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Development of a mechanistic model to represent the dynamics of particle flow out of the rumen and to predict rate of passage of forage particles in dairy cattle

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ABSTRACT

A mechanistic and dynamic model was developed to represent physiological aspects of particle dynamics in the reticulo-rumen (RR) and to predict rate of passage out of the RR (Kp) of forage particles quantitatively. The model consists of 2 conceptual pools with 3 spatial compartments of particles; the compartment the particle enters is based on functional specific gravity (FSG). The model assumes 2 major pressure gradient–driven flows of particles out of the RR through the reticulo-omasal orifice between 2 consecutive primary reticular contractions. One is associated with the second phase of primary reticular contraction and involves propulsion of particles in the vicinity of the honeycomb structure of the reticulum from the RR. The second flow involves movement of particles in the reticulum without selection by size. Particle outflow rate was assumed to be proportional to liquid outflow rate. The passage coefficient, defined as the ratio of particle to liquid outflow rate, was estimated for each particle group by an equation derived from the probability of passage based on FSG and particle size. Particles retained on a 1.18-mm screen were defined as large particles. When the model was evaluated with 41 observations in an independent database, it explained 66% of the variation in observed Kp of forage particles with a root mean square prediction error of 0.009. With 16 observations that also included measurements of liquid passage rate, the model explained 81 and 86% of the variation in observed Kp liquid and Kp forage, respectively. An analysis of model predictions using a database with 455 observations indicated that the assumptions underlying the model seemed to be appropriate to describe the dynamics of forage particle flow out of the RR. Sensitivity analysis showed that probability of a particle being in the pool likely to escape is most critical in the passage of large forage particles, whereas the probability of being in the reticulum as well as in the likely to escape pool is important in the passage of small forage and concentrate particles. The FSG of a particle is more important in determining the fate of a particle than its size although they are correlated, especially for forage particles. We conclude that this model can be used to understand the factors that affect the dynamics of particle flow out of the RR and predict Kp of particles out of the RR in dairy cattle.

Key words: rumen passage rate, ruminal particle dynamics, modeling

INTRODUCTION

When ruminal digestion is described as a competition between digestion and passage (NRC, 2001; Fox et al., 2004), accurate prediction of retention time in the reticulo-rumen (**RR**) is essential. Accuracy of previous models in predicting fractional rate of passage (**Kp**) of forage particles out of the rumen, however, was not satisfactory (Seo et al., 2006b), and it has been suggested that a more mechanistic approach may increase predictability of a passage model (Seo et al., 2006b). Using quantitative modeling and simulations based on sound logic and mathematical and biological constraints (Baldwin, 1995), Seo et al. (2007) previously developed a more dynamic and mechanistic liquid passage model, and accuracy of the model in predicting Kp of liquid out of the rumen was much improved. The liquid model is based on the dynamics of rumen physiology and liquid movement coordinated with the primary reticular contraction. Because the flow of particles out of the rumen is likely to follow the dynamics of liquid passage (Faichney et al., 1981; Poppi et al., 1981), implementation of particle dynamics into the previous liquid passage model should be helpful to expand our knowledge in particle dynamics and predict Kp of forage particle more accurately.

Ulyatt et al. (1986) suggested that passage through the reticulo-omasal orifice (**ROO**) was the rate-limiting

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step in clearing digesta from the rumen. Poppi et al. (1980) proposed the concept of critical particle size for rumen passage, in which the ROO serves as a sieve to retain particles above the critical size threshold. However, although there is a possibility that unguiform papillae and omasal leaves might prevent the flow of large particles, the structure of the ROO does not seem to act as a screen (Mathison et al., 1995). Moreover, the DM concentration of the reticular effluent passing through the ROO and that of the reticular contents sampled from the floor of the reticulum were similar (Harmeyer and Michalowski, 1991). As Mathison et al. (1995) have concluded, the ROO does not likely regulate passage of particles from the RR. Our hypothesis is that coordinated RR motility controls the digesta flow out of the rumen based on selective retention of small and large particles in 3 different compartments of the RR.

Functional specific gravity (**FSG**) of particles represents specific gravity of feed particles with associated gas-filled spaces and bound water (Hooper and Welch, 1985a). Particle size and FSG are important in determining the passage of particles from the rumen (Welch, 1982; Desbordes and Welch, 1984; Hristov et al., 2003). Sutherland (1988) developed a conceptual model that emphasizes the importance of stratification of particles in the rumen with buoyancy and sedimentation to examine digesta movement in and out of the rumen. However, no attempt was made to describe this model quantitatively or to predict Kp of forage particles out of the RR.

Thus, the objectives of this study were to develop a particle passage model that 1) is integrated with our liquid passage model (Seo et al., 2007), 2) can be used to help us understand the particle dynamics out of the rumen, and 3) can be used to predict the flow of particles out of the rumen more accurately.

MATERIALS AND METHODS

General Hypothesis

The structure for the model developed in this study was based on our liquid passage model (Seo et al., 2007). Briefly, the model is composed of 2 inflows (water consumption and salivary secretion), 1 outflow (liquid flow through ROO), and 1 in/out flow (liquid flux through the rumen wall). The model assumes that liquid flow through the ROO is coordinated with the primary reticular contraction, which is characterized by its frequency, duration, and amplitude during eating, ruminating, and resting. The rumen particles flow with liquid; however, there are constraints that prevent particles from escaping out of the rumen.

To represent physical constraints for passage of forage particles out of the rumen quantitatively, we adapted the concept of pools based on buoyancy as proposed by Sutherland (1988), using a compartmental model (Godfrey, 1983). The model describes pools of particles and predicts their behavior in the RR. Required inputs are DMI, chewing time, and chemical and physical properties of feed particles. We assumed that digesta has 2 chances to flow out of the rumen in a reticular contraction: 1) for a fixed time interval during the primary reticular contraction as measured by various investigators (McBride et al., 1983; Kelly et al., 1991; Froetschel et al., 1997), and 2) for a variable interval dependent on DMI, BW, and total digesta content in the rumen (Bueno, 1975; Deswysen and Ellis, 1988; Seo et al., 2007) between 2 consecutive reticular contractions. Seo et al. (2007) concluded that the ROO is likely to be open longer than indicated by endoscopic observations (McBride et al., 1983), and suggested it opens at least twice during a single reticular contraction cycle. Based on Reid (1984), Lechner-Doll et al. (1991), and Baumont and Deswysen (1991), we assumed that only particles that remain in the reticulum after the first phase of primary reticular contraction pass out of the RR during the opening associated with the second phase of primary reticular contraction. We assumed that no segregation of particles occurs during the other opening if the particles are in the reticulum. We assumed that the physical and chemical properties of a particle determine its dynamic behavior for both forage and concentrate particles.

Model Development

Structure of the Model. The model assumes 3 spatial compartments in the RR based on the FSG of particles: 1) dorsal rumen, 2) ventral rumen, and 3) reticulum. Figure 1 provides a graphical representation of these compartments. The particles in the dorsal rumen are more likely to be lightweight and buoyant than those in the ventral rumen and they have a low probability of escape before rumination or sedimentation (Sutherland, 1988). Therefore, this pool is termed inescapable. Because eventually all the feed particles are digested or pass out of the rumen (Welch, 1982), particles in the inescapable pool eventually become escapable after size reduction and sedimentation. The particles in the ventral rumen and reticulum are assumed likely to escape out of the RR because they are dense and tend to sediment and move to the vicinity of the ROO (Wyburn, 1984; Poppi et al., 2001). This pool is termed escapable. Although there are particles of different FSG in each of these compartments, a particle with a high FSG is likely to be located in the

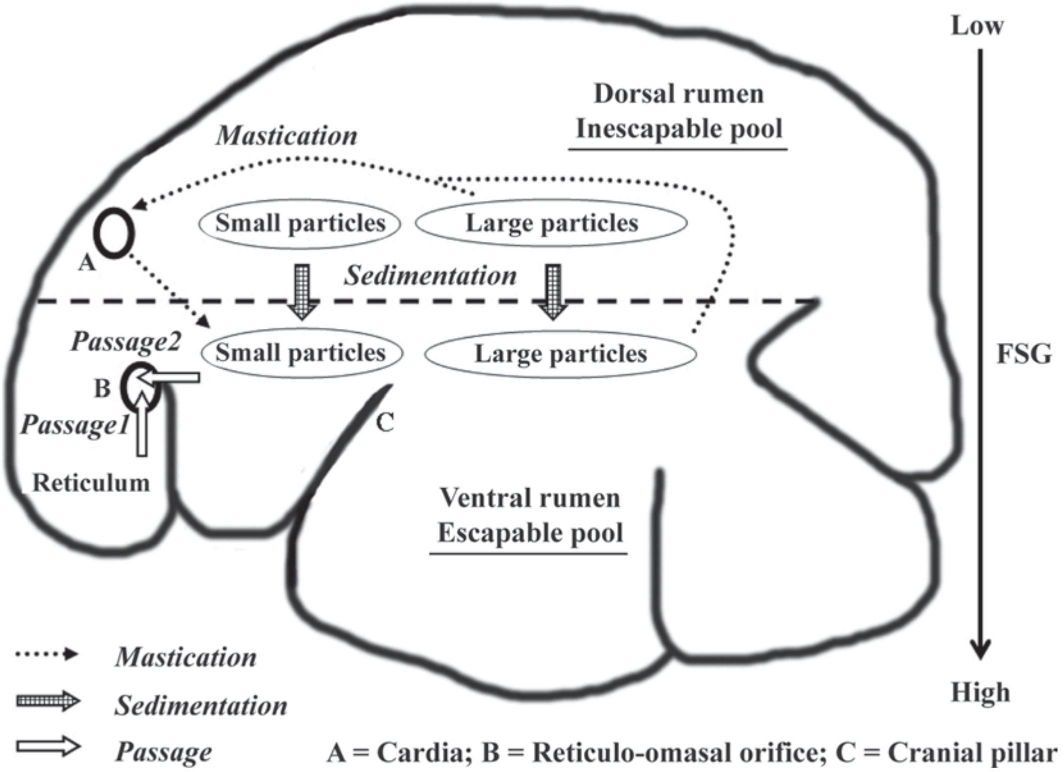

Figure 1. Spatial compartments and conceptual pools of feed particles in the reticulo-rumen. The dorsal rumen is defined as the inescapable pool and the ventral and cranial rumen and reticulum are defined as the escapable pool. Only particles that are in the reticulum can actually pass out of the rumen through the reticulo-omasal orifice (ROO). Functional specific gravity (FSG) of a particle determines its location. Three flows are presented in this diagram: 1) mastication during rumination and eating of large particle to small, 2) sedimentation of particles from the inescapable pool to the escapable pool, and 3) passage of particles out of the reticulum through the ROO. Particle selection for passage or retention occurs in passage 1 but not in passage 2. The basis for these assumptions is in the text.

escapable pool. Of the particles in the escapable pool, only particles that are located in the reticulum when flow occurs are assumed to pass through the ROO and flow into the omasum (Baumont and Deswysen, 1991; Lechner-Doll et al., 1991).

