Digesta Kinetics in Sheep and Cattle Fed Diets with Different Forage to Concentrate Ratios at High and Low Intakes

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ABSTRACT
Effect of maintenance and ad libitum intakes on digesta kinetics was studied with six ruminally fistulated cows and six ruminally fistulated wethers to validate the use of sheep as a model of cattle. Complete diets were made up of ratios of alfalfa:cracked corn and soybean meal of 80:20, 55:45, and 30:70. The rate of passage of Cl-mordanted alfalfa and soybean meal in the reticulo-rumen was negatively related to percentage of concentrate in the diet in both species at low intakes. Passage values of particulate and liquid markers were faster at high than at low intakes in both species for all diets. Rumen liquid volume increased with intake only in the cows on the low and intermediate concentrate diets.

No substantial differences were found in particulate passage values between sheep and cattle. However, liquid passage rates from the rumen and the differentials between liquid and particulate dilution rates were higher in cows than in sheep for all diets at both intakes. These results together with those for digestibility data reported in a previous communication suggest that caution should be exercised when extrapolating results from one species to the other.
(Key words: digesta kinetics, sheep and cattle, intake)

INTRODUCTION
In recent years, cereal grains have been a major source of energy in compounded feeds for high producing ruminant livestock. The yield of animal production required dictates, in general, the amount of grain in the diet. Diet formulation in ruminants requires information of nutrient requirements as well as reliable values for feed ingredients. The digestible energy of rations declines as intake increases and it does so at a greater rate when the concentrate portion of the diet increases (6). This is mainly an effect of shorter retention time of digesta in the gastrointestinal tract (5). Little information exists on the interactions between the forage and concentrate portions of the diet that affect digesta kinetics and utilization of feed. The few studies in this area have been carried out at intakes below those found in high producing animals. Therefore, information related to the retention time of digesta in mixed diets fed at different intakes is important in the estimation of degradability and in understanding feed utilization. The use of sheep as an experimental model for dairy cattle assumes that changes in intake and type of diet produce similar changes in digesta kinetics and in both species. Data from sheep, however, may not be applicable to the high yielding dairy cow. The assumption that sheep and cattle do not differ from a nutritional point of view has been tested mostly with animals fed high forage diets. No experimental results have been reported for different forage:concentrate ratios at high intakes. Data obtained in different experiments and analyzed by Warner (27) suggest that the mean retention time of digesta in cattle might be longer than in sheep. The reasons for differences between species are not clear. In a previous communication (6), we examined the effect of forage to concentrate ratios and intake on digestibility in sheep and cattle.

The objective of this experiment was to determine whether particulate and liquid passage rates in sheep fed diets with different forage:concentrate ratios at maintenance and ad libitum intakes are comparable with those obtained with dairy cattle at similar intakes.
MATERIALS AND METHODS

Animals, Diets, and Experimental Design

The diets, animals, and experimental design were described previously (6). In summary, three ratios of forage:concentrate were fed to six rumen-fistulated cows (nonpregnant) for ad libitum intake (cows-high) and maintenance (cows-low) intakes during the lactation and dry periods, respectively. Average milk production for cows-high was 28 kg/d (range 23 to 33 kg). The same diets were fed to six rumen-fistulated wethers at ad libitum (sheep-high) and maintenance (sheep-low) when the animals were 5 and 9 mo old, respectively. The complete diets were made up of ratios of chopped alfalfa hay: cracked corn and soybean meal of 80:20 (LC), 55:45 (IC), and 30:70 (HC). Body weights of experimental animals, organic matter intakes, energy digestibilities, and chemical composition of the complete diets are shown in Table 1. No supplemental mineral mix or vitamins were included in sheep diets. Sheep had continuous access to mineral blocks (6). Animals within species and intake were arranged in two 3 x 3 Latin square designs, making a total of 72 observations for each measurement. Each period lasted 35 d. The rate of passage of alfalfa was determined from d 19 to 25, liquid rate of passage from d 26 to 28, soybean meal rate of passage from d 29 to 33, and rumen osmolality on d 34.

Alfalfa Rate of Passage

Rate of passage of alfalfa particles was measured using mordanted Cr III stained on the cell walls of the alfalfa hay particles (Alf-Cr) (25). Alfalfa rate of passage studies were conducted in conjunction with the digestion trials (6). One hour after the morning feeding, cows and sheep were dosed via the ruminal cannula with 100 and 10 g, respectively, of the Cr-mordanted cell wall material. Between 30 and 35 fecal samples were collected from 9 to 167 h postdosing. Initial sampling times were closely grouped and were spaced further apart over time postdosing. This was done to detect as many points as possible in the ascending and peak portions of the excretion curve. At each collection time, feces were totally removed from galvanized feces pans attached to cattle stalls or for sheep from collection bags. Feces were weighed and...
sampled for marker analysis. Samples were dried at 70°C in a forced draft oven and weighed to calculate total DM voided since the previous time of sampling. Samples from cows were ground in a Wiley mill (Philadelphia, PA) with a 2-mm screen and stored for Cr analysis. Samples from sheep were stored unground.

