Relationship Between Fermentation Acid Production in the Rumen and the Requirement for Physically Effective Fiber

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ABSTRACT
The content of ruminally fermented OM in the diet affects the fiber requirement of dairy cattle. Physically effective fiber is the fraction of feed that stimulates chewing activity. Chewing, in turn, stimulates saliva secretion. Bicarbonate and phosphate buffers in saliva neutralize acids produced by fermentation of OM in the rumen. The balance between the production of fermentation acid and buffer secretion is a major determinant of ruminal pH. Low ruminal pH may decrease DMI, fiber digestibility, and microbial yield and thus decrease milk production and increase feed costs. Diets should be formulated to maintain adequate mean ruminal pH, and variation in ruminal pH should be minimized by feeding management. The fraction of OM that is fermented in the rumen varies greatly among diets. This variation affects the amount of fermentation acids produced and directly affects the amount of physically effective fiber that is required to maintain adequate ruminal pH. Acid production in the rumen is due primarily to fermentation of carbohydrates, which represent over 65% of the DM in diets of dairy cows and have the most variable ruminal degradation across diets. The non-fiber carbohydrate content of the diet is often used as a proxy for ruminal fermentability, but this measure is inadequate. Ruminal fermentation of both nonfiber carbohydrate and fiber is extremely variable, and this variability is not related to the nonfiber carbohydrate content of the diet. The interaction of ruminally fermented carbohydrate and physically effective fiber must be considered when diets for dairy cattle are evaluated and formulated.

(Key words: fiber requirements, ruminal fermentation, effective fiber)

Abbreviation key: BC = buffering capacity, PLI = particle length index (used with number), RDOM = OM truly digested in the rumen, RMSE = root mean square error, TCT = total chewing time.

INTRODUCTION
Ruminants require roughage in their diets to maximize production and to maintain health by sustaining a stable environment in the rumen. The ability of roughages to stimulate chewing has been investigated extensively because of the relationship between chewing and the flow of salivary buffers (6, 38) into the rumen, which are required to neutralize fermentation acids. Balch (7) proposed that the time spent chewing per unit of DM could be used as an index of roughage value, and many feedstuffs have been characterized for total chewing time (TCT) expressed as minutes per kilogram of DM (85). Welch and Smith (97) reported that NDF is the nutritional component of roughages that is related to chewing activity, now commonly reported in the literature as minutes per kilogram of NDF intake. However, chemical measures of fiber alone are inadequate to balance diets for high producing dairy cows because fiber varies in its effectiveness in stimulating chewing, primarily because of differences in particle length. Santini et al. (78) proposed that fiber (or roughage) intake be adjusted by mean particle length to create a roughage index that more closely corresponds to TCT. The National Research Council (69) gives minimum fiber requirements for NDF and ADF and recommends balancing rations with 75% of the diet NDF from forage to allow for the use of nonforage fiber sources that are less effective in stimulating chewing than forage fiber. However, the effectiveness of fiber within by-product feeds and forages is variable because of differences in size distribution of fiber particles and the retention time of fiber in the rumen. Chemical and physical characteristics alone should not be used as exclusive measures of fiber requirements because ruminal fermentation of fiber is variable (72) and because adjustment of diet fiber content affects fermentation acid production by dilution or concentration of the nonfiber fraction of the diet. No-
cek and Russell (71) suggested that an optimal ratio of nonstructural carbohydrate to NDF be used to formulate diets to maximize milk yield. However, ruminal fermentation of nonstructural carbohydrates is extremely variable (71), and variation in the effectiveness of NDF is not considered in this approach. Poore et al. (74) suggested that the ratio of forage NDF to ruminally degraded starch be maintained ≥1: 1 (wt/wt) to prevent a reduction in milk fat percentage when high NDF forage is substituted for low NDF forage. Although the starch content of dairy cows diets may exceed 30% of DM, ruminal degradation of other dietary components is variable and should be considered.

Milk fat response has been used to determine NDF effectiveness for nonforage fiber sources as a way of integrating these complex interactions (3, 23, 33, 87, 93). However, effectiveness, as determined with this strictly empirical relationship, might have limited application because effectiveness values have not been repeatable across different types of diets (24). Mid-lactation cows typically are used for this bioassay because milk fat percentage of cows in early lactation is less responsive to diet. Therefore, these data might not be applicable to early lactation cows. More importantly, milk fat percentage might not be the most appropriate measure of fiber effectiveness for cows in early lactation. Requirements for fiber and energy of cows in mid and late lactation are easily met, but fiber requirements of early lactation cows are critical because their energy expenditure exceeds the energy consumed. Diets with lower fiber and higher starch contents are fed to increase energy intake, which increases the risk of ruminal acidosis.

Ruminal pH is a more meaningful response variable for determining fiber requirements of dairy cows in early lactation. Diets should be balanced to maintain adequate ruminal pH; as ruminal pH decreases, appetite (81), ruminal motility (4, 81), microbial yield (53), and fiber digestion (53, 89) are reduced. Thus, low ruminal pH has direct, negative effects on energy intake and absorbed protein, which are primary factors limiting production of high producing dairy cows. When ruminal pH is reduced substantially, severe health problems, such as laminitis, ruminal ulceration, liver abscess, and even death could result (83). An index that weights the time spent under the optimal ruminal pH by the magnitude of the deviation from this pH has been suggested by Mackie and Gilchrist (65). Although this index might be better related to animal performance than is mean ruminal pH, variation in ruminal pH is more closely related to feeding management practices that affect meal frequency (16) and diet adaptation (26) than to diet formulation. The effects of feeding management on variation in ruminal pH should be considered when choosing the optimal mean ruminal pH, which is lower when variation over time is minimized.

Although milk fat and ruminal pH were positively related (Figure 1), prediction of ruminal pH from dietary characteristics might be more useful for diet formulation to meet the fiber requirements of dairy cows because the interactions among dietary components could be accounted for more accurately and could be applied across a wide range of feeds and feeding conditions. This paper addresses the fiber requirements of high producing dairy cows by considering the balance between production and neutralization of fermentation acids in the rumen.

