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Prediction of Ruminal Volatile Fatty Acids and pH Within the Net Carbohydrate and Protein System

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ABSTRACT: A steady-state model of the production, absorption, passage, and concentration of ruminal VFA and pH is developed from published literature data and is structured to use the feed descriptions and inputs from the net carbohydrate and protein system. Included are the effects of pH on growth rate and yield of structural and non-structural carbohydrate-fermenting bacteria; production of acetate, propionate, butyrate, lactate, and methane; conversion of lactate to VFA; ruminal absorption of acids; and prediction of ruminal pH from dietary measures and from ruminal buffering and acidity. The root mean square error of predicted total VFA concentration was

12 mM. Individual VFA fractions were inadequately predicted. In a review of literature data, effective NDF (eNDF) provided a better correlation with ruminal pH than forage or NDF. Digestion rate of NDF remained at normal levels above pH 6.2, which corresponds to a minimum eNDF of 20% of dietary DM. Further research is needed to determine the individual VFA produced from carbohydrate fractions at various pH, the appropriateness of partitioning the starch and pectin carbohydrate pool into slowly and rapidly degraded fractions, and the effect on microbial yield, total tract digestibility, and predicted energy values of feeds.

Key Words: Rumen, pH, VFA, Effective Fiber, Model

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Introduction

Prediction of absorbed VFA is an important goal for relating feed composition to milk production and composition, to changes in body composition, and to net energy values of diets (Hungate, 1966; Sutton, 1985; Bergman, 1990). Ruminal VFA production is closely related to ruminal pH, which is an important regulator of microbial yield and absorbed amino acids (Russell and Dombrowski, 1980). Prediction of these factors will be increasingly important as pricing systems for milk and meat evolve toward optimal content of protein and fat.

In a series of papers, a net carbohydrate and protein system was developed to use farm level information about cattle, intake, feed composition, and environment to evaluate animal performance (Fox et al., 1992; Russell et al., 1992; Sniffen et al., 1992; O'Connor et al., 1993). Central to the model is a

ruminal submodel that predicts steady-state carbohydrate fermentation, protein digestion, microbial growth, and ME from ingested feeds. An adjustment in microbial yield is made that varies with the amount of forage NDF in the diet, but ruminal pH and concentrations of VFA are not predicted. Existing models of ruminal VFA production and concentration (Baldwin et al., 1970, 1977; France et al., 1982; Dijkstra et al., 1992; Neal et al., 1992; Lescoat and Sauvant, 1995) are not easily integrated into the net carbohydrate and protein system because of wide differences in feed description inputs, levels of aggregation, and dynamic behavior (steady vs non-steady state).

The objective of this study was to develop a structure to predict ruminal VFA and pH using the inputs, assumptions, and equations in the net carbohydrate and protein system. The VFA submodel includes ruminal production and absorption of acetate, propionate, butyrate, lactate, and methane; effects of pH on microbial growth and yield; and prediction of ruminal pH from dietary measures. After evaluation of the model and identification of sources of error, implications for feed characterization and future research are discussed.

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Modeling Procedures for Predicting Ruminal VFA and pH

The general approach was to synthesize literature data relating to ruminal VFA and pH and to develop equations that utilize these data within the structure of the existing model. Because pH affects VFA production, the starting point is the effect of pH on microbial growth, microbial yield, and end product production. Following this, equations are presented for the production rates of individual VFA and lactate, the conversion of lactate to VFA, ruminal absorption of VFA and lactate, and steady-state mass balances to predict VFA concentrations. A procedure for predicting ruminal pH using these equations is then described.

Effects of Ruminal pH on Microbial Growth and Yield. Ruminal pH affects microbial growth, digestion of carbohydrate, and VFA production. The intent in this section is to model the best available information on pH effects on ruminal bacterial species and to adapt this information to the general microbial groups in the net carbohydrate and protein system. In Russell et al. (1992), microbial growth is divided between those fermenting structural carbohydrates (**SC**), which include digestible NDF (**B2**) carbohydrate, and those fermenting non-structural carbohydrates (**NSC**), which include sugar (**A**) and starch and pectic substances (**B1**). Digestion rates are specific to each fraction of each feed (Sniffen et al., 1992). The model described here includes effects of pH on the SC and NSC bacteria separately. For both groups, microbial yield at normal ruminal pH (i.e., 6.725; Russell and Baldwin, 1979) is calculated as in Russell et al. (1992), using feed specific digestion rates (Sniffen et al., 1992) and a maximum yield of .4.

In a continuous culture study of several species of ruminal bacteria (Russell and Dombrowski, 1980), the minimum pH at which the SC bacteria could maintain a growth rate above the dilution rate ranged from 5.7 to 6.15. Microbial yield dropped off sharply as pH approached the minimum. Based on the most acid-tolerant species (*Butyrivibrio fibriosolvens*) in this study (Russell and Dombrowski, 1980), the following equation was used to adjust microbial yield of SC bacteria with pH:

$$r_Y^{SC} = [1 - \exp(-5.624(\text{pH} - 5.7) \cdot .909)] / .9968, \text{pH} \geq 5.7$$

$$0, \text{pH} < 5.7 \quad [1]$$

where r_Y^{SC} = relative yield of SC bacteria as a function of pH.

Microbial yield from B2 carbohydrate for feed j, denoted Y_j^{B2} , was calculated as the product of yield at normal ruminal pH and the pH adjustment factor (vertical lines denote "at"):

$$Y_j^{B2} |_{\text{reduced pH}} = r_Y^{SC} \cdot Y_j^{B2} |_{\text{normal pH}} \quad [2]$$

With Eq. [1] and [2], SC yield is unchanged at pH 6.725, decreases to half at pH 5.8, and is reduced to 0 at pH 5.7.

For *Ruminococcus flavefaciens*, maintenance coefficient increases as pH decreases (Shi and Weimer, 1992). Regressing a line to the Shi and Weimer (1992) data produced $r^2 = .867$. To adapt this equation to mixed ruminal SC bacteria, the equation was multiplied by a constant to give the original value of .05 g/(g·h) at pH 6.725:

$$m^{SC} = .1409 - .0135 \text{ pH} \quad [3]$$

where m^{SC} = maintenance coefficient of SC bacteria, g/(g·h).

The digestion rate of SC at each pH could then be calculated using a reversal of the Pirt (1965) equation (with the assumption that true growth rate is approximated by digestion rate):

$$k_{dj}^{B2} = \left[\frac{m^{SC} Y_j^{B2} Y_{\max}^{SC}}{Y_{\max}^{SC} - Y_j^{B2}} + m^{SC} Y_{\max}^{SC} \right] \cdot 24 \quad [4]$$

where k_{dj}^{B2} = digestion rate of B2 carbohydrate on feed j, d⁻¹.

In Figure 1, calculated values of k_{dj}^{B2} vs pH are compared with published in vitro rates of NDF digestion (Grant and Mertens, 1992); these curves were forced to coincide with the published digestion rates at pH 6.8. Digestion rate was predicted to increase slightly as pH decreased to 6.2, then to decrease sharply as pH approached 5.7. In chemostat culture (Shriver et al., 1986), NDF digestibilities were found to vary from 32.0 to 33.1 to 8.1% when pH was decreased from 7.0 to 6.2 to 5.8, respectively.

For the NSC bacteria, only small adjustments in yield and digestion rate were made with decreasing pH, because the microbial population shifts to more acid-tolerant species such as *Streptococcus bovis* as pH decreases (Hungate, 1966). In a study on *Prevotella ruminicola* (Russell et al., 1979), growth rate was relatively unaffected by pH down to 5.8, then decreased linearly. It was assumed that, consistent with other lactate-producing ruminal bacteria, digestion rate reached zero at pH 4.0 (Hungate, 1966). The pH adjustment for digestion rate of the NSC bacteria was as follows:

$$r_{k_d}^{NSC} = 1, \text{pH} > 5.8$$

$$(\text{pH} - 4) / 1.8, 4 \leq \text{pH} \leq 5.8. \quad [5]$$

where $r_{k_d}^{NSC}$ = relative digestion rate as a function of pH.

The k_d at reduced pH was the product of k_d at normal pH and the adjustment factor, which was

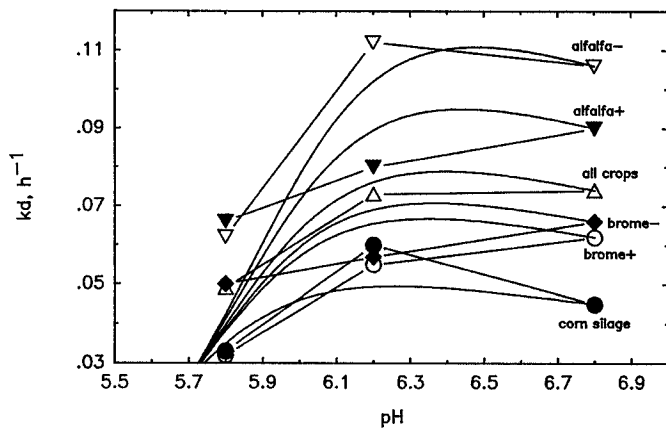


Figure 1. Effect of ruminal pH on digestion rate k_d of NDF. Shown are data from Grant and Mertens (1992) for various NDF sources without (-) or with (+) added starch. Curves show model-predicted values using the k_d at pH 6.8.

applied to both A and B1 digestion rates (the following is a composite of two equations, one each for A and B1 carbohydrates):

$$k_{dj}^{A,B1} \Big|_{\text{reduced pH}} = r_{k_d}^{\text{NSC}} \cdot k_{dj}^{A,B1} \Big|_{\text{normal pH}} \quad [6]$$

where $k_{dj}^{A,B1}$ = digestion rates of A or B1 carbohydrate for feed j, d^{-1} .

Similar to Eq. [1], an adjustment factor for NSC microbial yield was generated using a minimum pH of 4.5 and a 50% reduction in yield at pH 5.5 (Russell and Dombrowski, 1980).

$$r_Y^{\text{NSC}} = [1 - \exp(-.693(\text{pH} - 4.5)^{1.732})] \cdot .9373 \quad [7]$$

$$Y_j^{A,B1} \Big|_{\text{reduced pH}} = r_Y^{\text{NSC}} \cdot Y_j^{A,B1} \Big|_{\text{normal pH}} \quad [8]$$

where r_Y^{NSC} = relative yield of NSC bacteria as a function of pH; and $Y_j^{A,B1}$ = yield of NSC bacteria on A or B1 carbohydrate for feed j. Yield at normal pH is calculated with a maintenance coefficient of .15 g/(g·h) (Russell et al., 1992).

