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REVIEW

Methane abatement strategies based on genetics and dietary manipulation of ruminants: a review

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SUMMARY

The aim of this review was to analyze published data on ruminant management practices that mitigate enteric methane (CH_4) emissions. Recent studies on the effects of feeding and breeding on CH_4 production are discussed. This review was prepared on the basis of the available literature describing extensive and intensive management conditions. The current approaches in relation to future options to reduce enteric CH_4 emission are discussed. The review is divided into four sections (Feed intake and breeding, Animal management, Dietary manipulation, and Concentrates). Methane emissions from ruminant systems can be lowered by selecting animals with a low residual feed intake. The digestive physiology of ruminants result in different CH_4 production. It can be noted that the increase in dairy cow productivity results in a decrease in CH_4 emission per kg milk. Selection and breeding ruminant with low emissions per unit feed intake reduce CH_4 emissions. The ruminal digestion varies according to diet composition and quality. Methane production can be reduced by feeding high protein or low-fiber rations, specifically by feeding more concentrates. The proportion of the concentrate in the diet and the source of the grain influence CH_4 production in ruminants.

ADDITIONAL KEYWORDS

Feed.
Methane.
Ruminants.
Selection.

Estrategias de reducción de metano basadas en la genética y manipulación dietética de rumiantes: una revisión

SUMMARY

El objetivo de esta revisión fue analizar los datos publicados sobre las prácticas de manejo de rumiantes que mitigan las emisiones de metano entérico (CH_4). Se discuten estudios recientes sobre los efectos de la alimentación y la mejora en la producción de CH_4. Esta revisión fue preparada sobre la base de la literatura disponible que describía condiciones de manejo extensivas e intensivas. Los enfoques actuales en relación con las opciones futuras para reducir la emisión de CH_4 entérica se discuten. La revisión se divide en cuatro secciones (consumo de alimento y mejora, manejo de animales, manipulación dietética y concentrados). Las emisiones de metano de los sistemas de rumiantes pueden reducirse seleccionando animales con una ingesta de alimento residual baja. La fisiología digestiva de rumiantes resulta en diferentes niveles de producción de CH_4. Cabe señalar que el aumento de la productividad de las vacas lecheras produce una disminución de la emisión de CH_4 por kg de leche. Selección y cría de rumiantes con bajas emisiones por unidad de consumo de alimento reducen las emisiones de CH_4. La digestión ruminal varía según la composición y calidad de la dieta. La producción de metano puede reducirse alimentando raciones de alta proteína o baja en fibra, específicamente alimentando más concentrados. La proporción del concentrado en la dieta y la fuente del grano influyen en la producción de CH_4 en rumiantes.

PALABRAS CLAVE ADICIONALES

Alimento.
Metano.
Rumiantes.
Selección.

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Brief Annotation

The contemporary knowledge in relation to future options to reduce enteric CH_4 emission is showed. Methane emissions from ruminant systems can be lowered by selecting animals with a low residual feed intake. It can be noted that the increase in dairy cow productivity results in a decrease in CH_4 emission per kg milk. The ruminal digestion varies according to diet composition and quality. Methane production can be reduced by feeding high protein or low-fiber rations, specifically by feeding more concentrates.

INTRODUCTION

Genetic selection of animals is the most promising option for reduce enteric methane (CH_4) production without any hazard to animal or environment. However, ruminant selections are based on production efficiency of milk or meat. Genetic improvement is a tool that can be used to reduce enteric emissions. At present there are 3 ways to accomplish this: intensification of animal production; improvement of system efficiency, and the breeding for animals that are low CH_4 emitters (Bell et al. 2011, pp. 699-07; Crowley et al. 2010, pp. 885-94).

Genetic variation in feed intake provides a basis for genetic selection for feed-use efficiency of cattle (Chagunda, Römer & Roberts et al. 2009, pp. 323-32). As a result of increased productivity, CH_4 production could be decreased. Recent research suggests some animals produce less CH_4 than others, possibly because they have different microbes in their rumens (Cassandro, Mele & Stefanon 2013, pp. 450-8). The meta-analysis of Guyader et al. (2014, pp. 1816-25) showed a significant linear relationship between methane emission and protozoa concentration. At the work of Wallace et al. (2014, p. 5892), methane was correlated, irrespective of breed, with the abundance of archaea, bacteria, protozoa, Bacteroidetes, and *Clostridium* Cluster XIVa. However, the greatest limitation for a breeding scheme is in measuring feed intake or CH_4 emission on progeny of sires (Wall, Simm & Moran 2010, pp. 366-76).

Many factors influence ruminal CH_4 emissions, including diet, feed intake, energy consumption, animal size, housing, growth rate, milk production, and alterations in the ruminal microflora (Benson et al. 2010, 18933-8; Broucek 2015, pp. 122-39; Chilliard et al. 2009, pp. 5199-211; Garnsworthy et al. 2012, pp. 3166-80; Iqbal & Hashim 2014, pp. 91-3; Mirzaei-Aghsaghali & Maheri-Sis 2016, pp. 22-31; Pinares-Patiño et al. 2007a, pp. 30-46; Rzeźnik & Mielcarek 2014, pp. 169-77; Rzeźnik & Mielcarek 2016, pp. 1-9). The most important animal traits that affect CH_4 production, and which can be selectively bred for, are residual feed intake (RFI) and feed utilisation efficiency (Basarab et al. 2013, pp. 195-220; Hegarty et al. 2010, pp. 1026-33). Breeding to improve these factors is likely to be an ideal means towards future mitigation of CH_4 production. It has the potential to complement dietary management strategies that improve live body weight gain of an animal (LBWG) per unit CH_4 produced (Eckard, Grainger & de Klein 2010, pp. 47-56; Finn, Dalal & Klieve 2015, pp. 1-22).

