Variation in the Susceptibility to Ruminal Acidosis: Challenge or Opportunity?

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Take Home Messages

- Ruminal acidosis is highly prevalent and severe in dairy cattle, especially in early lactation
- There is considerable variation among cows in their susceptibility to ruminal acidosis
- Variation in the susceptibility to ruminal acidosis presents both a challenge and opportunity for producers
- The majority of the variation for the susceptibility to ruminal acidosis is explained by differences in the absorptive capacity of the rumen wall
- Future research is required to determine the genes involved in acidosis resistance and to determine whether they can be used as a selection tool for more acidosis resistant animals

Introduction

In the rumen, feed is fermented by microorganisms resulting in the production of short-chain fatty acids (**SCFA**; also known as volatile fatty acids). The predominant SCFA are acetate, propionate, and butyrate with lactate being a minor component. Short-chain fatty acids are absorbed across the rumen wall and are used as energy substrates. However, acid (H^+) is also produced with SCFA. Accumulation of acid decreases ruminal pH and can lead to ruminal acidosis which is known to have negative consequences on animal health and production efficiency (Stone, 2004). However, dairy producers and researchers alike have observed that cattle differ in their susceptibility to ruminal acidosis, even when managed similarly. This paper presents some recent findings demonstrating periods when ruminal acidosis may be most severe and some of the causes for variation in the susceptibility of cows to

ruminal acidosis.

■ Ruminal Acidosis

Ruminal acidosis occurs when the rate of acid production is greater than the rate of acid removal from the ruminal contents. For the dairy industry, ruminal acidosis is arguably one of the most prominent digestive disorders with prevalence rates, determined using 662 cows in 55 dairy herds in Wisconsin, ranging between 12 to 30% throughout lactation (Krause and Oetzel, 2006). In addition to high prevalence rates, cows fed typical diets in western Canada may also experience severe ruminal acidosis. For example, in a study conducted at the Lethbridge Research Centre, we found that on average, primiparous cows spent 7.3, 9.0, 8.3, and 6.1 h/d with a ruminal pH below 5.8 during the first 5 d of lactation, and on d 17-19, 37-39, and 58-60, respectively (Penner et al., 2007). Due to the high prevalence rates and severity of ruminal acidosis, we have conducted a number of studies to determine factors that affect the risk for ruminal acidosis.

Ruminal acidosis can be broadly characterized as acute or subacute in severity. Acute ruminal acidosis is caused by an abrupt increase in the intake of rapidly fermentable carbohydrate. This increases fermentation acid production decreasing pH, and ultimately increasing lactic acid production and accumulation leading to a further decrease in ruminal pH (Owens et al., 1998). Acute ruminal acidosis results in overt clinical signs including anorexia, diarrhea, and possibly death (Owens et al., 1998). In contrast, the decrease in pH associated with subacute ruminal acidosis (SARA) is driven by the accumulation of volatile fatty acids without a marked increase in lactic acid concentration (Krause and Oetzel, 2006), and animals experiencing SARA often do not present clinical signs (Nocek, 1997).

The severity of ruminal acidosis varies on a continuum from subacute to acute. As ruminal pH declines, the negative effect on the rumen microbial composition and activity and on the rumen wall are increased (Figure 1). For the context of this paper, we will consider ruminal acidosis to occur when ruminal pH is less than 5.8. Although more severe depressions in rumen pH may be required to elicit changes in rumen epithelial function, the use of pH 5.8 as a threshold also includes the negative impact of low pH on fibre digestibility.

