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A dynamic mechanistic model of lactic acid metabolism in the rumen

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ABSTRACT

Current feed evaluation systems for ruminants are too imprecise to describe diets in terms of their acidosis risk. The dynamic mechanistic model described herein arises from the integration of a lactic acid (La) metabolism module into an extant model of whole-rumen function. The model was evaluated using published data from cows and sheep fed a range of diets or infused with various doses of La. The model performed well in simulating peak rumen La concentrations (coefficient of determination = 0.96; root mean square prediction error = 16.96% of observed mean), although frequency of sampling for the published data prevented a comprehensive comparison of prediction of time to peak La accumulation. The model showed a tendency for increased La accumulation following feeding of diets rich in nonstructural carbohydrates, although less-soluble starch sources such as corn tended to limit rumen La concentration. Simulated La absorption from the rumen remained low throughout the feeding cycle. The competition between bacteria and protozoa for rumen La suggests a variable contribution of protozoa to total La utilization. However, the model was unable to simulate the effects of defaunation on rumen La metabolism, indicating a need for a more detailed description of protozoal metabolism. The model could form the basis of a feed evaluation system with regard to rumen La metabolism.
Key words: lactic acid, rumen, mechanistic model

INTRODUCTION

For many years researchers have recognized the importance of lactic acid (**La**) as an intermediary during the fermentation of NSC in the rumen (Phillipson and McAnally, 1942; Elsden, 1945; Waldo and Schultz, 1956). Within the rumen exist a group of La producers and a second group of La utilizers that ferment La to VFA (Dunlop and Hammond, 1965; Owens et al., 1998), the balance of which generally keeps the concentration of La in the rumen low. Accumulation of rumen La for animals fed large quantities of rapidly degradable starch or soluble sugars occurs when the rate of La production exceeds the capacity of the La-utilizing microbes for uptake. Nocek (1997) and Nagaraja and Titgemeyer (2007) speculated that as the concentration of La increases, rumen pH decreases, and lactic acidosis results. This further encourages the growth of acid-tolerant La-producing bacteria while inhibiting the growth of La utilizers, and results in a spiraling reduction of pH and elevating La concentration. Strategies to increase La utilizers or reduce La producers, or both, may be helpful in the prevention of acidosis. For example, feeding *Megasphaera elsdenii*, a major La utilizer, to beef cattle reduced rumen La concentration and increased pH (Calsamiglia et al., 2012).

High-yielding dairy cows fed energy-dense rations rich in rapidly fermentable starch or sugars are particularly susceptible to acidosis (Beauchemin and Penner, 2009), although feedlot beef cattle, sheep, goats and other ruminants are also prone to the disease (Braun et al., 1992). Rumen acidosis can be caused by improper adaptation to high-concentrate diets and the resulting accumulation of La in the rumen (acute acidosis; Nagaraja and Titgemeyer, 2007), or it can be caused by an accumulation of VFA within the rumen (subclinical acidosis; Oetzel et al., 1999; Beauchemin and Penner, 2009), both of which reduce rumen pH. In dairy and beef cattle, clinical and subclinical acidosis are causes of substantial production loss as animals reduce feed intake or become susceptible to associated physiological complications such as laminitis, reduced fiber digestion, milk fat depression, diarrhea, and liver abscesses (Plaizier et al., 2008). Current feed evaluation systems for dairy cows (e.g., NRC, 2001; Thomas, 2004) are unable to address the complex interrelationships in the rumen that give rise to lactic acidosis following the ingestion

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of certain feedstuffs or combinations of feedstuffs. In more recent approaches, empirical relationships were developed assessing fiber requirements to avoid low rumen pH (Zebeli et al., 2008). Adequate fiber levels were predicted to depend on both level of DMI and dietary content of rumen degradable starch from grain, but this approach still does not include levels of rapidly degradable sugars or degradation characteristics of fiber. A mechanistic approach to feed evaluation demonstrates a greater capacity for describing such rumen fermentation processes, although to date, these models have given only minimal consideration to ruminal La metabolism (Dijkstra et al. 1992; Baldwin, 1995; Danfær et al., 2006). Therefore, the objective of this investigation was to develop a model of La metabolism and integrate it into an existing mechanistic model of whole-rumen function. The model could be used as a method of feed evaluation that accounts for the potential risk of lactic acidosis in the dairy cow adapted to a particular diet.

