A GENERALIZED MODEL FOR DESCRIBING FIBER DYNAMICS IN THE RUMINANT GASTROINTESTINAL TRACT. 2. ACCOUNTING FOR HETEROGENEOUS POOLS IN THE RUMINORETICULUM

R.A.M. Vieira[1], L.O. Tedeschi[2] and A. Cannas[3]

[1]Laboratório de Zootecnia e Nutrição Animal, Universidade Estadual do Norte Fluminense Darcy Ribeiro, Campos dos Goytacazes, RJ, Brazil, [2]Department of Animal Science, Texas A&M University, College Station
[3]Dipartimento di Scienze Zootecniche, Università di Sassari, 07100 Sassari,Italy

Summary

There is considerable empirical evidence that at least two fiber pools might be encountered in forage-fed ruminants based on the digesta stratification within the ruminoreticulum. A mathematical model is proposed based on a generalized conceptual compartmental model to accommodate the heterogeneous nature of the digesta. Preliminary results agreed with behavioral concepts based on literature data. The model predicted a specific situation when ruminant diets are constrained enough to virtually avoid the formation of the rumen mat or raft. Such situations would include feedlot cattle eating large amounts of concentrates or small ruminants in which body size constrains intake to a selective feeding behavior that excludes coarse fiber from the diet. The simulation results indicated that the amount of digested fibrous carbohydrate and the fiber pool size in the ruminoreticulum are mostly affected.

Introduction

The most accepted paradigm concerning fiber retention and degradation dynamics treats the digesta fiber mass as a single pool. Nonetheless, there is an increasing number of studies suggesting the existence of anomalous observed behaviors that deviate from predictions based on a single pool model (Ellis et al., 1979; 2002; Huhtanen and Kukkonen, 1995; Vieira et al., 2000; Poppi et al., 2001; Lund et al., 2007). The fiber pool is heterogeneous whenever ruminants eat enough fiber to promote a natural stratification of the digesta. This phenomenon is believed to occur in larger species of ruminants such as cattle (Van Soest, 1996; Vieira et al., 2007). Therefore, an alternative model was developed and discussed in this paper to accommodate the digesta stratification that could be resolved either for steady-state or dynamic conditions; basically by treating the fiber mass in the ruminoreticulum as a sequential of two pools of fibrous particles.

Experimental Procedures

The concepts outlined below were used to develop the mathematical model. The bulk of the food matter consumed ($\dot{F}$, fiber intake rate, lb/h) is the fiber content of the j[th] feedstuff ($[NDF]_j$) times its intake rate ($\dot{X}_j$, lb/h):

$$\dot{F} = \sum_j \left([NDF]_j \cdot \dot{X}_j \right)$$
(Eq. 1)

We assume that neutral detergent solubles contribution to fill is negligible. Conceptually, fiber is a nutritional entity that contributes to the bulk of digesta by providing potentially digestible fibrous carbohydrates, and a remnant of the physical and chemical breakdown processes: an ideal nutritional entity called indigestible fibrous matter. Each feedstuff has its characteristic potentially digestible ($f_{d,j}$) and indigestible ($f_{i,j}$) fiber fractions that additively constitute the respective dimensionless potentially digestible (f_d) and indigestible (f_i) components of the diet, but constrained to $f_d + f_i = 1$.

The masticated food particles produced during eating will form the rumen floating mat, which is considered an unmixing pool of particles (RP, lb) that is formed by newly ingested and older, aged particles (such particles are usually larger in size). Older particles are derived from preceding meals that still remain in the RP. A recently ingested particle is not readily available for chemical breakdown via microbial digestion. Hydration, solubilization of digestion inhibitors, and microbial attachment and colonization of feed particles by rumen microbes are events that have to occur prior to digestion itself. These processes transform the unavailable potentially digestible RP entity into a form prone to be digested: an available entity of the same raft particle (RP_d, lb). The ideal indigestible entity of the raft particles (RP_i, lb) is recalcitrant to microbial enzymes in anoxic environments such as the rumen. Henceforth, it could only be broken down by rumination. The RP_d becomes available to be degraded by microbial enzymes after completion of the events above mentioned. The digestion process was kinetically described by the rate k_d, assumed to be exponentially distributed over time.