End Products of Carbohydrate Fermentation. In this section, we describe the allocation of degraded carbohydrates to the end products of fermentation as affected by ruminal pH. These end products include acetate, propionate, butyrate, lactate, carbon dioxide, methane, hydrogen gas, valerate, and isoacids (Van Soest, 1994). In the model, only acetate, propionate, butyrate, lactate, and methane are explicitly calculated (VFA production from peptide fermentation is not included).

Given that cell mass production is microbial yield (Y) times degraded carbohydrate (Russell et al., 1992), then the fraction of degraded carbohydrate going to end products should be $1 - Y$. However, some cell mass is derived from noncarbohydrate sources, so that a fraction greater than $1 - Y$ goes to end products. For the SC bacteria, which utilize ammonia, the cell mass not derived from carbohydrate is assumed to be N and ash. Based on a microbial composition of 10% N and 4.4% ash (Russell et al., 1992), 85.6% of SC cell mass comes from degraded carbohydrate. Thus, the rate of SC end product production is as follows:

$$\text{Endprod}^{B2} = \sum_j \text{degrB2}_j (1 - .856 Y_j^{B2}) \quad [9]$$

where Endprod^{B2} = end product production from B2 carbohydrate, g/d; and degrB2_j = degradation of B2 carbohydrate for feed j, g/d. Equations for calculating degrB2_j were provided by Sniffen et al. (1992) using digestion and passage rates. As microbial yield decreases with decreasing pH, the fraction of degraded B2 carbohydrate converted to end products is increased.

For NSC bacteria, which utilize peptides, amino acids, or ammonia (Russell et al., 1992), the portion of cell mass derived from noncarbohydrates includes N (10%), ash (4.4%), and the carbon skeletons of peptides. New cell mass derived from peptides is $6.25 \cdot (\text{peptide N uptake})$; the remainder of N is from ammonia (Russell et al., 1992). Thus, the end product production from A or B1 carbohydrate is calculated as follows:

$$\text{Cellmass}^A = \sum_j (Y_j^A \cdot \text{degrA}_j) \quad [10]$$

$$\text{Cellmass}^{B1} = \sum_j (Y_j^{B1} \cdot \text{degrB1}_j) \quad [11]$$

$$\text{Endprod}^A = \left(\sum_j \text{degrA}_j \right) - \left(\begin{array}{l} \text{Cellmass}^A - \text{NfromNH3}_A \cdot \text{fracA} \\ -6.25 \cdot \text{NfromPEP}_A \cdot \text{fracA} \\ -.044 \text{ Cellmass}^A \end{array} \right) \quad [12]$$

$$\text{Endprod}^{B1} = \left(\sum_j \text{degrB1}_j \right) - \left(\begin{array}{l} \text{Cellmass}^{B1} - \text{NfromNH3}_{B1} \cdot \text{fracB1} \\ -6.25 \cdot \text{NfromPEP}_{B1} \cdot \text{fracB1} \\ -.044 \text{ Cellmass}^{B1} \end{array} \right) \quad [13]$$

$$\text{fracA} = \text{Cellmass}^A / (\text{Cellmass}^A + \text{Cellmass}^{B1}) \quad [14]$$

$$\text{fracB1} = 1 - \text{fracA} \quad [15]$$

where

- Cellmass^{A,B1} = rates of cell mass produced from A or B1 carbohydrate, g/d;
- degrA_j = rate of A carbohydrate degraded from feed j, g/d;
- degrB1_j = rate of B1 carbohydrate degraded from feed j, g/d;
- Endprod_{A,B1} = rates of end product production from A or B1 carbohydrate, g/d;
- NfromNH3_{A,B1} = rates of N uptake as ammonia by bacteria fermenting A or B1 carbohydrate, g/d;
- NfromPEP_{A,B1} = rates of N uptake as peptides by bacteria fermenting A or B1 carbohydrate, g/d;
- fracA = fraction of NSC cell mass derived from A carbohydrate, g/g; and
- fracB1 = fraction of NSC cell mass derived from B1 carbohydrate, g/g.

Equations for degrA_j and degrB1_j are provided in Sniffen et al. (1992). Rate of ammonia and peptide uptake is described in Russell et al. (1992). It is assumed in the above equations that peptides taken up are divided between the A and B1 fermenting bacteria in proportion to their rates of cell mass production.

Based on gas production yields reported in the literature (Wolin, 1960; Sutton, 1985; Strobel and Russell, 1986; Pell and Schofield, 1993), it is assumed that 34.4% of the degraded A and B1 carbohydrates and 54% of the degraded B2 carbohydrate are converted to non-acid end products (sensitivity to this assumption is tested later). Thus, the acid production rates are as follows:

$$\text{Acidprod}^A = \text{Endprod}^A - .344 \sum_j \text{degrA}_j \quad [16]$$

$$\text{Acidprod}^{B1} = \text{Endprod}^{B1} - .344 \sum_j \text{degrB1}_j \quad [17]$$

$$\text{Acidprod}^{B2} = \text{Endprod}^{B2} - .540 \sum_j \text{degrB2}_j \quad [18]$$

where Acidprod^{A,B1,B2} = rates of acid production from A, B1, or B2 carbohydrate, g/d. Sutton (1985) reported VFA yields of 1.5 to 8.3 mol/kg of degraded carbohydrate for acetate and .8 to 3.8 mol/kg for propionate. Strobel and Russell (1986) indicated ranges of 1.6 to 6.1 mol/kg for acetate, 1.0 to 2.8 mol/kg for propionate, and .3 to .9 mol/kg for butyrate. Shriver et al. (1986) reported yields of 2.8 to 4.9 mol/

kg for acetate, 1.7 to 2.2 mol/kg for propionate, and 1.1 to 2.1 mol/kg for butyrate. The VFA yields from Eq. [16] to [18] were approximately 3.5, 2.2, and .7 mol/kg for acetate, propionate, and butyrate, respectively, within the range of most reported values.

The principal source of information on the division of end products among the four acids was an in vitro study by Strobel and Russell (1986), in which starch, sucrose, cellobiose, xylans, and pectin were provided to mixed ruminal bacteria in small doses on an hourly basis at two pH (6.7 and 6.0 at time zero). The reported yields of each end product were converted to mass fractions of lactate, acetate, propionate, and butyrate produced at each pH. Because there was no comparable information for NDF, the results for cellobiose and xylan were averaged and used as a first approximation of the end products of B2 digestion (sensitivity to this assumption is tested later). Substantial interconversion of VFA occurs during fermentation (Armentano and Young, 1983), so the results of Strobel and Russell (1986) were considered net production of individual VFA. Lacking information between pH 6.7 and 6.0, a simplistic linear relation was used to interpolate between the two pH (at the lower pH, the final values of 5.5 to 5.9 were used).

$$f_L^A = 2.444 - .308 \text{ pH} \quad [19]$$

$$f_L^{B1} = 3.292 - .473 \text{ pH} \quad [20]$$

$$f_L^{B2} = 0 \quad [21]$$

$$\text{Ac:PA} = -1.302 + .465 \text{ pH} \quad [22]$$

$$\text{Ac:PB1} = 5.013 - .535 \text{ pH} \quad [23]$$

$$\text{Ac:PB2} = .274 + .239 \text{ pH} \quad [24]$$

$$f_B^A = .567 - .0575 \text{ pH} \quad [25]$$

$$f_B^{B1} = .737 - .0922 \text{ pH} \quad [26]$$

$$f_B^{B2} = .482 - .060 \text{ pH} \quad [27]$$

where

$f_L^{A,B1,B2}$ = mass fraction of lactate produced from A, B1, or B2 carbohydrate, g/g;

Ac:PA,B1,B2 = acetate:propionate mass ratio produced from A, B1, or B2 carbohydrate, g/g; and

$f_B^{A,B1,B2}$ = mass fraction of butyrate produced from A, B1, or B2 carbohydrate, g/g.

For comparison, a set of equations to replace Eq. [19] to [27] was developed from the empirical stoichiometry of Murphy et al. (1982), in which ruminal concentrations of acetate, propionate, and butyrate were used to infer relative production rates of VFA from sugar, starch, and NDF in high-forage and high-concentrate diets. For the two types of diets, we assumed ruminal pH of 6.7 and 6.0, respectively, and linear interpolation was performed as before.

The rates of lactate and VFA production from each carbohydrate then are calculated as follows:

$$\text{Lactprod}^{A,B1,B2} = f_L^{A,B1,B2} \cdot \text{Acidprod}^{A,B1,B2} \quad [28]$$

$$\text{VFAProd}^{A,B1,B2} = (1 - f_L^{A,B1,B2}) \cdot \text{Acidprod}^{A,B1,B2} \quad [29]$$

$$\text{Butprod}^{A,B1,B2} = f_B^{A,B1,B2} \cdot \text{VFAProd}^{A,B1,B2} \quad [30]$$

$$\text{Proprod}^{A,B1,B2} = (1 - f_B^{A,B1,B2}) \cdot \text{VFAProd}^{A,B1,B2} / (1 + \text{Ac:P}^{A,B1,B2}) \quad [31]$$

$$\text{Acetprod}^{A,B1,B2} = \text{Proprod}^{A,B1,B2} \cdot \text{Ac:P}^{A,B1,B2} \quad [32]$$

where

$\text{Lactprod}^{A,B1}$ = rates of lactate production from A or B1 carbohydrate, g/d;

$\text{VFAProd}^{A,B1,B2}$ = rates of VFA production from A, B1, or B2 carbohydrate, g/d;

$\text{Butprod}^{A,B1,B2}$ = rates of butyrate production from A, B1, or B2 carbohydrate, g/d;

$\text{Proprod}^{A,B1,B2}$ = rates of propionate production from A, B1, or B2 carbohydrate, g/d; and

$\text{Acetprod}^{A,B1,B2}$ = rates of acetate production from A, B1, or B2 carbohydrate, g/d.

