Animal Feed Science and Technology 172 (2012) 22–33

Contents lists available at SciVerse ScienceDirect

Animal Feed Science and Technology

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

Ruminal pH regulation and nutritional consequences of low pH☆

J. Dijkstra[a,*], J.L. Ellis[a], E. Kebreab[b], A.B. Strathe[b], S. López[c], J. France[d], A. Bannink[e]

[a] Animal Nutrition Group, Wageningen University, P.O. Box 338, 6700 AH Wageningen, The Netherlands
[b] Department of Animal Science, University of California, Davis 95616, USA
[c] Instituto de Ganadería de Montaña (ULE–CSIC), Department Producción Animal, Universidad de León, 24071 León, Spain
[d] Centre for Nutrition Modelling, Department of Animal and Poultry Science, University of Guelph, Guelph, ON N1G 2W1, Canada
[e] Livestock Research, Animal Sciences Group, Wageningen University and Research Centre, Lelystad, The Netherlands

ARTICLE INFO

Keywords:
Rumen
pH
Volatile fatty acids
Fiber
Subacute ruminal acidosis
Methane

ABSTRACT

Volatile fatty acids (VFA) and lactic acid can build up in the rumen and reduce ruminal pH. Low ruminal pH for prolonged periods each day can affect feed intake, microbial metabolism and feed digestion, and has also been related to inflammation, diarrhea and milk fat depression. This paper considers aspects of pH regulation, as well as the effects of ruminal pH on rate of substrate degradation and on the profile of VFA available for absorption. Removal of VFA from the rumen by passage in the liquid phase and by absorption through the rumen wall are major processes that influence ruminal pH. The buffering capacity (BC) of rumen fluid is variable and is generally assumed to depend primarily on bicarbonate. Bicarbonate-dependent absorption is not just a primary absorption pathway of VFA but can also secrete bicarbonate at a capacity equal to that from saliva, thus removing protons from the rumen by neutralization. In addition, the inherent BC of the diet is involved in pH regulation, largely explained by the cation exchange capacity of feedstuffs. Empirical models to predict ruminal pH have had limited success. The inclusion of dietary characteristics in those models is needed to improve prediction accuracy. Representations of the effect of pH on fiber degradation adopted in models of ruminal function differ widely and include linear decline, saturation-type and sigmoidal relationships. In comparison with pH effects on degradation of fiber *in sacco*, most representations tend to overestimate the inhibiting effect of pH. Because the products of fiber hydrolysis are a major source of energy for microbial growth in the rumen, proper understanding and representation of fiber degradation at low pH is vital to predict microbial protein supply and VFA production satisfactorily. Variation in VFA profile is associated with variation in methane production, nutrient partitioning and milk composition. Various ruminal bacterial species have been observed to shift pathways in response to changes in pH while fermenting the same substrate. Mechanistic rumen models have adopted VFA stoichiometric coefficients related to type of substrate present in the feed or fermented in the rumen, but the majority of models do not include the effect of pH on VFA profile. In conclusion, ruminal pH is a major determinant of the profile of nutrients available for absorption. Shifting focus to factors other than salivary bicarbonate secretion will aid in better understanding ruminal pH regulation. Improved models to predict effects of ruminal pH on microbial metabolism and VFA profile will enable further optimization of dairy cow nutrition.

Abbreviations: BC, buffering capacity; peNDF, physically effective NDF; VFA, volatile fatty acids.

☆ This paper is part of the special issue entitled: Rumen Health: A 360° Analysis, Guest Edited by A. Van Vuuren, S. Calsamiglia and Editor for Animal Feed Science and Technology, P. Udén.

* Corresponding author. Tel.: +31 317 484082; fax: +31 317 484062.
E-mail address: jan.dijkstra@wur.nl (J. Dijkstra).

0377-8401/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.anifeedsci.2011.12.005

1. Introduction

Fermentation of feedstuffs in the reticulo-rumen (hereafter: rumen) produces volatile fatty acids (VFA) and lactic acid. These acids can accumulate and reduce ruminal pH if rumen buffering cannot keep pace with their accumulation (Plaizier et al., 2009). Low rumen pH for prolonged periods each day can negatively affect feed intake, microbial metabolism, and nutrient degradation, and low ruminal pH is related to inflammation, laminitis, diarrhea and milk fat depression (Stone, 2004; Krause and Oetzel, 2006; Enemark, 2008), although the extent of problems that occur and the precise mechanisms by which low ruminal pH increases these disorders have not been fully characterized. High yielding dairy cows fed energy dense rations rich in rapidly fermentable starch or sugars at high feed intake levels are particularly susceptible to acidosis, although goats, sheep and other ruminants are also prone to the disease (Braun et al., 1992). Subacute ruminal acidosis, which induces an elevation in rumen temperature (AlZahal et al., 2008), affects from 10% to 40% of dairy cattle in a herd, resulting in large financial losses and major concern for animal welfare reasons (Garrett et al., 1999; Kleen et al., 2009; Tajik et al., 2009).