OBJECTIVES AND PURPOSE

The aim of this review was to summarize published data on ruminant management practices that mitigate enteric methane (CH_4) emissions. The objectives are to identify the factors affecting CH_4 abatement in extensive and intensive management conditions.

FEED INTAKE AND BREEDING

Ruminants with a greater ability to convert feed into energy will eat less feed and ultimately produce less CH_4. As the daily feed intake increases, CH_4 production also generally increases (Kirchgessner et al. 1991, pp. 91-102; Shibata et al. 1993, pp. 790-6). Altering the amount and quality of the feed consumed can be used as a strategy to reduce CH_4 emissions from high feed efficient animals in the future. Feed consumption needs to be measured closely (Hegarty et al. 2007, pp. 1479-86).

Koch et al. (1963, pp. 486-94) developed residual feed intake (RFI) as an answer to the difficulties of using a feed conversion ratio to compare individual animals. To calculate RFI requires the measurement of actual individual feed intake. Residual feed intake represents the amount of feed consumed, net energy of the animal's requirements of body maintenance, growth, and lactation. The residual feed intake is an individual record, taken in long term feeding trials (at least 70 to 84 days) where animals are housed either in individual or group pens, and accurate measurements are made of daily feed offered and refused, as well as body weight. Once the trial is finished, the daily feed intake is calculated from the amounts of feed offered and refused, and the averages of live body weight (LBW) change for the same period.

Animals selected for low RFI can be used in intensive farming (Waghorn & Hegarty 2011, pp. 291-301). Data recorded on fattening cattle show that animals having a high RFI, produced 20 % less CH_4 than the less efficient ones (Hegarty et al. 2007, pp. 1479-86; Nkrumah et al. 2006, pp. 145-53). Differences between these animals could be due to individual differences in rumen microorganisms associated to the rate of degradation processes and to internal animal characteristics such as retention time of particles in the rumen. Pinares-Patiño et al. (2007b, pp. 601-13) showed that cows with a low retention time of particles in the rumen for a same intake produce less CH_4. Cattle that eat less than their peers of equivalent LBW and LBWG are more feed efficient, as shown by lines of cattle divergently selected for RFI. So, selection for reduced RFI will lead to substantial and lasting CH_4 abatement (Iqbal et al. 2008, pp. 2747-55).

There has been recent research on the mitigation benefits of using residual feed intake (RFI) as a selection tool for low CH_4 emitting animals; however, findings have so far been inconclusive (Waghorn & Hegarty 2011, pp. 291-301).

According to Cottle, Nolan & Wiedemann (2011, pp. 491-514), indirect selection via feed intake may be more cost-effective than via direct measurement of CH_4 emissions. The potential of using RFI as a selection tool for low CH_4 emitters is an interesting mitigation option, but the CH_4 reductions through RFI is considered at present as uncertain (Hristov et al. 2013b, pp. 5095-113).

Goopy & Hegarty (2004, pp. 75-8) identified steers as high and low emitters of CH_4 on identical feed and feed intakes. The factors responsible for such differences are the rate of passage, microbial activity, fermentation conditions and feeding behavior. This suggests that methane emission characteristics may not persist over time. While exploring the mechanistic basis CH_4 production, Shi et al. (2016, pp. 1517-25) revealed that methane yields are a reproducible, quantitative trait.

To breed grazing ruminants with reduced CH_4 emissions, it would need to demonstrate that there is repeatable individual variation in this trait and that a portion of this variation is genetically inherited (De Haas et al. 2011, pp. 6122-34; Eckhard, Grainger & de Klein et al. 1010, pp. 47-56). However, Lassey et al. (1997, pp. 2905-14) highlight the considerable diversity of methanogenic response to digestion, and may be significant in the search for strategies to control CH_4 emissions. Wallace et al. (2015, p. 839) applied metagenomics to the rumen microbial community to identify differences in the microbiota and metagenome that lead to high- and low-methane-emitting cattle phenotypes. The abundance of archaeal genes in ruminal digesta correlated strongly with differing methane emissions from individual animals, a finding useful for genetic screening purposes. Roehe et al. (2016, p. 1005846) identified 3970 microbial genes of which 20 and 49 genes were significantly associated with methane emissions and feed conversion efficiency respectively.