MATERIALS AND METHODS

Model Development

Existing models of rumen fermentation have tended to ignore the explicit description of La metabolism (Black et al. 1981; France et al. 1982; Dijkstra et al. 1992; Baldwin, 1995; Danfær et al., 2006). Where attempts have been made to account for La production and utilization, the approach taken has revolved around the manipulation of fermentation stoichiometry depending on rumen pH and fermentation substrate (Baldwin, 1995; Pitt et al. 1996). However, this technique is limited in its ability to describe reality, as several other factors associated with the fluctuations in the structure of the microbial population affect the potential for lactic acidosis. Rudimentary attempts at mechanistic modeling of La metabolism have since been made (Xu and Ding, 2006; Ding and Xu, 2006), but require a more advanced representation of underlying fermentation and metabolism. The requirement for a more detailed description of the microbial population structure is a prerequisite for a model capable of quantifying La metabolism. Dijkstra (1994) modified an existing mechanistic model of rumen function (Dijkstra et al., 1992) to consider protozoal metabolism in conjunction with both amylolytic (**Ba**) and fibrolytic (**Bc**) bacteria populations. However, La was not represented as a state variable and dietary La entered the amylolytic hexose pool directly. The objectives of the Dijkstra (1994) model make it suitable for modification to account for rumen La metabolism, especially because protozoa (**Po**) may have a considerable role in the production and utilization of rumen La (Nagaraja and Towne, 1990; Williams and Coleman, 1997). Therefore, the model described herein, introduced previously by Dijkstra et al. (2002), is a modified form of the dynamic, deterministic rumen model presented by Dijkstra (1994). Within the Dijkstra (1994) model, pH is determined from both VFA and La concentration. Thus, although VFA are not explicitly dealt with in the current modeling exercise, large amounts of VFA, without significant amounts of La, may also decrease pH and cause acidosis within the model. The principal nutrient flows herein are as described by Dijkstra (1994) with key additional elements shown in Figure 1. The additional state variables and modifications to the existing driving and state variables are described below. Notation used to describe nutrient flows is shown in Table 1.

Model Parameterization

Unless otherwise indicated, the rumen model is parameterized according to Dijkstra (1994). Parameters for the La metabolism module are displayed in Tables 2 and 3. To the extent possible, diet-specific input values were obtained from the published experiments used in model evaluation. For the description of in situ degradation kinetics of feed carbohydrate and protein, the data presented by Nocek and Grant (1987), Tamminga et al. (1990), Van Vuuren et al. (1990), Nocek and Tamminga (1991), and Bosch et al. (1992) were used.

Pulsed Dietary Inputs. The original rumen model was evaluated with regard to its ability to run with a continuous input of nutrients, therefore simulating rumen fermentation in a frequently fed cow. Although the simulation of a steady state within the rumen during continuous feeding has proved effective for the simulation of many aspects of rumen fermentation, the objectives of this investigation require pulsed model inputs, thus simulating rumen function in the cow fed a limited number of meals during the day. France et al. (1982), Baldwin, (1995), and Chilibroste et al. (2001, 2008) describe models of whole-rumen function for which inputs were either continuous or pulsed to represent discontinuous feeding schedules. Due to the objectives of the present model, the approach taken by France et al. (1982) is used to simulate discontinuous feeding where instantaneous values for nutrient inputs (D_x) are represented as follows:

$$D_x = \frac{x}{n_f \Delta_f} \sum_{i=1}^{n_f} \left[H\left(t^* - t_i^*\right) - H\left(t^* - t_i^* - \Delta_f\right) \right], \quad [1]$$

where x is the nutrient intake (kg/d) ingested over n_f equal meals, t^* is the fractional part of the time variable t (d), and Δ_f is the duration of each meal. Feeding begins at time of day t_i^* ($i = 1, 2, \ldots, n_f$) and

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