Chemical Engineering Journal 166 (2011) 315–323

Contents lists available at ScienceDirect

Chemical Engineering Journal

journal homepage: www.elsevier.com/locate/cej

Modelling the passage of food through an animal stomach: A chemical reactor engineering approach

Rodney Van Bentum [1], Mark Ian Nelson *

School of Mathematics and Applied Statistics, University of Wollongong, Wollongong, NSW 2522, Australia

ARTICLE INFO

Article history:
Received 22 January 2010
Received in revised form 7 October 2010
Accepted 8 October 2010

Keywords:
Continuous stir tank reactor
Cumulative excretion
Digesta
Gastrointestinal tract
Modelling
Non-ideal reactors
Ruminant
Segregated reactor model
Stagnant

ABSTRACT

Mathematical models have been extensively used in veterinary science to analyse data collected from experiments measuring the flow of digesta through the gastrointestinal tract (GIT) of ruminants. In this paper a classic two compartment digesta flow model is reformulated into a two compartment CSTR (continuous stir tank reactor) model. A segregated reactor model is then obtained by incorporating 'non-mixing' stagnant regions into the ideal CSTR model. The ability to incorporate non-ideal mixing into the model allows a more accurate representation of the conditions within the GIT.

In analyzing this model our main focus is on the cumulative excretion curve, as this is used to estimate the mean residence time through the GIT. The mean residence time is an important indicator of animal nutrition, directly affecting the feeding strategy of an animal. The effects of stagnant regions in a 'two stomach' GIT model are investigated by comparing the cumulative excretion curve with that obtained from an equivalent ideal 'two stomach' GIT model. This comparison characterises a trend that non-ideal mixing delays the excretion of waste from the GIT.

The effect upon the cumulative excretion curve of small changes in parameter values is then investigated. Small changes in the size of the first stomach, and the division of the initial digesta ingested between the 'well-mixed' and stagnant regions of the first stomach, are found to substantially effects the cumulative excretion of digesta from the GIT of a ruminant animal. This investigation is a good example of the applications of chemical engineering to a problem outside the traditional definition of the discipline.

1. Introduction

In this paper the principles of chemical engineering are applied to a problem in veterinary science. The problem is concerned with measuring the flow of digesta through the gastrointestinal tract (GIT), using a food tracer, to estimate the mean residence time (MRT) of food substances. The MRT impacts both the rate and proportion of nutrient absorption in an animal [1]. Furthermore the extent to which dietary components are fermented in the rumen is a function of both the residence time and the rate of fermentation of digesta in the rumen [2]. Traditionally digesta flow kinetics have been analysed using the two compartment model that is discussed in Section 1.1.

The use of mathematical models to analyze and fit data collected from the flow of nutrients through the gastrointestinal tract is well established [3]. Most of the articles relating to the digestive system of animals focus on modelling the flow of digesta through the gastrointestinal tract and its affect on animal nutrition and physiology [1,2,4–6]. Classic models assume that the digesta contained within the gastrointestinal tract is either a homogeneous mixture [4,5] or a mixture of large and small particle compartments following the digestive process of the rumen [7–9]. There have been complaints about the use of ideal mixing reactor models to simulate the flow of digesta through the GIT [2,10,11]. In [11, page 109] the assumptions of idealized reactor conditions, i.e. constant volume and instantaneous mixing of digesta within the reactor system, are identified as a weakness of deterministic models.

In veterinary science, methods have been developed that attempt to deal with the problem of non-ideal reactor conditions. The classic digesta flow models have been adapted to incorporate both the physical properties of digesta and the physicochemical properties of the GIT [7–9,12,13]. These approaches include a multicompartmental model in which each successive compartment contains particles of a smaller size. In general, food substances that have been largely digested form a solution of smaller particles that possess buoyant properties, and tend to flow more readily through the gastrointestinal tract than sedimentary particles, i.e.

* Corresponding author. Tel.: +61 2 4221 4400; fax: +61 2 4221 4845.
E-mail addresses: rodvb972@gmail.com.au (R. Van Bentum), nelsonm@member.ams.org, mnelson@uow.edu.au (M.I. Nelson).
[1] Tel.: +61 2 4862 1035.
[2] In the nomenclature a subscript i refers to the ith compartment of the reactor.

1385-8947/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.cej.2010.10.017

Nomenclature

M_0	the initial mass of non-digestable food in the GIT
V_i	volume of 'stomach'
c_i	concentration of digesta
$c_i(0)$	concentration of digesta a time $t=0$
c_{ia}	concentration of digesta in the well-mixed region
c_{ib}	concentration of digesta in the stagnant region
k_i	rate constant for digesta flow
$m_i(t)$	mass of digesta at time t
m_{ideal}	the mass of digesta deposited on the ground by an 'ideal' animal
m^*_{ideal}	the dimensionless mass of digesta deposited on the ground by an 'ideal' animal
$m_{\text{non-ideal}}$	the mass of digesta deposited on the ground by a 'non-ideal' animal
$m^*_{\text{non-ideal}}$	the dimensionless mass of digesta deposited on the ground by a 'non-ideal' animal
q	flowrate of food substance through the stomachs and digestive tracts
q_{ia}	the flow rate between the well-mixed compartment and the stagnant region
t	time
ε	the relative proportion of stomach volume divided between the well-mixed compartment and the stagnant region. $0<\varepsilon_i<1$
τ_d	time delay within the tubular compartment
τ_i	mean residence time

undigested food. Such models attempt to simulate the physical process by which complex food substances are broken down in stages within the various compartments of the GIT, into smaller molecules for absorption in the intestines. An overview of these approaches are provided by [14].

In this paper ideas from chemical reactor engineering are used to introduce stagnant regions into the classic compartment model. The effect of these stagnant regions upon the cumulative excretion of waste from the GIT is then investigated by comparing results from the incomplete mixing model against those produced by an equivalent well-mixed, i.e. 'classic', CSTR model. The aim of this comparison is to determine what affect the introduction of non-ideal mixing regions has on the cumulative excretion of waste from the GIT. Before incomplete mixing can be incorporated into the classic model it must be reformulated into the form of a CSTR model, this is discussed in Section 1.2. The extension of the reformulated model with incomplete mixing is given in Section 2.

The term gastrointestinal tract, or GIT, refers to the alimentary canal in animals that runs from the mouth through to the anus. It is involved with the absorption and the digestion of food into fuel molecules. In ruminant animals the gastrointestinal tract consists of a four-chambered stomach and an additional caecum to break down cellulose into fuel molecules [15]. It is important to note that the term "compartment or stomach", used throughout this article, may represent any specific organ in the GIT with a relatively large mean residence time. The incorporation of non-ideal mixing into the model allows a more accurate representation of the reactor conditions within the GIT.

