

THE ROLE OF RUMEN CILIATE PROTOZOA IN RUMINAL FERMENTATION, DIGESTION AND ENTERIC METHANE PRODUCTION

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ABSTRACT

First described in 1843, rumen ciliate protozoa were considered to be important in ruminant nutrition and contributed up to 50% of the total microbial biomass in the rumen. Recent studies on the presence or absence of rumen ciliate protozoa concluded that rumen protozoa are important, but not essential in the rumen ecosystem and to the well-being of host animals. Despite the fact that elimination of rumen protozoa (defaunation) negatively affects ruminal fermentation, plant cell wall digestion, defaunation results in an increase in the efficiency of bacterial protein synthesis and the rate of nitrogen flow to the duodenum, leading to increase average daily gain of host animals. Importantly, this increase in livestock productivity could occur alongside a reduction in enteric methane emissions.

Keywords: *ciliate, defaunation, microbial protein, methane*

INTRODUCTION

Rumen protozoa were first described in 1843 and considered to be important for the ruminant nutrition (Hungate, 1966). However, despite the fact that rumen protozoa contribute to as much as half the total microbial biomass in the rumen and actively participate in plant cell wall digestion (Williams and Coleman, 1992), elimination of rumen protozoa increases microbial protein supply to the host, leading to increase average daily gain by 11% and results in a 10.5 to 13% decrease in enteric methane production (Newbold et al., 2015; Eugène et al., 2004a). This paper aims at reviewing recent information on rumen ciliate protozoa and evaluating the role of protozoa on ruminal fermentation, digestion and enteric methane production.

Classification of rumen ciliate protozoa

Rumen protozoa are classified based on their cell morphology, and considered to be the simplest form of animal life, performing all the life processes as a eukaryotic cell (Dehority, 2003; Esteban et al., 2014). Further, the majority of protozoa identified in the rumen are ciliate species, with more than 100 species of rumen ciliate protozoa having been identified in two major sub-classes; being the entodiniomorphid (Table 1) and the holotrich ciliates (Table 2; Williams and Coleman, 1988, 1992). A few species of flagellate protozoa (Table 3) are also found in the rumen (Hungate, 1966; Williams and Coleman, 1992). However, the flagellates are easily confused with fungal zoospores (Dehority, 2003). In addition, flagellate protozoa are less numerous in terms of population density and have small body mass compared to the ciliates (Hungate, 1966; Clarke, 1977). Therefore, the flagellates are not well known and have not been the focus of attention in classifying or describing their activity and metabolism, leading to little information being available.

Table 1. Characteristics of some rumen entodiniomorphid protozoa (Williams and Coleman, 1988)

Genus	Dorsal cilia	Obvious skeletal plates	Macronucleus shape	Length (µm)	Width (µm)
Entodinium	0	0	Various	22-29	11-68
Eodinium	1 band ant.end [‡]	0	Rod-shaped	32-60	20-40
Diplodinium	1 band ant.end	0	Often bent rod	55-210	41-136
Eremoplastron	1 band ant.end	1 narrow	Often bent rod	45-500	21-260
Eudiplodinium	1 band ant.end	1 narrow	Hook shaped	105-198	56-120
Ostracodium	1 band ant.end	1 wide	Various	58-133	36-54
Polyplastron	1 band ant.end	2 narrow	Rod-shaped	123-205	98-123
Diploplastron	1 band ant.end	2 narrow close at post. End	Rod-shaped	88-120	47-65
Metadinium	1 band ant.end	2 narrow occ. Fused	Rod-shaped 2-3 lobes	110-288	61-165
Epidinium	1 band behind ant.end	3 variable width	Elongate	105-150	44-72
Enoploplastron	1 band ant.end	3 narrow close together	Elongate	60-140	32-90
Ophryoscolex	1 band round 3/4 of middle	3 variable width	Elongate	120-215	60-80
Epiplastron	1 band round 3/4 of middle	5 variables width	Elongate	90-140	41-60
Elytroplastron	1 band ant.end	3 narrow (2 on right 1 on left)	Elongate	110-160	67-97
Caloscolex	1 band round all middle	1 complex	Elongate	130-160	73-90
Opisthotrichum	1 band round 1/3 of middle	1 cylindrical	Elongate	60-80	21-28
Parentodium	0	0	Round	26-39	14-21

Note: [‡] anterior end

Table 2. Characteristics of some rumen holotrich ciliates (Williams and Coleman, 1992)

