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MODELLING ANIMAL SYSTEMS PAPER

Development and evaluation of empirical equations to predict ruminal fractional passage rate of forages in goats

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SUMMARY

The objectives of the present paper were to develop and evaluate empirical equations to predict fractional passage rate (*kp*) of forages commonly fed to goats using chemical composition of the diet and animal information. Two databases were created. The first (development database) was assembled from four studies that had individual information on animals, diets and faecal marker concentrations over time (up to 120 h post-feeding); it contained 54 data points obtained from Latin square designs. The second (evaluation database) was built using published information gathered from the literature. The evaluation database was comprised of five studies, containing 39 data points on diverse types of diets and animal breeds. The *kp* was estimated using a time-dependent model based on the Gamma distribution with at least two and up to 12 (rumen) + one (post-rumen) compartments (i.e. G2G1–G12G1) developed from the development database. Statistical analyses were carried out using standard regression analysis and random coefficient model analysis to account for random sources (i.e. study). The evaluation of the developed empirical equation was conducted using regression analysis adjusted for study effects, concordance correlation coefficient and mean square error of prediction. Sensitivity analyses with the developed empirical equation and comparable published equations were performed using Monte Carlo simulations. The G2G1 model consistently had lower sum of squares of errors and greater relative likelihood probabilities than other GnG1 versions. The *kp* was influenced by several dietary nutrients, including dietary concentration or intake of components such as lignin, neutral detergent fibre (NDF), hemicellulose, crude protein (CP), acid detergent fibre (ADF) and animal body weight (BW). The selected empirical equation, adjusted for study effects, ($kp_{/\mathrm{h}} = 0{\cdot}00161 \times \mathrm{NDF}_{\mathrm{g/kg\,BW}}^{1{\cdot}503 \pm 0{\cdot}371} \times e^{(0{\cdot}022 \pm 0{\cdot}0097 \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}00375 \pm 0{\cdot}0013 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}})}$) had an R^2 of 0·623 and root of mean square error (RMSE) of 0·0122/h. The evaluation of the adequacy of the selected equation with the evaluation database indicated no systematic bias (slope not different from 1), but a low accuracy (0·33) and a persistent mean bias of 0·0129/h. The sensitivity analysis indicated that the selected empirical equation was most sensitive to changes in dry matter intake (DMI, kg/d), BW(kg) and NDF (g/kg dry matter) with standardized regression coefficients of 0·98, −0·43 and −0·32, respectively. The sensitivity analysis also indicated that the greatest forage *kp* in goats is likely to be *c.* 0·0569/h. The comparison with a previously published empirical equation containing data on cattle, sheep and goats, suggested that the distribution of the present empirical equation, adjusted for mean bias, is wider and that *kp* of goats might be similar to cattle and sheep when fed high amounts of forage under confinement conditions.

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INTRODUCTION

In ruminants, the extent of digestion of feeds and their nutrients depends on: (i) the magnitudes of the fractional rate of fermentation (k_d) in the rumen and the fractional rate of passage (*kp*) from the rumen, (ii) the length of time that feed components are exposed to the enzymatic reactions and their absorption in the small intestine and (iii) possible fermentation in the hindgut. As fibre digestion is greater in the rumen than in any other compartment of the gastro-intestinal tract, the longer the fibre particulate remains in the rumen the greater the extent of fibre digestion is likely to be. The *kp* influences the retention of the particulate matter in the rumen. In addition to the extent of digestion of feeds, *kp* has also been related to maximal voluntary dry matter intake (DMI), amount of ruminally undegraded protein, efficiency of microbial growth, extent of methane loss and susceptibility of animals to bloating (Okine *et al.* 1998).

Clauss *et al.* (2006) indicated that the ratio between the rates of passage of liquids and solids is different between browsers and grazers, probably because grazers (or ruminants under a grazing condition) retain solids (fibre) for a longer period of time than browsers. Therefore, it is possible that the passage rate in goats (intermediate to concentrate selector) may be similar to that of cattle and sheep (grazers) when fed high-forage diets. However, Clauss & Lechner-Doll (2001) had previously concluded that browsers are not able to retain particles for as long as grazers because their retention selectivity factor in the rumen is narrower (1·14–1·80 mm) than grazers (1·56–2·80 mm), indicating that browsers may have a faster *kp*.

Mathematical models can be useful for describing and predicting the biological mechanisms involved in digestion of feeds by ruminants. In fact, nutrition mathematical models rely heavily on accurate predictions of *kp* to determine ruminal digestibility of feeds and their nutrients (Cannas *et al.* 2004; Fox *et al.* 2004; Tedeschi *et al.* 2008) and to allow different strategies for feeding and management of ruminant animals throughout the world. Different approaches have been used in predicting *kp* from empirical equations (Cannas & Van Soest 2000; Seo *et al.* 2006) to more complex dynamic models (Seo *et al.* 2007, 2009). Empirical equations can provide enough descriptive information of the variables involved and their relationship with dependent variables.

The objectives of the present paper were: (i) to develop and evaluate empirical equations to predict *kp* of forage in goats using chemical composition of the diet, (ii) to compare the predictions of the newly developed equation with those equations proposed by Cannas & Van Soest (2000) for ruminants and (iii) to perform a sensitivity analysis of influential variables that could impact the *kp* for goats.

MATERIALS AND METHODS

Database description

Table 1 shows the range of chemical composition of the diets, body weight (BW), DMI and number of data points for the development and evaluation databases.

Development database

The data from four studies that sequentially measured the concentration of a forage marker, ytterbium (Yb), in the faeces were gathered into a development database. Briefly, study 1 was comprised of a Latin square design with four mature Boer crossbred wether goats (51·4 kg BW) fed 0·37 of marked bermudagrass hay and 0·63 of concentrate containing 0, 0·13, 0·25 or 0·38 of distillers' dried grains with solubles (Gurung *et al.* 2008); all 16 (4 × 4) data points were used. Study 2 investigated the impact of levels of peanut skins (0, 0·10, 0·20 and 0·30), substituting soybean meal in the concentrate portion of the diet of four mature Boer crossbred wether goats (70·6 kg BW) fed 0·45 of marked bermudagrass hay (Kendricks *et al.* 2009); all 16 (4 × 4) data points were used. Study 3 had four mature wether goats (58·5 kg BW) fed 0·40 concentrate, 0·30 bermudagrass hay and 0·30 of *Lespedeza cuneata* and/or alfalfa at four different ratios (0:30, 10:20, 20:10 and 30:0, respectively) in a Latin square design (Wolc *et al.* 2009); only 15 out of 16 (4 × 4) data points were used. The marking technique used by Wolc *et al.* (2009) differed from the other studies in that they used rumen gelatine capsule containing Yb acetate to mark all feed particles (forages and concentrates) in the rumen. A limitation of this technique is that some Yb acetate probably remained free (i.e. unattached to any particle), escaped the rumen and reached the faeces in a free form, thus providing a faster *kp* than expected. Finally, study 4 also used an incomplete Latin square design to determine the impact of four levels of broiler litter (0, 0·13, 0·25 and 0·50) in the diet of wether goats (35·7 kg BW) (J. Bartlett, personal communication); only seven out of ten data points were used.

