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A meta-analysis of passage rate estimated by rumen evacuation with cattle and evaluation of passage rate prediction models

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ABSTRACT

A meta-analysis of studies using the flux/compartmental pool method with indigestible neutral detergent fiber (iNDF) as internal marker was conducted to study the effect of extrinsic characteristics and forage type on particle passage rate (k_p) in cattle. Further, the k_p prediction equations in the National Research Council (NRC) and the Cornell Net Carbohydrate and Protein System (CNCPS) were evaluated. Data comprised 172 treatment means from 49 studies conducted in Europe and the United States. In total, 145 diets were fed to dairy cows and 27 to growing cattle. A prerequisite for inclusion of an experiment was that dry matter intake, neutral detergent fiber (NDF), proportion of concentrate in the diet, body weight, and diet chemical composition were determined or could be estimated. Mixed model regression analysis including a random study effect was used to generate prediction equations of k_p and to investigate the relationships between NRC and CNCPS predictions and observed k_p of iNDF. Prediction equations were evaluated by regressing residual values on the predicted values. The best-fit model when forage type was not included was k_p (%/h) = 1.19 + 0.0879 × NDF intake (g/kg of body weight) + 0.792 × proportion of concentrate NDF of total NDF + 1.21 × diet iNDF:NDF ratio (adjusted residual mean square error = 0.23%/h). The best general equation accounting for an effect of forage type was as follows: k_p (%/h) = F + 1.54 + 0.0866 × NDF intake (g/kg of body weight) (adjusted residual mean square error = 0.21%/h), where F is the forage adjustment factor of the intercept. The value of F for grass silage, fresh grass, mixes of alfalfa and corn silage, and dry or ensiled alfalfa as sole forage component were 0.00, −0.91, +0.83, and +0.24, respectively. Relationships between predicted and observed k_p were y = 0.53(±0.187) + 0.41(±0.0373) × predicted k_p and y = 0.58(±0.162) + 0.46(±0.0377) × predicted k_p for the NRC and CNCPS models, respectively. Residual analysis of the NRC and CNCPS models resulted in both significant mean biases (observed − predicted) of −2.40 and −1.70% and linear biases of −0.59 and −0.53, respectively. The results from this meta-analysis suggest that ruminal particulate matter k_p is affected by forage type in the diet. Further, the evaluation of NRC and CNCPS models showed that passage rate equations developed from marker excretion curves markedly deviated from observed k_p of iNDF derived using the rumen evacuation technique.

Key words: cattle, indigestible neutral detergent fiber, passage rate, rumen evacuation

INTRODUCTION

A ruminant animal is unique because its digestive system is based on microbial degradation in the forestomachs. The utilization of fibrous plant material is made possible by a long retention time of feed particulate matter in the rumen. Feed residues must disappear from the rumen by either digestion or passage for further intake to occur, and physical constraints can limit intake. Thus, knowledge of the factors influencing the passage rate ($\mathbf{k_p}$) of fiber is essential for predictions of forage utilization by ruminants. Prediction equations of k_p are currently used in calculations of ruminal digestibility of carbohydrate and protein fractions in 1-compartment models and included in predictions of microbial efficiency (NRC, 2001; Fox et al., 2004; Danfær et al., 2006). Factors that influence particulate matter k_p can be described as extrinsic or intrinsic. Characteristics of the animal and total diet are then separated from attributes describing mechanistic digesta flow through the rumen like particle size, rate of particle size reduction, and functional specific gravity (Ellis et al., 1994; Huhtanen et al., 2006). Extrinsic factors are independent of intrinsic factors and can influence the potential digestibility of a feed. Stage of maturity, proportion of leaf to stem, primary or regrowth, and forage variety/species have been suggested to be determinants of the intrinsic properties that can influence ruminal particulate matter k_p in a typical cattle diet (Poppi et al., 2001; Lund, 2002; Kuoppala et al., 2009; 2010). The passage rate of

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indigestible NDF (**iNDF**) for diets based on corn and alfalfa silage has been higher than that predicted by an equation generated from a limited number of rumen evacuation studies (Huhtanen et al., 2006).

Prediction equations of k_p have been developed based on large sets of data using rare-earths or Cr-mordanted fiber as k_p markers (NRC, 2001; Seo et al., 2006). However, compartmental mean retention time estimated from the descending phase of marker excretion curves has been markedly shorter than the proportion of forestomachs to total mean retention time determined from lignin and iNDF recovery in slaughter studies (Paloheimo and Mäkelä, 1959; Walz et al., 2004; Ahvenjärvi et al., 2010). It could be hypothesized that equations generated from studies using the flux/compartmental pool method with iNDF as the internal marker would give more biologically relevant predictions. Previous prediction equations of k_p of iNDF have been generated from studies restricted to dairy cows primarily fed grass silage-based diets (Danfær et al., 2006; Krizsan et al., 2010).

The objective with this study was to summarize findings across published studies to generate empirical prediction equations of k_p of iNDF by conducting a meta-analysis of data from studies performed with cattle fed a range of different forages. Further, National Research Council (NRC, 2001) and Cornell Net Carbohydrate and Protein System (**CNCPS**; Seo et al., 2006) k_p prediction equations were evaluated with these data.