Soybean Meal Rate of Passage

On d 29, lactating cows, dry cows, and sheep were intraruminally dosed with 100, 70, and 10 g of Cr-mordanted soybean meal (SBM-Cr) (25) after the morning feeding. Between 20 and 25 fecal grab samples from the rectum of cows were obtained from 10 to 120 h postdosing. Cows were induced to defecate by manual palpation of the rectum and the last portion of the excrement was taken as the sample. This procedure proved unsuitable for sheep. Therefore, sheep were fitted with the nylon fecal collection bags used in the digestion trials. The samples were taken from the collection bags. Sampling time was taken as the midpoint of the collection period. Samples from cows and sheep were dried at 70°C in a forced-draft oven. Samples from sheep were stored unground in plastic bags; samples from cows were ground in a Wiley mill with a 2-mm screen and stored for chromium analysis.

Liquid Rate of Passage

Rumen liquid phase dilution rate was estimated with the Na salt of Co-EDTA as a liquid phase marker (25). On d 26, lactating cows, dry cows, and sheep were intraruminally dosed with 50, 40, and 5 g of Co-EDTA dissolved in water. The marker was mixed with 500 and 50 ml of distilled water (cows and sheep, respectively) and injected in different locations in the rumen 2 h after the morning feeding. Samples of rumen fluid (30 ml) were obtained at 0 (before dosing), 2, 4, 6, 8, 10, 12, 16, 20, 24, and 36 h postdosing. A 60-ml disposable syringe attached to a polyethylene sampling tube with a terminal wire screen was used to obtain the samples. The tube was moved to different positions in the rumen during collection. Samples were centrifuged at 16,000 rpm for 15 min, and the supernatant fraction was stored at -20°C for cobalt analysis.

Rumen Osmolality

On d 34, rumen samples were taken to measure osmolality. Samples were obtained starting before morning feeding (time 0) and at 1, 2, 4, and 6 h postfeeding. The samples (30 ml) were taken from the anterior floor of the ventral sac of the rumen using the procedure described in the liquid rate of passage section. Each sample was immediately placed on ice. The samples were centrifuged at 16,000 rpm for 15 min, and osmolality was measured in the supernatant within 4 h after the samples were taken.

Preparation of Markers

Chromium-Mordanted Alfalfa. Mordanted Cr III stained on the cell wall of the alfalfa hay particles was prepared using the procedures described by Udén et al. (25). Alfalfa fiber was prepared by soaking chopped alfalfa hay with commercial detergent in a galvanized metal trough. Hay was packed in cheesecloth and soaked in hot tap water (initial temperature, 60°C) and detergent overnight. Then it was washed with hot tap water (60°C) for several hours to extract as much of the cell solubles and detergent as possible. The procedure was repeated a minimum of six times. After that, the prepared fiber (average cell wall, 85 to 90% of DM) was dried in a forced-draft oven at 60°C for 24 h. Washing the material in acetone to remove remaining lipids as it was done originally (25) was not thought to be necessary. Three hundred grams of the prepared fiber were soaked in 1800 ml of a water solution of sodium dichromate (9 g Na2Cr2O7·2H2O/100 ml H2O) in aluminum pans covered with aluminum foil. The preparation was baked in an oven at 95°C for 24 h. After that the fiber was washed with hot tap water (60°C) through cheesecloth in a Buchner table-type funnel with an internal diameter of 308 mm (Fisher Scientific Co., Ltd., St. Louis, MO) under vacuum until the filtrate became colorless. The fiber was then suspended in water and treated with excess ascorbic acid (liquid near pH 4) to convert the Cr VI to Cr III. Although the change in color to green, which indicates the formation of Cr III, occurred in less than .5 h, mordanted fiber was kept in the solution overnight. Finally, the marked alfalfa was washed with hot tap water (60°C) for several hours and dried at 60°C.
Chromium-Mordanted Soybean Meal. The Cr-mordanted technique was devised to study the movement of cell wall particles through the gastrointestinal tract. Trivalent Cr forms strong ligands not only with plant cell wall components but also with proteins, which are insoluble and indigestible. Soybean meal and other high protein feeds can be treated directly with dichromate solutions to yield marked material. Batches of 800 g of SBM were soaked in 3200 ml of a water solution of sodium dichromate (6.25 g Na₂Cr₂O₇·2H₂O/100 ml H₂O) in aluminum pans covered with aluminum foil. The procedures used after this were identical to those used for mordant alfalfa cell wall.

Cobalt-Ethlenediaminetetraacetate. It was prepared according to Uden et al. (25). Batches of 125 g of Co(II) acetate·4H₂O, 146 g of ethylenediamine tetraacetic acid and 260 g of NaOH were dissolved in 1 L of distilled water with heating in 4-L beakers. After the solution cooled, 100 ml of 30% hydrogen peroxide were added, and the mixture was allowed to stand overnight in the laboratory. Next, 1500 ml (95% vol/vol) of ethanol were added and the beakers were stored at 5°C overnight. Finally, the crystals were washed with 80% vol/vol of ethanol. Yield of NaCo-EDTA·3H₂O was approximately 86 to 87%.