Table 1. *Summary of animal and diet composition of the development and evaluation studies*[*]

Studies†	N‡	BW (kg)	DMI (kg/d)	CP (g/kg DM)	NDF (g/kg DM)	ADF (g/kg DM)	Lignin (g/kg DM)	Ash (g/kg DM)	EE (g/kg DM)	*kp* (/h)	k_e (/h)
Development database											
1	16	51·1–51·9	0·82–0·91	135–145	312–344	146–157	–	43–45	27–47	0·0137–0·0274	0·0172–0·0408
2	16	51·1–51·9	1·07–1·25	138–168	444–567	342–431	39–80	69–76	13–104	0·0158–0·0296	0·0182–0·0515
3	15	52·9–66·6	1·05–1·57	153–197	394–473	226–292	39–54	49–67	23–32	0·0299–0·0746	0·0333–0·1112
4	7	34·7–36·5	0·89–1·02	141–178	279358	114–191	31–42	62–209	–	0·0212–0·0385	0·0239–0·09143
Evaluation database											
5	4	72·6±0·64	0·89–1·18	140–172	459–518	208–261	45–94	55–66	45–131	0·0299–0·0328	–
6	20	28·5	0·42–0·90	52–211	427–764	287–504	48–83	66–112	–	0·0250–0·0470	–
7	6	39·2	0·67–1·22	43–81	573–818	344–539	42–76	58–69	–	0·0140–0·0267	–
8	3	40·6±1·07	0·64–0·74	153–181	390–410	259–294	51–66	109–131	–	0·0240–0·0340	–
9	3	43·0±2·1	0·55–0·69	74–88	368–418	225–282	127–167	119–134	43·1–80·3	0·0210–0·0250	–

[*] BW, body weight; DMI, dry matter intake; CP, crude protein; NDF, neutral detergent fibre; ADF, acid detergent fibre; EE, ether extract; *kp*, calculated fractional passage rate and k_e is calculated fractional rate of escape of particles from the rumen. Values are minimum and maximum or mean ± S.E.

† Studies 1, Gurung *et al.* 2008; 2, Kendricks *et al.* 2009; 3, Wolc *et al.* 2009; 4, J. Bartlett, personal communication; 5, Solaiman *et al.* 2002; 6, Coleman *et al.* 2003; 7, Hadjigeorgiou *et al.* 2001; 8, Alcaide *et al.* 2000; and 9, Yanez Ruiz *et al.* 2004.

‡ Number of data points, considering all combinations of animals, diets and periods of Latin square designs.

The animals in study 4 were smaller (lighter) than in the other studies used for the development database. Study 3 had faecal collections at 0, 6, 12, 24, 36, 48, 60, 72, 96 and 120 h (ten time points), studies 1 and 2 had the same time points as study 3 plus faecal collection at 84 h (11 time points) and study 4 had 19 times of faecal collections (0, 6, 12, 18, 24, 30, 36, 42, 48, 54, 60, 66, 72, 78, 84, 90, 96, 108 and 120 h) after feeding the marker.

Evaluation database

Independent studies published in the literature were gathered into an evaluation database. Study 5 was comprised of four mature Nubian wether goats (72·6 kg BW) fed 0·45 bermudagrass hay and 0·55 concentrate, which had four levels of EasiFlo cottonseed replacing corn and soybean meal, so that diet dry matter (DM) contained 0, 0·16, 0·33 or 0·50 of EasiFlo cottonseed; Yb was used as a marker (Solaiman *et al.* 2002). For study 6, 20 different hays cut at two or three stages of maturity from cool-season and warm-season plant species were fed to yearling Alpine wether goats (28·5 kg BW) and the passage rate was determined using Yb (Coleman *et al.* 2003). The aim of study 7 was to investigate the digestibility of temperate forages with or without ammonia treatment using 12 Scottish cashmere male goats (39·2 kg BW); *n*-alkane was the marker used for temperate forages (Hadjigeorgiou *et al.* 2001). For study 8, four dry non-pregnant Granadina goats (40·6 kg BW) were fed with three diets based on alfalfa and combinations of beet pulp and oat grain; chromium mordant technique was used to mark alfalfa (Alcaide *et al.* 2000). Finally, study 9 also used dry non-pregnant Granadina goats (43 kg BW) to determine the ruminal degradation profiles and passage rates of olive leaves with or without supplementation with barley and faba beans; the chromium mordant technique was also used (Yanez Ruiz *et al.* 2004). These studies were selected because of their diversity of feed, animal and environment information.

Determination of the ruminal fractional passage rate

The direct comparison and use of the published *kp* from different studies may not be adequate because different studies may use different methodologies in fitting the data to passage rate models. Therefore, the raw data of the development database studies were used to estimate the *kp* using the GnG1 models

(Vieira *et al.* 2008*a*, *b*). The GnG1 models are based on the Gamma distribution and were selected because of their robustness, flexibility to describe different marker profiles and ability to standardize the method of determination of the age-dependent fractional passage rate among studies. The data were fitted to GnG1 models of at least two and to up to 12 orders of time dependency (e.g. compartments) in the rumen ($n=2$–12) and one-time dependency post-rumen (i.e. G2G1–G12G1). The GnG1 Models software (http://nutritionmodels.tamu.edu/gng1.htm, verified June 19 2011) was used to fit the data. Briefly, the parameter estimates are the order of time dependency related to transference mechanisms of the particles from the raft (unmixed) pool to the escapable (mixed) pool in the rumen (n), transit time, representing the time of an escaped particle to transit from the reticulo-omasal orifice to the faeces (τ, measured in h), asymptotic age-dependent fractional rate for transference of particles from the raft to the escapable pool (L_r or λ_r, measured /h), fractional rate of escape of particles from the escapable pool (k_e, /h), and the mass ratio between the marker dose and NDF mass in the raft pool (C0, g/g) (Vieira *et al.* 2008*b*). The kp was computed based on the parameters λ_r, k_e and n using Eqn (1) as proposed by Ellis *et al.* (1994).

$$kp = \frac{1}{(n/\lambda_r) + (1/k_e)} \tag{1}$$

where kp is the overall fractional passage rate (/h); λ_r is the asymptotic age-dependent fractional rate for transference of particles from the raft to the escapable pool (/h); k_e is the calculated fractional rate of escape of particles from the escapable pool (/h); and n is the order of time dependency.

