes, certain fresh grasses, silage, dried grass and hay. The calculated daily amounts of mixed saliva secreted were 110 l for lucerne silage, 149 l for hay, 123 l for dairy cubes and hay, 108 l for maize, groundnut cake and hay and 178 l for grass. WILSON (1963 b) found high secretion values in grazing sheep, but DENTON (1956, 1957) observed that finely shopped fresh lucerne (water content 65 %) brought about a considerably smaller secretion of parotid saliva than a diet consisting mainly of oaten chaff (water content 10 %). In the investigation of MEYER et al. (1965) with steers and cows it was observed that with an increasing moisture content of pasture or freshly cut alfalfa the flow of saliva decreased. The mean amount of saliva added per kg dry matter of freshly cut alfalfa was 2.70 kg and for hay 3.25 kg.

AUTREY (1964 b) observed the mean volume of the parotid saliva flow to be 493 ml per hour for corn silage, 363 ml for Coastal Bermuda-grass hay and 198 ml for green oat forage. For a ration high in crude fiber (7—8 kg hay) the daily secretion of saliva was about 10 per cent greater than for a ration high in starch (2 kg hay + 6—9 kg concentrates). Feeding pasture grass *ad lib.* gave similar results, i.e. with increasing contents of crude fiber the secretion of saliva increased (KAUFMANN and ORTH 1966).

It is apparent that the physical properties of the food rather than its chemical composition, affect the amount of saliva secreted. WILSON and TRIBE (1963) found that with a constant food intake the secretion of parotid saliva in sheep was increased by 25 % when the hay was ground using a 1/16 in. screen but was decreased by 61 % when using a 1/32 in. screen. A decrease in salivary flow as a result of pelleting hay was observed in the investigations of OLTJEN et al. (1965), YARNS et al. (1965 a) and PUTNAM et al. (1961 b).

The supply of certain mineral elements has been observed to influence not only the composition (p. 21) of the saliva but also the amount of saliva. DENTON (1956) investigated the effect of Na deficiency on the secretion of parotid saliva in sheep. The secretion of parotid saliva was 2.68 l per day when the Na supply was adequate, but 1.71 l per day with Na depletion.

BELL and WILLIAMS (1960) observed that the salivary output from the exteriorized parotid duct in calves decreased according to the degree of Na depletion. HAWKINS et al. (1965) used dairy steers with unilateral parotid and rumen fistulas to investigate the effect on the salivary flow of Na supplementation in a corn silage — ground snapped corn diet. With levels of Na supplementation of 0.22, 0.65 and 1.10 % on an air-dry basis the volumes of secretion measured at the right parotid gland were 8.49, 14.75 and 17.11 litres saliva/24 hours respectively. The secretion at the 0.22 % Na supplementation level was significantly ($P < 0.05$) lower than at the two higher levels, which did not differ significantly from each other. The differences became smaller if the values were calculated per kg dry matter eaten, because the animals on the lowest Na level ate less food compared with the other groups. DENTON (1956), however, observed that very large amounts of Na (2x595 m-equiv. $NaHCO_3$) added to a ration consisting of. 0.4 kg of lucerne chaff and 0.4 kg of oat chaff decreased the volume of saliva secreted daily by sheep.

The addition of volatile fatty acids to the rumen in some cases caused a slight increase in the amount of saliva secreted (COATS et al. 1956, KAY 1958 a, ASH and KAY 1959). The pH of the rumen was, however, below normal (pH 3—4). CLARK and WEISS (1952) observed no changes in the parotid secretion of sheep and goats when dilute acetic acid or lactic acid was placed into the rumen. BAILEY and BALCH (1961 b) found no changes in the rates of secretion of mixed saliva when the pH of the ruminal ingesta of cattle was changes from 6.8 to 5.4 by addition of acetic acid. YARNS et al. (1965 b) observed a tendency for the mixed salivary secretion to increase during infusion of VFA sodium salts into the rumen.

Ingested water

Water is introduced into the reticulo-rumen as part of the food and as drinking water. The sum of these has been observed to make up some 13—24 % of the total volume of fluid entering the reticulo-rumen (BAILEY 1961 a, POUTIAINEN and LAMPILA 1967). BALCH (1958 a) observed that during eating, when drinking of water was at its peak, the fluid entering the rumen consisted of saliva and drinking water in approximately equal amounts.

Grass and fodder beets, like other juicy roots and tubers, contain as much as 90 per cent by weight of water. If the ration consists mainly of foodstuffs like these, the amount of water entering the reticulo-rumen with the food may be 40—50 litres per day. The amount of water introduced with dry foodstuffs, for example hay and concentrates, on the other hand, is only 2—3 litres per day (BAILEY 1961 a, WALDO et al. 1965, CAMPLING 1966) and the direct effect on the flow of fluid must thus be considered slight. The amount of water drunk by the animals depends on how much of their requirements they receive with the food at a specific time (cf. p. 11).

BEILHARZ and KAY (1963) showed that the osmotic pressure of the blood is a more important factor determining the intake of water by drinking than the osmolality of the rumen contents. On the other hand, a low osmotic pressure of the plasma does not fully inhibit thirst in sodium depleted sheep (BEILHARZ et al. 1962). BOTT et al. (1964) observed that a hypertonic NaCl-solution (270 m-equiv./l) introduced directly into the rumen of sheep instead of plain water brought about a greater consumption of water than could be attributed to the osmotic effect.

ELAM and DAVIS (1962) reported that the addition of sodium chloride (5 % of the ration) increased the average water consumption of steers by some 9 litres per day (32 %). A gradual increase in the NaCl-ration from 50 g/day to 500 g/day increased the water intake of cows from about 37 l/day to about 50 l/day (PFEFFER et al. 1965). On the other hand, in the experiments of HELFFERICH et al. (1965) severely Na-depleted cows drank 2—4 times more water than when on an adequate sodium diet. The maximum water intake was 108 l/day.

Little is known about the effect of drinking water on the flow of fluid through the reticulo-omasal orifice. ASH (1962) observed a rapid flow of fluid following drinking. Surges (18—100 ml) of fluid flowed from the sheep omasum during and immediately after drinking. OYAERT and BOUCKAERT (1961) concluded that the most important factor influencing the very abundant passage of fluid (mean value 462 ml/h) through the sheep omasum in their experiment was the excessive intake of water.

SCHALK and AMADON (1928) observed that under ordinary conditions of feeding and watering, water enters the reticulo-rumen. This view has since been confirmed by results obtained with several different methods. It has been observed that the oesophageal groove in the adult animal functions only on rare occasions (DUKES 1947, p. 313, RIEK 1954, VALLENAS 1965, p. 151). Using polyethylene glycol as a reference substance in the drinking water of sheep it was shown that all of the water ingested entered the reticulo-rumen (ANON. 1964). The passage of milk along the contracted oesophageal groove of calves has been noted in several investigations. WISE and ANDERSON (1939), however, found that when water was offered to calves, 3—6 months of age, from an open pail almost all of the water drunk flowed into the rumen.

Movement of water across the rumen wall

Beside the passage from the reticulo-rumen via the reticulo-omasal orifice one also must consider the fluid transfer through the rumen wall. It exerts a decreasing or increasing effect on the flow of fluid into the omasum depending on the direction of net transfer of fluid through the wall.

PARTHASARATHY and PHILLIPSON (1953) showed that the water flowed across the rumen epithelium as a result of an osmotic gradient. The authors concluded from their experiments that in sheep on a normal diet the osmotic relations between the rumen fluid and the blood were such as to make the absorption of water possible. They also mention the theoretical possibility of the water flowing in the opposite direction under special circumstances. In sheep fasted for 12—16 hours DAVEY (1936) measured the osmotic pressure of the rumen fluid and the blood. He found no differences in osmotic pressure between the blood, or the rumen-, reticulum-, and abomasum content and suggested that the absorption from the compartments of the stomachs keeps the osmolality isotonic with the blood plasma. HYDÉN (1961 b) measured the transfer of water through the wall of the rumen in sheep, using polyethylene glycol as a reference substance and measured the secretion of saliva by use of a catheter (HYDÉN 1958) or estimating it on account of the concentration of phosphorous is the saliva and the rumen fluid (p. 19). The absorption of water from the normal rumen contents was evident in 11 cases, the influx of water in one case and in two cases no tranfer could be established with certainly. The mean absorption rate was 0.15 l/hour.

ENGELHARDT (1963 a and b) investigated the rate of flow of fluid through the rumen in goats. He determined the flow of fluid via the reticulo-omasal orifice by use of the PEG method and simultaneously measured the transfer of water through the rumen wall, using tritium oxide, which was injected in blood and introduced in the rumen. He observed an abundant flow of water through the rumen wall taking place in both directions the mean rate in each direction being 40 l/24 h. The osmolality in the rumen fluid was about 35 mosm. lower than in the blood, on account of which the water was able to move also against this gradient. During successive measurements of equal duration, the volume of water transferred from the rumen to the blood was about the same as the volume transferred from the blood to the rumen.

WARNER and STACY (1965) observed that deprivation of food and water for 3 days brought about almost a 10 % decrease in osmolality of the rumen contents, but that the plasma osmolality remained fairly constant. Feeding brought about a rapid rise in osmolality in the rumen, especially if deprivation of water was continued. WEETH et al. (1967) observed that the plasma osmolality after 4 days of water deprivation was 329 mosm./kg and under water *ad lib.* conditions 275 mosm./kg. The concentrations of several elements in the rumen fluid and the blood affect the osmotic relations between these two components, on which relationship the flow of water through the rumen wall in turn seems to be dependent. With regard to osmosis, the most important elements are sodium and potassium, which are to be discussed later (p. 23). Volatile fatty acid and other fermentation products continuously formed in the rumen are readily absorbed and have little influence on the osmotic pressure and water balance (ANNISON and LEWIS 1962, p. 124, HUNGATE 1966, p. 193). The ruminant saliva and blood plasma are nearly isotonic (KAY 1960, BAILEY 1961 b). The influence of saliva on the osmotical relations between the rumen contents and the blood is primarily a stabilizing one and apparently limits the flow of water through the rumen wall.

Methods used for measuring the secretion of saliva and the total flow of fluid

Secretion of saliva

Of the investigations concerning the secretion of saliva, the majority deal with the secretion of parotid saliva, the measuring technique of which has been developed to a considerable extent. The most common procedure for measuring the secretion of parotid saliva is perhaps the permanent fistulation of one of the glands. The surgical technique for sheep is described by DENTON (1957), and his method has been used by many workers (e.g. BAILEY and BALCH 1961 a, DENTON and SABINE 1961, BLAIR-WEST et al. 1963, WILSON and TRIBE 1963).

In connection with the parotid fistula different devices have been developed by which the saliva after measuring and sampling can be returned to the circulating fluid. In this way one avoids the loss of sodium, which causes Na-deficiency in the animal if one does not substitute the loss with some mineral containing Na (DENTON 1957, DENTON and SABINE 1961).

STEWART and DOUGHERTY (1958) cannulated the parotid duct with polyethylene tubing, and the rate of flow was recorded with a droprecorder while another catheter led the saliva back into the oral part of the duct. AUTREY (1964 a) reporported a technique for the quantitative collection of parotid saliva from a steer. The plastic tube was inserted into the fistulated parotid duct, and the other end of the tube into a rubber collection bottle. The method used by KAUFMANN and ORTH (1966) is in principle the same, but they connected the saliva collection bottle by a tube to a bottle placed above the animal into which the saliva was pumped periodically, using a pump with a timing attachment. The saliva was led by a tube from the container into the rumen via the rumen fistula. BRÜGGEMAN et al. (1965) describe a method for measuring the secretion of parotid saliva in sheep which makes it possible to register the secretion of saliva automatically and then to direct it into the rumen.

Inaccuracy in the evaluation of the total quantity of parotid saliva from the one fistulated gland is caused, among other things, by the different size of the glands (KAY 1960), possible damage produced by fistulation (DENTON 1957) and by reduced chewing on the operated side (WILSON 1963 a).

With regard to the measurement of the secretion of mixed saliva, no generally accepted method seems to have been developed. This is probably also in part the reason why investigations concerning the secretion of mixed saliva are less frequent than those concerning parotid saliva secretion.

The methods by which the saliva was collected from the mouth of the animal either as it dribbled from the mouth of an anaesthetized animal or by means of a sponge from a normal animal (MCDOUGALL 1948) have given quite unreliable results with regard to the average flow of mixed saliva. EMERY et al. (1960) inserted a tube into the cardiac orifice via the rumen fistula. SASAKI and UMEZU (1962) used an intraoesophageal glass funnel and CUNNINGHAM et al. (1958) an inflatable rubber catheter. HYDÉN (1958) blocked the oesophagus of sheep with a bladder, whereby the saliva flowing down the oesophagus could be removed by suction. Excitation in the cardiac orifice or in the oesophagus may cause changes in the secretion of saliva, at least in measurements performed for a short time (CLARK and WEISS 1952, KAY and PHILLIPSON 1959). When measuring the secretion of mixed saliva during resting, one can also use the fistulation of the oesophagus (MCMANUS 1962, TRIBE and PEEL 1963, YARNS et al. 1965 a and b).

BALCH (1958 a), BAILEY and BALCH (1961 b) and BAILEY (1961 a) collected a swallowed bolus (during eating) or saliva (during resting) at the cardiac orifice in a specially designed rubber bag held at the orifice by hand via the rumen fistula. The saliva secreted into the fodder during chewing was derived by determining the water content of the fodder and the water content of the collected food boluses, the difference thus representing the saliva. When collecting saliva during resting, part of the contents of the dorsal sac was removed to allow the collection of saliva in the rubber bag. The bag was held against the cardia for about 3 sec at each swallowing in order to avoid the effect caused by excitation. The method does not permit the measuring of mixed saliva secretion during rumination.

BAILEY (1966) reported that measurements of the rate of swallowing can be used to detect the changes in rate of mixed salivary secretion in resting cows. This is based on the finding that the relationship between the rate of swallowing and the rate of salivary secretion was approximately linear. HYDÉN (1961 b) suggested the possibility of evaluating the volume of salivary secretion from the net gain of phosphate in the rumen and the mean concentration in the rumen and the saliva. The transfer of phosphate through the wall of the rumen has been observed to be negligible (SPERBER and HYDÉN 1952, PARTHASARATHY et al. 1952, HYDÉN 1961 b). SMITH (1959) mentions the possibility of estimating the rate of the saliva flow based on the passage of fluid from the rumen, calculated with the aid of PEG. An indirect method for measuring the flow of mixed saliva into the reticulo-rumen based on the total flow of fluid is described by POUTIAINEN and LAMPILA (1967). The method is also described in the experimental part of the present investigation (p. 29).

Total flow of fluid through the reticulo-omasal orifice

The measurement of the flow of fluid requires the use of a substance soluble in water in order that its passage through the reticulo-omasal orifice should parallel with the flow of water. SPERBER et al. (1953) have defined the requirements to be placed on a suitable reference substance measuring the flow of fluid. The substance should preferably be homogenous and well defined from the chemical point of view and it ought to be possible to determine it with reasonable ease and accuracy. It should not be taken up or absorbed, produced or destroyed to a significant degree by the rumen microorganisms or by other parts of the contents and it should not influence the activity of these organisms or the rumen itself. The reference substance must not pass through the rumen wall in appreciable quantities.

The polyethylene glycol (PEG) is found to be a quite practicable reference substance. A detailed description of the method and its adaptation is given by HYDÉN (1961 a). This method has been used by many workers in recent years (CORBETT et al. 1958, 1959, LAMPILA and POIJÄRVI 1959, SMITH 1959, 1964, OYAERT and BOUCKAERT 1960, 1961, WELLER et al. 1962, ULYAT 1964 a and b, LAMPILA 1965).

Phenol red is also recommended for measuring the amount and passage of fluid through the alimentary tract (SMITH 1964, HECKER et al. 1964). This substance is poorly recovered after passing through the alimentary tract (SMITH l.c.).

HOGAN (1964) indicated that radioactive chromium (Cr^{51}) chelated with ethylenediaminetetra-acetic acid (EDTA) fulfills the requirements of a water soluble marker and can be used for studying the transfer of digesta from the rumen.

ULYAT (1964 b) found that lithium is unsuitable as a marker for measuring the volume of water in the rumen and the flow of fluid from the rumen. A method for estimating the volume of rumen fluid by use of antipyrine (AP) and N-acetyl-4-aminoantipyrine (NAAP) is used by some workers (REID et al. 1957).

Factors influencing concentrations of sodium and potassium in the rumen fluid

Inflow of sodium and potassium in saliva

Saliva secreted by different glands. — MCDOUGALL (1948) performed the first consistent and detailed investigation of the mineral composition of ruminant saliva. The sodium content in sheep parotid saliva was on an average 177 m-equiv./l and the potassium content 8 m-equiv./l. The Na content of mixed saliva varied from 160 to 200 m-equiv./l and the K content from 4 to 11 m-equiv./l. PHILLIPSON and MANGAN (1959) studied the composition of parotid and submaxillary saliva collected from cannulated ducts and the saliva secreted from the remaining salivary glands collected from the mouth of cattle. The Na contents of the different secretions were: parotid saliva 137 m-equiv./l, submaxillary 14 m-equiv./l and residual saliva 110 m-equiv./l. The K contents were: 14,14 and 17 m-equiv./l respectively. KAY (1960 a and b) observed that the inferior molar glands and the small mucous glands secrete saliva which is like parotid saliva in inorganic composition. It contains 175—185 m-equiv. Na/l and 4—9 m-equiv. K/l. The saliva secreted from the submaxillary, sublingual and labial glands is, however, quite different, containing from 15 to 40 m-equiv. Na/l and from 6 to 26 m-equiv K/l.

The contribution of the submaxillary and sublingual glands to the total of saliva is estimated to be quite small (KAY and PHILLIPSON 1959, KAY 1960 a) due to the slow rate of flow (KAY 1960 a) and the restricted time of activity (KAY 1958, ASH and KAY 1959, MEYER et al. 1965).

BAILEY and BALCH (1961 b) showed that the composition of mixed saliva obtained from resting cows was almost the same as that of the parotid saliva. The mean Na content in parotid saliva was 157 m-equiv./l and in mixed saliva 161 m-equiv./l. The K contents were 7.0

and 6.2 m-equiv./l, respectively. The close similarity in Na and K contents for parotid and mixed saliva of cattle and sheep under resting conditions has been observed in many investigations (Mc Dougall 1948, Phillipson and Mangan 1959, Kay 1960, Dobson et al. 1960, Dobson 1963, Tribe and Peel 1963).

Variations in the composition of mixed saliva. — The rate of secretion has been observed to change the composition of the saliva. The sodium concentration of parotid saliva has been noted to increase and the potassium concentration to decrease as the rate of secretion increases (Coats and Wright 1957, Kay 1960, Bailey and Balch 1961 a, Dobson 1963). The same tendency is also observed for the Na and K contents of mixed saliva in cows (Bailey and Balch 1961 b). The results of Boda et al. (1965) indicated, that when the rate of flow of mixed bovine saliva decreased from about 60—65 ml/min. to about half of this value, the level of K increased from a mean value of 5.4 m-equiv./l to a mean of 10.7 m-equiv./l. At the same time the Na content decreased from a mean value of 152 m-equiv./l to 143 m-equiv./l. The sum of these two cations thus remained on a fairly constant level. According to same investigations the rate of secretion of parotid saliva has not noticeably changed the Na/K ratio in the normal Na-repleted animal. In the Na-deficient animal the Na/K ratio increased with an increasing rate of secretion (Denton 1956, 1958, Goding and Denton 1960, Dobson 1963).

Kaufmann and Orth (1966) and Kaufmann (1966) observed that in cattle the Na concentration of parotid saliva decreased from a value of 145 mg/100 ml when the rate of secretion was 31.1 l/day (from one gland) to 113 mg/100 ml when rate of secretion was 22.5 l/day. The K concentration correspondingly rose from 309 to 394 mg/100 ml. The authors assume that the deficiency in sodium in part affected the change in the Na/K ratio.

The most noticeable changes in the Na and K contents of the saliva are influenced by the sodium deficiency of the animal. The great changes with regard to the Na/K ratio and the reciprocal compensating effect of these two cations was first observed by Denton (1956) in his experiments with sheep fitted with a parotid fistula. The Na/K ratio may drop from 18 to 0.5. A large intake of sodium raised the Na/K ratio to a value of 25. In some cases the Na/K ratio may drop to as low as 1/18 (Denton 1957).

Dobson et al. (1960) showed that during a progressive sodium depletion in sheep the sodium of the parotid and mixed saliva was successively replaced by potassium. Changes in the Na and K concentrations of the mixed saliva were in close correspondence with those of the parotid saliva ($P < 0.001$).

Kemp and Geuring (1966) and Kemp (1966) reported a decrease in Na concentration of the saliva from about 3.50 to 1.00 g/l and an increase in K concentration from about 0.25 to 3.50 g/l due to sodium deficiency in high-yielding dairy cows.

The noticeable decrease in Na concentration and increase in K concentration of the saliva of animals fed fresh grass or on pasture is connected with the low sodium content of grass, resulting in a sodium deficiency in the animal (Sellers and Dobson 1960, Dobson 1963, Dobson and McDonald 1963).

The adrenal secretion of aldosterone has been observed to regulate changes in the Na/K ratio of the saliva in connection with Na-deficiencies. The secretion of aldosterone increases during a period of Na-deficiency and at the same time the parotid gland becomes more sensitive to the effect of this hormone (Denton 1956, Blair-west et al. 1963, 1965, Bott et al. 1964, Scott 1966).

The relationship between the concentration of sodium and potassium in mixed saliva and rumen fluid. — Bailey (1961 b) presents results showing the interdependence of the sodium and potassium contents of mixed saliva and rumen fluid. On five different diets the Na concentration of the rumen contents remained on an average 17 % below the mean Na concentration of the mixed saliva. The Na content of mixed saliva varied between 28—168 m-equiv./l and that of rumen fluid at the same time between 60—180 m-equiv./l. The K content of mixed saliva (4—75 m-equiv./l) was invariably lower than that of rumen fluid (17—85 m-equiv./l). The sum of the Na and K in equivalents was about 166 m-equiv./l in mixed saliva. This value tended to decrease somewhat when the Na concentration dropped below 120 m-equiv./l and to increase somewhat when the K concentration rose above 164 m-equiv./l. The time elapsing after feeding seems to have no influence on the Na and K concentrations of mixed saliva.

