Examination of Methods for Estimating Rate of Passage in Grazing Steers

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Abstract

Understanding how rate of passage estimates are influenced by procedural variations may facilitate standardization of methodology and enhance comparisons among studies. Therefore, 12 ruminal-fistulated beef steers ($\bar{x}$ wt. = 294 kg) were used in two 6-day grazing trials to evaluate influences of sampling site, intraruminal mixing, and mathematical model on particle passage rate estimates. Steers grazed a 13-ha pasture of immature crested wheatgrass. We estimated particle passage rate from the rumen by intraruminal administration of a pulse dose of Yb-labeled forage followed by serial collection of ruminal digesta or fecal samples. Treatments were (1) rectal sampling; (2) ruminal sampling—ruminal contents mixed before subsampling digesta; (3) ruminal sampling—ruminal contents not mixed before subsampling digesta. All steers were fitted with vibracorders to monitor grazing time before and during sampling periods. Fecal Yb curves were fitted with a one compartment, time-dependent (ICMPT-TD), a two-compartment, sequential time-dependent—time-independent (2CMPT-TD), and a two-compartment, time-independent (2CMPT-TI) model. All ruminal Yb curves were fitted with a single exponential decay model. Comparisons among models were limited to rate constants associated with the slower escape process. Intraruminal mixing did not alter ($P>0.10$) passage rates. The 2CMPT-TD model failed to fit some fecal profiles. Particle passage rates from the 2CMPT-TI model were greater ($P<0.05$) than those from the ICMPT-TD model. Similarity among passage rate constants derived from fecal Yb curves and those derived by semilogarithmic regression of ruminal Yb concentration on time depended on the model used to fit fecal Yb curves. Grazing time decreased ($P<0.01$) during intensive sampling periods. We conclude that for steers grazing immature grass pastures, intraruminal mixing before subsampling does not significantly alter rate of passage estimates; however, site of sampling and mathematical model may be important factors to consider in choosing appropriate methodology for estimating rate of passage.

Key Words: solid turnover, ytterbium, rumen mixing, fecal output, particle passage, sampling methods

Knowledge of ruminal particulate kinetics enhances understanding of roughage utilization by ruminant animals (Grovum 1983). Grazing animals form a unique group of roughage utilizers due to their frequency of feeding and to the diversity of the diets they consume. Understanding influences of methods used to estimate rate of particle passage facilitates establishment of standardized procedures viable under grazing conditions and enhances comparisons among different studies.

Limited information is available regarding the influence of site of sample collection (Ellis et al. 1983) and mathematical model (Mader et al. 1982) on particle passage rates estimated in grazing animals. Results from confinement studies comparing sampling sites or mathematical models have been contradictory (Hartnell and Satter 1979, Prange et al. 1982, Coleman et al. 1984, Staples et al. 1984), and indicated treatments may interact with the procedure used to estimate passage rates (Mader et al. 1982, Goetsch and Galyean 1983, Snyder et al. 1984). Intraruminal mixing may facilitate collection of representative ruminal digesta samples, but this procedure has been inadequately evaluated. In addition, influences of procedures for estimating rate of passage and intake on time spent grazing by free-ranging ruminants remains poorly described. Therefore, this study examined effects of sampling site, mathematical model, and intraruminal mixing on particle passage rates, and monitored influences of sampling procedures on grazing time.

Materials and Methods

Twelve ruminal-fistulated Hereford × Angus steers ($\bar{x}$ wt. = 294 kg) were used in 2 grazing trials. All steers freely grazed a 13-ha crested wheatgrass *(Agropyron desertorum)* pasture during the early vegetative stage and had free access to water and a mixture of iodized salt and trace mineral product[1]. The 26-day experiment (30 April–25 May, 1984) consisted of 4 phases: (1) 7-d adaptation period; (2) 6-d collection period (trial 1); (3) 7-d rest period; (4) 6-d collection period (trial 2). Four steers were randomly assigned to each of 3 treatments: (1) rectal sampling; (2) rumen sampling—rumen contents mixed before subsampling digesta from 4 sites; (3) rumen sampling—rumen contents not mixed before subsampling digesta from 4 sites. Steers were rerandomized among treatments after trial 1.