Statistical analyses

All statistical analyses were performed with SAS *v*. 9.2 (SAS 2008) using PROC REG and PROC MIXED. The following variables, expressed either as g/kg DM or as daily intake (g/kg BW), were used in a stepwise selection process using PROC REG to predict kp either as observed kp values or as the logarithm of observed kp values: BW, dietary DM, crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), hemicellulose, lignin, ash, ether extract (EE) and the ratio of lignin to NDF. In addition, the logarithm of NDF, lignin and lignin to NDF ratio were used as independent dietary variables. Preliminary analyses indicated these variables were nonlinearly related to kp. This nonlinear relationship of the kp with other variables is in accordance with the work by Cannas & Van Soest (2000). As some of the studies did not have all variables, some variables (i.e. hemicellulose and ADF) were omitted in order to increase the number of data points in a parallel regression analysis. In the first random coefficient model, the PROC MIXED was used to evaluate the contribution of study, diet and animal variations to the total variance in predicting the average observed kp. The effects of study, and diet and animal within study, were assumed to be random effects and the variance component was used for the variance–(co)variance matrix structure (Littell *et al.* 2006). Additionally, a second random coefficient model (statistical model shown in Eqn (2)) was evaluated to estimate the empirical equation based on the fixed effect of the selected independent variables after adjustment for study effect (St-Pierre 2001). The kp adjusted for study effects (kp_{adj}) was computed with the fixed effects and the residue estimates ($\mu+X_{\text{ij}}+\varepsilon_{\text{ij}}$; Eqn (2)). The approximate coefficient of determination was calculated as the regression of kp_{adj} on the fixed effect variables (X_i). The plot of studentized residuals on predicted values was used to assess outliers, which were removed if outside of the range −2·5 to +2·5.

$$Y_{ij} = \mu + X_{ij} + \text{Study}_j + X_{ij} \times \text{Study}_j + \varepsilon_{ij} \tag{2}$$

where Y_{ij} is the dependent variable, μ is the overall mean, X_{ij} is the ith-independent variable of the jth study, Study_j is the random effect of the jth study on the intercept, $X_{ij} \times \text{Study}_j$ is the random interaction between the ith-independent variable and the jth study, study is identically, independently and normally distributed $\sim N(0, \sigma_s^2)$ and ε_{ij} is the identically, independently and normally distributed uncontrolled, random error $\sim N(0, \sigma_s^2)$.

Equation evaluation

A random coefficient model similar to that shown in Eqn (2) was used to remove the effect of study from the intercept and the slope and the adjusted, observed kp was used to determine the equation adequacy. The adequacy of the predictions of the kp of the evaluation database was assessed as described by Tedeschi (2006). Equation precision was measured with the coefficient of determination (R^2) of the linear regression between observed and predicted values and the simultaneous F-test of the intercept and slope (H_0: intercept = 0 and slope = 1), whereas the accuracy

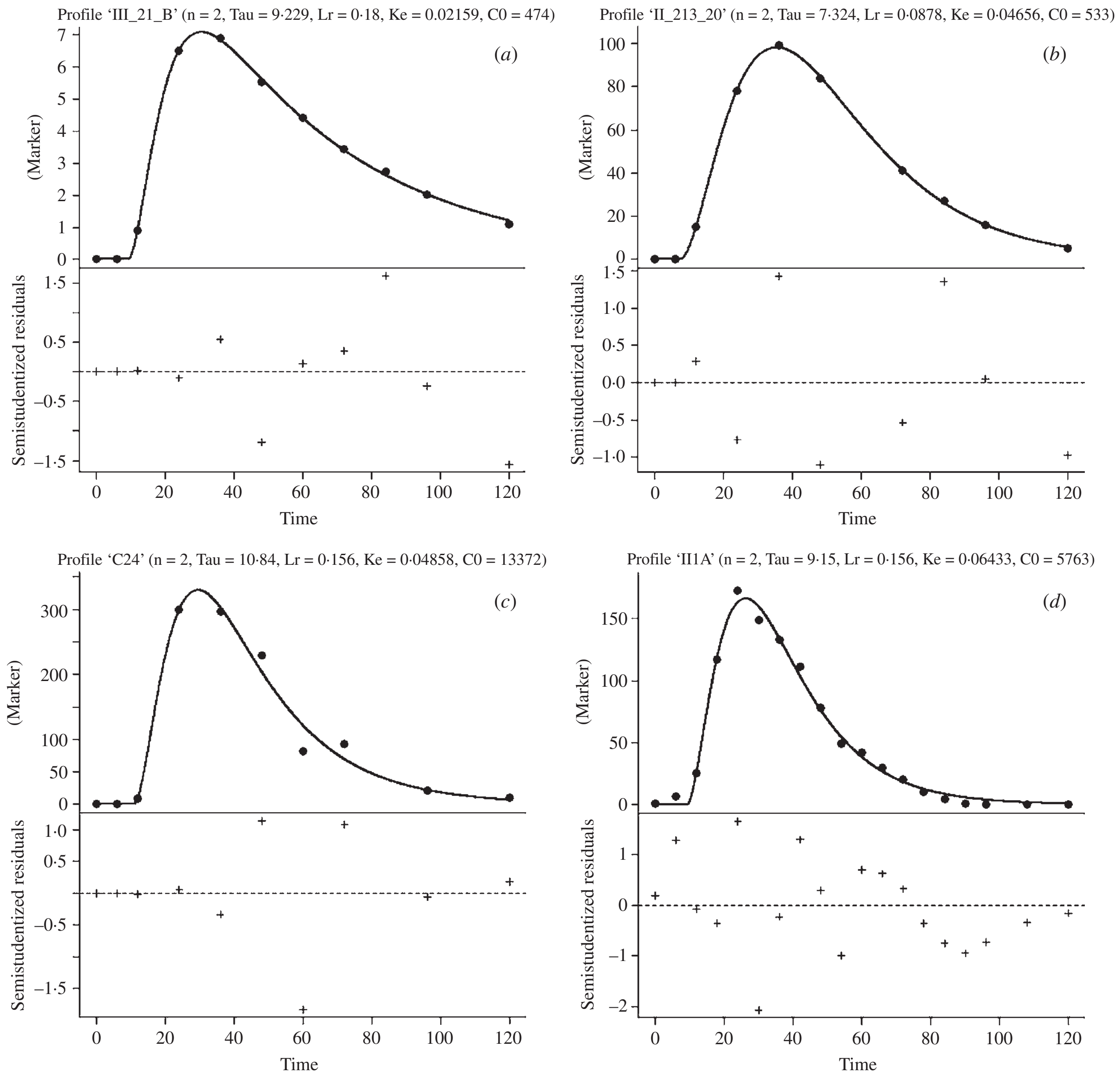

Fig. 1. Marker concentration (marker) profiles (blue dots) and G2G1 fitting line (solid, dark line) in the top part of the graphics and studentized residuals in the bottom part of the graphics versus incubation time (h, *X*-axis) of selected treatments from studies 1 (*a*), 2 (*b*), 3 (*c*) and 4 (*d*) of the development database. The parameter estimates shown in the top part of the graphics are: *n* is the order of time dependency; L_r is the asymptotic age-dependent fractional rate for transference of particles from the raft to the escapable pool (/h); σ is the transit time that represents the time of an escaped particle to transit from the reticulo-omasal orifice to the faeces (h); k_e is the calculated fractional rate of escape of particles from the escapable pool (/h); and C0 is the mass ratio between the marker dose and NDF mass in the raft pool (g/g).