Despite the impact of low ruminal pH on farm profitability and animal welfare, current empirical feed evaluation systems are unable to address the complex interrelationships in the rumen that result in acidosis following the ingestion of certain feeds. These systems aim to match nutrient requirements with nutrient intake at pre-defined production levels but are not suitable to predict the responses to dietary changes in terms of production level and product composition, digestion of nutrients and excretion of waste end-products to the environment, and nutrition related disorders. The change from a requirement to a response system to meet the needs of various stakeholders requires prediction of the profile of absorbed nutrients and its subsequent utilization for various purposes (Hanigan, 2005; Dijkstra et al., 2007; Kebreab et al., 2009). Mechanistic approaches to feed evaluation may address the relationships between host animal, feed and rumen micro-organisms, and demonstrate a greater capacity for describing ruminal fermentation processes that determine ruminal pH (Baldwin, 1995; Dijkstra et al., 2008). The development of these models to address prediction of ruminal pH requires concepts and data on the dynamics of nutrient degradation, microbial fermentation and acid removal from the rumen. Therefore, this contribution considers aspects of pH regulation, as well as effects of ruminal pH on rate of substrate degradation and on type of VFA formed.

2. Ruminal pH regulation

Fermentation of feed by microorganisms in the rumen produces VFA and sometimes lactic acid. Ruminal pH will drop when VFA or lactic acid accumulate in the rumen. To prevent this drop in pH related to production of acids in the rumen and acids ingested with the feed, the acids have to be removed from the rumen or buffered. Volatile fatty acids are removed from the rumen by passage in the liquid phase and by absorption through the rumen wall (Aschenbach et al., 2009). Acids accumulated in the rumen can be also buffered to some extent by bicarbonate secreted into the rumen, along with some dietary features that may result in buffering activity (cation exchange capacity of cell walls; addition of buffers to the ration; Allen, 1997; Kohn and Dunlap, 1998).

2.1. Relationship between VFA concentration and pH

In general, ruminal VFA concentration increases, and pH decreases, following a meal. Empirical models to predict ruminal fluid pH from acid concentration, however, have had limited success. Ruminal VFA concentration is related negatively to ruminal pH, but the relationship appears to be weak (Allen, 1997). This weak relationship is likely related to large variation between diets in removal, buffering and neutralization of acids in the rumen that affects the relationship between pH and VFA. It is interesting to compare this relationship between pH and VFA in the rumen with that in the hindgut, because the hindgut lacks salivary buffer secretion. Moreover, protozoa that have a moderating effect on the rate of fermentation of rapidly available carbohydrates in the rumen (Van Zwieten et al., 2008), are absent in the hindgut. Assuming that the pH and VFA in fresh feces resemble that in the hindgut, the relationship between VFA concentration and pH is much stronger and residual variation much less when compared with the rumen (Fig. 1), indicating a relatively less important influence of removal of VFA, buffering and neutralization in the hindgut.

In a series of experiments in sheep on a wide range of diets, the linear regression coefficient relating ruminal pH to VFA (in mM) varied significantly for different diets from −0.0060 to −0.0168 (Briggs et al., 1957). In these experiments, replacement of roughage by grain increased the absolute value of the regression coefficient significantly, and high protein diets had low regression coefficients. When buffers are fed, the equations predicting linear relationships between ruminal pH and VFA concentration had decreased slopes (Emmanuel et al., 1970) demonstrating that with buffers, ruminal pH is less sensitive to VFA concentration changes. Therefore the relationship between ruminal VFA concentration and pH appears to be diet specific and affected by various buffering mechanisms. Long forage particles in the diet affect digesta stratification in the rumen and promote ruminating and salivary secretion, which helps buffer the acids resulting from fermentation of feed. Thus, the amount of fiber in the diet and particle length of forages, combined in the diet characteristic physically effective NDF (peNDF), can have a significant impact on ruminal pH through the provision of salivary buffers (Yang and Beauchemin, 2007). The effect of peNDF is due to chewing and ruminating activities, meal size, rumen motility and shifts in the site of grain digestion (Allen, 1997). One of the drawbacks of the peNDF concept is that it does not take into consideration the