The RP particles are not eligible to escape the rumen. Instead, a transfer mechanism operates as an ageing chain process counterbalancing the RP buoyancy (resistance to flow) and the propelling forces produced by rumen motility and physical and chemical breakdown (increases flow) of RP. This results in the progressive transfer of matter between the RP to the mixing pool of fluid diluted particles (MP, lb). There is not a clear cut between these two pools and migrating particles (RP $\rightarrow$ MP) are commingled, but the pools were distinctly treated to simplify the model. The resultant of these processes was aggregated in a single rate, k_r, that is assumed to have a gamma distribution over time with parameters $\lambda_r \in \Re^+$ and $N_r \in \Im^+$, with $\bar{k}_r = \hat{\lambda}_r / N_r$.

The MP pool ventral to the RP pool contains particles eligible to leave the rumen. Particles of the MP pool share a remnant of the original potentially digestible entity of RP that remains to be digested at a k_d rate, or leave the rumen along with its indigestible counterpart. The escape process of MP is kinetically described by the rate k_e, that is assumed to be exponentially distributed over time.

Results and Discussion

Transfer mechanisms from the RP to the MP pools are as follows:

$$\dot{RP}_d = f_d \cdot \dot{F} - (k_r + k_d) \cdot RP_d$$

(Eq. 2)

$$\dot{RP}_i = f_i \cdot \dot{F} - k_r \cdot RP_i$$

(Eq. 3)

$$\dot{MP}_d = k_r \cdot RP_d - (k_d + k_e) \cdot MP_d$$

(Eq. 4)

$$\dot{MP}_i = k_r \cdot RP_i - k_e \cdot MP_i$$

(Eq. 5)

$$\dot{D} = k_d \cdot (RP_d + MP_d)$$

(Eq. 6)

Terms not yet defined were $\dot{D}$, the rate of digested amounts (lb/h), and MP_d and MP_i, the potentially digestible and indigestible fiber fractions of the MP pool. The dot above variables represents a differential with respect to time. The visual scheme of Eq. 2 to 6 is shown in Figure 1 using the stock and flow diagram of Vensim® (Ventana Systems Inc, Harvard, MA 01451) and Figure 2 depicts a simulation using the dynamic model.

Under the assumption of Steady-State, however, the following conditions are expected:

$\dot{RP}_d = \dot{RP}_i = \dot{MP}_d = \dot{MP}_i = 0$, $\dot{F} \cong \bar{F}$ (constant intake rate, $\dot{X} \cong \bar{X}$), $E(k_r) = \bar{k}_r = \dfrac{\hat{\lambda}_r}{N_r}$, $E(k_e) = k_e$, $E(k_d) = k_d$, $E(f_d) = f_d$, and $E(f_i) = f_i$. Therefore, the steady-state solution of the model allows solving for the digestible amounts and pool sizes:

$$\text{DIGESTIBILITY} = \frac{\dot{D}}{f_d \cdot \bar{F}} = \frac{k_d}{k_d + \bar{k}_r} \cdot \left(1 + \frac{\bar{k}_r}{k_d + k_e}\right)$$

(Eq. 7)

The dimensionless digestibility (Eq. 7) resumes to the single pool solution whenever conditions leading to the raft elimination operates in practice. Mathematically, mechanisms responsible by raft formation occurs so fast that $E(k_r) \rightarrow \infty$, and Eq. 7 becomes:

$$\text{DIGESTIBILITY} = \frac{k_d}{k_d + k_e}$$

(Eq. 80.21")

Here, k_e has the same meaning of the well known k_p for the single pool model.

The maximum fiber holding capacity of the ruminoreticulum (RR) scales isometrically (W to power one) with respect to size (Van Soest, 1996; Vieira and Tedeschi, 2007). The ruminal fiber mass (RFM, Eq. 9) provides a mean to estimate the amount of fiber that a given diet fills the RR.

$$RFM = \lim_{t \to \infty} (RP_d + RP_i + MP_d + MP_i) = \bar{F} \cdot \left[f_d \frac{k_d + k_e + \bar{k}_r}{(k_d + \bar{k}_r) \cdot (k_d + k_e)} + f_i \left(\frac{1}{\bar{k}_r} + \frac{1}{k_e} \right) \right]$$