ACID PRODUCTION VERSUS NEUTRALIZATION

Ruminal pH is very responsive to meals and chewing behavior; ruminal pH decreases following meals and increases during bouts of rumination (Figure 2). The rate of ruminal pH decline is faster following a meal as meal size increases and as dietary NDF concentration decreases (29). Dietary NDF concentration alone is not related to ruminal pH (Figure 3 and Table 1). Although dietary NDF is related to TCT for all forage diets (97) and, therefore, salivary buffer flow into the rumen, dietary NDF is not highly
related to TCT or to ruminal degradation of OM across the range of diets consumed by dairy cows. In addition, although ruminal VFA concentration is related negatively \((P < 0.001)\) to ruminal pH (Figure 4), the relationship is not strong \(r^2 = 0.13; \text{root mean square error (RMSE) } = 0.23\), presumably because of variation in buffering and neutralization in the rumen. Increased ruminal degradation is desirable to maximize microbial protein production and energy intake, but the increase in fermentation acids must be compensated for by increasing either NDF content of the diet or by increasing the physical effectiveness of the NDF to maintain pH by stimulating salivary buffer secretion via chewing activity (Figure 5). Increased NDF concentration increases TCT and salivary buffer flow and, for most diets, decreases production of fermentation acids by diluting more fermentable feed fractions such as starch. However, increased NDF concentration might decrease DMI because of constraints on ruminal fill (31) or on TCT per day. Increasing the physical effectiveness of NDF to increase salivary buffer flow might be a more desirable alternative to maintain ruminal pH because this increase would result in greater ruminal fermentation and production of microbial protein.

**Figure 2.** The relationship among ruminal pH, meals, and chewing activity for one cow fed a 35% NDF diet twice daily. Ruminal pH is represented by the top line. The weight of the feed remaining was measured by a manger suspended from a load cell and is represented by the middle line. Meals are represented by the shaded vertical bars. Increases in feed remaining that were recorded during eating bouts were due to downward pressure applied by the cow on the manger. Chewing activity is represented by the bottom line. Because many points are represented, chewing activity appears as blocks of eating and ruminating bouts. Ruminal pH decreased rapidly following meals and increased rapidly during rumination. Unpublished raw data from Dado and Allen (31).

**Figure 3.** The relationship between dietary NDF percentage and mean ruminal pH from experiments reported in the literature using ruminally cannulated, lactating dairy cows; ruminal pH is reported as within-day means. The relationship was not significant \((P = 0.27; n = 106)\) (1, 8, 9, 11, 12, 17, 18, 19, 21, 27, 28, 31, 40, 42, 51, 59, 60, 61, 62, 63, 64, 67, 75, 80, 82, 84, 101).

**EMPIRICAL PREDICTION OF RUMINAL pH**

Empirical relationships between ruminal pH and some independent variables were determined using 106 treatment means from 28 experiments in the literature. Only data from ruminally cannulated lactating dairy cows with pH determined as within-day means were used. Table 1 shows the mean and range for ruminal pH and the independent variables evaluated. Measurements of DMI or OM intake, dietary NDF, and ADF percentage were reported in all or most of the articles describing the experiments. However, the percentage of forage NDF was reported for only 6 of the experiments, and the percentage of forage ADF was reported in too few studies to be useful. Twelve of the experiments representing 48 treatment means measured ruminal OM digestion from duodenally cannulated cows. The relationships between each factor and ruminal pH were evaluated by regression analysis (Table 1) using the fit model procedure of JMP\textsuperscript{®} (56). Forage particle size was included as an ordinal variable to permit inclusion of studies with long hay as forage. Three categories were included: chopped forages with mean sieve aperture size <0.3 cm = particle length index (PLI)\(1\), chopped...
TABLE 1. Mean and range of ruminal pH and various dietary factors for lactating dairy cows and their relationships determined by regression.1

<table>
<thead>
<tr>
<th>Factor</th>
<th>X</th>
<th>SD</th>
<th>Range</th>
<th>no.2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruminal pH</td>
<td>5.97</td>
<td>0.24</td>
<td>5.51–6.60</td>
<td>106</td>
</tr>
<tr>
<td>NDF, % of DM</td>
<td>33.7</td>
<td>4.7</td>
<td>25.3–47.3</td>
<td>106</td>
</tr>
<tr>
<td>ADF, % of DM</td>
<td>19.7</td>
<td>3.4</td>
<td>12.6–28.4</td>
<td>92</td>
</tr>
<tr>
<td>Forage NDF, % of DM</td>
<td>19.7</td>
<td>3.8</td>
<td>12.3–26.5</td>
<td>26</td>
</tr>
<tr>
<td>OM Intake, kg/d</td>
<td>19.5</td>
<td>2.6</td>
<td>12.9–25.3</td>
<td>106</td>
</tr>
<tr>
<td>RDOM, % of OM</td>
<td>50.2</td>
<td>8.8</td>
<td>29.1–66.6</td>
<td>48</td>
</tr>
<tr>
<td>RDOM, kg/d</td>
<td>9.8</td>
<td>2.1</td>
<td>5.7–15.4</td>
<td>48</td>
</tr>
</tbody>
</table>

Regression results

<table>
<thead>
<tr>
<th>Factor (x)</th>
<th>P</th>
<th>r²</th>
<th>m</th>
<th>b</th>
</tr>
</thead>
<tbody>
<tr>
<td>Forage NDF, % of DM</td>
<td>&lt;0.0001</td>
<td>0.63</td>
<td>0.0578</td>
<td>4.80</td>
</tr>
<tr>
<td>RDOM, kg/d</td>
<td>0.003</td>
<td>0.18</td>
<td>0.0467</td>
<td>5.49</td>
</tr>
<tr>
<td>RDOM, % of OM</td>
<td>0.006</td>
<td>0.15</td>
<td>0.0100</td>
<td>5.43</td>
</tr>
<tr>
<td>PLI4</td>
<td>0.002</td>
<td>0.12</td>
<td>5</td>
<td>5.96</td>
</tr>
<tr>
<td>ADF, % of DM</td>
<td>0.16</td>
<td>0.02</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>NDF, % of DM</td>
<td>0.27</td>
<td>0.01</td>
<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>OM Intake, kg/d</td>
<td>0.87</td>
<td>&lt;0.001</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

1Ruminal pH = mx + b, where m = slope, and b = intercept.
2Number of treatment means from the literature (1, 8, 9, 11, 12, 17, 18, 19, 21, 27, 28, 31, 40, 42, 51, 59, 60, 61, 62, 63, 64, 67, 75, 80, 82, 84, 101).
3OM truly degraded in the rumen.
4Particle length index; number of treatment means from the literature = 103.
5Coefficient for PLI1 = 0, PLI2 = 0.0519, PLI3 = -0.2145.

Ruminal pH was related positively to forage NDF as a percentage of DM (P < 0.0001; r² = 0.63), amount of OM truly degraded in the rumen (RDOM) per day (P = 0.003; r² = 0.18), and RDOM percentage (P = 0.006; r² = 0.15). Ruminal pH also was related to PLI (P = 0.002; r² = 0.12). Ruminal pH was not related to ADF or NDF as a percentage of DM or to OM intake (P > 0.10). A positive relationship between forage NDF as a percentage of DM and ruminal pH was expected because of the greater chewing and salivary buffer flow, but the positive relationship between both amount and percentage of RDOM and ruminal pH was not, because greater fermentation acid production is expected with higher RDOM. In addition, the coefficient for PLI2 was positive relative to PLI1, and that for PLI3 was negative, which was unexpected. The negative coefficient for PLI3 might be due to an interaction between PLI and the RDOM percentage of the diet because most diets containing long hay also contained rolled barley, which is highly degraded in the rumen. Forage NDF percentage was closely related to ruminal pH. However, the data file including this dietary characteristic was limited (n = 26), and caution should be used when these results are interpreted. The relationships between most of these factors and ruminal pH were poor and the opposite of those expected, demonstrating the importance of the interactions among them.