Within each of the 3 RR compartments, the model assumes that there are 2 particle sizes: large and small (Baldwin et al., 1977; Sauvant et al., 1996). Large particles stimulate rumination, which reduces their size, whereas small particles do not engender cud-chewing. Large particles in this model are defined as particles retained on a 1.18-mm screen after wet sieving, because the particles retained on this sieve stimulate chewing and rumination (Mertens, 1997) and the relative amount of particles retained on the 1.18-mm sieve decreases after eating and rumination (Suzuki et al., 2001). Various methods have been used to measure particle size distribution, and the proportion of large particles in a sample may be quantified variably by different methods (Murphy and Zhu, 1997). In this study for development and parameterization of the particle passage model, the large particles were quantified using the method of Woodford and Murphy (1988a), which used wet sieving on a vibrational sieve shaker. Particles in all pools can be digested by microbes, but the fractional rates of degradation ($\mathbf{K_d}$) usually differ among different particle sizes because of differences in surface area (Weimer et al., 1990).

Figure 1 also shows the particles in the RR flow between the compartments in our model. The size of large particles both in the inescapable and escapable pool is reduced by mastication. When large particles are reduced in size through rumination to pass the 1.18-mm sieve, they are assumed to be located in the small and escapable pool. Even though gas production decreases the FSG of a particle during active microbial fermentation (Wattiaux et al., 1992), the FSG of a particle eventually increases when the trapped gas within the physical structure of the particle is released (Hooper and Welch, 1985b). The processes of particle size reduction and increases in FSG mean that both large and small particles initially in the inescapable pool eventually join the escapable pool. Based on Poppi et al. (2001), the fractional rate of movement of particles from ventral to dorsal was relatively low compared with the rates of movement from the ventral rumen to omasum and dorsal to ventral. Thus, the model assumes that particle movement from the inescapable to the escapable pool is irreversible. Not all the particles in the escapable pool have an equal probability of being located in the reticulum (Kennedy, 1995). Functional specific gravity primarily determines this probability. During the outflow associated with the second phase of a primary reticular contraction (passage 1), only particles that are located in the bottom of the reticulum can pass out of the rumen through the ROO because those particles would remain in the reticulum after the first phase of primary reticular contraction (Reid, 1984; Lechner-Doll et al., 1991). Particles can flow out of the RR if they are in the reticulum during the outflow not associated with the second phase of primary reticular contraction (passage 2).

It should be noted that unlike the commonly used age-dependent model using a gamma function (Matis et al., 1989), particles do not sequentially move from dorsal to ventral rumen and then to reticulum to pass out of the rumen in our model. The model accounts for the movement from dorsal to reticulum as well as the sequential movement from dorsal to ventral and then to reticulum, which was observed by a radiographical measurement (Wyburn, 1980).

Particle Outflow Rate. When we define passage coefficient (**PC**) as the ratio of particle to liquid outflow rate (**LOFR**), particles flow out of the rumen with liquid, and particle outflow rate (**POFR**, kg/h) can be expressed as follows:

$$POFR_i = PC_i \cdot LOFR,$$

where POFR is particle outflow rate of the ith particle pool, LOFR is liquid outflow rate, and PC is passage coefficient of the ith particle pool; LOFR is estimated by the liquid passage model (Seo et al., 2007), and the equations to estimate LOFR are shown in Table 5. The general term with a subscript was used to accommodate different types of particle pools; however, there are 2 particle pools in this study: forage and concentrate particles. After more research accumulates, the number of pools can be expanded. The PC is the ratio of particle to liquid in the escapable pool times the probability of the particle in the escapable pool of being located in the reticulum. Cattle typically maintain the DM concentration in the rumen in a range of 14 to 18% in the dorsal area and 6 to 9% in the ventral area, depending on the type of diet and DMI (Yokoyama and Johnson, 1988). Thus, the PC rarely exceeds 0.1. The PC for each particle pool is estimated with the following equation (see a detailed description of the development of this equation in the Appendix). In this model, we have 2 particle pools: forage and concentrate. The fibrous byproducts were categorized into concentrate as indicated by Seo et al. (2006a). The PC was estimated separately for these 2 pools:

$$PC_i = \frac{PPTD_i \cdot TPPE_i}{1 - PPTD_i \cdot TPPE_i} \times PPER_i,$$

where PC is passage coefficient, PPTD is the proportion of particles in the total ruminal digesta, TPPE is the theoretical probability of particles being in the escapable pool, and PPER is the probability of the particles in the escapable pool being located in the reticulum.

Theoretical Probability of Particle of Being in the Escapable Pool. The theoretical probability of particles being in the escapable pool (**TPPE**), a characteristic of particle, was defined as the proportion of particles in the escapable pool without any other factors such as filter-bed effect (Faichney, 1986). It is mainly determined by FSG of the particles by Stoke's law (Denn, 1980); however, we estimated the TPPE as a function of defined particle sizes of forage, based on the data of Evans et al. (1973), which was the only research article that contained appropriate data we could use for this purpose. Evans et al. (1973) provided data for time-series changes in distribution of particle sizes in different locations of the reticulo-rumen including dorsal and ventral rumen and reticulum, which allowed estimation of TPPE for each particle size category using the equations in the Appendix. For each particle size (coarse; 9.3 mm, medium; 3.5 mm, fine; 1 mm, and very fine; 0.05 mm) and intake level, TPPE was regressed on time after feeding. The parameter estimates from these regressions, initial TPPE, and the rates of change in TPPE over time were compared using ANOVA and pair-wise comparison. It turned out that the rates of change in TPPE over time were not significantly different among different levels of intake and particle sizes except for the very fine and soluble fraction. The rate of change in TPPE was 0.0136 (±0.0009) h^{-1}, estimated by the GLM procedure in SAS (SAS Institute Inc., Cary, NC) with a random size effect using pooled data. The initial TTPE, however, differed ($P < 0.01$) among particles of different sizes. This implies that initial TPPE is significantly different among particle sizes even though the rate of change is constant. A curve-fitting technique was used to find a quantitative relationship between initial TPPE and mean particle size. Mean particle size of fine or soluble particles that pass through a screen of 0.1 mm (diagonal) was assumed to be a half of the screen size (0.05 mm) as suggested by ASABE (2006); otherwise, the reported mean particle sizes were used. An inverse relationship was observed, and the best fit among possible simple models was obtained by logarithm of the mean particle size of a particle pool, assessed by the highest coefficient of determination (r^2) and the lowest sum of squares. The equation is as follows:

$$TPPE = 0.443(\pm 0.007) + \text{Ln}\left[MPS^{\,-0.145(\pm 0.004)}\right],$$

where TPPE is the theoretical probability of a particle of being in the escapable pool, Ln is the natural log, and MPS is the mean particle size of a particle pool (mm).

It should be noted that Evans et al. (1973) measured the actual sizes of particles that are retained on sieves with square apertures of 2.4, 1.2, 0.6, 0.3, and 0.075 mm on a side. Thus, the methods that we adopted to determine the particle size of feed particle pools are the same as that of Evans et al. (1973).

Model Simulation and Evaluation

The POFR and Kp of forage were predicted by simulation in our model. In the simulations of the model, the K_d of large forage, small forage, and concentrate particles were assumed to be 0.04, 0.06, and 0.08 h^{-1}, respectively, based on variation in K_d of forage due to fineness of processing for forages or concentrates in the feed libraries in NRC (2000), which is based on the CNCPS feed library (Fox et al., 2003). The K_d of concentrates differed by processing method (Chen, 1999), and these values can be entered into this model to predict passage rate. In the data used to evaluate the model, the description of processing method was not adequate to assign K_d by particle size; thus, the K_d of concentrates was assumed to be the same for large and small particles. The different probability of the particle in the escapable pool of being located in the reticulum (PPER) can be assigned for the flow of each pool. In this model, the PPER of large forage particle in passage 1 was assumed to be 0.54, based on the value of Kennedy (1995), and the rest of PPER were assumed to be 1. The TPPE of large and small forage particles were estimated to be 0.22 and 0.54, assuming mean particle sizes of 4.5 and 0.5 mm, respectively. The TPPE of concentrate was assumed to be 0.9 based on their higher and unchanging FSG (Ramanzin et al., 1994), even though TPPE may vary among feeds. The rate of movement from the inescapable pool to the escapable pool was assumed to be 0.0136 h^{-1} for both large and small particles of all forages in the database based on estimates from the data from Evans et al. (1973). The proportion of large particles in forage, proportion of large particles in concentrate and fractional rate of breakdown of large particles to small were assumed to be 0.66 (Van Soest, 1994; Yang et al., 2001), 0.45 (Woodford and Murphy, 1988a), and 0.07 h^{-1} (Woodford and Murphy, 1988a), respectively.