Sellers and Dobson (1960) observed a marked decrease in Na concentration of the saliva and an approximately equal increase in the K concentration after transferring sheep from a diet consisting of hay or hay and meal to grass feeding. The changes in Na and K concentrations of the rumen fluid were closely related to the Na/K-changes of the saliva. On a basal diet the Na concentration in the rumen fluid was about 100 m-equiv./l and that of K 30 m-equiv./l and on a grass diet the values were 25 and 100 m-equiv./l, respectively.

In the investigations of Emery et al. (1960) the Na concentration in the rumen fluid rose ($P < 0.05$) in accordance with the increase in the proportion of hay diet consisting of hay plus concentrates (the proportions of hay were: 20, 40, 60, 80 and 100 %). A corresponding tendency with regard to the Na concentration of the saliva could not be observed. No statistically significant differences could be found between the diets with regard to the Na concentrations of the saliva, but the lowest values for both of the experimental cows were noted on the pure hay diet. The sum of Na and K in the saliva increased as the proportion of grain increased ($P < 0.01$).

When transferring animals from indoor feeding to pasture (without NaCl supplement), some investigators have observed that sodium depletion is not the only factor causing changes in the Na/K ratio of the saliva and the rumen fluid. According to Dobson and McDonald (1963) Na/K ratio of the saliva gradually decreased in grass fed sheep although the animals were supplement with salt, and sodium deficiency thus should not have occurred. The drop in Na concentration and rise in K concentration of the rumen fluid occurred at a noticeably greater rate than the corresponding change in composition of the mixed saliva. An example of the unexpected changes in the Na/K ratio of the saliva and the rumen fluid connected with changes in the feeding is provided by the experiment carried out by Dobson et al. (1966). They observed that the K concentration of mixed saliva rose rapidly when sheep fed 9 days on a ration of grass (low in sodium) were transferred to a diet of hay and meal (high in sodium). At the same time an approximately equal decrease in Na concentration took place. The K concentration of the rumen fluid was high on a grass diet and low on a hay and meal diet, as one would expect the Na contents of the food. It was concluded that this phenomenon might be associated with a temporary increase in the sodium requirement of the animal.

Intake of sodium and potassium

The sodium content of the food consumed daily is generally quite small in comparison to the amount of this ion in the rumen fluid. For different combinations of foodstuffs comprising hay, concentrates, beets, silage or grass the amount of sodium received by the cow in the food ranges between about 3 and 20 g/day. The sodium entering the rumen with the food and drinking water does not seem to have a direct effect on the Na concentration of the rumen fluid. On the contrary, it has been observed that during the feeding interval the Na concentration of the rumen fluid is generally at its lowest immediately after feeding (Bailey 1961 b, Lampila 1964, 1965, Kemp and Geuring 1966). This phenomenon has been assumed to depend partly of the diluting effect of the drinking water (Lampila 1964) or even on the absorption of Na (Bailey 1961 b). Stacy and Warner (1966) observed an increase in the absorption rate of Na from the rumen fluid into the blood as a consequence of feeding.

In some investigations the effect of sodium supplementation on the Na concentration of the saliva and the rumen fluid has been investigated. HAWKINS et al. (1965) supplemented a basal diet of low Na content with 0.22, 0.65 and 1.10 % sodium on an air dry basis. The Na concentration in the parotid saliva averaged 81.4, 157.3 and 147.4 m-equiv./l respectively. KEMP and GEURING (1966) observed in their long-term experiments with dairy cattle that supplementing the diet with Na above the level adequate to keep the animals at a positive Na-balance does not increase the Na concentration of the saliva noticeably. Supplementing a basal diet poor in sodium with only 32 g NaCl increased the Na concentration of the saliva to above 3 g/l and decreased K concentration to below 0.5 g/l, and these values remained almost unchanged by supplementations of 38, 80, 110 and 220 g/day.

Dietary potassium is a quite important factor influencing on the K concentration of the rumen contents. An indication on this is, for example, the noticeable rise in K concentration of the rumen fluid as a consequence of feeding (BAILEY 1961 b, LAMPILA 1964, KEMP and GEURING 1966). The K content of foods is high compared to the Na content (BARNETT and REID 1961 p. 184). In ordinary foods the amount of K entering the rumen of the cow varies within the range 40—240 g per day depending on the mixture and amount of food (BAILEY 1961 b, HORROCKS 1964, LAMPILA 1964, 1965). Potassium as well as sodium in foods are found to a great extent in the form of inorganic and organic water soluble salts.

The high K concentration of the rumen contents during grass- or pasture feeding seems to be due partly to the direct effect of the high K content of young grass (DOBSON et al. 1966). The greater effect is, however, indirect in character because the low Na content of the grass causes a sodium deficiency in the animal whereby the K concentration of the saliva rises considerably (cf. p. 21), bringing about a rise in K concentration of the rumen fluid also (SELLERS and DOBSON 1963, DOBSON 1963).

Supplementing the rumen contents of sheep on a hay or grass-cube diet with a potassium salt solution (260—540 m-equiv./day) caused an increase in the K concentration of the mixed saliva as well as in the rumen fluid. The effect was similar in direction in Na-repleted and Na-depleted animals. As a consequence of potassium supplementation a drop in Na concentration was noted in the saliva as well as in the rumen fluid (GOODALL and KAY 1964, SCOTT 1966).

Passage of sodium and potassium through the rumen wall.

The passage of mineral elements through the rumen wall was first indicated in the studies of DANIELLI et al. (1945). They reported that the sodium ions are absorbed in roughly equal proportions to the anions. Accordind to MASSON and PHILLIPSON (1951) and ASH and DOBSON (1963) the uptake of fatty acid anions from the rumen through the wall is accompanied by a loss of CO_2 and the production of bicarbonate in the rumen content. SPERBER and HYDÉN (1952) expressed the opinion that Na ions pass from the rumen into the blood as a result of active processes in the rumen wall. Potassium moves in the opposite direction and against the concentration gradient. PARTHASARATHY (1952) reported that Na is absorbed against the concentration gradient, and K on account of its high concentration in the rumen fluid. PARTHASARATHY and PHILLIPSON (1953), on the other hand, found that Na and K are absorbed from the rumen only when their concentration there exceeds that of the blood. DOBSON (1955, 1959) found that Na can pass from the rumen contents against both electrical and concentration gradients. The active transportation of K could not be demonstrated (BARNETT and REID 1961, p. 172).

HYDÉN (1961 b) observed in his experiments with sheep that in most cases there was an absorption of Na and K or no definite movement through the rumen wall. He estimated the mean rate of absorption in his 18 experiments to be 0.5 g Na and 0.13 g K per hour. The animals had fasted for 2—12 hours before the experiment but had free access to water.

An electrical potential gradient seems to be a quite important aspect affecting the transportation of sodium and potassium. The contents of the reticulo-rumen of sheep have been observed to be some 30—40 mV negative relative to the blood (Dobson and Phillipson 1958, Sellers and Dobson 1960). The rumen potential is negatively correlated with the Na concentration and positively with the K concentration of the rumen (Dobson 1959, Sellers ans Dobson 1960, Scott 1966). A tenfold rise in the K concantration of the rumen fluid is observed to bring about a 43 mV rise in the potential (Scott 1966).

Stacy and Warner (1966) have observed an accelerated absorption of Na from the sheep rumen under hypertonic conditions as found after feeding, or adding solutions of KCl, mannitol or urea.

The influence of sodium and potassium absorption or influx on the increase or decrease in the concentrations of these elements in the rumen contents depends essentially on whether water transportation through the rumen wall has possibly occurred at the same time (cf. p. 18). In order to maintain the osmotic balance between the rumen fluid and the blood, any appreciable absorption of Na or K can hardly occur for a long period of time if water is not simultaneously absorbed.

Flow of sodium and potassium through the reticulo-omasal orifice

The daily outflow of any component from the reticulo-rumen can be estimated by multiplying its mean observed concentration in the rumen fluid by the measured flow of fluid during the same time. With regard to Na and K the amounts calculated in this way obviously fairly well represent the total amounts transported into the omasum. The flow of fluid is partly influenced by different factors and partly also by the factors affecting the concentrations of Na and K in the rumen fluid. These factors were discussed in the earlier paragraphs.

Investigations concerning the amounts of Na and K passing through the reticulo-omasal orifice of cows or sheep per unit of time are quite few. This is probably due to the fact that only in a few investigations have the both factors required for calculating the flow of these minerals been determined.

In one experiment carried out by Hydén (1961 b) it was observed that the outflow of Na from the rumen of a sheep was 0.4 g per hour and the outflow of K 0.1 g per hour. The animal was starved for 10 hour before the experiment, but had access to water and saltlick.

Lampila (1965) measured the passage of fluid in two cows using PEG as a reference substance and determined the Na and K contents of the rumen fluid. Estimating the volume of rumen fluid to be 50 litres, he calculated that the flow of Na from the rumen was 309 g/24 h for one of the cows and 379 g/24 h for the other. The flow of K was 211 and 428 g/24 h respectively. The differences in flow rate were chiefly due to the different rate of flow of fluid. The concentrations of these ions differed less.

In later work (Poutiainen and Lampila 1967) in which more precise calculations were made, the outflow of Na for two cows on different diets was 152 g/12 h and 145 g/12 h and the outflow of K 304 and 53 g/12 h respectively. Differences were noted for the rate of flow of fluid as well as for the Na and K concentrations in the rumen fluid.

EXPERIMENTAL METHODS AND CALCULATION OF RESULTS

Methods

Experimental animals and their feeding

The experiments were carried out with two Ayrshire cows, INA and IRPU, furnished with rumen fistulas. At the time of fistulation the animals were about 8 years old, in good condition and health. Rumen fistulas were made according to the procedure of Stoddard et al. (1951). The tube inserted into the aperture was plugged with an ordinary large sized cork, which was removed only when samples were taken. The fistulation of both cows was succesful. The quite insignificant outflow of rumen fluid taking place when the animals were resting on the fistulated side of the chest can be considered as negligible with regard to the effect on the results.

During the experimental period consisting of two indoor feeding periods, 1964—65 and 1965—66, cow INA calved on Febr. 28th 1965 whereas cow IRPU carried no calf. The average daily milk yield during the experimental periods varied within the range 22 kg to drying off for INA and from about 8 kg to drying off for IRPU. During the indoor feeding periods in question the animals were kept on the experimental diets almost continuously. Live weight measurements were carried out about once a month. The average live weight of INA during the whole experimental period was 530 kg (505—563 kg) and that of IRPU about 590 kg (540—625 kg). INA was all the time more or less in average condition, but at the end of the test IRPU fattened considerably due to rations exceeding the food requirements.

The animals remained healthy during the whole of the experimental period except for the severe mastitis contracted by cow INA, which caused the right hand quarter of the fore-udder to cease functioning. Three months after the sickness the animal was again included in the experiment.

Feeding took place twice a day, with a 12 hour interval, at 5 a.m. and 5 p.m. At each feeding half of the ration in question was given. The concentrate mixture containing the mineral supplementation was given first and the hay about half an hour later. When the ration consisted only of long hay it was placed before the animals at the same time as the hay given in connection with the other diets. The minerals were then given with the hay because the animals did not eat them evenly if they were offered separately. The finely ground hay (1.5 mm screen), when it was used, was mixed into the concentrates.

Table 1. Composition of the experimental diets

Diet No.	kg dry matter per day *)				Long hay % of total dry matter	NaCl supplement g/day
	long hay	ground hay	concentrate mixture **)	total		
1 *	7.0	—	7.0	14.0	50	100
2 *	7.0	—	7.0	14.0	50	50
3 *	7.0	—	7.0	14.0	50	0
4	6.0	—	6.0	12.0	50	100
5	6.0	—	6.0	12.0	50	50
6	6.0	—	6.0	12.0	50	0
7	4.5	—	4.5	9.0	50	100
8	4.5	—	4.5	9.0	50	50
9	4.5	—	4.5	9.0	50	0
10	9.0	—	—	9.0	100	50
11	2.25	2.25	4.5	9.0	25	50
12	0.9	3.6	4.5	9.0	10	50
13	3.0	—	3.0	6.0	50	50
14	3.0	—	3.0	6.0	50	0
15	6.0	—	—	6.0	100	50
16	1.5	1.5	3.0	6.0	25	50
17	0.6	2.4	3.0	6.0	10	50
18 *	3.0	—	—	3.0	100	50
19 *	1.5	—	1.5	3.0	50	50
20 *	0.3	1.2	1.5	3.0	10	50

* Only one cow on this diet
*) Dicalcium phosphate 100 g/day with all diets
**) Barley 45 %, oats 45 %, commercial protein rich mixture 10 %

In general the whole food ration was consumed within three hours from the beginning of the feeding. At higher levels of dry matter intake the eating some times proceeded for longer periods of time. Any food residue was removed and weighed before the beginning of the next feeding. When long hay was fed it was consumed completely. Shavings were used as bedding.

The animals had free access to water. On the days when samples were taken the amount of water drunk was determined by measuring the volume consumed during 3 hour periods (from 5 a.m. to 5 p.m.).

The diets used in the investigation are presented in Table 1. However the diets were not fed in the order seen in the table. When maintaining the experimental program the ration could not be composed exactly according to the respective food requirements of the animals. The length of the experimental periods and the order

Table 2. Mean chemical composition of foods and mean content of sodium and potassium in foods and drinking water.

Indoor period	Ingredient	Average % of dry matter					g per kg dry matter	
		ash	crude prot.	crude fat	crude fibre	N-free extr.	Na	K
1964—65	Hay, long	6.65	10.09	1.96	29.88	51.42	1.55	22.61
	Hay, ground	7.14	9.39	1.69	30.47	51.31	2.11	16.61
	Concentrate mixture ...	3.36	16.69	3.68	8.60	67.67	0.07	6.25
	Drinking water	—	—	—	—	—	22.4 *)	2.4 *)
1965—66	Hay, long	6.53	9.00	1.64	34.08	48.75	0.45	24.26
	Hay, ground	6.64	8.84	1.81	30.77	51.94	2.63	16.13
	Concentrate mixture ...	3.24	15.47	4.16	8.12	69.01	0.04	6.25
	Drinking water	—	—	—	—	—	20.5 *)	2.3 *)

*) ppm

of the periods are given in Appendix. Before the actual measurements were begun the animals were kept on each of the experimental diets for periods varying from 10 to 27 days and averaging 16 days.

The amounts of dry matter eaten by the animals on each diet are given in Appendix. On an average the animals consumed 93—108 % of the intended amount of dry matter at the different dosage levels. On diets 4—6 (Table 1) cow INA did not eat 12 kg dry matter per day as planned, but only about 11 kg. For this reason the diets 4—6 with regard to INA are in the presentation treated as being dosage levels of 11 kg dry matter/day. The average chemical composition of the foods used during the indoor feeding periods in question is presented in Table 2. Likewise the sodium and potassium concentrations of the foods and the drinking water are given as average of determinations made during different experimental periods.

Dosage of polyethylene glycol (PEG)

The reference substance used was CARBOWAX Polyethylene glycol 4 000 manufactured by Union Garbide. The dose was in general 300 g, but for diets 4 and 5 it was 200 g. For diets 2 and 3 the dosage was 2x200 g. The weighed amount of polyethylene glycol was first dissolved in one litre of tap water and the solution was introduced into the rumen via the fistula. The dosing was performed with the help of a funnel with a perforated metal tube extension, which facilitated the distribution of the dosage uniformly over the rumen contents. The dosing usually took place one hour before the beginning of the afternoon feeding (5 p.m.) with the exception of diets 4 and 5 (Table 1) where PEG was introduced into the rumen at times varying between 8 and 10 p.m. For diets 2 and 3 the first 200 g of the solution was given at 4 p.m. and then an equal amount at 8 p.m. The dosing of polyethylene glycol for a new period of measurement took place 24 hours after the previous one at the earliest.

Samling and preparation of samples

F r o m t h e r u m e n c o n t e n t s samples from the different parts of the rumen were taken at six different times during the 24 hour measuring period. The first samples were taken one hour after the dosing of PEG. The following samples were taken after 12 hours (5 a.m.) and during the day samples were taken regularly at 3 h intervals (3, 6, 9 and 12 hours from the beginning of feeding). For diets 4 and 5, however, sampling was begun at 5 a.m. In order to make the presentation more practicable for the later calculations, the 5 a.m. feeding is used as base time (0) from which the hours are counted forwards for the day period (+) and backwards for the night period (—).

At each time samples were taken from four different parts of the rumen in the following order: upper, central, lower and lower fore part. The samples from the upper and central parts were taken with a pair of forceps having long fluted jaws, and the fairly solid material obtained was squeezed by hand to obtain the sample of liquid. When samples were taken from the central part contents of the upper part often also were included, but this was avoided as far as possible. The samples from the fluid contents of the lower and lower fore parts were taken by means of a brass tube (7/8 in. diam.) having two 1 cm holes about 5 cm from the lower end (LAMPILA 1964, p. 29). A more exact description of the location of the points of sampling has been presented in an earlier paper (LAMPILA and POUTIAINEN 1966).

A 150 ml sample of liquid, representing different part of the rumen, was taken at each time. The solid material from which the fluid had been squeezed was pushed back into the rumen via the fistula.

From the mixed saliva samples were taken three times during the 12 hour day period at 0, 6 and 12 hours after the beginning of feeding. The saliva samples were taken by means of a perforated capsule inserted into the oesophagus of the animal. This device has been described in an earlier paper (POUTIAINEN and LAMPILA 1967). The capsule was kept in the oesophagus until the required amount of saliva (50—100 ml) had run into it. Usually this took only a few minutes. Only clear saliva containing no noticeable amounts of food debris from rumination was accepted as a sample.

The procedure described above for taking rumen and saliva samples was repeated three times for each diet, with a 24 hour non-sampling interval between each period of sampling. For the rumen fluid 72 samples per diet were usually obtained (60 for diets 4 and 5) and for the saliva 9 samples.

Both the rumen fluid and saliva samples were transported immediately to the laboratory in glass containers. After centrifuging for 20 minutes at 4 000 r.p.m. in order to separate the plant material, the chemical determinations were made of the supernatant, which was kept at +4°C. Whenever possible the analyses were made the same day the samples were taken or the following day. If for some reason the samples had to be stored a longer period of time, they were frozen.

Chemical analyses

Determination of PEG was made according to the method of HYDÉN (1956). In measuring the turbidity a nephelometer (EEL nephelometer head with a Unigalvo Type 20 Galvanometer) was, however, used instead of the spectrophotometer. The measurement was always carried out exactly 5 minutes after the addition of trichloroacetic acid. In calibrating the nephelometer two tubes of standard turbidity were used and a check of the standard curve was made, with each series of measurements using a solution of known concentration. The PEG concentration of the samples to be measured was always adjusted to 0.05—0.06 mg/ml. When the PEG dosage was 300 g the concentration in the rumen after 24 hours was still sufficiently high. As this dosage proved to be too small for diet 1, 200 g of PEG (cf. p. 26) was added in two portions to the other diets at the same dry matter level (diets 2 and 3).

Determination of sodium in the rumen fluid and mixed saliva was made using the supernatant fluid samples and the sodium electrode (POUTIAINEN and LAMPILA 1966). Using this method linearly 1.2 % higher values on an average were obtained for the rumen fluid and the saliva than when using a flame photometer. The sodium content of foods and drinking water was determined with a flame photometer. For the foods the determinations were made on ash extracts and for the water directly, diluting when necessary with distilled water. The burning procedure was carried out according to the method of SALONEN et al. (1962).

Determination of potassium in the rumen fluid and the mixed saliva was made on the diluted supernatant fluid directly with the flame photometer. The potassium content of the foods and drinking water was determined with a flame photometer, using samples prepared in the same manner as for the sodium determinations.

Calculations and statistical methods used

Flow of fluid

The factors needed for the calculations the volume of fluid flowing from the reticulo-rumen into the omasum during the certain time interval are the volume of fluid in the reticulo-rumen and the fluid flow rate per unit of volume. The calculation of these factors was made from the PEG concentration of the rumen fluid and the decrease in the concentration observed during the measuring period.

T h e v o l u m e o f f l u i d in the reticulo-rumen is calculated from the concentration of PEG which a given amount of polyethylene glycol (usually 300 g) calls forth in the rumen fluid. As the first samples were taken only one hour after the addition of PEG, the concentration of PEG at the time of dosing was found by extrapolation. This was done by use of the calculated PEG dilution equation for the night period (from —12 to zero hours). From this the $\log_{10}$ (PEG mg/l) concentration at time —13 was calculated and from that the concentration in g/l. An estimate of the volume of fluid in the rumen was obtained by dividing the amount of PEG (g) added to the dose by the observed concentration (g/l). For the diets 2 and 3 a PEG dilution equation could not be calculated for the time interval —12 to zero hours on account of the introduction of additional reference substance within the period (cf. p. 26) and for diets 4 and 5 account of the differing time of PEG dosage. The extrapolation of the concentration of reference substance to the time of dosing was in these cases done graphically, assuming that the concentration of PEG after dosing decreased at the same rate as during the day period of the diet in question, from the time of feeding during the corresponding interval. The concentrations of PEG used in the determination of the volume of fluid were also here measured immediately before the beginning of feeding.