1.1. Classic model

In veterinary science, classic models represent the GIT of animals as a series of compartments. The application of multicompartmental reactor models to model the movement of digesta through the gastrointestinal tract of ruminant animals was proposed by Blaxter et al. (1956) [4]. Blaxter et al. suggested that the ruminant gut (a ruminant is a mammal which digests its food in two steps) consists of two well-mixed compartments and a tubular compartment. The tubular compartment acts to delay the deposition of digesta by the animal. The model proposed by Blaxter et al. (1956) [4] is given by

$$\begin{aligned}\frac{dm_1(t)}{dt} &= -k_1 m_1(t),\\ \frac{dm_2(t)}{dt} &= k_1 m_1(t) - k_2 m_2(t),\\ \frac{dm_3(t)}{dt} &= k_2 m_2(t-\tau_d),\\ m_i(0) &= m_{i,0}.\end{aligned} \tag{1}$$

The rate of change in mass within a compartment is equal to the flow of mass into the compartment from the previous compartment minus the flow of mass out of the compartment. The third equation represents the rate of deposition of digesta from the GIT of the animal. It is assumed that no absorption of digesta takes place in any compartment and that the contents of each compartment are well-mixed. The rate constants, k_1 and k_2, are inversely proportional to the mean retention time in the first and second compartment respectively. Although the assigning of rate constants to specific ruminant organs has been debated [5], it is generally accepted that the first compartment represents the rumen stomach and the second compartment denotes the caecum stomach of ruminant animals [4,5,16]. As noted in Section 1, the use of a two compartment model does not necessarily mean that the animal has two stomachs.

In a typical experiment an ingestible external marker is added to a food source and the mass of the marker excreted in the faeces is measured over time. The cumulative excretion of the trace marker can be used to estimate the mean residence time of digesta through the GIT of animals. The rate of passage of food through the gastrointestinal tract significantly impacts the level of nutrition and feeding strategy of an animal [1]. The ability to analyse data using mathematical models has allowed for a greater understanding of the digestive process, enabling insights into the nutrition and feeding strategies of animals. Studies have shown that the retention time of digesta within the gastrointestinal tract has a substantial effect on digestion and uptake of nutrients in herbivores [17–19]. Thereby greater retention of food in the digestive tract results in a more complete extraction of energy and nutrients [20], but longer retention times (slower rates of digesta passage) also inhibit food intake [21] as the digestive tract has limited capacity.

1.2. Reformulation of the model

In this section the classic model devised by Blaxter et al. [4], system (1), is rewritten as an equivalent CSTR model so as to allow incomplete mixing to be modelled in Section 2. This reformulation, devised by Nelson et al. [22], describes the concentration of digesta rather than the mass of digesta in each compartment. The model equation becomes,

$$\begin{aligned}V_1\frac{dc_1}{dt} &= -qc_1,\\ V_2\frac{dc_2}{dt} &= qc_1 - qc_2,\\ c_1(0) &= 1, \quad c_2(0)=0.\end{aligned} \tag{2}$$

The initial concentration of digesta in the first stomach has been scaled to one whereas the initial concentration of digesta in the second stomach is zero, i.e. at time $t=0$ there is no marker deposited in the second stomach. The reason for investigating model (2) rather than model (1), is that it is straightforward to include non-ideal mixing into system (2). For the purpose of this study the tubular compartment equation is dropped from system (1). In general the time delay effect just acts to shift the solution.

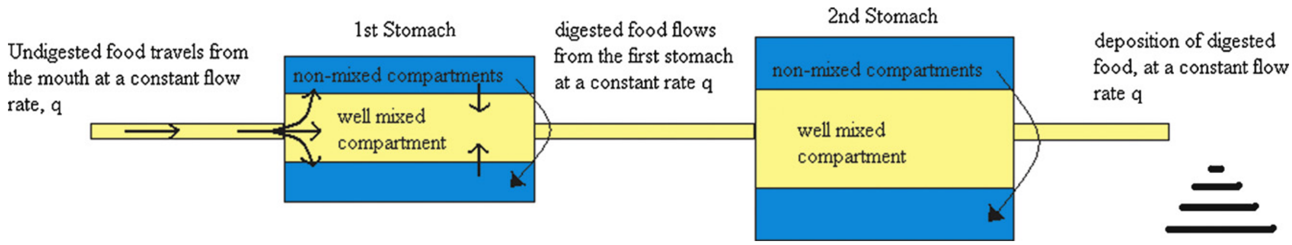

Fig. 1. The two stomach model with stagnant regions.

The problem of non-ideal mixing is well known in chemical engineering where combinations or modifications of ideal reactors can be used to represent reactors that are not perfectly mixed [23]. Segregated reactor models have been used to analyse incompletely mixed continuous-flow fermenters [24]. In such a model the reactor is divided into two regions: a well-mixed region, and a stagnant region (Fig. 6.20, pg 199 [24]).

In this article the classic veterinary science model is extended by introducing stagnant compartments into the ideal multicompartmental model. The stagnant compartments act as flow 'dead zones'; contents held within these compartments do not readily flow out of the reactor system. The introduction of stagnant regions produces a model that more accurately simulates the movement of digesta through the gastrointestinal system of ruminant animals [25]. To determine the effect of non-ideal mixing upon the cumulative excretion of waste from a ruminant animal the results from the 'two-stomach' incomplete mixing model are compared with those from an equivalent well-mixed 'two-stomach' model. The effect of changes in parameter values upon the cumulative excretion of waste from the GIT is also investigated.

2. The model with stagnant regions

The classic model for the passage of digesta through the gastrointestinal tract assumes that there are two stomachs of constant volume with perfect mixing in each compartment. Incomplete mixing along the gastrointestinal tract is simulated by a system of reactors with non-ideal mixing through the incorporation of internal compartments into system (2). A schematic of the model is shown in Fig. 1.

The model digestive tract is comprised of a system of cylindrical compartments joined in a particular arrangement. In Fig. 1, the stagnant region forms a cylindrical shell of non-flowing digesta around the central well-mixed compartment. At the boundary of these compartments, digesta is exchanged between the well-mixed compartment and stagnant region.

The model equations are,

First 'Stomach'

$$(1-\varepsilon_1)V_1\frac{dc_{1a}}{dt} = -qc_{1a} + q_{1a}(c_{1b} - c_{1a}), \tag{3}$$

$$\varepsilon_1 V_1\frac{dc_{1b}}{dt} = q_{1a}(c_{1a} - c_{1b}), \tag{4}$$

Second 'Stomach'

$$(1-\varepsilon_2)V_2\frac{dc_{2a}}{dt} = qc_{1a} - qc_{2a} + q_{2a}(c_{2b} - c_{2a}), \tag{5}$$

$$\varepsilon_2 V_2\frac{dc_{2b}}{dt} = q_{2a}(c_{2a} - c_{2b}), \tag{6}$$

Initial Conditions

$$c_{1a}(0) = \frac{\delta M_0}{(1-\varepsilon_1)V_1}, \quad c_{1b}(0) = \frac{(1-\delta)M_0}{\varepsilon_1 V_1},$$
$$c_{2a}(0) = 0, \quad c_{2b}(0) = 0,$$

The case $\varepsilon_1 = \varepsilon_2 = 0$ corresponds to a cascade of ideal reactors.