Dynamic simulations were conducted with Vensim professional version 5.0a (Ventana Systems Inc., Harvard, MA). Although we recognize that meal size and rumination pattern vary throughout the day (Fox and Tedeschi, 2002), this information was not available in most studies used to evaluate the model. In this model evaluation, we simulated steady-state conditions by assuming that an animal consumed the diet in 12 equal meals and ruminated after each meal. The 12 meals represented an average number of eating bouts of lactating dairy cows (Dado and Allen, 1995). The duration of each meal was estimated by dividing eating time by 12. The first feeding started 1 h after the simulation was begun. Water from the diet was consumed during each meal and drinking free water occurred right after the meal for 1.32 min (about 16 min/d; Dado and Allen, 1995). Rumination (daily ruminating time divided by 12) started 30 min after each of the 12 meals. Integration was conducted by the Euler method with a time step of 0.0078 h. The Kp value was calculated as flow rate divided by pool size for each digesta component. Simulations lasted 264 h to ensure that a stable oscillation was reached; it was typically reached in 72 to 96 h. The 24-h average from 240 to 264 h with 0.1-h intervals was utilized for the evaluations.

Data on chewing activity in cattle were searched using CAB Abstracts with data from 1910 until May 2005. The search term was "(chewing or time spent eating or time spent ruminating) and (cattle or cow) and (passage or turnover or flow) and (English in la)". Fifty-five records were included in the database. A subset of the database containing all needed input variables of the model was used to evaluate the model prediction of Kp forage. Table 1 shows descriptive statistics for the database. In this database, BW, DMI, concentrate concentration in the diet, DM concentration in the diet, and chewing activity were measured, and Kp forage was estimated using an external marker (e.g., chromium mordant or rare-earth). The passage database included a total of 41 observations in 10 experiments with lactating dairy cows (Woodford and Murphy, 1988a,b; Johnson and Combs, 1991; Okine and Mathison, 1991; Nelson and Satter, 1992; Beauchemin and Rode, 1994; Yang et al., 2001; Fernandez and Michalet-Doreau, 2002; Krause et al., 2002; Beauchemin and Yang, 2005). There were 16 observations in the database that also measured Kp liquid, using Co-EDTA as the liquid marker, from ruminal collections. Model predictions for Kp liquid and Kp forage were evaluated with this separate data set.

The r^2 was used to assess the precision of the model. Root mean square prediction error (**RMSPE**) calculated as the square root of the mean of the square of the

Table 1. Descriptive statistics for the database used to evaluate the model prediction of fractional rate of passage of forage

Item	n	Mean	Median	Minimum	Maximum
BW, kg	41	618	628	493	692
DMI, kg/d	41	20.2	20.5	11.0	25.6
Concentrates in the diet, % of DM	41	44.9	50.0	0	65.0
DM in the diet, %	41	68.3	70.6	19.0	93.1
NDF in the diet, % of DM	41	33.7	31.5	23.2	63.4
Time spent eating, min	41	297	276	165	437
Time spent ruminating, min	41	419	426	204	550
Fractional rate of passage of forage, h^{-1}	41	0.040	0.040	0.022	0.076

observed minus predicted value (Bibby and Toutenburg, 1977) was used to determine accuracy of the model. Residual analyses were also conducted to assess biases of the model prediction as described in St-Pierre (2003). The predicted values were centered around the mean predicted value before the residuals were regressed on the predicted values.

Sensitivity Analysis

Sensitivity of model predictions for Kp forage and concentrate to the input variables of the model were conducted with the Monte Carlo simulation technique using Vensim Professional version 5.0a (Ventana Systems Inc.). A treatment with a diet containing 60% concentrate, 30% corn silage, and 10% alfalfa hay fed to 8 lactating dairy cows (BW, 589 kg; DMI, 22.4 kg/d; time spent eating, 240 min; and time spent ruminating, 370 min) from Woodford and Murphy (1988a) was used to run the simulations. One input variable at a time was increased or decreased by 10% from the mean value to evaluate its effect on model predictions. The simulation was run for 72 h and then daily averages for predicted values were utilized for these analyses.

RESULTS

All variable names used in the equations for the particle passage model integrated with our liquid passage model (Seo et al., 2007) are described in Table 2, and the critical equations in the final model are listed in Table 3. The input variables used in this model are listed in Table 4 and the equations needed to implement the model are listed in Tables 5 and 6.

The model explained 66% of the variation in Kp forages in the independent database that contains 41 observations with RMSPE of 0.009 (Figure 2), and the residual analysis indicated that both mean (-0.002 ± 0.001) and slope (0.076 ± 0.123) biases were not significant ($P > 0.05$). When the model was evaluated for its predictions of both Kp liquid and Kp forage with the database that contained 16 observations (i.e., including measured Kp liquid rates), the model explained 81 and 86% of the variation with a RMSPE of 0.017 and 0.006, respectively, for Kp liquid and forage (Figure 3). Mean bias (-0.012 ± 0.002) was significant but no slope bias (-0.179 ± 0.105) was observed in prediction of Kp liquid, and no significant mean (-0.000 ± 0.002) and slope (0.088 ± 0.119) bias were observed in Kp forage prediction.

Table 7 summarizes the results of the sensitivity analysis. The results show the effect of a 10% change in the input variables on the percentage change in the model predictions for Kp and particle outflow rate. The sensitivity analysis indicated that the model prediction is the most sensitive to intake. A 10% increase in DMI increased Kp 10.7, 11.4, 21.0, and 22.1% for large and small forage particles, concentrate particles, and liquid, respectively.

Table 7 indicates that after DMI, the 3 most important parameters in prediction of Kp of large forage particles were TPPE of large forage particles, concentrate concentration in the diet, and BW. A 10% increase in each of these variables resulted in an 8.4, 5.9, and 4.8% increase, respectively, in the Kp of large forage particles. The percentage changes indicated that the Kp of small forage particles was the most sensitive to DMI (11.4%), followed by the proportion of large particles in forage (9.0%), TPPE of small forage particles (7.4%), and PPER of small forage particles (7.3%).

The sensitivity analysis indicated that the most important variables for predicting Kp of concentrates were DMI (21%), TPPE of concentrate particles (10.0%), BW (7.4%), and probability of small concentrate particles to be located in the bottom of the reticulum (6.7%). Despite the importance of proportion of DM in the rumen in predicting Kp liquid (Seo et al., 2007), the sensitivity analysis indicated that DMI (22.1%) and BW (7.8%) were the only significant parameters for estimation of Kp liquid. The sensitivity of POFR prediction differed from prediction of fractional rates: POFR varied less than 3% with a 10% increase or decrease in input variables except when DMI (16.2%) and soluble DM in concentrates (3.7%) were varied.

Table 2. Description and units of the abbreviations used in equations in the final model equations developed to predict liquid and particle passage rate from the rumen

Variable	Unit	Description
AF		Adjustment factor for opening of the reticulo-omasal orifice (ROO)
AMP	kPa	Amplitude of the second phase of primary reticular contraction (PRC)
AMP_EAT	kPa	Amplitude of the second phase of PRC during eating
AMP_RES	kPa	Amplitude of the second phase of PRC during resting
AMP_RUM	kPa	Amplitude of the second phase of PRC during ruminating
BW	kg	Body weight
ConcpDM	%	Concentrate as a percentage of dietary DM
CPCR	kg	Concentrate particle content in the rumen
CPMDM		Proportion of CP in the microbial DM
DDM		Proportion of DM content in the diet
diet TDN		Proportion of total digestible nutrients in the diet
DMCR	kg	DM content in the rumen
DMI	kg/d	Dry matter intake
DMI_M	kg	DMI per meal
DMIR_M	kg/h	DMI rate of each meal
DR_LPn_ER	kg/h	Digestion rate of large particle of feed n in the escapable pool of the reticulo-rumen
DR_LPn_IER	kg/h	Digestion rate of large particle of feed n in the inescapable pool of the reticulo-rumen
DR_SPn_ER	kg/h	Digestion rate of small particle of feed n in the escapable pool of the reticulo-rumen
DR_SPn_IER	kg/h	Digestion rate of small particle of feed n in the inescapable pool of the reticulo-rumen
DRINK		Drinking
DUR	s	Duration of opening of the ROO
DUR_EAT	s	Duration of opening of the ROO during eating
DUR_M	h	Duration of each meal
DUR_R	h	Duration of rumination per each meal
DUR_RES	s	Duration of opening of the ROO resting
DUR_RUM	s	Duration of opening of the ROO during ruminating
DUR_WC	h	Duration of water consumption
DWC	kg/d	Drinking free water consumption
EAT		Eating
FPCR	kg	Forage particle content in the rumen
FRQ	1/min	Frequency of PRC
FRQ_EAT	1/min	Frequency of PRC during eating
FRQ_M	1/d	Frequency of meal per day
FRQ_RES	1/min	Frequency of PRC during ruminating
FRQ_RUM	1/min	Frequency of PRC during resting
I_DM	h	Intake of DM during eating
I_DMn	kg/h	Intake of DM of feed n
I_ISDMn		Intake of insoluble DM of feed n
I_LPn	kg/h	Intake of large particle of feed n
I_LPn_ER	kg/h	Intake of large particle of feed n to the escapable pool of the reticulo-rumen
I_LPn_IER	kg/h	Intake of large particle of feed n to the inescapable pool of the reticulo-rumen
I_SDMn	kg/h	Intake of soluble DM of feed n
I_SPn	kg/h	Intake of small particle of feed n
I_SPn_ER	kg/h	Intake of small particle of feed n to the escapable pool of the reticulo-rumen
I_SPn_IER	kg/h	Intake of small particle of feed n to the inescapable pool of the reticulo-rumen
I_TDN	kg	Intake of total digestible nutrients
I_TSDM	kg/h	Intake of total soluble DM
I_WC	kg/h	Inflow rate of water via oral consumption
iLCR	kg	Initial liquid content in the rumen
iLPn_ER	kg	Initial large particle of feed n in the escapable pool of the reticulo-rumen
iLPn_IER	kg	Initial large particle of feed n in the inescapable pool of the reticulo-rumen
ILPR		Instant liquid proportion in the rumen
INTV_M	h	Interval between two meals
iSPn_ER	kg	Initial small particle of feed n in the escapable pool of the reticulo-rumen
iSPn_IER	kg	Initial small particle of feed n in the inescapable pool of the reticulo-rumen
iTPPE_LPn		Initial theoretical probability of particle of being located in the escapable pool of large particle of feed n
iTPPE_SPn		Initial theoretical probability of particle of being located in the escapable pool of small particle of feed n
iTSDM_R	kg	Initial total soluble DM in the rumen
Kbr	1/h	Fractional rate of particle breakdown
Kd_LPn_ER	1/h	Fractional rate of digestion of large particle of feed n in the escapable pool of the reticulo-rumen
Kd_LPn_IER	1/h	Fractional rate of digestion of large particle of feed n in the inescapable pool of the reticulo-rumen
Kd_SPn_ER	1/h	Fractional rate of digestion of small particle of feed n in the escapable pool of the reticulo-rumen
Kd_SPn_IER	1/h	Fractional rate of digestion of small particle of feed n in the inescapable pool of the reticulo-rumen
Kp_LPn	1/h	Fractional rate of passage of large particle of feed n