When calculating the r a t e o f f l o w o f f l u i d from the reticulo-rumen it was assumed that the PEG concentration decreases exponentially. Assuming the rate of flow of fluid and the volume of fluid to be constant on an average, one can define the change in PEG concentration with time by the general equation (Hydén 1961 a p. 55—56):

$$C_t = C_0 \cdot e^{-kt}$$, where
C_t = concentration of PEG at time t
C_0 = concentration of PEG at time 0
e = base of natural logarithms
k = rate constant

In this investigation the equations depicting the dilution of PEG have been calculated by placing the $\log_{10}$-values of the PEG concentration on the ordinate and the time in hours on the abscissa. The equation obtained is thus:

$$\log_{10}C_t = \log_{10}C_0 — bt$$

From the equations given, $k = 2.3026 \cdot b$. By use of the constant k one can calculate the following values defining the flow of fluid through the reticulo-omasal (R—O) orifice:

$p = 100k$
$u = kV$
$F = kVt$, where
V = volume of fluid in the reticulo-rumen (l)
p = rate of flow of fluid as a percentage from the rumen fluid volume per hour (vol. %/h)
u = rate of flow of fluid (l/h)
F = passage of fluid in t hours (l)

N u m e r i a l e x a m p l e o f t h e c a l c u l a t i o n s.

Diet 1 (cf. Fig. 1 p. 31 and Table 3 p. 33)

Volume of fluid in the reticulo-rumen

$y = 2.85 — 0.0749\ X$ (night period)
$\log PEG_{-13} = 2.85 — 0.0749 \cdot (—13)$
$= 3.8237$
$N \log PEG_{-13} = 6\,664$ mg/l i.e. 6.664 g/l

Dose of PEG 300 g

$V = 300$ g/6.664 g/l
V = 45.0 l

The flow of fluid through the reticulo-omasal orifice

$$y = 2.84 - 0.0961\ X \text{ (day period)}$$
$$k = 2.3026 \cdot 0.0961$$
$$k = 0.2213 \text{ (rate constant)}$$
$$p = 100 \cdot 0.2213$$
$$p = 22.1 \text{ vol. \%/h}$$
$$u = 0.2213 \cdot 45.0$$
$$u = 9.95\ l/h$$
$$F_{12h} = 12 \cdot 9.95$$
$$F = 119.3\ l/12\ h$$

The statistical calculations concerning the rate and volume of flow of fluid were made according to methods described in the book »Statistical Methods» by SNEDECOR (5th Ed. 1956).

The calculation of terms used in computing the regression equations are given on p. 158 of the book (Model I, fixed X). The confidence limits for the rate of flow in vol.% were calculated by taking $b \pm t_{0.01} \cdot s_b$ (p. 136).

The confidence limits given in figures 1—7 and 10—14 were computed from the formula:

$$S_{\hat{Y}} = s_{y \cdot k} \sqrt{1/n + x^2/\Sigma x^2} \quad \text{(SNEDECOR 1956, p. 137—138)}$$

The calculations were performed by substituting the values 0, +6 and —6 for the deviation x $(= X - \overline{X})$ in the equations for the day period as well as for the night period. The confidence limits were computed using a 99 % probability level $(t_{0.01} x \pm s_{\hat{Y}})$. The confidence limits for the estimate of the volume of fluid in the reticulo-rumen were calculated from the above formula using the computed equation for the night period, taking x as equal to —6.

The standard error of the total flow of fluid (Table 3 and 5) was calculated by taking into account the standard deviation of the rate constant $(s_{\bar{k}})$ as well as that of the volume of fluid $(s_{\overline{V}})$. The calculation of the standard error of the product was made in the following way (VOLK 1958 p. 141—143):
When the product is $u = kV$ its standard error is

$$s_{\bar{u}} = kV \sqrt{\frac{s_{\bar{k}}^2}{\bar{k}} + \frac{s_{\overline{V}}^2}{\overline{V}}}$$

The 99 % confidence limits for the flow of fluid during a given period of time were computed from s_u · number of hours · statistical t-value.

The difference in the rate of flow of fluid between the night and day period was tested by calculating the difference between the regression coefficients in the equations of the two periods at the same diet. The procedure was that described by SNEDECOR (p. 397—398).

All calculations and tests described above were performed on a computer using specially written programs.

Flow of mixed saliva

The contribution of saliva to the flow of fluid was calculated by subtracting the water of the food and the drinking water from the total flow of fluid. The same confidence limits were used for the calculated mean saliva secretion as for the mean total flow of fluid, because the error occurring in measuring the water intake can be considered negligible compared to the error in measuring the flow of fluid. The effect of different factors (cow, dosage levels of dry matter and sodium chloride, proportion of coarse fodder from the dry matter) on the flow of saliva has been tested by an analysis of variance with a factorial arrangement of the experiment (SNEDECOR 1956, p. 360).

Flow of sodium and potassium

The mean concentration of sodium and potassium in the mixed saliva for each diet was calculated during a period of 3 days and at 3 different times (0, 6 and 12 h) as an average of the samples taken (cf. p. 00). The dispersion lines (Figs. 17—20) give the 99 % confidence limits for the means of the concentrations. The mean concentration of Na and K $(C_{\overline{X}})$ in the rumen fluid during the 12 hour day period was calculated from the mean concentration of samples representing the four different parts of the rumen (cf. p. 27) collected over a period of 3 days at C_0, C_3, C_9 and C_{12} respectively, using the following equation:

$$C_{\overline{X}} = \frac{\frac{C_0 + C_{12}}{2} + C_3 + C_6 + C_9}{4}$$

When calculating the confidence limits of the mean concentrations, only the variation caused by the localities and days of sampling was included in the standard error while systematic variation between the time periods was eliminated.

The flow of Na and K into the rumen in saliva was calculated by multiplying the volume of saliva (in 12 hours) by the mean concentration of these elements in the saliva during the same time interval. The outflow of Na and K in the rumen fluid was correspondingly calculated by multiplying the volume of the fluid by the concentration in the fluid during the same time. The confidence limits for the inflow of Na and K in the saliva and the outflow in the rumen fluid were calculated using the equation already presented (cf. p. 29). The factors making up the product are: the volume (l) · concentration (m-equiv./l).

RESULTS

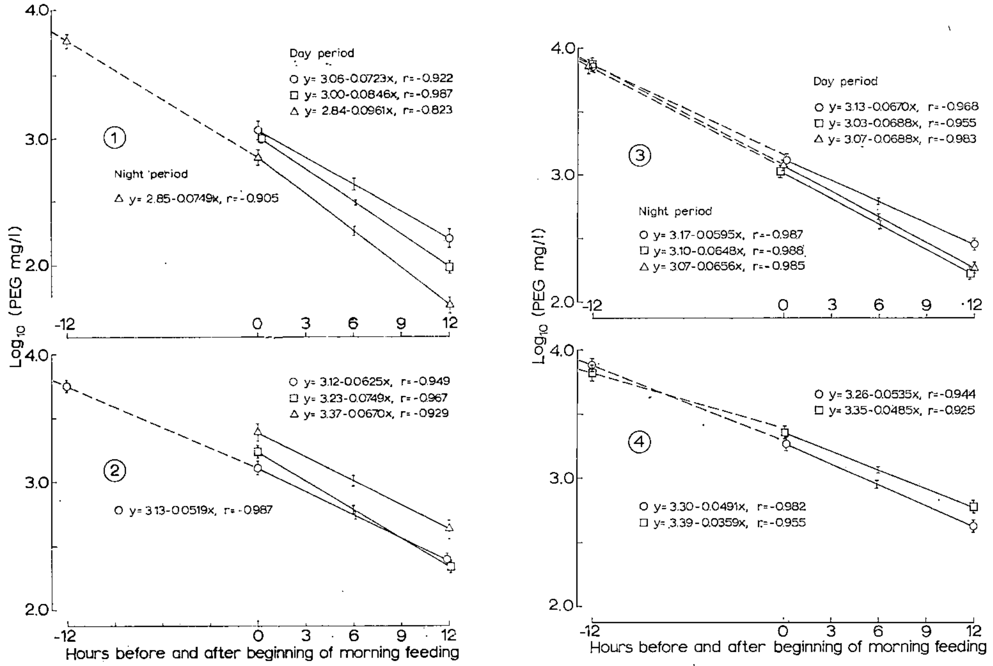
The effect of the factors studied on the flow of fluid and saliva through the reticulo-omasal orifice

Effect of dry matter intake and NaCl supplementation

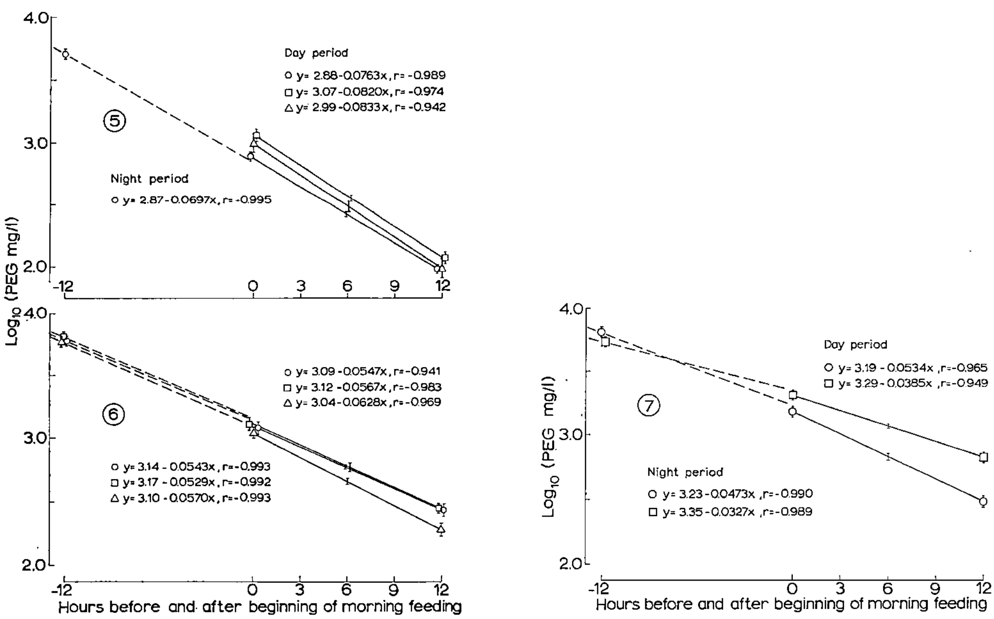
When studying the effect of the dry matter intake and sodium chloride dosage on the flow of fluid and saliva, the ration always consisted of 50 % long hay and 50 % of a concentrate mixture (cf. p. 25). The amount of dry matter eaten was 14, 11, 9 and 6 kg dry matter per day (cow INA) and 12, 9 and 6 kg dry matter per day (cow IRPU). Three dosage levels of sodium chloride were used at each dry matter level except at the dry matter level 6 kg per day when the highest dosage of NaCl was not used. The lowest level corresponded to the ordinary diet without supplementation while the second comprised 50 g NaCl per day and the third 100 g/day. The amount of Na received by the animal with each diet was dependent not only on the NaCl supplementation but also on the Na content of the foods and the drinking water. The actual amounts of dry matter eaten and amounts of water drunk as well as the amount of sodium received (12 h) in the foods and the drinking water are given in Appendix.

T o t a l f l o w o f f l u i d. — The straight lines in Figs. 1—7 and their equations sow the flow of fluid. The equations concerning the day period are based on the results of the 60 measurements and those for the night period on 24 measurements. Due to the different dosage levels of PEG, it was not always possible to calculate an equation for the night period. The vertical lines show the 99 % confidence limits of the mean decrease in the concentration of polyethylene glycol with regard to time. The confidence limits for zero time were drawn using the values of the day period. The equations and the lines show that the rate of dilution of the reference substance in the rumen contents decreased with decreasing intake of dry matter. With a constant food intake the addition of sodium cloride generally increased the rate of flow of fluid. The most distinct differences are observed when the dry matter level is 14 kg per day (Fig. 1). The differences decrease with decreasing levels of dry matter (Figs. 2, 3 and 5, 6). When the amount of dry matter consumed was 6 kg/day (Figs. 4 and 7) the rate of flow of fluid was faster for diets without NaCl supplementation than for diets with 50 g of additional NaCl/day.

When the dosage of PEG was the same, the observed differences between the diets, in the constants of the equations depicting the dilution of the polyethylene glycol, are due to differences in the volume of fluid in the rumen. The concentration of PEG found by extrapolation to the dosing time (—13 h) rises when the volume of fluid in the rumen decreases, in which case the calculated line for the night period intersects the ordinate at a higher level. Judging from the original concentration of PEG the amount of fluid in the reticulo-rumen decreased somewhat



Figs. 1—4. Decrease of the polyethylene glycol (PEG) concentration in the rumen fluid of cow INA fed 14 kg (Fig. 1), 11 kg (Fig. 2), 9 kg (Fig. 3) and 6 kg (Fig. 4) dry matter per day. Additional NaCl: △—△ 100 g, □—□ 50 g, ○—○ 0 g, per day. Vertical line segments indicate the 99 % confidence limits.



Figs. 5—7. Decrease of the polyethylene glycol (PEG) concentration in the rumen fluid of cow IRPU fed 12 kg (Fig. 5), 9 kg (Fig. 6) and 6 kg (Fig. 7) dry matter per day. Additional NaCl: △—△ 100 g, □—□ 50 g, ○—○ 0 g, per day. Vertical line segments indicate the 99 % confidence limits.

with decreasing amount of dry matter. The effect of the level of salt dosage can be seen in Figs. 3, 4, 6 and 7. The volume of fluid in the rumen seems to be more or less independent of the salt dosage at the 9 kg dry matter level. On the other hand, when the amount of dry matter consumed was 6 kg, the addition of 50 g NaCl seems to have increased the volume of fluid in the reticulo-rumen as compared to a diet without salt supplementation.

The 99 % confidence limits calculated for the lines defining the dilution of the reference substance are fairly narrow, which shows that the removal of the fluid from the reticulo-rumen occurred at a similar rate on the various days of measuring (3 days). The concentration of PEG measured in the different parts of the rumen each time likewise varied only slightly.

The linear correlation coefficients are negative, strong and highly significant ($P < 0.001$). Judging from the high correlations the linear model depicts the dilution of PEG fairly well and therefore it was not found necessary to fit equations of a higher order to the data.

Examination of the equations of the day and night periods for the same diet shows that the rate of dilution of the reference substance was higher during the day than during the night. In order to facilitate comparison, the constant of the equations describing the flow of fluid during the night period were also calculated to zero time.

The flow of total fluid for different diets and the partial factors of the flow (volume of fluid in the rumen l and flow of fluid vol.%/hour) calculated on the basis of the regression equations, are presented in Table 3. The results are given separately for the day and night periods. The total flow of fluid in 24 hours was calculated as the sum these whenever the results for both day and night periods were available.

The volume of fluid in the rumen as measured 1 hour before the beginning of feeding varied, according to the different levels of dry matter and salt intake, from 47 to 34 litres for cow INA and from 51 to 42 litres for cow IRPU. The general tendency is that the amount of fluid in the rumen decreases when the amount of dry matter consumed decreases. The decrease in the volume of fluid was not quite linear, but most pronounced when the dry matter intake decreased from 11 to 9 kg for INA and from 12 to 9 kg for IRPU. The addition of sodium chloride did not exert any influence upon the volume of fluid of the rumen contents exept at the dry matter level of 6 kg/day, when the addition of 50 g NaCl/day increased the volume by about 20 % for both cows as compared with no addition of salt.

The flow of fluid expressed as percentage of rumen fluid volume per hour (vol.%/h) decreased (at the salt dosage level 50 g/day) from 19.5 to 11.2 for cow INA when the corresponding decrease in the amount of dry matter consumed was from 14 to 6 kg/day. Likewise the ration of flow of fluid for cow IRPU decreased from 18.9 to 8.9 vol.%/h when the amount of dry matter decreased from 12 to 6 kg/day.

The comparison between the rates of flow of fluid for the day and night periods was carried out by testing the differences between the regression coefficients of the PEG dilution equations with a covariance test. Of the 13 cases tested the difference was significant ($P < 0.05$ or $P < 0.01$) in four and highly significant ($P < 0.001$) in three.

The decrease in the total flow of fluid with decreasing intake of dry matter was influenced primarily by the reduction in the rate of flow and secondly by the decrease in the volume of fluid in the rumen. The same applies to the effect of the level of salt intake with the exception of the dry matter level of 6 kg/day. Thus a negative association seems to exist between the component factors controlling the total flow of fluid. At the salt dosage level 0 g/day volume of fluid was smaller than at 50 g/day, but the rate of flow fluid per unit of volume was correspondingly greater. Therefore as for the total flow of fluid the differences became smaller.

Calcuting the total flow of fluid for the 24 hour period as the sum of the flow of the 12 hour long night and day periods is not perhaps

Table 3. Volume of rumen fluid and the flow of fluid through the reticulo-omasal orifice at different levels of dry matter intake and NaCl dosage. The results are the means of measurements on three days, with the 99 % confidence limits.

Dry matter intake kg/day	NaCl supplement g/day	Diet No.	Volume of fluid in the reticulo-rumen litres	Rate of flow of fluid vol. %/h		Difference in rate of flow betw. night and day F (1,80)	Total flow of fluid through the reticulo-omasal orifice, litres		
				night period	day period		night period 12 h	day period 12 h	night + day 24 h
Cow INA									
14	100	1	45.0±2.7	17.8±1.6	22.1±2.3	18.4***	96.1±9.7	119.3±12.9	215.4±22.6
	50	2	45.4±2.7	—	19.5±1.1	—	—	106.2± 8.7	—
	0	3	45.0±2.7	—	16.6±2.4	—	—	89.6±14.0	—
11	100	4	45.8±3.3	—	15.4±2.2	—	—	84.6±13.5	—
	50	5	46.0±3.3	—	17.2±1.6	—	—	94.9±11.2	—
	0	6	46.9±3.3	12.0±1.2	14.4±1.7	8.2**	67.2±8.1	81.0±11.0	148.2±19.1
9	100	7	35.6±3.1	15.1±1.7	15.8±1.2	1.2	64.4±8.1	67.5± 7.3	131.9±15.4
	50	8	34.2±2.8	14.9±1.4	15.8±1.7	1.0	61.2±7.6	65.0± 8.9	126.2±16.5
	0	9	34.2±2.7	13.7±1.3	15.4±1.4	5.2*	56.3±7.0	63.4± 7.7	119.7±14.7
6	50	13	41.6±3.9	8.3±1.5	11.2±1.6	11.4***	41.2±8.6	55.8± 9.5	97.0±18.1
	0	14	34.4±2.7	11.3±1.3	12.3±1.5	1.6	46.5±4.6	50.8± 7.4	97.3±14.0
Cow IRPU									
12	100	4	49.0±2.8	—	19.2±2.4	—	—	112.9±15.5	—
	50	5	50.8±2.8	—	18.9±1.5	—	—	115.2±11.1	—
	0	6	50.0±2.8	16.1±0.9	17.6±0.9	9.2***	96.4±7.7	105.4± 8.0	201.8±15.7
9	100	7	43.6±2.5	13.1±1.0	14.5±1.3	3.9	68.6±6.4	75.5± 8.0	144.1±14.4
	50	8	41.7±2.4	12.2±0.9	13.0±0.9	3.4	61.0±5.8	65.4± 5.7	126.4±11.5
	0	9	42.6±2.3	12.5±0.9	12.6±1.6	0.0	63.9±5.6	64.5± 8.8	128.4±14.4
6	50	13	50.4±2.1	7.5±0.7	8.9±1.0	6.4*	45.6±4.6	53.6± 6.6	99.2±11.2
	0	14	42.4±2.4	10.9±0.9	12.3±1.2	5.3*	55.4±5.6	62.5± 6.9	117.9±12.5

completely justified because the values for the night period are based on a considerably smaller number of measurements (cf. p. 30). On account of the differences in the rate of flow between the night and day periods the sum of these has, however, been assumed to represent better the average flow during the 24 hour period than the result of doubling the flow of the day periods.

The total flow of fluid through the reticulo-omasal (R—O) orifice ranged from 215 to 97 litres per 24 hours for cow INA when the corresponding dry matter levels varied between 14 and 6 kg/day. For cow IRPU the flow of fluid decreased from 202 to 99 litres per 24 hours when the amount of dry matter consumed decreased from 12 to 6 kg per day.

The effects of the levels of dry matter and sodium chloride intake on the volume of fluid passing through the R—O orifice during the day period (12 hours) can be compared in Figs. 8 and 9. The volumes of the flow of fluid were calculated to correspond exactly to the reported levels of dry matter intake. The corrections made on basis of the amount of dry matter consumed did not noticeably change the measured values (cf. Appendix).

The effect of the amount of dry matter consumed on the flow of fluid is observed to be large and fairly constant. Including all levels of dry matter and salt dosage the average flow of fluid per kg dry matter consumed for cow INA was 15.7 litres (variation 17.7—12.6) and for cow IRPU 17.8 litres (variation 20.0—14.4). The flow per kg dry matter consumed was greatest at the 6 kg level. A distinct decreasing tendency with decreasing level of dry matter intake was not observed because usually the smallest flow of fluid occurred when the ration contained 9 kg dry matter per day. The differences in total flow of fluid between the animals on

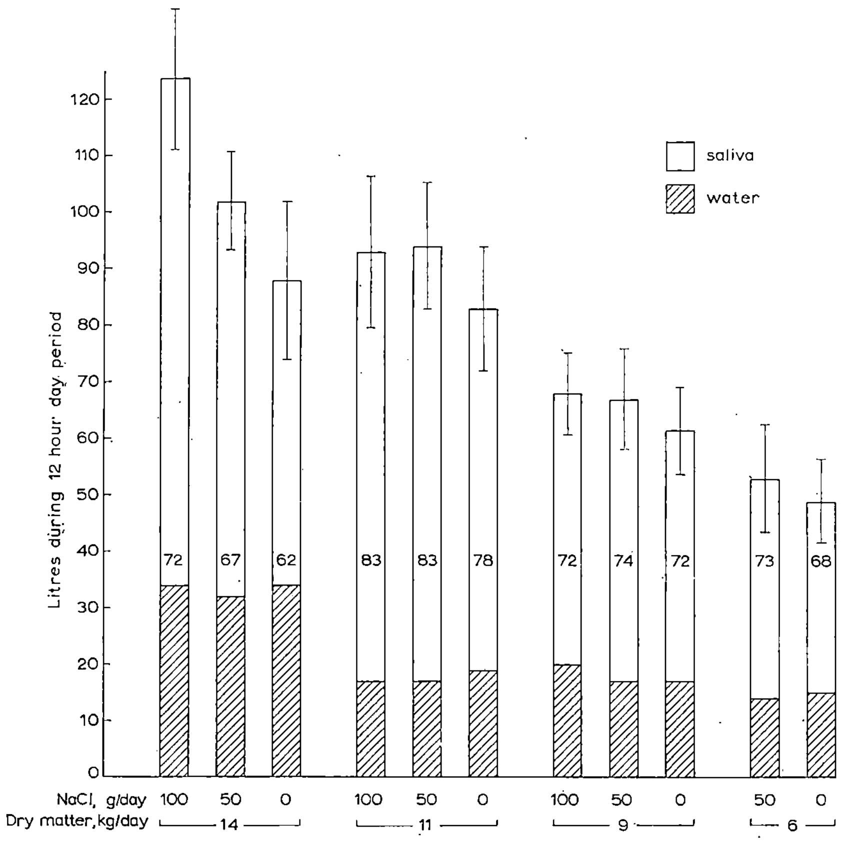


Fig. 8

the same diet were primarily due to differences in the volume of fluid in the rumen. This was 5 litres less on an average for INA than for IRPU.