It is assumed that initially all the contents of the GIT are contained within the compartments of the first stomach. The terms δM_0 and $(1-\delta)M_0$ denote the mass of the non-digestable food initially in the well-mixed and stagnant compartments respectively.

3. Solution to model equations

The two stomach model forms a set of four linear differential equations that can be solved through the rearrangement of the time-dependant variables.

3.1. The first reactor solution

An equation for $c_{1b}(t)$ in terms of the time dependant variable $c_{1a}(t)$ is obtained by rearranging Eq. (3)

$$c_{1b}(t) = \frac{(1-\varepsilon_1)V_1}{q_{1a}}\frac{dc_{1a}}{dt} + \frac{q+q_{1a}}{q_{1a}}c_{1a}. \tag{7}$$

A homogeneous linear second order ODE, with constant coefficients, is obtained by substituting relationship (7) into Eq. (4) $c_{1a}(t)$,

$$\frac{d^2c_{1a}}{dt^2} + \left(\frac{q+q_{1a}}{(1-\varepsilon_1)V_1} + \frac{q_{1a}}{\varepsilon_1 V_1}\right)\frac{dc_{1a}}{dt} + \frac{qq_{1a}}{\varepsilon_1(1-\varepsilon_1)V_1^2}c_{1a} = 0. \tag{8}$$

The solution in the well-mixed compartment of the first stomach, c_{1a}, is given by

$$c_{1a}(t) = Ae^{u_1 t} + Be^{u_2 t}, \tag{9}$$

where A and B are the constants of integration and the parameters u_1 and u_2 are given by

$$u_1 = -\frac{a_1}{2} + \frac{\sqrt{a_1^2 - b_1}}{2}, \tag{10}$$

$$u_2 = -\frac{a_1}{2} - \frac{\sqrt{a_1^2 - b_1}}{2}. \tag{11}$$

The parameters a_1 and b_1 are

$$a_1 = \frac{q+q_{1a}}{(1-\varepsilon_1)V_1} + \frac{q_{1a}}{\varepsilon_1 V_1},$$
$$b_1 = \frac{4qq_{1a}}{\varepsilon_1(1-\varepsilon_1)V_1^2}.$$

The discriminant, $\sqrt{a_1^2 - b_1}$, is always greater than zero. Thus u_1 and u_2, are real and negative.

The solution to the concentration of digesta in the stagnant region of the first stomach, $c_{1b}(t)$ is given by

$$c_{1b}(t) = \frac{Ae^{u_1 t}((1-\varepsilon_1)V_1u_1 + q + q_{1a})}{q_{1a}} + \frac{Be^{u_2 t}((1-\varepsilon_1)V_1u_2 + q + q_{1a})}{q_{1a}}. \tag{12}$$

Using the initial conditions the constants of integration are found to be,

$$A = \frac{M_0}{(1-\varepsilon_1)V_1(u_1-u_2)}\left(\frac{q_{1a}}{\varepsilon_1 V_1} + \delta u_1\right), \tag{13}$$

$$B = \frac{M_0}{(1-\varepsilon_1)V_1(u_1-u_2)}\left(\frac{q_{1a}}{\varepsilon_1 V_1} - \delta u_2\right). \tag{14}$$

This completes the solution in both compartments of the first stomach.

3.2. The second reactor solution

The following expression for $c_{2b}(t)$ is obtained by rearranging Eq. (5)

$$c_{2b}(t) = \frac{(1-\varepsilon_2)V_2}{q_{2a}}\frac{dc_{2a}}{dt} - \frac{qc_{1a}}{q_{2a}} + \frac{q+q_{2a}}{q_{2a}}c_{2a}. \tag{15}$$

A non-homogeneous linear second order ODE is obtained by substituting this expression into Eq. (6),

$$\frac{d^2c_{2a}}{dt} + \left(\frac{q+q_{1a}}{(1-\varepsilon_2)V_2} + \frac{q_{2a}}{\varepsilon_2 V_2}\right)\frac{dc_{2a}}{dt} + \frac{qq_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}c_{2a} = \frac{q}{(1-\varepsilon_2)V_2}\frac{dc_{1a}}{dt} + \frac{qq_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}c_{1a}. \tag{16}$$

The complementary solution, $c_{2ac}(t)$, is given by

$$c_{2ac}(t) = Xe^{w_1 t} + Ye^{w_2 t},$$

where X and Y are constants of integration and the parameters w_1 and w_2 are given by

$$w_1 = -\frac{a_2}{2} + \frac{\sqrt{a_2^2 - b_2}}{2},$$
$$w_2 = -\frac{a_2}{2} - \frac{\sqrt{a_2^2 - b_2}}{2}.$$

The parameters a_1 and b_2, are

$$a_2 = \frac{q+q_{2a}}{(1-\varepsilon_2)V_2} + \frac{q_{2a}}{\varepsilon_2 V_2},$$
$$b_2 = \frac{4qq_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}.$$

The discriminant, $\sqrt{a_2^2 - b_2}$, is always greater than zero. Thus w_1 and w_2, are real and negative.

The particular solution, $c_{2ap}(t)$, is given by

$$c_{2ap} = \frac{Aq}{(1-\varepsilon_2)V_2}\left(\frac{1}{u_1^2 + a_2u_1 + b_2/4}\right)\left(u_1 + \frac{q_{2a}}{\varepsilon_2 V_2}\right)e^{u_1 t} + \frac{Bq}{(1-\varepsilon_2)V_2}\left(\frac{1}{u_2^2 + a_2u_2 + b_2/4}\right)\left(u_2 + \frac{q_{2a}}{\varepsilon_2 V_2}\right)e^{u_2 t}.$$

Thus the solution for the well-mixed compartment of the second stomach, $c_{2a}(t)$, is

$$c_{2a}(t) = Xe^{w_1 t} + Ye^{w_2 t} + \frac{Aq}{(1-\varepsilon_2)V_2}\left(\frac{1}{u_1^2 + a_2u_1 + b_2/4}\right)\left(u_1 + \frac{q_{2a}}{\varepsilon_2 V_2}\right)e^{u_1 t} + \frac{Bq}{(1-\varepsilon_2)V_2}\left(\frac{1}{u_2^2 + a_2u_2 + b_2/4}\right)\left(u_2 + \frac{q_{2a}}{\varepsilon_2 V_2}\right)e^{u_2 t}. \tag{17}$$

Substituting the solution for $c_{2a}(t)$ (Eq. (17), into Eq. (15), the concentration of digesta in the stagnant region of the second stomach, c_{2b}, is found to be

$$\begin{aligned} c_{2b}(t) = {} & Xe^{w_1 t}((1-\varepsilon_2)V_2w_1 + q + q_{2a}) + Ye^{w_2 t}((1-\varepsilon_2)V_2w_2 + q + q_{2a}) \\ & + \frac{Aqe^{u_1 t}}{q_{2a}}\left[\left(\frac{(1-\varepsilon_2)V_2u_1 + q + q_{2a}}{u_1^2 + a_2u_1 + b_2/4}\right)\left(\frac{u_1}{(1-\varepsilon_2)V_2} + \frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}\right) - 1\right] \\ & + \frac{Bqe^{u_2 t}}{q_{2a}}\left[\left(\frac{(1-\varepsilon_2)V_2u_2 + q + q_{2a}}{u_2^2 + a_2u_2 + b_2/4}\right)\left(\frac{u_2}{(1-\varepsilon_2)V_2} + \frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}\right) - 1\right]. \end{aligned} \tag{18}$$

The constants of integration (X and Y) are found using the initial conditions. As these are complicated, they have been placed in Appendix A. The solutions $c_{1a}(t)$, $c_{1b}(t)$, $c_{2a}(t)$, and $c_{2b}(t)$ form the solution to the two stomach model.

