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Review article

The role of dissolved carbon dioxide in both the decline in rumen pH and nutritional diseases in ruminants

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ABSTRACT

Rumen pH has been central to theories of nutritional disease and nutrient digestion in ruminants for decades. In particular, rumen pH is the measurement of a physical phenomenon that describes the balance between bases and acids in a solution. Here, I take a closer look at rumen pH and suggest that its decline during acidosis is a sign of an increased concentration of dissolved carbon dioxide (dCO_2), which is the acid in the main buffer system. Rumen dCO_2 concentrations are thought to be constant and low, but modern feeding practices can lead to carbon dioxide (CO_2) holdup, which is defined as a decline in CO_2 fugacity due to changes in the physicochemical properties of the rumen liquor. Gas holdup might thus be responsible for increasing rumen dCO_2 concentrations, with a concomitant pH decline. Dissolved CO_2 is a biologically active molecule that directly influences bacterial metabolism and that, if found at high concentrations, might enhance rumen CO_2 diffusion into the blood, leading to hypercapnia or high blood CO_2 concentrations. Hypercapnia has known cellular and physiological effects that are closely associated with rumen acidosis. In this review, I discuss the implication of a high rumen dCO_2 concentration for the onset of nutritional diseases and highlight the need to explore rumen acidosis from a physicochemical point of view and beyond pH decline.

Contents

Abbreviations: CO_2, carbon dioxide; pCO_2, partial pressure of CO_2; dCO_2, dissolved CO_2; HCO_3^-, bicarbonate; H_2CO_3, carbonic acid; H_3O^+, hydronium; OH^-, hydroxide; H^+, hydrogen; SARA, subacute rumen acidosis; AD, abomasal dysplasia.

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1. Introduction

In recent decades, research has shed light on several of the mechanisms responsible for nutritional diseases in ruminants; however, many aspects of these diseases remain elusive (Nagaraja and Titgemeyer, 2007; Enemark, 2008; Plaizier et al., 2008). For example, rumen acidosis has been linked to a decline in rumen pH, but continuous monitoring of pH has failed to accurately predict the onset of rumen acidosis (Dohme et al., 2008; DeVries et al., 2009; Sato et al., 2012). In fact, disease models for rumen acidosis have shown a decline in pH, although clinical signs are not always observed (Krause and Oetzel, 2005; Gozho et al., 2007; Nagaraja and Titgemeyer, 2007). Researchers have attributed the failure to observe clinical signs in animals with low pH to the individual susceptibility of ruminants to rumen acidosis (Dohme et al., 2008; DeVries et al., 2009). Alternatively, rumen pH fluctuations reflect the equilibrium between different carbon dioxide (CO_2) species, as shown in early experimental work in sheep rumen fluid (Turner and Hodgetts, 1955a, 1955b). Moreover, rumen pH describes the balance between bases and acids in solution, although current research has neglected the contribution of dissolved CO_2 (dCO_2) to the acid pool because its concentrations are thought to be constant and low (Dawes, 1965; Kohn and Dunlap, 1998; Aschenbach et al., 2011). The present review presents evidence that this assumption may not be true and that a high dCO_2 concentration during rumen acidosis drives rumen pH decline. Rumen dCO_2 may also have direct physiological and microbiological effects that can explain the pathogenesis of nutritional diseases.

2. Relationship between rumen pH and carbon dioxide species

The pH of a solution is the measurement of the electrical field between a cell and a reference electrode (Covington et al., 1985). In simple solutions, pH represents hydrogen ion activity (αH^+), which is equivalent to the hydrogen ion (H^+) concentration as the acidity of the solution increases (Dawes, 1965; Covington et al., 1985). For instance, pure water ionisation leads to the formation of the hydroxide ion (OH^-) and H^+, or more precisely the hydronium ion (H_3O^+), as H^+ does exist alone in solutions (Dawes, 1965; Covington et al., 1985). Nevertheless, in more complex solutions, such as the rumen liquor, pH is better defined as the equilibrium between bases and acids according to the Henderson-Hasselbalch equation (Eq. (1)) (Dawes, 1965) and the dissociation contact of the reaction (pK_a):

$$pH = pK_a + \log \frac{[Base]}{[Acid]} \tag{1}$$

Conversely, CO_2 is a chemical compound that is mainly found in a gaseous state, and it plays a key role in respiration and blood buffering (Klocke, 1987). When evaluating CO_2 exchange between the blood and the alveoli, blood CO_2 concentrations are expressed in pressure units (Siggaard-Andersen et al., 1984). However, the use of this convention might be misleading, given that in the rumen, gaseous CO_2 is found mainly in the gas cap over the liquid compartment (Waghorn, 1991). Nevertheless, due to the high solubility of CO_2 in water, most of the CO_2 in the rumen is either in a liquid state (mM), as a base (bicarbonate, or HCO_3^-) or an acid (carbonic acid, or H_2CO_3), or in a hydrated state (dCO_2). Moreover, the equilibrium between CO_2 species is critical to understanding the role of dCO_2 in modulating the pH of the rumen.

As found in the blood, the main buffer system in the rumen is CO_2/HCO_3^- (Turner and Hodgetts, 1955a; Counotte et al., 1979; Kohn and Dunlap, 1998). According to many researchers, high CO_2 partial pressure (pCO_2) is responsible for the lower pH range and better buffering capacity of the rumen (Counotte et al., 1979; Kohn and Dunlap, 1998). It is also thought that pCO_2 controls rumen CO_2 species via the equilibrium characterised by Henry's law constant for CO_2 in water (k_H = 0.0229 M/atm at 37 °C and 0.15 M) and the following equation (Counotte et al., 1979; Russell and Chow, 1993; Kohn and Dunlap, 1998):

$$pH = pK_a + \log \frac{[HCO_3^-]}{[pCO_2 * k_H]} \tag{1.a}$$

However, Eq. (1.a) provides only a partial view of a more complex relationship between pH and CO_2 species in the rumen liquid (Eq. (2)). For instance, CO_2 hydration, CO_2 and more H_3O^+ (Eq. (2)) result in the formation dCO_2, which in turn leads to of H_2CO_3 formation; H_2CO_3 has a similar acid strength as formic acid (pKa = 3.75) (Loerting et al., 2000; Adamczyk et al., 2009; Loerting and Bernard, 2010). This increase in H_2CO_3 formation leads to rumen pH decline.

$$\begin{array}{llll} \text{Rumen Gas Cap} & & \text{Fugacity} & \text{Rumen Liquid} \\ & \mathbf{CO_2} & \underset{1}{\Leftrightarrow} & \mathbf{d}CO_2(CO_2 + nH_3O^+) \underset{2}{\Leftrightarrow} H_2CO_3 + nH_3O^+ \underset{3}{\Leftrightarrow} HCO_3^- + nH_3O^+ \end{array} \tag{2}$$

However, H_2CO_3 has a limited lifetime in liquid solutions and quickly dissociates to form HCO_3^- (Eq. (2), $_3$) (Edsall, 1969; Adamczyk et al., 2009). Moreover, due to the slow conversion from dCO_2 to H_2CO_3 (Eq. (2), $_2$), the majority of the CO_2 in solution is dCO_2, and only small fraction (1%) is H_2CO_3 (Loerting et al., 2000; Adamczyk et al., 2009; Loerting and Bernard, 2010). Accordingly, dCO_2 behaves as an acid, reflecting the equilibrium between H_2CO_3 formation and dissociation to HCO_3^-