(Eq. 9)

If a given RFM predicted for the formulated diet is greater than the fiber holding capacity of the ruminoreticulum (FHCRR) determined for a given animal in a specified physiological condition, two constraints should be accommodated in current feeding systems for diet formulation and optimization:

$$\sum_j \left\{ [\mathrm{NDF}]_j \cdot \bar{X}_j \cdot \left[f_{d,j} \frac{k_{d,j} + k_{e,j} + \bar{k}_{r,j}}{(k_{d,j} + \bar{k}_{r,j}) \cdot (k_{d,j} + k_{e,j})} + f_{i,j} \left(\frac{1}{\bar{k}_{r,j}} + \frac{1}{k_{e,j}} \right) \right] \right\} \leq \text{Max FHCRR}$$

(Eq. 10)

$$\frac{\bar{F}}{\sum_j \bar{X}_j} \geq \text{Min DIET}[\mathrm{NDF}]$$

(Eq. 11)

Subscript j refers to the j[th] feedstuff, and Max is the maximum FHCRR. In Eq. 11, the minimum requirement of fiber is Min DIET [NDF] and dry matter intake is

$\sum_j \bar{X}_j$.

Meanwhile, k_r and k_e could be estimated by fitting compartmental models to time excretion profiles of particulate markers in the feces. We assumed that larger retention pools are either within the rumen, and that caudal segments of the gastrointestinal tract promotes a random walk flow of the digesta with a mean retention time equals to τ (Ellis et al., 1994).

$$C(t) = C(0)\left\{ \delta^{N_r} \exp[-k_e(t-\tau)] - \exp[-\lambda_r(t-\tau)] \sum_{i=1}^{N_r} \delta^i [\lambda_r(t-\tau)]^{N_r - i} / (N_r - i)! \right\}$$

(Eq. 12)

Where C(t) and C(0) are the respective marker concentrations in the feces and in the unmixing compartment, $\delta = \lambda_r / (\lambda_r + k_e)$ and λ_r, N_r and k_e were as specified previously.

Passage estimates could be obtained by administration of marked feedstuffs to animals and inferences should not extrapolate the physiological stage of the animal, e.g. during the course of lactation, growth, or late pregnancy.

The k_d seems to be the same rate as in the single pool model. However, fractional degradation rates have different estimates in practice and the reader should be aware of that. We discussed methods to estimate rates of degradation within the proposed model in a companion report.

Blaxter et al. (1956) derived mathematical relationships of the passage of food residues through the gastrointestinal tract of sheep. They ascribed first-order kinetic rates respectively to the emptying of the rumen and the abomasum, although they were well aware about inexistence of experimental proof regarding rate association to a specific segment of the tract at that time. Grovum and Williams (1973) studying the flow of markers through segments of the sheep digestive tract concluded that the first-order rates (analogous to $\lambda_r/1$, i.e. $N_r = 1$, and k_e) should be ascribed to the rumen (the lower rate, usually k_e), and to the cecum and proximal colon (the faster rate, usually $\lambda_r/1$).

Theoretical Simulation

Let us assume that a late spring pasture with a non-limiting crude protein content (65% NDF with a k_d = 4%/h) was grazed by a 990 lb cow. A hypothetical sample of the grazed pasture was taken from an esophageal cannulated steer and the extrusa marked with chromium mordant ($Cr_2O_7^{-2}$) was fed to the cow and yielded estimates for passage parameters of 20%/h for λ_r and 3%/h for k_e. Let us assume that N_r = 1. In such situation, the digestibility amounted to 0.54 or 54%, according to Eq. 8 (single pool model).

The k_d estimate used in the proposed model is quite different from the single pool model, although they share the same biological meaning. The same hypothetical *in vitro* kinetic analysis used to obtain the single pool k_d estimate was used and yielded a k_d = 5%/h to be used in the generalized model. This resulted in a digestibility estimate of 70%, according to Eq. 7. Even if the estimate of 5%/h is used in Eq. 8, the digestibility achieved would be 63%, still lower than the integrated kinetic flow estimates of the generalized model (Eq. 7).