The stoichiometric procedure of Wolin (1960) was used to calculate methane production as follows:

$$Y_{\text{CH}_4}^{A,B1,B2} = \left(\frac{1}{2 \cdot \text{fracP}^{A,B1,B2}} - \frac{3}{4} \right) \frac{16}{74} \quad [33]$$

$$\text{fracP}^{A,B1,B2} = [\text{Proprod}^{A,B1,B2}/74] / [(\text{Acetprod}^{A,B1,B2}/60) + (\text{Proprod}^{A,B1,B2}/74) + (\text{Butprod}^{A,B1,B2}/88)] \quad [34]$$

where $Y_{\text{CH}_4}^{A,B1,B2}$ = mass of methane per mass of propionate produced from A, B1, or B2 carbohydrate, g/g; and $\text{fracP}^{A,B1,B2}$ = propionate produced as a molar percentage of VFA from A, B1, or B2 carbohydrate, mol/mol. Multiplying methane yield by rate of propionate production (Eq. [31]) gives rate of methane production. Calculated methane yields were within 15% of those measured by Strobel and Russell (1986) at pH 6.7; at pH 6.0, methane production was virtually eliminated in these experiments. A simple relation was used to reduce methanogenesis to zero at pH 6.0:

$$r_{\text{CH}_4}^{\text{pH}} = \begin{cases} (\text{pH} - 6)/.7, & 6 \leq \text{pH} \leq 6.7 \\ 0, & \text{pH} < 6 \end{cases} \quad [35]$$

$$\text{Methprod}^{A,B1,B2} = Y_{\text{CH}_4}^{A,B1,B2} \cdot \text{fracP}^{A,B1,B2} \cdot r_{\text{CH}_4}^{\text{pH}} \quad [36]$$

where $r_{\text{CH}_4}^{\text{pH}}$ = relative methane production as a function of pH; and $\text{Methprod}^{A,B1,B2}$ = rates of methane production from A, B1, or B2 carbohydrate, g/d.

Lactate Conversions in the Rumen. In the rumen, a portion of the lactate is converted to acetate, propionate, and butyrate. Counotte et al. (1981) found that *Megasphaera elsdenii* was responsible for the majority of ruminal lactate fermentation; propionate was the principal product. In this section, equations are developed to describe growth and end product production by *M. elsdenii* as affected by pH.

In Therion et al. (1982) net growth rate of *M. elsdenii* on lactate was .58/h at an optimum pH of approximately 6.0, and the pH range for growth was 4.0 to 7.5 when the inocula had been cultured on lactate. On the basis of these data, the following equation is used to relate net growth rate to pH (respective r^2 of .998 and .998):

$$\mu^L = \begin{cases} -3.631 + 1.255 \text{ pH} - .0925(\text{pH})^2, & 4.18 \leq \text{pH} \leq 6.07 \\ -6.906 + 2.636 \text{ pH} - .2311(\text{pH})^2, & 6.07 \leq \text{pH} \leq 7.33 \end{cases} \quad [37]$$

where μ^L = net growth rate of *M. elsdenii* on lactate, h^{-1} .

Yield of *M. elsdenii* was measured at four pH and three dilution rates in continuous culture (Russell and Allen, 1984). At each pH, a Pirt plot was formed, and estimates of maintenance coefficient and maximum yield were obtained ($r^2 = .751, .999, .990, .979$ at pH 5.4, 5.8, 6.2, 6.6, respectively). Linear regression of these variables against pH gave the following (respective r^2 of .972 and .953):

$$Y_{\text{max}}^L = \begin{cases} -1.176 + .232 \text{ pH}, & \text{pH} \geq 5.07 \\ 0, & \text{pH} < 5.07 \end{cases} \quad [38]$$

$$m^L = -2.779 + .664 \text{ pH} \quad [39]$$

where Y_{max}^L = maximum yield of *M. elsdenii* on lactate, g/g; and m^L = maintenance coefficient of *M. elsdenii* on lactate, g/(g·h). The observed yield calculated with the Pirt equation is 0 at pH 5.07, .149 at pH 6.0, and .142 at pH 6.7. The digestion rate of lactate then is obtained from

$$k_d^L = (\mu^L + m^L Y_{\text{max}}^L) \cdot 24 \quad [40]$$

where k_d^L = digestion rate of lactate, d^{-1} .

Of the cell mass produced by *M. elsdenii* on lactate, 14.4% is assumed to derive from ash and N from ammonia; the remaining 85.6% is from lactate. In Counotte et al. (1981), propionate as a fraction of total end products reached a minimum of .33 at pH 6, acetate fraction reached a minimum of .19 at pH 5.65, and butyrate fraction reached a maximum of .3 at pH 5.5. Piecewise linear equations are used to represent these data:

$$f_A^L = \begin{cases} 1.035 - .154 \text{ pH}, & 4 \leq \text{pH} \leq 5.65 \\ -1.089 + .222 \text{ pH}, & 5.65 < \text{pH} \leq 8 \\ 0, & \text{otherwise} \end{cases} \quad [41]$$

$$f_P^L = \begin{cases} 1.568 - .206 \text{ pH}, & 4 \leq \text{pH} \leq 6 \\ -1.408 + .29 \text{ pH}, & 6 < \text{pH} \leq 8 \\ 0, & \text{otherwise} \end{cases} \quad [42]$$

$$f_B^L = \begin{cases} -1.181 + .27 \text{ pH}, & 4.4 \leq \text{pH} \leq 5.5 \\ 1.316 - .184 \text{ pH}, & 5.5 < \text{pH} \leq 7 \\ 0, & \text{otherwise} \end{cases} \quad [43]$$

where f_A^L = mass fraction of acetate from lactate, g/g; f_P^L = mass fraction of propionate from lactate, g/g; and f_B^L = mass fraction of butyrate from lactate, g/g. The sum $f_A^L + f_P^L + f_B^L$ is less than unity because of valerate, which accounts for 4 to 10% of VFA production (Counotte et al., 1981).

Ruminal Absorption of Volatile Fatty Acids and Lactate. Ruminal absorption of fermentation acids is associated with uptake and metabolism by the rumen epithelium and transport into the bloodstream. In this section, a simple equation is presented and coefficients are estimated for describing VFA and lactate absorption rates in the rumen.

Early studies with VFA infusion showed that the individual VFA were absorbed at different rates in the rumen and that absorption rate increased as pH decreased (Danielli et al., 1945; Gray, 1947; Johnson, 1951; Pfander and Phillipson, 1953; Tsuda, 1956). This suggests that the rumen epithelium is more permeable to undissociated acids than to dissociated acids. However, Ash and Dobson (1963) found that at pH 7 approximately half of the absorbed acetate was in the dissociated form. As in Dijkstra et al. (1993), four factors are included in modeling absorption: acid species, acid concentration, ruminal pH, and rumen epithelial surface area. On the basis of a summary in Van Soest (1994), rate of absorption is assumed to be proportional to ruminal acid concentration, which is consistent with absorption being a diffusion process. Absorption rate is also assumed proportional to epithelial surface area, a quantity difficult to determine but which can be adjusted in a relative manner with ruminal volume. Absorption coefficients for dissociated and undissociated forms of each acid are determined separately. The equation embodying these assumptions is as follows:

$$q_{\text{abs},x} = A_{\text{Ru}} C_x [K_{\text{xu}} f_{\text{xu}} + K_{\text{xd}} (1 - f_{\text{xu}})] \quad [44]$$

where

- x = A for acetate, P for propionate, B for butyrate, L for lactate;
- $q_{\text{abs},x}$ = absorption rate of acid x, mol/d;
- C_x = ruminal concentration of acid x, mol/m³;
- A_{Ru} = rumen epithelial surface area, m²;
- K_{xu} = absorption coefficient of acid x in the undissociated form, m/d;
- f_{xu} = fraction of acid x in the undissociated form, mol/mol; and
- K_{xd} = absorption coefficient of acid x in the dissociated form, m/d.

The fraction of acid in the undissociated form is a function of pH from the titration curve:

$$f_{\text{xu}} = \left[1 + 10^{(\text{pH} - \text{pK}_x)} \right]^{-1} \quad [45]$$

where $\text{pK}_x = 4.76$ for x = A, 4.87 for x = P, 4.81 for x = B, 3.86 for x = L.

To estimate the coefficients, studies were used in which rates of disappearance from isolated rumens of cattle or sheep were measured at known pH, VFA concentrations, and ruminal liquid volumes (Danielli et al., 1945; Masson and Phillipson, 1951; Thorlacius and Lodge, 1973). For each acid, the coefficients K_{xu} and K_{xd} in Eq. [44] were obtained from the absorption rates at two pH, giving two equations in the two unknown coefficients. To obtain stable estimates, the two pH had to be sufficiently different so that the system of equations was linearly independent.

Adjustment of surface area with ruminal volume is made using the following equation:

$$A_{\text{Ru}} = 4.836 \cdot (V_{\text{Ru}})^{2/3} \quad [46]$$

where V_{Ru} = ruminal liquid volume, m³. The coefficient 4.836 (derived for a sphere) is arbitrary because the absorption coefficients are determined assuming this value. The exponent 2/3 is a standard conversion from volume to surface area (Peters, 1986).

Table 1 shows the pH ranges and absorption coefficients obtained for a single trial in each of three studies (Danielli et al., 1945; Masson and Phillipson, 1951; Thorlacius and Lodge, 1973). Except for the concentrate diet of Thorlacius and Lodge (1973), the coefficients for butyrate in the dissociated form were consistent across the three studies, and those for the other acids were consistent in two of the three studies. When an exponent of 3/4 (as for metabolic body weight) was used in Eq. [46], the discrepancy among the three studies increased. For the model, the largest of the three coefficients is used (Table 1). Absorption coefficients for the undissociated forms are 3 to 10

Table 1. Empirical absorption coefficients for acetate, propionate, and butyrate estimated from three studies

Parameter ^a	Danielli et al. (1945)	Masson and Phillipson (1951)	Thorlacius and Lodge (1973)		Selected value
			Hay diet	Concentrate diet	
pH range	5.85–7.5	5.7–8.15	5.41–6.55	5.78–6.53	
K _{Au} , m/d	—	.48	.18	1.11	.48
K _{Ad} , m/d	—	.12	.12	.17	.12
K _{Pu} , m/d	.28	.29	.67	2.00	.67
K _{Pd} , m/d	.21	.068	.12	.18	.21
K _{Bu} , m/d	1.43	.55	1.42	4.41	1.43
K _{Bd} , m/d	.15	.13	.14	.15	.15

^aK_{xu} = absorption coefficient for undissociated VFA; K_{xd} = absorption coefficient for dissociated VFA; x = A for acetate, P for propionate, B for butyrate.

times higher than for the dissociated forms.