As can be observed especially in Fig. 8, the effect of the NaCl dosage is different at different levels of dry matter intake. When the dosage of dry matter was 14 kg/day, distinct differences can be observed between all salt dosage levels. A dose of 100 g NaCl/day brought about a 41 % greater and a dose of 50 g/day a 16 % greater flow of fluid than was observed without additional salt. When the amount of dry matter consumed was 11 kg (INA) or 12 kg (IRPU) a difference in the flow observed only between the 0-salt level and the 50—100 salt levels, the difference being 9—12 %. Between the dosage levels 100 g and 50 g no differences were observed for either animal. With regard to INA no effect of the salt dosage could be observed at the dry matter levels 9 and 6 kg, although the flow was least without addition of salt. At the corresponding dry matter levels the flow of fluid for IRPU was almost the same when the salt dosage was 0 or 50 g/day. Contrary to the general tendency the dose 100 g NaCl/day at the 9 kg dry matter level increased the flow about 25 % compared to the dosage level 50 g/day.

F l o w o f s a l i v a. — The effect of absolute and relative magnitudes of the component factors, water intake and calculated amount of saliva, on the total flow of fluid during the 12 hour day period are presented in Figs. 8 and 9. The amount of water consumed in foods and as drinking water varied from about 35 litres to 11 litres during the 12 hour feeding interval. The moisture of the food was only a very

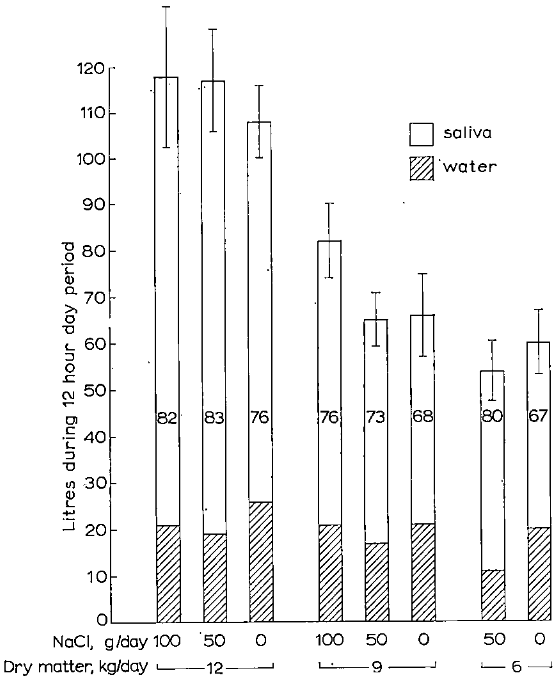


Fig. 9

Figs. 8—9. Total flow of fluid through the reticulo-omasal orifice of cow INA (Fig. 8) and cow IRPU (Fig. 9) during the 12 hour day period on diets containing different amounts of dry matter and additional NaCl. The total flow is divided into water and saliva fractions. Vertical line segments express the 99 % confidence limits for the mean amount of fluid. The number in the columns indicate the proportion of saliva (%) in the total flow of fluid.

insignificant part of this amount (1.3—0.5 l/12 h). The water intake averaged 4.2 litres per kg dry matter consumed, varying from 3.0 to 6.6 litres. The drinking decreased with decreasing amounts of dry matter eaten. It was somewhat greater for diets without additional NaCl than for diets with 50 or 100 g NaCl.

The estimated proportion of saliva in the total flow at different dosage levels of dry matter and salt for cow INA varied during the 12 hour day period from 86 to 35 litres and for cow IRPU from 96 to 42 litres. The relative proportion of saliva in the total flow was 74 % on an average, varying from 62 to 83 % (Figs. 8 and 9).

The flow of saliva was primarily dependent on the amount of dry matter consumed, decreasing almost linearly with decreasing amounts of dry matter eaten. The calculated flow of saliva per kg dry matter eaten was 11.5 litres on an average for cow INA and 13.5 litres for cow IRPU, taking into account all dosage levels of dry matter and salt.

The differences in the flow of saliva seem to have caused the differences in the total flow of fluid between the different dosage levels of salt. The flow of saliva decreased absolutely as well as relatively with decreasing levels of NaCl dosage. The calculated amount of saliva per kg dry matter eaten at the NaCl dosage levels 100, 50 and 0 g/day was 12.5, 12.0 and 10.2 litres for cow INA and 14.9, 13.4 and 12.4 litres for cow IRPU respectively.

The effect of the investigated factors (amount of dry matter, NaCl dosage) on the flow of saliva was tested by an analysis of variance. The test was made separately for the measured values of each cow because all the diets were not the same. The 6 kg dry matter level was not included in the calculations as it lacked the 100 g NaCl dosage level. The results of the analysis of variance are presented in Table 4.

Table 4. Analysis of variance of the flow of saliva during the 12 hour day periods of two cows. Treatments: level of dry matter intake (14, 11 and 9 kg/day for cow INA and 12 and 9 kg/day for cow IRPU), NaCl supplement (100, 50 and 0 g/day).

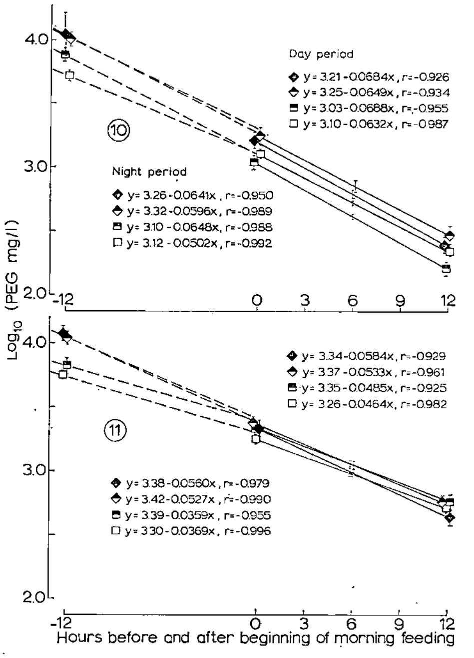
Source of variation	Degrees of freedom	Sum of squares	Mean squares	F-value
Cow INA				
Days	2	190.97	95.49	1.19
Dry matter	2	3 487.83	1 743.92	21.82***
Amount of NaCl	2	1 546.44	773.22	9.67**
Dry matter × NaCl	4	1 045.62	261.41	3.27*
Error	16	1 279.07	79.94	—
Total	26	7 549.93	—	—
Cow IRPU				
Days	2	175.14	87.57	1.38
Dry matter	1	7 188.01	7 188.01	113.30***
Amount of NaCl	2	1 126.45	563.22	8.88**
Dry matter × NaCl	2	45.02	22.51	0.35
Error	10	634.37	63.44	—
Total	17	9 168.99	—	—

*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

The amount of dry matter consumed had a highly significant effect ($P < 0.001$) on the flow of saliva in both of the experimental animals. The observed differences between the different NaCl dosage levels (100, 50 and 0 g additional NaCl per day) were significant ($P < 0.01$). The salt addition had a different effect at the different dry matter dosage levels (cow INA) judging from the statistical significance of the interaction between dry matter intake and amount of NaCl. This phenomenon was not as distinctly observed for the other cow. The effect of the salt addition seems to have increased with increasing amounts of dry matter eaten, which fact is apparent already from examining Figs. 8 and 9.

The differences in amount of saliva between the different measuring days are not statistically significant.

With regard to the 6 kg dry matter level, not included in the analysis of variance, Figs. 8 and 9 show that the salt dosage does not seem to have a noticeable effect on the flow of saliva.



Figs. 10—11. Decrease of the polyethylene glycol (PEG) concentration in the rumen fluid of cow INA fed 9 kg (Fig. 10) and 6 kg (Fig. 11) dry matter per day. The proportion of coarse fodder (long hay) in the dry matter: □—□ 100 %, ⊟—⊟ 50 %, ⬘—⬘ 25 %, ◈—◈ 10 %. Vertical line segments indicate the 99 % confidence limits.

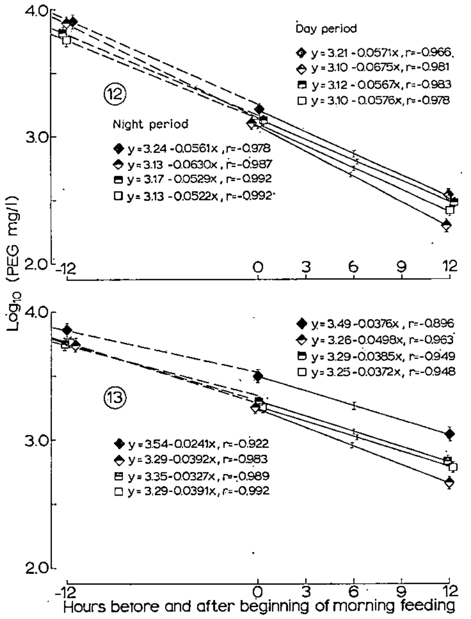
Effect of dry matter intake and proportion of coarse fodder in the ration

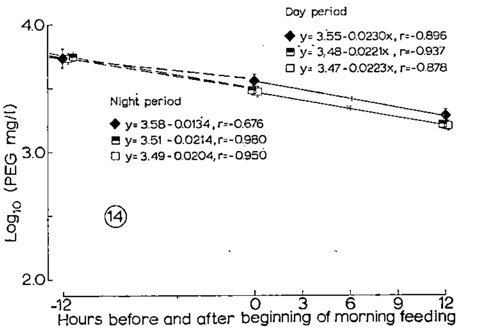
The effect of the relative amount of coarse fodder on the total flow of fluid and on the flow of saliva through the R—O orifice was investigated at the dry matter dosage levels 9 and 6 kg per day with both of the cows and also at the 3 kg level with cow IRPU. Coarse fodder is in this investigation defined as long hay. The proportion of long hay of the dry matter in the diet was 100, 50, 25 and 10 % when the amount of dry matter consumed was 9 or 6 kg/day. At the 3 kg dosage level of dry matter the proportion of long hay was 100, 50 and 10 % of the dry matter.

When the proportion of coarse fodder was 100 % the whole of the ration consisted of long hay and in the other cases one half of the ration consisted of a concentrate mixture, the other half being long hay plus ground hay.

When investigating the effect of the proportion of coarse fodder on the flow of fluid and saliva the dosage of salt for all diets was 50 g/day.

T o t a l f l o w o f f l u i d. — The lines and their equations describing the dilution of polyethylene glycol in the rumen fluid at different dry matter levels and for diets containing different amounts of coarse fodder are presented in Figs. 10—11 (INA) and in Figs. 12—14 (IRPU). Again a reduction of the flow of fluid can be observed as the amount of dry matter consumed decreases (cf. p. 30). The differences in slope of the lines describing the removal of PEG with the diets containing different amounts of coarse fodder are fairly small. More distinct differences can be observed for the constants of the equations. They depend on the volume of fluid in the rumen when the time and amount of dosage of PEG have been the same for different diets. For diets containing only 25 or 10 % long hay the PEG concentration during the whole of the measuring period (24 h) remained at a higher level than for diets containing 50 or 100 % long hay.





Figs. 12—14. Decrease of the polyethylene glycol (PEG) concentration in the rumen fluid of cow IRPU fed 9 kg (Fig. 12), 6 kg (Fig. 13) and 3 kg (Fig. 14) dry matter per day. Proportion of coarse fodder (long hay) in the dry matter: □—□ 100 %, ■—■ 50 %, ◆—◆ 25 %, ◆—◆ 10 %. Vertical line segments indicate the 99 % confidence limits.

Table 5. Volume of rumen fluid and the flow of fluid through the reticulo-omasal orifice with varying dry matter intake and proportion of coarse fodder (long hay). The results are the means of measurements on three days, with the 99 % confidence limits.

Dry matter intake kg/day	Proportion of coarse fodder % of total dry matter	Diet No.	Volume of fluid in the reticulo-rumen litres	Rate of flow of fluid vol. %/h		Difference in rate of flow betw. night and day F (1,80)	Total flow of fluid through the reticulo-omasal orifice, litres		
				Night period	Day period		night period 12 h	day period 12 h	night + day 24 h
Cow INA									
9	100	10	50.5±2.6	11.6±0.9	14.6±0.8	44.9***	70.1± 6.4	88.3± 6.8	158.4±13.2
	50	8	34.2±2.8	14.9±1.4	15.8±1.7	1.0	61.2± 7.6	65.0± 8.9	126.2±16.5
	25	11	24.4±1.8	13.7±1.2	15.0±2.0	1.5	40.1± 4.7	43.7± 6.7	83.8±11.4
	10	12	23.9±4.2	14.8±2.9	15.7±2.2	0.5	42.3±11.2	45.1±10.2	87.4±21.4
6	100	15	49.9±1.4	8.5±0.4	10.7±0.7	36.6***	50.8± 3.0	64.0± 4.6	114.8± 7.6
	50	13	41.6±3.9	8.3±1.5	11.2±1.6	11.4***	41.2± 8.6	55.8± 9.5	97.0±18.1
	25	16	23.7±1.4	12.1±1.0	12.3±1.2	0.0	34.4± 3.6	34.8± 4.1	69.2± 7.7
	10	17	23.3±2.3	12.9±1.6	13.4±1.9	0.3	36.0± 5.7	37.6± 6.4	73.6±12.1
Cow IRPU									
9	100	10	46.2±2.6	12.0±0.9	13.2±1.0	5.7*	66.5± 6.3	73.6± 6.9	140.1±13.2
	50	8	41.7±2.4	12.2±0.9	13.0±0.9	3.4	61.0± 5.8	65.4± 5.7	126.4±11.5
	25	11	33.3±2.9	14.5±1.4	15.6±1.1	2.7	58.0± 7.6	62.2± 6.9	120.2±14.5
	10	12	31.9±3.2	12.9±1.7	13.1±1.2	0.1	49.4± 8.0	50.2± 6.9	99.6±14.9
6	100	15	47.4±1.9	9.0±0.7	8.6±1.0	0.7	51.2± 4.3	48.7± 6.0	99.9±10.3
	50	13	50.4±2.1	7.5±0.7	8.9±1.0	6.4*	45.6± 4.6	53.6± 6.6	99.2±11.2
	25	16	47.9±2.9	9.0±1.0	11.5±1.1	17.2***	51.8± 6.6	65.9± 7.6	117.7±14.2
	10	17	42.3±3.6	5.6±1.4	8.7±1.5	15.1***	28.1± 7.5	43.9± 8.5	72.0±16.0
3	100	18	52.2±2.9	4.7±0.9	5.1±1.0	0.7	29.4± 7.1	32.2± 6.4	61.6±13.5
	50	19	49.0±1.8	4.9±0.6	5.1±0.7	0.2	29.0± 3.7	29.9± 4.0	58.9± 7.7
	10	20	53.3±6.5	3.1±2.0	5.3±0.9	10.9***	19.7±13.1	33.9± 7.2	53.6±20.3

The linear correlation coefficients are negative, strong and highly significant ($P < 0.001$). The dilution of PEG in the rumen contents, followed the linear model quite well judging from the high correlation. The values obtained for the volume of fluid in the rumen and for the flow of fluid on different diets, calculated from the regression equations of the dilution of the reference substance, are given in Table 5. The volume of fluid in the reticulo-rumen 1 hour before the beginning of feeding varied greatly for the different diets and was primarily dependent on the proportion of long hay in the diet. When the proportion of long hay expressed as percentage of the dry matter decreased as follows: 100, 50, 25 and 10, the volume of fluid in the rumen in litres was 50, 38, 24 and 24 respectively (INA) and 47, 46, 40 and 37 (IRPU). A difference of 3 kg in the dry matter intake (9 and 6 kg dry matter/day) did not seem to influence significantly the volume of fluid in the reticulo-rumen. When the amount of dry matter consumed was 3 kg per day, the average volume of fluid in the rumen was 51.5 litres and remained practically the same regardless of the proportion of long hay.

A test of the differences in regression based on the equations for the flow of fluid for the night and day period showed that the rate of flow is faster during the day than during the night. The difference in 8 cases out of 19 was significant ($P < 0.05$) or highly significant ($P < 0.001$). The diet did not seem to have an influence on the differences in flow of fluid in this material.

The rate of flow of fluid expressed as percentage of rumen fluid volume per hour (vol.%/h) was appromately the same for diets containing different proportions of coarse fodder, decreasing only with decreasing amounts of dry matter consumed. At the 9 kg dry matter level it was 15.3 on an average for cow INA (variation 14.6—15.8) and for IRPU on an average 13.7 (variation 13.0—15.6). When the dry matter intake was 6 kg/day the corresponding rates of flow of fluid were 11.9 (10.7—13.4) and 9.4 (8.6—11.5) respectively. The rate of flow of fluid was very slow, on an average only 5.2 vol.%/hour when IRPU received 3 kg dry matter per day.

The absolute and relative amounts of water and saliva in the total flow of fluid are presented in Figs. 15 and 16. The measured values were slightly changed in order to make them correspond exactly to the dry matter dosage levels given in the figures (cf. Appendix).

Decreasing the proportion of long hay from 50 to 10 % decreased the flow of fluid through the R—O orifice for cow INA by about 30 %, regardless of the dry matter dosage level (9 and 6 kg/day). An approximately equal decrease in the flow of fluid in this animal was caused already by decreasing the proportion of long hay from 50 to 25 %. For the other animal the decrease in the proportion of long hay from 50 to 10 % decreased the flow of fluid by approximately 20 % regardless of the amount of dry matter consumed (9 or 6 kg/day). The flow of fluid remained practically unchanged when the proportion of long hay was decreased from 50 to 25 % at the 9 kg/day dosage level. The corresponding change in the proportion of long hay at the 6 kg/day level on the other hand increased the flow of fluid by about 20 %. Increasing the proportion of long hay from 50 to 100 % increased the flow of fluid in different cases by 10—30 % (exept on the 6 kg day matter level cow IRPU). When the amount of dry matter consumed is only 3 kg/day the amount of long hay does not seem to have any noticeable influence on the flow of fluid through the R—O orifice.

F l o w o f s a l i v a. — The proportions of water and saliva (calculated by difference) in the total flow of fluid are presented in Figs. 15 and 16.

The water intake was primarily dependent on the amount of dry matter consumed, and the proportion of coarce fodder did not seem to influence it noticeably. The volume of water passing into the reticulo-rumen of cow INA averaged 4.9 litres per kg dry matter consumed (9 and 6 kg/day). The corresponding value for IRPU was 4.5 litres per kg. When the amount of dry matter was 3 kg/day the relative water intake was slightly larger, about 5 l/kg dry matter on an average.

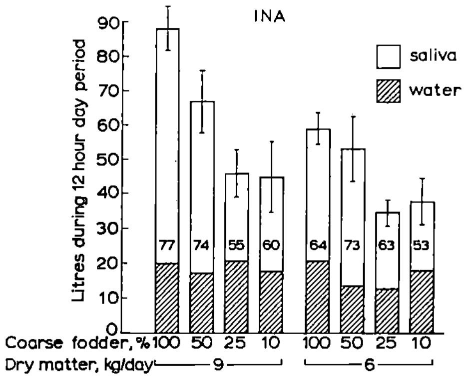


Fig. 15

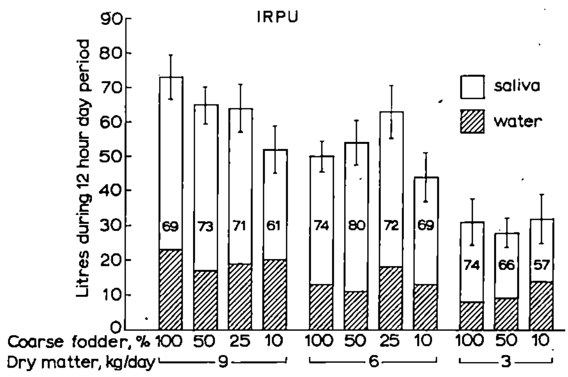


Fig. 16

Figs. 15—16. Total flow of fluid through the reticulo-omasal orifice of cow INA (Fig. 15) and cow IRPU (Fig. 16) during the 12 hour day period on diets containing different amounts of dry matter and proportions of coarse fodder (long hay) in the dry matter. The total flow is divided into water and saliva fractions. Vertical line segments express the 99 confidence limits for the mean amount of fluid. The numbers in the columns indicate the proportion of saliva (%) in the total flow of fluid.

The flow of saliva decreased both absolutely and relatively as the proportion of long hay from the dry matter decreased. The decrease for INA was about 48 % at the 9 kg dry matter level when the proportion of long hay decreased from 50 to 25 or 10 %. The corresponding changes in the relative amounts of coarse fodder decreased the amount of saliva about 54 % at the 6 kg dry matter level. For IRPU the decrease in the proportion of long hay from 50 to 25 % did not seem to change the amount of saliva. The smallest proportion of long hay (10 %), however, decreased the flow of saliva about 33 % at the 9 kg dry matter level and about 28 % at the 6 kg level.