Crested wheatgrass used for labeling was collected from a single pasture by 8 esophageal-fistulated steers ($\bar{x}$ wt. = 595 kg). Forage samples were collected 1 h after sunrise over a 3-d period. Steers were withheld from grazing for approximately 1 h before collections were made. Forage samples were composited and dried at 50°C

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[1]Each kg of mix contained the following (g): salt (iodized), 492.5; sulfur, 13.5; magnesium, 100; manganese, 22; zinc, 60; iron, 51; cobalt, 1.2; copper, 6.6; iodine, 1.5

in a forced-air oven. After drying, forage was labeled with $YbCl^{32}$ by immersion and subsequent rinsing (Teeter et al. 1984). On day 1 of each trial, 230 g of Yb-labeled forage (2.6 g Yb) was placed in the rumen of each steer and stratified by placing approximately equal portions of the labeled forage at successively higher levels intraruminally, beginning with the midventral region and stopping at the middorsal region of the rumen (McCollum and Galyean 1985). Fecal grab samples were collected immediately before dosing and at 4, 8, 12, 16, 20, 24, 28, 32, 36, 42, 54, 60, 72, 84, 96, 108, and 120 h thereafter. Similarly, we collected ruminal digesta samples immediately before dosing and at 4, 8, 12, 16, 20, 24, 32, and 48 h thereafter. Fecal samples were collected by inducing defecation by rubbing the dorsal rectal wall and saving the final 150 to 300 g of feces excreted (Hartnell and Satter 1979). Ruminal digesta samples were composites of a single subsample collected from each of the dorsal, ventral, mid-cranial, and midcaudal regions. Rumen contents of steers assigned the intraruminal mixing treatment were mixed by hand for 1 to 2 min until solid and liquid phases were throughly commingled. Samples were collected in the same order that steers were dosed and within 3 min of designated sampling time. Three days before each trial began, we fitted all steers with vibacorders[3] for estimating grazing time (Stobbs 1970). Vibracorders remained on steers through day 5 of each collection period. On day 1 of each trial all steers were fitted with fecal collection bags and fecal output was recorded on days 2 through 6. We mixed feces from each animal and subsampled them each day. Forage samples were collected from the study pasture on day 4 of each trial by 4 esophageal-fistulated steers (Table 1). Esophageal-fistulated steers were maintained on a similar crested wheatgrass pasture and were moved to the study pasture 1 d before forage sample collection. We collected forage samples in the morning following a 12-h fast. Fecal, forage, and ruminal digesta samples were dried at 50 °C in a forced-air oven, ground with a Wiley mill (1-mm screen), and stored for future analyses.

Table 1. Chemical composition[a] and in vitro organic matter digestibility (IVOMD) of crested wheatgrass[b] samples collected by esophageal-fistulated steers.

Item	Trial 1	Trial 2	Forage used for labeling
Organic matter	89.3	89.1	83.7
Crude protein	13.9	13.7	13.9
Neutral detergent fiber	57.2	63.5	59.3
IVOMD	74.9	76.4	75.7

[a]Percent of dry matter.
[b]International feed number = 2-05-420.

Forage samples and fecal samples from total fecal collection were analyzed for dry matter, ash, and Kjeldahl N (forage samples only) by standard procedures (AOAC 1980). In vitro organic matter digestibility was determined for forage samples by the Tilley and Terry (1963) procedure with urea (.5 g/liter) added to the buffer/inoculum mixture. Neutral detergent fiber content in forage samples was determined as described by Goering and Van Soest (1970). Ground residues from fecal grab samples and ruminal digesta samples were placed in aluminum tins and dried at 100° C in a forced-air oven for 24 h. After cooling in a desiccator for 1 h, 200 mg of dry fecal or rumen sample was weighed into a 50-ml glass extraction vial. Ytterbium was extracted from samples with .05 M EDTA by the procedure of Hart and Polan (1984). We determined concentration of Yb in the extract by atomic absorption spectrophotometry (nitrous oxide/acetylene flame). Common matrix standards were used in preparing standard curves.