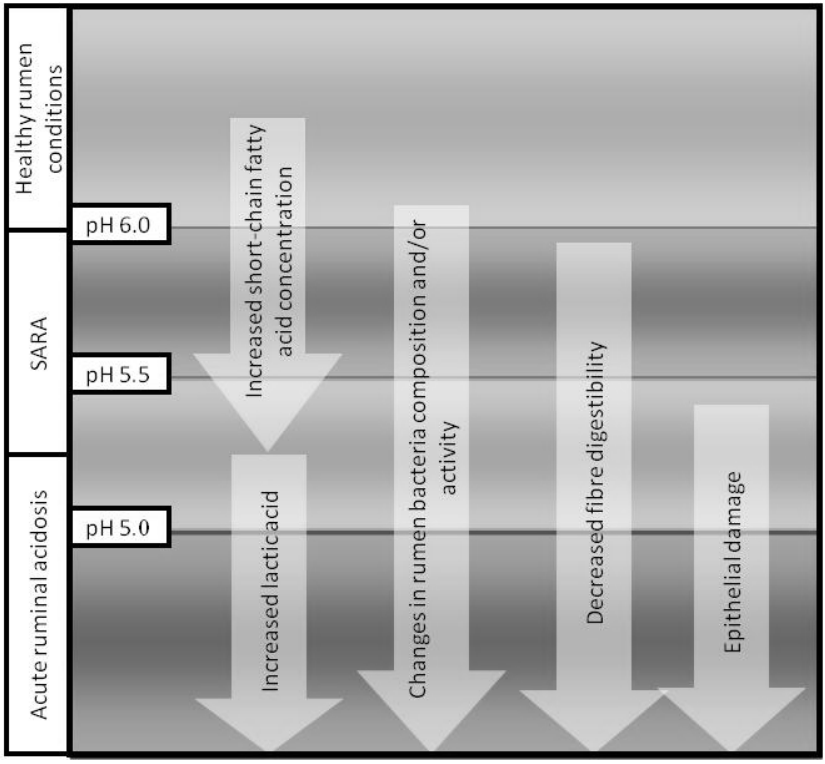

Figure 1. Impact of changes in pH on short-chain fatty acid production, bacterial composition and activity, fibre digestibility, and epithelial function.

■ Acid Production in the Rumen

Microbial fermentation of organic matter (mainly fibre, starch, and protein) in the rumen provides a source of nutrients for ruminal microbes to carry out maintenance and growth functions. Fermentation also yields by-products including SCFA, carbon dioxide (CO_2), and hydrogen gas (Russell and Hespell, 1981). The primary SCFA arising from microbial fermentation are acetate, propionate, and butyrate; however, other minor acids including isobutyrate, valerate, isovalerate and lactate are also produced. As mentioned above, these SCFA are absorbed across the rumen wall and provide the main energy source for dairy cattle.

The quantity of acid (i.e. protons, H^+) produced depends on the type of SCFA arising from fermentation. Figure 2 illustrates the pathway by which microbes

convert carbohydrates such as starch or fibre to SCFA. Carbohydrates are cleaved into their individual sugar units denoted in Figure 2 as glucose. Glucose is then fermented by the microbes yielding either 2 acetate + H^+, 2 propionate + H^+, or 1 butyrate + H^+. Thus, fermentation that promotes the production of butyrate may result in lower rates of acid production.

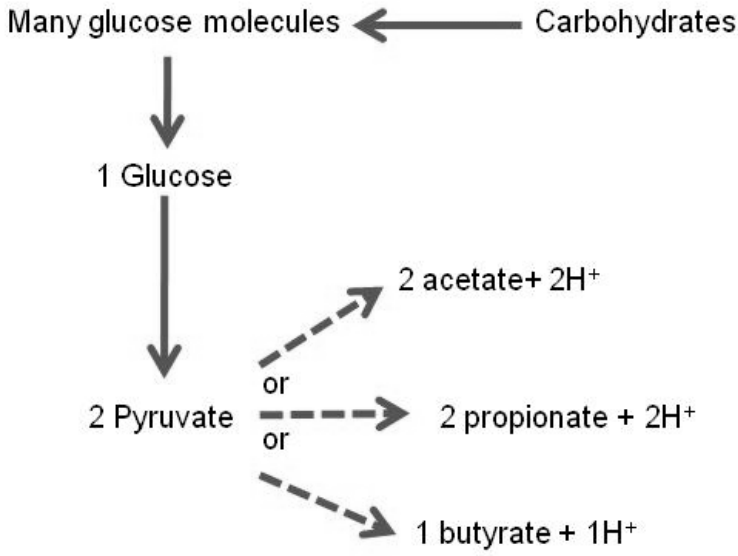

Figure 2. Pathway for the microbial conversion of carbohydrates to SCFA and the resulting production of acid (H^+).