Analytical Methods

Chromium. Chromium was determined in fecal samples by atomic absorption spectroscopy (28), with a Varian Techtron Model AA-4, Atomic Absorption Spectrophotometer (Varian Techtron Pty. Limited, Australia). The samples (up to 2.5 g depending on Cr concentration) were weighed in a 100-ml Pyrex beaker and ashed at 550°C overnight. This temperature was high enough to ash the sample without damaging the beaker. The acid digestion was performed directly in the beaker, eliminating the need to transfer the ashed sample to a second container and reducing losses of Cr through incrustation during ashing. More than 4000 samples were analyzed by this method.

Cobalt. Cobalt in rumen fluid was analyzed by atomic absorption spectroscopy, using the same equipment described for Cr. After centrifuging (16,000 rpm for 15 min), the samples of rumen fluid (diluted or undiluted) were directly aspirated into the flame of the atomic absorption apparatus. Cobalt concentration in the samples was calculated against Co standards (1, 3, 5, 10, and 15 ppm), prepared from a 1000-ppm stock solution (Fisher Scientific Co., NJ). All readings were done relative to that of distilled water, which was set at 0 absorbance. Impurities in the rumen fluid samples could cause interferences with Co determination. As a check on accuracy of the method, a recovery test of Co-EDTA added to centrifuged rumen fluid was made. Approximately 500 ml of rumen fluid were collected from a fistulated steer, eating an alfalfa and cracked corn (50:50 ratio) diet. The sample was centrifuged 15 min at 16,000 rpm in 50-ml plastic centrifuge tubes. Supernatant was used to make the dilutions. A solution with 5100 ppm of Co as Co-EDTA was diluted 850 times with distilled water or rumen fluid. Cobalt concentration in the water and rumen fluid samples was 6.12 and 6.07 ppm, respectively. The results indicate that the method is reliable for the determination of Co as Co-EDTA in rumen fluid samples.

Osmolality. Osmolality in rumen fluid was measured by freezing point depression with an osmometer (Advance Osmometer, Model 3W, Advance Instruments, Inc., MA).

Mathematical Calculations of Different Parameters

Chromium Rate of Passage Parameters. The Alf-Cr and SBM-Cr excretion curves were analyzed similarly. The model (Equation [1]), consisting of two exponential exponents and a time delay (4, 13), was used to analyze the curves:

\[ y = \begin{cases} Ae^{-k_1(t-TT)} & \text{for } t > TT \\ Ae^{-k_2(t-TT)} & \text{for } t < TT \end{cases} \]

where y is marker concentration, A is a scale parameter, t is sampling time, TT transit time or an estimate of time of first appearance of marker in feces, \( k_1 \) is the rate of passage of marker in the reticulorumen, and \( k_2 \) is an estimate of the rate of passage of marker in the lower tract (cecum and proximal colon). The numerical values of \( k_1, k_2, \) TT, and A were derived using the nonlinear regression procedure (NLIN, iterative Marquardt method) of SAS (22). A total of 140 fecal excretion curves for both Alf-Cr and SBM-Cr were analyzed.

To fit each excretion curve, 1) Chromium concentration in the feces (μg/g DM) was plot-
The descending portion of the curve (linear) was evaluated by regression of the natural logarithm (ln) of Cr concentration (y) against time of sampling (t). The model used

\[ \ln y = \ln A - kt \]

was fitted to the data using the General Linear Models procedure (22); the first point to start the analysis was selected by visual inspection. 3) The k value, estimated by linear regression, was used as a starting value for the k₁ parameter in the NLIN procedure; starting values for the other parameters (k₂, T₁, and A) were estimated by visual inspection of the semilogarithmic plot. Using this procedure to fit excretion curves, the program converged in less than 20 iterations in most of the cases. The parameters k₁, k₂, and TT were designated Ak₁, Ak₂, ATT, and Sk₁, Sk₂, STT to denote values for alfalfa (A) and soybean meal (S). Mean retention times (R₁) in the mixing compartments (reticulorumen, T₁, and cecum-proximal colon, T₂) of the model, were calculated as the sum of reciprocals of the exponential constants (1/k₁ and 1/k₂, respectively). Total mean retention times (R₂) were calculated as the sum of the mean retention times in both compartments (R₁) plus time delay (TT).

\[ R₁ = T₁ + T₂ \]
\[ R₂ = R₁ + TT \]

These parameters were designated AR₁, AR₂, SR₁, and SR₂ to denote values for alfalfa (A), soybean meal (S), and R as defined before.

**Cobalt Rate of Passage Parameters.** The passage rate constant (k₁Co) of the water-soluble marker (Co-EDTA) was calculated as the slope of the semilog plot of Co concentration against time. Rumen fluid volume (VOL, L) was estimated by dividing the amount of Co dosed by the antilog of the intercept (A) at zero time. The equation describing the curve is:

\[ y = Ae^{-k₁t} \]

where y is the marker concentration at time t, A is marker concentration at t₀, and k₁ is the dilution rate constant for Co (k₁Co). The model was fitted to the data using the GLM procedure (22). Flow (FLOW, L/h) was calculated as k₁Co × VOL. The difference in body weight between cows and sheep is reflected in the respective values of VOL and FLOW. To establish a meaningful comparison between the two species, these values were expressed as a percentage of BW. The adjusted volume and flow parameters were designated VOLc (L/100 kg BW) and FLOWc (L/h per 100 kg BW) respectively.