MATERIALS AND METHODS

Database Construction and Calculations

A database was constructed from experiments with cattle where the experimental objective was to study dietary effects on digestion and passage kinetics of fiber fractions. In all trials, k_p of iNDF was determined using the flux/compartmental pool method (Ellis et al., 1994):

$$k_p\ (\%/\text{h}) = 100 \times \text{flux of indigestible component into the compartment (kg/h)/rumen pool of indigestible component (kg).} \quad [1]$$

A total of 49 studies, using ruminally cannulated animals and comprising 172 treatment means, was pooled in a database. Forty (n = 145) of these were conducted with dairy cows and 9 (n = 27) were with growing cattle. Studies included in the database were conducted in Europe and in the United States. The diets in the experiments consisted of different types of forages; fresh grass, grass hay or silage, legume, whole crop (barley and a pea-barley mix), corn, and mixtures of alfalfa and corn silages were fed at different levels of concentrate feeding. The concentrate fed with the different forages differed in amount and composition, but were offered at fixed levels or proportions throughout a study. In the database, 26 experiments were primarily targeted on forage source, 13 studies dealt with different sources or levels of concentrate supplementation, and 8 studies had factorial arrangement of treatments including both forage type and level of concentrate supplementation. One experiment used different feeding levels to induce differences in digesta kinetic parameters to study methodological aspects; another study looked primarily at feeding frequency and rumen evacuation schedule effects on digestion kinetics. The list of studies used in this meta-analysis is given in the Appendix.

The prerequisite for an experiment to be included in the analysis was that k_p was calculated for iNDF, preferably based on flow of iNDF from intake (n = 159) or fecal output of iNDF (n = 13) and rumen pool size of iNDF. The rumen evacuation technique is based on assumptions of a steady-state rumen pool size and no disturbance of the normal rumen function (Robinson et al., 1987). In the experiments included in this database, rumens were evacuated several times, except for 3 studies with single evacuations (n = 10). Rumen iNDF pool size has shown little variation between different rumen evacuation time points equally spaced over 3 d for cattle fed twice daily (Huhtanen et al., 2007). Rumen digesta pool size was judged as representative of diurnal mean values. Concentration of iNDF in feed or feed ingredients, rumen contents, and fecal samples was determined either by long-term rumen incubations of the samples in nylon bags for a minimum of 96 h up to 504 h (n = 140), or by in vitro incubation in buffered rumen fluid without addition of pepsin for 120 or 240 h (n = 32). In one study, k_p was determined based on the indigestible component of ADF (n = 2) instead of iNDF. A further prerequisite for inclusion of an experiment was that production parameters (forage and total DMI, milk production, and BW) and diet chemical composition (concentrations of CP, NDF, ether extracts, ash, and iNDF) were determined or could be estimated. If concentrate chemical composition was not completely reported, default feed table values from the country where the experiment was performed were used. Dietary concentration of NFC for each observation was calculated as OM (% of DM) − [CP (% of DM) + NDF (% of DM) + ether extracts (% of DM)]. When silage iNDF concentrations were not reported, the estimates were back-calculated from given numbers of k_p of iNDF according to equation [1], concentration of iNDF in concentrate, concentrate and forage DMI, and rumen iNDF pool size. Concentrate iNDF values were given in most experiments, but values for 2 studies (n = 8) were estimated from ingredient composition and iNDF concentration in ingredients derived from data sets from MTT Agrifood Research Finland. Two treatments reported by Dado and Allen (1995), where inert bulk was introduced in the rumen of the cows, were not included in the database.

The NRC (2001) and CNCPS (Seo et al., 2006) give separate k_p prediction equations for concentrate and forage feed:

$$k_p \text{ of concentrates } (\%/h) = 2.904 + 1.375 \times \text{DMI } (\% \text{ of BW}) - 0.020 \times X_2, \quad [2]$$

$$k_p \text{ of dry forages } (\%/h) = 3.362 + 0.479 \times \text{DMI } (\% \text{ of BW}) - 0.007 \times X_2 - 0.017 \times X_3, \quad [3]$$

$$k_p \text{ of wet forages (silages and fresh; } \%/h) = 3.054 + 0.614 \times \text{DMI } (\% \text{ of BW}), \quad [4]$$

and

$$k_p \text{ of concentrates } (\%/h) = 1.169 + 0.1375 \times \text{FpBW} + 0.1721 \times \text{CpBW}, \quad [5]$$

$$k_p \text{ of forages } (\%/h) = 2.365 + 0.0214 \times \text{FpBW} + 0.0734 \times \text{CpBW} + 0.069 \times \text{FDMI}, \quad [6]$$

respectively, where X_2 = percentage of concentrate in diet DM, X_3 = percentage of NDF in DM, FpBW = forage DMI (g/kg of BW), CpBW = concentrate DMI (g/kg of BW), and FDMI = forage DMI (kg/d). Therefore, an aggregated k_p was calculated using the prediction equations [2], [3], and [4] for NRC and equations [5] and [6] for CNCPS as follows:

$$\text{Aggregated } k_p (\%/h) = (\text{CiNDFI} + \text{FiNDFI}) / [(\text{CiNDFI}/k_p \text{ of concentrates}, \%/h) + (\text{FiNDFI}/k_p \text{ of forages}, \%/h)], \quad [7]$$

where CiNDFI = concentrate iNDF intake (g/kg of BW) and FiNDFI = forage iNDF intake (g/kg of BW). The aggregated k_p calculations in equation [7] were based primarily on concentrate and forage iNDF intake (n = 165), but when not available concentrate and forage NDF intake were used (n = 7).