Although dairy cattle utilize SCFA as a source of energy, under normal conditions in the rumen, SCFA dissociate (i.e. release a proton [H^+]). The release of the proton drives the reduction in pH causing ruminal acidosis. The point at which a compound releases a proton or accepts a proton is pH dependent. The term 'dissociation constant' has been used to define the point at which 50% of the compound would be in each the dissociated and un-dissociated states. A greater proportion of compounds in the dissociated state indicates that these compounds have released a proton and thus have acted as an acid. On the other hand, when compounds have a greater proportion in the un-dissociated state, they have accepted a proton and have acted as a buffer. Figure 3 illustrates the relationship between pH and the proportion of various compounds that would occur in the dissociated state. As can be seen from Figure 3, the majority of the lactate and SCFA would be in the dissociated state under normal rumen conditions indicating that these compounds act as acids. In contrast, bicarbonate and hydrogen phosphate can accept protons and therefore function as bases.

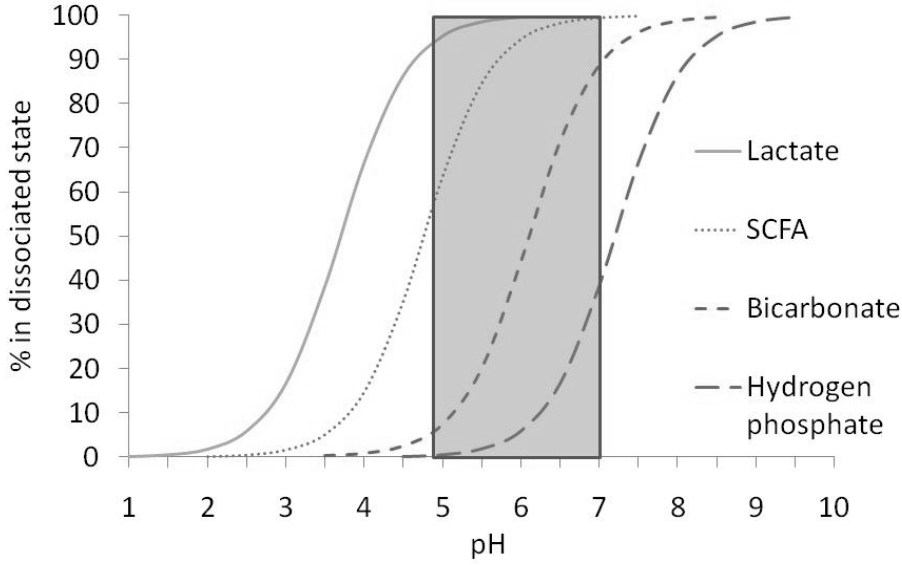

Figure 3. Impact of pH on the proportion of lactate, SCFA, bicarbonate, and phosphate in the dissociated state. Compounds are considered to be acids (i.e. they donate a proton) when less than 50% are in the dissociated state and bases (i.e. they accept a proton) when more than 50% are in the dissociated state. The grey box indicates the typical range observed for ruminal pH in dairy cows.

■ Acid Removal

Acid production in the rumen is a valuable process supplying energy substrates and microbial protein. However, to prevent the accumulation of acid in the rumen, dairy cattle have a number of mechanisms to remove acid. Removal of acid is facilitated through clearance of the acid from the rumen (absorption across the rumen wall and passage out of the rumen), and by neutralization (a chemical reaction converting bicarbonate and H^+ to CO_2 and water). Figure 4 illustrates the main mechanisms for acid removal from the rumen.