Greater variation was explained when these factors were used in combination to predict ruminal pH. The best fit equation (P < 0.0001; RMSE = 0.07; n = 26), explaining 95% of the variation in ruminal pH (RpH), is

\[
R_pH = 3.98 + 0.011 \times NDF + 0.040 \times OMI + 0.031 \times FNDF + 0.18 \times PLI2 - 0.15 \times PLI3
\]

where OMI = OM intake (kilograms per day), and FNDF = forage NDF (percentage of DM).

Although the r² is extremely high, the subset of data including these factors included only 26 treat-
ment means from 6 experiments. All dietary factors were significant (P < 0.05). Dietary NDF, OM, and forage NDF percentage were related positively with ruminal pH. Again, the coefficient for PLI2 was positive relative to PLI1, and that for PLI3 was negative, which might have been due to an interaction with RDOM percentage. Forage particle length had the most influence on the range in ruminal pH; pH range was 0.33 units between PLI2 and PLI3, attainable by a 28-unit difference in dietary NDF percentage, an 11-unit difference in forage NDF percentage, or an 8-kg/d difference in OM intake. Data including measurements of both RDOM and forage NDF percentage are limited to only one experiment; therefore, RDOM was not included. However, RDOM percentage may have been included implicitly in this data file because RDOM probably was related negatively to both forage NDF and dietary NDF percentage, which were related positively with each other (r² = 0.15; P < 0.05). Removing forage NDF percentage included more data with Equation [2] but decreased the variation explained (r² = 0.54; P = 0.0001; RMSE = 0.17; n = 48).

\[ RpH = 8.38 + 1.91 \times PLI2 + 0.38 \times PLI3 - 0.088 \times RDOMP + 0.067 \times NDF - 0.258 \times OMI + 0.499 \times RDOMKG - 0.060 \times PLI2 \times NDF - 0.014 \times PLI3 \times NDF \]  

[2]

where RDOMP = ruminally degraded OM (percentage of total OM), RDOMKG = ruminally degraded OM (kilograms per day), and other terms are as defined for Equation [1].

The relationships between individual factors and ruminal pH were as expected; NDF as a percentage of DM was positively related, and RDOM percentage and OM intake were negatively related, to ruminal pH. Although the coefficients for both PLI2 and PLI3 were positive relative to PLI1, the coefficient for PLI2 was much higher than that for PLI3, which has no obvious explanation. Ruminal pH was influenced highly by PLI and RDOM as a percentage of OM and less influenced by the normal ranges in OM intake and NDF as a percentage of DM. The pH difference of 1.9 units between coarsely chopped and finely chopped forages would result from a 22-unit difference in RDOM percentage, a 29-unit difference in NDF percentage, or a 7.4-kg difference in OM intake. This range in RDOM is common among diets for dairy cows, although this range for NDF percentage is not. However, the effect of NDF in this model was independent of its effect on RDOM percentage, which was included separately. Because a negative relationship between NDF and RDOM concentrations would be expected, NDF should have exerted a greater influence on ruminal pH than was demonstrated by Equation [2]. Because of the expected relationships of NDF and forage NDF with RDOM and because of the separate data files for forage NDF and RDOM, their relative importance for the prediction of ruminal pH is difficult to establish. However, both are related to ruminal pH and should be considered in order to meet the fiber requirements for dairy cows. The more mechanistic approach that follows is required to evaluate further the dietary factors affecting ruminal pH.

**RUMINAL ACID PRODUCTION**

Acids that are produced in the rumen are derived from feedstuffs as end products of OM fermentation in the rumen (primarily acetic acid) or consumed in silage (primarily lactic acid). Carbohydrates normally account for more than 65% of the DM of dairy cattle diets, and the extent of carbohydrate fermentation is extremely variable among feedstuffs. This variation has been reviewed extensively for ruminal degradation of DM, CP, NDF (71), and starch (72). Variation in ruminal degradation of DM across feeds...
has been reported to range from 29 to 90% (71). Although diets for dairy cows are normally composed of several ingredients and the range in RDOM across diets would be expected to be less than the range across individual diet components, experiments with duodenally cannulated dairy cows still showed a wide range of RDOM from 29 to 67% of DM (Table 1).

The variation within feed type tends to be much less than the variation across feeds, and a reasonable prediction of RDOM for diets might be possible using tabular values. However, variation is only partially due to feed characteristics because it is highly influenced by interactions among the diet, the animal, and ruminal microbes, affecting residence time in the rumen and microbial activity. Variation in ruminal degradation within feeds tends to be higher for fine, nonforage fiber sources because of differences in ruminal retention time (41), which are probably affected by ruminal consistency (46). Variation in ruminal degradation is also high for certain ground grains; ruminal degradation of starch in ground corn (n = 11) and ground sorghum (n = 9) ranged from 51 to 93% and 42 to 91%, respectively (72). The values included in these ranges were from experiments with different animal types and levels of intake. Fractional passage rates from the rumen were most likely to be variable for these animals, and differences in ruminal residence time probably were largely responsible for these differences. The few experiments that have measured ruminal degradation of starch from ground corn supported this concept. Ruminal degradation of starch from ground corn was reported as 92% for steers with DMI at 1.32% of BW (43), 64% for steers with DMI at 1.65% of BW (45), and a mean of 45% for data from four experiments with high producing dairy cows with DMI at 3.8% of BW (19, 21, 64, 67). Although the experiments with dairy cows used mixed diets containing corn silage, ground corn was the primary source of starch. Much less variation was reported within grain type for ruminal starch degradation of cracked, ensiled, steam-flaked, or whole grains (72). A possible explanation for this difference in variation is that fine particles of ground grain are more likely to flow from the rumen suspended in the liquid fraction than are large particles, and large differences in liquid passage rate are expected between steers at maintenance intake and dairy cattle at four times maintenance intake. Although little variation in the ruminal degradation of starch was reported for ground barley or ground wheat (72), those ground grains might have been so rapidly fermented in the rumen that variation in fractional passage rate had little effect; variation in fractional passage rate exerts its greatest influence on ruminal digestibility when rates of digestion are low. Data from experiments with high producing dairy cows should be used when RDOM are being predicted from tabular values because ruminal retention time varies among animals and production levels.