Continued

Table 2 (Continued). Description and units of the abbreviations used in equations in the final model equations developed to predict liquid and particle passage rate from the rumen

Variable	Unit	Description
Kp_SPn	1/h	Fractional rate of passage of small particle of feed n
Kp_TLP	1/h	Fractional rate of passage of total large particles
Kp_TP	1/h	Fractional rate of total particles
Kp_TSP	1/h	Fractional rate of passage of total small particles
Kpf	1/h	Fractional rate of forage passage out of the rumen
Kpc	1/h	Fractional rate of concentrate passage out of the rumen
Kpl	1/h	Fractional rate of liquid passage out of the rumen
LCR	kg	Liquid content in the rumen
LFRW	kg/h	Liquid flux through the rumen wall
LOFR	kg/h	Liquid outflow rate through the ROO
LOFR1	kg/h	Liquid outflow rate at the first flow
LOFR2	kg/h	Liquid outflow rate at the second flow
LPn_ER	kg	Large particle of feed n in the escapable pool of the reticulo-rumen
LPn_IER	kg	Large particle of feed n in the inescapable pool of the reticulo-rumen
LPn_R	kg	Large particle of feed n in the rumen
MCP	kg	Microbial crude protein
MDM_R	kg	Microbial DM in the rumen
MLPR		Mean liquid proportion in the ruminal content
MPS	mm	Mean particle size
MP_SPn_ER	kg/h	Masticate particle flow of small particle of feed n to the escapable pool of the reticulo-rumen
MP_SPn_IER	kg/h	Masticate particle flow of small particle of feed n to the inescapable pool of the reticulo-rumen
MP_SPn_R	kg/h	Masticated particle flow to small particle of feed n in the rumen
OFR_TSDM	kg/h	Outflow rate of soluble DM
PBR_LPn_ER	kg/h	Particle breakdown rate of large particle of feed n in the escapable pool of the reticulo-rumen
PBR_LPn_IER	kg/h	Particle breakdown rate of large particle of feed n in the inescapable pool of the reticulo-rumen
PBR_LPn_R	kg/h	Particle breakdown rate of large particle of feed n in the rumen
PC1_LPn		Passage coefficient at the first flow of large particle of feed n
PC1_SPn		Passage coefficient at the first flow of small particle of feed n
PC2_LPn		Passage coefficient at the second flow of large particle of feed n
PC2_SPn		Passage coefficient at the second flow of small particle of feed n
PDMn		Proportion of DM of feed n in total dry matter intake
PLPn		Proportion of large particle in insoluble DM of feed n
PM_LPn_ER		Proportion of masticated large particle of feed n of being located in the escapable pool of the reticulo-rumen
POFR_C	kg/h	Particle outflow rate of concentrate particles
POFR_F	kg/h	Particle outflow rate of forage particles
POFR_LPn	kg/h	Particle outflow rate of large particle of feed n
POFR_SPn	kg/h	Particle outflow rate of small particle of feed n
POFR_TLP	kg/h	Particle outflow rate of total large particles
POFR_TP		Particle outflow rate of total particles
POFR_TSP	kg/h	Particle outflow rate of total small particles
POFR1_LPn	kg/h	Particle outflow rate 1 of large particle of feed n
POFR1_SPn	kg/h	Particle outflow rate 1 of small particle of feed n
POFR2_LPn	kg/h	Particle outflow rate 2 of large particle of feed n
POFR2_SPn	kg/h	Particle outflow rate 2 of small particle of feed n
PPER1_LPn		Probability of the particle in the escapable pool of being located in the reticulum at the first flow of large particle of feed n
PPER1_SPn		Probability of the particle in the escapable pool of being located in the reticulum at the first flow of small particle of feed n
PPER2_LPn		Probability of the particle in the escapable pool of being located in the reticulum at the second flow of large particle of feed n
PPER2_SPn		Probability of the particle in the escapable pool of being located in the reticulum at the second flow of small particle of feed n
PPTD_LPn		Proportion of particle in total ruminal digesta of large particle of feed n
PPTD_SPn		Proportion of particle in total ruminal digesta of small particle of feed n
PSDMn		Proportion of soluble DM in feed n
RUM		Ruminating
SPn_ER	kg	Small particle of feed n in the escapable pool of the reticulo-rumen
SPn_IER	kg	Small particle of feed n in the inescapable pool of the reticulo-rumen
SPn_R	kg	Small particle of feed n in the rumen
SR_LPn	kg/h	Sedimentation rate of large particle of feed n
SR_SPn	kg/h	Sedimentation rate of small particle of feed n
SSR	kg/h	Saliva secretion rate
SSR_EAT	kg/h	Saliva secretion rate during eating
SSR_RES	kg/h	Saliva secretion rate during resting

Continued

Table 2 (Continued). Description and units of the abbreviations used in equations in the final model equations developed to predict liquid and particle passage rate from the rumen

Variable	Unit	Description
SSR_RUM	kg/h	Saliva secretion rate during ruminating
T_EAT	h/d	Time spent eating daily
T_RES	h/d	Time spent resting daily
T_RUM	h/d	Time spent ruminating daily
TCR	kg	Total digesta content in the rumen
TLP_ER	kg	Total large particles in the escapable pool of the reticulo-rumen
TLP_IER	kg	Total large particles in the inescapable pool of the reticulo-rumen
TLP_R	kg	Total large particles in the rumen
TPCR	kg	Total particle content in the rumen
TPPE_LPn		Theoretical probability of particle of being located in the escapable pool of large particle of feed n
TPPE_SPn		Theoretical probability of particle of being located in the escapable pool of small particle of feed n
TSDM_R	kg	Total soluble DM in the rumen
TSP_ER	kg	Total small particles in the escapable pool of the reticulo-rumen
TSP_IER	kg	Total small particles in the inescapable pool of the reticulo-rumen
TSP_R	kg	Total small particles in the rumen
TWC	kg/d	Total water consumption
WCF	kg/d	Water content in the diet
WIC	kg/d	Water inflow into the rumen via oral consumption daily
WIC_M	kg	Water inflow into the rumen via oral consumption per meal
WID	kg/d	Water inflow into the rumen via drinking

DISCUSSION

Others have concluded that coordinated RR motility is an important factor in selective retention of large particles in the RR (Reid, 1984; Wyburn, 1984; Baumont and Deswysen, 1991; Lechner-Doll et al., 1991; Mathison et al., 1995; Okine et al., 1998). Although there is no direct experimental evidence that the biphasic primary reticular contractions control the digesta flow and the selective retention of large particles, several pieces of indirect evidence support this hypothesis. Stevens et al. (1960) reported that an orifice about 20 mm in diameter forms at the peak of the second reticular contraction and fluid digesta flows from the ventral floor of the reticulum toward the omasal canal through the orifice. Also, there were more large particles in the feces when reticular contractions were disturbed by adding weights in the reticulum of cows (Okine et al., 1989, 1990) and sheep (Kaske and Midasch, 1997) or due to traumatic reticulo-peritonitis (Holtenius et al., 1971). The observation that the time interval between the first and second reticular contractions was precisely

Table 3. The key equations used in the final model to predict liquid and particle passage from the rumen