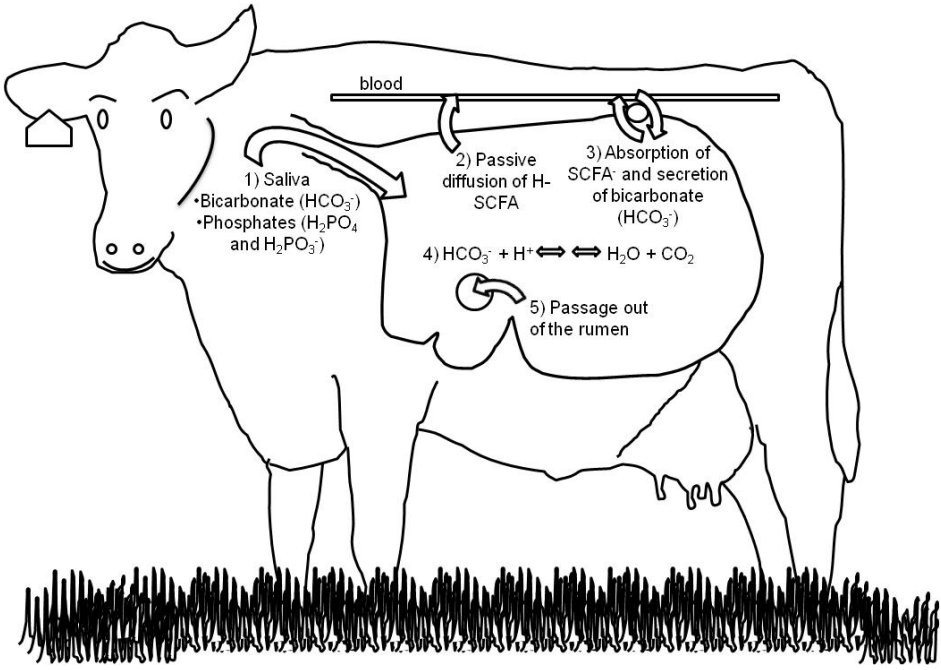

Figure 4. Main mechanisms for the removal of acid from the rumen: 1) saliva containing bicarbonate [neutralizes acid through the carbonic anhydrase reaction; step 4] and hydrogen phosphate enters the rumen, 2) passive diffusion of undissociated SCFA across the rumen wall [protons may be removed with the absorption process], 3) absorption of dissociated SCFA in exchange for bicarbonate [supply of bicarbonate neutralizes acid; step 4], 4) carbonic anhydrase reaction [bicarbonate and a proton (acid) are converted to CO_2 and water], and 5) passage of acid out of the rumen.

Neutralization of Acid with Salivary Buffers

A considerable emphasis has been placed on the role of salivary buffer supply towards the stabilization of ruminal pH. Because saliva contains relatively consistent proportions of bicarbonate and hydrogen phosphate buffers (Bailey and Balch, 1961), estimates of salivary secretion during eating, ruminating, and resting can provide reliable estimates of the salivary buffer supply to ruminal contents. The most important buffer in saliva is bicarbonate. Bicarbonate reacts with acid through a two-step reaction that converts bicarbonate and acid to CO_2 and water. This reaction is facilitated through an enzyme called carbonic anhydrase (see Figure 4).

Rates of saliva secretion during resting, and eating have been estimated to

range between 88 to 173 mL/min while resting and 166 to 253 mL/min during eating (Cassida and Stokes, 1986; Maekawa et al., 2002a,b). It has been estimated that saliva can neutralize approximately 30% of the total H^+ production/d (Allen, 1997).

Absorption of SCFA as A Mechanism for Acid Removal

Short-chain fatty acids are absorbed across the rumen wall and serve as energy substrates. There are two main mechanisms for SCFA absorption (Figure 5). Previously, it was thought that SCFA absorption occurred exclusively through passive diffusion. Passive diffusion requires that SCFA be in the un-dissociated state (bound to H^+). However, as shown in Figure 3, under normal rumen pH conditions, the vast majority of the SCFA would be in the dissociated state (released the H^+). Passive diffusion of SCFA is beneficial in terms of the regulation of ruminal pH as the H^+ is removed with the SCFA.

The second mechanism for SCFA is through a transport protein that facilitates the exchange of bicarbonate for the dissociated SCFA (Aschenbach et al., 2009). In this process SCFA are removed, while the rumen epithelium supplies bicarbonate. The secreted bicarbonate then can react with protons through the carbonic anhydrase reaction to yield CO_2 and H_2O. The CO_2 can then be removed through eructation. It is estimated that for every SFCA absorbed, 0.53 HCO_3^- is secreted (Gäbel et al., 1991).