In Thorlacius and Lodge (1973), coefficients for the concentrate diet are 2.7 times larger, on average, than those for the hay diet, despite the similarity in ruminal pH (Table 1). Dirksen et al. (1985) observed that in cattle acclimated to a diet with 11% fiber, papillary surface area was increased by a factor of 3.6 compared with cattle fed diets of 32 to 37% fiber; absorption rates were approximately 2.3 times higher for low-fiber diets than for high-fiber diets. Thus, a surface area adjustment is used to increase absorptive area by a factor of 2.3 as dietary NDF decreases from 32 to 11% NDF:

$$r_{A_{Ru}}^{NDF} = 3 - .062 (\%NDF), \%NDF \leq 32$$

$$1, \%NDF > 32 \quad [47]$$

$$A_{Ru} = 4.836(V_{Ru}^{2/3}) r_{A_{Ru}}^{NDF} \quad [48]$$

where $r_{A_{Ru}}^{NDF}$ = ruminal surface area adjustment factor.

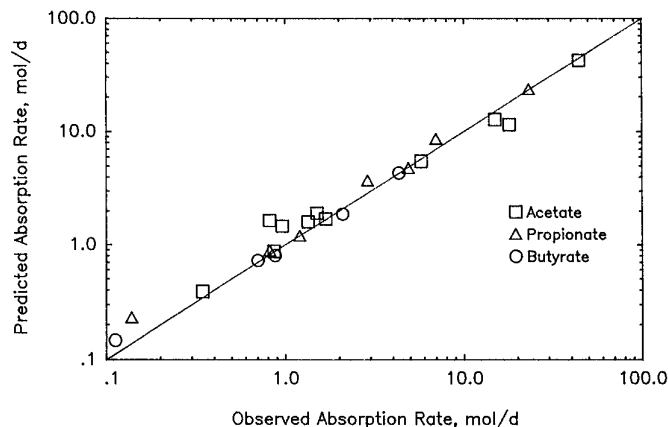


Figure 2. Predicted vs observed absorption rates of VFA from the rumen for several validation studies ($r^2 = .985$). Solid line is $y = x$.

In using these equations, we assume that diets have been fed long enough that the rumen has adapted. Equation [48] is used in place of Eq. [46].

Figure 2 shows comparisons between predicted and observed absorption rates in trials not used in obtaining the coefficients (Danielli et al., 1945; Masson and Phillipson, 1951; Dirksen et al. 1985), as well as data for steers (Peters et al. 1990, 1992) and sheep (Williams and MacKenzie, 1965). Linear regression between observed and predicted data produced a slope of .938 and an r^2 of .985.

Dijkstra et al. (1993) developed a model of ruminal VFA absorption as dependent on VFA species and concentration, pH, and ruminal volume; five empirical coefficients were estimated from data collected from isolated rumens of dairy cattle at several pH. Compared with the test data of Figure 2, the Dijkstra et al. (1993) equation predicted absorption rates that were consistently high by a factor of 2.2 on average. This indicates that absorption rates measured in the Dijkstra et al. (1993) study were higher than those of the test data of Figure 2. This discrepancy raises the

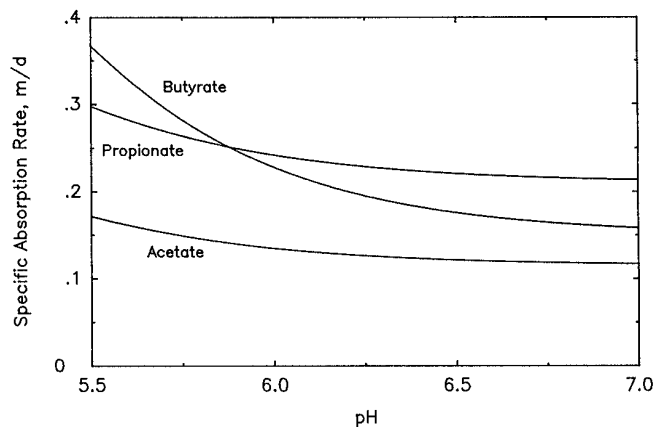


Figure 3. Predicted effect of pH on specific absorption rate (absorption rate per unit rumen surface area and per unit concentration) for acetate, propionate, and butyrate, calculated using the current model.

Table 2. Equations for silage lactate C_L^j , acetate C_A^j , and butyrate C_B^j concentrations (% of DM) as a function of percentage DM content x (%)

Crop type ^a	Lactate C_L^j	Acetate C_A^j	Butyrate C_B^j
Legumes ($20 \leq x \leq 50$)	$4 + (x - 20)^{2.94} e^{-.59(x - 20)}$	1.5	$8e^{-[(x - 20)/4.04]^5}$
Grasses ($20 \leq x \leq 50$)	$-29.2 + 1.61x, x \leq 23.75$ $14.9 - .25x, x > 23.75$	$2.7 - .029x$	$9e^{-[(x - 20)/4.04]^5}$
Cereals ($20 \leq x \leq 40$)	$-19.4 + 1.07x, x \leq 23.75$ $11.1 - .21x, x > 23.75$	$2.5 - .047x$	$6e^{-[(x - 20)/4.04]^5}$

^aRange of x in parentheses.

possibility that absorption rates should be higher than are presently in the model (sensitivity to absorption rate is considered later).

Figure 3 shows calculated absorption rates at various pH for each VFA. Absorption rate is predicted to increase significantly as pH falls below 6.0, and this effect is most pronounced for butyrate. Below pH 5.8, absorption rate increases with VFA molecular weight; above pH 5.8, propionate and butyrate are reversed in their order of absorption. These results are consistent with the VFA absorption rankings of Gray (1947), Johnson (1951), and Pfander and Phillipson (1953).

Lactate absorption rates were based on published data for sheep (Williams and MacKenzie, 1965). Two pH (4 and 5) and two concentrations (60 and 120 mM) of lactate were used in these experiments, with pH within .3 units of initial values. Averages (\pm SD) for the seven animals in their trials are as follows:

$$\begin{aligned} K_{Lu} &= .00405 \pm .00130 \text{ m/d} \\ K_{Ld} &= .00139 \pm .00060 \text{ m/d.} \end{aligned} \quad [49]$$

These values are approximately 100 times smaller than those for the VFA and are from trials in which only lactate (no VFA) was introduced into the rumen; when VFA were present at pH 5.5, lactate absorption was even lower (Williams and MacKenzie, 1965).

Intake, Production, and Concentration of Lactate and Volatile Fatty Acids. Here we present equations to estimate intake of acids from silages; steady-state mass balances are then used to predict VFA and lactate concentrations in the rumen. Acids in silages include lactate, acetate, and possibly butyrate. Equations for predicting silage acid concentrations (Table 2) were based on data from McDonald et al. (1991) and a silage fermentation model (Pitt et al., 1985; Leibensperger and Pitt, 1987). Lactate and acetate concentrations increase as DM content decreases to 25%, after which lactate becomes partially replaced by butyrate due to clostridial spoilage. Acid concentrations increase with crop buffering capacity in the order

of cereals, grasses, and legumes. For grass and legume mixtures, an average of the two crops is used.

Intake of each acid is calculated from the acid concentration and intake of each feed:

$$\text{Lactin} = \sum_j C_L^j \cdot \text{Intake}_j / 100 \quad [50]$$

$$\text{Acetin} = \sum_j C_A^j \cdot \text{Intake}_j / 100 \quad [51]$$

$$\text{Butin} = \sum_j C_B^j \cdot \text{Intake}_j / 100 \quad [52]$$

where

- Lactin = intake of lactate from all feeds, g/d;
- Acetin = intake of acetate from all feeds, g/d;
- Butin = intake of butyrate from all feeds, g/d;
- C_L^j = concentration of lactate in feed j , % DM;
- C_A^j = concentration of acetate in feed j ; % DM;
- C_B^j = concentration of butyrate in feed j , % DM;
- and
- Intake $_j$ = DMI of feed j , g/d.

The NSC contents of silages, which previously included fermentation acids (Sniffen et al., 1992), are reduced by the calculated acid concentrations.

Production and concentrations of lactate and VFA in the rumen are obtained from steady-state mass balances, giving

$$K_{\text{abs},x} = \left(\frac{A_{\text{Ru}}}{V_{\text{Ru}}} \right) [K_{xu} f_{xu} + K_{xd}(1 - f_{xu})], \quad x = A, P, B, L \quad [53]$$

$$\text{Lact}_{\text{tot}} = \text{Lactprod}^A + \text{Lactprod}^{B1} + \text{Lactin} \quad [54]$$

$$\text{degrL} = \text{Lact}_{\text{tot}} \cdot k_d^L / (k_d^L + K_1 + K_{\text{abs},L}) \quad [55]$$

$$\text{VFAprod}^L = \text{degrL} \cdot (1 - .856Y^L) / (1 + f_A^L \frac{44}{60}) \quad [56]$$

$$\text{Acetprod}^L = f_A^L \cdot \text{VFAprod}^L \quad [57]$$

$$\text{Proprod}^L = f_P^L \cdot \text{VFAprod}^L \quad [58]$$

$$\text{Butprod}^L = f_B^L \cdot \text{VFAprod}^L \quad [59]$$

$$\text{Acet}_{\text{tot}} = \text{Acetprod}^A + \text{Acetprod}^{B1} + \text{Acetprod}^{B2} + \text{Acetprod}^L + \text{Acetin} \quad [60]$$

$$\text{Prop}_{\text{tot}} = \text{Proprod}^A + \text{Proprod}^{B1} + \text{Proprod}^{B2} + \text{Proprod}^L \quad [61]$$

$$\text{But}_{\text{tot}} = \text{Butprod}^A + \text{Butprod}^{B1} + \text{Butprod}^{B2} + \text{Butprod}^L + \text{Butin} \quad [62]$$

$$C_A = \text{Acet}_{\text{tot}} / [(K_1 + K_{\text{abs},A}) \cdot V_{\text{Ru}} \cdot 60] \quad [63]$$

$$C_P = \text{Prop}_{\text{tot}} / [(K_1 + K_{\text{abs},P}) \cdot V_{\text{Ru}} \cdot 74] \quad [64]$$

$$C_B = \text{But}_{\text{tot}} / [(K_1 + K_{\text{abs},B}) \cdot V_{\text{Ru}} \cdot 88] \quad [65]$$

$$C_L = \text{Lact}_{\text{tot}} / [(k_d^L + K_1 + K_{\text{abs},L}) \cdot V_{\text{Ru}} \cdot 90] \quad [66]$$

where

$K_{\text{abs},x}$ = fractional absorption rate of acid x, d^{-1} ;

Lact_{tot} = total rate of lactate production and intake, g/d;

degr^L = degradation rate of lactate, g/d;

Endprod^L = end product production rate from lactate, g/d;

Acetprod^L = rate of acetate production from lactate, g/d;

Proprod^L = rate of propionate production from lactate, g/d;

Butprod^L = rate of butyrate production from lactate, g/d;

Acet_{tot} = total rate of acetate production and intake, g/d;

Prop_{tot} = total rate of propionate production and intake, g/d;

But_{tot} = total rate of butyrate production and intake, g/d; and

K_1 = liquid passage rate, d^{-1} .