Species	Morphology	Size range, average (μm)	Length: width range, average	Macronucleus
Isotricha prostoma	Elongated ovoid to elipsoidal	80-200×50-120; 135×70	1.69-2.55; 2.03	Elongated
Isotricha intestinalis	Elongated ovoid to elipsoidal	90-200×45-150; 110×60	1.65-1.93; 1.76	Ovoid, 30×20
Dasytricha ruminantium	Ovoid	35-75×20-40; 57×27	1.70-2.70; 2.11	Elongated/ellipsoidal, 16-18×8-9
Dasytricha hukuokaensis	Ovoid	120-180×68-122; 151×95	1.47-1.76; 1.59	Ellipsoildal, 24-38×16-20; 31×18
Oligoisotricha bubali	Ovoid	12-20×8-15; 16×12	1.07-1.60; 1.30	Spherical-elliptical
Buetschlia parva	Ovoid	30-67×20-48; 55×35	1.58-2.38; 1.91	Spherical
Buetschlia neglecta	Ovoid	40-60×20-30	2.0	Spherical
Buetschlia lanceolate	Spear-shaped	48×20	2.4	Large
Buetschlia omnivore	Ovoid/spherical	Variable; 35-110×27-97		Elongated
Buetschlia nana	Ovoid	17-21×12-17; 19×15		spherical
Parabundleia ruminantium	Ovoid	37.5-50 × 27.5-32.5; 42.5 × 30.5	1.25-1.54	Elliptical, 16 μm long
Polymorphella bovis	Ovoid to bottle-like	26-37.5 × 20-26; 34× 22	1.30-1.80; 1.56	Subspherical, 2.5 μm long
Blepharoprosthium parvum	Pyriform	26-32 × 16-20; 29 × 18		Spherical
Blepharoconus krugerensis	Ovoid with anterior knoblike protuberence	30-65 × 21-60; 46 × 35	1.11-1.80; 1.34	Disc-shaped 7-15 × 4-8; 11 × 5.5 μm
Microcetus lappus	Ovoid/elongate	18-29 × 7.5-18; 23.6 × 13		Spherical

Table 3. Characteristics of some rumen flagellate protozoa (Williams and Coleman, 1992)

Species	Shape	Size	Number of flagella	Size of nuclear (µm)
<i>Chilomastix caprae</i>	Piriform	8.3×4.4	4	
<i>Monocercomonas ruminantium</i>	Piriform	4.8×4.1	4	1.8×1.6
<i>Monocercomonoide bovis</i>	Elliptical	5.4×2.8	4	1.6×1.4
<i>Monocercomonoide caprae</i>	Elliptical	9×6	4	Large
<i>Pentatrichomonas hominis</i>	Elliptical	7.5×5.6	5	2.5×2.0
<i>Tetratrichomonas buttrei</i>	Elliptical	5.3×4.8	4	2.0×1.7
<i>Trichomonas ruminantium</i>	Elliptical	12×10	3	

Anaerobic rumen ciliates are extremely abundant, ranging from 10^4 to 10^6 cells/mL of rumen liquor and are capable of engulfing bacteria and digesting plant materials such as cellulose and other structural carbohydrates (Finlay and Esteban, 2013; Esteban et al., 2014).

Rumen protozoa account for as much as half the total microbial biomass in the rumen and up to 50% of total fermentation products (Williams and Coleman, 1992; Newbold et al., 2015). They actively participate in the ruminant digestion process. The absence of rumen protozoa, therefore, results in modifying ruminal digestion of plant cell walls and starch which are considered to be two main sources of energy supply for ruminants (Jouany and Martin, 1997). The ruminal ecosystem and environment can be slightly altered by the absence of rumen protozoa with significant influence on bacterial activity, affecting the retention time of the digesta, the concentrations and proportion of ruminal VFA and ammonia (NH_3) concentration (Eugène et al., 2004a; Newbold et al., 2015) and therefore the supply of metabolites to the host, especially amino acids.

Plant cell wall digestion

Early studies on the role of rumen protozoa in ruminal digestion concluded that rumen protozoa did not digest plant cell components (Becker, 1929). In later years, enzymatic and microscopic evidence showed that cellulose was digested by entodiniomorphs (Hungate, 1966). Further, the rumen ciliate protozoa were confirmed in their ability to colonize and damage plant tissues in studies with scanning electron microscopic technology. *Epidinium crawleyi* was found to cause primary degradation of plant tissues (Bauchop and Clarke, 1976) as it attached and damaged areas of the stem. *Entodinium* spp. and *Ophryoscolex caudatum*, however, rarely attached themselves to the large tissue fragments, but to damaged tissues exposed through fractures (Orpin, 1984).