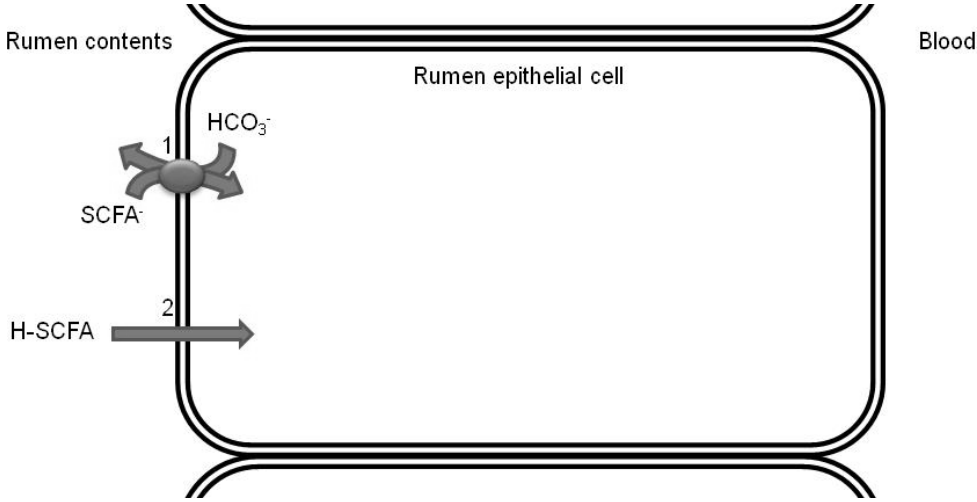

Figure 5. Pathways for SCFA absorption across the rumen wall (epithelium): 1) Dissociated SCFA can be absorbed in exchange for bicarbonate thereby supplying a buffer to the rumen contents and 2) SCFA can be absorbed via passive diffusion across the rumen epithelium. Passive diffusion removes an acid associated with the SCFA.

■ Variation in the Susceptibility

Dairy producers and researchers alike have observed that there is tremendous variation in the susceptibility of individual cows to ruminal acidosis. In a past study, we found that the duration that ruminal pH was below 5.8 ranged between 0 and 22 h/d during the first 5 d of lactation, 0 and 18 h during d 17-19, 0 and 21 h/d during d 37-39, and 0 and 16 during d 58-60 (Figure 6). Variation among animals for the susceptibility to ruminal acidosis provides a challenge for nutritional management, as there is an inherent trade-off between diet fermentability and the risk for ruminal acidosis. However, it also presents an opportunity to select for increased resistance to ruminal acidosis. Despite the common knowledge that variation is present, few studies have investigated the cause for such variation. A physiological understanding of why animals differ in their tolerance to SARA may provide new strategies to reduce SARA.

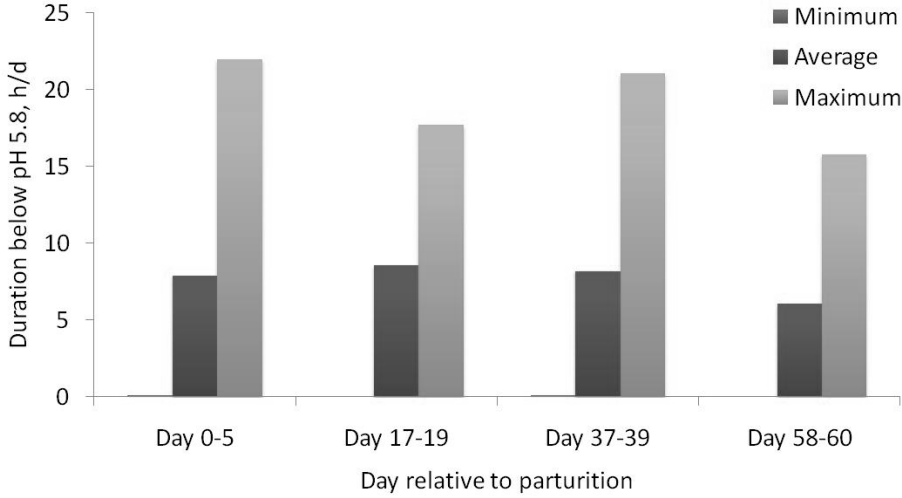

Figure 6. Minimum, average, and maximum values for the duration that ruminal pH was below 5.8 for 14 primiparous Holstein cows during early lactation. Minimum duration was near 0 h/d for all time points.