(Cb) was determined based on the concordance correlation coefficient (CCC) and the mean square error of prediction (MSEP) and its decomposition into mean bias, systematic bias and random errors (Tedeschi 2006). The Cb statistic measures how far (or close) the regression line deviates from the $Y=X$ line. Evaluations were performed by means of the Model Evaluation System *v*. 3.1.11 (http://nutritionmodels.tamu.edu/mes.htm, verified June 19 2011) as discussed by Tedeschi (2006). In addition to the prediction equation derived in the present study, the equation proposed by Cannas & Van Soest (2000)

(CVS) to predict *kp* (Eqn (3)) was also tested with the evaluation database.

$$kp_{\mathrm{CVS},/\mathrm{h}} = 0{\cdot}0182 \times (0{\cdot}1 \times \mathrm{NDF}_{\mathrm{g/kg\,BW}})^{0{\cdot}40} \times e^{0{\cdot}0046 \times \mathrm{CP}_{\mathrm{g/kg\,DM}}} \tag{3}$$

where kp_{CVS} is the fractional passage rate predicted by the Cannas & Van Soest's (2000) equation (/h), NDF is expressed as a g/kg BW, and CP is expressed as a g/kg dry matter.

Sensitivity analysis

Sensitivity analysis was performed using the Monte Carlo technique, which randomly samples input variables based on a probability density distribution to assess their concurrent impact on the value and distribution of output variables. The Monte Carlo simulation was performed with @Risk *v.* 5.7 (Palisade Corporation 2010) using 10 000 iterations and Latin hypercube sampling as discussed by McKay *et al.* (1979). The determination of most influential variables on the simulation output was accomplished by using standardized regression coefficients (SRC) (Kutner *et al.* 2005). The SRC reflects the change in the S.D. of the dependent (output) variable associated with 1 unit change in the S.D. of the independent (input) variable at a *ceteris paribus* condition, that is, when all other input variables are fixed, unchanged (Helton & Davis 2002). Spearman correlations were assigned to input variables to maintain the expected correlations between independent variables during the simulations.

RESULTS AND DISCUSSION

The G2G1 model consistently had a lower sum of squares of errors and greater relative likelihood probabilities (data not shown) than other GnG1 versions (Vieira *et al.* 2008*a*). Therefore, the G2G1 model was chosen to converge the passage profiles of all studies of the development database. Figure 1 depicts the marker concentration profiles and the fitted line for selected treatments of the development database studies.

Development of empirical equations

For the untransformed *kp*, hemicellulose (g/kg BW), BW (kg), natural logarithm of lignin to NDF ratio and ash (g/kg BW) were selected by the stepwise selection process. These variables explained 0·714 of the variation and had a root of mean square error (RMSE) of 0·0069/h with 38 data points (Eqn (4)).

$$kp_{/\mathrm{h}} = \left(\begin{array}{l} -5{\cdot}266 \pm 1{\cdot}51 + 1{\cdot}418 \pm 0{\cdot}451 \\ \times \ln(\mathrm{Lignin}_{\mathrm{g/kg\,DM}}/\mathrm{NDF}_{\mathrm{g/kg\,DM}}) \\ + 1{\cdot}122 \pm 0{\cdot}142 \\ \times \mathrm{Hemicellulose}_{\mathrm{g/kg\,BW}} \\ + 0{\cdot}421 \pm 0{\cdot}21 \times \mathrm{Ash}_{\mathrm{g/kg\,BW}} \\ + 0{\cdot}132 \pm 0{\cdot}0199 \times \mathrm{BW}_{\mathrm{kg}} \end{array} \right) \Big/ 100 \tag{4}$$

When the ln(*kp*) was used as the dependent variable, hemicellulose (g/kg DM), BW (kg), NDF (g/kg DM) and ADF (g/kg BW) were selected; they explained 0·747 of the variation and had RMSE of 0·189 ln(*kp*) (0·0121/h) with 38 data points (Eqn (5)).

$$\begin{aligned} \ln(kp_{/\mathrm{h}}) = & -4{\cdot}95 \pm 0{\cdot}315 + 0{\cdot}209 \pm 0{\cdot}062 \\ & \times \mathrm{ADF}_{\mathrm{g/kg\,BW}} - 0{\cdot}00722 \pm 0{\cdot}00165 \\ & \times \mathrm{NDF}_{\mathrm{g/kg\,DM}} + 0{\cdot}00904 \pm 0{\cdot}00154 \\ & \times \mathrm{Hemicellulose}_{\mathrm{g/kg\,DM}} \\ & + 0{\cdot}0358 \pm 0{\cdot}0054 \times \mathrm{BW}_{\mathrm{kg}} \end{aligned} \tag{5}$$

The ln(*kp*) yielded slightly better predictions than the original, untransformed *kp*, and the residual plot of the ln(*kp*) had a more homoskedastic variance (not shown). Therefore, the ln(*kp*) was selected for further evaluation.

In the present study, nonetheless, few data points were used because of missing values for some dietary variables across studies. Thus, a reduced model that did not contain certain variables with missing values (i.e. lignin, cellulose and hemicellulose) was re-fitted; therefore including more data points. With the reduced model, the ln(*kp*) equation contained CP (g/kg BW), ADF (g/kg BW), ln(NDF) (g/kg BW) and BW (kg) as independent variables. These variables explained 0·722 of the variation and had an RMSE of 0·202 ln(*kp*) (0·0122/h) with 54 data points (Eqn (6)).

