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Review

# Influence of hydrogen on rumen methane formation and fermentation balances through microbial growth kinetics and fermentation thermodynamics

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A B S T R A C T

A descriptive model is presented that can explain changes in the amount of methane ($CH_4$) formed in the rumen in relation to passage rate, feed type, and the effects of pH and inhibitors of methanogenesis. The model is based on methanogen growth kinetics in continuous systems. The growth rate of hydrogen ($H_2$) utilising methanogens in the rumen and the prevailing $H_2$ concentration are dynamically linked. Higher $H_2$ concentrations are required to permit a growth rate sufficient to prevent washout of methanogens from the rumen at higher ruminal passage rates, at suboptimal ruminal pH values, or in the presence of inhibitors. Lower $H_2$ concentrations are possible when the passage rate is lower, when the pH is near optimum, or when methanogens are less affected by inhibitors. Analysis of the literature confirms that increased particulate passage rate is associated with higher rumen $H_2$ concentrations, less $CH_4$ formation, and increased importance of propionate as a fermentation endproduct. Published data also show that partial inhibition of methanogens results in higher $H_2$ concentrations, less $CH_4$ formation, and more propionate formation. The model suggests that the prevailing $H_2$ concentration influences the thermodynamics of rumen fermentation. $H_2$ producing fermentation pathways are favoured at low $H_2$ concentrations. Therefore, feeds and conditions that result in low $H_2$ partial pressures will result in more $H_2$ formation, and less propionate formation, and so more $CH_4$ is formed per mole of feed monomer fermented in the rumen. Conversely, feeds and additives that favour high $H_2$ concentrations result in less $H_2$ formation per mole of feed monomer fermented in the rumen, and so result in production of less $CH_4$ and more propionate.



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## 1. Description of ruminal digestion

Feed ingested by ruminants is fermented by microbes in the rumen, the reticulum and the omasum, the first three compartments of the so-called four stomachs of ruminants. These three compartments are often collectively termed the reticulo-rumen or, as in this review, the rumen. The three-compartment rumen can be simplistically described as an open system with discontinuous solid (*i.e.*, the plant material the animal eats) and liquid (*i.e.*, saliva, water in the feed, and drinking water) inputs, and contains multiple fractions that have different turnover rates (Wolin, 1979). Feed is physically broken down to smaller particles by initial mastication as it is eaten, by re-chewing during rumination, and by disintegration due to microbial degradation (Hungate, 1966). In the rumen, the ingested feed and liquids are mixed and maintained under anaerobic conditions, normally at a pH 5.6–6.7, and at 39 °C (Hungate, 1966; Kolver and de Veth, 2002). Microbes degrade many of the polymeric components of the feed, and then ferment the resultant monomers and oligomers. This microbial community consists of many bacterial, archaeal, protozoal and fungal species. Details of the rumen fermentation and the microbes involved have been published many times, and the reader is referred to reviews for more information (Hungate, 1966; Wolin, 1979; Van Soest, 1994; Hobson and Stewart, 1997; Ellis et al., 2008; Janssen and Kirs, 2008). The products of fermentation are mainly the volatile fatty acids (VFA) acetate, propionate and butyrate, although formate, ethanol, lactate, succinate and branched chain volatile fatty acids are also formed. In addition, ammonia, carbon dioxide and hydrogen gas are produced. Longer chain fatty acids are released from lipids, and a wide variety of end products result from the microbial degradation of minor components of the feed. The acetate, propionate and butyrate form an important part of the ruminant's energy and carbon requirements, and are largely absorbed across the rumen wall. Amino acids, oligopeptides, and ammonia released by microbial degradation of proteins and non-protein N compounds can be taken up by microbes and converted to microbial protein. This microbial protein, and ingested plant proteins, are the sources of dietary amino acids for the animal. The microbes, small feed particles, and unabsorbed compounds dissolved in the rumen liquid, can be utilised by the animal when they exit the rumen and enter the true stomach (abomasum) and lower digestive tract. The activities of the microbial community in the rumen therefore convert feed components to VFA and microbial cells, and also pre-digest feed before it enters the remainder of the digestive tract.

Hydrogen gas produced during microbial fermentation of feed is used as an energy source by methanogenic archaea (*i.e.*, methanogens), which produce methane. Formate can also be used by methanogens in the rumen, but is much less important as a $CH_4$ precursor than $H_2$ (Hungate et al., 1970). The central role of $H_2$ in rumen fermentation (Hungate, 1967) means that $H_2$ utilising methanogens are important in rumen function and animal nutrition, even though they only make up a small part of the rumen microbial biomass (Janssen and Kirs, 2008). Efficient $H_2$ removal is postulated to increase the rate of fermentation by eliminating the inhibitory effect of $H_2$ on the microbial degradation of plant material (Wolin, 1979; McAllister and Newbold, 2008). The total pool of $H_2$ in the rumen is small, and the dissolved $H_2$ concentration is usually about 0.1–50 $\mu$M, which is 0.014 to 6.8% of its maximal solubility at 39 °C and one atmosphere pressure (described in more detail in Section 4). The rate of $CH_4$ formation is determined by the rate at which $H_2$ passes through this dissolved pool, and the amount of $CH_4$ formed is determined by the amount of $H_2$ that passes through the pool. The $CH_4$ produced by the ruminal methanogens is released by the ruminant, by eructation, to the atmosphere. Cattle each produce about 150–420 l of $CH_4$ per day and sheep about 25–55 l per day (Czerkawski, 1969; Holter and Young, 1992; McAllister et al., 1996). This ruminant derived $CH_4$ accounts for about one quarter of all anthropogenic $CH_4$ emissions, and is implicated as a driver of global climate change (Wuebbles and Hayhoe, 2002). $CH_4$ formation also represents a loss of energy from the diet of the animal (Blaxter, 1967; Johnson and Johnson, 1995). Development of mitigation strategies to reduce $CH_4$ emissions from ruminants is currently the subject of scientific and public interest (Iqbal et al., 2008; Leslie et al., 2008; Martin et al., 2010).

## 2. Subject of this review

In this review, factors that affect $CH_4$ formation, and their association with each other and with other rumen characteristics, are summarized (Section 3). Effects of these factors on dissolved $H_2$ in the rumen are then described (Section 4), and a