**Statistical Analysis**

Passage rate constant, retention parameters, and rumen osmolality were analyzed using the General Linear Models procedure (22). Details of the statistical model used are given elsewhere (6). Data in Figures 1 to 4 were analyzed by regression techniques. Equality of slopes (sheep versus cows) was tested by including species and the interaction between species and the independent variable in the regression model (22).

**RESULTS**

**Particulate Rate of Passage**

*Effect of Type of Diet.* The rate of passage of Alf-Cr in the reticulorumen (Ak₁) was linearly and negatively related to the percentage of concentrate in the diet in both species at low intake (P<.005, Table 2). At high intake, both sheep and cattle fed the HC diet showed a passage rate slower than, but not significantly different from, the others. Lower tract rate of passage of SBM-Cr (Ak₂) was not altered with changes in the proportion of concentrate in the diet. The estimated time of first appearance of marker in the feces (ATT) increased linearly with increasing amounts of concentrate in the diet in sheep-low (P<.005) in both species and at high intakes (P<.05) in cows. In sheep-high, the relationship between total tract retention and amount of concentrate in the diet was nonlinear (P<.05), with a minimum value for the IC diet.

With regard to rates of passage of SBM-Cr, increasing the amount of concentrate in the diet caused a reduction in Sk₁ and Sk₂ average
In cows caused an increase in Ak2 values for all diets in sheep-high, cows-low, and cows-high increased linearly with increasing proportions of concentrate in the diet (P<.05). Total tract retention of SBM-Cr (SR1 and SR2) in sheep-high, cows-low, and cows-high increased linearly with increasing proportions of concentrate in the diet (P<.05). In sheep fed at maintenance (sheep-low), retention time increased, but because of a high variation between animals, a larger difference for statistical significance was required.

**Effect of Intake.** At high intakes, rumen rate of passage values for alfalfa (Ak1) in sheep were 1.16, 1.64, and 1.67 times faster than at low intakes for LC (P<.05), IC (P<.001), and HC (P<.001) diets, respectively (Table 2). Corresponding values for the cows were 1.34, 1.58, and 2.16 (P<.05). Increasing the intake of feed in cattle increased Ak2 values for all diets in both species (P<.01). Both measurements of total tract retention (AR1 and AR2) substantially decreased (32 to 50% reduction) with increasing intake for all diets in both species (P<.001), except for the LC diet in sheep which exhibited a lesser reduction (AR1, 16%; AR2, 17%) (P<.05).

Increasing intake caused an increase in the rumen rate of passage values of SBM-Cr (Sk1) in both species. In sheep at high intakes, passage rates of SBM from the rumen were 1.62, 2.25, and 1.91 times faster (P<.01) than those at low intakes for the LC, IC, and HC diets, respectively. Corresponding values for cattle (P<.001) were 1.81, 2.68, and 2.42. The rate of passage of SBM-Cr in the lower tract (Sk2) followed the same pattern as Sk1 for all the diets in both species. In cows, Sk2 values for diet HC were higher at high intakes, but the increase from the low intake value was not

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**Table 2.** Least squares means for rate of passage of Cr-marked alfalfa in the rumen (Ak1, %h), rumen retention time (AT1, h), rate of passage in the lower tract (Ak2, %h), rumen retention time (AT2, h), rate of passage in the lower tract (Ak2, %h), and in sheep low concentration (LC), intermediate concentration (IC), and high concentration (HC) at low and high intake.1

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1Mean square error from complete mixed effects model [see reference (6)].
significant. Values at high intake were 1.74 (P<.001), 1.47 (P=.056), and 1.54 (P<.05) times higher for the LC, IC, and HC diets in sheep, respectively, and 1.88 (P<.01), 1.87 (P<.01), and 1.51 (P>.10) in cows. The STT values of the three diets decreased at high intakes in sheep and cattle (P<.05).

Total tract retention values (SR1 and SR2) decreased (45 to 63% reduction) with increasing intakes in cows fed the three diets (P<.05). Sheep also had reduced retention time values at high intakes in the three diets (P<.01), with the exception of SR1 for diet LC (P>.05).

Effect of Species. At the low intakes, cows had higher AR2 (P<.001) (Table 2) values than sheep for diet LC. The ATT values at low intake were also higher for cows than for sheep for diets LC (P<.001) and IC (P<.01). Other Alf-Cr parameters did not differ greatly between species.

At the high intake, sheep had smaller ATT values than cows for diet IC (P<.05) and a greater total tract retention (both AR1 and AR2) (P<.05) for diet HC. Other Alf-Cr parameters did not show significant differences, except for Ak2, which was smaller (P<.05) in sheep than in cows (sheep, 5.98%, cows, 9.16%).

No significant differences were found between species in any of the SBM-Cr rumen and lower tract kinetic parameters (Table 3). Sheep-low had shorter (P<.05) total tract retention (SR2) values of SBM-Cr than did cows-low for the IC diet. Transit time of SBM-Cr (STT) was shorter in sheep than in cows for diets LC (P<.001) and IC (P<.01).