$$\begin{aligned} \ln(kp_{/\mathrm{h}}) = & -8{\cdot}155 \pm 0.538 + 1{\cdot}791 \pm 0{\cdot}398 \\ & \times \ln(\mathrm{NDF}_{\mathrm{g/kg\,BW}}) + 0{\cdot}21 \pm 0{\cdot}08 \\ & \times \mathrm{CP}_{\mathrm{g/kg\,BW}} \\ & - 0{\cdot}23 \pm 0{\cdot}036 \times \mathrm{ADF}_{\mathrm{g/kg\,BW}} \\ & + 0{\cdot}024 \pm 0{\cdot}0041 \times \mathrm{BW}_{\mathrm{kg}} \\ \therefore kp_{/\mathrm{h}} = & (0{\cdot}000287 \times 1{\cdot}713^{\pm 1}) \times \mathrm{NDF}_{\mathrm{g/kg\,BW}}^{1{\cdot}791 \pm 0{\cdot}398} \\ & \times e^{\left(\begin{array}{l} 0{\cdot}21 \pm 0{\cdot}08 \times \mathrm{CP}_{\mathrm{g/kg\,BW}} - 0{\cdot}23 \pm 0{\cdot}036 \times \mathrm{ADF}_{\mathrm{g/kg\,BW}} \\ + 0{\cdot}024 \pm 0{\cdot}0041 \times \mathrm{BW}_{\mathrm{kg}} \end{array} \right)} \end{aligned} \tag{6}$$

Equation (6) suggests that *kp* increases with dietary CP, ln(NDF) and BW but decreases with dietary ADF, as shown by their coefficient estimates. These variables are in agreement with Cannas & Van Soest (2000), in which *kp* was positively correlated with NDF and CP. The dairy NRC (2001) also uses dietary NDF in predicting *kp* of dry forage, and the work of Seo *et al.* (2006) confirmed that *kp* of forage is related to forage proportion in the diet of dairy cows. In contrast to these publications, Eqn (6) included CP (g/kg BW), suggesting that CP is important in the *kp* of goats in addition to fibre and body size for the present data. However, note that the coefficient of variation (S.D. divided by the mean) of the CP coefficient estimate was *c.* 0·38, which is quite large.

As ADF is not always reported as it should be, an additional regression excluding ADF was also performed and Eqn (6) was re-fitted using NDF, DM, CP, ash and BW. Equation (7) explained only 0·595 of the variation of the ln(*kp*) and had RMSE of 0·241 ln(*kp*) (0·0127/h) with 54 data points. Interestingly, CP was no longer significant when ADF was not included as an independent variable.

$$\begin{aligned}\ln(kp_{/\mathrm{h}}) &= -\,7{\cdot}125 \pm 0{\cdot}424 + 2{\cdot}164 \pm 0{\cdot}267 \\ &\quad \times \ln(\mathrm{NDF}_{\mathrm{g/kg\,BW}}) + 0{\cdot}039 \pm 0{\cdot}0062 \\ &\quad \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}0078 \pm 0{\cdot}0011 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}} \\ \therefore kp_{/\mathrm{h}} &= \left(0{\cdot}0008 \times 1{\cdot}528^{\pm 1}\right) \times \mathrm{NDF}_{\mathrm{g/kg\,BW}}^{2{\cdot}164 \pm 0{\cdot}267} \\ &\quad \times e^{\left(0{\cdot}039 \pm 0{\cdot}0062 \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}0078 \pm 0{\cdot}0011 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}}\right)}\end{aligned} \tag{7}$$

Development of empirical equations adjusted for study effects

The first random coefficient model analysis indicated the (co)variance of study, animal and diet accounted for 0·564, 0·158 and 0·00002 of the total variance, respectively. Even though study accounted for more than 0·50 of the random variation, its (co)variance estimate was not significantly different from zero ($P=0{\cdot}134$). Similarly, the diet (co)variance was not significantly different from zero ($P=0{\cdot}479$). However, there was a very strong trend for the animal (co) variance to be different from zero ($P=0{\cdot}059$). The average *kp* was 0·0283/h.

The second random coefficient model was performed using the variables identified in Eqn (7), but the random effect of study was included in the statistical model as shown in Eqn (2). The parameter estimates of the fixed effects are shown in Eqn (8). The approximate R^2 was 0·623 with a RMSE of 0·196 ln(*kp*) (0·0122/h). As Eqn (8) is adjusted for the impact of studies, it should be used to predict *kp* for goats.

$$\begin{aligned}\ln(kp_{/\mathrm{h}}) &= -\,6{\cdot}429 \pm 0{\cdot}71 + 1{\cdot}503 \pm 0{\cdot}371 \\ &\quad \times \ln(\mathrm{NDF}_{\mathrm{g/kg\,BW}}) + 0{\cdot}022 \pm 0{\cdot}0097 \\ &\quad \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}00375 \pm 0{\cdot}0013 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}} \\ \therefore kp_{/\mathrm{h}} &= (0{\cdot}00161 \times 2{\cdot}034^{\pm 1}) \times \mathrm{NDF}_{\mathrm{g/kg\,BW}}^{1{\cdot}503 \pm 0{\cdot}371} \\ &\quad \times e^{(0{\cdot}022 \pm 0{\cdot}0097 \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}00375 \pm 0{\cdot}0013 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}})}\end{aligned} \tag{8}$$

Evaluation of empirical equations

Equation (8) was used to predict the *kp* using the animal and dietary information of the evaluation database. Studies in the evaluation database were also analysed as random factors. The study (co)variance affected mostly the intercept ($\sigma^2_{\mathrm{Study}}=0{\cdot}399$, $P=0{\cdot}130$) rather than the slope ($\sigma^2_{\mathrm{Study}}=0{\cdot}013$, $P=0{\cdot}403$) of the regression of observed on predicted mean *kp*. The intercept was greatly affected by studies 6 and 7, probably because of the lighter BW of the animals; their points are more sparsely distributed than the other studies. Figure 2 depicts the plot of observed and predicted values. After adjusting for study effects, Eqn (8) was able to account for *c.* 0·46 of the variation in the observed *kp*. Even though the intercept and slope differed simultaneously ($P<0{\cdot}001$) from zero and unity, respectively, the slope was not different ($P=0{\cdot}172$) from unity. This suggests that Eqn (8) was able to predict *kp*, but there was a significant mean bias. In fact, Eqn (8) underpredicted the mean *kp* by 0·0129/h. The CCC was extremely low (0·22; theoretical range from 0 to 1) with an accuracy of 0·33 (theoretical range from 0 to 1). The root of MSEP (RMSEP) was 0·0139/h and the decomposition of the MSEP indicated that 0·86 of this error was associated with mean bias, 0·132 was due to random errors, and only 0·0076 was caused by systematic bias.