We fit fecal Yb excretion curves with a two-compartment, time-independent (2CMPT-TI) model (Grovum and Williams 1973) and with one-compartment, time-dependent (1CMPT-TD) and two-compartment, sequential time-dependent—time-independent (2CMPT-TD) models described by Ellis et al. (1979). The time-dependent models were evaluated using the nonlinear regression option (Marquardt method) of the Statistical Analysis System (Helwig and Council 1979). Gamma 2 time dependency was used in fitting time-dependent models (Ellis et al. 1983). Initial parameter estimates (multiple estimates indicate use of grid search option available within the system used), bounds and covergence criterion for time-dependent models were as follows: (1) 1CMPT-TD—initial parameter estimates: k_0 = 50,000, λ_1 = .05, .1, 1, tau = 12; bounds: $k_0 > 0, \lambda_1 > 0$, tau > 0; covergence criterion: .00001 and (2) 2CMPT-TD—initial parameter estimates: k_0 = 10,000, k_1 .1, .3, 3, λ_2 = .05, tau = 12; bounds: k_0 > .00001, k_1 > .0001, λ_2 > .0001, tau > .00001; covergence criterion: .0001. All ruminal Yb curves were fitted with a single exponential decay model and the slope (β_1) was considered as representing passage of undigested particles from the rumen. The 2CMPT-TD model failed to fit some fecal profiles; therefore, only slopes derived by fitting fecal Yb curves with the 1CMPT-TD and 2CMPT-TI models were used for comparison with the single exponential model applied to ruminal Yb decline. The slopes from fecal models used in statistical comparisons with β_1 from ruminal curves were those associated with the slower rate process (k_1 for 2CMPT-TI and λ_1 for 1CMPT-TD) and were also considered to be primarily representative of the passage of undigested particles from the reticulorumen. We calculated ruminal mass of indigestible particles as described by Grovum and Williams (1977) with the exception that we used fecal output as an estimate of the outflow (or intake) of indigestible particles. Since the rectally sampled treatment did not have direct estimates of passage of Yb from the rumen, we used passage rate constants from the 2CMPT-TI model in calculating mass of indigestible particles for the rectally sampled steers. Organic matter intake was determined for all steers by dividing measured fecal organic matter output by percentage organic matter indigestibility derived from the in vitro digestibility procedure described above (Cordova et al. 1978). In addition, fecal organic matter output was calculated for the rectally sampled treatment group from the ICMPT-TD model as described by Pond et al. (1982). The predicted values were compared with observed fecal matter output.

Data from particle passage, fecal output, and intake estimates were analyzed by factorial analysis of variance. Factors were trial and treatment (treatment = rectal sampling, rumen sampling—mixed, rumen sampling—not mixed). Treatment × trial interactions were evaluated. Orthogonal contrasts were used to partition treatment sums of squares from the particle passage rate analysis. Grazing time data were analyzed by analysis of variance for completely randomized designs. We confined analysis to data from 2 d before each trial began through 0600 h of day 3 of each trial (shortly before the last sample was collected from ruminally sampled steers). Terms for treatment, trial, time (before vs during collection period), day within time, and their interactions were included in the model.

Results and Discussion

Treatment effect was not significantly dependent on trial for any independent variables. Estimated daily organic matter intake (OMI; Table 2) did not differ ($P>0.10$) among treatments; however, OMI for all steers was larger ($P<0.01$) in trial 2 than in trial 1 (25.4 vs 19.8 g/kg body weight, respectively). Time spent grazing did not differ ($P>0.10$) among treatments and, in spite of increased forage intake during trial 2, was similar ($P>0.10$) among trials. Similarly, grazing time did not differ ($P>0.10$) among days within a time period (time period = 2 d before or 2 d during sample collection). Average daily grazing time was 9.2 h/steer. Although grazing time did not differ among treatments, trials, or days within time period, more ($P<0.01$) time was spent grazing before the

[2]Research Chemicals, P.O. Box 14588, Phoenix, Ariz. 85063.
[3]Argo Instruments Inc., P.O. Box 2997, Winchester, Va. 22601.

Table 2. Daily organic matter intake (OMI) and fecal organic matter output (FOMO) from grazing steers sampled at different anatomical sites.