Co-EDTA Parameters and Rumen Osmolarity

Osmolality in rumen fluid increased for all diets following feeding, with the highest values occurring 1 to 2 h after feeding in sheep and cows at both intakes. Statistical analysis of rumen osmolality data by sampling time did not differ from that performed on average values over time; therefore, only results on the latter will be reported.

Effect of Type of Diet. Dilution rate of liquid in the rumen (k1Co) decreased linearly (P<.05) as the proportion of concentrate in the diet increased in both species at low intakes (Table 4). However, differences in k1Co among the three dietary treatments at high intakes were small and not statistically significant. Estimates
TABLE 4. Least squares means for rumen liquid turnover rate of Co-EDTA ($k_1$Co, %/h), rumen mean retention time of Co-EDTA ($T_1$, h), rumen volume (VOL, L; VOLc, L/100 kg BW), rumen liquid flow (FLOW, L/h; FLOWc, L/h/100 kg BW), and rumen fluid osmolality (mOsmol/kg) on diets low in concentrate (LC), intermediate in concentrate (IC), and high in concentrate (HC) fed at low and high intakes.1

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1Six observations in each mean, except for osmolality in cows-low where n = 4 in each diet.
2Mean square error from complete mixed effects model [see reference (6)].
3Mean square error for sheep.
4Mean square error for cows.
5Rumen fluid osmolality average values over sampling time (0, 1, 2, 4, and 6 h postfeeding).
6Rumen fluid osmolality maximum observed values.
of rumen fluid volume decreased linearly ($P<.05$) as diet varied from LC to HC in both species at low and high intakes. The same results were obtained when these values were expressed as a percentage of BW ($VOL_e$). Linear changes ($P<.05$) were found in the two estimates of rumen fluid flow (FLOW and $FLOW_c$) with alterations in diet composition, the maximum mean FLOW value for diet LC being 1.25 and 1.60 times higher than for diets IC and HC in sheep-low. Corresponding values for the other groups were 1.14 and 1.40, 1.31 and 1.56, and 1.33 and 1.89 for sheep-high, cows-low, and cows-high, respectively (Table 4).

The average rumen osmolality values over time (0, 1, 2, 4, and 6 h after feeding) are given in Table 4. In sheep-low, rumen osmolality decreased linearly ($P<.05$) as the proportion of concentrate in the diet increased. However, in sheep at high intake and cows at low and high intakes, osmolality was unaffected by diet. The maximum values of rumen osmolality are also given in Table 4.

**Effect of Intake.** Larger feed intakes were associated with faster liquid rate of passage values ($k_1Co$) in both species for the three diets ($P<.001$) (Table 4). For sheep-high, $k_1Co$ values were $1.51, 1.80$, and $1.96$ times higher than for sheep-low for diets LC, IC, and HC respectively. Corresponding values for cattle were $1.53, 1.69$, and $1.81$. The marker estimate of VOL significantly increased only in the cows for diets LC ($P<.001$) and IC ($P<.01$). In sheep and cows, no changes were found in VOL with intake. The adjusted values of volume ($VOL_e$, L/100 kg BW), increased with intake in sheep ($P<.001$) and cows ($P=.06$) only for diet LC. Flow parameter values (FLOW and $FLOW_c$) showed an increase of more than 65% as intake increased in both species ($P<.01$), except for $FLOW_c$ for diet HC in the cows, in which the increment was 50% ($P=.06$). The FLOW values in sheep-high were $1.65, 1.81$, and $1.88$ times higher than in sheep-low for diets LC, IC, and HC, respectively, whereas in cows corresponding values were $2.12, 2.09$, and $1.75$. Rumen osmolality increased with increasing intake in sheep ($P<.01$) and cows ($P<.05$). The degree of change of rumen fluid osmolality from low intake to high intake increased from diet LC to HC.

**Effect of Species.** Rate of passage of liquid ($k_1Co$) was faster in cattle than in sheep ($P<.05$) at both intakes (Table 4), cattle values being 1.40, 1.42, and 1.48 times faster than those for sheep at the low intake and 1.42, 1.34, and 1.36 at the high intake for LC, IC, and HC, respectively. Comparisons of unadjusted values of rumen fluid volume or flow are meaningless because of the differences in BW between species. Therefore, only BW adjusted values of the parameters are considered here. Rumen volume ($VOL_e$) values did not significantly differ between species at both intakes (Table 4), except for diet HC at high intake, where sheep VOL values were 1.29 times greater ($P<.05$) than those for cattle.

At low intake, cattle had greater adjusted flow ($FLOW_c$) values for diets LC ($P<.01$), IC ($P=.056$) and HC ($P=.066$) than did sheep. At high intake, cattle had higher values than sheep for diet LC ($P<.01$) and IC ($P=.06$). $FLOW_c$ values in cows-low were 1.58, 1.47, and 1.61 times higher than in sheep-low for LC, IC, and HC, respectively; values at high intake were 1.47, 1.22, and 1.05.