Hydrogen ion concentration also is affected by differences in the acid dissociation constant, which is 10-fold higher for lactic acid than for the major VFA, which are similar to one another. Although the degree of dissociation is pH dependent and at ruminal pH above 6 little difference exists among all fermentation acids because they are almost completely dissociated, VFA buffer at a pH higher than that of lactic acid and exert less influence on ruminal pH than lactic acid does as pH decreases. Lactic acid accumulates when glycolytic flux (hexose units fermented per unit time per microorganism) is high, which is typical during diet adaptation (26). In chemostats, Streptococcus bovis produced up to 10 times more lactic acid per molecule of maltose at a high dilution rate (0.36/h) than at a lower (0.12/h) dilution rate (77). At normal ruminal pH, lactic acid is slowly absorbed from

![Figure 6](image-url)
the rumen because it is almost completely ionized because of its high acid dissociation constant. However, lactic acid normally is rapidly metabolized in the rumen; 90% of lactic acid that was infused into the rumen of sheep was metabolized to acetic (61%), propionic (34%), and butyric (5%) acids (44). Coumoute and Prins (26) reported that 60 to 80% of the lactate produced in the rumen by dairy cattle was metabolized by Megasphaera elsdenii. Lactate utilization decreases as pH declines toward 5 because growth of M. elsdenii is inhibited, and lactate production might greatly exceed its utilization in the rumen (76). As lactic acid concentration increases and pH decreases, lactic acid concentration becomes an important influence on ruminal pH. However, even though lactic acid can have a major effect on ruminal pH during adaptation to dietary changes, it normally is only a minor intermediate in ruminal metabolism and has little influence on ruminal pH (26).

Prediction of production of fermentation acid in the rumen requires estimation of RDOM and the assumption of a constant microbial cell yield from the hexose equivalents fermented. Equation [3] can be used to estimate the daily milliequivalents of fermentation acid produced in the rumen (RFA):

$$RFA = \frac{(OM \times RDOM)}{(MM \times WH)} \times (1.0 - MCY) \times VFA$$

where MM = molecular mass of hexose (0.180 kg/mol), WH = correction for water added from hydrolysis of OM to hexose (0.9), MCY = microbial cell yield from hexose fermented (0.33), and VFA = yield of VFA per mole of available hexose determined by fermentation balance (1800 meq of VFA/mol of hexose for 60% acetic acid, 25% propionic acid, and 15% butyric acid).

The amount of OM that was degraded in the rumen per day (as the product of OM intake and RDOM percentage) was converted to hexose equivalents by dividing the molecular mass of hexose [C\textsubscript{6}H\textsubscript{12}O\textsubscript{6} (180)] adjusted for water added from hydrolysis of OM to hexose equivalents (0.9). Microbial cell yield is variable and directly affects the amount of fermentation acid produced per kilogram of RDOM. Microbial N yields ranged from approximately 10 to 50 g of microbial N/kg of RDOM with a mean of approximately 33 g of microbial N/kg of RDOM for treatment means from experiments with dairy cows in the literature (22). The microbial cell yield of 0.33 from fermented hexose was calculated using this mean microbial N yield and a mean microbial N content of 10% (92). The yield of VFA, expressed as milliequivalents per mole of available hexose, could be calculated by fermentation balance given the molar proportions of VFA produced (99). Assuming a constant microbial cell yield, the amount of fermentation acid produced is related to OM intake and RDOM percentage. The amount of fermentation acid produced in the rumen of a cow consuming 20 kg of OM/d with an RDOM of 50% is over 74,000 meq/d, calculated with Equation [3]. Ruminal pH could be maintained by increasing acid neutralization or by decreasing ruminal acid production; the amount of fermentation acids produced in the rumen is very easily manipulated by substitution of dietary ingredients. Dietary substitution of 5 kg of dry ground corn OM (50% RDOM) for 5 kg of wet high moisture corn OM (90% RDOM) will reduce ruminal fermentation acid production by nearly 15,000 meq/d. As previously mentioned, microbial yield per kilogram of OM fermented is extremely variable, which has a large effect on fermentation acid production in the rumen; a 20% increase (or decrease) in microbial cell yield from 0.33 g/g of hexose fermented will increase (or decrease) fermentation acid production by nearly 7800 meq/d. Thus, the formulation of diets to maximize microbial yield should decrease the production of fermentation acids and might reduce the incidence of ruminal acidosis.

Although all hydrogen ions eventually are removed from the rumen by absorption and passage, ruminal pH fluctuates, depending upon the rate of VFA absorption, rate of fluid passage, water flux into the rumen or out across the rumen wall, meal patterns, and the fractional rates of OM degradation and passage.

**REMOVAL OF FERMENTATION ACIDS FROM THE RUMEN**

Fermentation acids are removed from the rumen by absorption across the rumen wall and by passage from the rumen through the omasal orifice. There is little or no absorption of VFA from the rumen in the ionized form (5), so VFA absorption results in the net removal of hydrogen ion from the rumen. At high ruminal pH, little VFA exists in the associated form, and the fractional rate of absorption is reduced (5). Under these conditions, VFA absorption from the rumen occurs by carbonic acid secretion into the rumen, which supplies the hydrogen ions necessary for absorption (5, 66). Although fractional rate of absorption increases as pH decreases because a greater fraction of the VFA is in the associated form, absorption rates vary by type of VFA. Acetic, propionic, and butyric acids are absorbed at similar rates at neutral pH; but, as pH decreases, absorption rates increase at
a greater rate as molecular mass increases (32, 35, 90, 96). Dijkstra et al. (35) reported the effect of ruminal pH on fractional absorption rates for acetic, propionic, and butyric acids from the rumen. Ruminal pH had no effect on fractional absorption rate of acetic acid (0.31/h), but the fractional absorption rate increased for propionic and butyric acid from 0.35 to 0.68/h and 0.28 to 0.85/h, respectively, as pH decreased from 7.2 to 4.5. The difference in the fractional absorption rates among the VFA might be due to a greater concentration gradient between the rumin and the portal circulation for butyrate and, to some extent, propionate, depending upon the extent of metabolism in ruminal epithelium (35). Although the major VFA have similar acid dissociation constants, they have different effects on ruminal pH because of their differential rates of absorption. Acetic acid has a greater effect of reducing ruminal pH than does propionic acid, which is greater than butyric acid; the magnitude of the differences increases as ruminal pH decreases. The concentration gradient is also affected by mixing in the rumin, which increases the VFA concentration at the ruminal epithelium, and the rate of VFA absorption would be expected to increase with greater mixing in the rumin.