There are a number of possible mechanisms that may alter the susceptibility of individual cows to ruminal acidosis. Past studies have comprehensively evaluated chewing activity as a management strategy to reduce the risk for ruminal acidosis. To evaluate the impact of saliva production on ruminal pH, we re-evaluated data from Maekawa et al. (2002). In that study, cows were fed diets with forage-to-concentrate ratios of 40:60, 50:50, and 60:40 and the salivation rate was determined from the amount of moisture added to feed consumed. In that study, they reported a positive correlation between dry matter intake and saliva production but no information on the relationship between saliva production and ruminal pH were presented. To address this, we evaluated the relationship between the duration that pH was below pH 5.8 and the rate of saliva production and found a positive correlation (Figure 7). These data indicate that while the rate of saliva production increases with the level of DMI, increased rate of saliva production did not result in improved ruminal pH status.

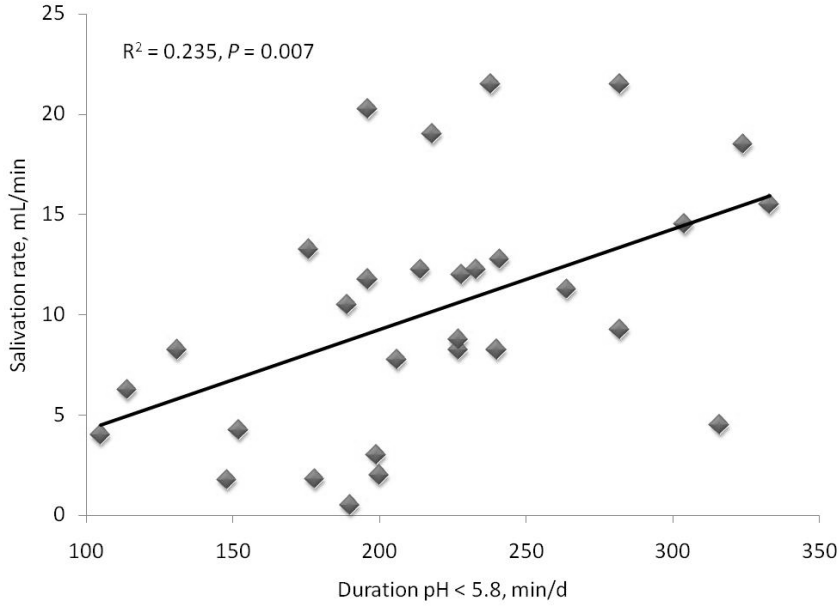

Figure 7. Relationship between the duration that ruminal pH is below 5.8 and the rate of saliva production. The positive correlation indicates that although the rate of secretion increases, the increased saliva is not able to ameliorate the duration that pH is below 5.8.

Based on the estimate that absorption of SCFA accounts for approximately 53% of acid removal from rumen (Allen, 1997), we evaluated whether differences in the absorptive capacity could explain differences in susceptibility of individual animals to ruminal acidosis (Penner et al., 2009). For this study, we used 24 sheep as a model for ruminants. Sheep were assigned to either SHAM or GLUC infusion treatments. Sheep on the GLUC treatment received an oral drench of glucose designed to induce ruminal acidosis. Sheep on the SHAM treatment received an oral drench of water of equivalent volume to GLUC sheep. Administering the drench reduced ruminal pH for GLUC sheep but not for SHAM sheep (Figure 8); however, there was tremendous variation observed for the ruminal pH response within the GLUC treatment. To understand the cause for this variation, sheep on the GLUC treatment were classified as non-responders (NR) or responders (RES) based on the area that pH was below 5.8. Sheep classified as NR had a smaller area that pH was below 5.8 with minimum, average, and maximum values of 0.0, 6.8, and 12.3 pH × min, respectively with RES having values of 29.2, 47.8, and 84.0 pH × min, respectively. Clearly, the NR and RES were two groups of animals with drastic differences in their response to the acidosis challenge.