Rumen osmolality was higher ($P<.01$) for cows than for sheep at low and high intakes on all diets, except for diet HC at high intake, where the difference between cows and sheep was smaller (sheep, 306 mOsmol/kg; cows, 321 mOsmol/kg; $P=.12$).

**DISCUSSION**

**Particulate Rate of Passage**

**Effect of Type of Diet.** Sheep and cattle data indicate that in the rumen of animals fed mixed diets, there are at least two particular passage pools with different kinetic rate constants: one for the concentrate (SBM-Cr) and another for the forage (ALF-Cr). The speed of passage was always greater for the concentrate than for the forage portion of the diet (Tables 2 and 3). Values of rate of passage of alfalfa from the rumen ($Ak_1$) plotted against those of SBM ($Sk_1$) for sheep and cattle are shown in Figure 1. The slopes of the regression equations (sheep, $391 \pm 0.066$; cows, $355 \pm 0.043$) were less than unity ($P<.001$). A test of heterogeneity of slopes, as well as a covariate analysis on these two variables, indicated that values for both species are contained within a common line (Figure 1). For each unit of increase in $Sk_1$, $Ak_1$ changed by only $369 \pm 0.74$ (95% confidence interval) in sheep and cows. This obser-
Figure 1. Relationship between rumen outflow rates (%/h) of Cr-mordanted alfalfa hay (Ak1) and SBM (Sk1) in sheep and cows fed at low and high intakes ($Y = 1.91 + 0.369 X$; SE of $b = 0.037$, $n = 68$, $r = .77$, $P<.001$).

The effect of forage:concentrate ratios on kinetics of the particulate fractions of digesta has not been well studied. Information is limited on the effect that proportion of concentrate in the diet has on retention time of roughage and vice versa. In some studies the forage:concentrate ratio effects are confounded with food intake. Studies have shown that increasing the proportion of concentrates in the diet increases the retention time of indigestible hay particles in the gastrointestinal tract (5, 17). Contrary to our own results, Bines and Davey (3) found no differences in retention times for diets containing 40 to 100% concentrates. Several factors complicate interpretation of studies relating forage:concentrate ratios with turnover in the rumen. Physical (particle size, density, and distribution of particle sizes) and chemical (cell wall contents, cell wall composition, and protein content) quality of the roughage seem to be critical. For instance, mean retention time of straw particles increased in sheep fed a diet of sodium hydroxide-treated straw in which concentrates provided 45% of the total diet. However, when the same amount of concentrates was added to untreated straw, retention times did not change (7).

Effect of Intake. The increased rate of passage of marker through the gastrointestinal tract of both sheep and cows with increased feed intake agrees with other results for cattle (5) and for sheep (4, 14, 17). Increased passage rates for the reticulum have also been demonstrated in cows (5, 8, 17) and in sheep (8, 14). The reduction of retention times in the cecum-proximal colon ($k_2$) resulting from increasing feed intake agrees with other results reported in cows (5) and in sheep (11, 14).

The amount of feed consumed is probably the most important variable associated with retention time of digesta in the gastrointestinal tract of ruminant animals. Changes in retention time with variation in intake have been demonstrated in almost all the experiments in which these two parameters were studied (27). This association is expected given the fact that in ruminant animals, an increase in the amount of feed entering the gastrointestinal tract must be coupled with either an expansion of the organ or a faster rate of disappearance (through digestion or passage). Both phenomena might operate at the same time. The magnitude of the response of these two mechanisms is likely to be dependent on physical and chemical composition of the diet (density, particle size, cell walls, starch, and protein concentrations). Density and particle size effects on rate of passage are apparent in our results by the different response of Ak1 and Sk1 to intake. The differentials between high and low intakes were greater for Sk1 (higher density and smaller particle size) than for Ak1. This could explain the greater increase in passage rate for the HC diet when intake was increased in our experiment. Similarly, Colucci et al. (5) observed that intake variations caused greater changes in retention times in low forage diets than in high forage diet. Also, the effect of intake on the rate of passage of alfalfa in the rumen (Ak1) and cecum-proximal colon (Ak2) varied with diet. For instance, in sheep, doubling intake increased rate of passage 16% in the rumen and 48% in the cecum-proximal colon for diet LC. For diet HC, doubling intake markedly increased rate of passage through the rumen (67% increase), whereas the increase was only 15% in the lower tract (Table 3).
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Effect of Species. A few direct comparisons on retention of digesta between sheep and cattle have been made, mostly with animals fed high forage diets. No experimental results have been reported for different forage:concentrate ratios at high intakes. When interpreting data from the literature, one should be cautious in extrapolating results obtained with forage diets to animals fed mixed diets.