The flux of VFA absorbed also depends on the effective surface area for absorption; fractional absorption rate decreased as ruminal liquid volume increased from 10 to 30 L (35). The fractional rates of absorption that have been reported in the literature are higher than those that normally would be observed because the ratio of surface area to rumin volume was higher when the rumin was partially emptied during the experiments and because mixing was greater when particulate matter was removed. The rate of VFA absorption from the rumin was positively related to ruminal papillae surface area, which was affected by diet (36). The adaptive changes of ruminal papillae length to diets varying in RDOM might be an important factor affecting the susceptibility of animals to ruminal acidosis.

Fermentation acids pass from the rumin through the omasal orifice primarily with the liquid fraction. Although some acids pass with particulate matter, liquid flow is much greater because of a larger liquid pool size and a faster turnover rate. Passage from the rumin has no effect on the relative distribution of associated versus ionized VFA because differential flow of the two forms is not expected. Passage of free hydrogen ions from the rumin is negligible because of the small pool size of hydrogen ions in the rumin. A considerable fraction of VFA passes from the rumin and is absorbed postruminally. Estimates of the fractional rates of absorption passed have been reported as 15% for sheep (94), 15 to 20% for calves (37), 29% for dairy cows at maintenance intake to 39% for dairy cattle at four times maintenance intake (88), and from 20 to 35% for dairy cows, depending upon ruminal pH (35). The fraction that passes from the rumin increases as rate of liquid passage from the rumin increases and as ruminal pH increases.

WATER DYNAMICS

Water flux into the rumin from drinking, feed consumption, and saliva and water removal through the omasal orifice and flux across the ruminal wall determine the volume of ruminal liquid that dilutes hydrogen ions and the passage of hydrogen ions through the omasal orifice. Saliva is the primary source of water flow into the rumin and has been calculated to range up to 308 L/d for dairy cows (20). Water intake of early lactation cows averaged 89 L (SD = 19) and was dependent on feed consumption, milk production, sodium intake, and environmental temperature (68). Water influx from drinking and saliva may have a diminished effect on hydrogen ion removal because of incomplete mixing in the rumin. Woodford et al. (102) reported that 18% of drinking water bypassed the rumin when water was withheld for 4.5 h following feeding. Some bypass of saliva also could be expected because of incomplete mixing in the rumin. Water influx from the diet is much less than that from saliva and drinking, ranging from 2 to 14 L/d for cows consuming 20 kg of DM/d with dietary moisture contents of 10 to 70%.

Hydrogen ion concentration also is affected by water flux across the ruminal wall. Transient fluxes of water across the ruminal wall may have little effect on ruminal pH; a rapid increase or decrease in ruminal volume of 20% changes ruminal pH less than 0.1 unit at pH 6.0. However, net flux decreases the ruminal liquid pool and must be considered. Warner and Stacy (95) summarized several studies with sheep and showed no net flux of water across the ruminal wall; ruminal osmolality ranged from 295 to 360 mmol/kg. Argyle and Baldwin (2) suggested that, because daily and mean ruminal osmolalities are usually below this range, there is a net flux of water out of the rumin through the ruminal wall. Increasing ruminal osmolality acts to increase ruminal pH by reversing the flow of water out of the rumin through the ruminal wall and by increasing the flow of water through the omasum. Water passage through the omasal orifice removes hydrogen ions from the rumin as dihydrogen phosphate, ammonium ions, and associated with VFA.
NEUTRALIZATION

Although hydrogen ions produced in the rumen are removed rapidly by absorption as VFA, hydrogen ions remaining in the rumen must be removed from solution to maintain physiological pH. Hydrogen ions are removed by alkalization and buffering by saliva, by feed, and by feed degradation products. Of these, saliva is by far the most important mechanism for removal of hydrogen ions from solution. Saliva contains bicarbonate and hydrogen phosphate ions that remove hydrogen ions from solution by a combination of alkalization and buffering. Bailey and Balch (6) reported that bicarbonate and phosphate concentrations averaged 126 and 26 meq/L for 48 samples of mixed saliva collected from four dry Shorthorn cows. Saliva composition has been reported to be relatively constant and not greatly affected by diet or feed intake (39).

The mechanism of hydrogen ion removal is different for bicarbonate and hydrogen phosphate. In the carbonate system, hydrogen ions are incorporated into water, and, in the phosphate system, hydrogen ions are removed by flow through the omasal orifice. At pH 6, approximately 94% of the potential buffering capacity (BC) of hydrogen phosphate (pK_a = 7.2) is used, and the associated hydrogen ions flow from the rumen as dihydrogen phosphate. Although the pK_a for bicarbonate is 6.1, more than 50% of the potential BC is used when the pH is equal to the pK_a at 6.1 because the rumen is an open system in which the concentration of dissolved CO_2 is maintained at relatively constant levels. The carbonate buffer system acts differently from the phosphate system (although some phosphate is removed from solution by microbial metabolism) because the associated form is removed from the system by dehydration of carbonic acid to H_2O and CO_2 and removal of CO_2 gas:

\[
H^+ + HCO_3^- \leftrightarrow H_2CO_3 \leftrightarrow H_2O + CO_2 \leftrightarrow CO_2 \text{ (gas)}. \quad [4]
\]

Carbon dioxide formed from the dehydration of carbonic acid equilibrates with the gas phase and is expelled by belching. Thus, hydrogen ions are removed from the rumen by incorporation into water. The equilibrium constant for dehydration of carbonic acid favors the production of CO_2 and H_2O at 5 \times 10^{-3} (79). The acid titration curve is shifted, and bicarbonate in the rumen has its maximum BC at a pH higher than its reported pK_a (which was determined in a closed system). The extent to which the curve is shifted is directly proportional to the partial pressure of CO_2 in the gas phase. Turner and Hodgetts (91) reported that the pH of ruminal fluid from a sheep ranged from 8.44 to 6.55 at pCO_2 of 0.2 to 580 mm Hg, respectively. The fraction of the neutralizing capacity of bicarbonate used in the rumen is determined by ruminal pH and relative differences in rates of carbonic acid removal and passage of bicarbonate ion with liquid flow through the omasal orifice. Because the total BC of saliva can be estimated as a sum of bicarbonate and hydrogen phosphate concentrations (152 meq/L), as reported by Bailey and Balch (6), the actual BC of saliva probably ranges from 50% of this value at neutral pH to close to 100% at pH 5.5.