It would be necessary to demonstrate that dry matter intake or feed intake is heritable (Berry, Crowley, 2013, pp. 1594–613). According to Crowley et al. (2010, pp. 885-94), the heritability of feed intake was 0.49 in growing beef bulls. Berry (2013, pp. 28-36) showed that daily methane emission is not heritable, but may still exhibit heritable variation. This is confirmed by the authors Lassen and Løvendahl (2016, pp. 1956-67). They concluded that estimated enteric CH_4 emission from dairy cattle is a heritable trait. The positive genetic correlation between RFI (residual feed intake) and predicted methane emission indicated that cows with lower RFI have lower predicted methane emission (estimates ranging from 0.18 to 0.84) (De Haas et al. 2011, pp. 6122-34).

According to Pinares-Patiño et al. (2013, pp. 316-321), heritability of g $CH_4.d^{-1}$ was $h^2 = 0.29$, and for g $CH_{4.}kg^{-1}$ DMI was $h^2 = 0.13$ in sheep. Repeatability between measurements 14 days apart were 0.55 and 0.26. The genetic and phenotypic correlations of CH_4 outputs with various production traits were weak and not significantly different from zero for the g $CH_{4.}kg^{-1}$ DMI. These results of Pinares-Patiño et al. (2013, pp. 316-321) indicate that there is genetic variation between animals for CH_4 emission traits even after adjustment for feed intake and that these parameters are repeatable. The heritability for total CH4 production and CH4 emissions per kilogram of feed intake were in beef cattle heritability 0.40 and 0.19 (Donoghue et al., 2013, pp. 290-93).

The study of Dong et al. (2015, pp. 1807-1812) informed that cow genetic merit has little effect on enteric CH_4 emissions as a proportion of feed intake. Instead enteric CH_4 production may mainly relate to total feed intake and dietary nutrient composition. At the work of Zou et al. (2015, pp. 616-622) there was no significant effect between two suckle cow genotypes on the enteric methane emissions.

Animal breeding is a further strategy to enhance productivity and thereby lower CH_4 emission intensities. Two approaches are currently being taken; breeding animals with improved feed conversion efficiency (Hegarty et al. 2007, pp. 1479-86) and breeding animals with low emissions per unit of feed consumed (Pinares-Patiño & Clark 2008, pp. 223-9). From a range of traits, breeding studies found feed efficiency to have a large impact on reducing the CH_4 emissions from dairy systems (Bell et al. 2011, pp. 699-07). The enteric CH_4 emission of dairy cattle appears to be related to feed intake and dietary nutrient composition (Moss, Jouany & Newbold 2000, pp. 231-253). Breeding programs that select dairy cows with high production efficiencies can reduce feed intake per kg milk yield, and thus reduce enteric CH_4 emissions per unit of feed intake or energy intake (Dong et al. 2015, pp. 1807-1812).

The possible selection of animals based on low CH_4 production and more likely on their high efficiency of digestive processes has been discussed in the last few years. It has been established by several researchers that between-animal variability, at the same level of performance and using similar diets, is high. Differences in feed intake explain only a part of the variability. Genetic variation between animal variation in CH_4 emissions and CH_4 intensity (as CH_4 per unit intake) have also been reported in animals fed the same diet (Vlaming et al. 2008, pp. 124-7).

Selected genetic line cows fed under low forage regime were estimated to reduce emission production by 24 % compared to control genetic line cows fed under a high forage regime (Ross et al. 2014, pp. 158-171). The high forage regime group was fed a total mixed ration (TMR) comprising 25 % concentrates (including distillers grains and rapeseed meal), the low forage regime group were fed a TMR consisted of 55 % concentrates (including wheat, distillers grains, sugar beet pulp, and soymeal).

The ranking of animals in CH_4 production per DMI is determined by physiological stages with a change in diet (Pinares-Patiño et al. 2007b, pp. 601-13) or dietary changes at the same physiological stage (Goopy & Hegarty 2004, pp. 75-8; Münger & Kreuzer 2008, pp. 77-82; Vlaming et al. 2008, pp. 124-7).

The repeatability between animals was evaluated from 47 % to 73 % according to the diets (Martin, Morgavi & Doreau 2010, pp. 351-65). However, the apparent lack of persistence of individual animal differences in methane yields suggests that genetic determination of this trait is of minor importance in dairy cows. None of the statistical approaches showed clear and persistent individual animal differences in methane yield (Goopy & Hegarty 2004, pp. 75-8). Methane emissions were within published ranges (136.4 $g.d^{-1}$) in the study of Münger & Kreuzer (2008, pp. 77-82); however, differences in actual vs predicted production between high- and low- ranked animals were diminished, while several animals changed in rankings.

This suggests that methane emission characteristics may not persist over time, and that any selection of animals for low methane emission may need to be diet specific (Münger & Kreuzer 2008, pp. 77-82). These results show that the genetic component of CH_4 production may be low (Goopy & Hegarty 2004, pp. 75-8). According to Clark, Kelliher & Pinares-Patiño (2011, pp. 295-02), a breeding approach to CH_4 mitigation is possible.