Ruminal Volume and Liquid Passage Rate. Ruminal liquid volume and passage rate are required in the above equations and must be estimated for studies in which these quantities are not measured. Fox et al. (1990) used the following equation for liquid passage rate:

$$K_1 = 1.059 + .0458 \text{ DMI/BW} \quad [67]$$

where BW = body weight, kg; and K_1 has units of per day and DMI has units of grams per day. Liquid passage rates from Eq. [67] were compared with measured values in the literature (Rogers and Davis, 1982a,b; Sharp et al., 1982; Johnson et al., 1988; Vanzant et al., 1990; Cameron et al., 1991; Klusmeyer et al., 1991; Nocek, 1992; Beauchemin and Rode, 1994; Mansfield and Stern, 1994), giving an r^2 of .748. The equation underestimated liquid passage rate when it exceeded 13%/h. The accuracy might be improved by incorporating the effect of osmotic pressure on liquid flow (Argyle and Baldwin, 1988).

A relation between liquid volume and BW was developed from published data on dairy cows, sheep, and steers (Davis, 1967; Haaland and Tyrell, 1982; Rogers and Davis, 1982a,b; Sharp et al., 1982; Colucci, 1984; Siddons et al., 1985; Stokes et al., 1986; Johnson et al., 1988; Nelson and Satter, 1992; Nocek, 1992; Robinson and McQueen, 1992). Ruminal volumes ranged from 4.9 to 110 L and BW from 47 to 650 kg. Regression of a log-log relationship gave the following ($r^2 = .931$):

$$V_{\text{Ru}} = .0888(\text{BW})^{1.034}/1000 \quad [68]$$

with BW in kilograms and V_{Ru} in cubic meters. Although the r^2 was $>.9$, liquid volumes would not be predicted accurately within a given animal type because of fluctuations with intake, fiber level, stage of lactation, and time relative to feeding (Argyle and Baldwin, 1988).

Prediction of Ruminal pH. Ruminal pH is required as an input to the foregoing equations for digestion, end product production, and absorption. Two approaches to predicting ruminal pH are presented. The first approach relates empirical values of pH to simple dietary measures from diets reported in the literature. The second approach uses the above equations for acid production rates and combines them with new equations for ruminal buffering. The congruence of the two approaches is considered later.

Chewing activity, production of ruminal buffers, and ruminal pH are increased as forage and fiber content in the diet increases (Bailey, 1961; Cassida and Stokes, 1986; Beauchemin, 1991). Ruminal pH and dietary measures were correlated from published studies with lactating dairy cows, steers, and, in one case, sheep (Haaland and Tyrell, 1982; Haaland et al., 1982; Rogers and Davis, 1982a,b; Sharp et al., 1982; Casper and Schingoethe, 1986; Coppock et al., 1986; Olumeyan et al., 1986; Stokes et al., 1986; Sutton et al., 1986; West et al., 1986; Atkins et al., 1988; Johnson et al., 1988; Leonard and Block, 1988; Tucker et al., 1988; BenGhedalia et al., 1989; Ghorbani et al., 1989; McCarthy et al., 1989; Moran and Trigg, 1989; Voelker et al., 1989; Casper et al., 1990; Grant et al., 1990a; Newbold and Rust, 1990; Vanzant et al., 1990; Cameron et al., 1991; Klusmeyer et al., 1991; Petit and Veira, 1991; Robinson and Kennelly, 1991; Erasmus et al. 1992; Nagel and Broderick, 1992; Robinson and McQueen, 1992; Feng et al., 1993; Huhtanen et al., 1993; Oliviera et al., 1993). In studies with multiple diets, results were averaged if the diet fiber contents and pH values were similar; otherwise the diets were treated separately. Diets containing added buffers were excluded.

Figure 4 shows ruminal pH vs percentage of forage in the diets ($r^2 = .148$, $P < .05$). There was a slight increase in pH as the percentage of forage increased. The relation between ruminal pH and total NDF in

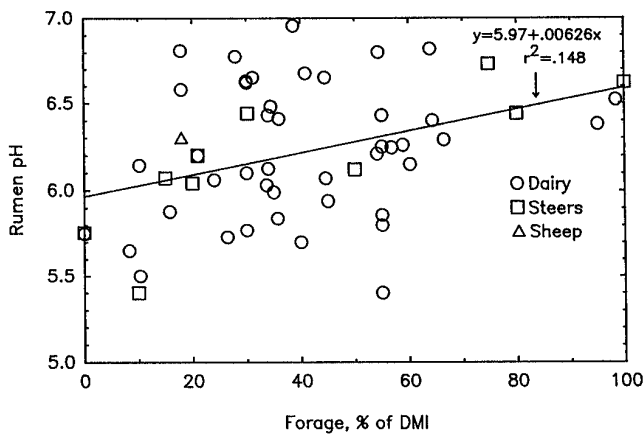


Figure 4. Empirical relation between ruminal pH and total forage in the diet DM from a number of studies.

these same studies was somewhat better (Figure 5; $r^2 = .296$, $P < .01$).

Particle size also affects rumination (Welch, 1982), and grinding the feed tends to reduce ruminal pH (Grant et al., 1990a,b). Effective fiber has been defined as the percentage of NDF in each feed, depending on its physical processing, that contributes to meeting NDF requirements (Mertens, 1992). In Figure 6, ruminal pH in these studies is plotted vs effective NDF (eNDF) in the diets, where eNDF is calculated as the sum of each dietary component as tabulated in Sniffen et al. (1992). None of the variation in ruminal pH was explained for eNDF greater than 30%, but as eNDF decreased, ruminal pH decreased. Differences among animal types were not apparent (although more data on sheep might seem to be anomalous because of their longer rumination times). A line was regressed to the data below 30%

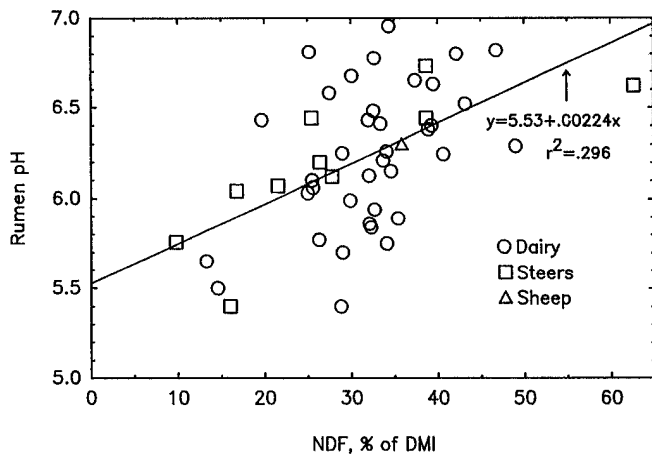


Figure 5. Empirical relation between ruminal pH and total NDF in the diet DM from the same studies as in Figure 4.

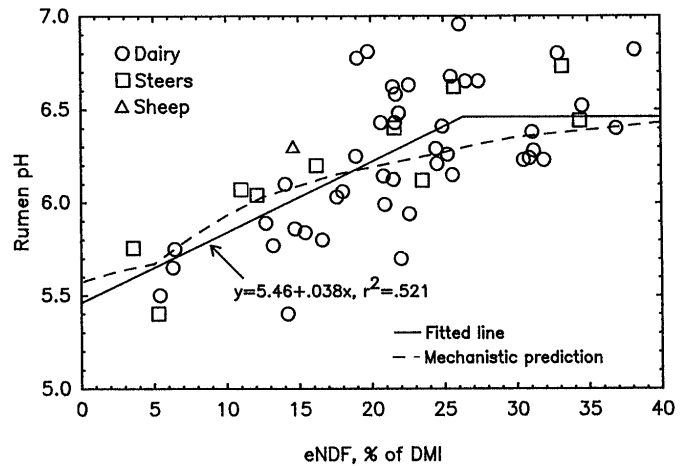


Figure 6. Empirical relation between ruminal pH and effective NDF (eNDF) in the diet DM from the same studies as in Figure 4. Also shown is the mechanistically predicted curve based on ruminal buffering and acidity.

eNDF ($r^2 = .521$, $P < .001$); for eNDF higher than 30%, a simple average was calculated. The empirical equation for ruminal pH is as follows:

$$\text{pH} = \begin{cases} 5.46 + .038 (\text{eNDF}), & \text{eNDF} < 26.3\% \\ 6.46, & \text{eNDF} > 26.3\% \end{cases} \quad [69]$$

Equation [69] is restricted to diets without added buffers.

In the mechanistic approach to predicting ruminal pH, the acidity of ruminal liquid is calculated through a range of pH values using the VFA production and concentration equations. The buffering of ruminal liquid is also calculated through a range of pH. The pH at which buffering and acidity are equal is taken as the equilibrium ruminal pH.