There is a special case that is not accounted for in our solution for the second stomach. This corresponds to the situation in which the stomach reactors have identical volume ($V_1 = V_2$), the size of the well-mixed and stagnant compartments are equal ($\varepsilon_1 = \varepsilon_2$), and there is a identical flow rate between the compartments in each stomach ($q_{1a} = q_{2a}$). This solution is not of physical interest and is investigated elsewhere [26].

In analyzing the solution of the non-ideal model, our main focus is on the cumulative excretion curves produced by the system. Differences in the excretory curves of an ideal and non-ideal two stomach model are compared to investigate the characteristics of the non-ideal mixing model.

The mass of digesta deposited on the ground, the cumulative excretion curve, is given by

$$m_{\text{non-ideal}}(t) = M_0 - (1-\varepsilon_1)V_1c_{1a}(t) - \varepsilon_1 V_1 c_{1b}(t) - (1-\varepsilon_2)V_2c_{2a}(t) - \varepsilon_2 V_2 c_{2b}(t). \tag{19}$$

The dimensionless mass of digesta deposited on the ground, $m^*_{\text{non-ideal}}$, is defined by

$$\begin{aligned} m^*_{\text{non-ideal}} &= m_{\text{non-ideal}}/M_0, \\ &= 1 - (1-\varepsilon_1)\frac{V_1}{M_0}c_{1a}(t) - \varepsilon_1\frac{V_1}{M_0}c_{1b}(t) - (1-\varepsilon_2)\frac{V_2}{M_0}c_{2a}(t) - \varepsilon_2\frac{V_2}{M_0}c_{2b}(t). \end{aligned} \tag{20}$$

4. Model simulations

In this section cumulative excretion curves for the non-ideal model are calculated and compared against equivalent curves for the ideal model. Prior to making this comparison a set of parameter values for ruminant animals must be determined. The main parameters of interest are related to the mean residence time, τ, of digesta through the gastrointestinal tract, by the relation $\tau_i = (V_i/q)$. By combining relevant values of τ_i, and known data on the volume of the rumen and caecum stomachs of different ruminant animals values for the flow rate q are determined for an ideal model. The mean residence time of digesta through the gastrointestinal tract is usually defined in terms of a rate constant k_i. Comparing definitions, it follows that

$$\tau_i = \frac{1}{k_i}. \tag{21}$$

This equation allows us to determine parameter values for τ_i, and hence to determine specific values for the variables, q and V_i. The rate-constants k_1 and k_2 are associated with the caecum and rumen respectively [5].

4.1. An ideal model

Before the dimensionless cumulative deposition curves for a ruminant with two non-ideal mixing chambers can be compared against that of an 'equivalent' animal having two ideal mixing

Table 1
Values of variables within the two compartment model.

Ruminant	Rumen τ_1 (h)	Caecum τ_2 (h)	Rumen V_1 (L)	Caecum V_2 (L)	q ($\mathrm{L\,h^{-1}}$)	τ_{tot} (h)	V_{tot} (L)	Source
Sheep[a]	32.3	31.3	5.30	5.13	0.164	63.6	10.43	[4,27]
Red deer[b]	17.0	2.8	13.20	2.17	0.776	19.8	15.37	[6,28]
Cattle[c]	38.8	5.6	24.00	3.46	0.619	43.8	27.46	[2,29]

[a] Data gathered on a 60 kg sheep.
[b] Data gathered on an 'average weighted' male red deer.
[c] Data gathered on a 150 kg cow.

chambers the dimensionless mass of digesta deposted on the ground, m^*_{ideal}, must be calculated for the ideal mixing model. The solution of system (2) is

$$c_1(t) = e^{-(q/V_1)t}, \tag{22}$$

$$c_2(t) = \frac{V_1}{V_1 - V_2}(e^{-(q/V_1)t} - e^{-(q/V_2)t}), \tag{23}$$

for $V_1 \neq V_2$. The cumulative excretion curve, m_{ideal}, is given by

$$m_{\text{ideal}}(t) = m(0) - V_1 c_1(t) - V_2 c_2(t),$$
$$= V_1 - V_1 c_1(t) - V_2 c_2(t).$$

Non-dimensionalizing, we obtain

$$m^*_{\text{ideal}}(t) = (1 - e^{-(q/V_1)t}) - \frac{V_2}{V_1 - V_2}(e^{-(q/V_1)t} - e^{-(q/V_2)t}). \tag{24}$$