These findings suggested the G2G1 model may underpredict the *kp* or that reported values for *kp* in the evaluation database are overpredicted. In fact, simple models or one compartment model (Grovum & Williams 1973; Mertens & Loften 1980) may overpredict the *kp* because it does not account for the age-dependent fractional rate between compartments within the rumen (λ_r in Eqn (1)) before the marked particulate effectively escapes the rumen. The reported *kp* in the literature is more likely to be associated with k_e in Eqn (1), shown in Table 1, than with the

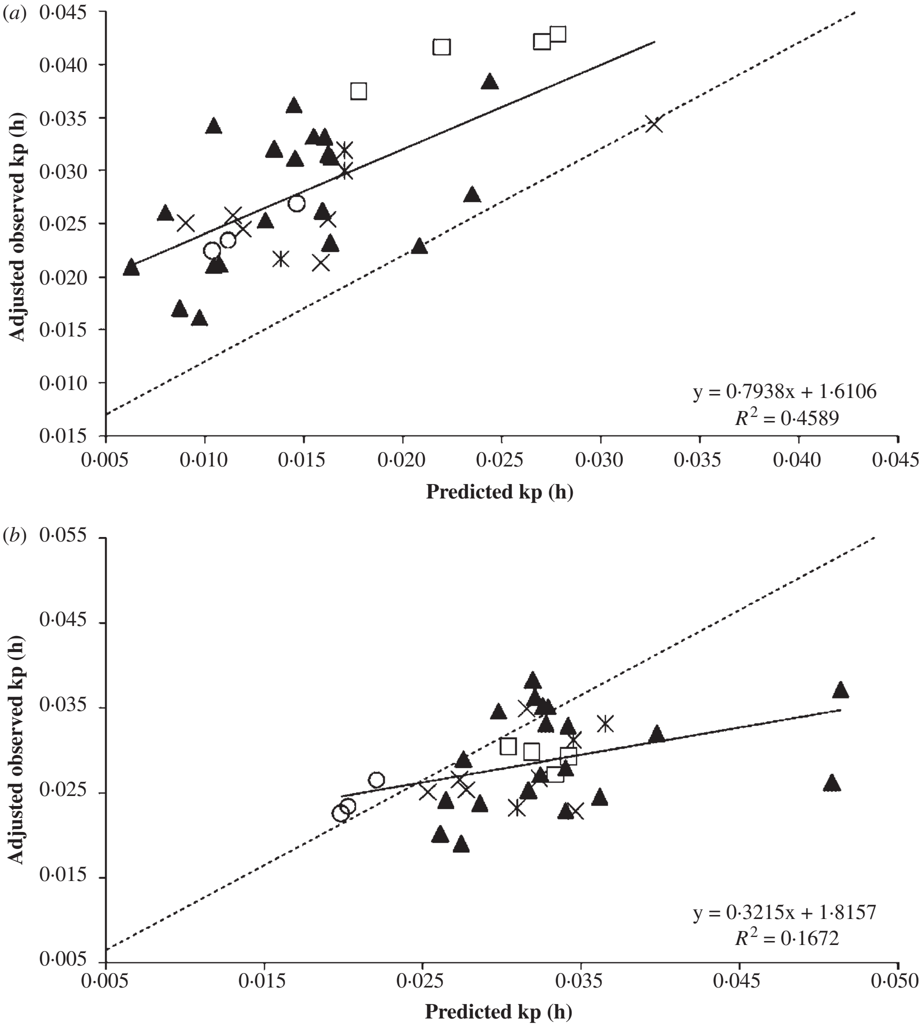

Fig. 2. Regression between observed fractional passage rates (*kp*) adjusted to study effect and predicted *kp* using (*a*) the developed empirical equation or (*b*) the equation published by Cannas & Van Soest (2000). Symbols are data from study 5 (□), study 6 (▲), study 7 (×), study 8 (*) and study 9 (○). The dashed line is the $Y = X$ line.

kp calculated with GnG1 models. The averages ± standard deviations (S.D.) of calculated *kp* and k_e in the development database were 0·028 ± 0·0115 and 0·041 ± 0·0212/h, respectively. The difference between *kp* and k_e is 0·0135/h, which is similar to the mean bias of 0·0129/h. This remarkably similar difference and the negligible systematic bias suggest that Eqn (8) can predict the true fractional passage rate, assuming two compartments in the rumen. Furthermore, predicted values by Eqn (8) could be adjusted for the mean bias that was found when evaluating literature data by simply adding 0·0129/h to Eqn (8) as shown in Eqn (9). The reason for this discrepancy is likely because the literature data were based on one compartment in the rumen using a time-independent fractional rate.

$$kp_{\mathrm{adj.}/\mathrm{h}} = 0{\cdot}0129 + (0{\cdot}00161 \times 2{\cdot}034^{\pm 1}) \times \mathrm{NDF}_{\mathrm{g/kg\,BW}}^{1{\cdot}503 \pm 0{\cdot}371} \times e^{(0{\cdot}022 \pm 0{\cdot}0097 \times \mathrm{BW}_{\mathrm{kg}} - 0{\cdot}00375 \pm 0{\cdot}0013 \times \mathrm{NDF}_{\mathrm{g/kg\,DM}})} \tag{9}$$

A similar meta-regression was performed with Eqn (3) (Cannas & Van Soest 2000). The precision was less than Eqn (8) (R^2 of 0·17) but as expected, the accuracy was greater (mean bias of 0·00344/h, RMSEP of 0·00716/h, CCC of 0·34 and accuracy of 0·83), probably because the authors used literature data that are comparable to the values in the evaluation database of the present study. This means that their