Two contributions to ruminal buffering are saliva and rumen-resident NDF. Dijkstra et al. (1992) developed an equation from literature data (Bailey, 1961; Cassida and Stokes, 1986) to predict salivary flow in dairy cows from DMI and diet NDF. To incorporate the effect of particle size on rumination, we converted the NDF values in these diets to eNDF (Sniffen et al., 1992), and saliva flow was then regressed against DMI and percentage of eNDF ($r^2 = .978$):

$$D_s = -177.2 + .01638(\text{DMI}) + 4.766(\text{eNDF}) \quad [70]$$

where D_s = saliva production, L/d; and DMI is in grams per day and eNDF is a percentage of diet DM. This equation is valid only for D_s greater than 100 L/d.

The buffering of saliva is proportional to saliva volume. Concentration of saliva in the rumen is calculated from

$$C_s = \frac{D_s}{1000V_{Ru}K_1} \quad [71]$$

where C_s = saliva concentration in the rumen, L/L; and V_{Ru} is in cubic meters and K_1 is per day. The buffering capacity of saliva (Van Soest, 1994) is approximated by a theoretical titration curve with pK of 6.4:

$$BC_s = -33.3 + \frac{165.8}{1 + 10^{(pH - 6.4)}} \quad [72]$$

where BC_s = buffering capacity of saliva from pH 7 to any given pH, mEq/L of saliva.

Buffering curves for NDF (McBurney et al., 1983) were approximated by an exponential relationship:

$$BC_{NDF} = -.004 + .3e^{-(pH - pH_c)} \quad [73]$$

where BC_{NDF} = buffering capacity of NDF, mEq/g of NDF; and pH_c = reference pH. Reference pH varies with the source of NDF and is related to NDF cation exchange capacity for different feeds (McBurney et al., 1983) ($r^2 = .655$):

$$pH_c = 2.388 + .00078(CEC_{NDF}) \quad [74]$$

where CEC_{NDF} = cation exchange capacity of cell wall, mmol/kg of NDF.

Concentration of NDF resident in the rumen is calculated from a steady-state mass balance:

$$C_{NDF} = \sum_j (\text{degr}B2_j/k_{dj}^{B2}) / (1000V_{Ru}) \quad [75]$$

where C_{NDF} = NDF concentration in the rumen, g/L.

The total buffering of ruminal liquid is the sum of the contributions from saliva and NDF:

$$BC_1 = C_s BC_s + C_{NDF} BC_{NDF} \quad [76]$$

where BC_1 = buffering capacity of ruminal liquid from pH 7 to any given pH, mEq/L.

Total acidity of ruminal liquid is the sum of the contributions from acetate, propionate, butyrate, and lactate, adjusted for degree of dissociation using the titration function:

$$C_{acid} = C_A(1 - f_{Au}) + C_P(1 - f_{Pu}) + C_B(1 - f_{Bu}) + C_L(1 - f_{Lu}) \quad [77]$$

where C_{acid} = total acidity of the rumen, mEq/L; and f_{xu} is from Eq. [45]. Each variable on the right side of Eq. [76] and [77] is a function of ruminal pH. After calculation of BC_1 and C_{acid} through a range of pH, the pH at which $C_{acid} = BC_1$ is taken as equilibrium ruminal pH.

Results

Model Evaluation and Sources of Error. Predictions of total VFA concentration and VFA fractions were compared with studies in which diet, intake, ruminal pH, and in some cases ruminal liquid volume and liquid passage rate were measured (Rogers and Davis, 1982a,b; Stokes et al., 1986; Johnson et al., 1988; McCarthy et al., 1989; Grant et al., 1990a; Vanzant et al., 1990; Cameron et al., 1991; Klusmeyer et al., 1991; Robinson and Kennelly, 1991). In some studies, more than one diet was tested. The primary objective was to test predictions of VFA production, absorption, and concentration. Reported ruminal pH was used as an input to the model. These studies were not used to develop the VFA production, absorption, or passage equations.

In initial comparisons, predicted VFA concentrations were high by 50 to 75%. Potential sources of bias include low VFA absorption rates and high VFA production rates. As discussed earlier, the VFA absorption model was low in comparison to the model of Dijkstra et al. (1993) but was unbiased when tested against other studies (Figure 2).

Production rates of acetate and propionate in comparison with one study (Rogers and Davis, 1982b) were high by 50 and 30%, respectively (11.1 vs 7.3 mol/d for acetate, 6.5 vs 4.8 mol/d for propionate). Production rates would be high if the yield of VFA per unit of degraded carbohydrate was high, but calculated yields were shown earlier to be within reported ranges (Sutton, 1985; Shriver et al., 1986; Strobel and Russell, 1986).

Production rates of VFA are inflated if carbohydrate digestion in the model is too high. Low passage rates, high pH, or high digestion rates would increase carbohydrate digestion (Chalupa et al., 1991). For the B2 carbohydrate, digestion rates are 4 to 9%/h (Sniffen et al., 1992), which are comparable to literature values (Grant and Mertens, 1992; Grant and Weidner, 1992; Pell and Schofield, 1993). Digestion rates for B1 carbohydrate are 15 to 30%/h, and rates for A carbohydrate are 150 to 300%/h (Sniffen et al., 1992). Model runs were performed in which digestion rates for both the A and B1 carbohydrates were limited to 13%/h, but the resulting VFA concentrations were reduced by less than 6% and were therefore still high.

In the model, 80 to 90% of dietary starch and pectin is ruminally digested. Ruminal starch digestion in lactating dairy cows in three of the validation studies was reported to be 50 to 75% (McCarthy et al., 1989), 40 to 50% (Klusmeyer et al., 1991), and 35 to 50% (Cameron et al., 1991) in diets with 40 to 45% ground shelled corn and 20% corn silage. Kung et al. (1992)

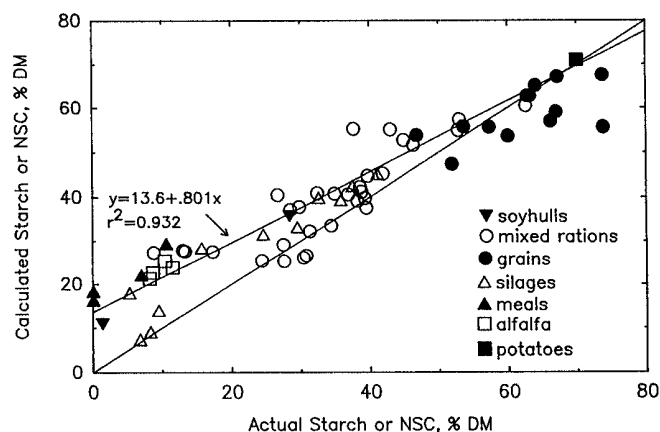


Figure 7. Relation between enzymatically determined starch or NSC contents of feeds or whole diets, and the values calculated by subtraction of NDF, CP, fat, and ash from 100%. Line shown is a regression of the data for less than 50% starch or NSC.

measured ruminal starch digestion of 75 to 80% in diets of 50% ground corn fed to steers. In a diet of 25% ground shelled corn and 25% corn silage fed to lactating dairy cattle (Stokes et al., 1991), ruminal starch digestion was 45 to 75%. An *in vitro* study on barley and cornstarch (McAllister et al., 1993) found ruminal digestibility to be 70%, which is also close to the 66 and 73% digestibilities of sorghum and cornstarch, respectively (Theurer, 1986). In a broad summary by Nocek and Tamminga (1991), ruminal starch digestibility varied from 50 to 90% and was highly dependent on source and processing of starch. Thus, one change in the model was to apply a 70% ruminal digestibility to the B1 carbohydrate for all feeds, although this figure should depend on individual feed, its processing, and its starch and pectin characteristics.

In the model, starch or NSC contents of feeds were calculated by subtraction of CP, NDF, fat, and ash from 100% (Sniffen et al., 1992). However, these calculations are known to differ from starch or NSC contents determined by enzymatic procedures (Mertens, 1992; Feng et al., 1993). Figure 7 shows calculated vs measured starch or NSC contents in feeds and whole diets reported in the literature (McDonald et al., 1981; Theurer, 1986; Rosenberg and Rinne, 1987; Sniffen, 1988; Colucci et al., 1989; Nakamura and Owen, 1989; Schoenherr et al., 1989; Valdez et al., 1989; Weiss et al., 1989; Cone and Wolters, 1990; Vanzant et al., 1990; Robinson et al., 1991; Robinson and Kennelly, 1991; Shockey and Barta, 1991; Stokes et al., 1991; Waybright and Varga, 1991; Wilks et al., 1991; Kung et al., 1992; Sarwar et al., 1992; Wester et al., 1992; Feng et al., 1993; McAllister et al., 1993). For feeds less than 50% starch or NSC, including alfalfa, soybean meal,

cottonseed meal, and corn silage, calculated values were generally higher than actual values. For feeds high in starch or NSC, including grains and potatoes, calculated values were satisfactory or even low. For whole diets, the discrepancies were intermediate. A regression line was formed between measured and calculated starch or NSC contents for feeds less than 50% starch or NSC (Figure 7, $r^2 = .932$). Reversing this equation gave the second change in the model:

$$\text{NSC} = \begin{cases} 0, & \text{NSC}_{\text{calc}} \leq 13.59\% \\ -16.97 + (1.249 \cdot \text{NSC}_{\text{calc}}), & 13.59 < \text{NSC}_{\text{calc}} < 50\% \\ \text{NSC}_{\text{calc}}, & \text{NSC}_{\text{calc}} > 50\% \end{cases}$$

[78]

where NSC = corrected NSC content of feeds, % DM; and NSC_{calc} = NSC content of feeds calculated by subtraction, % DM. The division of NSC between A and B1 carbohydrate was not changed from Sniffen et al. (1992).

After incorporation of these changes, predicted and observed ruminal concentrations of VFA (sum of acetate, propionate, and butyrate) for the validation studies were closer (Figure 8). Regression gave a slope of .956, an r^2 of .892 ($P < .001$), and a root mean square error in VFA concentration of 11.6 mM.

Predicted and observed molar fractions of acetate, propionate, and butyrate are plotted in Figure 9. Linear regression produced a slope of .926 and an r^2 of .943. However, taken separately, predicted VFA fractions were poorly correlated with the data and were insensitive to variations in the evaluation studies. When the equations for VFA fractions based on Murphy et al. (1982) replaced those based on Strobel and Russell (1986) (Figure 10), the slope was .985 but r^2 decreased to .881. Using only the acetate:propionate ratios from Murphy et al. (1982) reduced the scatter in Figure 10, but the acetate fraction was high and the propionate fraction was low. Ruminal lactate concentrations were measured in one study (Robinson and Kennelly, 1991). Predicted values were low, varying from 3 to 10 mM compared with 5 to 23 mM (slope = .250, $r^2 = .214$).