On diets consisting only of long hay the flow of saliva was approximately the same as when the proportion of long hay was 50 %. An exception to this was that the flow of saliva for cow INA about 35 % greater the proportion of long hay being 100 % compared with a diet at the same dry matter level (9 kg) containing 50 % long hay. At the 3 kg dry matter per day level the proportion of coarse fodder did not seem to influence the amount of saliva at all.

The relative proportion of saliva in the total flow of fluid decreased as the proportion of coarse fodder decreased because the water intake remained more or less constant. The proportion of saliva in the total flow of fluid varied for INA from 64 to 77 % and for cow IRPU from 69 to 80 %, when the proportion of coarse fodder was 50 or 100 %. On diets containing less coarse fodder (25 or 10 %) the proportion of saliva in the total flow of fluid was from 53 to 63 % for INA and from 57 to 72 % for IRPU.

In order to determine the statistical significance of the observed variation in the flow of saliva,

Table 6. Analysis of variance of the flow of saliva during the 12 hour day periods. Treatments: level of dry matter intake (9 and 6 kg/day), proportion of coarse fodder in the ration (100, 50, 25 and 10 % long hay), cows (INA and IRPU).

Source of variation	Degrees of freedom	Sum of squares	Mean squares	F-value
Days	2	23.19	11.60	0.26
Dry matter (DM)	1	779.24	779.24	17.73***
Proportion of coarse fodder (P)	3	2 923.52	974.51	22.17***
Cows (C)	1	210.00	210.00	4.78*
DM × P	3	828.66	276.22	6.28**
DM × C	1	83.22	83.22	1.89
P × C	3	1 409.04	469.68	10.68***
DM × P × C	3	103.96	34.66	0.79
Error	30	1 318.79	43.96	—
Total	47	7 679.62	163.40	—

*** $P < 0.001$
** $P < 0.01$
* $P < 0.05$

an analysis of variance was made. The level of dry matter intake (9 and 6 kg/day) and the proportion of coarse fodder (100, 50, 25 and 10 %) were chosen as factors. The results of three different measuring days for each diet were considered as replications (days). The results are presented in Table 6.

The amount of dry matter as well as the proportion of coarse fodder in the diet had a highly significant ($P < 0.001$) effect on the flow of saliva. The difference between the animals was significant ($P < 0.05$). Judging from the highly significant interaction P x C ($P < 0.001$) it can be concluded that the difference between the cows appears primarily as a different effect of the coarse fodder on the secretion of saliva. This seems obvious already by examining Figs. 15 and 16. The significance ($P < 0.01$) of the interaction P x D shows that the effect of the proportion of coarse fodder was different at different dry matter levels. In the analysis of variance test of the factors influencing the secretion of saliva the 3 kg dry matter level was not included because it lacked the ration containing 25 % coarse fodder.

The effect of the factors studied on the concentration of sodium and potassium in mixed saliva and rumen fluid and on the flow of these cations through the reticulo-omasal orifice

The flow of sodium and potassium through the reticulo-rumen was calculated on the basis of the mean concentration of the 12 hour long day period and the volume of fluid passing the reticulo-omasal orifice.

The flow of sodium and potassium into the reticulo-rumen during the 12 hour time interval consist of the amounts introduced with foods, drinking water and saliva. The proportions in the foods and the drinking water were calculated from the determined average percentage of Na and K and the mean intake. Samples were collected for analyses from all foods during the last 14 days of each diet. Samples from the drinking water were taken on days when the measurements of the flow of fluid were carried out. The amounts of Na and K introduced into the reticulo-rumen with the saliva were calcuted as the product of the determined mean concentration in the saliva and the flow.

Effect of dry matter intake and NaCl supplementation

Concentration of sodium and potassium in mixed saliva and rumen fluid. — The mean concentration of Na and K during the 12 hour feeding interval of the day period at the different dosage levels of dry matter and salt are given in Figs. 17 and 18.

The effect of the amount of dry matter consumed on the Na and K concentrations can be seen most clearly when the salt dosage is 50 g/day, the Na supply being then apparently adequate.

The Na concentration in the mixed saliva of cow INA was 155, 154, 145 and 148 m-equiv./l when the levels of dry matter intake were 14, 11, 9 and 6 kg/day respectively. The same tendency for the Na concentration to decrease slightly with decreasing levels of dry matter can be observed for cow IRPU, the values being 152, 154, 145 and 136 m-equiv./l at the dry matter levels 12, 9, 6 and 3 kg/day (Fig. 20).

The Na concentration of the rumen fluid very closely followed the Na concentration in the saliva. The Na concentration of the rumen fluid was about 20 % lower, on an average, than that of the mixed saliva on the same diet. When the amount of dry matter decreases the Na concentration of the rumen fluid seems to decrease in the same way as in mixed saliva. The Na concentration in the rumen fluid of INA decreased from 119 m-equiv./l at the 14 kg/day dry matter level to 113 m-equiv./l at the 6 kg/day dry matter

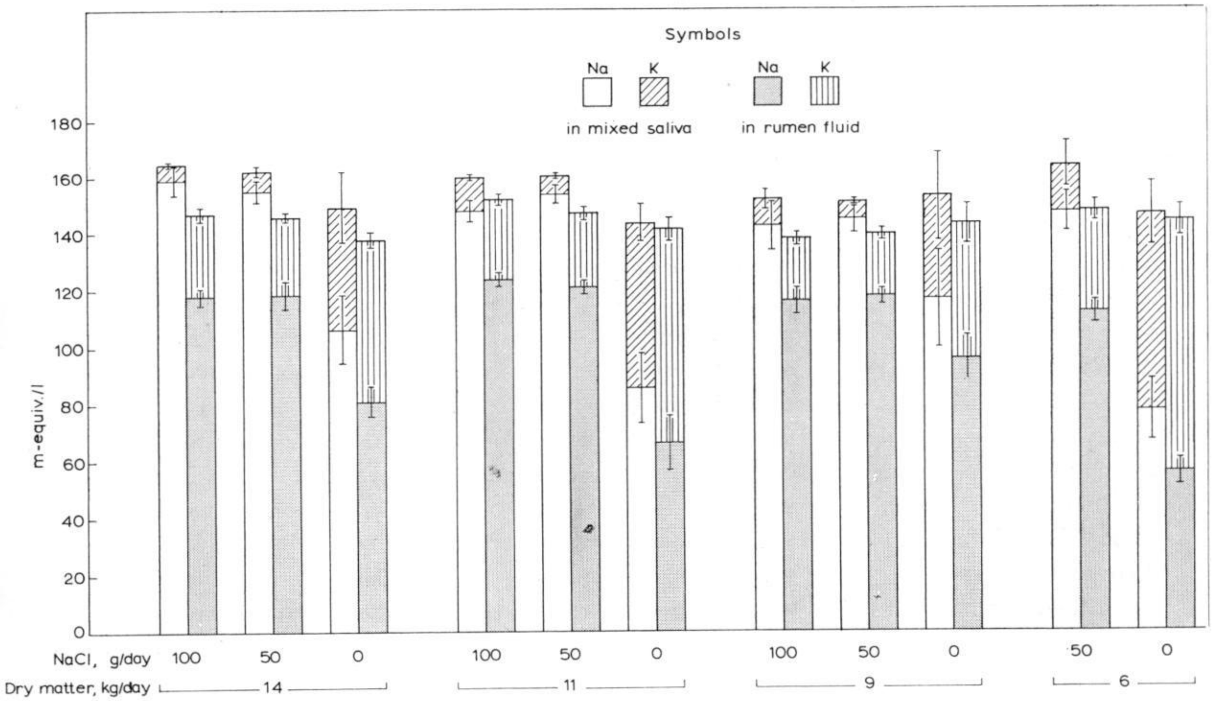


Fig. 17

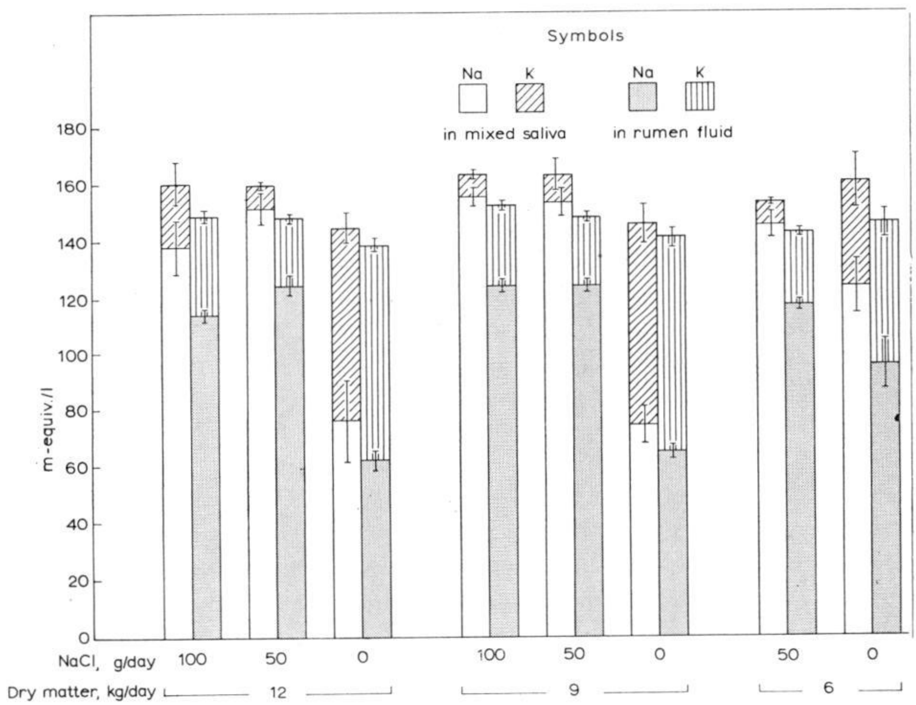


Fig. 18

Figs. 17—18. Mean concentrations of sodium and potassium in mixed saliva and rumen fluid of cow INA (Fig. 17) and cow IRPU (Fig. 18) on diets containing different amounts of dry matter and additional NaCl. Vertical line segments indicate the 99 % confidence limits of the mean concentrations.

level. The Na concentration of the rumen fluid of IRPU was 124 m-equiv./l when the amount of dry matter consumed was 12 kg/day, but 111 m-equiv./l when the amount of dry matter consumed was only 3 kg/day (Fig. 20).

The potassium concentration in the mixed saliva of both cows was about 9 m-equiv./l on an average (variation 6—17) when the salt dosage was 50 g/day at all levels of dry matter intake. The corresponding K concentration of the rumen fluid was about 26 m-equiv./l on an average (variation 21—36). The K concentration in mixed saliva on the same diet was 65 % lower on an average than that of the rumen fluid when the salt dosage was 50 g/day.

The effect of the NaCl dosage on the Na and K concentrations of the mixed saliva and the rumen fluid can be observed by comparing the average concentrations at different levels of salt dosage (Figs. 17 and 18). At the dosage levels 100 and 50 g systematic differences can be observed neither in the Na concentrations of the saliva nor in those of the rumen fluid. The average Na concentrations of the mixed saliva for these diets, including all levels of dry matter intake, was about 151 m-equiv./l (142—159) for INA and about 149 m-equiv./l (138—156) for IRPU.

The Na concentration of the mixed saliva was, however, noticeably lower without addition of salt. Including all levels of dry matter intake it averaged 97 m-equiv./l (86—117) for INA and 91 m-equiv./l (74—124) for IRPU. A consideralbe variation in Na concentration of the mixed saliva can be observed at different levels of dry matter intake for diets without additional NaCl. These differences in Na concentration are partly due to the fact that at different dry matter levels the Na-supply relatively speaking apparently accounted for an unequal portion of the requirement and partly because the animal was on a poor Na-dosage at various times in various cases (cf. Appendix). The Na concentration of the mixed saliva at the 0-salt dosage levels seemed to have a decreasing tendency all the time. For this reason a greater variation in concentration was observed for these diets, which also is apparent from the 99 % confidence limits of the mean concentration.

The Na concentration of the rumen fluid followed very closely the concentration of the saliva. Without salt addition the Na concentration of the rumen fluid, including the different dry matter levels, was 75 m-equiv./l on an average (57—96) for INA and 74 m-equiv./l (62—96) for IRPU. These concentrations were about 36—38 % lower than when the salt dosage was 100 g (119 m-equiv./l) and 50 g (120 m-equiv./l).

The relative difference between the Na concentration of the rumen fluid and the saliva did not seem to be dependent on the concentration level. The Na concentration of the rumen fluid at the salt dosage levels 100, 50 and 0 g NaCl per day was for INA 21—23 % lower and for IRPU at all levels 19 % lower on an average than the corresponding concentration of the mixed saliva at the same time.

The K concentration of the mixed saliva at the salt dosage levels 100 and 50 g/day was 10 m-equiv./l. It rose on diets without additional NaCl to an average of 52 m-equiv./l (36—69) for INA and 59 m-equiv./l (37—72) for IRPU.

The K concentration on the rumen fluid rose from an average of about 28 m-equiv./l on diets containing 100 or 50 g additional NaCl to about 68 m-equiv./l on diets without NaCl supplementation (Figs. 17 and 18). It can, however, be observed that the K concentration of the rumen fluid was all the time maintained at a higher level than that of the saliva. The relative difference decreased at the 0-salt dosage levels to 15—20 %, being 60—65 % at the levels 100 or 50 g NaCl per day.

The same factors influencing the Na concentration seemed to affect the variation in K concentration on the diet at the 0-salt dosage level and between the different dry matter dosage levels.

The changes in K concentration of the mixed saliva and rumen fluid are observed to be opposite to those of Na. The sum of the amounts of Na and K in equivalent was thus changed only slightly. The sum in the mixed saliva was, however, on average about 6 % less on diets

Table 7. Flow of sodium and potassium into and from the reticulo-rumen calculated in equivalents for the 12 hour day period on diets containing different amounts of dry matter and additional NaCl. The results are the means of measurements on three days, with the 99 % confidence limits.

Dry matter intake kg/day	NaCl supplement g/day	Diet No.	SODIUM equiv. per 12 h: Flow into the rumen: in saliva	in food + drinking water	total	Outflow in rumen fluid	Difference inflow-outflow	POTASSIUM equiv. per 12 h: Flow into the rumen: in saliva	in food + drinking water	total	Outflow in rumen fluid	Difference inflow-outflow
Cow INA												
14	100	1	13.71±2.10	1.21	14.42±2.10	14.09±1.87	0.83	0.51±0.11	2.76	3.27±0.11	3.47±0.48	—0.20
	50	2	11.03±1.38	0.79	11.82±1.38	12.60±1.14	—0.78	0.53±0.15	2.85	3.38±0.15	2.90±0.28	0.48
	0	3	5.89±1.63	0.20	6.09±1.63	7.28±1.24	—1.19	2.37±0.93	2.92	5.29±0.93	5.12±0.83	0.17
11	100	4	10.67±2.07	0.92	11.59±2.07	10.49±1.69	1.10	0.50±0.10	1.93	2.43±0.10	2.37±0.42	0.06
	50	5	12.04±1.73	0.76	12.80±1.73	11.47±1.38	1.33	0.53±0.11	1.92	2.45±0.11	2.50±0.36	—0.05
	0	6	5.40±1.22	0.17	5.57±1.22	5.38±1.05	0.19	3.68±0.77	1.90	5.58±0.77	6.07±0.87	—0.49
9	100	7	6.89±1.12	0.98	7.87±1.12	7.82±0.90	0.05	0.47±0.19	1.89	2.36±0.19	1.48±0.22	0.88
	50	8	6.98±1.31	0.51	7.49±1.31	7.69±1.07	—0.20	0.29±0.05	1.70	1.99±0.05	1.39±0.23	0.60
	0	9	5.34±1.19	0.09	5.43±1.19	6.07±0.87	—0.64	1.66±0.76	1.59	3.25±0.76	3.04±0.58	0.21
6	50	13	6.04±1.43	0.61	6.65±1.43	6.28±1.09	0.37	0.67±0.35	1.30	1.97±0.35	1.99±0.41	—0.02
	0	14	2.70±0.69	0.15	2.85±0.69	2.87±0.48	—0.02	2.39±0.64	1.05	3.44±0.64	4.47±0.71	—1.03
Cow IRPU												
12	100	4	12.77±2.31	0.93	13.70±2.31	12.85±1.77	0.85	2.10±0.75	2.07	4.17±0.75	4.01±0.60	0.16
	50	5	14.50±1.77	0.77	15.27±1.77	14.31±1.43	0.96	0.79±0.15	2.00	2.79±0.15	2.78±0.33	0.01
	0	6	6.12±1.33	0.19	6.31±1.33	6.54±0.61	—0.23	5.52±0.71	2.09	7.61±0.71	8.12±0.65	—0.51
9	100	7	8.93±1.26	1.07	10.00±1.26	9.40±0.99	0.60	0.45±0.12	1.60	2.05±0.12	2.10±0.26	—0.05
	50	8	7.37±0.91	0.69	8.06±0.91	8.14±0.84	—0.08	0.47±0.29	1.82	2.04±0.29	1.59±0.17	0.45
	0	9	3.26±0.71	0.21	3.47±0.74	4.19±0.59	—0.72	3.15±0.70	1.47	4.62±0.70	4.91±0.70	—0.29
6	50	13	6.20±0.96	0.49	6.69±0.96	6.31±0.77	0.38	0.35±0.06	1.36	1.71±0.06	1.36±0.18	0.35
	0	14	5.19±0.94	0.12	5.31±0.94	5.98±0.86	—0.67	1.55±0.48	1.25	2.80±0.48	3.18±0.46	—0.38

without additional NaCl than on diets containing 100 or 50 g per day. No difference can be observed in the equivalent sum of Na and K for the two last mentioned dosage levels. The total sum of Na and K in mixed saliva was smallest when the Na concentration was lowest.

The same decreasing tendency in the Na+K concentrations in the rumen fluid can be observed when no salt was given. The deviation as compared to diets containing salt (100 or 50 g/day) averaged 3—5 %, being at the most 6—9 %.

Flow of sodium and potassium. — The flow of sodium and potassium leaving the rumen via the R—O orifice, calculated on the basis of the average concentration and the volume of fluid, are seen in Table 7. The amounts entering the reticulo-rumen with the saliva, food and drinking water are also given in the same table.

The flow of Na decreases noticeably with decreasing amounts of dry matter consumed. The passage of Na from the reticulo-rumen during the 12 hour feeding interval was for cow INA 12.6, 11.5, 7.7 and 6.3 equiv. at the dry matter levels 14, 11, 9 and 6 kg/day respectively. The salt dosage was here in all cases 50 g/day. For IRPU sodium was discharged in the rumen fluid at the rate of 14.3, 8.1 and 6.3 equiv./12 hours, when the amount of dry matter consumed was 12, 9 and 6 kg/day respectively. The differences between the amounts of sodium leaving the reticulo-rumen via the R—O orifice at different dry matter levels were primarily due to differences in the flow of fluid, as the Na concentration of the rumen fluid was approximately the same at the different levels of dry matter intake. Without salt supplementation the outflow of Na from the reticulo-rumen with the fluid at the dry matter levels 14, 11 and 6 kg (INA) and 12 and 9 kg/day (IRPU), was only about 50 % of the amount on the corresponding diets containing 50 g salt per day. Without salt supplementation the amout of dry matter consumed being 9 kg/day (INA) and 6 kg/day (IRPU), the rate of outflow of sodium was only 5—10 % less than that with a dosage of 50 g/day. In these cases the Na concentration of the rumen fluid was quite high also at the 0-salt dosage level (Figs. 17 and 18).

The slower flow of sodium on diets without additional NaCl was due partly to the lower Na concentration of the rumen fluid (Figs. 17 and 18) and partly to the smaller volume of the flow of fluid (Table 3).

In table 7 the amount od sodium entering the reticulo-rumen is divided into two parts: the amount arriving with the saliva and the amount arriving with the food and the drinking water. The ratio of these parts does not seem to be dependent on the amount of dry matter consumed. For all diets the proportion entering with the saliva was about 94 % on an average. The proportion entering with the food and the drinking water varied for the different diets between 12.5 and 1.7 %.

The proportion of dietary sodium of the sodium entering the rumen during the 12 hour feeding interval at the salt dosage levels 100, 50 and 0 g/day was 9, 7 and 4 % respectively. The amounts of sodium entering and leaving the reticulo-rumen during the feeding interval (12 h) are much the same, as can be observed from Table 7. The difference inflow minus outflow is on all diets smaller than the calculated 99 % confidence limits of the inflow.

The amount of dry matter consumed influenced the outflow of potassium via the R—O orifice only insofar as it decreased the total flow of fluid, because the changes in concentration due to the levels of dry matter intake were very slight (Figs. 17 and 18). The outflow of K in the rumen fluid on diets without salt addition was 1.5—2 times greater compared to diets containing the same amounts of dry matter with 100 or 50 g salt/day. The difference is due to the considerable increase in K concentration in the rumen fluid when the Na-supply is low. The flow of K in equivalents at the 0-salt dosage levels was of the same magnitude as, or even greater than, that of Na. When the salt dosage was 100 or 50 g/day the outflow of Na in equivalents was 3—5 times greater than the outflow of K.

The food and the drinking water are considerably more important as suppliers of potassium than of sodium. On an average 79 % (66—89) of the K entering the rumen during the 12 hour feeding interval was supplied by these when the salt dosage was 50 g/day. The proportion of the dietary potassium decreased to about 38 % on diets without salt supplementation. This was primarily due to the considerable increase in salivary K concentration on these diets (Figs. 17 and 18).

The outflow of potassium from the reticulo-rumen during the 12 hour feeding interval was in 13 cases out of 19 equivalent, at the 1 % probability level, to the inflow during the same period of time. On five diets it appeared that more potassium flowed into the rumen than was released from it during the same period of time, and in one case the outflow was larger than the flow into the rumen.

Effect of dry matter intake and proportion of coarse fodder in the ration

Sodium and potassium concentrations in mixed saliva and rumen fluid. — The influence of dry matter consumed and the proportion of coarse fodder on the mean sodium and potassium concentrations in mixed saliva and rumen fluid are seen in Figs. 19 and 20. The NaCl-dosage for all diets was 50 g/day.