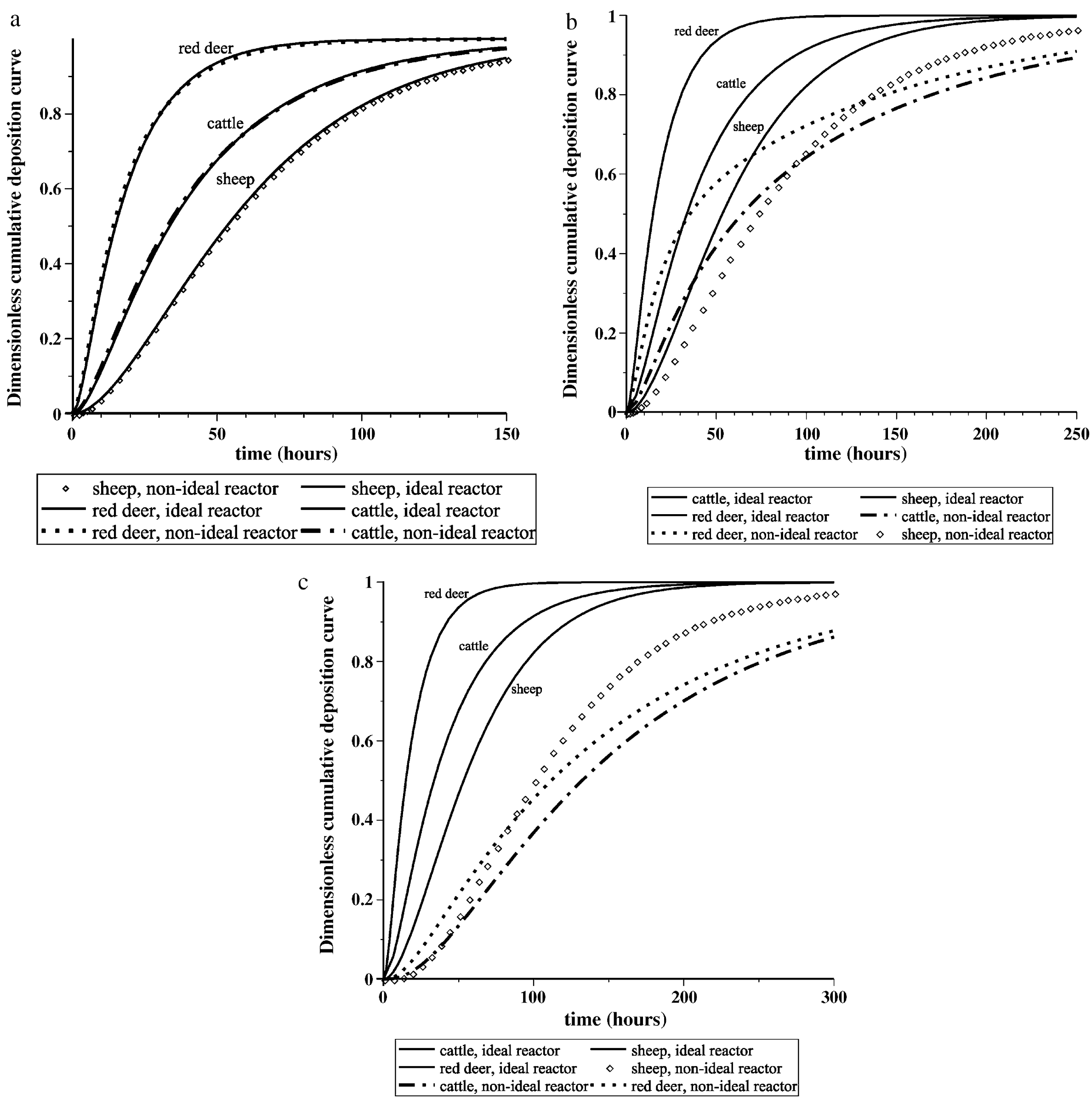

Fig. 2. Comparing two stomach ideal and non-ideal reactor models for the ruminant animals displayed in Table 1 for a) $\delta = 1$, b) $\delta = 0.5$, c) $\delta = 0$. In this figure the discrete data corresponds to the non-ideal stomach model ($\varepsilon_i \neq 0$), and the solid line, to the ideal stomach models ($\varepsilon_i = 0$).

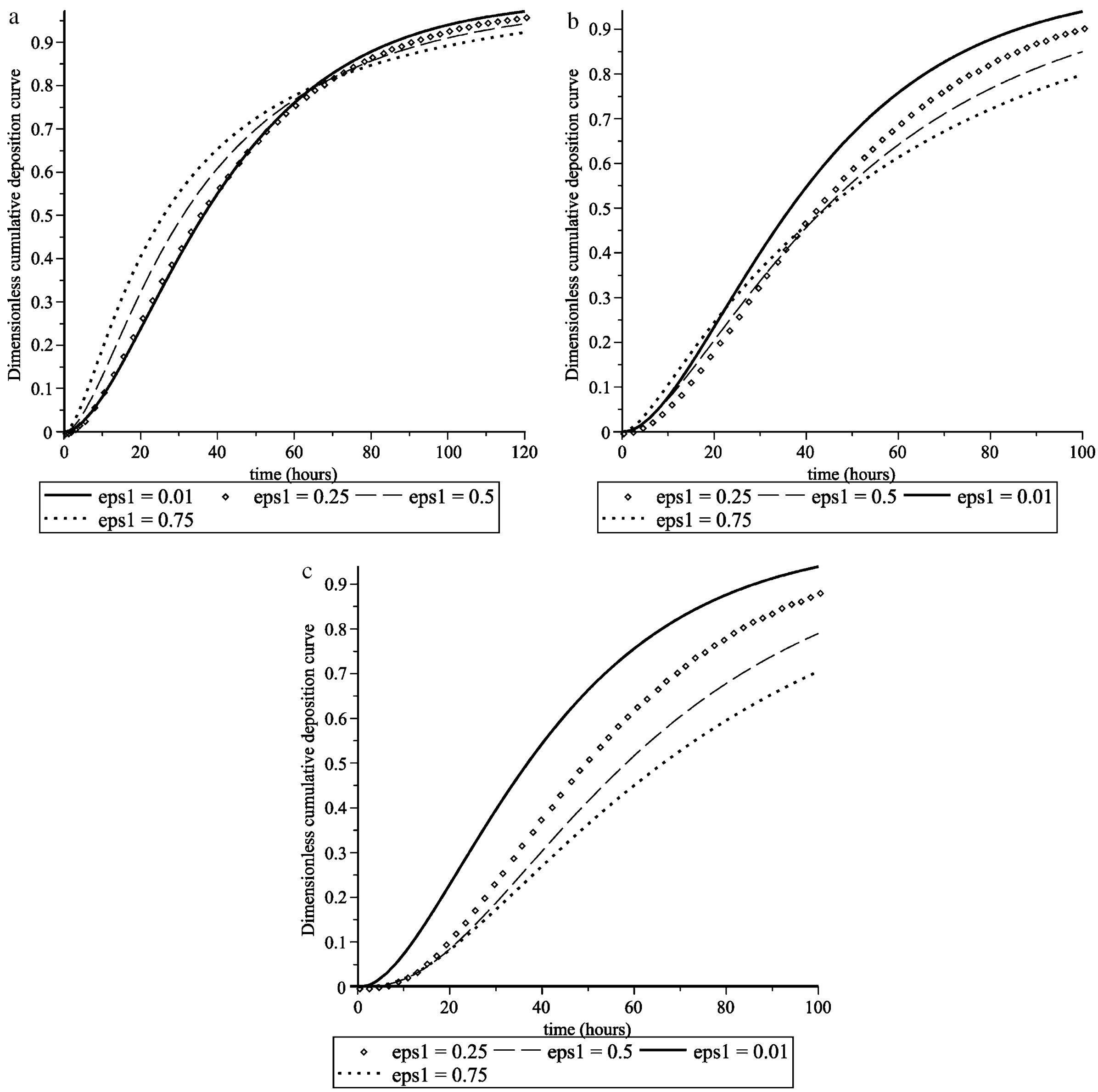

Fig. 3. The effect of varying the size of the well-mixed and stagnant compartments in the first stomach, ε_1, in sheep for a) $\delta = 1$, b) $\delta = 0.5$, c) $\delta = 0$.