Data obtained in different experiments and analyzed by Warner (27) suggest that the mean retention time of digesta in cattle might be longer than in sheep. Similarly, Puppi et al. (20) concluded that cattle had a longer retention time of digesta than sheep. They pointed out that the relationship between intake and passage for both species changed according to the unit of intake expression. The regression lines were different for sheep and cattle when the .9 power of BW was used, but when the unit of intake was changed to grams of intake per kilogram of BW, then a common line for both species was obtained. Their conclusion was based on the fact that the unadjusted values of retention were smaller in sheep than in cattle. However, one can also argue that the differences found could be more an effect of intake than an effect of species. This view agrees with results obtained by Mansbridge and Ørskov (18), who found no consistent differences between sheep and cattle in passage of SBM-Cr at similar intakes. The common regression line indicates that per unit of intake (BW), both species had similar retention values. Our own results suggest that at low intakes, retention times for Alf-Cr (AR2) are longer in cows (74.7 h) than in sheep (58.2 h) fed the low concentrate diet HC. The increase in the ratio VOL/klCO from LC to HC diet. The increase in the ratio VOL/klCO was greater in cows high concentrate diet and lower in sheep. Values of differential rate of passage of Co-EDTA and particulate from the reticulorumen in cows and sheep at both intakes. This is consistent with several reports (12, 25). Values of differential rate of passage of Co-EDTA and particulate matter from the reticulorumen (ratios of k1Co to Ak1 and Sk1) are shown in Table 5. These ratios indicate an increase in differential passage rates of water and particulate matter from LC to HC diet. The increase in the ratio value from LC to HC must be due to differential effects on fluid volumes: flows or on particulate volumes: flows:digestion rates. The data indicate that increasing the amount of concentrates in the diet (or decreasing the fiber content) did not have the same effect upon kinetics of liquid and particulate phases in the rumen.

Rumen Osmolality

Effect of Type of Diet. The rate of marker disappearance from the rumen in sheep-low and cows-low was slower when the proportion of concentrate in the diet increased (Table 4). This finding is generally supported by results with liquid markers for sheep (13, 23) and for cattle (2, 10, 21, 23). Mathers and Miller (19), however, found no significant differences in fluid dilution rates in sheep fed chopped alfalfa hay supplemented with different proportions of barley at 23 g DM/kg BW. The lack of effect of diet on dilution rate in that study (19) was attributed to the moderate amount fed. However, they also pointed out a large animal variation in passage rate within diets. Our results indicate that the effect of diet is apparent at low intakes, but at high intakes, differences in fluid dilution rates between diets are small (Table 4). Similarly, fluid dilution rates of Co-EDTA were reduced by increasing the proportion of concentrate in the diet in cows fed at maintenance, but at ad libitum intake, dilution rate values did not change with diet (Colucci et al., unpublished). In those experiments in which proportion of concentrate in the diet had an effect on liquid dilution rate, intakes were low (21, 23) moderate (10, 13), and high (2).

Rumen fluid volume decreased with increasing amounts of concentrate in the diet (Table 4). This observation concurs with previous results in cows (10). On the contrary, the results of Bauman et al. (2) and Rogers et al. (21) with cows do not support this conclusion.

Differences in liquid flow (FLOW and FLOWc) from the rumen between the three dietary treatments were anticipated, since FLOW and FLOWc were calculated as the product of VOL and k1Co. As expected, Co-EDTA was eliminated faster than Alf-Cr and SBM-Cr from the reticulorumen in cows and sheep at both intakes. This is consistent with several reports (12, 25). Values of differential rate of passage of Co-EDTA and particulate matter from the reticulorumen (ratios of k1Co to Ak1 and Sk1) are shown in Table 5. These ratios indicate an increase in differential passage rates of water and particulate matter from LC to HC diet. The increase in the ratio value from LC to HC must be due to differential effects on fluid volumes: flows or on particulate volumes: flows: digestion rates. The data indicate that increasing the amount of concentrates in the diet (or decreasing the fiber content) did not have the same effect upon kinetics of liquid and particulate phases in the rumen.

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TABLE 5. Differential rate of passage of Co-EDTA (kICO), Co-mordanted alfalfa (AK), and soybean meal (SK) in sheep and cows fed diets low in concentrate (LC), intermediate in concentrate (IC), and high in concentrate (HC) at low and high intakes.

<table>
<thead>
<tr>
<th></th>
<th>Sheep-low</th>
<th>Sheep-high</th>
<th>Cows-low</th>
<th>Cows-high</th>
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<tr>
<td></td>
<td>LC</td>
<td>IC</td>
<td>HC</td>
<td>LC</td>
</tr>
<tr>
<td>kICO/AK</td>
<td>1.55</td>
<td>1.86</td>
<td>2.22</td>
<td>2.03</td>
</tr>
<tr>
<td>kICO/SK</td>
<td>1.21</td>
<td>1.63</td>
<td>1.53</td>
<td>1.14</td>
</tr>
</tbody>
</table>

Values are ratios of kICO to AK and SK.

Effect of Intake. The higher dilution rate of Co-EDTA observed at high intakes in both species is consistent with other results in sheep (14, 26) and in cows (1, 16, 24).

Interpretation of the effect of intake on rumen volume is complicated in this study by the different response observed in sheep and cows. In sheep, no changes were found in VOL with intake, whereas in cows VOL increased in the LC and IC diets and did not change at all in the HC diet. Published results in which rumen fluid volume was related to DM intake are contradictory and often confused. In sheep fed three different forage diets, rumen fluid volume increased with increasing feed intake (26). Similarly, Grovum and Williams (14) showed that the amount of water in the rumen of sheep fed alfalfa chaff was positively related to feed intake. In cows, increasing DM intake causes an increase (16), no change (24), or a decrease (1, 9) in rumen fluid volume.