Rumen protozoa produce fibre-degrading enzymes and the cellulolytic enzymes produced by rumen protozoa are distinguished from those of bacterial and fungal origin. This was observed by the characterization of protozoal genes encoding cellulase enzymes (Jouany and Martin, 1997). Further, polysaccharidase activities were greater in animals with ciliate protozoa compared to animals without ciliate protozoa (Santra and Karim, 2002; Eugène et al., 2004b). However, effects of rumen protozoa on ruminal digestion are inconsistent in the literature. There are reports of decreased organic matter (OM) digestibility (Eugène et al., 2004a; Newbold et al., 2015), and neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) digestibility (Newbold et al., 2015) in the absence of rumen protozoa, probably due to the loss of protozoal fibrolytic activity. The absence of rumen protozoa, in contrast, increases cellulolytic ruminococci populations (Mosoni et al., 2011). This increased cellulolytic ruminococci in the absence of rumen protozoa may compensate for the loss of protozoal fibrolytic activity, and therefore the digestibility of OM, NDF and ADF was not different between defaunated and faunated animals (Jouany et al., 1995). Zeitz et al. (2012) observed no effects of individual ciliate protozoa such as *Entodinium caudatum*, *Epidinium ecaudatum* and *Endiplodium maggii* on whole tract digestibility of OM, NDF or ADF and suggested that ciliate protozoa may not always improve plant cell wall digestion.

Carbohydrates and starch digestion

Both holotrich and entodiniomorph ciliate protozoa are believed to ferment carbohydrates to meet their energy requirement. Holotrich ciliates utilise soluble carbohydrates, while *Entodinium* spp. and *Epidinium* spp. preferably digest starch (Williams, 1989). De Smet et al. (1992) showed that the total protozoal population density was nearly double in a high concentrate diet compared to a high roughage diet, with holotrich ciliates increasing accordingly. *Entodinium* spp. and *Epidinium* spp. have their largest numbers with a high concentrate diet.

Wereszka and Michałowski (2012) found that *Diploplastron affine* possessed enzymes degrading starch and its derivatives. A protozoal cell extract for enzymatic studies found *Diploplastron affine* ciliate capable of digesting starch, released about 45 pmol VFA per protozoa per hour and utilised liberated energy for their energy requirement. The rate of starch degraded by *Diploplastron affine* is equivalent to $2.4 \pm 0.47 \mu\text{mol/L}$ glucose per mg protein per min and the degradation rate of maltose is approximately $0.05 \mu\text{mol/L}$ glucose per mg protein per min (Wereszka and Michałowski, 2012). The ciliate *Diploplastron affine* is also found to digest insoluble 1,3- β -glucans such as pachyman and 1,6- β -glucans such as pustulan as energy substrates (Belzecki et al., 2012).

Apart from being able to digest and utilise plant carbohydrates, rumen protozoa also ferment chitin of the rumen fungus. Morgavi et al. (1994) found *Piromyces* spp. strain OTS1 in monocultures or in the presence of rumen protozoa in vitro and reported that rumen protozoa adversely affect the growth of *Piromyces* spp. strain OTS1 and are able to digest fungal cell walls, resulting in 42% reduction of chitin which is a carbohydrate component of the fungal cell wall. *Diploplastron affine* and *Entodinium caudatum* are found to possess a chitinolytic

enzyme (Miltko et al., 2015b) and utilise chitin as a source of energy for ciliate metabolism (Miltko et al., 2015a).

Protein digestion and protozoal synthesis in the rumen

Ruminants with protozoa in the rumen (faunated) support a higher ruminal NH₃ concentration than do animals with rumen protozoa removed (defaunated), indicating that rumen protozoa degrade dietary proteins (Jouany, 1996) and engulf bacteria for their amino acid requirement (Coleman, 1989; Esteban et al., 2014). Ueda et al. (1975) who incubated the isotrich ciliates with soluble casein found that peptide-nitrogen and amino-nitrogen produced by the isotrich reached its highest level between 3 and 15 hours of incubation, accounting for 47% and 58% of non-protein nitrogen (NPN), respectively. Incubation of the ophryoscolecid ciliates with insoluble casein showed a peak of peptide-nitrogen at 3 hours, which accounted for 36% of NPN while amino-nitrogen increased linearly and accounted for 47% of NPN at 15 hours of incubation (Ueda et al., 1975).