No significant differences could be observed between the Na and K concentrations of the saliva and the rumen fluid at the dry matter levels 9 and 6 kg per day. When the proportion of coarse fodder (long hay) was decreased the Na concentrations in the mixed saliva show a tendency to increase. When the long hay proportions (on a dry matter basis) were 100, 50, 25 and 10 %, the Na concentration in the mixed saliva of cow INA was 134, 147, 152 and 154 m-equiv./l, respectively. A similar tendency is observed for the change in concentration of the mixed saliva of IRPU, the values being 147, 150, 152 and 154 m-equiv./l respectively. The same tendency is also evident for the Na concentration of the rumen fluid. When the proportions of long hay were 100, 50, 25 and 10 % the Na concentration of the rumen fluid of INA was 102, 116, 123 and 122 m-equiv./l, and of IRPU 115, 121, 127 and 125 m-equiv./l, respectively.

In contrast, when the amount of dry matter consumed was 3 kg per day (IRPU) there was a tendency for the Na concentration of the mixed saliva to decrease as the proportion of long hay was decreased. The Na concentration of the rumen fluid was, however, maintained at approximately the same level regardless of the proportion of coarse fodder.

Changing the proportion of long hay in the diet altered the K concentrations of mixed saliva and rumen fluid in the opposite direction to the Na concentrations. The K concentration of mixed saliva at the 9 and 6 kg dry matter dosage levels decreased for cow INA from a level higher than 20 m-equiv./l to about half of this value when the proportion of long hay was decreased from 100 to 10 %. The decreasing tendency in K concentration of the saliva is less pronounced for cow IRPU. The decrease in K concentration of the rumen fluid seemed to occur mainly when changing from a 100 % long hay diet to a 50 % diet. On some diets the decreasing tendency in K concentration continued also for the lower levels of dry matter intake (Figs. 19 and 20).

When the amount of dry matter consumed was 3 kg/day the K concentration of the saliva increased with decreasing proportion of coarse fodder, but that of the rumen fluid decreased simultaneously (Fig. 20). This contradiction might be due to the difficulties in getting a clean saliva sample from the oesophagus when the coarse fodder proportion was 50 or 10 %. Inclusion of even a small amount of food particles might cause an increase in the K concentration and a decrease in the Na concentration.

The sum of sodium and potassium in equivalents in mixed saliva was fairly constant on all diets. It averages 159 m-equiv./l varying from 151 to 169. In the rumen fluid the sum of the sodium and potassium concentrations was 146 m-equiv./l on an average (134—153).

F l o w o f s o d i u m a n d p o t a s s i u m. — The results of the calculations concerning the inflow and outflow of sodium and potassium are presented in Table 8. The amount of sodium leaving the rumen decreases with decreasing amounts of dry matter consumed, as was already noted from the results given in Table 7.

A decrease in the proportion of coarse fodder appears to reduce the flow of sodium through the R—O orifice The outflow of sodium in the rumen fluid of cow INA during the 12 hour day period was 25—30 % smaller on diets containing 25 or 10 % long hay than that with diets containing 50 %. For cow IRPU decreasing the proportion of long hay to 10 % reduced the flow of Na by about 18 % compared to diets containing 50 % long hay. The flow of Na did not change (9 kg dry matter/day) or slightly increased (6 kg dry matter/day) when the proportion of coarse fodder in the ration of cow IRPU was reduced from 50 to 25 %.

Increasing the proportion of coarce fodder from 50 to 100 % in general slightly decreased the amount of sodium flowing through the R—O orifice. In one case a considerable increase in the Na outflow was observed and in two cases the outflow was approximately the same.

When the level of dry matter intake was 3 kg/day, the effect of the proportion of coarse fodder on the Na outflow was fairly slight. This is due primarily to the small differences observed in the flow of fluid (cf. p. 39).

The differences in the amounts of Na removed from the reticulo-rumen associated with the different diets were due mainly to the differences

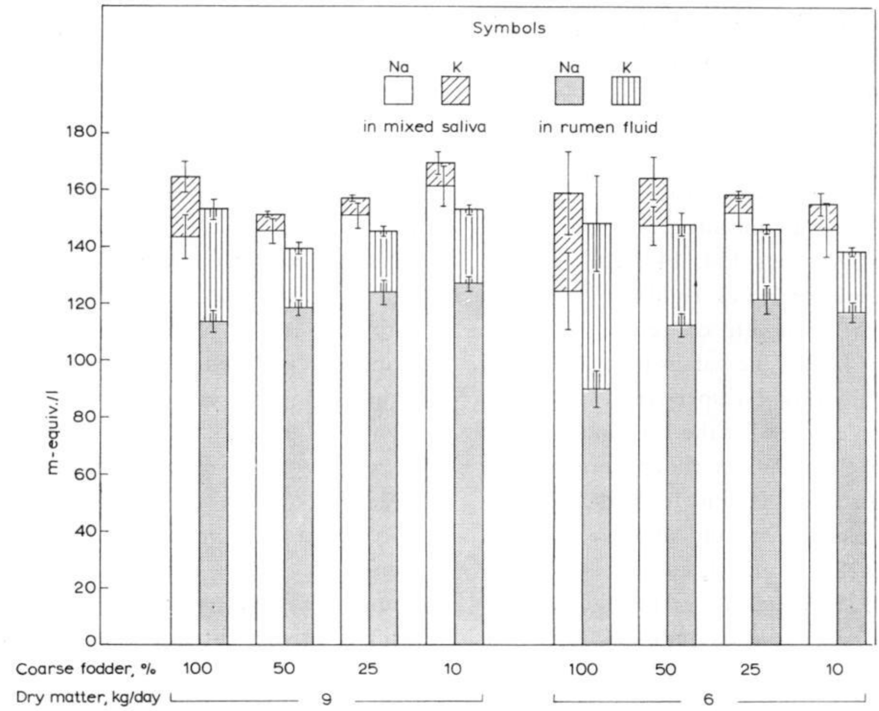


Fig. 19

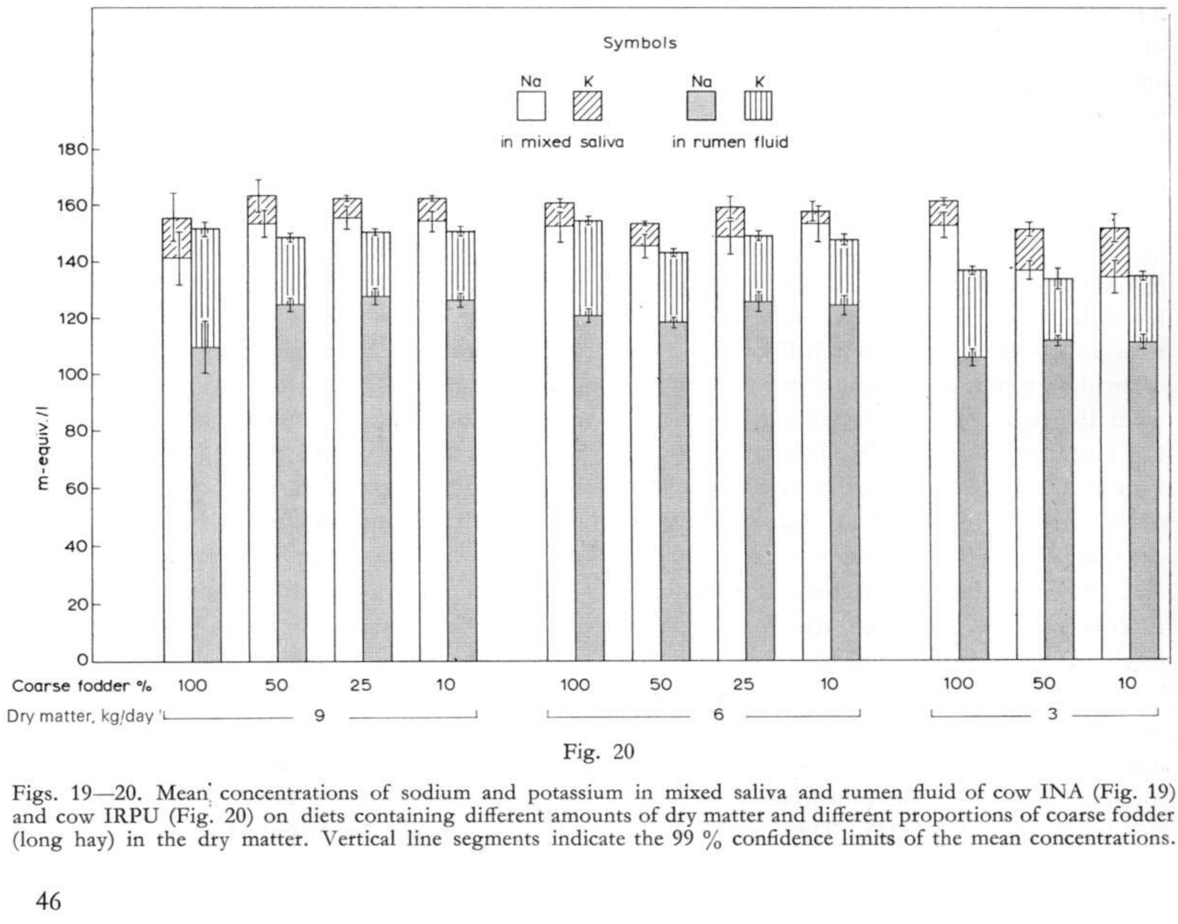


Fig. 20

Figs. 19—20. Mean concentrations of sodium and potassium in mixed saliva and rumen fluid of cow INA (Fig. 19) and cow IRPU (Fig. 20) on diets containing different amounts of dry matter and different proportions of coarse fodder (long hay) in the dry matter. Vertical line segments indicate the 99 % confidence limits of the mean concentrations.

Table 8. Flow of sodium and potassium into and from the reticulo-rumen calculated in equivalents for the 12 hour day period on diets containing different amounts of dry matter and proportions of coarse fodder in the ration. The results are the means of measurements on three days, with the 99 % confidence limits.

Dry matter intake kg/day	Proportion of coarse fodder % of dry matter	Diet No.	SODIUM equiv. per 12 h					POTASSIUM equiv. per 12 h				
			Flow into the rumen					Flow into the rumen				
			in saliva	in food + drinking water	total	Outflow in rumen fluid	Difference inflow-outflow	in saliva	in food + drinking water	total	Outflow in rumen fluid	Difference inflow-outflow
Cow INA												
9	100	10	9.74±1.10	0.56	10.30±1.10	10.00±0.85	0.30	1.37±0.39	2.62	3.99±0.39	3.52±0.43	0.47
	50	8	6.98±1.31	0.51	7.49±1.31	7.69±1.07	−0.20	0.29±0.05	1.70	1.99±0.05	1.39±0.23	0.60
	25	11	3.64±1.02	0.61	4.25±1.16	5.41±0.95	−1.16	0.14±0.04	1.30	1.44±0.04	0.93±0.15	0.51
	10	12	4.37±1.64	0.69	5.06±1.64	5.73±1.30	−0.67	0.22±0.14	1.42	1.64±0.14	1.18±0.28	0.46
6	100	15	5.12±0.79	0.57	5.69±0.79	5.75±0.60	−0.06	1.43±0.61	1.50	2.93±0.61	3.76±0.73	−0.83
	50	13	6.04±1.43	0.61	6.65±1.43	6.28±1.09	0.37	0.67±0.35	1.30	1.97±0.35	1.99±0.41	−0.02
	25	16	3.32±0.63	0.60	3.92±0.63	4.24±0.53	−0.32	0.14±0.03	0.95	1.09±0.03	0.86±0.11	0.23
	10	17	2.89±0.95	0.61	3.50±0.95	4.39±0.75	−0.89	0.18±0.10	0.86	1.04±0.10	0.82±0.15	0.22
Cow IRPU												
9	100	10	7.19±1.09	0.55	7.74±1.09	8.04±1.01	−0.30	0.74±0.43	2.93	3.67±0.43	3.03±0.34	0.64
	50	8	7.37±0.91	0.69	8.06±0.91	8.14±0.84	−0.08	0.47±0.29	1.82	2.04±0.29	1.59±0.17	0.45
	25	11	6.90±1.08	0.63	7.53±1.08	7.94±0.90	−0.41	0.31±0.07	1.43	1.74±0.07	1.41±0.17	0.33
	10	12	4.74±1.07	0.67	5.41±1.07	6.33±0.87	−0.92	0.24±0.06	1.41	1.65±0.06	1.22±0.18	0.43
6	100	15	5.46±0.93	0.51	5.97±0.93	5.85±0.73	0.12	0.30±0.07	1.71	2.01±0.07	1.68±0.22	0.33
	50	13	6.20±0.96	0.49	6.69±0.96	6.31±0.77	0.38	0.35±0.06	1.36	1.71±0.06	1.36±0.18	0.35
	25	16	7.00±1.16	0.83	7.83±1.16	8.28±0.99	−0.45	0.50±0.20	0.88	1.38±0.20	1.54±0.22	−0.16
	10	17	4.67±1.31	0.88	5.55±1.31	5.45±1.06	0.10	0.13±0.11	0.90	1.03±0.11	1.04±0.22	−0.01
3	100	18	3.61±0.98	0.46	4.07±0.98	3.39±0.68	0.68	0.20±0.06	0.92	1.12±0.06	1.00±0.20	0.12
	50	19	2.70±0.58	0.47	3.17±0.58	3.34±0.45	−0.17	0.29±0.07	0.56	0.85±0.07	0.65±0.14	0.20
	10	20	2.60±0.97	0.53	3.13±0.97	3.75±0.80	−0.62	0.34±0.16	0.45	0.79±0.16	0.82±0.18	−0.03

in the flow of fluid (Table 5). As was pointed out, a reduction in the proportion of coarse fodder caused an increase in the Na concentration (Figs. 19 and 20) and consequently increased the Na outflow from the rumen.

Of the sodium entering the reticulo-rumen in all cases more than 80 % came in the mixed saliva. The proportion of dietary sodium increased somewhat when the proportion of long hay decreased. Of the total Na inflow the dietary sodium, including all levels of dry matter intake, accounted for 7.8, 8.0, 12.2 and 14.8 % on an average when the coarse fodder proportions were 100, 50, 25 and 10 %, respectively. The observed tendency was due apparently to the reduction in salivary secretion with decreasing amounts of coarse fodder (Figs. 15 and 16). In food and drinking water, however, approximately the same amounts of sodium were carried into the rumen regardless of the coarse fodder proportion.

The outflow of sodium from the reticulo-rumen via the R—O orifice during the 12 hour day period equalled, at the 1 % probability level, the inflow. Without regarding the statistical significance it can be observed that the outflow of sodium from the rumen in most cases was slightly larger than the inflow. This is particularly true for diets containing the smallest proportions of coarse fodder (25 or 10 %).

The outflow of potassium in the rumen fluid was clearly most abundant when the diet consisted of long hay only. When the proportion of long hay is reduced, the K outflow generally seems to decrease. The reduction in the outflow of K with decreasing proportions of coarse fodder is due partly to the decreasing tendency observed in the K concentration of the rumen fluid and partly to the simultaneous reduction in volume of the total flow.

Of the potassium inflow, on all diets, 77.5 % on an average came with the food and the drinking water. The smallest proportion of dietary potassium, on an average 70.5 %, in the total inflow was observed for the long hay diets. When the coarse fodder proportions were 50, 25 and 10 %, the inflow of dietary potassium in percent of the total flow of potassium during the feeding interval was 80.0, 80.9 and 85.6 %, respectively. The differences between the potassium inflow and outflow indicate that the amounts of K entering the reticulo-rumen during a 12 hour interval were on an average slightly larger than the amounts removed during the same period of time. The difference in 14 cases out of 19 was greater than the calculated 99 % confidence limits for the inflow or outflow.

DISCUSSION

Methods

The polyethylene glycol (PEG) method, developed by SPERBER et al. (1953), has proved to be very suitable for measuring the flow of fluid through the reticulo-omasal (R—O) orifice, and it has been used in several investigations. The difficulties in measuring PEG, mentioned by CORBETT et al. (1958), can to a great extent be avoided by adjusting the concentration in the sample to a suitable level (HYDÉN 1961 c) and by using a nephelometer when measuring the turbidity (ENGELHARDT 1963 a). In this investigation a dosage of 300 g PEG proved almost without exception to be sufficient for a 24 hour period.

The semilogarithmic relationship between polyethylene glycol concentration in the rumen fluid and time has been observed to follow closely the linear model (HYDÉN 1961 a). A more complex model might in some cases describe the dilution of the reference substance in the rumen contents more exactly (ULYAT 1964 a), but in general the deviation from linearity is not statistically significant (HYDÉN l.c.). In this investigations only the linear model was used, which judging from the high correlation coefficients obtained described the release of fluid from the reticulo-rumen quite well (Figs. 1—7 and 10—14).

The difficulties connected with the use of PEG are described in an earlier paper (POUTIAINEN and LAMPILA 1967). They are connected mainly with the measuring of the volume of fluid in the rumen. HYDÉN (1961 a) observed when measuring the volume of rumen fluid in sheep that the volume measured with PEG was 95 % of the actual volume. The size of the error depends, among other things, on the fineness of the food (HYDÉN l.c.) and on the dry matter percentage of the rumen contents (BROBERG 1960, p. 30). In the *in vitro* tests performed by Poutiainen and Lampila (l.c.) the volume of fluid obtained by the use of PEG was 3—6 % lower than the actual volume. Taking this and the measuring time of the volume (1 hour before the beginning of feeding) into account the observed volumes of fluid in the rumen in the present experiments is estimated to be 5—10 % lower than the actual values. In the comparisons between different diets this fact cannot be regarded as very important as the procedure used was the same throughout.

In the present investigation the total flow of fluid through the R—O orifice divided into two compents by subtracting the water supplied by foods and drinking water from the total flow of fluid during the corresponding 12 hour day period. The difference is considered to represent the proportion of saliva in the total flow of fluid, which consideration is valid assuming that there has been no net passage of fluid through the rumen wall during the 12 hour period. The osmotic pressure differences in blood and rumen fluid affect the transfer of water. The salts supplied in the food increase the osmotic pressure in the rumen fluid as well as in the blood (BEILHARZ and KAY 1963, BOTT et al. 1966, WARNER and STACY 1965), which in turn makes the animal thirsty. The osmotic pressure differences thus partly outweighed. STACY and WARNER (1966) observed an increase in the rate of sodium absorption after feeding when the osmotic pressure in the rumen fluid is higher.

During resting and rumination saliva makes the main contribution to the fluid entering the rumen. Its effect on the osmotic balance is slight because it is approximately isotonic to the blood (KAY 1960 a, BAILEY 1961 b). The continuous flow of saliva apparently reduces osmotic pressure differences and limits the transmission of water through the rumen wall.

Investigations concerning the net transmission of water through the rumen wall performed under normal conditions are few in number. The transmission of water seems to occur in both directions (ENGELHARDT 1963 a and b), but the absorption from the rumen is in most cases greater than the influx (HYDÉN 1961 b). In estimations of the flow of saliva based on the total outflow of fluid the net influx of water was regarded as saliva, or on the other hand the net absorption of water was subtracted from the actual amount of saliva. Whenever a net transmission of water through the rumen wall occurs apparently also a transfer of sodium and potassium takes place simultaneously in the same direction, because the amounts of these mineral elements entering and leaving the rumen during the same period of time are quite similar (Table 7 and 8). The flow of saliva and the amounts of sodium and potassium included in it represents the portion of the salivary volume and minerals being transported from the reticulo-rumen into the omasum. This is apparently true for the main portion of the saliva and the minerals it contains, because the apparent volumes of salivary secretion observed in this study agree well with the results obtained for the secretions of saliva and minerals (using varying measuring methods) in other investigations carried out on correcponding diets (BAILEY 1961 a, MEYER et al. 1964, PUTNAM et al. 1966 a).

The mixed salivary samples were taken by inserting a perforated capsule into the oesophagus of the animal (POUTIAINEN and LAMPILA 1967). The excitation in the cervical oesophagus has been observed to stimulate the secretion of saliva to a certain extent (CLARK and WEISS 1952, KAY 1958, ASH and KAY 1959) and the changes in the rate of secretion cause changes in the composition of the saliva. It has been observed that the Na concentration rises and the K concentration decreases as the rate of secretion increases (COATS and WRIGHT 1957, KAY 1960 a, BAILEY and BALCH 1961 a, DOBSON 1963, BODA et al. 1965). The change in the composition of the saliva due to the stimulation effect is similar to the change caused by the increasing rate of secretion of saliva during eating and rumination (STEWART and DOUGHERTY 1959, BAILEY and BALCH 1961 a, YARNS et al. 1965 a). The measured Na and K concentrations of the samples taken by capsule thus apparently represent the average concentration during the feeding interval quite satisfactorily.

Results

Total flow of fluid. — Some earlier investigations indicated the volume of fluid transport from the reticulo-rumen of the cow into the omasum is 200—150 litres per 24 hours (SPERBER et al. 1953, LAMPILA and POIJÄRVI 1959, LAMPILA 1965). In the present investigation the flow of fluid via the R—O orifice was observed to vary from about 215 litres to 60 litres per 24 hours. Here certain dietary effects were used intentionally in order to influence the amount of flow of fluid.

The amount of dry matter consumed proved to be the factor influencing most the flow of fluid through the R—O orifice. During the

12 hour period about 16—18 litres of fluid was released from the reticulo-rumen into the omasum per kg dry matter consumed on diets containing 50 % hay and 50 % concentrates. The flow of fluid decreased almost linearly as the amount of dry matter consumed was decreased (Figs. 8 and 9). In the investigation of LAMPILA (1965) the flow of fluid, calculated per kg air-dry food (hay + conc.), was 12.6 litres in one case and 14.4 in another. BAILEY (1961 a) estimated that about 20 litres of fluid flowed into the reticulo-rumen per kg dry matter consumed.