To evaluate if the relationships between independent variables and k_p were curvilinear, the basic and most correct type of nonlinear regression in this case was transformed data regression (i.e., a natural logarithm transformation). Further, the accuracy of the best generated passage kinetic model was evaluated by comparing NDF digestibility predictions based on passage kinetic parameters with observed in vivo NDF digestibility. The passage kinetic parameters estimated by the best prediction equation generated from this database were used in a 2-compartment rumen model as described by Allen and Mertens (1988). The total mean rumen retention time ($1/k_p$) was divided in the ratio of 0.4:0.6 between nonescapable and escapable pools and the digestion rate of potentially digestible NDF (**pdNDF**) was assumed to 5.0%/h. Mean values for the proportion of concentrate on an NDF basis and iNDF:NDF ratio were obtained from the data set of digestibility trials in dairy cows (Huhtanen et al., 2009; Nousiainen et al., 2009) to calculate passage kinetic parameters at different NDF intakes.

Statistical Analysis

The relationships between k_p of iNDF and independent variables were analyzed using the mixed model procedure of SAS (Littell et al., 1996). The model was $Y = B_0 + B_1X_{1ij} + b_0 + b_1X_{1ij} + B_2X_{2ij} + \ldots + B_nX_{nij} + e_{ij}$, where B_0, B_1X_{1ij}, B_2X_{2ij} . . . X_{nij} were the fixed effects and b_0, b_1, and e_{ij} were the random experiment effects (intercept, slope, and error), where i = 1 . . . n studies and j = 1 . . . n_i values. In multivariate models, only the first independent variable was treated as a random factor. The best-fit model was chosen based on the lowest residual mean square error (**RMSE**) and Akaike's information criterion (**AIC**). Akaike's information criterion indicates the model likely to be the most correct with the smallest number of parameters. In the tables, RMSE values adjusted for the random study effect are presented. Variation in the experimental units, experimental designs, different measurement methods, and laboratory assays would contribute to the random effect of study. Rationale and further details of using mixed model analysis to integrate quantitative findings from multiple studies are described by St-Pierre (2001) and Sauvant et al. (2008).

Model adequacy was controlled by generating residual values from observed minus predicted values from the mixed model regression. Mixed model regression analysis was used to test for differences in k_p of iNDF between forage types, and between growing cattle and dairy cows. Passage rate predictions of different forage types were compared with that predicted for grass silage-based diets. The forage component of the diets was initially classified into 13 different groups: grass silage with <550 g of NDF/kg of DM (1; n = 52),

Table 1. Description of the experimental animal and diet characteristics in the database for prediction and evaluation of passage rate in cattle

Item	n	Mean	SD	Minimum	Maximum
Intake (g/kg of BW)					
DM	172	29.0	7.93	8.4	45.6
NDF	172	10.6	2.68	3.8	16.6
Forage DM	172	17.7	5.27	2.9	32.5
Forage NDF	172	8.6	2.49	1.5	16.0
Apparent total-tract digestibility (%)					
OM	155	71.8	8.21	32.7	86.4
NDF	157	59.7	12.8	25.0	86.1
Milk production (kg/d)	145	26.1	8.68	0	42.5
BW (kg)	172	574	87.8	315	710
Diet composition (% of DM)					
NDF	172	38.2	9.32	18.4	66.1
NFC	172	34.4	8.55	12.5	56.5
CP	172	16.7	2.91	5.98	24.1
iNDF[1]	172	8.87	3.61	2.37	17.4
Concentrate proportion, DM basis	172	0.37	0.182	0	0.75
Concentrate proportion, NDF basis	172	0.20	0.144	0	0.60
Passage rate (k_p) of iNDF, %/h	172	2.56	0.668	1.10	5.11
Aggregated k_p NRC[2] (%/h)	172	5.01	0.655	2.95	6.25
Aggregated k_p CNCPS[2] (%/h)	172	4.23	0.726	2.71	5.92

[1]iNDF = indigestible NDF.

[2]CNCPS = Cornell Net Carbohydrate and Protein System. Aggregated k_p is predicted based on either NRC or CNCPS equations and calculated according to the flux/compartmental pool method.

grass silage with >550 g of NDF/kg of DM (2; n = 20), legume silages (3; n = 17), whole crop silage (4; n = 6), whole-crop silage mixed with grass silage (5; n = 5), alfalfa mixed with corn silage (6; n = 22), fresh grass (7; n = 7), hay of grasses and legumes (8; n = 20), ryegrass silage (9; n = 8), grass silage mixed with legumes (10; n = 9), corn silage (11; n = 3), wheat straw (12; n = 3), and dried or ensiled alfalfa (13; n = 11). Forage treatments overlapped in groups 3, 8, and 13. Numbers in parentheses therefore exceeded the total number of treatment means. With no indication of differences ($P \geq 0.10$), the observations for the forage type tested were pooled with the observations of the grass silage group.