In order to compare the dimensionless cumulative deposition curves of a ideal and non-ideal animal, the initial mass of digesta ingested must be the same for both models. Hence

$$m^*_{\text{non-ideal}}(0) = m^*_{\text{ideal}}(0),$$
$$1 - \delta M_0 - (1 - \delta)M_0 = 0,$$
$$\Rightarrow M_0 = 1.$$

4.2. Comparing ideal and non-ideal models

In this section the effect that stagnant regions have on the cumulative flow of digesta through the GIT is investigated by comparing the cumulative excretion curves produced by the ideal and non-ideal models. The effect of the non-specified parameter values (i.e. δ and ε_1) upon the flow of digesta through the GIT is also considered. These simulations include varying the relative initial concentration of digesta within the given compartments of the first stomach, δ, and varying the volumetric proportion of the well-mixed and stagnant compartments in the first stomach, ε_1. Unless otherwise stated the following parameter values are used: $\varepsilon_1 = 0.1$, $\varepsilon_2 = 0.1$, $\delta = 1$, $M_0 = 1$, $q = 2$, $q_{1a} = 0.01$ and $q_{2a} = 0.01$. All other parameter values are supplied in Table 1.

Fig. 2 compares the cumulative excretory curves produced by the ideal and non-ideal reactor models. It is evident that decreasing the value of δ, i.e. increasing the initial proportion of digesta in the stagnant region of the stomach, decreases the rate at which food substances are excreted from the system. This trend is explained by the fact that the introduction of stagnant regions into the model reduces the amount of digesta flowing through and out of the system, reducing the cumulative excretion curve. Another important note is that the difference between the cumulative excretion depositions of the ideal and non-ideal models is dependant upon the initial proportion of digesta in the well-mixed compartment, δ, of the non-ideal stomach model.

Fig. 3 investigates the effects of varying the proportional size of the well-mixed and stagnant compartments in the first stomach, ε_1, on different initial conditions. The cumulative excretory curves, shown in Fig. 3, are strongly dependant upon both the values for delta (δ) and epsilon (ε). The first trend observed is that increasing the relative size of the stagnant region in the first stomach, i.e.

ε_1, decreases the cumulative excretion of waste from the system over long periods of time. This trend is reversed for smaller values of time. Fig. 3a demonstrates that for smaller values of time, and larger values of delta, a ruminant whose first 'stomach' contains a relatively large stagnant region will excrete a greater amount of digesta than those with a smaller stagnant region. This observation can be explained by the definition: concentration = mass/volume. Consider the case when epsilon and delta are large, i.e. $\varepsilon = 0.75$ and $\delta = 1$. By taking epsilon to be large the volume of the well-mixed compartment is made smaller in proportion to the volume of the stagnant region. Thereby the initial mass of digesta is contained in a well-mixed compartment with smaller volume. This increases the concentration of digesta in the well-mixed compartment. The increase in concentration results in an increase in the probability that digesta will flow out of the stomach. Therefore, for a short period of time, when epsilon and delta are large, digesta flows more readily through the stomach system. As time increases the concentration of digesta in the well-mixed compartment decreases as more digesta passes into the stagnant regions. As the stagnant region is relatively large in volume, when epsilon is large, digesta that flows into this compartment will remain in low concentration and hence there is a smaller probability that digesta will flow out of the stagnant region, and eventually out of the stomach system.

After a certain time this trend will be reversed, as systems that contain smaller stagnant regions will contain a larger concentration of digesta, allowing for a greater flow out of digesta from the stagnant region. Thus after this time more digesta will reside in the well-mixed compartment, increasing the probability that digesta will flow out of the stomach. The cross over trend in the Fig. 3 is independent of the value of the flow rate parameters q and q_{1a}. As the initial proportion of digesta in the stagnant region increases, i.e. as δ tends towards 0, ruminant animals with larger well-mixed compartments pass food through the GIT at a faster rate than those with larger secondary compartments. This trend is a direct result of all the digesta being located in the stagnant region. Hence the reactor systems with a smaller stagnant region, i.e. as ε tends towards 0, will contain a greater concentration of digesta. Consequently there is a greater probability that digesta will flow out of the stagnant region into the well-mixed compartment, and hence out of the system.

A second observable trend is that decreasing the proportion of digesta initially in the well-mixed compartment, i.e. decreasing δ, increases the difference observed between excretory curves for the different values of epsilon (ε). Thus the initial location of digesta significantly affects the rate at which digesta is excreted from the system. Hence large changes in the proportion of digesta in the respective compartments (δ) results in large changes in the cumulative excretion curve. Simulations in which the proportional size of the stagnant region in the second stomach, ε_2, was varied showed identical trends to those obtained by varying ε_1.

Fig. 4 shows how varying the initial proportion of digesta within the well-mixed and stagnant compartments (δ) of the first stomach, affects the cumulative excretion of waste from the two stomach model. When $\delta = 1$ all the initial mass of digesta lies within the well-mixed compartment. Decreasing δ increases the initial proportion of digesta contained within the stagnant region of the first stomach. Fig. 4 shows that the greater the initial proportion of digesta in the well-mixed compartment of the first stomach, the faster waste is excreted from the system.

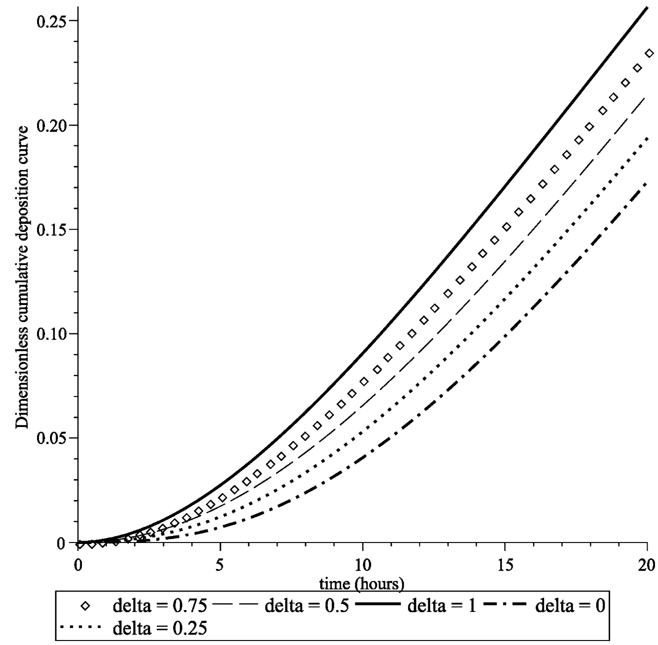

Fig. 4. Varying the initial proportion of digesta in the respective compartments, δ, for sheep in a non-ideal two stomach model.

5. Discussion

In this paper the classic model for the flow of digesta through the GIT of animals has been extended by incorporating non-ideal mixing. Additional extensions are possible to incorporate more information about digesta flow kinetics. These include incorporating variable volume (the change in volume caused by the flow of gastric secretions into the stomach compartments) and increasing the number of stomach reactors.