Item	Rectal sampling	Rumen Sampling: Contents mixed	Rumen Sampling: Contents not mixed
OMI (g/kg body weight)			
Trial 1[a]	19.8[b]	20.4[b]	19.4[b]
Trial 2[a]	24.7[c]	24.6[c]	26.8[c]
SE[d]	.8	.8	.8
FOMO[e] (kg/d)			
Trial 1[a]	1.4[f]	1.5[f]	1.4[f]
Trial 2[a]	1.8[g]	1.7[g]	1.9[g]
SE[d]	.1	.1	.1

[a]Row means do not differ ($P>0.10$).
[b,c]Column means for OMI with different superscripts differ ($P<0.01$).
[d]SE = Standard error, n = 4.
[e]FOMO = output measured by total fecal collection.
[f,g]Column means for FOMO with different superscripts differ ($P<0.01$).

Table 3. Estimated particle passage rates in the rumens of grazing beef steers sampled at different anatomical sites.

Treatment and Model[a,b]	Turnover rate constant (%/h): Trial 1	Trial 2	$\bar{x}$	SE[c]
Rectal sampling				
One compartment, time dependent (A)	5.9	5.4	5.6	.3
Two compartment, time independent (B)	6.2	6.5	6.4	.3
Rumen sampling, (contents mixed)				
Exponential decay (C)	7.0	6.3	6.7	.4
Rumen sampling, (contents not mixed)				
Exponential decay (D)	6.3	6.6	6.5	.4

[a]Orthogonal contrasts: A vs B, ($P<0.05$); C vs D ($P>0.10$); $\frac{C+D}{2}$ A vs $\frac{C+D}{2}$, ($P<0.05$); B vs $\frac{C+D}{2}$ ($P>0.10$).
[b]Row means within treatments were not different ($P>0.10$).
[c]SE = standard error, (n=4).

collection period began (10.0 h • head^{-1} • d^{-1}) than during sample collection period (8.3 h • head^{-1} • d^{-1}). We surmise that differences in grazing time before versus during sample collection indicated a negative influence of sampling procedures on grazing behavior. However, our observations of the influences of digesta or fecal sampling on grazing time are confounded with fitting animals with fecal collection bags. These procedures could act independently or may interact in various ways to influence grazing behavior. Therefore, we urge caution in the development of experimental methodologies for use with grazing ruminants, and suggest that controlled research evaluating influences of experimental procedures on grazing behavior is needed.

Fecal organic matter output followed the same trend as organic matter intake. Output measured by total fecal collection was less ($P<0.01$) in trial 1 (1.4 kg organic matter • hd^{-1} • d^{-1}) than trial 2 (1.8 kg organic matter • hd^{-1} • d^{-1}). Fecal output predicted by the 1CMPT-TD model resembled ($P>0.10$) measured output from the rectally grab-sampled treatment group in both trials (1.5 and 1.9 kg organic matter • hd^{-1} • d^{-1} for trials 1 and 2, respectively). This finding concurs with results reported for sheep maintained in confinement (Krysl et al. 1985); however, Mader et al. (1982) and Judkins et al. (1984) noted considerable variation in the ability of 1CMPT-TD and 2CMPT-TD models to predict fecal output in grazing beef steers. This conflict warrants additional study of the potential of these models to accurately predict fecal output in grazing animals.

Rate parameter estimates occasionally failed to converge when fit to the 2CMPT-TD model (Ellis et al. 1983). This has been suggested as indicating that the process under evaluation would be more appropriately described by a 1CMPT-TD model (Pond 1982). We observed no problems in rate parameter convergence when the 2CMPT-TI model was used to fit fecal marker profiles. Therefore, statistical comparisons were confined to slopes associated with the slower rate process from the 1CMPT-TD and 2CMPT-TI models and the single first-order fractional rate constants determined for ruminal exponential decay. Estimates of particle passage rate (Table 3) were greater ($P<0.05$) when fecal Yb excretion curves were fit with the 2CMPT-TI model than when fit with the 1CMPT-TD model.