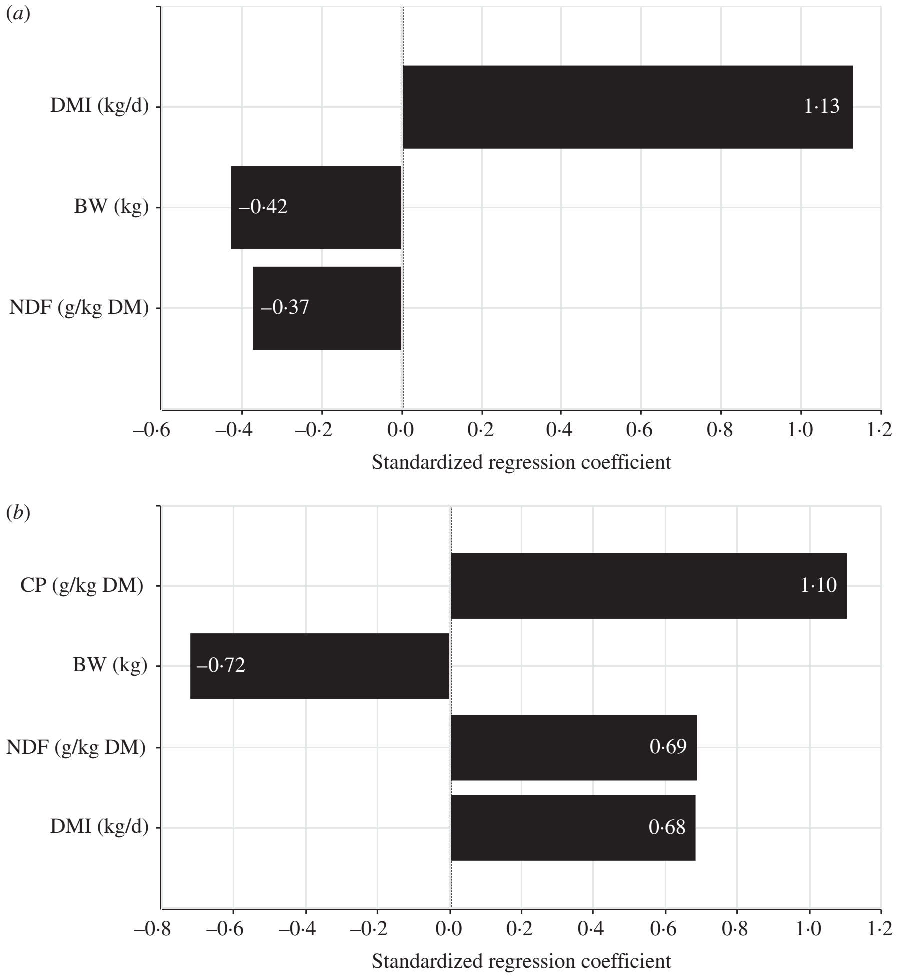

Fig. 3. SRC obtained from Monte Carlo simulation of predictions of fractional passage rate using (*a*) the developed empirical equation or (*b*) the equation published by Cannas & Van Soest (2000). Generated with @Risk 5·7.

kp were computed using time-independent models. The decomposition of MSEP indicated a more equally distribution of the MSEP among mean bias (0·23), systematic bias (0·363) and random errors (0·406) than Eqn (8).

A revision of the equation published by Cannas & Van Soest (2000) (Eqn (3)) has been developed (L. O. Tedeschi, personal communication; Eqn (10)) by adjusting for the study effects of the database used by Cannas & Van Soest (2000).

$$kp_{\mathrm{CVS2,/h}} = 0{\cdot}0217 \times (0{\cdot}1 \times \mathrm{NDF}_{\mathrm{g/kg\ BW}})^{0{\cdot}371} \times e^{0{\cdot}00321 \times \mathrm{CP}_{\mathrm{g/kg\ DM}}} \qquad (10)$$

When using the evaluation database to evaluate the revised equation of Cannas & Van Soest (2000) (Eqn (10)), a slightly improved R^2 was obtained of 0·24, RMSEP of 0·00625/h and CCC of 0·39. However, mean bias (–0·00366/h) was similar with the sign changed, and accuracy decreased slightly (Cb = 0·79). The major enhancement in using the kp_{CVS2} for study effects (Eqn (10)) was the partitioning of the MSEP that decreased the systematic bias from 0·363 to 0·139, suggesting that the adjustment for studies allows for a more consistent prediction.

Even though there was a slight improvement in the Cannas & Van Soest (2000) equation when their study effects were accounted for, the adequacy of Eqn (10) was less than Eqn (9) in predicting *kp* for goats. Therefore, either equation could be used for predictive purposes.

Sensitivity analysis

The data from the development and evaluation databases ($N = 90$ data points) were combined to identify the most likely distribution of CP (g/kg DM), NDF (g/kg DM), BW (kg) and DMI (kg/d) of goats consuming high-forage-based diets under

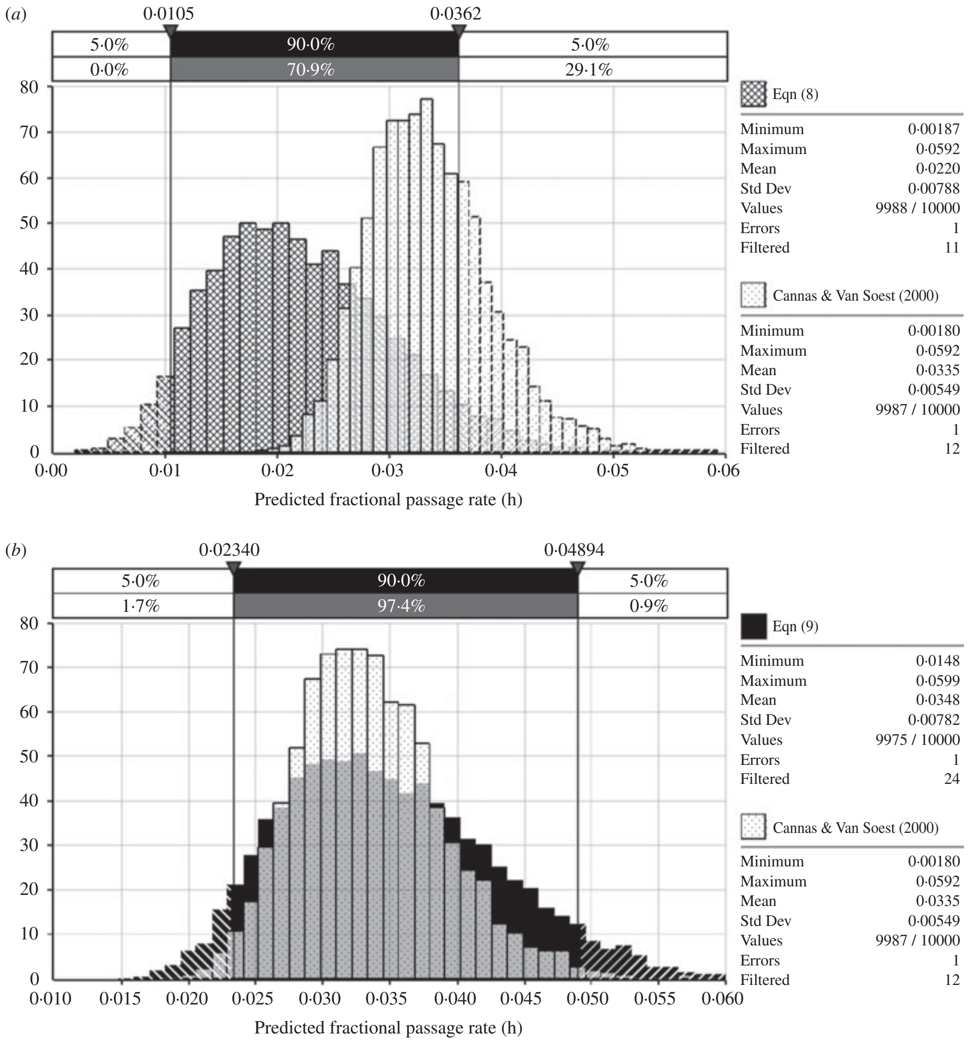

Fig. 4. Histogram of the distributions of predicted fractional passage rate (/h) using Monte Carlo simulation technique of the empirical equation published by Cannas & Van Soest (2000) and the developed empirical equation without (*a*, Eqn (8)) or with (*b*, Eqn (9)) adjustment for the mean bias. Generated with @Risk 5·7.

confinement conditions. The best distribution fit for CP (g/kg DM) was the normal distribution with mean = 132 and s.d. = 41·7; for NDF (g/kg DM) it was the Weibull distribution with alpha and beta parameters equal to 1·40 and 244·3, respectively; for BW (kg) it was the normal distribution with mean = 46 and s.d. = 12·4; and for DMI (kg/d) it was the beta general distribution with alpha1 and alpha2 parameters of 2·58 and 3·56, respectively. The correlation between CP (g/kg DM) and NDF (g/kg DM) was −0·695 and for BW (kg) and DMI (kg/d) it was 0·725. These correlations are in agreement with those obtained from the database of Cannas & Van Soest (2000) of −0·77 and 0·87, respectively.