The aggregated k_p calculated from the prediction equations of NRC (2001) and CNCPS (Seo et al., 2006) were centered by subtracting the mean of all predicted values from each prediction within each system. This transformation centered the data points to a mean value of zero. The slope and intercept estimates in the regression is thereby made orthogonal and will allow for a proper interpretation of the regression model. Residual values were calculated from observed k_p of iNDF minus the predicted k_p. Prediction equations were evaluated by regressing residual values on the predicted values. Mean biases were assessed by using the intercepts of the regression equations, and the slopes of the regression equations were used to determine the presence of linear biases (St-Pierre, 2003).

RESULTS

Description of the Database

The experimental data for dairy cows and growing cattle combined are described in Table 1. Considerable variation existed in both diet composition and animal parameters. The range in DMI was much larger for dairy cows than for growing cattle (8.7 to 46.6 g/kg of BW vs. 8.4 to 20.1 g/kg of BW, respectively), whereas the difference in intake range between animal type was much smaller on an NDF basis (3.8 to 16.6 g/kg of BW vs. 4.0 to 12.0 g/kg of BW for dairy cows and growing cattle, respectively). Mean BW for dairy cows and growing cattle was 606 and 405 kg, respectively. Concentration of NDF was generally lower in dairy cow diets compared with diets fed to growing cattle (36.7 vs. 46.0% of DM, respectively). This is consistent with an on-average higher proportion of concentrate fed to dairy cows than growing cattle (0.38 vs. 0.30, respectively). Small differences were found in mean and variability of k_p of iNDF between animal types in the data set (Table 1).

Intake of NDF (**NDFI**) was negatively related to proportion of concentrate on an NDF basis [**CProp (NDF)**]: NDFI, g/kg of BW = 11.9 − 6.42 × CProp (NDF); $P = 0.01$, adjusted RMSE = 1.00 g/kg of BW. Forage intake on an NDF basis (**FNDFI**) was negatively related to concentrate intake on an NDF basis: FNDFI, g/kg of BW = 9.66 − 0.574 × concentrate intake on

NDF basis, g/kg of BW; $P = 0.02$, adjusted RMSE = 0.93 g/kg of BW. Forage intake also was negatively related to CProp (NDF): FNDFI, g/kg of BW = 11.7 – 15.8 × CProp (NDF); $P < 0.01$, adjusted RMSE = 0.71 g/kg of BW, but only the last relationship was strong. No other univariate mixed model regressions between independent variables of biological and predictive relevance to k_p displayed significant ($P \geq 0.28$) relationships.

Effect of Animal Type on Passage Rate of iNDF

Animal type did not give any adjustment of either intercept separately ($P \geq 0.17$) or of both intercept and slope ($P \geq 0.20$) in univariate mixed model regressions with any of the independent variables DMI, NDFI, forage DMI, or FNDFI. Further, only NDFI as an independent variable was associated ($P = 0.04$) with k_p of iNDF when animal type was included as a fixed effect in the regression equation. There were no further improvements of the prediction equation of k_p of iNDF for growing cattle and dairy cows separately in bivariate regressions including either concentrate NDFI (expressed in g/kg of BW) or CProp (NDF) in addition to NDFI as independent variables.

Regressions of Extrinsic Characteristics and Forage Type on Passage Rate of iNDF

The effects of extrinsic diet and animal characteristics on k_p in univariate and multivariate linear regressions estimated by mixed model regression analysis are presented in Table 2. All 4 independent variables in the univariate regressions of Table 2 showed a significant relationship with k_p of iNDF ($P \leq 0.02$). Intake of NDF performed slightly better as a predictor in the univariate regressions of k_p than did the other independent variables as indicated by a low adjusted RMSE (Table 2). The mean response in k_p of iNDF to increased NDFI was more than twice as high as for increased DMI (0.0760 vs. 0.0375%/h per g intake of NDF and DM per kg of BW, respectively; Table 2). Neither concentrate DMI (expressed as g/kg of BW) nor CProp on a DM basis [**CProp (DM)**] had a significant effect ($P \geq 0.60$; equations not presented) when included in bivariate models with DMI. Including CProp (NDF) in a bivariate model with NDFI did not show a significant effect on k_p ($P = 0.08$; Table 2). However, this bivariate regression lowered AIC compared with the univariate model based on NDFI (Table 2). Segregating total intake to forage and concentrate intake on an NDF basis in bivariate models did not result in any further improvements. When adding a third variable descriptive of the chemical characteristics of the diets (concentration of NDF, NFC, or CP) to the best bivariate regressions, none of these variables had significant effect ($P \geq 0.08$) on k_p. Only the equations with dietary ratio of iNDF:NDF as a third independent variable gave significant effects of all variables on k_p ($P \leq 0.05$; Table 2). There was comparable goodness of fit of 2 multivariate regressions including NDFI, CProp (NDF), and iNDF:NDF, or FNDFI, CProp (NDF), and iNDF:NDF (Table 2). The equation based on FNDFI as the first independent variable had higher standard errors of the regression coefficients for the first and second independent variable when compared with the equation based on NDFI (0.103 and 0.505 vs. 0.0879 and 0.404, respectively). Examining plots of residuals against predicted values and residuals against the regressor NDFI, neither obvious model defects nor a nonconstant variance pattern was observed for these equations (results not presented). The density of the residuals plotted in a histogram supported the assumption of normally distributed data for both models. The curvilinear model of k_p of iNDF, adjusted to the data with transformed data regression (i.e., a natural logarithm transformation) generated the following equation:

$$k_p,\ \%/\text{h} = 0.828 \times \text{NDFI}^{0.373} + e^{(0.435 \times \text{CProp (NDF)} + 0.551 \times \text{iNDF:NDF})}$$
$$(\text{adjusted RMSE} = 0.25\%/\text{h}).$$