If only cattle data of Cannas et al. (2003) were used, assuming that FHCRR scales to W^1, the hypothetical cow could hold 0.010 lb per lb of W or 9.9 lb of NDF. In addition, her NDF intake scaled to the same power was expected to be 0.010 lb per lb of W per day or 9.9 lb/d. Additionally, if we assumed the NDF of our pasture had f_d and f_i values of 0.7 and 0.3, it will fill the cow's rumen with 9 lb or .009 lb per lb of live weight according to Eq. 10. This value is lower than 0.010 lb/lb of W and intake is not expected to be limited (Figure 3a) unless other constraints force an increase in intake such as metabolic demand for energy of lactating cows. Similar calculations performed within the single pool solutions would render a 0.008 lb/lb of W, which means one fill lower than that estimated with the proposed model. The lower flow estimates are (↓ k_r and ↓ k_e) the greater will be the filling effect of the diet (Figure 3c) and this situation probably occurs with less digestible forages (↓ k_d and higher ↑ f_i, Figures 3b and 3d).

Implications

A generalized model based on the natural stratification of the ruminoreticular digesta was developed and preliminary results are in concordance with literature concepts. Nevertheless, proper evaluation methods should be performed to verify its broader applicability.

Literature Cited

Blaxter, K.L., Graham, McC., Wainman, F.W. 1956. Some observations on the digestibility of food by sheep, and on related problems. Brit. J. Nutr., 10:69-91.

Cannas, A., Van Soest, P.J., Pell, A.N. 2003. Use of animal and dietary information to predict rumen turnover. Anim. Feed Sci. and Technol., 106:95-117.

Ellis, W.C., Matis, J.H., Lascano, C. 1979. Quantitating ruminal turnover. Fed. Proc., 38:2702-2706.

Ellis, W.C., Wylie, M.J., Matis, J.H. 2002. Validity of specifically applied rare earth elements and compartmental models for estimating flux of undigested plant tissue residues through the gastrointestinal tract of ruminants. J. Anim. Sci., 80(10):2753-2758.

Grovum, W.L., Williams, V.J. 1973. Rate of passage of digesta in sheep. 4. Passage of marker through the alimentary tract and the biological relevance of rate-constants derived from the changes in concentration of marker in faeces. Brit. J. Nutr., 30:313-329.

Huhtanen, P., Kukkonen, U. 1995. Comparison of methods, markers, sampling sites and models for estimating digesta passage kinetics in cattle fed at two levels of intake. Anim. Feed Sci. Technol., 52:141-158.

Lund, P., Weisbjerg, M.R., Hvelplund, T. 2007. Digestible NDF is selectively retained in the rumen of dairy cows compared to indigestible NDF. Anim. Feed Sci. Technol., 134:1-17.

Pond, D.P., Ellis, W.C., Matis, J.H., Ferreiro, H.M., Sutton, J.D. 1988 Compartmental models for estimating attributes of digesta flow in cattle. Brit. J. Nutr., 60:571-595.

Poppi, D.P., Ellis, W.C., Matis, J.H. et al. Marker concentration patterns of labeled leaf and stem particles in the rumen of grazing bermuda grass (*Cynodon dactylon*) analysed by reference to a raft model. Brit. J. Nutr., 85:553-563, 2001.

Van Soest, P.J. 1996. Allometry and ecology of feeding behavior and digestive capacity in herbivores: a review. Zoo Biol., 15:455-479.

Vieira, R.A.M., Pereira, J.C., Malafaia, P.A.M., Queiroz, A.C., Jordao, C.P., Goncalves, A.L. 2000. Simulation of the nutrient dynamics in the gastrointestinal tract: application and validation of a mathematical model for grazing cattle. Rev. Bras. Zoot. (Braz. J. Anim. Sci.), 29(3):898-909 (Portuguese).

Vieira, R.A.M., Tedeschi, L.O., Cannas, A. 2007. A generalized model for describing fiber dynamics in the ruminant gastrointestinal tract. 1. The heterogeneity of the pool of fiber particles in the ruminoreticulum. Beef Cattle Res. Texas, submitted.