Protozoal nitrogen (N) can account for 53% of the total microbial N in the bovine rumen (Michałowski, 1979), which is about 24 to 46 g N (Leng et al., 1981). However, rumen protozoa contribute only 20% of the total microbial N entering the duodenum (Jouany et al., 1988). The smaller protozoal biomass in the duodenum of the ruminants could be due to 65% to 74% of protozoa lysing and being degraded in the rumen (Leng, 1982; Ffoulkes and Leng, 1988), suggesting only 24 to 35% of protozoa enter the lower digestive tract. The relatively high numbers of rumen protozoa that complete their life span in the rumen (Leng, 1982) and are retained within the omasum of ruminants (Czerkawski, 1987; Nguyen and Hegarty, 2019) mean rumen protozoa contribute a small proportion of the total microbial protein supply. The principal detrimental effect of rumen protozoa, therefore, may be competition for substrate with bacteria and engulfment and digestion of bacteria by protozoa, leading to decreased bacterial biomass and flow of protein in the duodenum (Leng, 1982).

Ruminal lipid metabolism

The role of rumen protozoa in bio-hydrogenation is not well defined and understood (Williams and Coleman, 1992), although they contribute significantly to flow of unsaturated fatty acids to the duodenum (Newbold et al., 2015; Yáñez-Ruiz et al., 2006). Yáñez-Ruiz et al. (2006) reported rumen protozoa accounted for between 30-40% of conjugated linoleic acid (CLA) and 40% of vaccenic acid (VA) leaving the rumen. Mixed protozoa from the sheep rumen contain at least two to three times more unsaturated fatty acids, including CLA and VA, than do bacteria. Different species have different composition, with larger fibrolytic species such as *Epidinium ecaudatum caudatum* containing more than ten times more CLA and VA than some small species, including *Entodinium nanellum* (Devillard et al., 2006). This high level of polyunsaturated fatty acids in protozoal cells is a consequence of ingestion and/or engulfment of chloroplasts (Huws et al., 2009) and this chloroplasts uptake is specifically found in entodiniomorphids (Huws et al., 2012). Rumen protozoa, therefore appear to increase the duodenal flow of mono or polyunsaturated fatty acids by protecting chloroplasts unsaturated fatty acids from rumen bio-hydrogenation.

Factors affecting protozoal population densities in the rumen

Rumen ciliate protozoa represent approximately 10^4 - 10^6 cells/mL of rumen contents (Dehority 2003; Esteban et al., 2014), but the concentration of rumen protozoa varies among animals and is dependent on many factors such as ruminant species, geographical location (Akbar et al., 2009), diet (Whitelaw et al., 1984), frequency of feeding and rumen pH (Clarke, 1977).

Diet composition

Ruminants fed highly digestible diets often show the largest populations of rumen protozoa (Hungate, 1966), while small populations of rumen protozoa are found in animals on low quality roughage diets (Abe et al., 1973). De Smet et al. (1992) fed sheep low and high concentrate diets containing 4.3% or 17.3% starch respectively, observing total protozoal population was nearly two-fold higher in the high concentrate diet. Rumen protozoa are able to reduce the rate of fermentation, contributing to the maintenance of a stable ruminal ecosystem when a high concentration of grain is suddenly introduced in the diet (Mackie et al., 1978). However, the protozoa are significantly affected by the environment's acidity or alkalinity, with the protozoa unable to survive if rumen pH is above 7.8 or below 5.0 (Clarke, 1977). Mackie et al. (1978) also found that the protozoal population decreased by 50-80% as rumen pH fell below 5.4. Cellulolytic ciliates almost disappeared when cattle were fed barley only (Kudo et al., 1990) and steers became protozoa-free for a period of a few weeks by ad libitum feeding of barley (Whitelaw et al., 1984).

Dietary fatty acid supplement

Capric acid (C10:0), lauric acid (C12:0) and myristic acid (C14:0) show strong protozoal toxicity and are useful rumen defaunating agents (Matsumoto et al., 1991). Matsumoto et al. (1991) observed that rumen protozoa, except *Entodinium* spp. were undetectable after 3 days of feeding 30 g of hydrated coconut oil (CO) containing 52% lauric acid. Feeding 250g of refined CO to beef heifers reduced rumen protozoal population by 62% (Jordan et al., 2006) and protozoal populations in beef heifers were decreased by 63% and 80% by 300 g/d CO after 45 and 75 days, respectively (Lovett et al., 2003). Machmüller (2006) reported a reduction in rumen protozoa by 88 and 97% when feeding sheep with 3.5 and 7% CO, respectively. This suppressive effect of CO on rumen protozoa persisted 5 weeks after finishing feeding sheep with CO (Sutton et al., 1983). Rumen protozoa were reduced to half of the original population by cottonseed, with holotrich and cellulolytic protozoa apparently lost from the rumen of sheep and only *Entodinium* spp. remained (Dayani et al., 2007).