Breeding can be used to decrease predicted CH_4 production based on milk fatty acids (Van Engelen et al. 2015, pp. 8223-6). Milk fatty acids profile can be considered a potential indicator of in vivo methane output in ruminants (Chilliard et al. 2009, pp. 5199-211) and it can be used to predict the formation of CH_4 in dairy cattle (Dijkstra et al. 2011a, pp. 590-5). According to Yin et al. (2015, pp. 5748-62), predicted CH_4 emissions had moderate heritabilities over lactation and ranged from 0.15 to 0.37 (h^2), with highest heritabilities around 100 days of milk. Genetic correlations between CH_4 with days open and with calving interval increased from 0.10 at the beginning to 0.90 at the end of lactation. Genetic relationships between CH_4 and stillbirth (intrauterine fetal death) were negative from the beginning to the peak phase of lactation.

Significant breed differences in CH_4 emissions of cattle have been reported by Thackaberry et al. (2010, pp. 10-11). It could suggest that indeed genetic differences exist among dairy cows (Jersey, Holstein-Friesian, and Jersey×Holstein-Friesian F1). However, methane emissions on a g.kg milk solids^{-1} basis were not significantly different between breed groups. Differences between genotypes were most apparent during periods of high productivity (Thackaberry et al. 2010, pp. 10-11). Boadi & Wittenberg (2002, pp. 201-6) compared enteric CH_4 emissions from dairy (Holstein) and beef (Charolais x Simmental) heifers of similar LBW and age, fed ad-libitum and restricted feeding. Methane production was not different (238.0 L.d^{-1} vs. 228.6 L.d^{-1}). The data of Robertson & Waghorn (2002, pp. 213-8) showed that cattle selected for high productivity on high concentrate diets produced 8 to 11 % less CH_4 than animals selected in a pasture system.

O'Brien et al. (2010, pp. 3390-402) reported a difference of 9 % in emissions per kilogram of milk yield (MY) between two genotypes of Holstein–Friesian animals differing in replacement rate (18 % vs. 35 %). De Haas et al. (2011, pp. 6122-34) estimated a heritability of 0.35 for predicted CH_4 emissions in dairy cows (predicted CH_4 emissions were derived from feed intake and maintenance). Also, others authors (Berry 2013, pp. 28-36; Koenen & Veerkamp 1998, pp. 67-77) consider more reliable to use the heritability of DMI and LBW. Therefore, the benefit of such measurements in selecting programs which routinely available likely correlated traits as MY, or LBW in breeding for reduced environmental load need to be quantified (Dehareng et al. 2012, pp. 1694-701; Lassen, Løvendahl & Madsen 2012, pp. 890-898).

ANIMAL MANAGEMENT

There are a wide range of management practices that improve animal productivity, resulting in reduced CH_4 emissions in ruminants (Borhan et al. 2012, p. 51175; Lovett et al. 2006, pp. 156-79). Increasing animal productivity can be a very effective strategy for reducing CH_4 emissions per unit of livestock product (Hristov et al. 2013b, pp. 5095-113). Generally, an enhancement in production efficiency in terms of MY was associated with a decrease in enteric methane emissions per litre of milk (Chagunda, Römer & Roberts et al. 2009, pp. 323-32). Especially, increasing survival, decreasing MY, LBW, and DMI per live unit can mitigate the CH_4 emissions per cow (Bell et al. 2013, pp. 7918-31). A more accurate estimation could be made, by taking into account the whole productive life of the cow (Garnsworthy 2004, pp. 211-23).

Improving fertility and longevity can reduce the environmental load of the production system. Of course, prolong life will increase the generation interval thereby reducing annual genetic gain; the impact needs to be quantified once genetic parameters for environmental traits are available (Berry 2013, pp. 28-36). Garnsworthy (2004, pp. 211-23) reported a reduction of 10-11 % in CH_4 emissions if dairy fertility is improved. Fertility has a major effect on the replacement rate of the herd because poor reproductive performances are associated to a higher number of young livestock to be reared. Moreover, although first calving at 24 months of age is a target, many herds calve heifers at an older age. All these aspects have a direct effect on the total herd emissions of CH_4 (Cassandro, Mele & Stefanon 2013, pp. 450-8).

The impact of fertility on environmental load differs also through alterations on the diet fed and the associated implications, especially in seasonal calving production systems (Berry 2013, pp. 28-36). Increased MY is beneficial to reductions of CH_4 emissions per unit of product, but it is important that effects of reduced fertility do not outweigh them. Therefore, over the long term, fertility traits included in a selection index should be considered a positive way to reduce environmental impact as much as to preserve fertility (Cassandro, Mele & Stefanon 2013, pp. 450-8). A reduction of 4 % to 5 % in CH_4 emissions was expected in the United Kingdom, if fertility levels were restored to 1995 levels from 2003 levels. These improvements were primarily because of a reduced number of non-producing replacement animals and to a lesser extent greater MY when fertility was improved (Garnsworthy 2004, pp. 211-23).

Selection for MY or LBWG and thus intensification of production could result in lower CH_4 production per kg product, although daily emissions per animal increase. However, it should be noted that CH_4 emissions during a cow lifetime should be split between milk and meat productions. The meat produced should take into account not just the cow but also that from the male offspring (Martin, Morgavi & Doreau 2010, pp. 351-65).

Reduce the number of animals in the herd would increase feed availability and performance of individual animals, thus lowering CH_4 emission intensity (Mihina, Kazimirova & Copland 2012, pp. 1-99). Reducing age at slaughter of finished cattle and the number of days that animals are on feed can have a significant impact on reduce CH_4 emissions. Improved animal health and reduced mortality and morbidity are also expected to reduce CH_4 emission intensity (Hristov et al. 2013b, pp. 5095-113).