Eq.	Variable[1]	Unit	Prediction equation
[1]	WIC	kg/d	$[0.8 \times 4.893 + 0.2 \times (100/\mathrm{DDM} - 1)] \times \mathrm{DMI}$
[2]	SSR_EAT	kg/h	12.60
[3]	MLPR	%	$91.688 - 0.363 \times \mathrm{DMI}$
[4]	SSR_RUM	kg/h	$12.60 + 40 \times (\mathrm{MLPR} - \mathrm{ILPR}$[2]$)$
[5]	SSR_RES	kg/h	$1.266 \times e^{(0.091 \times \mathrm{DMI})}$
[6]	LFRW	kg/h	4.6
[7]	FRQ_EAT	min^{-1}	$1.345 + 0.035 \times \mathrm{DMI}/\mathrm{T\_EAT} + 0.003 \times \mathrm{ConcpDM}$
[8]	FRQ_RUM	min^{-1}	1.122
[9]	FRQ_RES	min^{-1}	$1.494 - 0.026 \times \mathrm{T\_RES}$
[10]	AF	s/s	$-6.798 + 0.210 \times \mathrm{DMI} + 0.003 \times \mathrm{BW} + 0.039\ \mathrm{TCR}$
[11]	LOFR[3]	kg/h	$0.82 \times \mathrm{FRQ} \times \mathrm{DUR} \times \mathrm{AF} \times \sqrt{\mathrm{AMP}}$
[12]	Kpl	h^{-1}	LOFR/LCR
[13]	TPPE	kg/kg	$0.443 + \mathrm{Ln}(\mathrm{MPS}^{-0.145})$
[14]	PC	kg/kg	PPTD[4] $\times\ \mathrm{TPPE}/(1 - \mathrm{PPTD} \times \mathrm{TPPE}) \times \mathrm{PPER}$
[15]	POFR	kg/h	$\mathrm{PC} \times \mathrm{LOFR}$
[16]	Kpp	h^{-1}	POFR/PCR

[1] SSR_EAT = salivary secretion rate during each activity; Kpp = fractional rate of particle passage out of the rumen. All other variables are as defined in Table 2.

[2] ILPR = LCR/TCR × 100, where LCR is liquid content in the rumen at time *t* of simulation, TCR is the sum of LCR and PCR, where PCR is particle content in the rumen at time *t* of simulation.

[3] For LOFR, DUR = 2.74, 3.18, and 2.97 s during eating, ruminating, and resting, respectively, and AMP = 1.30, 1.24, 1.58 kPa during eating, ruminating, and resting, respectively.

[4] PPTD = PCR/TCR.

Table 4. Input variables to the final model[1]

Variable	Unit	Constant/equation
DMI[2]	kg/d	22.4
BW[2]	kg	589
ConcpDM[2]	%	60
PDMn[2,3]		0.4 (if n = 1), 0.6 (if n = 2)[4]
DDM[2]		0.75
T_EAT[5]	h/d	4
T_RUM[5]	h/d	6.17
T_RES	h/d	24 – T_EAT – T_RUM
Assumed parameters		
FRQ_M	1/d	12
diet TDN		0.75
PSDMn		0.4 (if n = 1), 0.4 (if n = 2)
PLPn		0.66 (if n = 1), 0.45 (if n = 2)
MPS_LP$_1$	mm	4.5
MPS_SP$_2$	mm	0.5
iTPPE_LP$_2$		0.9
iTTPE_SP$_2$		0.9
SR_LPn	kg/h	0.0136 (if n = 1), 0.0136 (if n = 2)
SR_SPn	kg/h	0.0136 (if n = 1), 0.0136 (if n = 2)
PPER1_LPn		0.54 (if n = 1), 1.00 (if n = 2)
PPER2_LPn		1.00 (if n = 1), 1.00 (if n = 2)
PPER1_SPn		1.00 (if n = 1), 1.00 (if n = 2)
PPER2_SPn		1.00 (if n = 1), 1.00 (if n = 2)
Kd_LPn_ER	1/h	0.04 (if n = 1), 0.08 (if n = 2)
Kd_LPn_IER	1/h	0.04 (if n = 1), 0.08 (if n = 2)
Kd_SPn_ER	1/h	0.06 (if n = 1), 0.08 (if n = 2)
Kd_SPn_IER	1/h	0.06 (if n = 1), 0.08 (if n = 2)
PM_LPn_ER		1.0 (if n = 1), 1.0 (if n = 2)

[1] The basal data were obtained from Woodford and Murphy (1988a). Variables are as defined in Table 2.

[2] The key variables that should be available when the model is implemented.

[3] The nth feed in the total of N feeds in a diet.

[4] n of 1 is forage and n of 2 is concentrate.

[5] If chewing activity is not available in lactating dairy cows, the user may assume 4.4 and 6.4 h for T_EAT and T_RUM, respectively, which are the average of lactating dairy cows (Beauchemin, 1991).

controlled relative to other intervals also supports this hypothesis. By analyzing the data from Dracy et al. (1972), we found that the time interval between the biphasic contractions had an average coefficient of variation (**CV**) of 4% with a mean of 3.0 s. The average CV of periods of reticular contraction, on the contrary, was 13.6%.

It is also possible that the omasum rather than the primary reticular contraction mediates the flow of digesta flow through the ROO, as significant backflow from the omasum to the reticulum has been observed (Stevens et al., 1960; McBride et al., 1984). Stevens et al. (1960) proposed that the omasum is a two-stage pump, aspirating reticular contents into the omasum and pumping large material back to the reticulum. However, removal of laminae from a sheep, reducing the area to about half, showed little change in digesta flow and its composition (Bueno, 1972). Because of a lack of information, the effect of omasum on control of digesta flow out of the RR has not been incorporated into the model presented in this paper. More research is needed to reveal the function of the omasum on controlling the digesta passage out of the RR.

Another assumption related to selective retention of large forage particles was that the physical and chemical properties of forage particles itself controls selective retention of large particles in the RR. It has been known for decades that the density of a particle is very important in determining passage rate (Balch and Kelly, 1950; King and Moore, 1957). Dense particles tend to sediment to the bottom of the RR, whereas light particles are buoyant and form a rumen mat in cattle (Welch, 1982). Moreover, RR motility seems to stimulate stratification of ruminal particulate matter by density (Constable et al., 1990). In this model, we describe this phenomenon using TPPE. The TPPE of a particle should be estimated from its FSG because it determines the direction of the initial movement of a particle. However, because of a lack of information, we parameterized the value of forage particles based on size with data from a single experiment by Evans et al. (1973), and we arbitrarily chose a value for concentrate. The TPPE is a function of chemical and physical properties of a particle, and quantification of each pool size of inescapable and escapable pool is not needed. However, more research is needed to improve the equation

Table 5. Equations used in the liquid passage model

Variable[1]	Unit	Constant/equation
Water inflow via oral consumption		
TWC	kg/d	4.893 × DMI
WCF	kg/d	(100/DDM – 1) × DMI
DWC	kg/d	TWC – WCF
WID	kg/d	0.8 × DWC
WIC	kg/d	WID + WCF
WIC_M	kg	WIC / FREQ_M
DUR_WC	h	0.022
DRINK		1 (during drinking); 0 (otherwise) PULSE TRAIN[2] (1+DUR_M, DUR_WC, INTV_M, FINAL TIME[3])
I_WC	kg/h	WIC_M / DUR_WC × DRINK
Salivary secretion		
SSR_EAT	kg/h	12.60
MLPR		91.688 – 0.363 × DMI
SSR_RUM	kg/h	12.60 + 40 × (MLPR – ILPR)
SSR_RES	kg/h	1.266 × $e^{(0.091 \times \mathrm{DMI})}$
SSR	kg/h	SSR_EAT × EAT + SSR_RUM × RUM + SSR_RES × (1 – EAT – RUM)
Liquid flux through the rumen wall		
LFRW	kg/h	4.6
Liquid outflow through the ROO		
AMP_EAT	kPa	1.30
AMP_RUM	kPa	1.24
AMP_RES	kPa	1.58
AMP	kPa	AMP_EAT × EAT + AMP_RUM × RUM + AMP_RES × (1 – EAT – RUM)
DUR_EAT	s	2.74
DUR_RUM	s	3.18
DUR_RES	s	2.97
DUR	s	DUR_EAT × EAT + DUR_RUM × RUM + DUR_RES × (1 – EAT – RUM)
FRQ_EAT	1/min	1.345 + 0.035 × DMI / T_EAT + 0.003 × ConcpDM
FRQ_RES	1/min	1.122
FRQ_RUM	1/min	1.494 – 0.026 × T_RES
FRQ	1/min	FRQ_EAT × EAT + FRQ _RUM × RUM + FRQ_RES × (1 – EAT – RUM)
AF		−6.798 + 0.210 × DMI + 0.003 × BW + 0.039 × TCR
LOFR1	kg/h	0.82 × FRQ × DUR × $\mathrm{AMP}^{1/2}$
LOFR2	kg/h	(AF – 1) × LOFR1
LOFR	kg/h	LOFR1 + LOFR2
iLCR	kg	55
LCR	kg	$\frac{d(LCR)}{dt} = I\_WC + SSR - LOFR - LFRW$
Kpl	1/h	LOFR / LCR

[1] Variables are as defined in Table 2.

[2] A built-in function of Vensim professional version 5.0a (Ventana Systems Inc., Harvard, MA). PULSE TRAIN ({start}, {duration}, {repeat time}, {end}): returns 1.0, starting at time {start}, and lasting for {duration} and then repeats this pattern every {repeat time}; 0.0 is returned at all other times.

[3] A built-in variable of Vensim professional version 5.0a (Ventana Systems Inc.), standing for the time when a simulation ends.

to quantify TPPE in accounting for different changes in particle size and FSG of variable feed particles.

The inescapable pool in this model is a spatial location in the RR and is not necessarily identifiable by physical properties of rumen digesta, known as rumen mat. As Wyburn (1980) described, the circular movement of digesta within the RR differs between the dorsal (counterclockwise) and the ventral (clockwise) sacs of the rumen. Therefore, spatial location of particles within the RR affects the dynamic behavior of the particles in each location. A similar definition was used and discussed when the particle movement from dorsal to ventral rumen was described by introducing an age-dependent pool using gamma functions (Poppi et al., 2001). However, our model is quite different in several aspects: 1) we do not assume sequential movement of particles, 2) we separated the ventral sac of the rumen and the reticulum, and 3) we do not describe the flow out of the RR as a first-order process.