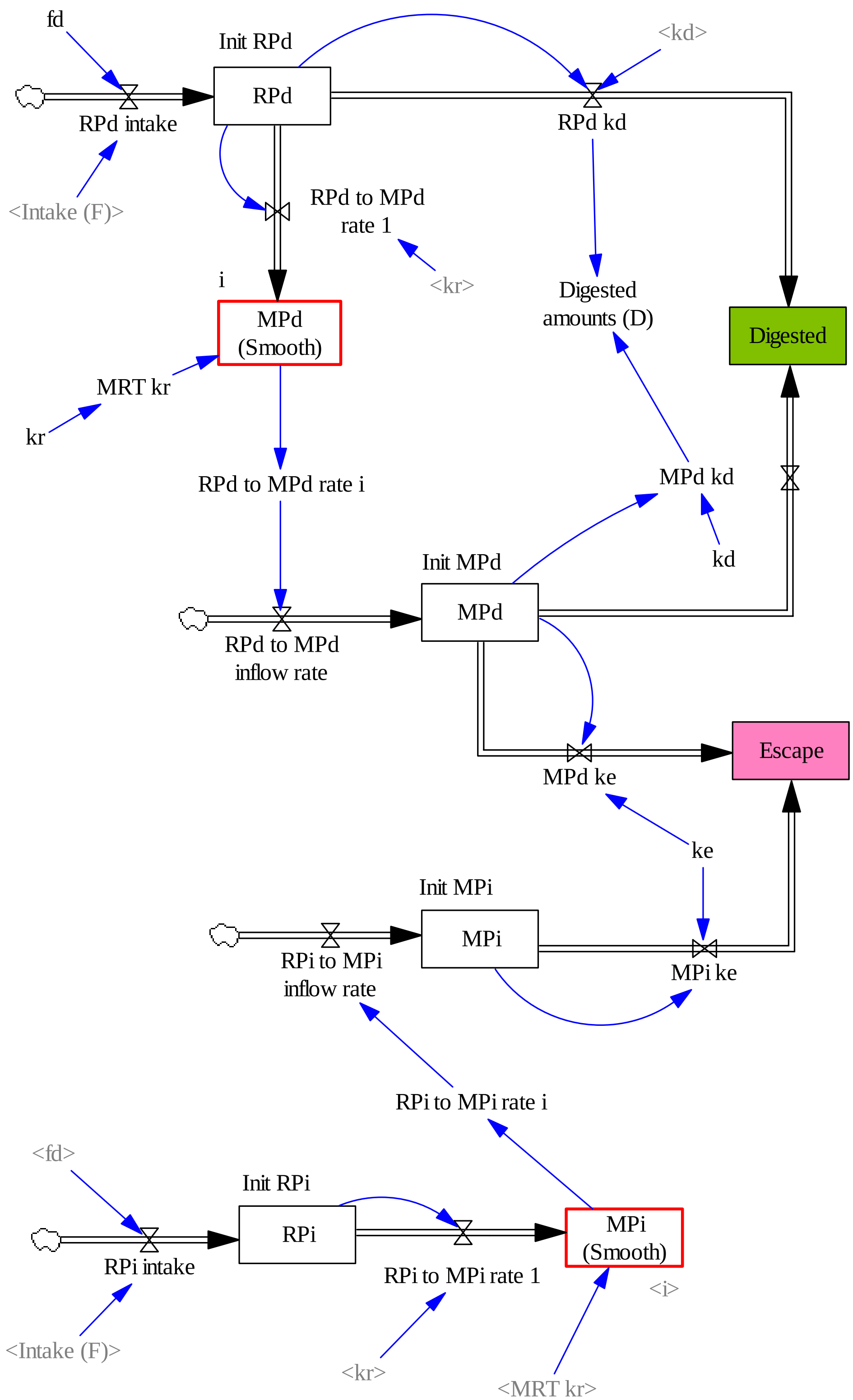

Figure 1. Schematic representation of the dynamic model to predict flow of fiber particles from the rumen using stock and flow diagram.