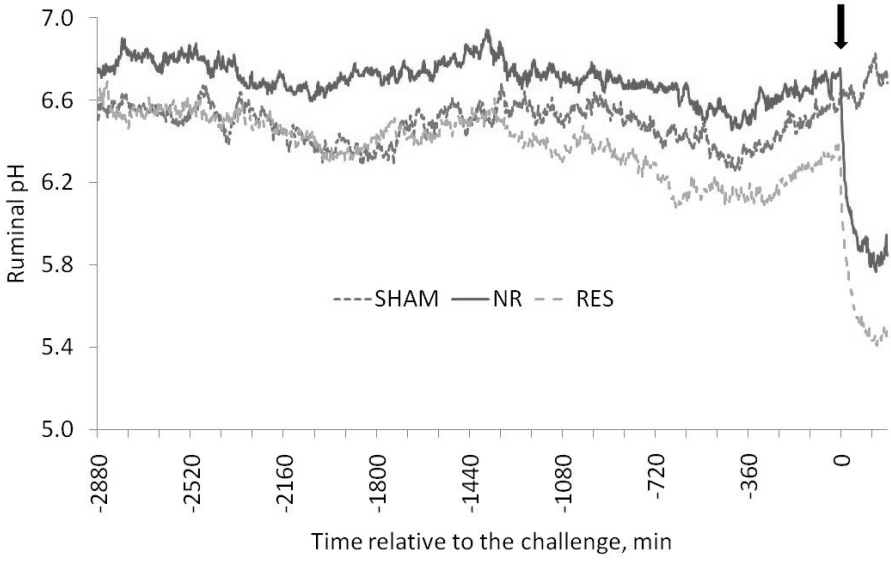

Figure 8. Ruminal pH for sheep receiving the SHAM treatment and GLUC treatments. Due to the significant variation within the GLUC treatment, sheep were classified as non-responders (NR) or responders (RES).

Three hours after administering the oral drench, ruminal epithelia was harvested and mounted in Ussing Chambers. Ussing Chambers are an in vitro method that can be used to determine the rate of nutrient absorption across the ruminal epithelium. We decided to compare the rate of acetate and butyrate uptake by the ruminal epithelia including the currently known pathways for absorption (passive diffusion, bicarbonate exchange (described in Figure 5) and another less characterized pathway.

Results showed that the uptake of acetate and butyrate were not different between RES and SHAM sheep indicating that low ruminal pH for RES compared to SHAM did not negatively affect epithelial function. This was a critical finding allowing for comparisons between NR and RES. Interestingly, NR had much greater rates of total acetate and butyrate uptake than RES (Figure 9).

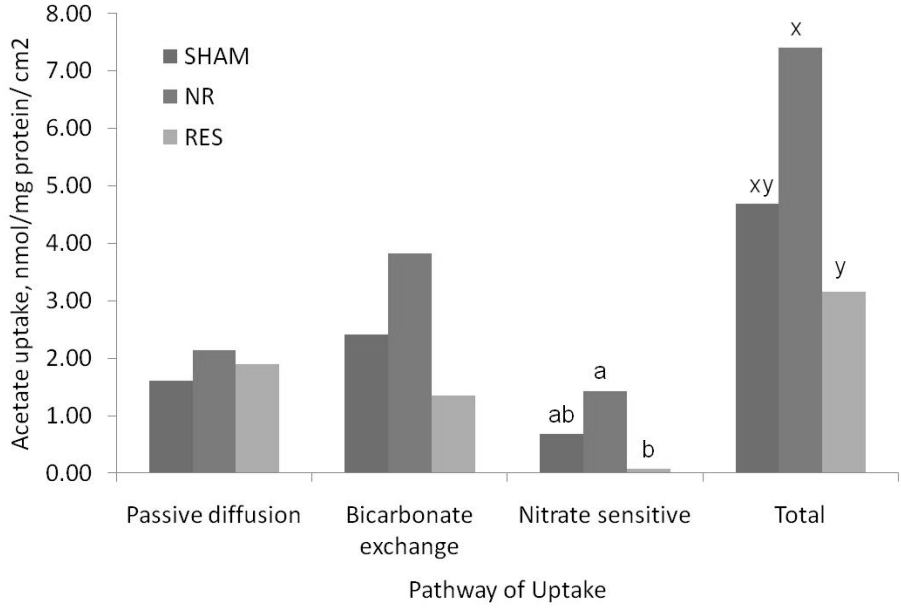

Figure 9. Acetate uptake by the isolated ruminal epithelia in Ussing Chambers. Treatments with differing superscripts within a pathway for absorption differ (P <0.05).