DIETARY MANIPULATION

Diet had the greatest influence on methane emissions (Wallace et al. 2014, p. 5892). Nutritional strategies to mitigate CH_4 emissions from ruminants are developing and they are not always applicable in practice. Feed rations and feed intake have been proposed as a means of reducing CH_4 emissions from cattle (Beauchemin et al. 2008; pp. 21-27; Boadi et al. 2004, pp. 319-335; Eckard, Grainger & de Klein 2010, pp. 47-56; Hünerberg et al. 2015, pp. 1760-5; Moss, Jouany & Newbold 2000, pp. 231-53). Abatement of CH_4 emissions from ruminant animals has been focused on rumen and animal manipulations, such as improving forage quality, adding dietary supplement, reducing unproductive animals, and supplementing probiotics to change microbial population in rumen (Borhan et al. 2012, p. 51175).

The chemical composition of diet is an important factor which affects rumen fermentation and CH_4 emission by the animals. Digestion in the rumen is dependent on the activity of microorganisms, which need energy, nitrogen and minerals. Guyader et al. (2014, pp. 1816-1825) showed that a reduction of protozoa concentration was in most cases indicative of a reduction of CH_4 emission. The effects of the amount and type of diet on CH_4 production in sheep and cattle were also determined.

The CH_4 production rate is depended on the fiber content (Shibata & Terada 2010, pp. 2-10). Methane production tends to decrease as the protein content of feed increases, and increases as the fiber content of feed increases (Shibata et al. 1992, pp. 1221-7; Johnson & Johnson, 1995, pp. 2483-92; Kurihara et al. 1997, pp. 227-234).

The improving forage quality and the efficiency of dietary nutrient use is an effective way of decreasing CH_4 (Chagunda, Flockhart & Roberts 2010, pp. 250-6; Hristov et al. 2013a, pp. 5045-69). The study of Boadi, Wittenberg & McCaughey (2002, pp. 151-7) implies that pasture quality plays a major role in the extent to which CH_4 production can be reduced with grain supplementation in grazing animals. The quality of forage affects the activity of rumen microbes and CH_4 production in the rumen. Mirzaei-Aghsaghali & Maheri-Sis (2016, pp. 22-31) wrote that CH_4 emissions in ruminants generally increase with forage maturity. Robertson & Waghorn (2002, pp. 213-8) found that CH_4 production from grazing dairy cows increased with forage maturity from 5 % to 6.5 % of gross energy intake in spring and summer, respectively. Forage species and the proportion of forage in the ration also influence CH_4 production in ruminants. Boadi, Wittenberg & McCaughey (2002, pp. 151-7) write that CH_4 production declined with grazing on high-quality forages; steers on early pastures had 44 % and 29 % lower energy loss as CH_4 than animals on mid and late pastures, respectively.

An expected decrease in CH_4 with young fresh forages may be explained by a higher content of soluble sugars and linolenic acid (Martin, Morgavi & Doreau 2010, pp. 351-65). CH_4 yield (emission expressed per unit of feed intake) can change, possibly in association with physiological drivers affecting intake. The effects of animal-related factors are most apparent at high intake levels, for example during lactation. Absolute emissions were strongly associated with feed intake (especially of digestible fiber) (Pinares-Patiño et al. 2007b, pp. 601-13). Pasture management, including forage species selection, stocking rate and continuous vs. rotational grazing strategies have all been shown to influence enteric CH_4 emissions. Waghorn, Tavendale & Woodfield (2002, pp. 167-71) fed sheep with fresh cut, good quality forages. They observed a difference in CH_4 emissions, from 11.5 g CH_4.kg^{-1} DMI with lotus and dried lucerne to 25.7 g CH_4.kg^{-1} DMI with a ryegrass and white clover pasture. All forages had a DM digestibility of 70 % or greater, although DMI was not the same.

It depends on the physical property (consistency, compactness or firmness) of the mixed feed ration. Since the growth rates of methanogens are slow (Ushida et al. 1997, pp. 209-20), the passage rate of digesta from the rumen also influences CH_4 production in the rumen. Methane production tends to decrease as the protein content of feed increases, and it increases as the fiber content of feed increases (Shibata et al., 1992, pp. 1221-7; Johnson & Johnson, 1995, pp. 2483-92; Kurihara et al., 1997, pp. 227-34). Forages are composed of several types of carbohydrates. These fibrous carbohydrates play an important role in providing plants with their structural rigidity. However, this also makes them difficult to digest (Drogoul, Poncet & Tisserand et al., 2000, pp. 117-30; Niderkorn & Baumont, 2009, pp. 951-60). Honing van der (1975, pp. 1-156) showed that forage processing, i.e. grinding and pelleting, increased the feed intake of ruminants. This increase, due to a reduction in particle size distribution of the forage, depends mainly on the forage quality, and nutrient requirements of the cow. Processed forages offered to ruminants depressed their digestibility, which the animals compensated for by the lower production of methane. Digestibility of organic matter and energy from pelleted diets was 6.9 % lower than from unprocessed diets. Methane loss per unit of diet can be reduced 20–40 % by using ground or pelleted forage at high intakes because of the increased rate of passage (Shibata & Terada 2010, pp. 2-10).