A decrease in the amount of food seems to influence the outflow of fluid and solid matter similarly, as the rate of passage of food residues also is reduced with decreasing amounts of dry matter (cf. p. 9). When the contents of the rumen in general become more watery as the amount of dry matter consumed decreases the reason for the slower transport may be a weakening of the contractions of the forestomachs transporting the contents. (cf. p. 13).

It was found that the reduction in the total flow (rate × volume) of fluid with decreasing amounts of dry matter consumed depended mainly on the decrease in the rate of flow (per unit of volume of the rumen fluid), because the level of food intake had only a small effect on the volume of fluid in the rumen. Many investigators have observed that the amount of fresh contents of the rumen and especially its fluidal part remains fairly constant when the ration consumed varies (NEVENS 1928, MÄKELÄ 1956, 1960, PALOHEIMO and MÄKELÄ 1959, HYDÉN 1961 a, BATH et al. 1966).

Adding sodium chloride to a diet low in Na increased the flow of fluid through the R—O orifice. The rate of flow per unit of volume increased as the volume of fluid in the reticulo-rumen remained approximately constant. Only at the dry matter level of 6 kg/day was a greater amount of fluid measured in the rumen of both animals on a diet containing 50 g NaCl per day as compared to a diet without supplementary NaCl.

The addition of minerals has in some investigations been observed to exert a decreasing influence upon the dry matter percentage of the rumen contents (NICHOLSON et al. 1963) and to increase the transfer of the contents from the reticulo-rumen (MURRAY et al. 1962, ELAM 1961).

According to the present investigation the physical form of the food affected the volume of fluid in the rumen and the flow of fluid through the R—O orifice to a considerable extent. The physical form of the food was changed by finely grinding a certain proportion of the hay ration. When the proportion of coarse fodder (long hay) was 10 % of the dry matter the volume of fluid in the reticulo-rumen of cow INA was about 30—40 % and that of cow IRPU about 15—25 % lower than the volume on diets containing 50 % coarse fodder in the ration. On diets containging small amounts of coarse fodder (0.8—1.0 kg long hay) the rumen contents were a frothy mass, in which the amount of free fluid was very small. A similar description of the rumen contents on diets containing ground material is given, among others, by BALCH (1950), CAMPLING et al. (1963) and ORTH and KAUFMANN (1964) for cattle and BLAXTER and GRAHAM (1956) for sheep. A reduction in the hay proportion of the diet has generally been observed to exert a decreasing influence upon the rumen contents (BALCH et al. 1955, NICHOLSON and GUNNINGHAM 1961).

When the proportion of coarse fodder was 25 % of the dry matter consumed the flow of fluid of cow INA decreased considerably (about 30 %), but did not change, or increased slightly, for cow IRPU compared to a diet with 50 % coarse fodder in the ration (Figs. 15 and 16). The rumen contents of cow INA was observed to become somewhat frothy, containging little free fluid. The ratio between the fine material introduced with the ration and the volume of fluid in the rumen may have influenced the observed difference between the animals. The volume of fluid for INA was 5 litres less on an average than for IRPU.

The decrease in the flow of fluid apparently did not prolong the removal of dry matter from the reticulo-rumen, because the rate of flow ir creased somewhat as the proportion of coarse fodder in the diet was reduced. The dry matter percentage of the material transported into the omasum has been observed to increase when the ration is rich in finely ground food (CAMPLING et al. 1963).

The flow of fluid was observed to be faster during the day period than during the night period with most of the diets tested. The difference was in many cases statistically significant. HYDÉN (1961 a), working with sheep, obtained results showing the flow of fluid to be faster in the day than during the night. The difference in flow of fluid between the two periods may be due either to differences in water intake or in the volume of saliva secreted (PUTNAM et al. 1966 a, YARNS et al. 1965 b).

The water intake varied on different diets from 35 to 8.5 litres and the apparent contribution of saliva from 96 to 20 litres per 12 hours of the day period. The relative proportion of the saliva of the total flow on an average was 74 % (62—83). BAILEY (1961 a) estimated that 70—90 % of the fluid entering the rumen in 24 hours was saliva.

The water intake depended mainly on the amount of dry matter consumed, being about 4.7 litres per kg dry matter consumed. The drinking of water was on an average slightly greater on the ordinary diets than on diets with NaCl supplementation. Addition of salt has been observed to increase the water intake (ELAM and DAVIS 1962, PFEFFER et al. 1965), but the dosage was higher than that used in the present investigation. At the dry matter level of 3 kg dry matter/day a dose of 50 g NaCl/day was equivalent to about 1.6 % of the dry matter, which may be the reason for the greater water intake (5.2 l/kg dry matter).

F l o w o f s a l i v a. — The variation observed in the total flow of fluid was due primarily to the variation in the flow of saliva on different diets. The apparent flow of saliva decreased approximately linearly with decreasing amounts of dry matter consumed (Figs. 8 and 9). A similar relationship between salivary secretion and amount of dry matter consumed was observed by WILSON and TRIBE (1963) in sheep and by HAWKINS et al (1965) and PUTNAM et al. (1966 a) in cattle.

When the ration consisted of 50 % long hay + 50 % concentrate mixture the amount of saliva secreted per kg dry matter was almost independent of the level of food intake (in the range 14—3 kg dry matter/day). The salivary flow of cow INA was on an average 12.0 litres and that of cow IRPU 13.4 litres per kg dry matter consumed (NaCl 50 g/day). These values are somewhat lower than those reported by BAILEY (1961 a) for a diet of approximately the same composition (about 16 l/kg dry matter consumed), but they are slightly higher than those given by PUTNAM et al. (1966 a) for beef steers on a pelleted (9 mm) 89 % hay ration (13.4—6.5 l /kg dry matter consumed). The last mentioned authors observed that the amount of saliva secreted per kg dry matter consumed decreased with increasing dry matter level. This tendency was also observed by WILSON and TRIBE (1963) in sheep.

The flow of saliva increased 6—30 % when 50 g NaCl/day was added to a diet consisting of 50 % hay + 50 % concentrates. On the ordinary diets without NaCl supplementation the animals apparently suffered from a slight Na-deficiency (cf. p. 52). It has been observed that a deficiency in Na reduce the secretion of saliva in sheep (DENTON 1957) and in calves (BELL and WILLIAMS 1960). In the experiments of HAWKINS et al. (1965) with steers the secretion of parotid saliva was increased when Na in the diet was increased. (cf. p. 16). Judging from the Na concentration of the saliva (157 m-equiv./l), the effect was positive even when the Na-supply to the animals was adequate. Generally the effect of the salt addition in the present investigation was relatively most pronounced when the Na-deficiency was most obvious. The effect of an abundant Na-dose remains uncertain, because the addition of 100 g NaCl resulted in an increase in the flow of saliva only at the dry matter levels 14 kg/day (INA) and 9 kg/day (IRPU). In the former case the Na-requirement, due to the fairly high milk yield (about 21 kg/day), was moderately high and judging from the values of the measuring days the Na concentration of the saliva showed a decreasing tendency when the salt dosage was 50 g/day.

A decrease in the salivary flow seemed to cause a reduction in the total flow of fluid from the reticulo-rumen as the proportion of coarse fodder in the diet was decreased (Figs. 15 and 16). The coarse fodder (long hay) required much chewing, during which the secretion of saliva is abundant (STEWART and DOUGHERTY 1959, BAILEY and BALCH 1961 a, BAILEY 1961 a, YARNS et al. 1965). The finely ground food is swallowed after little chewing and the rumination time is shortened, or even the finely crushed food is transported from the rumen without being ruminated at all (BALCH 1955, 1958 a, OLTJEN et al. 1962 b, GORDON 1965). The excitation of the reticulo-rumen fold caused by the coarse material increases the secretion of saliva (cf. p. 16).

Grinding and pelleting of coarse fodder has been observed to cause a reduction in salivary secretion (WILSON and TRIBE 1963, OLTJEN et al. 1965, YARNS et al. 1965, KAUFMANN and ORTH 1966, PUTNAM et al. 1966 b). Even quite a small change in the coarseness of the hay meal or in the size of the pellets may considerably influence the amount of saliva (WILSON and TRIBE l.c.).

In the present investigation no diet was included consisting only of ground material, because during a preliminary test period it was observed that the daily consumption of such food was very irregular. A coarse fodder proportion of 10 % of the dry matter (0.8—1.0 kg long hay/day) was not sufficient to maintain the salivary flow at the same level as a proportion of 50 % (3.6—5.6 kg long hay/day). When the proportion of coarse fodder was 25 % of the dry matter (1.8—2.8 kg long hay/day) the salivary flow of one of the cows decreased considerably, but that of the other did not change or increased slightly compared to a diet with 50 % coarse fodder in the ration.

S o d i u m a n d p o t a s s i u m c o n c e n t r a t i o n s. — The sodium and potassium concentrations of mixed saliva and rumen fluid found in the present investigation agree with the values obtained in several other investigations on corresponding diets (EMERY et al. 1960, BAILEY and BALCH 1961 b, ORTH and KAUFMANN 1964, HAWKINS et al. 1965, KEMP and GEURING 1966).

On diets containing apparently sufficient Na (100 or 50 g NaCl/day) the Na concentration of mixed saliva and rumen fluid showed a slight decreasing tendency while that of K simultaneously showed an increasing tendency as the amount of dry matter consumed decreased. The sum of the Na and K concentrations expressed in equivalents per litre was thus almost independent of the dry matter level. Change in Na and K concentrations is thought to be connected primarily with a reduction in salivary secretion due to the decrease of the dry matter level. It has been observed that when the salivary secretion decreases the Na concentration of the saliva drops and the K concentration increases (BAILEY and BALCH 1961 b, BODA et al. 1965, KAUFMANN and ORTH 1966, KAUFMANN 1966).

The sodium concentration of the saliva decreased considerably and that of potassium increased noticeably on diets without Na-supplementation compared to diets with 100 or 50 g additional NaCl per day. A considerably decrease in the Na/K ratio of saliva has been observed in animals suffering from Na-deficiency (DENTON 1956, DOBSON et al. 1960, SELLERS and DOBSON 1960, DOBSON and MCDONALD 1963, KEMP and GEURING 1966). The Na concentration of mixed saliva varied in the present investigation on diets without salt supplementation from 74 to 124 m-equiv./l and that of K correspondingly from 92 to 36 m-equiv./l. The experimental animals were thus apparently suffering from a slight Na-deficiency, because according to the Na-balance experiments of KEMP and GEURING (l.c.) a Na concentration of the saliva below 130 m-equiv./l indicates a slight deficiency in sodium.

The sum of the sodium and potassium concentrations expressed in equivalents/l in both mixed saliva and rumen fluid was reduced as the

Na concentration decreased. This phenomen has also been observed by BAILEY and BALCH (1961 b).

Judging from the Na concentration of the saliva the additional dose of 50 g NaCl/day was on all diets sufficient to prevent the appearance of Na-deficiency at least during the relatively short experimental periods. Increasing the dose to 100 g/day did not increase the Na concentration of the saliva nor of the rumen fluid. The results of HAWKINS et al. (1965) and KEMP and GEURING (1966) also indicate that by adding more Na to the ration the Na-level of the saliva cannot be increased, or at least only slightly, when the animals are already getting amounts of sodium sufficient for their requirements.

The Na concentration of the rumen fluid on all diets was on an average 20 % lower than that of the mixed saliva. The difference remained approximately the same regardless of the concentration. In the investigations of BAILEY (1961 b) the Na concentration of the rumen fluid was 17 % lower on an average than that of the saliva, but at very low (25—60 m-equiv./l) and very high (over 160 m-equivl./l) concentrations the rumen fluid contained more sodium than the saliva. The differences observed in the present investigation between the Na concentrations of the saliva and the rumen fluid (20 %) seems to be due primarily to the diluting effect of the water introduced in food and as drinking water. Water intake supplied 25—27 % on an average of the total amount of fluid entering the rumen (cf. p. 35, 39), but on the other hand about 6—10 % of the sodium flowing into the rumen was introduced with the food (cf. p. 44, 47). The flow of sodium through the rumen wall may also have influenced partly the difference in concentrations.

The potassium introduced with food seems to exert a direct influence upon the K concentration of the rumen contents, indicated by the rise in K concentration of the rumen fluid following feeding. The same observation was made, among others, by BAILEY (1961 b), LAMPILA (1964), and KEMP and GEURING (1966). The K concentration of the saliva on diets containing adequate sodium was on an average 60—65 % lower than of the rumen fluid. The corresponding figure on the ordinary diets (deficient in Na) was 15—20. The difference in the said concentration during the feeding interval is at its greates immediately after feeding, decreasing then gradually, due partly to the diluting effect to the saliva in the rumen and partly perhaps because of the absorption of potassium from the rumen.

As the proportion of long hay in the diet was deceased, in increasing tendency was observed in the Na concentration of the rumen fluid a decreasing one in the K concentration. The observed change seemed to be connected with the K content of the diet (Appendix). GOODALL and KAY (1964) and SCOTT (1966) observed that an abundant dosage of potassium introduced into the rumen of sheep caused an increase not only in the K concentration of the rumen fluid but also an increase in the K concentration and a decrease in the Na concetration of the saliva. According to EMERY et al. (1960) on the other hand, the Na concentration of the rumen fluid rises when the proportion of hay in the food is increased and that of concentrates is decreased.

F l o w o f s o d i u m a n d p o t a s s i u m. — On diets adequate in Na the flow of fluid influenced the variation in Na and K amounts passing through the R—O orifice more than did the concentration of these cations in the rumen fluid. On diets without NaCl supplementation (mild Na-deficiency) the changes in Na and K concentration significantly affected the outflow of these cations.

On diets containing 100 or 50 g additional NaCl/day the outflow of Na, expressed in equivalents, was 3—5 times greater than that of K. Without addition of NaCl approximately the same equivalent amounts of Na and K were removed from the rumen. LAMPILA (1965) estimated the outflow of Na to be 1.5—2.5 times as great as that of K (in equivalents). The Na supply to the animals was rather low, which can be seen in the Na concentration of the rumen fluid (below 100 m-equiv./l).

The results of the present investigation confirm the view of the dominating role of the saliva as a maintainer of the Na concentration of the rumen compared with that of the dietary sodium (McDougall 1948, Bailey and Balch 1961 b, Lampila 1965). On an average only 6 % of the Na entering the rumen during the 12 hour day period came from food and drinking water, the rest (at least the major part) being introduced with the saliva. The total amount of sodium entering the rumen during the 12 hour period ranged on different diets from 15.3 to 2.9 equiv. Increasing the dietary Na dosage significantly increases the rate of flow of sodium into the rumen apparently for as long as it raises the Na concentration of the saliva, that is until the animal's sodium requirement is satisfied. The effect is enhanced partly because the salivary secretion seems to increase when additional sodium is given to an animal with a Na deficiency (cf. p. 35). At least in some cases an overdose of Na seems to have a positive effect on the flow of saliva, and consequently the amount of sodium entering the rumen is increased. The direct effect of the dietary Na apparently remains quite small, unless the added Na is not included in the sodium circulation maintained by the saliva. The effect of the Na-supplement given as sodium chloride on the neutralization of the rumen contents evidently occurs solely via the saliva.

On the different diets from 7.6 to 0.8 equiv. potassium was introduced into the reticulo-rumen during the 12 hour day period. On diets adequate in Na supply the proportion of K introduced with the food was nearly 80 % of the total inflow. On diets poor in Na supply more potassium on an average was introduced into the rumen in the saliva than together in food and drinking water.

The total amount of sodium and potassium entering the reticulo-rumen during the 12 hour day period varied on different diets from 18.2 to 3.9 equiv. As Na and K together constitute about 98 % of the cations in the mixed saliva (McDougall 1948, Phillipson and Mangan 1959) and about 95 % of the most common cations removed with the rumen fluid (Lampila 1965) their total sum provides a good estimate of the total amount of the cations in both of these fluids. Of the sum of the Na and K in equivalents on all diets an average of 77 % (66—85) was introduced into the rumen with the saliva. The total neutralizing effect of Na and K introduced with the saliva during the 12 hour period was equivalent to 1190—240 g $NaHCO_3$. The Na and K introduced with the food into the rumen probably influence the neutralization of volatile fatty acids only to a small degree, because in most cases they apparently occur in the rumen fluid as neutral salts. The Na and K transported with the saliva consequently have a greater importance in the neutralization of the volatile fatty acids formed by fermentation than might be expected from the proportion of these cations in the total flow.

Per kg dry matter consumed the flow of Na and K during the 12 hour period was almost independent of the dry matter level. On the other hand it was observed that the flow of Na + K in equivalents was reduced as the NaCl dosage and the proportion of coarse fodder were decreased. On the salt dosage levels 100, 50 and 0 g/day the total flow of Na and K per kg dry matter consumed average during the 12 hour period 2.8, 2.6 and 2.1 equiv., respectively. The sum of the Na and K equivalents per kg dry matter consumed averaged about 2.9, 2.5, 2.7 and 1.9 during the 12 h period for the coarse fodder proportions of the dry matter 100, 50, 25 and 10 %, respectively.

The neutralization level of the rumen contents cannot, however, be estimated from the total amount of neutralizing cations alone, because the required neutralization depends on the other hand on the concentration of volatile fatty acids in the rumen. Results (unpublished) of measurements of the neutralization capacity, however, indicate that the neutralization capacity was increased when the flow of sodium and potassium was accelerated.

SUMMARY

In the present investigation studies were made on the effect of some dietary factors on the flow of fluid, saliva and cations sodium and potassium through the reticulo-omasal (R—O) orifice of the cow. The factors in question were 1) the level of dry matter intake, 2) the dosage of sodium chloride, and 3) the physical character of the ration. The flow of fluid was determined by means of polyethylene glycol (PEG) a water soluble substance, which is not absorbed from the forestomachs. The flow of saliva was calculated by substracting the total water intake from the total flow of fluid. The mean concentrations of Na and K in mixed saliva and rumen fluid were determined and the amounts of Na and K entering and leaving the reticulo-rumen during the same period of time were estimated.

Two cows, INA and IRPU, equipped with rumen fistulas, were used as the experimental animals. The levels of dry matter intake varied from 14 to 3 kg/day. Na was supplied as NaCl at three rates: 0, 50 and 100 g/day. The effect of the physical character of the diet was investigated by giving part of the hay in ground form. The proportion of coarse fodder (long hay) in the dry matter of different diets was 100, 50, 25 and 10 %. With the exception of the pure long hay diet, 50 % of the dry matter of the ration consisted of hay (long or ground) and 50 % of a concentrate mixture. The animals had free access to water and 100 g/day dicalcium phosphate was given on all diets.

The results concern mainly the day period (from 5 a.m. to 5 p.m.) of the 12 hour feeding interval. With regard to the total flow of fluid a value was calculated also for the night period (from 5 p.m. to 5 a.m.) based on 17 of the 20 diets investigated. On each diet the results were calculated as averages of three measuring days. A resting period of 1—2 days generally alternated with the measuring days.

The total amount of fluid flowing through the R—O orifice during the night and day period (in 24 hours) varied from 215 to 59 litres as the amount of dry matter consumed varied from 14 to 3 kg per day. The flow was more abundant during the day period than during the night period. The difference in 13 cases out of 28 was statistically significant.

The flow of fluid per kg dry matter consumed during the 12 hour day period (feeding interval) averaged about 17 litres, for the different levels of food intake and NaCl dosage. The flow of fluid decreased approximately linearly as the dry matter level was decreased.

Addition of NaCl (100 or 50 g/day) increased the flow of fluid via the R—O orifice compared to a diet without NaCl supplementation containing the same amount of dry matter. The increase varied from 0 to 41 %, depending primarily on the adequacy of the Na-supply in the basic diet.

On a given dry matter level the flow of fluid was most abundant on the long hay diet, decreasing when the proportion of long hay was reduced. When the proportion of long hay was reduced to 10 % of the dry matter, the flow of fluid decreased by 20—30 % compared to a diet containing 50 % long hay. Reducing correspondingly the proportion of long hay to 25 % reduced the flow of fluid by about 30 % in one of the cows, but resulted in either no change or only a slight increase in the flow in the other cow.

The average volume of fluid in the reticulo-rumen, measured with PEG 1 hour before the beginning of feeding, varied on all diets from 47 to 24 litres for cow INA and from 51 to 37 litres for cow IRPU. In INA the rate of flow of fluid during the 12 hour day period per one hour varied from 22.1 to 10.7 % of the fluid volume in the rumen and in IRPU from 19.2 to 5.1 %.

On all diets the contribution of the saliva to the total flow of fluid averaged 69.0 % (52.7—82.5) for cow INA and 71.6 % (57.2—83.0) for cow IRPU.

The water intake was primarily influenced by the amount of dry matter consumed, being on an average about 4.7 litres per kg dry matter

consumed. The major part of the intake was drinking water, as the moisture in the food accounted for a flow rate into the rumen of only 0.3—1.3 litres of water per 12 hours.

The flow of saliva decreased approximately linearly as the amount of dry matter consumed was reduced. The effect of the dry matter level on the amount of saliva was statistically highly significant ($P < 0.001$). It was estimated that an average 11.5 and 13.5 litres of saliva per kg dry matter consumed entered the reticulo-rumen in INA and IRPU respectively.

The effect of the NaCl-supplementation on the calculated amount of saliva was statistically significant ($P < 0.01$) for both animals. At the NaCl dosage levels of 100, 50 and 0 g/day the amount of saliva was 12.5, 12.0 and 10.2 litres per kg dry matter consumed (INA) and 14.9, 13.4 and 12.4 litres (IRPU), respectively.

Decreasing the proportion of long hay in the diet reduced ($P < 0.001$) the amount of saliva in the total flow absolutely as well as relatively. When the proportion of long hay was 100, 50, 25 and 10 % of the dry matter (levels 9 and 6 kg), the amount of saliva was 13.9, 12.0, 6.5 and 6.3 (INA) and 11.6, 12.4, 12.6 and 8.6 (IRPU) litres per kg dry matter consumed respectively. The observed difference between the animals was significant ($P < 0.05$) appearing primarily as a different effect of the amount of long hay on the flow of saliva.