The physical breakdown of food substances flowing through a non-ideal GIT system can be included in the present model through the addition of a first order differential equation representing digestive processes. Furthermore, the model may be adapted, by varying the default value for the flow rate parameter, q, to model systemic stomach diseases, such as dumping syndrome. Dumping syndrome describes the process when digesta is released from the stomach before being properly digested, i.e. the flow rate of digesta through the stomach is faster than normal [30].

In veterinary science alternate methods have been developed to deal with the problem of non-ideal reactor conditions. These models attempt to simulate the physical process by which complex food substances are broken down in stages within the various compartments of the GIT, into smaller molecules for absorption in the intestines. A more accurate estimations of the mean residence time of food particles in the GIT can be obtained by combining a non-ideal mixing model with knowledge of the physicochemical properties of the GIT.

A limitation of compartmental models for ruminants and equids [4,5,2,31] is that they do not describe the residence time of the digesta in the different regions of the gut. This imposes a limit in our understanding of the link between the speed and extent of digestibility/fermentability and nutrient absorption. Thus an attempt to match stagnant areas with physical areas within the gut would lead to improved insight into these issues.

6. Conclusion

In this paper a standard model from veterinary science used to study the flow of digesta through the gastrointestinal tract of animals has been reformulated from a chemical engineering perspective. This reformulation enables the incorporation of non-ideal mixing into the model, creating a more accurate representation of the conditions within the GIT. The reformulated model includes the classic Blaxter model as a limiting case. Thus parameter fitting of the model would identify the role played by stagnant regions in digesta flow. However, a drawback of our model is that the physiological location of the stagnant areas is not specified.

The dimensionless cumulative excretion of waste was simulated under varying biological conditions. The comparative differences in the excretory curves produced by equivalent ideal and non-ideal two stomach models were investigated. 'Stomachs' containing stagnant regions were found to excrete digesta at a slower rate than ideal 'stomachs'. The difference between the cumulative excretion depositions of the ideal and non-ideal models was dependant upon the initial proportion of digesta in the well-mixed compartment, δ.

Changes in the values of ε and δ, were shown to substantially effect the cumulative excretion curve from the GIT of a ruminant animal. Increasing the relative size of the stagnant region in the first stomach, i.e. increasing ε_1, decreased the cumulative excretion of waste over long periods of time. Similarly, increasing the proportion of contents in the stagnant non-mixing region within the system, i.e. reducing δ, decreased the excretion rate. Conversely, increasing the proportion of digesta initially in the well-mixed compartment of the first stomach, increasing δ, increased the excretion rate. For smaller values of time, and larger values of δ, a ruminant whose first 'stomach' contains a relatively large stagnant region excretes a greater amount of digesta than those with a smaller stagnant region.

This problem is a good example of the applications of chemical engineering to an application outside the traditional definition of the discipline.

Acknowledgements

(RVB) thanks the School of Mathematics and Statistics at the University of Wollongong, for providing the Austin Keane scholarship to allow him to undertake this research.

The authors would like to thank the referee and the editor for their very constructive comments on our paper.

Appendix A. Constants of integration, *X* and *Y*, for the two stomach non-ideal model

The constants of integration, X and Y, derived from the solution to the second stomach reactor in the two stomach model with constant volume in a non-ideal reactor, are given below,

$$
\begin{aligned}
X = {} & \frac{Aq}{(1-\varepsilon_2)V_2(w_2-w_1)}\left(\frac{(u_1(1-\varepsilon_2)V_2+q+q_{2a})}{(u_1{}^2+a_2u_1+b_2/4)}\left(\frac{u_1}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2{}^2}\right)-1\right)\\
& +\frac{Bq}{(1-\varepsilon_2)V_2(w_2-w_1)}\left(\frac{(u_2(1-\varepsilon_2)V_2+q+q_{2a})}{(u_2{}^2+a_2u_2+b_2/4)}\left(\frac{u_2}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2{}^2}\right)-1\right)\\
& -\frac{Aq}{(1-\varepsilon_2)^2V_2{}^2}\left(\frac{(1-\varepsilon_2)V_2w_2+q+q_{2a}}{(w_2-w_1)(u_1{}^2+a_2u_1+b_2/4)}\right)\left(u_1+\frac{q_{2a}}{\varepsilon_2V_2}\right)\\
& -\frac{Bq}{(1-\varepsilon_2)^2V_2{}^2}\left(\frac{(1-\varepsilon_2)V_2w_2+q+q_{2a}}{(w_2-w_1)(u_2{}^2+a_2u_2+b_2/4)}\right)\left(u_2+\frac{q_{2a}}{\varepsilon_2V_2}\right),
\end{aligned}
\tag{25}
$$

and

$$
\begin{aligned}
Y = {} & \Bigg(-\Bigg(\frac{Aq}{(1-\varepsilon_2)V_2(w_2-w_1)}\Bigg(\frac{(u_1(1-\varepsilon_2)V_2+q+q_{2a})}{u_1{}^2+a_2u_1+b_2/4}\\
& \left(\frac{u_1}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2^2}\right)-1\Bigg)+\frac{Bq}{(1-\varepsilon_2)V_2(w_2-w_1)^{-1}}\\
& \left(\frac{(u_2(1-\varepsilon_2)V_2+q+q_{2a})}{(u_2{}^2+a_2u_2+b_2/4)}\left(\frac{u_2}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2{}^2}\right)-1\right)\\
& -\frac{((1-\varepsilon_2)V_2w_2+q+q_{2a})}{(w_2-w_1)(u_1{}^2+a_2u_1+b_2/4)}\frac{Aq}{(1-\varepsilon_2)^2V_2{}^2}\left(u_1+\frac{q_{2a}}{\varepsilon_2V_2}\right)\\
& -\frac{((1-\varepsilon_2)V_2w_2+q+q_{2a})}{(w_2-w_1)(u_2{}^2+a_2u_2+b_2/4)}\frac{Bq}{(1-\varepsilon_2)^2V_2{}^2}\left(u_2+\frac{q_{2a}}{\varepsilon_2V_2}\right)\Bigg)((1-\varepsilon_2)V_2w_1+q+q_{2a})\\
& -Aq\left(\frac{(u_1(1-\varepsilon_2)V_2+q+q_{2a})}{(u_1{}^2+a_2u_1+b_2/4)}\left(\frac{u_1}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2{}^2}\right)-1\right)\\
& -Bq\left(\frac{(u_2(1-\varepsilon_2)V_2+q+q_{2a})}{(u_2{}^2+a_2u_2+b_2/4)}\left(\frac{u_2}{(1-\varepsilon_2)V_2}+\frac{q_{2a}}{\varepsilon_2(1-\varepsilon_2)V_2{}^2}\right)-1\right)\Bigg)\\
& ((1-\varepsilon_2)V_2w_2+q+q_{2a})^{-1}.
\end{aligned}
\tag{26}
$$

References

[1] P. Uden, T.R. Rounsaville, G.R. Wiggans, P.J. van Soest, The measurement of liquid and solid digesta retention in ruminants, equines and rabbits given timothy (Phleum pratense) hay, British Journal of Nutrition 48 (1982) 329–339.