Feed preservation and treatment processing also affect enteric CH_4 production. Methanogenesis tends to be lower when forages are ensiled than when they are dried, and when they are finely ground or pelleted than when coarsely chopped (Beauchemin et al. 2008, pp. 21-7; Boadi et al. 2004, pp. 319-335). Agrawal & Kamra (2010, pp. 27-39) found that wheat straw treated with urea or urea plus calcium hydroxide, and stored for 21 days before feeding, reduced CH_4 emission from sheep by 12-15 %. Moss (1994, pp. 786-806) recommends reducing CH_4 production by chemical treatments such as sodium hydroxide or ammonia. Pinares-Patiño et al. (2016, pp. 7-12) concluded that enhanced dietary lipids contents is an effective means of reducing CH_4 emissions from grazed pasture.

An effective tool to reduce CH_4 emissions is proven to be dietary manipulation. For example, feeding cattle with a high starch and low fiber diet reduces creation of acetate in the rumen and leads to lower CH_4 production (Borhan et al. 2012, p. 51175). Authors Agrawal & Kamra (2010, pp. 27-39) found that methanogenesis decreased significantly after a green maize inclusion to the feed ration.

Methane production was significantly lower in the sheep fed on green sorghum and wheat straw in the ratio of 90:10 as compared to where the ratio was 60:40 (31.5 vs. 46.91 CH_4.kg^{-1} DM). Improvement in the digestibility of lignocellulose feeds with different treatments also resulted in lower methanogenesis by the animals (Agrawal & Kamra 2010, pp. 27-39). Kurihara et al. (1995, pp. 21-107) showed that CH_4 production per DMI of cows given Italian ryegrass hay (lower digestibility) was lower than that of cows given corn silage (higher digestibility). However, in lactating cows, CH_4 production per DMI was 35 % higher in high roughage feeding with lower digestibility than in high concentrate feeding with higher digestibility. Shioya et al. (2002, pp. 191-4) showed CH_4 production (L.d^{-1}) to be 260 and 146 and CH_4 production per FCM (L.kg^{-1} FCM) to be 48.1 and 25.5 for hay alone and hay with sweet potato, respectively. The effect of sweet potato feeding may be attributed to a higher rate of rumen fermentation, a higher passage rate of digesta and enhanced propionic acid production (Shibata & Terada 2010, pp. 2-10).

According to the prediction model of Benchaar, Pomar & Chiquette (2001, pp. 563-574), the substitution of timothy hay by lucerne decreases CH_4 emissions by 21 % (expressed as % of digestible energy). Replacing grass silage with maize silage is a feeding strategy to reduce enteric CH_4 emission (Hristov et al. 2013a, pp. 5045-69; Van Middelaar et al. 2013, pp. 9-22). Dijkstra, Oenema & Bannink (2011b, pp. 414-22) showed that replacing 50 % of the grass silage with maize silage in a diet containing on average 30 % concentrates and 70 % grass silage, reduces enteric CH_4 levels by approximately 8 %. So, increasing maize silage at the expense of grass and grass silage in a dairy cow's diet is a promising strategy with an immediate effect on emissions (Van Middelaar et al. 2013, pp. 9-22).

The inclusion of wheat grain in the diet of dairy cows also results in a substantial reduction in methane yield (Moate et al. 2015, pp. 1017-34). It is unclear how much wheat should be in the feed. The feed ration of Moate et al. (2011, pp. 254–64) contained 303 g.kg DM^{-1} of cracked wheat grain. In another study by the same authors, the concentration of wheat grain ranged from 0 to 567 g.kg DM^{-1} and the methane yield declined quadratically with an increasing dietary wheat concentration (Moate et al., 2014, pp. 121-40). According to Moate et al. (2015, pp. 1017-34), Australian dairy herds consume to 38 % of metabolisable energy intake as wheat. Moate et al. (2017, pp. 7139-53) offered to dairy cows corn, wheat, and two types of barley diet. The mean methane emissions and methane yields of cows fed the wheat diet were significantly lower than those of cows fed with the other diets. Indeed, the corn- and two- barley diets were associated with 49, 73, and 78 % greater methane emissions, respectively, compared with the emissions from the wheat diet.

McCaughey, Wittenberg & Corrigan (1999, pp. 221-6) found 10 % decrease in CH_4 production over the course of a grazing season in beef cattle (0.53 vs. 0.58 g.kg^{-1} LBW.d^{-1}, respectively) when grasses were replaced by a mixture of lucerne and grasses (70: 30). These authors concluded that this was due to the higher digestibility rate of lucerne and an increased passage of feed particles out of the rumen. However, this effect on methanogenesis is not a characteristic of all legumes; clover did not differ from ryegrass on CH_4 emissions of cattle significantly (Beever et al. 1985, pp. 763-75). Also, findings of Van Dorland et al. (2007, 57-69) imply that clover supplementation to a high-protein ryegrass based diet did not result in a significant reduction in CH_4 emission.