Sensitivity Analysis. Given the uncertainty in several model parameters, the sensitivity of the model to variations in certain parameters was tested. The objective was to determine which parameters need to be known with the greatest certainty.

Table 3 shows model results as various inputs and parameters were changed. The base run (first column) was for a published diet (Johnson et al., 1988) with dairy cows fed 40% corn silage, 10% alfalfa silage, 36.5% corn grain, 11% soybean meal 44, and .5% urea. Dry matter intake was 19.5 kg/d, ruminal pH was 6.1, liquid passage rate was 11.4%/h, and ruminal liquid volume was 87 L. Each column shows the results of changing only a single variable, leaving all others the same as in the base run.

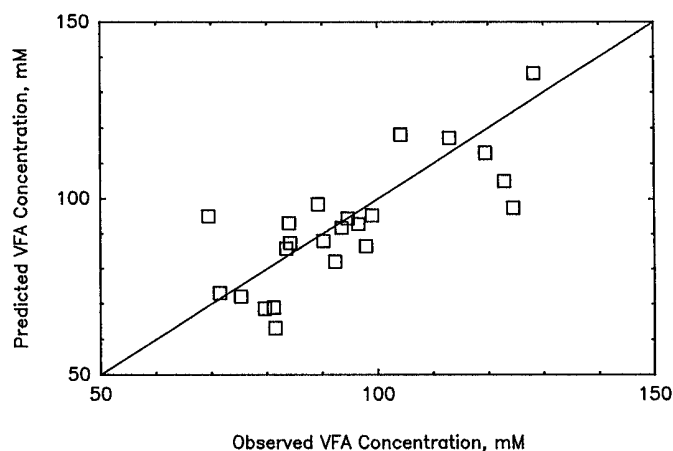


Figure 8. Predicted vs observed total VFA concentrations for the validation studies ($r^2 = .862$). Solid line is $y = x$.

Ruminal pH was first increased to 6.7 and then decreased to 5.7 (Table 3). At the lower pH, amounts of A and B1 carbohydrate degraded were only slightly reduced, whereas digestion of B2 carbohydrate decreased slightly at pH 6.7 and decreased by 35% at pH 5.7. Total concentrations of VFA varied by approximately 10% as pH increased or decreased. Lactate concentrations varied inversely with and were sensitive to pH. Fractions of individual VFA were minimally affected at the higher pH, but at the lower pH, propionate was increased and acetate was decreased. The absorbed fraction of VFA increased as pH decreased; acetate had the lowest absorbed fraction of the three VFA, whereas butyrate absorption was most sensitive to pH.

Ruminal liquid volume was increased by 26% to 110 L or decreased by 26% to 64 L (Table 3). This spans

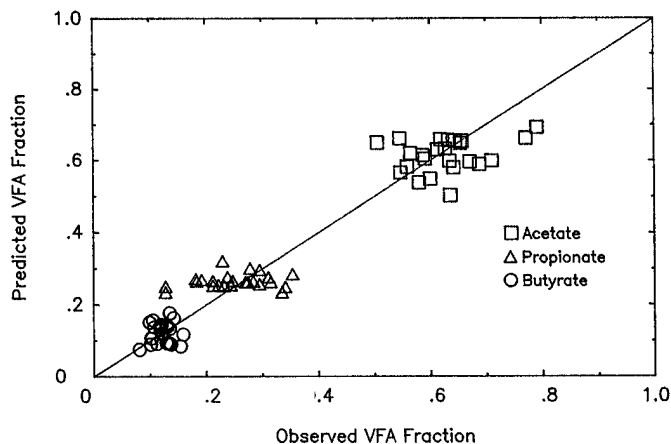


Figure 9. Predicted vs observed VFA molar fractions of acetate, propionate, and butyrate for the validation studies ($r^2 = .943$). Solid line is $y = x$.

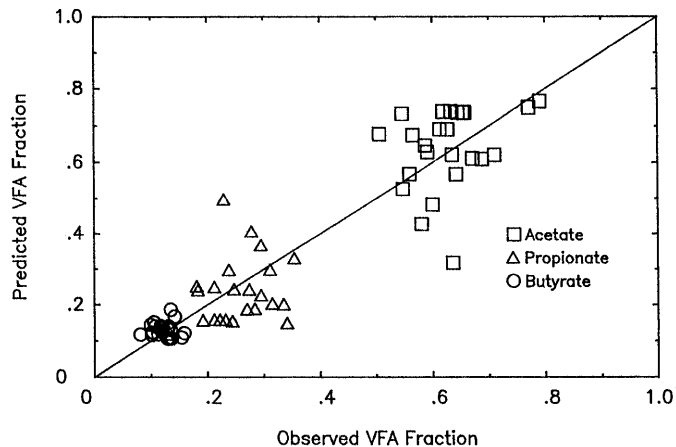


Figure 10. Predicted vs observed VFA molar fractions of acetate, propionate, and butyrate for the validation studies ($r^2 = .881$), using the empirical coefficients of Murphy et al. (1982). Solid line is $y = x$.

the range of values for dairy cows in the studies used to develop Eq. [68]. Total VFA and lactate concentrations varied inversely with ruminal volume, indicating the importance of liquid volume in VFA predictions. As ruminal volume increases, surface:volume ratio decreases, thereby reducing absorption of VFA (Table 3).

When absorption coefficients for the VFA were varied by a factor of two (Table 3), absorbed fractions varied by less than two because of competition between absorption and passage. Molar fractions changed with absorption because of differences in the absorption coefficients among the individual VFA (Table 1).

Limiting digestion rates of A and B1 carbohydrates to 13%/h reduced the digestion of A carbohydrate substantially, owing to its initially high digestion rate of 150 to 300%/h; digestion of B1 carbohydrate was only slightly affected. Because most VFA was produced from B1 carbohydrate, total VFA and lactate concentrations were largely unaffected.

When the coefficients for production of end products other than acids were varied by 20% (.344 and .54 in Eq. [16] to [18]), total VFA concentrations were changed by 14 to 17% (Table 3), indicating sensitivity.

Changing liquid passage rate by 50% significantly affected total VFA concentration. Acetate became slightly more predominant with lower liquid passage rate because of different rates of absorption of propionate and acetate (Table 1).

When yield of SC and NSC bacteria was varied by 20%, total VFA and lactate concentrations were affected very little (Table 3). Digestion of B2 carbohydrate was slightly affected by microbial yield, because digestion rates were adjusted for microbial yield at various pH (Eq. [4]).

Table 3. Sensitivity of the volatile fatty acid model to changes in selected inputs or parameters^a

Item	Base run ^b	pH 6.7	pH 5.7	V _{Ru} × 1.26	V _{Ru} × .74	K _{abs} × 2	K _{abs} /2	K _d ^{max} = 13%/h	non-VFA non-VFA × 1.2	K _i × 1.5	K _i /1.5	Y × 1.2	Y /1.2	D ^{B1} = 85%	D ^{B1} = 100%	A.P:B2 × 1.5	Ac:P:B2 × 2.5
degrA, g/d	820	820	820	820	820	820	820	590	820	820	820	820	820	820	820	820	820
degrB1, g/d	2,860	2,860	2,810	2,860	2,860	2,860	2,860	2,770	2,860	2,860	2,860	2,860	2,860	3,470	4,090	2,860	2,860
degrB2, g/d	2,190	2,140	1,590	2,190	2,190	2,190	2,190	2,190	2,190	2,190	2,190	2,420	2,040	2,190	2,190	2,190	2,190
CVFA, mM	94	108	86	77	123	68	118	93	78	108	71	91	97	104	115	95	96
Molar fractions																	
Acetate	.62	.64	.56	.62	.62	.64	.60	.62	.62	.61	.63	.62	.62	.62	.62	.64	.66
Propionate	.26	.28	.29	.26	.26	.25	.28	.26	.26	.27	.25	.26	.26	.26	.26	.24	.23
Butyrate	.12	.08	.15	.12	.12	.11	.12	.12	.12	.12	.12	.12	.12	.12	.12	.12	.12
Fraction absorbed																	
Acetate	.34	.32	.38	.33	.37	.51	.21	.34	.34	.26	.44	.34	.34	.34	.34	.34	.34
Propionate	.48	.46	.52	.46	.51	.65	.32	.48	.48	.38	.58	.48	.48	.48	.48	.48	.48
Butyrate	.46	.40	.54	.44	.48	.63	.30	.46	.46	.36	.56	.46	.46	.46	.46	.46	.46
C _L , mM	7.1	3.7	11.7	5.6	9.6	7.1	7.1	6.9	6.5	6.7	7.4	6.9	7.3	7.9	8.6	7.1	7.1
Methane, mol/d	1.07	8.56	0	1.07	1.07	1.07	1.07	1.05	.84	1.07	1.07	1.03	1.10	1.19	1.32	1.15	1.23

^aV_{Ru} = rumen liquid volume; K_{abs} = VFA absorption coefficients; k_d^{max} = maximum digestion rate for A and B1 carbohydrates; non-VFA = yield of non-acid end products from carbohydrate digestion; K_i = ruminal liquid passage rate; Y = yield of all microbial groups; D^{B1} = maximum ruminal digestibility of B1 carbohydrate; A:P:B2 = acetate to propionate ratio of VFA produced from B2 carbohydrate; degrA, degrB1, degrB2 = rates of ruminal digestion of A, B1, B2 carbohydrate; CVFA = total VFA concentration in the rumen; C_L = lactate concentration in the rumen.

^bBase run: pH = 6.7, V_{Ru} = 10.5 L/h, DMI = 10.5 L/h, Y = 11.4 g/h.

Increasing ruminal B1 digestibility from 70 to 85 or 100% caused substantial increases in VFA and lactate concentrations (Table 3). This reiterates the importance of ruminal B1 carbohydrate digestibility in VFA predictions.

Finally, the acetate:propionate ratio for VFA produced from B2 carbohydrate (Eq. [24]) was increased by a factor of 1.5 or 2.5 (Table 3). The resulting acetate:propionate ratios in the rumen were changed by much less than this, because most VFA were produced from the B1 fraction.