The mechanism causing increased total acetate uptake was primarily the bicarbonate exchange mechanism although differences were not significant. For butyrate, the increase in total uptake was due to passive diffusion (data not shown). Collectively, these data show that differences among sheep for the capacity of SCFA uptake strongly affects ruminal pH.

Additional evidence for the role of absorption for the regulation of pH is presented in Figure 10. As shown in this graph, the mean pH prior to the oral drench was significantly correlated to the rate of acetate and butyrate uptake. Thus, sheep with a greater capacity for SCFA absorption had higher ruminal pH.

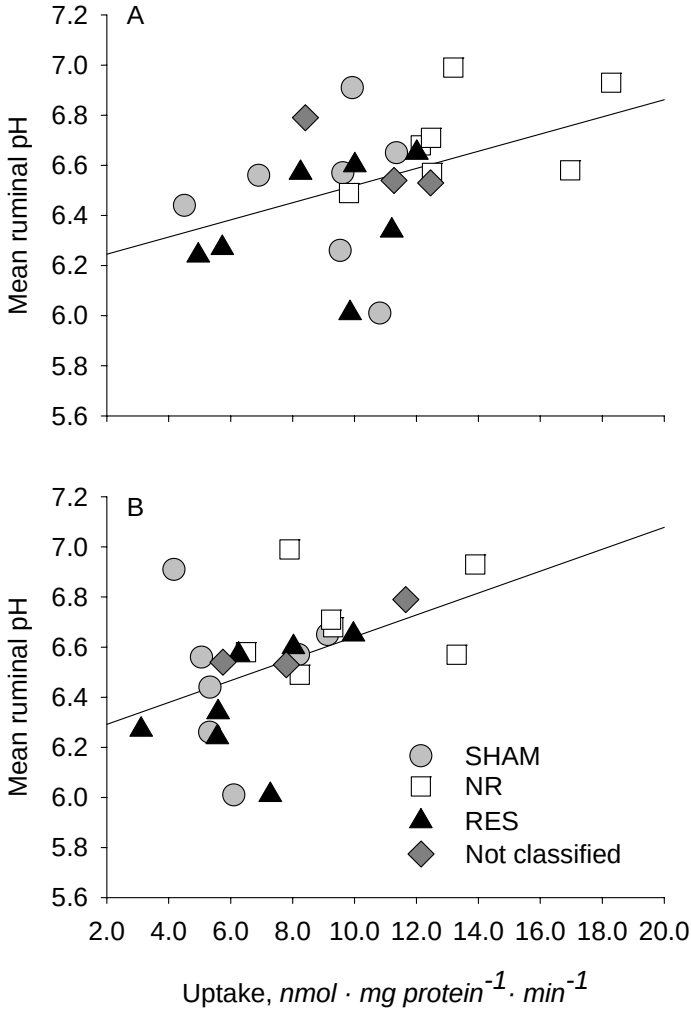

Figure 10. Relationship between the total uptakes of acetate (A) or butyrate (B) and the 48-h mean pH of each individual sheep prior to the oral drench. Regressions were (A) mean ruminal pH = 0.0460 × total acetate uptake, nmol · mg protein^{-1} · min^{-1} + 6.31 (n = 24, P = 0.024, r^2 = 0.212) and (B) mean ruminal pH = 0.0343 × total butyrate uptake, nmol · mg protein^{-1} · min^{-1} + 6.18 (n = 24, P = 0.033, r^2 = 0.191). The figure includes data for SHAM (n = 7), NR (n = 7) and RES sheep (n = 7), as well as for glucose-drenched sheep not classified into NR or RES (n = 3).

Summary

Ruminal acidosis is a highly prevalent and severe digestive disorder in dairy cows. One particular challenge with ruminal acidosis is the considerable variation observed among cows, even when fed a common diet. Recent research has demonstrated that differences in the rate of SCFA absorption among animals explain the differences observed for ruminal pH. Future research is still required to determine the molecular regulation for these mechanisms and whether a certain genotype is involved.

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