Increasing forage digestibility and digestible forage intake was one of the major recommended CH_4 mitigation practices (Blaxter & Clapperton 1965, pp. 511-22). These authors showed that the CH_4 production rate could be changed by the digestibility of the feed, especially crude fiber. According Sauvant & Giger-Reverdin (2007, pp. 561-2) CH_4 production efficiently compensated for the influence of feeding level on diet digestibility.

Hegarty (1999, pp. 1321-7) found that CH_4 production per LBWG was reduced significantly when animals were shifted from low digestible pasture to high digestible pasture. The use of more digestible forage (less mature and processed forage) resulted in a reduction of CH_4 production (-15 % and -21 %).

Mitigating CH_4 emissions can be achieved by changing type of forage offered (legumes, condensed tannins) but there are practical and cost barriers to the use of alternative feeds (Clark, Kelliher & Pinares-Patiño 2011, pp. 295-302; Waghorn, Tavendale & Woodfield 2002, pp. 167-171). Methane production was lower with legume than with grass forage by 28 %. Legumes generally have higher DMI and produce more milk solids. This reduces CH_4 emissions per unit of milk or meat production (Benchaar, Pomar & Chiquette 2001, pp. 563-574; Iqbal et al. 2008, pp. 2747-55).

Feeding legume silages could also lower CH_4 emissions compared to grass silage due to their lower fiber concentration. Hristov et al. (2013a, pp. 5045-69) explained lowered methane loss observed with legumes to the lower proportion of structural carbohydrates and faster rate of passage of legumes, which will shift the fermentation pathway towards higher propionate production.

Study of Woodward et al. (2001, pp. 23-6) with wether sheep showed lower daily CH_4 outputs per DMI when fed *Lotus pedunculatus* (a condensed tannin containing legume) than ryegrass-based pasture or lucerne (14.5 vs. 20.4 vs. 19.0 g CH_4.kg^{-1} DMI). Friesian dairy cows fed either *Lotus corniculatus* silage or perennial ryegrass silage had similar total CH_4 outputs. However, methane emissions were significantly lower from cows fed *Lotus* silage (26.90 vs. 35.13 g CH_4.kg^{-1} DMI; 378 vs. 434 g CH_4.kg^{-1} milk solids). The results of dairy cow trials confirm the beneficial effects of *Lotus*: improved feeding value for both growing sheep and lactating cows, together with reduced methane emission per unit of feed intake. The mitigation of CH_4 emissions from animals fed *Lotus* species was due in part to a higher nutritive value relative to pasture but effects of condensed tannins on methanogenesis warrants further investigation (Woodward et al. 2002, pp. 227-30).

Condensed tannins, a constituent of some legumes, have been associated with reduced enteric CH_4 emissions. Several studies reviewed by Frutos et al. (2004, pp. 191-202) have shown that fibre degradation in the rumen can be drastically reduced in animals that consume tannin-rich feeds. Tannins can react with microbial (both bacterial and fungal) enzymes, inhibiting their activity. Waghorn, Tavendale & Woodfield (2002, pp. 167-171) observed the impact of condensed tannins on rumen methanogenesis to be small but significant; a 16 % reduction. Jones et al. (1994, pp. 1374-8) showed that tannins reduced the ability of some bacterial species to colonize on plant particles. Other authors have shown that including tannin rich legumes (sainfoin, lotus, sulla) and shrubs in the diet contribute to a decrease in methanogenesis (Waghorn and Dewhurst 2007, pp. 111-23).

CONCENTRATES

The composition of the feed has been shown to influence enteric fermentation and CH_4 emissions from the rumen or hindgut (Mirzaei-Aghsaghali & Maheri-Sis, 2016, pp. 22-31). The increasing the high levels of grain based concentrate in the ruminant diet leads to a reduction in CH_4 emissions as a proportion of energy intake or expressed by unit of animal product (Beauchemin & McGinn 2005, pp. 653-61; Beauchemin et al. 2008, pp. 21-7; Boadi et al. 2004, pp. 319-35; Chagunda, Flockhart & Roberts 2010, pp. 250-6; Finn, Dalal & Klieve et al. 2015, pp. 1-22; Hristov et al. 2013a, pp. 5045-69; Lovett et al. 2006, pp. 156-79; McAllister & Newbold 2008, pp. 7-13; Sejian & Naqvi 2012, pp. 255-76; Yan et al. 2000, pp. 253-263). The proportion of concentrate within the diet has been reported to be negatively correlated with CH_4 emissions (Holter & Young 1992, pp. 2165-75; Sauvant & Giger-Reverdin 2007, pp. 561-2; Yan et al. 2000, pp. 253-63). Methane losses appear relatively constant for diets containing up to 30 % to 40 % concentrate (above 40 % of DMI) and then decrease rapidly to low values for diets containing 80 % to 90 % concentrate (Beauchemin & McGinn 2005, pp. 653-61; Lovett et al. 2003, pp. 135-46).