Sedimentation of particles from the dorsal to ventral rumen was more important than control by reticular contractions in lactating dairy cows in terms of selective retention of large forage particles. The sensitivity analysis indicated that the Kp of large forage particles is 4.7-fold more sensitive to their probability of being in the escapable pool than their probability of being located in the reticulum (Table 7), because the former determines the probability of a particle passing through

Table 6. Equations used in the particle passage model

Variable[1]	Unit	Constant/equation
I_DM	h	DMIR_M × EAT
I_DMn	kg/h	I_DM × PDMn
I_SDMn		DMIn × PSDMn
I_ISDMn		DMIn × (1 – PSDMn)
iTPPE		0.443 + Ln (MPS$^{-0.145}$), when n = 1
Large particles		
I_LPn	kg/h	I_ISDMn × PLPn
I_LPn_ER	kg/h	I_LPn × iTPPE_LPn
I_LPn_IER	kg/h	I_LPn × (1 – iTPPE_LPn)
TPPE_LPn		LPn_ER / LPn_R
PPTD_LPn		LPn_R / TCR
PC1_LPn		PPTD_LPn × TTPE_LPn / (1 – PPTD_LPn × TTPE_LPn) × PPER1_LPn
PC2_LPn		PPTD_LPn × TTPE_LPn / (1 – PPTD_LPn × TTPE_LPn) × PPER2_LPn
POFR1_LPn	kg/h	PC1_LPn × LOFR1
POFR2_LPn	kg/h	PC2_LPn × LOFR2
POFR_LPn	kg/h	POFR1_LPn + POFR2_LPn
Kp_LPn	1/h	POFR_LPn / LPn_R
POFR_TLP	kg/h	$\sum_{n}^{N}(POFR\_LPn)$
Kp_TLP	1/h	POFR_TLP / TLP_R
PBR_LPn_IER	kg/h	Kbr × LPn_IER
PBR_LPn_ER	kg/h	Kbr × LPn_ER
PBR_LPn_R	kg/h	PBR_LPn_IER + PBR_LPn_ER
DR_LPn_ER	kg/h	Kd_LPn_ER × LP_ER
DR_LPn_IER	kg/h	Kd_LPn_IER × LP_IER
iLPn_ER	kg	0.1968 (if n = 1); 0.4356 (if n = 2)
LPn_ER	kg	$\frac{d(LPn\_ER)}{dt}$ = I_LPn_ER + SRLPn – DR_LPn_ER – PBR_LPn_ER – POFR_LPn
iLPn_IER	kg	0.8364 (if n = 1); 0.0484 (if n = 2)
LPn_IER	kg	$\frac{d(LPn\_IER)}{dt}$ = I_LPn_IER – SRLPn – DR_LPn_IER – PBR_LPn_IER
LPn_R	kg	LPn_ER + LPn_IER
TLP_ER	kg	$\sum_{n}^{N}(LPn\_ER)$
TLP_IER	kg	$\sum_{n}^{N}(LPn\_IER)$
TLP_R	kg	TLP_ER + TLP_IER
Small particles		
I_SPn	kg/h	I_ISDMn × (1 – PLPn)
I_SPn_ER	kg/h	I_SPn × iTPPE_SPn
I_SPn_IER	kg/h	I_SPn × (1 – iTPPE_SPn)
TPPE_SPn		SPn_ER / SPn_R
PPTD_SPn		SPn_R / TCR
PC1_SPn		PPTD_SPn × TTPE_SPn / (1 – PPTD_SPn × TTPE_SPn) × PPER1_SPn
PC2_SPn		PPTD_SPn × TTPE_SPn / (1 – PPTD_SPn × TTPE_SPn) × PPER2_SPn
POFR1_SPn	kg/h	PC1_SPn × LOFR1
POFR2_SPn	kg/h	PC2_SPn × LOFR2
POFR_SPn	kg/h	POFR1_SPn + POFR2_SPn
Kp_SPn	1/h	POFR_SPn / SPn_R
POFR_TSP	kg/h	$\sum_{n}^{N}(POFR\_SPn)$
Kp_TSP	1/h	POFR_TSP / TSP_R
MP_SPn_R	kg/h	PBR_LPn_R
MP_SPn_ER	kg/h	PBR_LPn_R × PM_LPn_ER
MP_SPn_IER	kg/h	PBR_LPn_R × (1 – PM_LPn_ER)
DR_SPn_ER	kg/h	Kd_SPn_ER × SP_ER
DR_SPn_IER	kg/h	Kd_SPn_IER × SP_IER

Continued

Table 6 (Continued). Equations used in the particle passage model

Variable[1]	Unit	Constant/equation
iSPn_ER	kg	0.6586 (if n = 1) 0.90 (if n = 2)
SPn_ER	kg	$\frac{d(SPn\_ER)}{dt}$ = I_SPn_ER + SRSPn + MP_SPn_ER – DR_SPn_ER – POFR_SPn
iSPn_IER	kg	0.4608 (if n = 1) 0.10 (if n = 2)
SPn_IER	kg	$\frac{d(SPn\_ER)}{dt}$ = I_SPn_IER + MP_SPn_IER – SRSPn – DR_SPn_IER
SPn_R	kg	SPn_ER + SPn_IER
TSP_ER	kg	$\sum_{n}^{N}(SPn\_ER)$
TSP_IER	kg	$\sum_{n}^{N}(SPn\_IER)$
TSP_R	kg	TSP_ER + TSP_IER
Total particles		
TPCR	kg	TLP_R + TSP_R
POFR_TP		POFR_TLP + POFR_TSP
Kp_TP	1/h	POFR_TP / TPR
POFR_F	kg/h	POFR_LP$_1$ + POFR_SP$_1$
FPCR	kg	LP$_1$_R + SP$_1$_R
Kpf	1/h	POFR_F / FPCR
POFR_C	kg/h	POFR_LP$_2$ + POFR_SP$_2$
CPCR	kg	LP$_2$_R + SP$_2$_R
Kpf	1/h	POFR_C / CPCR
Soluble DM		
I_SDMn	kg/h	DMIn × PSDMn
I_TSDM	kg/h	$\sum_{n}^{N}(I\_SDMn)$
OFR_TSDM	kg/h	SDM_R × Kpl
iTSDM_R	kg	2.297
TSDM_R	kg	$\frac{d(TSDM\_R)}{dt} = I\_TSDM - OFR\_TSDM$
Microbial DM		
I_TDN	kg	DMI × diet TDN
MCP	kg	0.13 × I_TDN
CPMDM		0.625
MDM_R	kg	MCP/CPMDM
Ruminal digesta		
DMCR	kg	TPCR + TSDM_R + MDM_R
TCR	kg	DMCR + LCR
ILPR		LCR/TCR

[1] Variables are as defined in Table 2.

the ROO during passage 1. This may be because more digesta pass through the ROO with high levels of intake (Okine and Mathison, 1991); thus, the relative importance of the control by reticular contraction is decreased. This result is consistent with the results of Poppi et al. (2001), who found that escape from the raft is a rate-limiting component of passage of forage particles.

Because of limitations in data available to test the model, the results of this study could not prove or disprove our hypothesis on how passage of particles from the rumen is controlled. However, the variation accounted for in predicting particle passage by the model indicates that the assumptions underlying this model seem to be appropriate. Although the number of observations used in the evaluation is relatively small (n = 41 and 16 in the 2 databases), predictability of Kp by the model was higher than published empirical equations (Seo et al., 2006b). The Kp forage equation, developed by Seo et al. (2006b), which was the best equation among those tested, explained only 39% of variation in observations (n = 88) with 0.011 of RMSPE.

Moreover, our results indicate that this model adequately represents the difference in Kp between liquid

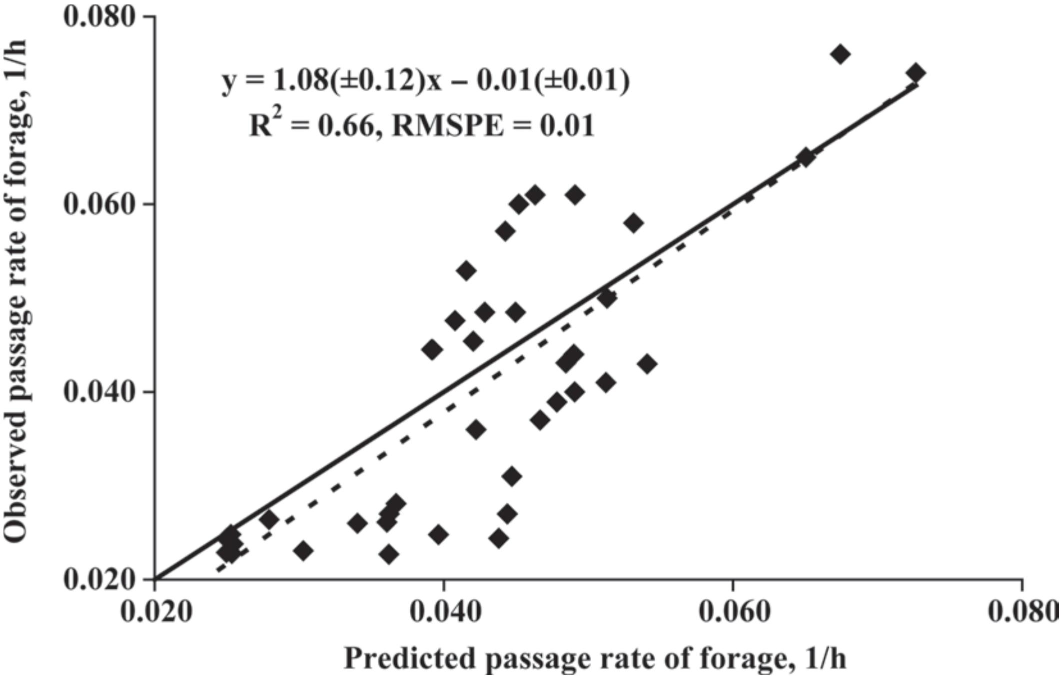

Figure 2. Plots of regression of observed on predicted for fractional forage passage rate (h^{-1}) in the evaluation database containing 41 observations. Solid and dotted lines represent y = x and the best fit linear regression, respectively, and the regression equations (dotted line) are presented. RMSPE = root mean square prediction error.