Similarity among passage rate constants derived from fecal Yb curves and those derived by semilogarithmic regression of ruminal Yb concentration on time depended on the model used to fit fecal Yb curves. Passage rates from ruminal sampling were similar ($P>0.10$) to passage rates from fecal sampling when the 2CMPT-TI model was fit to fecal Yb excretion curves. This observation concurs with the results of Ellis et al. (1983) where the slow rate constants from the time-independent portion of a 2CMPT-TD model were similar to rate constants derived from a single exponential decay model applied to ruminal Yb decline. In contrast, we observed that passage rates from fecal Yb curves fit with the 1CMPT-TD model were smaller than rate estimates derived by ruminal sampling. Although describing the faster rate process from fecal excretion curves remains problematic (Ellis et al. 1983, Grovum 1983), our data indicate that, in grazing steers, the slower rate process can be described equally well by an exponential decay model applied to ruminal marker disappearance or to the downslope of marker in the feces. However, under the conditions of this study, the time-dependent models either failed to fit some fecal excretion curves (such as the 2CMPT-TD model) or yielded different rate constants than ruminally derived rates. Ellis et al. (1983) have suggested that the rate constant from the 1CMPT-TD model may represent a "composite mixing-rumination-passage" process. This may explain the observed differences in exponential decay rates derived from ruminal sampling and rate constants from the 1CMPT-TD model fit to fecal Yb excretion curves.

Mixing rumen contents before collecting subsamples of rumen digesta did not influence ($P>0.10$) particle passage estimates. Similar passage rates among mixed and nonmixed groups suggest mixing due to reticuloruminal contractions, or other natural processes, was sufficient to thoroughly distribute labeled forage throughout the rumen. No apparent difficulties were encountered in collecting representative rumen digesta samples from steers grazing crested wheatgrass.

Although daily organic matter intake increased by about 28% during trial 2, particle passage rate constants (%/h) were not altered regardless of sampling site or mathematical model used. Particle passage rate (the reciprocal of retention time) is thought to represent the rate at which undigested particles exit from the reticulorumen (Ellis et al. 1983). Ruminal passage rate constants are determined from the ratio of the outflow rate of undigested particles (wt • time^{-1}) to the mass of ruminally indigestible particles (wt) Grovum 1983). Therefore, if both outflow rate and the mass of indigestible particles held in the rumen change in the same direction, it is possible for particle passage rate constants to be unaffected. Fecal output can be viewed as an estimate of the outflow rate of undigested particles. By combining fecal output values (or intake of indigestible particles) with the passage rate constants derived by marker dilution procedures, one can calculate estimates of the total mass of indigestible particles in the rumen (Grovum and Williams 1977). In the present study, such calculations (Table 4) suggest that the mass of indigestible particles contained in the rumen increased ($P<.01$) by approximately 28%

Table 4. Estimated mass of indigestible particles in the rumens of grazing beef steers sampled at different anatomical sites.

Item	Rectal sampling[a]	Rumen sampling	
		Mixed	Not mixed
Mass of indigestible particles (kg)			
Trial 1[b]	1.2[c]	1.1[c]	1.2[c]
Trial 2[b]	1.5[d]	1.5[d]	1.5[d]
SE[e]	.1	.1	.1

[a]Calculated using turnover rate constants from the 2CMPT-TI model. Mass of indigestible particles (kg) = fecal dry matter output (kg/h) ÷ k_1.
[b]Row means do not differ ($P>0.10$).
[c,d]Column means for digesta mass with different superscripts differ ($P<0.01$).
[e]SE = Standard error, (n=4).

during trial 2. Since measured fecal organic matter output (i.e., estimated outflow rate) also increased by 25–26% during trial 2, passage rate expressed as a percentage per hour value would not be expected to change appreciably. This observation highlights the fact that given the described relationship (outflow ÷ mass = rate), at least 2 of the 3 components comprising this equation must be available in order to adequately interpret the influence of a treatment on ruminal kinetics.

In conclusion, mathematical model altered rate of passage measurements and influences the interpretation of kinetic information. When using a time-independent model to fit fecal Yb curves, particle passage rates were similar to rates from a single exponential decay model fit to ruminal Yb decline. However, fitting the time-dependent model to fecal Yb curves yielded smaller passage rates than those derived by fitting a single exponential decay model to ruminal Yb decline. In steers grazing immature forage, intraruminal mixing did not appear to enhance the probability of obtaining a representative ruminal digesta sample when sampling was done by compositing subsamples from various ruminal locations. Procedures used for measuring intake, particle passage and grazing time had a negative influence on time spent grazing. Fecal output predicted by the 1CMPT-TD model was similar to observed fecal output.

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