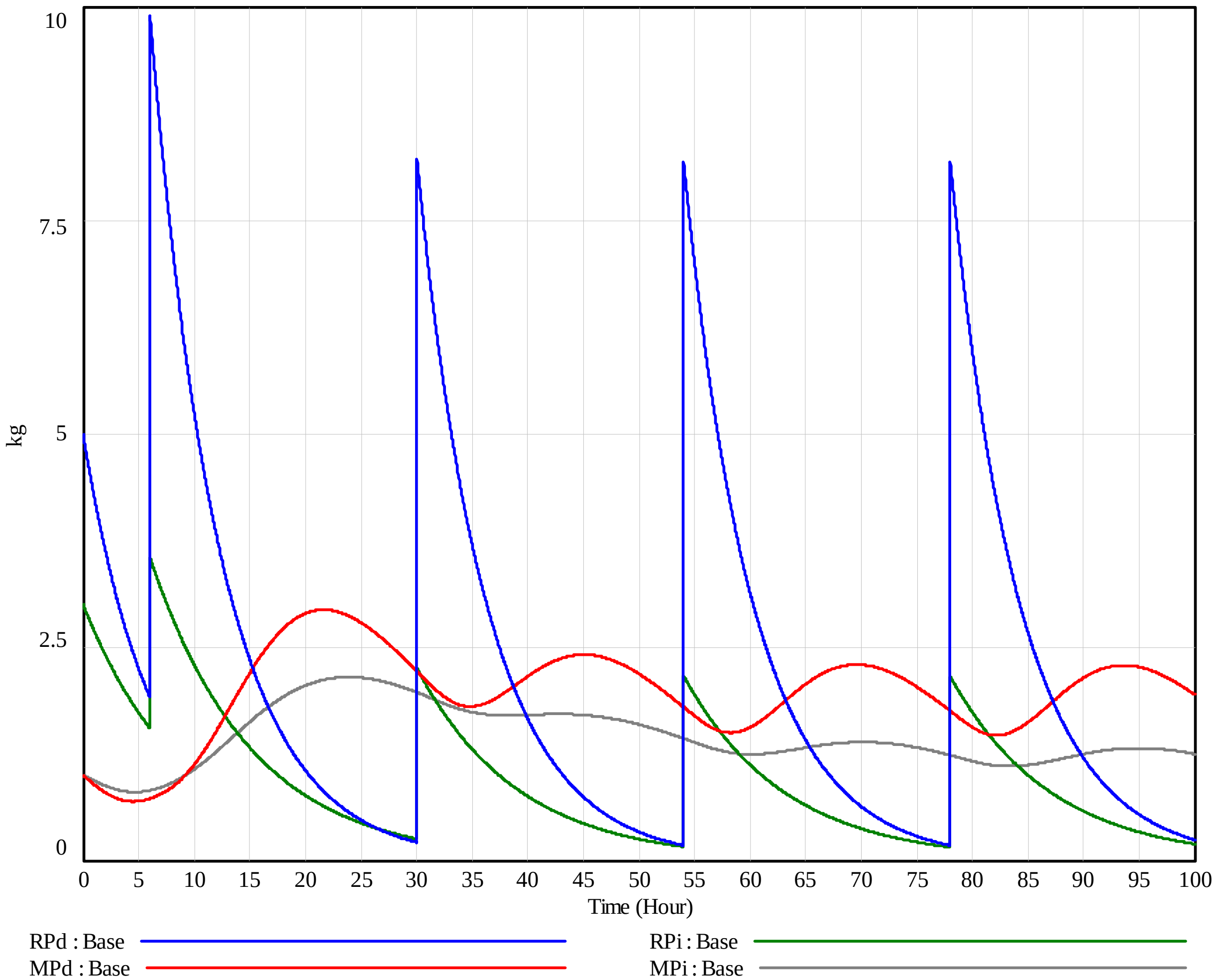

Figure 2. Simulation using the dynamic model assuming intake of 10 kg/d (22 lb/d) of fiber, initial RP_d, RP_i, MP_d, and MP_i of 5 (11 lb), 3 (6.6 lb), 1 (2.2 lb), and 1 kg (2.2 lb), respectively, k_d of 5%/h, k_r of 11%/h, k_e of 7%/h, and four multi-compartments (i = 3 in the MPd smooth stock). The average digested amount ($\dot{D}$) was 0.21 kg/h (0.46 lb/h) and varied from 0.096 (0.21 lb/h) to 0.53 kg/d (1.17 lb/h).