and forage particles. When differences between Kp liquid and Kp forage were regressed on Kp liquid with a total of 455 observations in the NRC database (Seo et al., 2006a) using a random coefficient model, the intercept and the slope were -0.02 (± 0.00) and 0.77 (± 0.02), respectively (Figure 4, panel A). With the predicted Kp liquid and Kp forage for the observations in this study, the intercept and the slope were -0.01 (± 0.00) and 0.78 (± 0.01) (Figure 4, panel B). Strong linear correlations between 2 variables were observed in both cases. It can be speculated that as liquid flow out of the RR increases, forage particle flow also increases (Faichney et al., 1981; Poppi et al., 1981); however, the rate of increase in forage particles is lower than that in liquid because a certain mechanism prevents forage particles from flowing like liquid. The linear relationship also implied that effect of the mechanism is constant. Because the slope of regression with model predictions was not significantly different from that with actual observations, the underlying mechanisms are not significantly different. Thus, this suggests that the model in this study successfully represents the mechanism preventing forage particles from flowing out of the RR with liquid.

However, regression of differences between Kp liquid and Kp concentrate on Kp liquid from the model indicated that model predictions were not consistent with those in the NRC database (Seo et al., 2006a). The intercepts were -0.020 (± 0.004) and -0.003 (± 0.001) and the slopes were 0.628 (± 0.044) and 0.242 (± 0.004) for the NRC database and the model predictions, respectively, which implies that the model overall overpredicts Kp concentrate. This may be because of 1) inappropriate estimation of parameters, and 2) diversity of concentrate particles that were marked in the NRC database. Processing of different types of grain results in changes in FSG (Siciliano-Jones and Murphy, 1991) and digestion and passage characteristics of a concentrate particle (Taylor and Allen, 2005). For instance, fibrous feed by-products containing appreciable amounts of fiber (e.g., soy hull, 1.08) have low FSG (Bhatti and Firkins, 1995) and thus they have low TPPE, whereas ground shelled corn and ground corn gluten feed have high FSG (Siciliano-Jones and Murphy, 1991) and thus may have high TPPE. It should be pointed out that a large concentrate particle that has a high FSG may have low PPER because it may sediment rapidly to the floor of the ventral rumen based on the Stoke's Law, which dictates that larger particles sediment faster than small particles when their densities are the same (Denn, 1980). Particles with FSG between 1.17 and 1.42 pass more rapidly compared with those with higher or lower FSG (Welch, 1986). Further research on estimating model input parameters for different concentrates, especially for TPPE and PPER, is required.

Sensitivity analysis gives useful information for evaluating the relative importance of the model parameters. The TPPE of large particles was more important than a

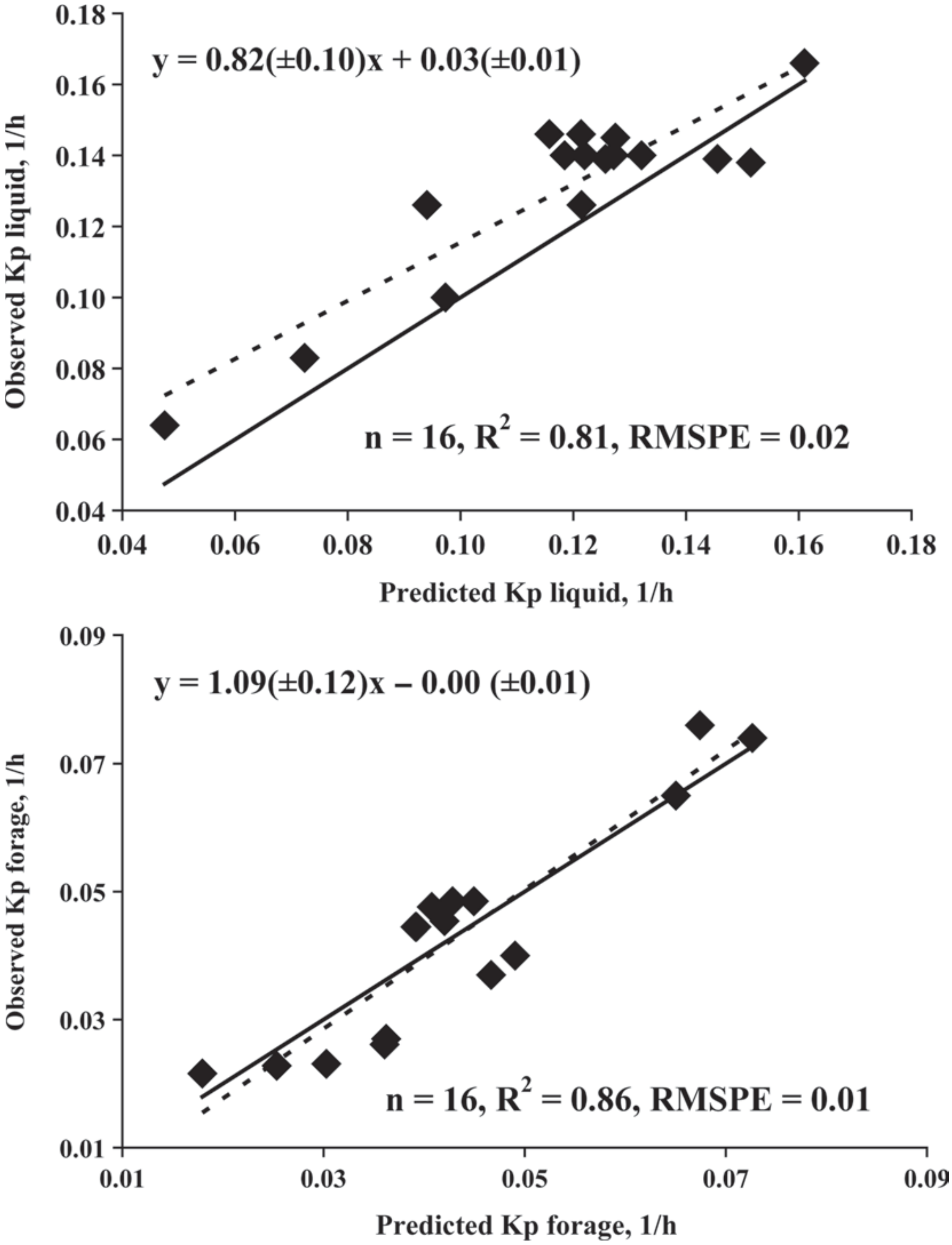

Figure 3. Plots of regression of observed on predicted for fractional liquid passage rate (1/h, panel A) and fractional forage particle passage rate (1/h, B) for the evaluation database containing 16 observations of both liquid and particle passage data. Solid and dotted line represent y = x and the best fit linear regression, respectively. The regression equations (dotted line) are presented. Kp = fractional passage rate. RMSPE = root mean square prediction error.

fast large-particle digestion rate even though the model assumes that masticated particles become small particles in the escapable pool (Table 7). The effect of K_d of large particles on Kp concentrate was negligible. These results imply that sedimentation of particle was more important than particle size reduction in this study. This is consistent with the report that particle size and specific gravity accounted for 28 and 59%, respectively, of the variation in retention time of plastic particles in the RR of sheep (Kaske and Engelhardt, 1990).

Table 7. Sensitivity of the model predictions (% change) to a 10% increase in the input variables of the model[1]

Input variable[2]	Effect of a 10% increase in input variable on output variables (% change)				
	Kp large forage	Kp small forage	Kp concentrate	Kp liquid	Particle outflow rate
DMI	10.7	11.4	21.0	22.1	16.2
BW	4.8	5.1	7.4	7.8	2.3
Concentrate content in the diet	5.9	4.0	0.2	−0.1	−0.4
Time spent eating	2.1	1.1	1.4	0.3	−0.1
Time spent ruminating	0.3	0.4	0.5	0.6	0.2
PPER large concentrate[3]	—[4]	—	−3.3	0.1	0.5
PPER small concentrate[3]	0.1	—	−6.7	0.1	−2.4
PPER large forage	1.8	—	—	—	0.1
PPER small forage[3]	0.1	−7.3	—	0.1	−1.2
PMIE[3]	—	1.4	—	—	0.2
TPPE of large forage particle	8.4	−0.2	—	—	0.4
TPPE of small forage particle	−0.1	7.4	—	−0.1	1.2
TPPE of concentrate particle	−0.1	—	10.0	−0.1	1.7
K_d large concentrate	—	—	—	—	−0.3
K_d small concentrate	−0.1	—	−0.1	−0.1	−2.2
K_d large forage	1.3	−0.4	—	−0.1	−0.8
K_d small forage	−0.1	2.6	—	−0.1	−1.1
Large particle breakdown rate	2.3	0.5	—	−0.1	1.2
Sedimentation rate of large particles	3.5	−0.1	—	—	0.2
Sedimentation rate of small particles	—	2.4	—	—	0.4
Large particles in concentrate	—	—	—	—	−2.7
Large particles in forage	−3.1	9.0	—	—	0.5
Soluble DM in concentrates	—	—	−0.1	0.1	−3.7
Soluble DM in forages	2.4	1.5	—	−0.1	−2.7

[1] One input variable at a time was increased or decreased by 10% from the values from Woodford and Murphy (1988a): a treatment with a diet containing 60% concentrate, 30% corn silage, and 10% alfalfa hay fed to lactating dairy cows (BW, 589 kg; DMI, 22.4 kg/d; time spent eating, 240 min; time spent ruminating, 370 min). The simulation was run for 72 h and then daily averages for predicted values were compared. Kp = fractional rate of passage; K_d = fractional rate of degradation.