Saliva flow rates vary with chewing activity. Cassida and Stokes (20) used cardial collection and measured resting and eating saliva flow with multiparous Holstein cows in early lactation. Mean saliva flows during resting and eating were 151 and 177 ml/min, respectively; saliva flow from cows at rest increased from 130 to 173 ml/min at 4 to 8 wk postpartum. However, the resting flow rates of saliva might have been overestimated in this experiment because of cardial stimulation during collection. Saliva flow rate during rumination was 1.8 times higher than the resting flow for 19 published values in the literature (20). Argyle and Baldwin (2) argued that the use of this factor produced a volume of saliva that is much greater than the amount of liquid that could enter the rumen based upon measured ruminal volumes and liquid dilution rates. However, incomplete mixing and water flux across the ruminal wall could explain this inconsistency. Although better estimates of saliva flow are needed, it is apparent that flow varies with chewing activity and that total saliva flow should be a function of time spent resting, eating, and ruminating and their respective rates of flow. Equation [5] can be used to estimate salivary buffer flow into the rumen per day:

\[
SBF = [(IT \times IF) + (ET \times EF)] \times BCS \quad [5]
\]

where

- SBF = salivary buffer flow (milliequivalents per day),
- IT = time spent resting (minutes per day),
- IF = resting flow (liters per minute),
- ET = time spent eating (minutes per day),
- EF = eating flow (liters per minute),
- RT = time spent ruminating (minutes per day),
- RF = ruminating flow (liters per minute), and
- BCS = BC of the saliva (152 meq/L).

Salivary buffer flow is determined as the product of saliva flow and the BC of saliva, which, as previously
mentioned, is approximately 152 meq/L. Total saliva flow for a lactating dairy cow eating 270 min/d and ruminating 400 min/d is estimated to be 273 L/d using flow rates of 0.151, 0.177, and 0.272 L/min for resting, eating, and ruminating, respectively (20). Thus, salivary buffer flow is nearly 41,500 meq/d.

The BC of feedstuffs vary considerably; cereal grains have low BC, low protein and grass forages have intermediate BC, and legume forages and high protein feeds have high BC (55). Among forages, BC tends to increase with maturity (55) and with ensiling (39). Total cation contents of feeds have been reported (55) to be good indicators of total BC from pH 4 to 9. However, the total BC of feeds will not be realized because acid titration curves (98) show that feeds have little buffering effect in the functional range in the rumen of healthy lactating cows (pH 5.5 to 6.8). Most of the buffering by feeds occurs under pH 5, which, along with buffering by VFA, is important to resist dramatic decreases in ruminal pH but has less effect at normal pH. Turner and Hodgetts (91) found little difference in BC of ruminal fluid from a sheep grazing rich alfalfa and ryegrass pasture containing 3.5% particulate matter and BC of the same fluid that had been clarified; those researchers concluded that the particulate matter added little to the BC of the total ruminal fluid.

The direct buffering by the diet is much less than buffering by saliva; consumption of 22 kg/d of a diet with a total BC of 400 meq/kg of DM provides the capability of buffering 8800 meq/d of acid, which is approximately one-fifth of the BC from saliva. However, most of the BC from saliva will be used compared with a fraction of the BC from feed. Although direct buffering by the feed might not be of great importance compared with that of saliva, some additional buffering occurs with ammonia produced by protein degradation in the rumen. Hydrogen ions are removed from solution by rapid association with ammonia in the rumen to form ammonium ions because the normal range of ruminal pH is well below the pK_a for ammonia (52). However, the ammonium pool in the rumen is fairly low because ammonia is readily absorbed across the rumen wall (52) and is rapidly utilized by ruminal bacteria (54). Net loss of hydrogen ions from the rumen occurs as ammonium ions pass through the omasal orifice with liquid flow.

**PREDICTION OF TIME SPENT CHEWING**

Prediction of salivary buffer flow from Equation [5] requires prediction of the time spent resting, eating, and ruminating per day. Empirical predictions of the TCT and the fraction of TCT that was due to ruminating provide this information because time spent resting can be calculated by difference. Treatment means from the literature reporting chewing time per day for both eating and ruminating (132 treatment means from 32 experiments) or for TCT only (24 treatment means from 3 experiments) were used to develop empirical relationships from DMI and dietary characteristics. Thirteen experiments reported both time and number of chews during eating and ruminating, and the two measures were very closely correlated across experiments (Figure 7). Table 2 shows the mean and range for TCT and the factors evaluated.

![Figure 7. The relationships between the time spent chewing per day and the number of chews per day from experiments reported in the literature. The number of chews and time spent chewing per day were positively correlated for eating (+), ruminating (x), and total chewing (o) activity. Eating chews (number per day) = ±5854 + 84.75 \times eating time (minutes per day) (P < 0.0001; r^2 = 0.89; root mean square error = 2069; n = 58); ruminating chews (number per day) = ±4281 + 71.29 \times ruminating time (minutes per day) (P < 0.0001; r^2 = 0.95; root mean square error = 803; n = 58); total chews (number per day) = ±12,390 + 80.59 \times total chewing time (minutes per day) (P < 0.0001; r^2 = 0.94; root mean square error = 2214, n = 58) (9, 10, 11, 12, 13, 14, 15, 30, 31, 62, 73; C. S. Mooney and M. S. Allen, 1993, unpublished).](image-url)
described. Concentrations and intake of fiber (NDF and ADF) and PLI were related positively (P < 0.0001) to TCT, explaining from 26 to 32% of the variation. Forage NDF concentration and forage percentage were also related positively (P < 0.0001) to TCT, as was forage NDF intake (P < 0.01), explaining from 10 to 20% of the variation. Particle length of chopped forage, forage type (grass, legume, or mixed), and DMI were not related to TCT (P > 0.5). Although particle length was not related to TCT across experiments, it was related to TCT within experiment as previously discussed. The TCT was independent of a wide range of DMI (14.5 to 26.3 kg/d) although TCT and DMI have been previously reported to be positively related within an experiment (86). Also, ADF and NDF had similar relationships to TCT even though they were not highly related to each other in this data file (r² = 0.43).

Two-factor models also were evaluated using PLI and each other factor (Table 2). In combination with PLI, both concentration and intake of forage NDF were related positively (P < 0.0001) to TCT and accounted for 66 and 64% of variation, respectively. Other dietary factors that were related positively (P < 0.0001) to TCT in models that included PLI explained 38 to 42% of the variation and included NDF, ADF, and forage percentage and NDF and ADF intakes.

When all factors were used, combination in 69% of the variation in TCT was explained. The best fit model (r² = 0.69; RMSE = 77.6; response mean = 666), determined using 82 treatment means (limited by the articles reporting forage NDF percentage), is described by Equation [6].

\[
TCT = 544.6 + 159.9 \times PLI2 + 317.1 \times PLI3 - 12.1 \times DMI + 9.2 \times FNDF
\]  

All factors included were significant (P < 0.01). Particle length had a large effect on TCT with 160 min more TCT for chopped forage ≥0.3 cm and 317 min more TCT for long hay than for finely chopped forage. Although DMI was not related to TCT in previous models, DMI was related negatively in this model. Forage NDF percentage was related positively to TCT as expected.