The best general equation correcting for the effect of forage type was as follows: k_p, %/h = F + 1.54 + 0.0866 × NDFI, g/kg of BW (adjusted RMSE = 0.21%/h), where F = forage adjustment factor of the intercept. The effect on k_p of fresh grass ($P = 0.02$), mixes of alfalfa and corn silage ($P < 0.01$), and dry or ensiled alfalfa as the sole forage component ($P = 0.10$) was estimated by adjusting the intercept in the general equation accounting for forage. The adjustment factor on the intercept for grass silage, fresh grass, mixes of alfalfa and corn silage, and dry or ensiled alfalfa were 0.00, −0.91, +0.83, and +0.24, respectively.

Evaluation of Passage Rate Models

Both the NRC and CNCPS models overestimated ruminal passage rate (i.e., underestimated total retention time of particulate matter in the rumen). Relationships between predicted and observed k_p were y = 0.53(±0.187) + 0.41(±0.0373) × predicted k_p and y = 0.58(±0.162) + 0.46(±0.0377) × predicted k_p for the NRC and CNCPS models, respectively. The evaluation of the NRC and CNCPS prediction equations of k_p by regressing residual values on the predicted values are

Table 2. Effects of extrinsic diet characteristics on passage rate of indigestible NDF (iNDF; %/h) estimated by mixed model regression analysis ($Y = A + BX_1 + CX_2 + DX_3$)[1]

X_1	X_2	X_3	A[2]	B[3]	C	P-value	D	P-value	RMSE[4]	AIC[5]
DMI			1.44	0.0375					0.25	214
NDFI			1.77	0.0760					0.22	210
FDMI			2.03	0.0314					0.23	219
FNDFI			2.07	0.0584					0.22	215
NDFI	CNDFI		1.67	0.0697	0.0790	0.05			0.23	211
NDFI	CProp (NDF)		1.52	0.0861	0.756	0.08			0.23	207
FNDFI	CNDFI		1.77	0.0660	0.109	<0.01			0.23	212
NDFI	CNDFI	iNDF:NDF	1.33	0.0709	0.0857	0.03	1.24	<0.01	0.23	203
NDFI	CProp (NDF)	iNDF:NDF	1.19	0.0879	0.792	0.05	1.21	<0.01	0.23	199
FNDFI	CProp (NDF)	iNDF:NDF	1.07	0.103	1.73	<0.01	1.15	0.01	0.23	198

[1]DMI in g/kg of BW; NDFI = intake of NDF in g/kg of BW; FDMI = forage DMI in g/kg of BW; FNDFI = forage NDFI in g/kg of BW; CNDFI = concentrate NDFI in g/kg of BW; CProp (NDF) = concentrate proportion on NDF basis; NDF = diet NDF concentration (% of DM); and iNDF:NDF = ratio between diet iNDF and NDF concentrations.

[2]A: $P \leq 0.03$.

[3]B: $P \leq 0.02$.

[4]RMSE = residual mean square error. The values are adjusted for random study effect.

[5]AIC = Akaike's information criterion.

presented in Figure 1. Residual analysis of the NRC and CNCPS models resulted in both significant ($P < 0.001$) mean biases of −2.40 and −1.70%/h and linear biases of −0.59 and −0.53, respectively.

DISCUSSION

Effect of Animal Type on Predictions of Ruminal Particulate Matter Passage Rate

This database used data on growing cattle, and dry and lactating dairy cows. Using pooled data of cattle in this evaluation of the effect of animal and feed variables on k_p of iNDF was justified from statistical testing of animal type in mixed model regressions. In these data, large differences were observed in the range of DMI, but not in NDFI (both in g/kg of BW) between dairy cows and growing cattle. Pooled cattle data were also used in the development of empirical prediction equations of k_p in NRC (2001) and CNCPS (Seo et al., 2006). However, Cannas (2002) compared predictions of k_p from the CNCPS model developed for cattle with observed k_p in sheep and found that the predictions underestimated the ruminal passage of feed particles in sheep. Both the prediction model and the observed k_p were based on data using the marker technique. It has been suggested by Van Soest (1994) and Cannas (2002) that sheep tend to have higher passage rates than cattle at similar physiological stages. The equations in the CNCPS sheep model (Cannas et al., 2004) were developed from a database where passage rate measurements on small (sheep and goat) and large (cattle and buffaloes) ruminants were pooled. Animal species was not significant in these predictions (Cannas and Van Soest, 2000). Many of the rumen evacuation studies on sheep found in the literature used lignin as an indigestible marker; however, lignin has given faster estimates of k_p than iNDF (Huhtanen and Kukkonen, 1995). The effect of markers would have been confounded with animal species and it was therefore decided not to proceed with data also trying to cover k_p predictions in small ruminants. More research would be needed to clarify the difference between small and large ruminants on intake and passage rate of particulate matter, also with the aim of giving a more mechanistic explanation.