The high-concentrate diet resulted in lower methane emissions than the medium-concentrate diet (Wallace et al. 2014, p. 5892). Methane production with high-concentrate feed ration was found lower than that with high-roughage feed in heifers, sheep and goats (Hegarty et al. 2007, pp. 1479-86; Shibata et al. 1992, pp. 1221-7), as well as in lactating cows (Kurihara et al. 1997, pp. 199-208). Martin, Morgavi & Doreau (2010, pp. 351-65) described a comparison of the grass system with low-producing cows and the winter feeding system based on concentrates with high-yielding cows. The second system with concentrate produced 37 % less enteric CH_4 than the first one. In beef heifers and feedlot systems, concentrate supplementation into finishing diets have been also shown to reduce CH_4 emissions (Beauchemin & McGinn 2005, pp. 653-61; Finn, Dalal & Klieve 2015, pp. 1-22; Lovett et al. 2003, pp. 135-146).

The depressive effect of concentrate on methanogenesis likely resulted from a lower residence time of digesta in the rumen when feeding level increased. Ruminal digestive interactions depend on the microbial activity, especially of the ability of these bacteria to attach to particles, and the particle retention time in the rumen (Michalet-Doreau, Martin & Doreau 1997, pp. 103-12).

It is obvious that type of dietary nonstructural carbohydrates (starch and sugars) or structural carbohydrates (cellulose and hemicellulose) influences emissions from the animal. Studies of Beever et al. (1989, pp. 1-33) determined the effect of starch-based and fiber-based concentrates on enteric CH_4 production. Concentrates rich in starch (wheat, barley, maize) have a more important negative effect on CH_4 production than fibrous concentrates (beet pulp). When was the beet pulp replaced by barley in a high concentrate diet (70 %) and fed to dairy cows, CH_4 emissions were reduced by 34 % (Beever et al. 1989, pp. 1-33).

Martin, Morgavi & Doreau (2010, pp. 351-65) recorded lower CH_4 emissions from bulls fed the diet containing 45 % starch compared to those fed other two diets containing 30 % starch. Beauchemin & McGinn (2005, pp. 653-61) measured CH_4 emissions from feedlot cattle fed backgrounding and finishing diets containing maize (slowly degradable starch) or barley grain (rapidly degradable starch). They recommend a high-forage backgrounding diet and a barley-based finishing diet in the production cycle of feedlot cattle as a dietary strategy to decrease CH_4 emissions of cattle.

Doreau et al. (2011, pp. 2518-28) evaluated the effects of three high-concentrate diets on enteric CH_4 production of beef cattle. Diets consisted of 49 % hay, 41 % ground corn grain, and 10 % soybean meal (hay diet); 63 % corn silage, 21 % ground corn grain, and 16 % soybean meal (corn silage diet); and 70 % ground corn grain, 16 % soybean meal, and 14 % wheat straw (corn grain diet). Daily CH_4 emission was similar for the hay and corn silage diets and was 56 % ($P<0.001$) greater than for the corn grain diet. Lovett et al. (2005, pp. 2836-42) demonstrated that increased fiber-based concentrate use at pasture reduced enteric CH_4 per kilogram of animal product (19.26 and 16.02 g of CH_4. kg^{-1} of fat-corrected milk). Plant fibre substitution in the diet with starch induces a shift of volatile fatty acid production from acetate towards propionate occurs, which results in less hydrogen production. The depression in CH_4 production was accompanied with an increase in propionate concentration in the rumen liquor (Agrawal & Kamra 2010, pp. 27-39); Martin, Morgavi & Doreau 2010, pp. 351-65; Singh 2010, pp. 142-58).

However, enteric CH_4 emission per unit of estimated feed intake (DM or gross energy) or milk output (gross or energy corrected) was not affected by level of concentrate supplementation (Muñoz et al. 2015, pp. 37-46). The studies of Klevenhusen, Kreuzer & Soliva (2011, pp. 450-61) and Finn, Dalal & Klieve (2015, pp. 1-22) recorded that feeding mixed forage-concentrate diets instead of forage-only diets is not generally useful to mitigate CH_4 formation, in case diets are nutritionally balanced.

CONCLUSIONS

Methane emissions from ruminant systems can be lowered by selecting ruminants with a low residual feed intake and by selection or breeding ruminants with low CH_4 production.

The increase in dairy cow productivity results in a decrease in CH_4 emission per kg milk. Increasing ruminants productivity can be a very successful strategy for mitigating CH_4 emissions. However, selection for high productivity should not be expensive and shall not affect other essential traits such as fertility and health condition.

The values suggest that breeding animals with low CH_4 emissions but unchanged performance would be a helpful way for CH_4 mitigation in future. Improving the genetic potential of animals through cross-breeding or selection within breeds are effective approaches for reducing CH_4 emission intensity.

The ruminal CH_4 varies according to diet composition and quality, specifically by feeding more grain. Concentrate supplements in ruminant diets have been recognized as an effective CH_4 mitigation strategy. Also, concentrate feeding has shown to reduce methane output by reducing the protozoal population and this feeding type may result in health problems e.g. acidosis.

The CH_4 emissions are highly dependent on the management strategies implemented on a farm. Consequently, improvements in practices and changes in demand for livestock products will affect future CH_4 emissions.

Further research is needed to consider a possible selection of animals on CH_4 production and more likely on microbial and digestive processes. New approaches will be need in genetics and nutrition to provide perspective on the contribution of CH_4 emissions.

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