Overall, ruminal VFA predictions were least sensitive to A and B1 digestion rates, microbial yield, and acetate:propionate ratios from NDF digestion. Predictions were most sensitive to ruminal pH, ruminal liquid volume, yield of non-acid end products, liquid passage rate, and ruminal B1 digestibility.

Model Results with Added Buffers. Here we use the model to determine which of several reported effects were most important in a study with dietary buffers. In a study by Rogers and Davis (1982b), Holstein steers were fed diets of 50% corn silage, 42% ground shelled corn, and 6.5% soybean meal with or without 5% sodium bicarbonate. Without the buffer, DMI was 5.15 kg/d, ruminal liquid volume was 15.5 L, liquid passage rate was 10.6%/h, and ruminal pH was 5.8. With added buffer, ruminal pH was increased to 6.04, liquid volume increased to 18.7 L, liquid passage rate increased to 11.3%/h, and DMI increased to 5.58 kg/d.

Table 4 shows a series of calculations in which each effect was incorporated individually in the model. When ruminal pH was increased (2nd row), VFA concentration and the acetate:propionate ratio predicted by the model were increased. Lactate concentration was decreased, and the absorbed fraction decreased slightly for all VFA. When DMI was increased (3rd row), total VFA and lactate concentrations were increased. Next, solid passage rate was increased (4th row) due to increased DMI (Sniffen et al., 1992), causing acid concentrations to decrease slightly. The increase in ruminal volume (5th row) caused a large decrease in acid concentrations, and when liquid passage rate was increased, acid concentrations were decreased further (6th row). Thus, the predicted effect of added buffers was decreased VFA concentrations, higher butyrate fraction, and lower ruminal propionate concentration. These results agree qualitatively with the actual results (Rogers and Davis, 1982b) and suggest that the most important effects of buffers in this experiment were associated with ruminal volume and liquid dilution rate (Erdman, 1988; Russell and Chow, 1993).

Ruminal pH Prediction. In this section we compare the empirical pH prediction based on eNDF in the diet and the mechanistic approach based on buffering and acidity in the rumen. Using a high-forage diet, saliva production, and other data from a study with dairy cows (Cassida and Stokes, 1986), cumulative buffer-

Table 4. Changes in VFA predictions over a series of effects associated with added buffers^a

Changes	C_{VFA} (mM)	Molar fractions			C_L (mM)	Absorbed fraction		
		A	P	B		A	P	B
Control run	84.3	.609	.259	.132	14.9	.61	.74	.74
pH increased 5.8 to 6.04	91.1	.642	.240	.118	10.3	.59	.72	.71
DMI increased 5.15 to 5.58 kg/d	98.3	N/C			11.1	N/C		
K_p increased	96.8	N/C			11.0	N/C		
V_{Ru} increased 15.5 to 18.7 L	83.8	.640	.242	.119	9.2	.58	.71	.69
K_l increased 10.6 to 11.3%/h	81.6	.638	.243	.119	9.1	.56	.70	.68

^aA = acetate; P = propionate; B = butyrate, K_p = solid passage rate; V_{Ru} = rumen liquid volume; N/C = no change from above row; K_l = rumen liquid passage rate.

ing and acidity curves were calculated as a function of pH (Figure 11). These curves were generated by implementing the model at a series of pH values; lactate and VFA concentrations, total acidity, NDF in the rumen, and total buffering were calculated at each pH. The crossover point between buffering and acidity occurred at pH 6.1, which was taken as the equilibrium pH. The actual value is also shown in the figure.

To test the relation between eNDF and ruminal pH, a low-concentrate diet for early-lactation cows (Robinson and Kennelly, 1991) was used as a model input. The eNDF in this diet was varied with DMI held constant. Varying eNDF in the model changed saliva production in Eq. [70] and solid passage rate (Sniffen et al., 1992). Ruminal pH was calculated from the equilibrium between ruminal acidity and buffering as in Figure 11. Figure 6 shows the mechanistic predictions plotted with the empirical correlation. The predicted curve was high at low eNDF and low at high eNDF but was within .2 pH units of the regression line.

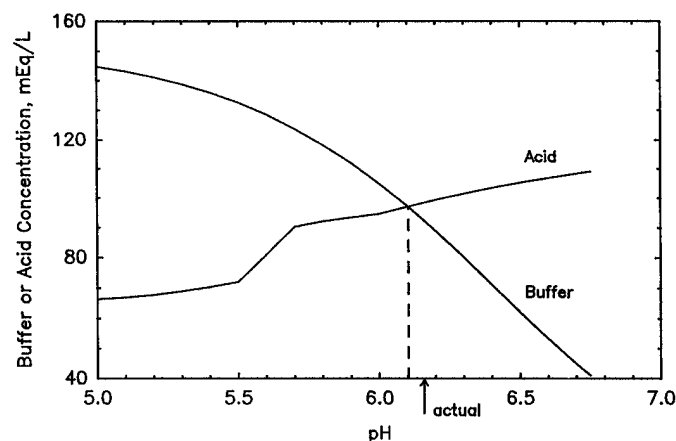


Figure 11. Calculated ruminal acidity and buffering for the high-forage diet of Cassida and Stokes (1986), showing the crossover point representing acid-base equilibrium and predicted steady-state ruminal pH. Actual ruminal pH is shown on the horizontal axis.

Applications of the Model

Applications of the net carbohydrate and protein system have included evaluation of feed, animal, and environmental factors in predicting efficiency of nutrient use by cattle in production settings; interpretation of research results; evaluation of interactions among feed composition, feeding management, and animal requirements; and development of nutrient requirements that are mechanistic (Fox et al., 1995). The current model contributes to these goals. Prediction of absorbed VFA and ruminal pH is the next step in predicting ME in terms of substrates. The VFA model should also provide a basis to develop a metabolism model. Moving to this level of aggregation will be necessary to account for the effect of diet on milk and tissue composition and the efficiency of absorbed substrates.

One of the important contributions of modeling is in helping establish research agenda and priorities (Fox et al., 1995). Establishing research agenda comes not from models performing perfectly, but from models performing imperfectly. Thus, one of the applications of the VFA and pH model is to identify areas in which further information is needed.

There are two primary areas in which the present model has highlighted the need for more research. The first of these is in the description and ruminal digestibility of starch and pectic substances (B1 carbohydrate). On the basis of comparisons with Cameron et al. (1991), Klusmeyer et al. (1991), Kung et al. (1992), McCarthy et al. (1989), and Stokes et al. (1991), the model predicted ruminal B1 digestion that was substantially greater than actual digestion. The limiting of B1 digestibility in the VFA model in effect divides the B1 carbohydrate into slowly and rapidly degraded fractions. This is consistent with the reviews of Theurer (1986) and Nocek and Tamminga (1991) and is closer to the models of Baldwin et al. (1970) and Dijkstra et al. (1992). The sensitivity analysis in the present study confirmed the importance of B1 digestibility on ruminal VFA. More work is needed to develop a method to describe and quantify these fractions for various feeds as dependent on processing.

Subdividing the B1 carbohydrate has other implications. If ruminal B1 digestion is reduced in the model, this will also reduce microbial protein production, which was previously shown to be well predicted (Russell et al., 1992). Thus, further research is needed to resolve the effect of partitioning of B1 carbohydrate on microbial yield, total tract digestibility, and predicted energy values of diets.

A second area of weakness identified by the model is the distribution of end products from the carbohydrate fractions at various pH. Even when total concentrations of VFA were approximately predicted (Figure 8), the fractions of acetate, propionate, and butyrate predicted by the model did not account for variations in the evaluation studies (Figures 9, 10). Neal et al. (1992) encountered the same difficulty in their rumen model. In vitro incubation of individual carbohydrate fractions over a range of pH should provide information useful to the current structure.

In the summary of literature data, ruminal pH was better correlated with eNDF than with forage or NDF as a percentage of dietary DM. However, considerable variability exists in ruminal pH and its measurement. In some of the studies used to develop Figures 4 through 6, multiple pH measurements were averaged, whereas in other studies a single reading was taken at a set time, usually a few hours after feeding; because pH fluctuates with time, a single value may not be representative (Fischer et al., 1994). Sampling of ruminal fluid was in some studies by cannula and in other studies by esophageal tube. In some studies, a number of locations in the rumen were sampled, whereas in others only a single location was sampled. Frequency of feeding varied from twice daily to essentially continuous feeding; more frequent feeding results in a more stable pH (Sutton et al., 1986).

The relationship between pH and eNDF accounts for none of these factors. However, the approximate agreement between empirical and mechanistic pH relationships supports the consideration of eNDF as a predictor of steady-state pH. Describing fiber by its proportion of eNDF should provide a quantitative way to relate feed chemical and physical characteristics to stimulation of chewing, rumination, rumen motility, and buffering of the rumen (Mertens, 1992), all of which affect ruminal pH (Beauchemin, 1991). Further investigation is warranted to test the relationship.

The relation of pH to fiber digestion and microbial yield provides further utility to the model. In Figure 1 fiber digestion rate decreased when pH was less than 6.2. From the relationship between pH and eNDF (Figure 6), this suggests that fiber digestion is inhibited when eNDF is less than approximately 20% of dietary DM. Diets with eNDF less than 15%, such as high-grain diets used in feedlots, are predicted by Eq. [69] to result in ruminal pH below 6.0.

Taken together, the feed library containing eNDF values (Barry et al., 1994; Sniffen et al., 1992), the

ruminal pH prediction based on eNDF, and the effect of pH on cell wall digestion and microbial yield provide a simple starting point for diagnosing problems related to dietary fiber and for tailoring recommendations for fiber processing and dietary level in specific production settings. Continued research into the description of effective fiber in various feeds should improve the usefulness and accuracy of these relations (Mertens, 1992).

Implications

A structure has been developed to predict ruminal VFA production and absorption, ruminal pH, and dietary fiber requirements within the net carbohydrate and protein system. Evaluation of the model shows that more work is needed to determine the individual VFA produced from carbohydrate fermentation at various pH and the effect of partitioning starch and pectin into slowly and rapidly degraded fractions on microbial yield, total tract digestibility, and predicted energy values of feeds. The empirical and mechanistic relation between effective fiber and ruminal pH, combined with the model for the effect of pH on fiber digestion and microbial yield, provides a beginning structure for relating feed physical and chemical composition to problems with fiber processing and dietary level in specific production settings.

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