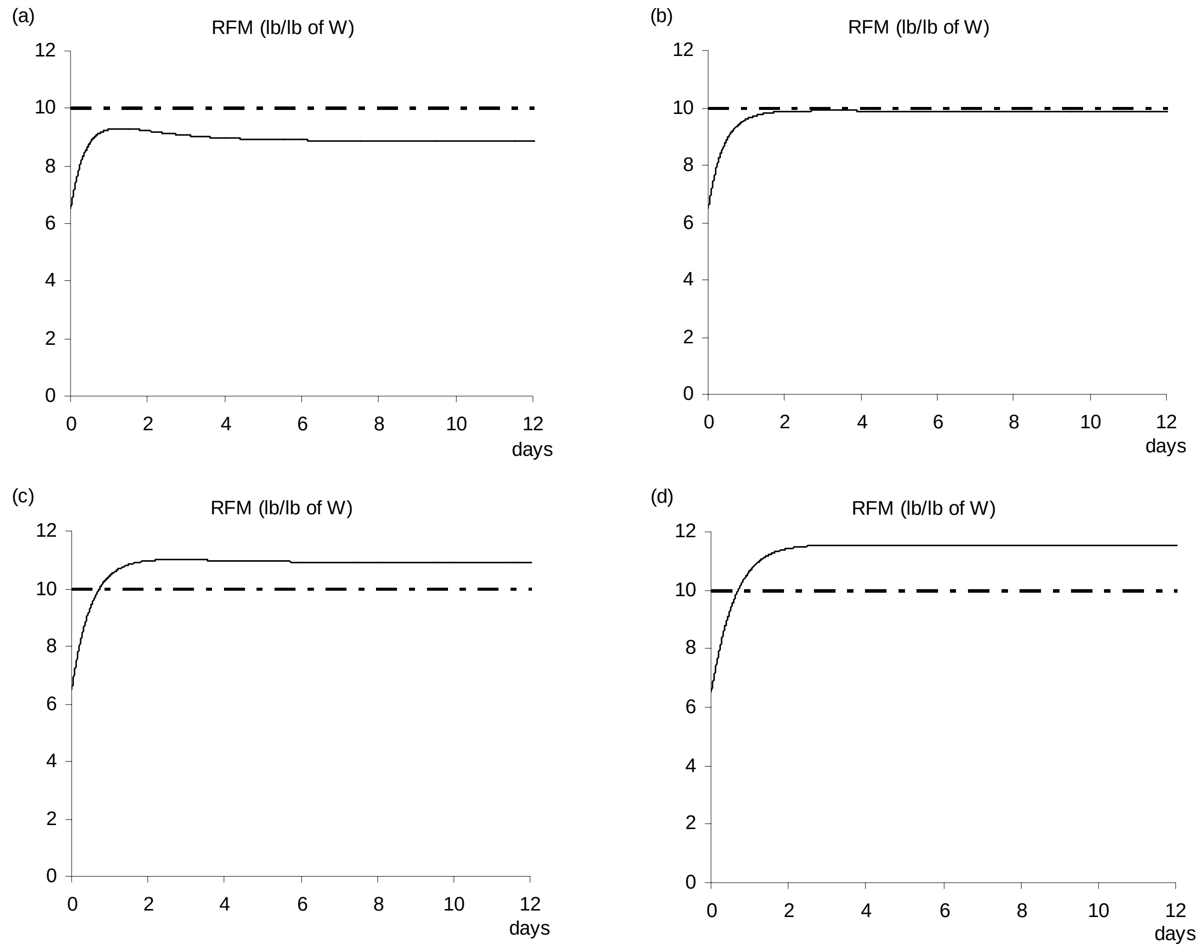

Figure 3. Simulated behaviors of the ruminoreticular fiber mass (RFM). The solid curves represent RFM (lb/lb of W) and the dashed lines represent the fiber holding capacity of the ruminoreticulum (FHCRR) from our hypothetical cow. Plots were obtained according to the following parameters: in (a), fd = 0.7, fi = 0.3, λr = 0.2, ke = 0.03 and kd = 0.05; in (b), only fd = 0.6 and fi = 0.4 were different from (a); in (c), only λr = 0.15 and kd = 0.04 were different from (a); and in (d), fd = 0.6, fi = 0.4, λr = 0.15 and kd = 0.04 were different from (a). Note that the pasture consumed could not fill the FHCRR in the cases (a) and (b), but the pasture in the cases (c) and (d) could. A limitation on intake is thus expected according to Eq. 10.