When the amount of dry matter was 3 kg per day the proportion of long hay in the diet did not seem to affect the flow of saliva noticeably. The secretion was about 20 litres per 12 hours, i.e. 13.3 litres per kg dry matter consumed.

The principal factor affecting the Na and K concentrations of the saliva and rumen fluid was the NaCl-dosage. With 100 or 50 g/day NaCl supplement the concentration of sodium in mixed saliva averaged 151 m-equiv./l. On diets without additional NaCl the Na concentration decreased to approximately 94 m-equiv./l. At the same time the K concentration rose from about 10 m-equiv./l (with 100 and 50 g NaCl/day) to about 55 m-equiv./l (with no additional NaCl). The sum of the Na and K concentrations in equivalents per litre was slightly lower on the ordinary diets without supplementary NaCl than on diets with additional NaCl.

When the dry matter level was decreased a slight increasing tendency was observed in the Na concentration of mixed saliva and a slight decreasing one in the K concentration.

The sodium and potassium concentrations of the rumen fluid followed the corresponding concentrations of the saliva very closely. The Na concentration of the rumen fluid was on an average 20 % lower than the concentration in mixed saliva at the same time; the ratio between the two remained the same regardless of the diet. On diets containing 100 or 50 g additional NaCl the K concentration in the saliva was on an average 60—65 % lower than that of the rumen fluid. On diets without additional NaCl the K concentration in the saliva was 15—20 % lower than that in the rumen fluid.

On different diets the amount of sodium leaving the reticulo-rumen with the rumen fluid during the 12 hour day period ranged from 15.3 to 2.9 equiv., the potassium figures ranging correspondingly from 0.7 to 8.1 equiv. The variation was due partly to differences in the amounts of fluid removed of different diets and partly to differences in the Na and K concentrations in the rumen fluid.

The amount of Na entering the reticulo-rumen in the food drinking water and saliva were equal to the amounts removed from there during the same period of time (12 h) using a 1 % risk level. The amounts of K entering the rumen were likewise equal to the amounts leaving it, when the differences were compared with the error of the means using 99 % confidence limits. In 15 cases, however, the amounts of K entering the rumen seemed to exceed the amounts leaving via the reticulo-omasal orifice during the corresponding time.

Of the Na entering the rumen during the 12 hour period, 94 % was introduced with the saliva. The proportions of dietary sodium with the NaCl dosage levels of 100, 50 and 0 g/per day were 9, 7, and 4 % respectively. As the proportion of coarse fodder in the diet was reduced, the proportion of dietary sodium of the Na entering the rumen increased slightly due to a reduction in the amount of saliva. At the most the dietary sodium accounted for only about 15 % (10 % long hay in the ration) of the Na entering the rumen.

As transporter of K the food was considerable more important than the saliva. When the Na-ration of the animals was adequate (100 and 50 g NaCl) the proportion of dietary potassium of the potassium entering the rumen during the 12 hour feeding interval averaged almost 80 %. On diets without additional NaCl, leaving the animals slightly Na-deficient, the importance of the saliva as a transporter of potassium increased and the proportion of the dietary potassium was about 40 % of the K entering the rumen.

On diets supplemented with NaCl the total amount of Na in the rumen during the 12 hour feeding interval was 3—5 times greater than that of potassium, and on diets without NaCl supplementation 1.5—2.0 times greater.

The total flow of Na and K averaged 2.4 equiv. per kg dry matter consumed almost independently of the dry matter intake. On the other hand this flow decreased when both the salt level or the proportion of long hay in the diet was reduced.

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Diet No.	Milk kg/day	Days on the diet before sampling	Sampling period No.	Date of sampling	Food intake, kg/dry matter/12 h				Intake of water litres/12 h			Intake of cations including supplements g/12 h	
					long hay	ground hay	concentr. mixt.	total	in food	as drinking water	total	Na	K
Cow INA													
1	22.2	22	6	23—25—27/3 —65	3.6	—	3.1	6.7	1.2	32.0	33.2	27.8	107.8
2	21.5	23	7	21—23—26/4 —65	3.8	—	3.3	7.1	1.3	33.7	35.0	18.2	111.2
3	17.4	26	8	24—29/5, 1/6 —65	3.8	—	3.3	7.1	1.1	33.2	34.3	4.5	113.9
4	9.6	11	1	28—30/9, 5/10 —64	2.8	—	2.3	5.1	1.0	13.8	14.8	21.2	75.0
5	3.0	13	2	19—21—23/10 —64	2.9	—	2.7	5.6	1.0	15.6	16.6	17.4	74.7
6	0.2	22	3	17—20—24/11 —64	2.8	—	2.6	5.4	1.1	16.7	17.8	4.0	74.2
7	5.2	16	9	27—30/8, 1/9 —65	2.5	—	2.0	4.5	0.7	18.4	19.1	22.6	73.4
8	4.6	17	10	20—22—24/9 —65	2.3	—	2.1	4.4	0.8	16.1	16.9	11.7	66.2
9	3.7	20	11	16—18—22/10 —65	2.3	—	2.2	4.5	0.9	16.8	17.7	2.0	62.0
10	2.6	10	14	11—13—15/1 —66	4.5	—	—	4.5	1.1	19.4	20.5	13.0	102.3
11	3.4	10	12	9—11—13/11 —65	1.1	1.0	2.2	4.3	0.9	18.7	19.6	14.1	50.4
12	3.1	10	13	20—22—24/11 —65	0.4	1.9	2.2	4.5	0.9	17.1	18.0	15.8	55.4
13	2.6	27	5	12—14—16/1 —65	1.6	—	1.5	3.1	0.6	14.3	14.9	14.0	50.6
14*	—	14	4	9—12—15/12 —64	1.6	—	1.5	3.1	0.6	15.6	16.2	3.4	41.0
15	—	10	17	22—25—27/4 —66	3.2	—	—	3.2	0.5	22.3	22.8	13.1	58.4
16	2.7	12	15	1— 3— 5/3 —66	0.7	0.8	1.5	3.0	0.6	12.4	13.0	13.8	37.0
17	2.3	10	16	21—23—25/3 —66	0.3	1.2	1.5	3.0	0.6	17.2	17.8	13.9	33.8
Cow IRPU													
4	8.3	16	1	21—23—25/9 —64	2.9	—	2.9	5.8	1.1	19.2	20.3	21.3	80.5
5	7.6	25	2	12—14—16/10 —64	3.0	—	2.9	5.9	0.9	18.6	19.5	17.7	77.8
6	5.0	25	3	12—16—19/11 —64	3.0	—	2.9	5.9	0.9	24.2	25.1	4.4	81.4
7	2.8	12	6	2— 4— 6/2 —65	2.2	—	2.0	4.2	0.9	17.2	18.1	24.5	62.7
8	2.8	26	5	12—14—16/1 —65	2.3	—	2.2	4.5	0.9	16.5	17.4	15.8	62.3
9*	3.3	16	4	9—11—15/12 —64	2.2	—	2.2	4.4	0.8	19.8	20.7	4.9	57.6
10	2.3	10	9	29/4, 3—5/5 —65	4.6	—	—	4.6	1.0	21.7	22.7	12.7	114.3
11	2.8	18	7	9—11—16/3 —65	1.2	1.0	2.2	4.4	0.9	16.9	17.8	14.4	55.6
12	2.6	10	8	5— 7— 9/4 —65	0.4	1.7	2.2	4.3	0.8	18.7	19.5	15.5	54.8
13	1.2	22	11	20—22—24/9 —65	1.5	—	1.5	3.0	0.5	10.4	10.9	11.2	53.1
14	2.6	15	10	24—26—29/5 —65	1.6	—	1.5	3.1	0.5	20.1	20.6	2.7	48.7
15	—	24	14	24—26—28/1 —66	3.0	—	—	3.0	0.8	12.0	12.8	11.8	66.8
16	—	10	12	16—18—22/10 —65	0.7	0.7	1.5	2.9	0.4	18.1	18.5	19.2	34.3
17	—	10	13	9—11—13/11 —65	0.3	1.2	1.5	3.0	0.6	12.8	13.4	20.2	35.3
18	—	15	15	1— 3— 5/3 —66	1.6	—	—	1.6	0.2	8.3	8.5	10.6	35.6
19	—	10	16	21—23—25/3 —66	0.8	—	0.8	1.6	0.3	9.8	10.1	10.8	21.7
20	—	17	17	18—20—22/4 —66	0.2	0.6	0.8	1.6	0.3	14.2	14.5	12.1	17.5

*) These rations were fed after diet No. 6. Thus cow INA was without additional NaCl on diet 14 in all 36 days before sampling and cow IRPU on diet 9 in all 41 days.

SELOSTUS

Tekijöitä, jotka vaikuttavat nesteen, syljen ja eräiden kationien kulkuun lehmän verkkomaha-satakerta-aukosta

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Tutkimuksessa on selvitetty eräiden ruokinnallisten tekijäin vaikutusta nesteen, syljen sekä natriumin ja kaliuminvirtaukseen lehmän verkkomaha-satakerta aukon kautta. Kysymyksessä olevat tekijät olivat (1) syödyn kuiva-aineen määrä, (2) natriumkloridin annostus ja (3) rehuannoksen fysikaalinen olomuoto. Nestevirtauksen mittauksessa käytettiin johtoaineena polyetylenglykolia (PEG), joka on vesiliukoinen pötsistä imeytymätön aine. Syljen määrä laskettiin vähentämällä kokonaisnestevirtauksesta juomaveden ja rehujen sisältämän veden osuus. Natriumin ja kaliumin osalta laskettiin pötsiin syljessä sekä rehuissa ja juomavedessä saapuneet ja sieltä samana aikana pötsinesteessä satakertaan poistuneet määrät.

Koe-eläiminä käytettiin kahta pötsifistelillä varustettua lehmää INA ja IRPU. Kuiva-aineen annostus vaihteli 14:stä 3:een kg/p. Eläinten natriumin saanti järjestettiin kolmelle tasolle. Alimman tason muodosti perusdieetti ilman suolalisää, toisella tasolla annettiin NaCl:a 50 g ja kolmannella 100 g/p. Dieetin fysikaalisen olomuodon merkitystä tutkittiin antamalla osa heinästä jauhetussa muodossa. Karkearehun (pitkän heinän) prosenttinen osuus kuiva-aineesta oli eri dieeteissä 100, 50, 25 ja 10 %. Pelkkää heinädieettiä lukuunottamatta oli rehuannoksen kuiva-aineessa 50 % heinää (pitkänä tai jauhettuna) ja 50 % väkirehuseosta. Vettä oli vapaasti saatavana ja rehufosfaattia annettiin 100 g/p kaikissa dieeteissä.

Tulokset koskevat pääasiassa 12 tunnin pituisen ruokintavälin päiväjaksoa (klo 5—17). Totaalinestevirtauksen arvio on laskettu myös yöjaksolle (klo 17—5), joka koski 17 dieettiä 20:stä tutkitusta. Tulokset on laskettu kullakin dieetillä kolmen mittauspäivän keskiarvoina. Mittauspäivien välillä oli 1—2 lepopäivää.

Pötsi-verkkomahasta satakertaan yö- ja päiväjaksolla (24 t) poistunut nestemäärä vaihteli 215:sta 59:ään litraan ja syöty kuiva-ainemäärä 14:sta 3:een kg/p. Nestevirtaus oli runsaampaa päivällä kuin yöllä. Ero oli testatusta 28 tapauksesta 13:sta tilastollisesti merkitsevä. Syötyä kuiva-ainekiloa kohti laskettu nestevirtaus oli 12 tunnin päiväjaksolla (ruokintaväli) keskimäärin noin 17 litraa kuiva-aineen ja suolan eri annostustasot mukaan lukien. Kuiva-ainetason alentuessa virtaus pieneni jokseenkin suoraviivaisesti.

Natriumkloridi (100 tai 50 g/p) lisäsi nestevirtausta verrattuna saman verran kuiva-ainetta sisältäneeseen dieettiin ilman NaCl:a. Lisäys oli 0—41 %, riippuen lähinnä Na:n saannin riittävyydestä perusdieetin aikana.

Tietyllä kuiva-ainetasolla nestevirtaus oli runsainta rehun ollessa yksinomaan pitkää heinää ja väheni pitkän heinän osuuden pienentyessä. Pitkän heinän osuuden vähentäminen 10 %:iin kuiva-aineesta vähensi nestevirtausta 20—30 % verrattuna dieettiin, jossa oli pitkää heinää 50 %. Vastaavasti pitkän heinän määrän alentaminen 25 %:iin pienensi nestevirtausta noin 30 % toisella lehmällä, mutta ei aiheuttanut muutosta tai hieman lisäsi virtausta toisella.

Keskimääräinen pötsin nestevolymi vaihteli INA-lehmällä 47:stä 24:ään litraan ja IRPU-lehmällä 51:stä 37:ään litraan. INA-lehmällä nestevirtauksen nopeus vaihteli 12 tunnin päiväjaksolla ilmaistuna prosentteina pötsin nestevolymista tunnissa 22.1—8.9 % ja IRPU-lehmällä 19.2—5.1 %.

Syljen osuus nesteen kokonaisvirtauksesta oli kaikilla dieeteillä keskimäärin 69.0 % (52.7—82.5) INA-lehmällä ja 71.6 % (57.2—82.5) IRPU-lehmällä.

Veden saanti määräytyi pääasiassa syödyn kuiva-ainemäärän mukaan ja oli kaikilla dieeteillä keskimäärin noin 4.7 litraa/kg kuiva-ainetta. Valtaosa tästä oli juomavettä, sillä rehujen mukana tuli pötsiin vettä vain 0.3—1.3 litraa 12 tunnissa.

Syljen virtaus väheni syödyn kuiva-ainemäärän pienentyessä jokseenkin suoraviivaisesti. Kuiva-aineen annostustason vaikutus syljen määrään oli tilastollisesti erittäin merkitsevä ($P < 0.001$). Keskimäärin laskettiin pötsi-verkkomahaan tulleen sylkeä 11.5 litraa (INA) ja 13.5 litraa (IRPU) syötyä kuiva-ainekiloa kohti.

NaCl:n lisäyksen vaikutus syljen laskettuun määrään oli tilastollisesti merkitsevä ($P < 0.01$) molemmilla eläimillä. NaCl-annostuksen tasoilla 100, 50 ja 0 g/p oli syljen määrä vastaavasti 12.5, 12.0 ja 10.2 litraa/kg k.a. (INA) ja 14.9, 13.4 ja 12.4 l (IRPU).

Pitkän heinän osuuden pienentäminen dieetissä vähensi syljen määrää ($P < 0.001$) sekä absoluuttisesti että suhteellisesti osana totaalivirtauksesta. Pitkän heinän osuuden ollessa 100, 50, 25 ja 10 % kuiva-aineesta (tasot 9 ja 6 kg) oli sylkimäärä vastaavasti 13.9, 12.0, 6.5 ja 6.3 (INA) ja 11.6, 12.4, 12.6 ja 8.6 (IRPU) litraa/kg k.a. Eläinten välillä havaittiin ero karkearehun osuuden vaikutuksessa syljen määrään.

Kuiva-ainemäärän ollessa 3 kg päivässä ei pitkän heinän osuudella dieetissä näyttänyt olevan sanottavaa vaikutusta syljen määrään. Eritys oli noin 20 litraa 12 tunnissa eli noin 13.3 litraa/kg k.a.

NaCl-annostusta oli syljen ja pötsinesteen Na- ja K-konsentraatioihin voimakkaimmin vaikuttava tekijä. NaCl annostuksen ollessa 100 tai 50 g/p oli konsentraatio seossyljessä keskimäärin 151 me./l. Dieteeteillä ilman

suolalisää Na-konsentraatio aleni noin 94 tasolle me./l. Kaliumin konsentraatio nousi samanaikaisesti tasoita noin 10 me./l (100 ja 50 g NaCl/p) tasolle noin 55 me./l ilman NaCl:n lisäystä. Natriumin ja kaliumin summa ekvivalenteissa oli hieman pienempi perusdieeteillä kuin niillä dieeteillä, joihin oli lisätty NaCl:a.

Kuiva-aineen saannin pienentyessä ilmeni seossyljen Na-konsentraatiossa lievästi aleneva ja K-konsentraatiossa nouseva tendenssi.

Pötsinesteen Na- ja K-konsentraatiot seurasivat hyvin kiinteästi syljen vastaavia konsentraatioita. Na-konsentraatio oli pötsinesteessä keskimäärin 20 % alempi kuin samanaikaisesti syljessä. Suhde pysyi samana dieetistä riippumatta. Dieeteillä, joihin kuului 100 tai 50 g NaCl:a, kaliumin konsentraatio oli syljessä keskimäärin 60—65 % alempi kuin pötsinesteessä. Dieeteillä ilman natriumkloridin lisäystä K-konsentraatio oli syljessä 15—20 % alempi kuin pötsinesteessä.

Pötsi-verkkomahasta poistui pötsinesteessä 12 tunnin päiväjaksolla natriumia eri dieeteillä 15.3:sta 2.9:ään ekvivalenttia ja kaliumia 0.7:stä 8.1:een ekvivalenttia. Vaihtelu johtui osaksi poistuvien nestemäärien eroista eri dieeteillä ja osaksi natriumin ja kaliumin konsentraatioiden eroista pötsinesteessä.

Rehuissa, juomavedessä ja syljessä pötsi-verkkomahaan saapuneet natriummäärät vastasivat sieltä saman ajan (12 t) kuluessa poistuneita määriä (1 %:n riskillä). Kaliumin pötsiin saapuneet määrät vastasivat samoin sieltä poistuneita määriä, kun eroa verrattiin keskiarvoille laskettuihin 99 %:n varmuusrajoihin, paitsi 15 tapauksessa, jolloin pötsiin näytti saapuneen enemmän kaliumia kuin sitä oli samana aikana verkkomaha-satakerta aukosta poistunut.

Päiväjakson 12 tunnissa pötsiin tulleesta natriumista oli 94 % syljen osuutta. Rehuissa ja juomavedessä tulleen natriumin osuus lisääntyi NaCl-annostuksella 100 g/p noin 9 %:iin ja annostuksella 50 g/p 7 %:iin, verrattuna 4 %:n osuuteen perusdieeteillä. Karkearehun osuuden pieneneminen lisäsi jonkin verran ruokinnassa välittömästi pötsiin tulleen natriumin suhteellista osuutta, johtuen lähinnä syljen määrän vähenemisestä.

Rehut ovat olleet kaliumin tuojana tärkeämpi lähde kuin sylki. Eläinten Na:n saannin ollessa riittävä (100 ja 50 g NaCl/p) oli rehujen sisältämän kaliumin osuus pötsiin 12 tunnin ruokintavälinä saapuneesta kaliumista keskimäärin lähes 80 %. Dieeteillä ilman NaCl-lisäystä, jotka jättivät eläimet lievään Na:n puutteeseen, syljen merkitys kaliumin tuojana lisääntyi ja rehujen kaliumin osuus oli noin 40 % pötsiin saapuneesta kaliumista.

Natriumin kokonaismäärä pötsissä 12 tunnin ruokintavälinä oli ekvivalentteina 3—5 -kertainen kaliumiin verrattuna dieeteillä, joihin kuului 100—50 g/p NaCl:a, ja 1.5—2.0 -kertainen dieeteillä ilman NaCl-lisäystä.

Pötsiin tulleen natriumin ja kaliumin yhteinen ekvivalenttimäärä oli keskimäärin 2.4 ekvivalenttia syötyä kuiva-ainekiloa kohti, ja se oli kuiva-ainetasosta jokseenkin riippumaton. Sen sijaan summa pieneni suolan annostuksen vähentyessä ja karkearehun osuuden dieetissä alentuessa.

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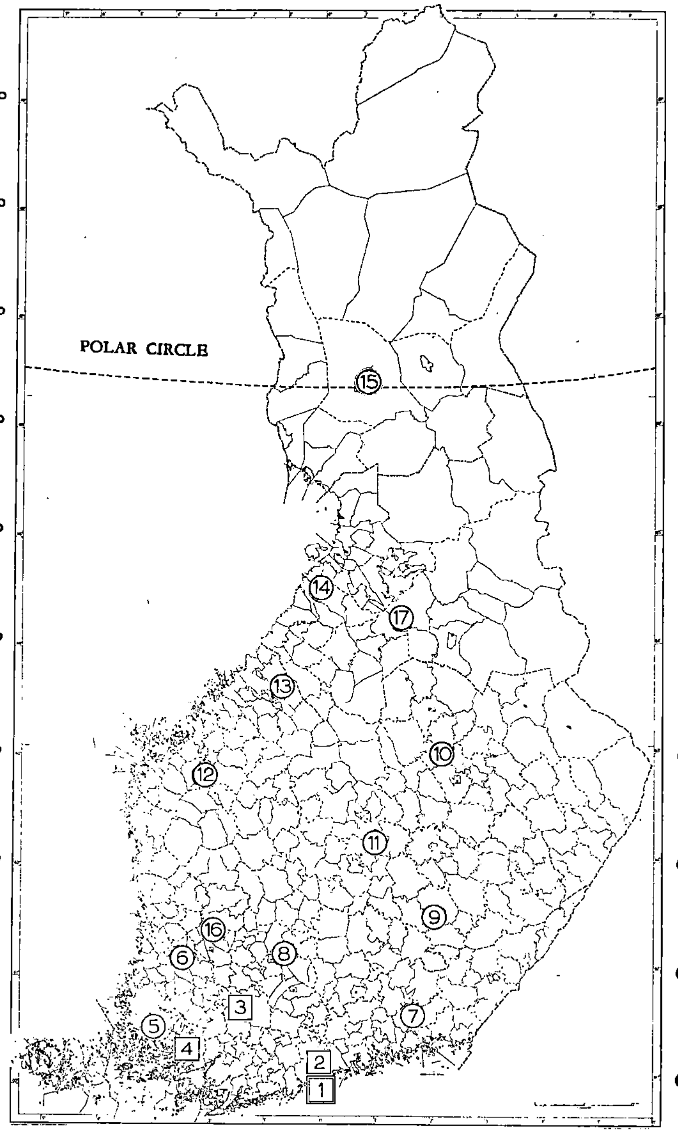

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