Effect of Extrinsic Characteristics and Forage Type on Ruminal Particulate Matter Passage Rate

Intake of NDF performed better as a predictor of k_p of iNDF than DMI at all levels of regression in this data material. Lund (2002) and Rinne et al. (2002) observed faster k_p of iNDF in dairy cows fed grass silages made from material harvested at later maturity stages. Despite increased k_p, rumen pool size of fresh matter, DM, OM, NDF, and iNDF increased with progressing maturity of the grass silage in the study by Rinne et al. (2002). A biological reasoning for the better performance of NDFI than DMI as a predictor of particulate matter k_p has been thoroughly discussed by Huhtanen et al. (2006) and further evaluated in the study by Krizsan et al. (2010). A proportionality factor of 1.6 was introduced in the Nordic dairy cow model Karoline to account for the higher k_p of concentrates in relation to k_p of forages (Danfær et al., 2006). In this meta-analysis, the faster k_p of concentrate particles compared with forage particles was modeled by a positive coefficient for CProp (NDF) in the best multivariate model. Shaver et al. (1988) and Colucci et al. (1990) reported a generally faster k_p of concentrate particles than of forage particles labeled with different markers when measured in early lactating dairy cows. Cannas and Van Soest (2000) used experiments where both forage and concentrate k_p was measured at the same time and found a slope of 1.57 when regressing concentrate k_p on forage k_p. Ahvenjärvi et al. (2010) observed that differences in retention time of rapeseed meal were consistent with the differences in forage retention time. This suggested that k_p of concentrate could be predicted successfully from k_p of forages. However, rumen conditions can be affected by diet type or amount of concentrate provided in the total diet. Robinson et al. (1987) and Stensig et al. (1998) reported that increased starch supplementation in the diet to dairy cows decreased ruminal particle passage rate. Using the marker technique, Colucci et al. (1990) observed that k_p of both forage and concentrate