To calculate saliva flow from Equation [5], TCT must be divided into time spent eating and time spent ruminating. The percentage of TCT that was due to rumination, calculated from the data from experiments represented in Table 1, varied from 43 to 74% (59.6 ± 6.4; mean ± SD) and was predicted from dietary characteristics with Equation [7]:

\[
RP = 57.50 - 4.70 \times PLI3 - 0.26 \times FNDF + 1.52 \times NDFI
\]  

where RP = ruminating time, percentage of total chewing time, and NDFI = NDF intake (kilograms per day).

Equation [7] predicted ruminating time as a percentage of TCT (r² = 0.76; RMSE = 2.53), which was related negatively (P < 0.01) to PLI3 and forage NDF.

---

**Table 2. Mean and range of total chewing time and various dietary factors for lactating dairy cows and their relationships determined by regression.**

<table>
<thead>
<tr>
<th>Factor</th>
<th>X</th>
<th>SD</th>
<th>Range</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total chewing time, min/d</td>
<td>668</td>
<td>126</td>
<td>364-962</td>
<td>149</td>
</tr>
<tr>
<td>DMI, kg/d</td>
<td>21.7</td>
<td>2.5</td>
<td>14.5-26.3</td>
<td>140</td>
</tr>
<tr>
<td>Forage, % of DM</td>
<td>48.1</td>
<td>12.8</td>
<td>18.4-98.2</td>
<td>145</td>
</tr>
<tr>
<td>ADF, % of DM</td>
<td>18.9</td>
<td>3.3</td>
<td>13.1-30.7</td>
<td>104</td>
</tr>
<tr>
<td>ADF Intake, kg/d</td>
<td>4.15</td>
<td>0.77</td>
<td>2.74-6.29</td>
<td>104</td>
</tr>
<tr>
<td>NDF, % of DM</td>
<td>29.1</td>
<td>4.3</td>
<td>19.0-41.9</td>
<td>139</td>
</tr>
<tr>
<td>NDF Intake, kg/d</td>
<td>6.29</td>
<td>0.96</td>
<td>3.93-8.59</td>
<td>142</td>
</tr>
<tr>
<td>Forage NDF, % of DM</td>
<td>19.2</td>
<td>5.5</td>
<td>11.5-36.3</td>
<td>82</td>
</tr>
<tr>
<td>Forage NDF intake, kg/d</td>
<td>4.37</td>
<td>1.26</td>
<td>2.23-7.45</td>
<td>78</td>
</tr>
</tbody>
</table>

---

1. Number of treatment means from the literature (9, 10, 11, 12, 13, 14, 15, 23, 25, 30, 31, 34, 42, 47, 48, 49, 50, 57, 58, 62, 70, 73, 78, 80, 87, 93, 100, 101; C. S. Mooney and M. S. Allen, 1993, unpublished).

2. Total chewing time (minutes per day) = mx + b, where m = slope, and b = intercept.

3. Particle length index.

4. Coefficient for PLI1 = 0, PLI2 = 13.31, and PLI3 = 149.76.

5. Grass, legume, or mixed.

6. Total chewing time (minutes per day) = m₁x₁ + m₂x₂ + b, where m₁ and m₂ = slopes, b = intercept, and x₂ = particle length index.

---

percentage and related positively (P < 0.01) to NDF intake. The percentage of TCT spent ruminating decreased for long hay, which might have been due to the greater time required for chewing during eating. However, ruminating time per day was higher for long hay than for chopped forage because of a higher TCT predicted from Equation [6]. The same was true for forage NDF (percentage of DM) because it was related positively to TCT in Equation [6].

Equations [5], [6], and [7] can be used to predict salivary buffer flow from dietary characteristics. For example, a cow with a DMI of 22 kg/d and consuming a diet including coarsely chopped forage with 21% of DM as forage NDF and 28% of DM as NDF, was estimated to have a TCT of 632 min/d, of which 61% was spent ruminating, and to have secreted saliva at a rate of 271 L/d with a total BC of approximately 41,000 meq.

**CHEWING VERSUS FERMENTATION ACID PRODUCTION**

The rate of acid production by fermentation of OM in the rumen (74,000 meq/d) is nearly twice the rate of salivary buffer secretion (41,000 meq/d) from the examples calculated. Table 3 shows the amount and fraction of hydrogen removal from the rumen by various routes at pH 6.0 with the given assumptions. Absorption of VFA removes about 53% of total hydrogen ions from the rumen under the conditions stated. More than 28% is incorporated into H₂O by the dehydration of carbonic acid, and about 9% flows from the rumen as dihydrogen phosphate. A minor fraction (<7%) flows from the rumen associated with VFA, ammonia, and particulate matter. A negligible quantity flows from the rumen as free hydrogen ions because of the small pool size (<0.1 mmol) at pH 6. More than 96% of the total hydrogen ion production is accounted for with these routes of removal. Additional removal of hydrogen ions by the carbonate buffer system is likely due to the previously mentioned increase in neutralization from removal of carbonic acid from the rumen. Because the example calculated neutralization from bicarbonate (61%) directly from the Henderson-Hasselbach equation (79) without consideration of a constant pCO₂, neutralization was underestimated. However, incomplete mixing of bicarbonate and dihydrogen phosphate ions from saliva before passage from the reticulorumen decreases the estimated neutralization. If the RDOM percentage is very high and total fermentation acid production exceeds the BC of the reticulorumen, pH decreases, forcing the animal to decrease DMI to adjust the amount of RDOM consumed.

<table>
<thead>
<tr>
<th>Route of removal</th>
<th>Amount removed (meq/d)</th>
<th>Percentage of total produced per day (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Absorbed as VFA</td>
<td>39,168</td>
<td>52.9</td>
</tr>
<tr>
<td>Incorporated into H₂O via carbonic acid</td>
<td>&gt;20,752</td>
<td>28.0</td>
</tr>
<tr>
<td>H₂PO₄⁻</td>
<td>6599</td>
<td>8.9</td>
</tr>
<tr>
<td>VFA</td>
<td>2316</td>
<td>3.1</td>
</tr>
<tr>
<td>NH₄⁺</td>
<td>1537</td>
<td>2.1</td>
</tr>
<tr>
<td>Particulate matter</td>
<td>1000</td>
<td>1.4</td>
</tr>
<tr>
<td>Free H⁺</td>
<td>&lt;1</td>
<td>Negligible</td>
</tr>
<tr>
<td>Total</td>
<td>71,372</td>
<td>96.4</td>
</tr>
</tbody>
</table>

1Assumptions: pH 6.0, ruminal liquid pool size = 80 L, liquid rate of passage = 0.15/h, ruminal particulate pool size = 13 kg, particulate fractional rate of passage = 0.035/h, saliva flow = 270 L/d, saliva HCO₃⁻ = 126 meq/L, saliva H₂PO₄²⁻ = 26 meq/L, ruminal ammonia concentration = 8 mg/dL, ruminal VFA concentration = 120 mmol/L, fractional rate of VFA absorption = 0.17/h (calculated as total rate of disappearance minus liquid passage rate; total rate of disappearance calculated as production rate per hour divided by ruminal VFA pool size), and digesta buffering = 100 meq/kg at pH 6.0.