Frequency of feeding

The concentration of protozoa in the rumen liquor varies according to the daily feeding regime, reaching a maximum before feeding and decreasing by approximately 60-80% from 4 to 12 hours after feeding (Michalowski and Muszyński, 1978). More specifically, the holotrich population in the fluid decreases for a period of 12 to 20 hours after feeding and the population returns to its original numbers within 4 to 6 hours pre-feeding, while the entodiniomorphid population in the fluid decreases for up to 16 hours after feeding and then

increases to the pre-feeding numbers (Williams, 1986). The increase of the holotrich population is mainly caused by the increase in dasytrichs while the isotrich population remains relatively low (Clarke, 1965). The highest concentration of rumen protozoa occurs when the animal is fed three or four meals per day rather than once (Bonhomme, 1990).

Defaunating the rumen

Rumen protozoa are important, but not essential in the rumen ecosystem and to the well-being of host animals (Williams and Coleman, 1992; Newbold et al., 2015). Elimination of rumen protozoa (defaunation) has led to reported increases in growth rate and liveweight gain of ruminants (Bird and Leng, 1978; Bird et al., 1979; Eugène et al., 2004a; Newbold et al., 2015) especially when the feed is deficient in protein relative to energy content (Nguyen et al., 2015). In addition, rumen protozoa are significant hydrogen (H₂) producers and synthesise mainly acetate and butyrate rather than propionate (Williams and Coleman, 1992). Defaunation is therefore expected to induce a greater proportion of propionate in the ruminal VFA (Eugène et al., 2004a), but this phenomenon is not always observed (Williams and Coleman, 1992; Newbold et al., 2015). The reduced CH₄ emissions caused by defaunation also reported by several authors (Whitelaw et al., 1984; Hegarty, 1999; McAllister and Newbold, 2008; Newbold et al., 2015) may reflect reduced H₂ availability by removing endosymbiotic methanogens (Finlay et al., 1994; Tokura et al., 1997; Finlay and Esteban, 2013).

Effect of defaunation on extent of ruminal fermentation

An in vitro study by Yoder et al. (1966) reported cellulose digestion by rumen protozoa (7%), by bacteria (40%) and by protozoa and bacteria combined (exceeded 60%), showing a beneficial effect of rumen protozoa on cellulose digestion. Bauchop and Clarke (1976) observed rumen ciliate protozoa contribute to fibre digestion as they are capable of colonizing and damaging plant tissues. Cellulolytic, polysaccharide depolymerases and glycoside hydrolase enzymes produced by protozoa are significant contributors to cellulose and hemicellulose fermentation (Coleman, 1989). Therefore, the absence of rumen protozoa can lead to a 5-15% reduction in carbohydrate digestion of plant cell walls (Jouany et al., 1988).

Removing protozoa reduces the rumen digestibility of fibre components of the diet (Newbold et al., 2015). Ruminal digestion of NDF and ADF were reduced by 31% and 22% respectively by defaunation of sheep when fed a low soluble N diet (Ushida and Jouany, 1990). Defaunation also reduced degradation of a mainly chopped hay diet by up to 18% in sacco (De Smet et al., 1992). The absence of rumen protozoa did not affect rumen digestibility in lambs offered a diet with a high protein/energy ratio, but reduced total tract digestibility of OM (10%) and NDF (7%; Eugène et al., 2010). In addition, Ushida and Jouany (1990) found that defaunated ruminants require an increased supply of NPN in order to maintain fibrolytic activity in the rumen compared to faunated animals. Although fibre digestion is moderately suppressed by defaunation, improving protein supply is far more important in growing animals with high protein demand and when protein is a limiting factor in the diet (De Smet et al., 1992).

Effect of defaunation on animal productivity

A positive effect of defaunation on ruminants is the increased rumen bacterial biomass and passage of ruminal undegraded protein from the diet (Jouany, 1996). Duodenal N and duodenal CP/kg DMI outflow significantly increased after defaunation (Eugène et al., 2004a; Newbold et al., 2015), indicating an increase in the efficiency of microbial protein synthesis and leading to an average increased daily gain of 11%.