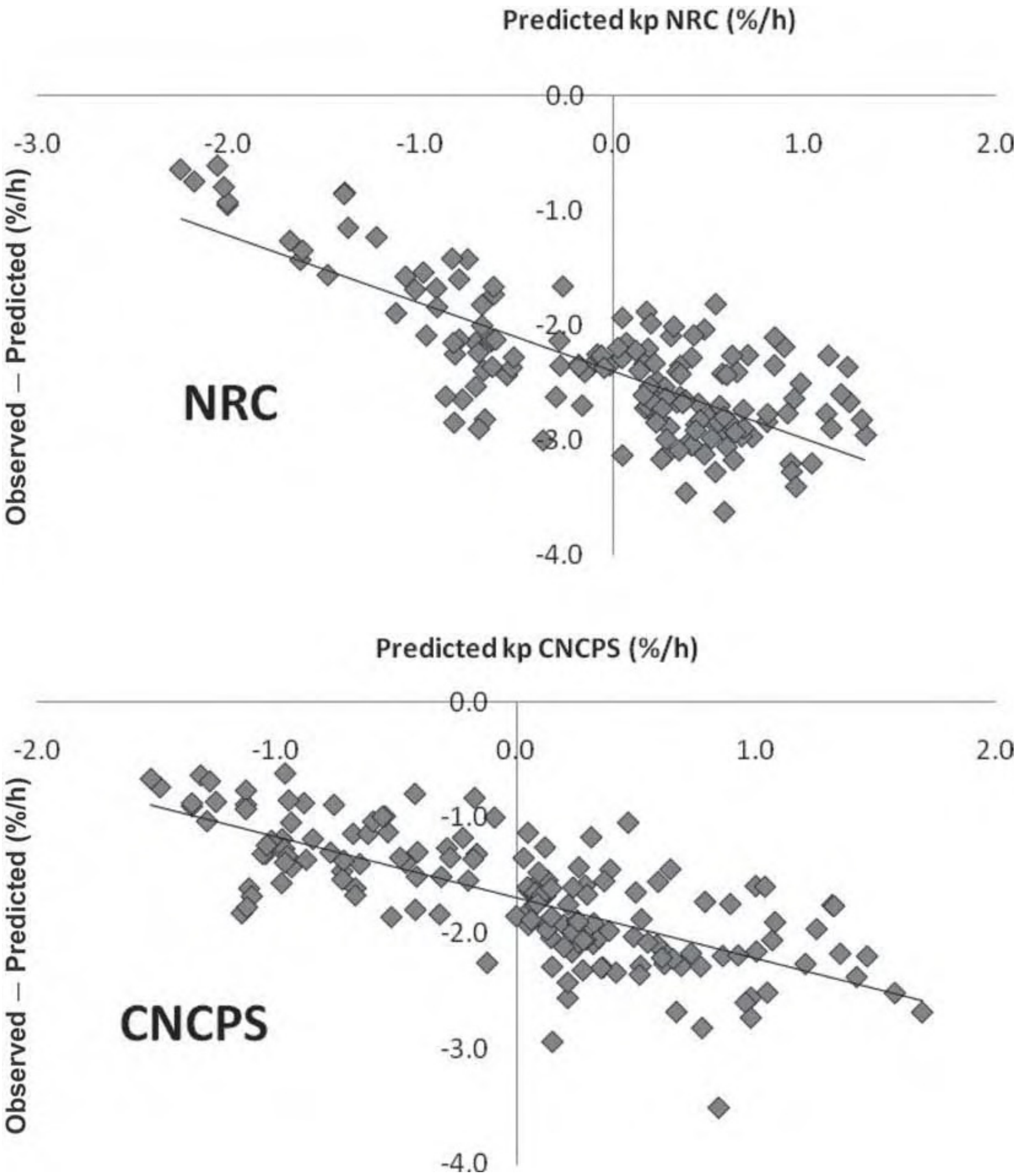

Figure 1. Plot of residuals (observed − predicted) versus predicted passage rate (k_p) estimated according to the NRC and the Cornell Net Carbohydrate and Protein System (CNCPS). The regression lines in the graph represent the equations y = −2.40(±0.0287) − 0.59(±0.0372) × predicted k_p and y = −1.70(±0.0270) − 0.53(±0.0373) × predicted k_p for the NRC and CNCPS models, respectively. Predicted k_p for concentrate and forage feed from NRC and CNCPS equations were combined in an aggregated k_p according to the flux/compartmental pool method. Predicted values were centered by subtracting the mean of all predicted values from each predicted value.

particles decreased when the proportion of concentrate in the diet to dairy cows increased. The decrease in k_p of forage particles was more pronounced at low levels of intake than at high levels of intake. This implies that the relationship between k_p of concentrate and forage particles is not necessarily constant over the range of feed intake by cattle.

Passage rate can also be related to feed characteristics (intrinsic factors) other than particle size (e.g., functional specific gravity, proportion of leaf to stem, and factors associated with the resistance of cell walls to comminution; Huhtanen et al., 2006). The positive coefficient for iNDF:NDF in the best multivariate equations in this meta-analysis is related to the fact that k_p increases when NDF potential digestibility decreases in feed particles. The iNDF:NDF ratio determined in feeds is related to the type of feed (generally higher iNDF:NDF ratio in concentrates than forages) or forage maturity. The results from this study suggested that, except for NDFI, other regressors describing diet composition were not relevant when an effect of forage type was included in the prediction of k_p.

The NRC (2001) developed separate k_p equations for dry and wet forages, whereas one k_p equation for all forages is used in CNCPS (Seo et al., 2006). Huhtanen and Jaakkola (1993) did not observe any differences between forage types on rumen evacuation-based k_p when comparing grass hay and grass silage fed to growing cattle with different inclusions of concentrate supplementation. The statistical analysis in this study did not separate k_p of hays from k_p of grass silage-based diets ($P = 0.95$). The only forage types that were separated from the grass silage-based diets were fresh grass, mixes of alfalfa and corn silage, and dry or ensiled alfalfa as sole forage component. The slower k_p with diets based on fresh grass is consistent with experimental data. The mean NDFI and k_p of iNDF for 4 diets in the studies with cattle by Owens et al. (2008a,b) were 7.89 g/kg of BW and 1.45%/h, respectively. Further, the mean NDFI and k_p of iNDF for 3 diets in the study with dairy cows by Sairanen et al. (2005) were 16.2 g/kg of BW and 1.83%/h, respectively. The faster estimated k_p of diets based on alfalfa and corn silage than of diets based on grass silage in this meta-analysis is in agreement with the results of Lund (2002). The fastest k_p of iNDF was reported for corn silage diets (2.66 and 2.87%/h); the alfalfa hay diet was in between (1.65 and 2.17%/h), and k_p was lowest for grass hay (1.27 and 1.34%/h) when fed to dairy cows supplemented with concentrate or without any supplementation. Huhtanen et al. (2006) suggested that the effect of forage type on particulate matter k_p would arise from differences in the consistency of the rumen raft. Further, there was no explanatory value of any extrinsic characteristics or diet chemical composition parameters except NDFI in prediction of k_p of iNDF when an effect of forage type was included in the model.

Linear or Curvilinear Predictions of Ruminal Particulate Matter Passage Rate

In the present study, the curvilinear model using natural logarithmic transformed NDFI did not improve the model compared with the linear model. This is in contrast with the study of Cannas et al. (2003), who observed that a logarithmic model gave a better fit of the data than a linear model. The difference is because turnover time was used as the dependent variable, whereas passage rate was used in this study (i.e., the reciprocal of turnover time). The relationship between NDF intake and passage rate calculated from Cannas et al. (2003) turned out to be linear. Their model predicted shorter turnover times compared with our model, especially at high NDF intakes. In a direct comparison, based on the rumen evacuation technique, passage rate of ADL was 14% faster than that of iNDF (Huhtanen and Kukkonen, 1995). It is possible that some soluble phenolic compounds are released from particulate matter and flow in the rumen fluid phase, thereby lending to overestimates of fiber passage rate. Large lignin disappearance from grass samples incubated in nylon bags in the rumen supports this assertion (Huhtanen and Vanhatalo, 1997).

The predicted depression in NDF digestibility of 0.48% U/kg of increase in DMI compares well with the observed depression of 0.49% U in the meta-analysis of data from digestibility trials with dairy cows (Huhtanen et al., 2009). In addition, the predicted ruminal NDF digestibility at the mean DMI of the data set (62.0%) was close to the observed NDF digestibility (62.7%). Total-tract digestibility of pdNDF in dairy cows was 75.4% on average (Nousiainen et al., 2009). Using the proportion of ruminal digestion of total NDF digestion (95%) determined by omasal sampling technique (Huhtanen et al. 2010) gave a ruminal pdNDF digestibility of 71.3%. Assuming a 1-compartment rumen model and k_p calculated according to the NRC (5.0%/h), digestion rate should be 12.4%/h to reach 71.3% ruminal pdNDF digestibility and 8.8%/h assuming a 2-compartment system (Allen and Mertens, 1988). Both of these values for digestion rate of pdNDF are unrealistically high for average dairy cow diets. Although these calculations are based on several assumptions, accurate predictions of both total NDF digestibility and depression in digestibility with increased DMI provide some evidence of the accuracy of passage kinetic models derived from rumen evacuation data.