[2] PPER = probability of the particle in the escapable pool of being located in the reticulum; PMIE = proportion of masticated large particle of being located in the inescapable pool; TPPE = theoretical probability of particle of being located in the escapable pool.

[3] A 10% decrease in parameter value.

[4] The values are not applicable or insignificant ($-0.05 < x < 0.05$).

In predicting Kp of large forage particles, PPER of large forage particles was not an important variable compared with TPPE; however, predictions of Kp of small forage particles and concentrates were very sensitive to both. This may be because of the relatively small proportion of large forage particles in the escapable pool. Because TPPE determines the escape of particles from inescapable pool to escapable pool and PPER determines the movement of particles from rumen to reticulum within the escapable pool, these results suggest that the flow from inescapable to escapable pool is a rate-limiting step of movement of large particles, whereas the flow from escapable pool to reticulum as well as escape from the inescapable pool is the rate-limiting step of passage of small forage and concentrate particles.

Sensitivity analysis showed independence among different pools in the model. The Kp of one pool was insensitive to the variations in pool-specific parameters of the others. This is because of the lack of interactions among pools in the model. The model assumes that distribution of chewing activity and DMI, which account for the interaction of different particle pools, are known. Based on this, the dynamics of particle can be theoretically and mathematically represented in a simple manner using a factorial approach. A more complete model, which also predicts chewing activity and DMI, requires accounting for interactions among different particle pools, rumen microbes, and the animal.

The model developed in this study demonstrated the potential for using mechanistic and dynamic modeling to improve our understanding of physiological processes in animal nutrition and to more accurately predict escape of nutrients from the RR, which is important in precision feeding to reduce nutrients in manure. However, more research on estimating the model parameters for individual feeds is needed.

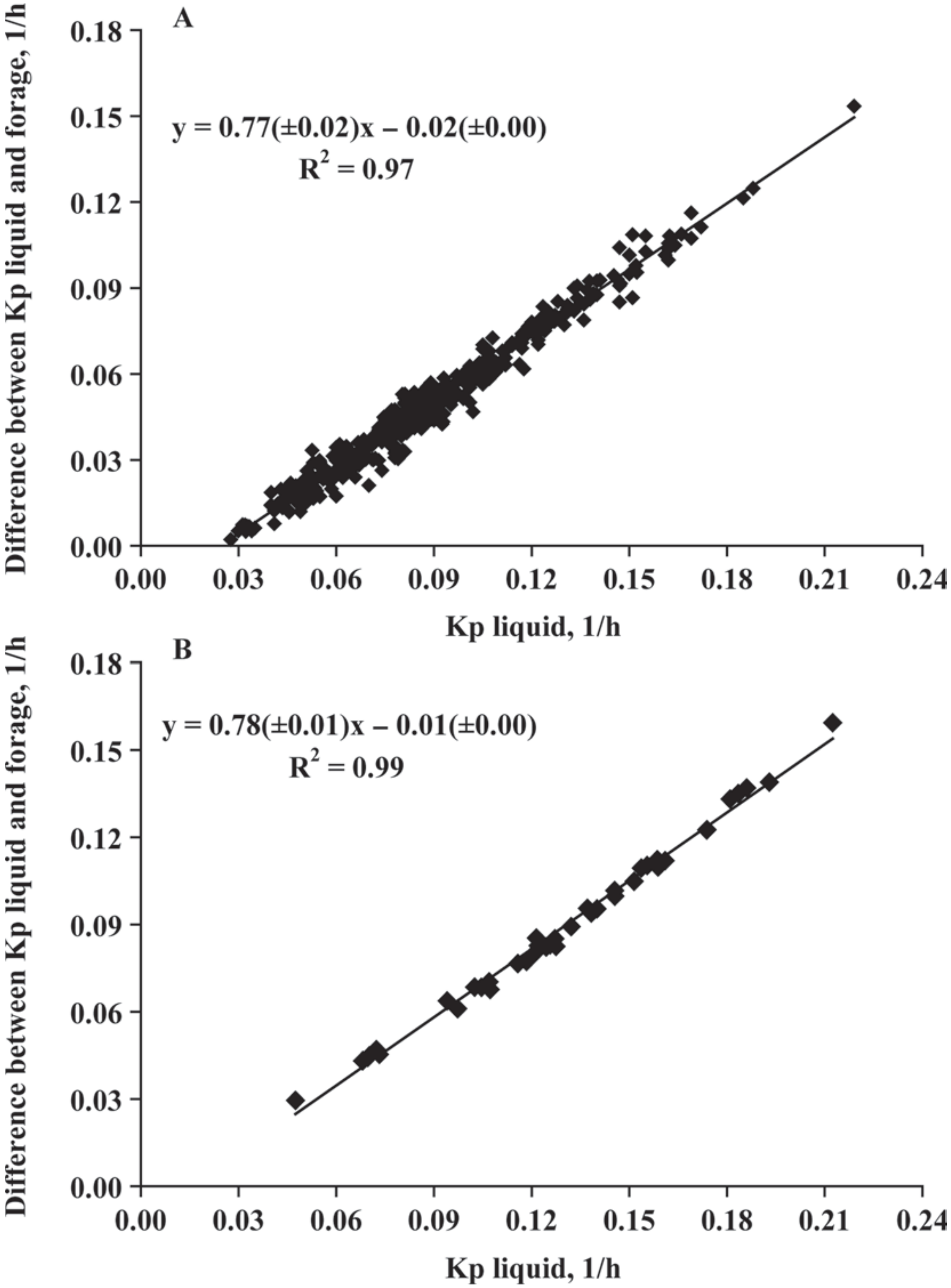

Figure 4. Plots of difference between fractional liquid passage rate (1/h) and fractional forage particle passage rate (1/h) on fractional liquid passage rate (1/h) in the database described in Seo et al. (2006a; panel A) and predictions from the model with the independent database in this study (panel B). The numbers of observations were 455 in A and 41 in B, respectively. Solid lines represent the best fit linear regression, and the regression equations are presented. Kp = fractional passage rate.

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APPENDIX

Assuming P, L, and W are particle, liquid and wet digesta in the rumen, respectively, $W = P + L$. Assuming E, U, and T are escapable pool, inescapable pool, and total, respectively, $T = E + U$.

The passage coefficient (PC) is defined as the ratio of particle to liquid in the escapable pool times the probability of the particle in the escapable pool of being located in the reticulum (PPER). The ratio of particle to liquid in the escapable pool (k) is estimated as follows:

$$k = \frac{P_E}{L_E},$$

where P_E and L_E are particle and liquid in the escapable pool, respectively.

Thus, the equation for PC is PC = k·PPER.

Let $M = \frac{P_T}{W_T}$ be the proportion of particle in the ruminal digesta (PPTD), $E = \frac{W_E}{W_T}$ be the proportion of escapable pool in the rumen, and $a = \frac{P_E}{P_T}$ be the proportion of particles in the escapable pool to total particles in the rumen. The proportion of particles in the escapable to total particles in the rumen (a) is equivalent to the probability of particle of being in the escapable pool.

$$\frac{P_E}{W_E}E + \frac{P_U}{W_U}\left(1 - E\right) = \frac{P_T}{W_T}$$

$$\begin{aligned}\frac{P_E}{W_E} &= \frac{1}{E}\left(\frac{P_T}{W_T} - \frac{P_U}{W_U}\left(1 - E\right)\right)\\ &= \frac{1}{E}\left(\frac{P_T}{W_T} - \frac{P_U}{W_U}\frac{W_U}{W_T}\right)\\ &= \frac{1}{E}\cdot\frac{P_E}{W_T} = \frac{1}{E}\cdot M\cdot a\end{aligned}$$

$$\frac{P_E}{W_E} = M\frac{a}{E}.$$

The presence of an inescapable pool may affect the proportion of particles in the escapable pool. For example, large particles in the dorsal rumen are known to form a rumen mat and entrap small particles under some dietary conditions in cows (Faichney, 1986).

Assuming a' is a theoretical proportion of particles in the escapable pool without a presence of inescapable pool (TPPE) and a is affected by the amount of the pool, then $a = f\,(E)\cdot a'$

By definition, $f\ (0) = 0$, $f\ (1) = 1$, and there are 5 possible shapes of $f\ (E)$. However, we assume the simplest form, $f\,(E) = E$, which means the effect of raft to the proportion of particles in the escapable pool is constant for all the particles regardless of its property. Then,

$$\frac{P_E}{W_E} = M\frac{a}{E} = M\frac{E\cdot a'}{E} = M\cdot a'$$

$$\frac{P_E}{L_E} = k = \frac{M\cdot a'}{1 - M\cdot a'}.$$

We may assume that E, M, and a' are independent.

Therefore, the equation for estimating the particle coefficient is as follows:

$$PC_i = \frac{PPTD_i\cdot TPPE_i}{1 - PPTD_i\cdot TPPE_i}\times PPER_i,$$

where PC is passage coefficient, PPTD is the proportion of particle in total ruminal digesta, TPPE is the theoretical probability of particle to be in the escapable pool, and PPER is the probability of the particle in the escapable pool of being located in the reticulum.