In pen-feeding studies, defaunated lambs showed 18% faster growth rate and greater wool growth and wool fibre diameter over faunated or refaunated lambs offered a 50:50 concentrate and roughage ration (Santra et al., 2007). Birth weight of lambs born from defaunated ewes was 13% heavier than from faunated ewes on single-born lamb and pre-weaning growth rates were 10% and 14% heavier in lambs reared free of ciliate protozoa for both single and twin-born lambs, respectively (Hegarty et al., 2008). On high energy and low protein diets, defaunated cattle grew at a 43% faster rate than faunated cattle on the same intake (Bird and Leng, 1978) and lambs without rumen protozoa showed significantly increased growth rates and efficiency of utilisation of feed when fed a low level of protein. Wool growth increased by 50% compared to faunated animals that were fed a low protein diet (Bird et al., 1979).

In grazing studies, Bird and Leng (1984) observed a greater rate of body weight gain (23%) and wool growth (19%) in defaunated compared to faunated lambs grazed on a green oats pasture. Protozoa-free lambs born from defaunated ewes were significantly (4-8%) heavier than were lambs born from faunated ewes measured from 2 months of age to 5 months of age and wool growth was also greater in protozoa-free lambs grazed on fescue dominant pastures (Hegarty et al., 2000).

Effect of defaunation on enteric methane production

As stated earlier, ciliate protozoa are significant producers of H₂ and produce acetic and butyric acids rather than propionic acid (Williams and Coleman, 1992). Defaunation is generally associated with fermentation shifting to a greater proportion of propionic acid, therefore reducing the amount of CH₄ produced (Eugène et al., 2004a).

The methanogens existing as endo- and ecto-symbionts with ciliate protozoa (Finlay et al., 1994; Tokura et al., 1997; Finlay and Esteban, 2013) have been estimated to account for 37% of ruminal methane production (Finlay et al., 1994). The proportion of methanogens in the total bacterial population was lower in protozoa-free lambs, with 26% lower CH₄ emissions compared to faunated lambs (McAllister and Newbold, 2008). While the archaeal community of methanogens in liquid and solid rumen contents were similar in faunated wethers, a lower proportion of methanogens occurred in the liquid phase with defaunation (Morgavi et al., 2012). However, Mosoni et al. (2011) while observing a 20% reduction in CH₄ emissions in short-term (10 week) and long-term (2 year) defaunated sheep, found methanogens per gram of DM of rumen content increased with defaunation while the diversity of the dominant methanogenic community was not changed. Therefore, it may not be reasonable to attribute the reduced CH₄ production from defaunation to a loss of methanogens (Morgavi et al., 2012).

The presence of protozoa did not change enteric CH₄ production in lambs raised with/without protozoa from birth (Hegarty et al., 2008) or from 10 to 25 weeks after chemical defaunation (Bird et al., 2008). Defaunation was associated with a reduced number of methanogens in rumen fluid, but did not reduce CH₄ production (Morgavi et al., 2012; Kumar et al., 2013). This could be explained as defaunation induces changes in bacterial or fungal populations (Eugène et al., 2004a) and the absence of protozoa in the rumen leads to changes in the methanogen community (Morgavi et al., 2012).

Ruminal acetogens were found able to grow on CO₂ and H₂, and produce acetate, but reductive acetogenesis was not likely to be occurring because of lower H₂ affinity, making reductive acetogenesis unable to compete with methanogens in the rumen (Joblin, 1999). In normal fermentation, methanogens reduce H₂ to a low level in which reductive acetogenesis is below detectable levels (Ungerfeld, 2015), but if pyruvate-derived acetate is produced when methanogenesis is inhibited, H₂ may accumulate and stimulate reductive acetogenesis (Ungerfeld, 2013). Reductive acetogens established in the rumen lacking methanogens can replace methanogens as a sink for H₂ in the rumen (Fonty et al., 2007). The reduced CH₄ emissions from defaunated animals associated with a rise in acetate proportion is a desirable condition in the rumen where reductive acetogens may be occurring.

CONCLUSION

Rumen ciliate protozoa are important in the ruminant nutrition, but they are not essential in the rumen ecosystem and to the well-being of host animals. Though elimination of rumen ciliate protozoa slightly decreases total VFA and plant cell wall digestion, defaunation largely impacts on the reduced NH₃ concentration, CH₄ production in the rumen and increased microbial protein supply to the hosts.

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