The relative importance of the different routes of removal changes as the amount of VFA produced and pH change. As VFA production increases and pH decreases, a greater fraction of VFA would be absorbed because of a higher fractional absorption rate. More hydrogen ions would be incorporated into H₂O via carbonic acid because the lower pH drives the reaction in this direction. Hydrogen ion flow from the rumen that is associated with VFA and particulate matter increases because the associated fraction increases as pH decreases. Lower pH should have little effect on the flow from the rumen as dihydrogen phosphate and ammonium ions because they already are highly associated at pH 6. Little flow of unassociated hydrogen ions occurs because of a small relative pool size, even at low pH. Neutralization by salivary buffers is important in maintaining ruminal pH, but the relative importance of neutralization in hydrogen ion removal from the rumen changes with the amount of VFA produced.

The rate of fermentation acid production and salivary buffer secretion into the rumen is predicted for four different diets using Equations [3], [5], [6], and [7] (Table 4). The basal diet (A) had moderate percentages of RDOM and forage NDF and was predicted to have a fermentation acid production of 74,519 meq/d and a salivary buffer flow of 40,888 meq/d. When the RDOM was increased from 50 to
60% (diet B), fermentation acid production increased 20% to 89,423 meq/d. The substitution of finely chopped forage (diet C) for coarsely chopped forage (diet A) decreased salivary buffer flow by nearly 5%, from 40,888 to 38,912 meq/d, and an increase of the forage NDF of diet A (20% of DM) to 24% of DM in diet D increased salivary buffer flow less than 1%. Variation in RDOM appeared to have a much greater effect on ruminal pH than variation in PLI or forage NDF percentage with the assumptions made. Although forage NDF percentage was closely related to both TCT and ruminal pH, the relatively minor effect on salivary buffer flow suggests that forage NDF has effects on ruminal pH other than through its relationship with TCT. Forage NDF may also increase ruminal motility, resulting in greater mixing of ruminal contents. Increased mixing will increase the concentration of fermentation acid at the ruminal epithelium, which can result in a greater rate of fermentation acid absorption and removal from the rumen because of a higher concentration gradient. Another explanation is that the effect of TCT on saliva flow was underestimated because the saliva flow rates that were used were not accurate. Overestimation of the resting flow rate of saliva, because of cardial stimulation during collection, would decrease the effect TCT has on hydrogen ion removal in this model.

**TABLE 4. Prediction of daily fermentation acid production and salivary buffer flow for four different diets.**

<table>
<thead>
<tr>
<th>Diet</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ruminally degraded OM, %</td>
<td>50</td>
<td>60</td>
<td>50</td>
<td>50</td>
</tr>
<tr>
<td>Particle length index</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Forage NDF, % of DM</td>
<td>20</td>
<td>24</td>
<td>20</td>
<td>24</td>
</tr>
<tr>
<td>Total chewing time, min/d</td>
<td>622</td>
<td>622</td>
<td>462</td>
<td>659</td>
</tr>
<tr>
<td>Ruminating time, min/d</td>
<td>388</td>
<td>388</td>
<td>288</td>
<td>402</td>
</tr>
<tr>
<td>Eating time, min/d</td>
<td>234</td>
<td>234</td>
<td>174</td>
<td>257</td>
</tr>
<tr>
<td>Saliva flow, L/d</td>
<td>269</td>
<td>269</td>
<td>256</td>
<td>271</td>
</tr>
<tr>
<td>Salivary buffer flow, meq/d</td>
<td>40,888</td>
<td>40,888</td>
<td>38,912</td>
<td>41,192</td>
</tr>
<tr>
<td>Fermentation acid production, meq/d</td>
<td>74,519</td>
<td>74,519</td>
<td>74,519</td>
<td>74,519</td>
</tr>
</tbody>
</table>

1DMI = 22 kg/d, NDF = 30% of DM, and OM = 91% of DM.
2A = Basal diet [moderate percentages of OM truly digested in the rumen (RDOM) and forage NDF]. B = RDOM increased from 50 to 60%. C = substitution of finely chopped forage for coarsely chopped forage (diet A), and D = increased forage NDF to 24% of DM (diet A = 20% of DM).
3Predicted using Equation [6].
4Predicted using Equations [6] and [7].
5Predicted using Equation [5].
6Predicted using Equation [3].

**CONCLUSIONS**

Fiber requirements for dairy cattle should be determined by considering both the physical effectiveness of fiber and the production of fermentation acids. Relationships of ADF and NDF to TCT were similar. However, NDF from forage was superior to concentrations of total dietary NDF or ADF for prediction of TCT with PLI in the model. The same might be true for ADF from forage, but this result was reported for too few experiments to permit this theory to be evaluated. Although saliva flow is necessary to neutralize fermentation acids, differences in RDOM percentage among diets might be the most important single factor affecting ruminal pH. Fiber exerts its influence on ruminal pH by increasing saliva flow via its effect on chewing and by diluting more fermentable feed components, which reduces fermentation acid production. Forage NDF generally has lower ruminal degradation than nonforage NDF and nonstructural carbohydrates (68) and was related positively to TCT, the combination of which may be responsible for the high positive relationship with ruminal pH that was observed for the small (n = 26) data file. The prediction of the hydrogen ion pool in the rumen requires iterative methods because the primary route of hydrogen ion removal from the rumen is by VFA absorption, the fractional rate of absorption of which is affected by pH. Future models must account for the effect of removal of CO₂ gas on bicarbonate buffering in the rumen. The effects of several factors on ruminal pH are not adequately understood; among those factors are saliva flow and composition, surface area for VFA absorption in the rumen, and variation in microbial cell yield (which affects fermentation acid yield from fermented OM). However, even with a greater understanding of these areas, mechanistic modeling of ruminal pH as hydrogen ion concentration in the rumen may be futile; at pH 6.0, the pool of hydrogen ions is less than 0.1 meq with a ruminal volume of 80 L, and daily production of hydrogen ions is normally in excess of 60,000 meq/d. Empirical models give reasonably accurate predictions, and accuracy may be improved further by including percentages of forage NDF or measurements of physical effectiveness of NDF combined with estimates of RDOM.

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SYMPOSIUM: MEETING THE FIBER REQUIREMENTS OF DAIRY COWS