Evaluation of Passage Rate Models

Prediction equations of k_p in NRC and CNCPS are used in calculations of ruminal digestibility of carbohydrate and protein fractions in 1-compartment models (NRC, 2001; Fox et al., 2004). Generally, k_p equations have been developed separately for forage and concentrate feed, and for predictions of ruminal liquid outflow. In all k_p equations in NRC and CNCPS, intake of feed (i.e., either concentrate, forage, or total intake) is on a DM basis (NRC, 2001; Seo et al., 2006). Intake of NDF was a better explanatory variable in univariate as well as multivariate regressions compared with DMI in this meta-analysis. Further, the linear bias showed that the absolute difference between observed k_p of iNDF and NRC and CNCPS predictions increased at higher values of k_p. However, DM- or NDF-based k_p predictions alone cannot explain the observed negative mean biases (i.e., overestimation) on ruminal particulate matter k_p predictions by the NRC and CNCPS models. Marker excretion curves from duodenal and fecal samples have indicated that passage of feed particles in ruminants is at least a 2-compartmental process. The ascending phase of duodenal marker excretion curve has been interpreted as selective retention of feed particles in an inescapable pool, and the concomitant descending phase of the curve as a compartment with mass action dilution turnover (Ellis et al., 1994). With the marker technique, ruminal passage rate of feed particles has usually been estimated from the descending phase of duodenal or fecal marker excretion curves. Compartmental mean retention time estimated from the descending phase of marker excretion curves has been markedly shorter than the proportion of fore-stomachs to total mean retention time determined from lignin or iNDF recovery in slaughter studies (Paloheimo and Mäkelä, 1959; Huhtanen and Ahvenjärvi, 2008). The rumen evacuation technique is an alternative to measuring rumen contents by slaughter. The technique is based on first-order kinetics and a 1-compartment model; passage kinetics of the reticulo-rumen are determined for the whole diet, and it is not possible to separate k_p of forages and concentrate particles.

The equations in NRC and CNCPS have been developed based on large sets of empirical data using rare earths alone (NRC) or with data of Cr-mordanted fiber as a k_p marker (CNCPS). Longer retention times when Cr-mordanted fiber was compared with Yb-labeled fiber (Beauchemin and Buchanan-Smith, 1989; Huhtanen and Kukkonen, 1995) suggest that marker type influences estimated values. Cannas and Van Soest (2000) presented a significant effect of marker when comparing rare earths with Cr in k_p regressions based on DMI but not NDFI. Passage rate equations of forages and concentrates in CNCPS were not corrected for the effect of marker (Seo et al., 2006). The NRC (2001) did not include data of Cr-mordanted feeds because no independent variables could be related to k_p of concentrate particles when these data were included. Particle density or level of Cr mordanted to the fiber (Lirette and Milligan, 1989), labeling method of rare earths (Ellis et al., 1994), and particle size or particle distribution of the mordanted feed (Bruining and Bosch, 1992) are factors that in addition to relative differences due to animal and feed characteristics have affected the passage rate or retention time estimates.

This analysis suggests that rumen residence time of feed particles is markedly longer than the k_p values predicted in the current feed protein evaluation systems (e.g., NRC and CNCPS). Using the current passage rate estimates would increase calculated values of ruminal protein degradability. The results of this meta-analysis suggest that differences in omasal feed protein flow are smaller than predicted by the NRC (2001) system (Broderick et al., 2010). Similarly, the small effects of ruminal protein degradability on milk protein yield and efficiency of N utilization in milk production studies (Huhtanen and Hristov, 2009) suggest that the true differences in ruminal protein degradability could be smaller than those in the tabulated values.

CONCLUSIONS

In agreement with previous conclusions, intake of NDF was the best single predictor of ruminal particulate matter passage rate in this study. The positive coefficient for dietary proportion of concentrate on NDF basis is related to the faster k_p of concentrate particles compared with forage particles. An increased ratio of iNDF:NDF in the diet indicated that k_p increases when NDF potential digestibility decreases. The iNDF:NDF ratio in feeds is related to the type of feed (concentrate vs. forage or forage type) or forage maturity. Further, when forage type was accounted for in the prediction of k_p no other independent variables in addition to intake of NDF improved the model. Considering different ruminal passage rates between forage types, future feed evaluations for ruminants could contribute to more precise estimates of ruminal digestibility of carbohydrate and protein fractions. However, more research is needed to confirm the importance of relative forage differences in a rumen model and to separate animal effects from feed factors in predictions of ruminal particulate matter k_p. The k_p estimates derived from rumen evacuation data were lower than predictions of ruminal particulate matter k_p from NRC and the CNCPS. Rumen evacuation-derived k_p estimates include the retention time in the large particle pool, whereas k_p estimated from marker kinetics are derived from the descending phase of the marker curve that represents retention time in the small particle compartment.

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APPENDIX

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