The increase in liquid flow from the rumen (L/I/h) observed when intake was increased can be attributed principally to an increase in salivation, water consumption and possibly diffusion of water through the rumen wall.

Effect of Species. The lower digestibility of starch, as well as other feed fractions, in cattle than in sheep at high intakes found in the digestion study (6) may be partly related to the fact that liquid turnover rates (Table 4) and the differentials between fluid and particular turnover were greater in cattle than in sheep (Table 5). However, the greater rumen fluid osmotic pressure found in cattle compared with sheep might also explain the differences in liquid dilution rate observed. The higher rumen fluid osmolality values in cows could be an effect of a higher mineral intake, because no minerals were added to the diets of sheep. Nevertheless, ruminal osmotic pressure probably is involved in establishing the rumen liquid dilution rates that were observed because kICO values increased as osmolality increased (Figure 2). An increase in osmolality promoted a faster dilution rate in the rumen of sheep (15). The linear regression equations for sheep and cow data are given in Table 6. The slopes of the sheep and cow regression lines shown in Table 6 were not different (P>0.05), so subsequent calculations were made according to a model constrained to have the same regression coefficients for both species (Figure 2). The adjusted group mean or predicted value of kICO using the overall osmolality mean in prediction was smaller (P<0.01) for sheep than for cattle (sheep, 9.49 ± 0.42; cows, 11.33 ± 0.46; mean ± SE). This analysis shows that although osmolality values are related to liquid turnover rate, osmolality itself does not completely explain the differences in liquid turnover rate in cows and in sheep.

![Figure 2. Relationship between rumen fluid dilution rate (kICO, %/h) and rumen fluid osmolality (mOsmol/kg) in sheep and cows fed three different diets at low and high intakes. Common slope of the lines for sheep and cows is 0.076 (SE 0.011).](image-url)
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TABLE 6. Regression equations of rumen rate of passage of Co-EDTA (k₃Co, %/h) and rumen fluid osmolality (mOsmol/kg), Cr-mordanted alfalfa (Ak₁, %/h) and soybean meal (Sk₁, %/h).

<table>
<thead>
<tr>
<th>Y</th>
<th>X</th>
<th>Species</th>
<th>a</th>
<th>b</th>
<th>SEb</th>
<th>α</th>
<th>n</th>
</tr>
</thead>
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<tr>
<td>k₃Co</td>
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<tr>
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<td></td>
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<td>.020</td>
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<tr>
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<tr>
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<td></td>
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<td>1.040</td>
<td>.250</td>
<td>.038</td>
<td>.75</td>
<td>36</td>
</tr>
<tr>
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<td>.101</td>
<td>.81</td>
<td>32</td>
</tr>
<tr>
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<td></td>
<td>Cows</td>
<td>-1.218</td>
<td>.574</td>
<td>.086</td>
<td>.75</td>
<td>36</td>
</tr>
</tbody>
</table>

*Correlation coefficients significant at P<.001.

1Y = a + bx.

The graph indicates that for a given osmolality value, liquid turnover rate was still faster in cows than in sheep.

The same statistical approach described for k₃Co and osmolality was used in analyzing the relationships between rumen particulate outflow rates (Sk₁ and Ak₁) and liquid outflow rate (k₃Co). Outflow rates of particulate marker (Sk₁ and Ak₁) and the liquid marker (k₃Co) from the rumen were closely related in sheep and cattle (Figures 3 and 4). Although there were different lines for sheep and cattle for each of the relationships (Table 6), sheep and cattle regression coefficients were not different either for Ak₁ vs. k₃Co (P>.05) or for Sk₁ vs. k₃Co (P>.1). Sheep adjusted mean values for Ak₁ and Sk₁ were 1.34 and 1.60 times higher (P<.001) than those for cows (Figures 3 and 4). This suggests that at a given fluid outflow rate, the rate of passage of particles is faster in sheep than in cattle.

In summary, passage values (particulate and liquid) were linearly and negatively related to the percentage of concentrate at low intakes in both species. At high intakes, differences were small. Rumen fluid volume and liquid flow values decreased linearly from diet LC to HC in all the groups. Intake affected rate of passage of particulate and liquid fractions of digesta as well as FLOW in a positive way in both species. However, intake caused an increase in VOL only in cows fed diets LC and IC. The effect of intake on kinetic parameters was greater in diet HC than in the other. No big differences were found in particulate passage...
values between sheep and cattle, except for diet LC at low intake, in which ATT values were smaller in sheep than in cows. At high intake, sheep retained the Al-f-Cr for a longer time in diet HC. Significant species differences were found in liquid turnover rates and osmolality values (higher values for cows than for sheep).

The differentials between fluid and particulate turnover were greater for cows than for sheep. These results together with those for digestibility data reported on a previous communication (6) suggest that caution should be exercised when extrapolating results from one species to the other. The greater differential passage rates of liquid and particulate markers in cows than in sheep has significant implications with respect to biology and to management of ruminants.

REFERENCES