Figure 3 shows the SRC for the simulated predictions of *kp* using Eqns (3) and (8). Both equations were positively related to DMI (kg/d) and negatively related to BW (kg/d) with varying intensities (different SRC values). Interestingly, however, whereas NDF (g/kg DM) had a negative impact on the *kp* predicted with Eqn (8) (for each s.d. increase in the NDF value, *kp* would decrease by 37% of its s.d.), it had a positive impact on Eqn (3) (for each s.d. increase in the NDF value, *kp* would increase by 69% of its s.d.). The mean and s.d. for the *kp* predicted with Eqn (3) were 0·034 and 0·0056/h and for Eqn (8) they were 0·022 and 0·0079/h, respectively. Therefore, assuming the s.d. of NDF was 155 g/kg DM, an increase in dietary NDF by the s.d. value would increase the *kp* from Eqn (3) by 0·0039/h whereas the *kp* from Eqn (8) would be decreased by 0·0029/h. The inclusion of dietary CP in the prediction equation greatly impacted on the

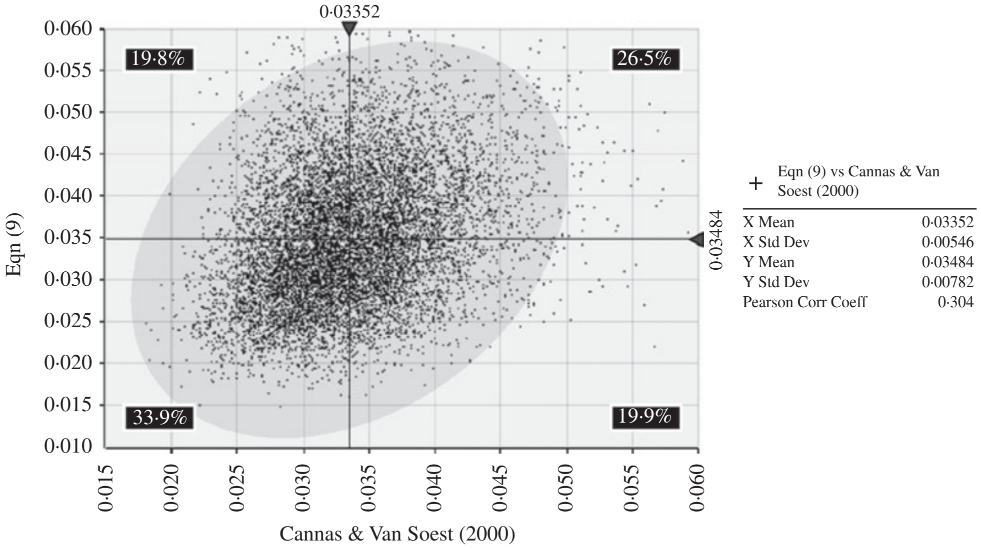

Fig. 5. Scatter plot of predicted fractional passage rate (/h) using Monte Carlo simulation technique of the developed empirical equation (Eqn (9), *Y*-axis) and the equation published by Cannas & Van Soest (2000) (*X*-axis). The shaded area is the confidence ellipse assuming bivariate normal distribution. Generated with @Risk 5·7.

kp predicted by the equation of Cannas & Van Soest (2000), which was based on papers in which time-independent models were probably used, in contrast to the present study. This is likely to be the same for the present evaluation database, as discussed above. Even though DMI affected both empirical equations, it had a greater impact in Eqn (8) than in Eqn (3), in which the SRC was 1·66 times greater (1·13/0·68). A possible explanation for these discrepancies in directions and intensities (SRC values) between these empirical equations is that the fitting technique used in obtaining the *kp* in each case was different. For Eqn (8), the G2G1 model (Vieira *et al.* 2008*a*, *b*) was used, whereas the studies in the database used by Cannas & Van Soest (2000) might have used the G1G1 model, which is probably the same model used by the studies in the present evaluation database.

Figure 4*a* has the distribution of simulated predicted *kp* using Eqns (3) and (8). Equation (8) had a wider distribution ($P<0{\cdot}01$ was 0·0105–0·0362/h) compared with Eqn (3) ($P<0{\cdot}01$ was 0·0253–0·0434/h, not shown). The least value that Eqn (3) is likely to predict in practice is about 0·0217/h (lower $P<0{\cdot}001$) and the greatest *kp* that Eqn (8) is likely to predict is 0·044/h (upper $P<0{\cdot}001$). This suggests that, assuming the *kp* predictions of Eqn (9), it is likely to have an upper limit of *kp* around 0·0569/h (0·044 + 0·0129/h). In fact, the greatest *kp* of the evaluation database was 0·047/h. The partial correlation between the simulated *kp* of Eqns (3) and (9) was low ($r=0{\cdot}32$), indicating that these equations are not compatible even though the mean predicted values are similar (0·0335 and 0·0349/h, respectively, Fig. 5). The distribution of *kp* shown in Fig. 4 does not support the claim that browsing ruminants have faster *kp* than grazing ruminants (Hoffmann 1989), even though most of the ruminants used in scientific experimentations are not free-ranging animals and therefore a direct comparison with grazing ruminants may not be adequate because animals cannot exert their normal behaviour of feed selection.

Figure 4*b* suggests that 0·748 of the simulated *kp* from Eqn (9) are within $P<0{\cdot}01$ of the simulated *kp* from Cannas & Van Soest (2000) or the $P<0{\cdot}01$ of Eqn (9) (0·0244–0·0501/h) contains 0·973 of the simulated *kp* values with Cannas & Van Soest's (2000) equation (not shown). These findings support the hypothesis that the *kp* in goats may behave like cattle and sheep when fed high-forage diets (Clauss *et al.* 2006). The average NDF of the development and evaluation databases was 0·50 g/kg DM, ranging from 0·28 to 0·82 g/kg DM.

Implications

The current results suggest that *kp* of goats is impacted differently by dietary nutrients when compared with grazers such as cattle and sheep. The sensitivity analysis indicated a theoretical upper limit of 0·0569/h for *kp* for goats based on the developed empirical equation. Furthermore, standardization of the prediction of the true *kp* is needed among different laboratories so that improvements in the predictions of *kp* for goats can be achieved. Data with different dietary compositions are needed to further evaluate the equation devised in the present paper.

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