[2] M.S. Dhanoa, R.C. Siddons, J. France, D.L. Gale, A multicompartmental model to describe marker excretion patterns in ruminant faeces, British Journal of Nutrition 53 (1985) 663–671.

[3] A. Dumas, J. Dijkstra, J. France, Mathematical modelling in animal nutrition: a centenary review, Journal of Agricultural Science 146 (2008) 123–142, Cambridge University Press.

[4] K.L. Blaxter, N.McC. Graham, F.W. Wainman, Some observations on the digestibility of food by sheep and on related problems, British Journal of Nutrition 10 (1956) 69–91.

[5] W.L. Grovum, V.J. Williams, 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, British Journal of Nutrition 30 (1973) 313–329.

[6] J.A. Milne, J.C. Macrae, A.M. Spence, S. Wilson, A comparison of the voluntary intake and digestion of a range of forages at different times of the year by sheep and red deer (Cervus elaphus), British Journal of Nutrition 40 (1978) 347–357.

[7] R.L. Baldwin, L.J. Koong, M.J. Ulyatt, N. Smith, Towards a synthesis, in: T.M. Sutherland, J.R. McWilliam, R.A. Leng (Eds.), Reviews in Rural Science. 2. From Plant to Animal Protein, University of New England Publishing Unit, Armidale, 1976, pp. 175–181.

[8] W.C. Ellis, J.H. Matis, K.R. Pond, C.E. Lascano, J.P. Telford, Dietary influences on flow rate and digestive capacity, in: F.M.C. Gilchrist, R.I. Mackie (Eds.), Herbivore Nutrition in the Subtropics and Tropics, The Science Press, Craighall, 1984, pp. 269–293.

[9] R.E. Hungate, The Rumen and its Microbes, Academic Press, New York, NY, 1966.

[10] W.C. Ellis, J.H. Matis, T.M. Hill, M.R. Murphy, in: G.C. Fahey, M. Collins, D.R. Mertens, L.E. Moser (Eds.), Methodology for Estimating Digestion and Passage Kinetics of Forages: Forage Quality Evaluation and Utilisation, American Society of Agronomy, Madison, WI, USA, 1994, pp. 682–756.

[11] M.J.S. Moore-Colyer, H.J. Morrow, A.C. Longland, Mathematical modelling of digesta passage rate mean retention time and in vivo apparent digestibility of two different lengths of hay and big-bale grass silage in ponies, British Journal of Nutrition 90 (2003) 109–118.

[12] T.M. Sutherland, Particle separation in the forestomachs of sheep, in: A. Dobson (Ed.), Aspects of Digestive Physiology in Ruminants, Cornell University Press, Ithaca, NY, 1988, pp. 43–73.

[13] R.A.M. Vieira, L.O. Tedeschi, A. Cannas, A generalized compartmental model to estimate the fibre mass in the ruminoreticulum: 2. Integrating digestion and passage, Journal of Theoretical Biology 255 (2008) 357–368.

[14] W.C. Ellis, M.J. Wylie, J.H. Matis, Validity of specifically applied rare earth elements and compartmental models for estimating flux of undigested plant tissue residues through the gastrointestinal tract of ruminants, Journal of Animal Science 80 (2002) 2753–2758.

[15] B. Knox, P. Ladiges, B. Evans, R. Saint, Biology: An Australian Focus, 3rd ed., McGraw-Hill Australia, Sydney, 2006, ISBN 0 074 71664 6.

[16] G.J. Faichney, R.C. Boston, Interpretation of the faecal excretion patterns of solute and particle markers introduced into the rumen of sheep, Journal of Agricultural Science, Cambridge 101 (1983) 575–581.

[17] D. Cuddeford, R.A. Pearson, R.F. Archibald, R.H. Muirhead, Digestibility and gastro-intestinal transit time of diets containing different proportions of alfalfa and oat straw given to Thoroughbreds, Shetland ponies, Highland ponies and donkeys, Animal Science 61 (1995) 407–417.

[18] J.D. Pagan, P. Harris, T. Brewster-Barnes, S.E. Duren, S.G. Jackson, Exercise affects digestibility and rate of passage of all-forage and mixed diets in thoroughbred horses, Journal of Nutrition 128 (1998) 2704–2707.

[19] R.A. Pearson, R.F. Archibald, R.H. Muirhead, The effect of forage quality and level of feeding on digestibility and gastrointestinal transit time of oat straw and alfalfa given to ponies and donkeys, British Journal of Nutrition 85 (2001) 599–606.

[20] D. Afik, W.H. Karasov, The trade-offs between digestion rate and efficiency in warblers and their ecological implications, Ecology 76 (1995) 2247–2257.

[21] R.M. Sibly, Strategies of digestion and defaecation, in: C.R. Townsend, P. Calow (Eds.), Physiological Ecology: An Evolutionary Approach, Sinauer, Sunderland, Massachusetts, 1981, pp. 109–139.

[22] M.I. Nelson, H.S. Sidhu, X.D. Chen, The passage of food through animal stomachs: a chemical engineering approach, in: Proceedings of the 36th Australasian Chemical Engineering Conference, CHEMECA 2008, Engineers Australia, 2008, pp. 533–542.

[23] H.S. Fogler, Elements of Chemical Reaction Engineering, 3rd ed., Prentice Hall, New Jersey, 1999, ISBN 0 13 531708 8.

[24] M.L. Shuler, F. Kargi, Bioprocess Engineering, 2nd ed., Prentice Hall, New Jersey, 2002, ISBN 0 13 081908 5.

[25] D.L. Penry, P.A. Jumars, Modeling animal guts as chemical reactors, The American Naturalist 129 (1987) 69–96.

[26] R. Van Bentum, A Fundamental Analysis of Mathematical Modelling of the Gastrointestinal Tract, B. Mathematics (Adv). Hons., University of Wollongong, 2009.

[27] D.B. Purser, R.J. Moir, Rumen volume as a factor involved in individual sheep differences, Journal of Animal Science 25 (1966) 509–515.

[28] J. Kamler, J. Dvofiák, K. Kamlerová, Differences in relative volume and weight of stomach among four free living ruminants, Acta Veterinaria Brno 72 (2003) 33–39.

[29] A.S. Shakespeare, Rumen management during aphagia, Journal of the South African Veterinary Association 79 (3) (2008) 106–112.

[30] P.S. Barie, R.R. Bollinger, A.E. Chang, S.F. Lowry, S.J. Mulvihill, J.A. Norton, H.I. Pass, R.W. Thompson, Surgery: Basic Science and Clinical Evidence, 2nd ed., Springer Science and Business Media, New York, 2008, p. 855.

[31] K.R. Pond, W.C. Ellis, J.H. Matis, H.M. Ferreiro, J.D. Sutton, Compartment models for estimating attributes of digesta flow in cattle, British Journal of Nutrition 60 (3) (1988) 571–595.