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## Between-cow variation in digestion and rumen fermentation variables associated with methane production

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### ABSTRACT

A meta-analysis based on an individual-cow data set was conducted to investigate the effects of between-cow variation and related animal variables on predicted CH<sub>4</sub> emissions from dairy cows. Data were taken from 40 change-over studies consisting of a total of 637 cow/period observations. Animal production and rumen fermentation characteristics were measured for 154 diets in 40 studies; diet digestibility was measured for 135 diets in 34 studies, and ruminal digestion kinetics was measured for 56 diets in 15 studies. The experimental diets were based on grass silage, with cereal grains or by-products as energy supplements, and soybean or canola meal as protein supplements. Average forage:concentrate ratio across all diets on a dry matter basis was 59:41. Methane production was predicted from apparently fermented substrate using stoichiometric principles. Data were analyzed by mixed-model regression using diet and period within experiment as random effects, thereby allowing the effect of experiment, diet, and period to be excluded. Dry matter intake and milk yield were more repeatable experimental measures than rumen fermentation, nutrient outflow, diet digestibility, or estimated CH<sub>4</sub> yield. Between-cow coefficient of variation (CV) was 0.010 for stoichiometric CH<sub>4</sub> per mol of volatile fatty acids and 0.067 for predicted CH<sub>4</sub> yield (CH<sub>4</sub>/dry matter intake). Organic matter digestibility (OMD) also displayed little between-cow variation (CV = 0.013), indicating that between-cow variation in diet digestibility and rumen fermentation pattern do not markedly contribute to between cow-variation in CH<sub>4</sub> yield. Digesta passage rate was much more variable (CV = 0.08) between cows than OMD or rumen fermentation pattern. Increased digesta passage rate is associ-

ated with improved energetic efficiency of microbial N synthesis, which partitions fermented substrate from volatile fatty acids and gases to microbial cells that are more reduced than fermented carbohydrates. Positive relationships were observed between CH<sub>4</sub> per mol of volatile fatty acids versus OMD and rumen ammonia N concentration versus OMD; and negative relationships between the efficiency of microbial N synthesis versus OMD and digesta passage rate versus OMD, suggesting that the effects of these variables on CH<sub>4</sub> yield were additive. It can be concluded that variations in OMD and efficiency in microbial N synthesis resulting from variations in digesta passage contribute more to between-animal variation in CH<sub>4</sub> emissions than rumen fermentation pattern.

**Key words:** digestibility, rumen fermentation, passage rate, variance component

### INTRODUCTION

Enteric CH<sub>4</sub> emissions from ruminants represent a loss of dietary energy and contribute to greenhouse gas emissions. Depending on feeding level and diet composition, 2 to 12% of feed gross energy (GE) can be lost as CH<sub>4</sub> (Blaxter and Clapperton, 1965; Johnson and Johnson, 1995). Thus, strategies that mitigate CH<sub>4</sub> emissions are not only environmentally beneficial, but can also result in greater efficiency of feed energy utilization by the animal. Methane production in cattle is strongly and positively correlated with DMI (e.g., Yan et al., 2000; Hristov et al., 2013). Because CH<sub>4</sub> can be produced only from potentially digestible substrate, CH<sub>4</sub> production in the rumen can be expected to be positively related to feed digestibility. In addition, diet composition, which is closely associated with digestibility, influences passage and digestion kinetics of feed particles in the gastrointestinal tract, and finally CH<sub>4</sub> production.

Forage-to-concentrate ratio and dietary fat content are important variables influencing CH<sub>4</sub> emissions per unit intake (CH<sub>4</sub> yield; Hristov et al., 2013; Ramin and Huhtanen, 2013). Low CH<sub>4</sub> yields have been reported

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when high-concentrate feedlot diets are fed to growing cattle (Johnson and Johnson, 1995), reflecting increased propionate production from the higher supply of starch in these diets. Conversely, fat supplementation clearly decreases CH<sub>4</sub> production (Moss et al., 2000). In addition to manipulation of diet composition, many other mitigation strategies (e.g., ionophores, electron acceptors, and plant bioactive compounds) have been extensively studied (Hristov et al., 2013).

The common assumption that CH<sub>4</sub> production is affected mainly by the diet has been challenged since the large variation in CH<sub>4</sub> emissions also has been attributed to animal factors (Ellis et al., 2007; Yan et al., 2009). In a study by Blaxter and Clapperton (1965), the coefficient of variation between-animal of CH<sub>4</sub> yield was 7 to 8% in a respiration chamber study with sheep and cattle fed restrictively. In dairy cows fed ad libitum, the coefficient of variation for CH<sub>4</sub> yield was considerably greater (8–18%) when measured by the SF<sub>6</sub> technique (Vlaming et al., 2008). Studies conducted in sheep have shown that the variation in ruminal digesta retention time or passage rate is related to CH<sub>4</sub> emissions, with high CH<sub>4</sub> emitters having a larger rumen volume and digesta pools than low emitters (Pinares-Patiño et al., 2003; Pinares-Patiño et al., 2011; Goopy et al., 2014). Other studies have shown that the host animal controls the archaea populations in the rumen (Weimer et al., 2010; Roehe et al., 2016). Although deep metagenomic and metatranscriptomic sequencing has shown similar abundance of methanogens and methanogenesis pathway genes in high and low CH<sub>4</sub> emitters, the transcription of methanogenesis pathway genes was substantially increased in sheep with high CH<sub>4</sub> yields (Shi et al., 2014). The mechanisms explaining the between-animal variation in CH<sub>4</sub> emissions are not fully understood. The examination of the between-animal differences in a large data set originating from variations in digestion physiology and rumen microbial ecology could help to elucidate it.

Because the animal variation is likely to be under genetic control, one option to mitigate CH<sub>4</sub> emissions that has been suggested is to select for animals that emit less. Pinares-Patiño et al. (2013) demonstrated that there is repeatable individual variation in this trait and part of this variation is genetic, but that the heritability estimate was lower for CH<sub>4</sub> yield than for total daily CH<sub>4</sub> emissions (0.13 and 0.29, respectively). Therefore, in addition to heritability, further progress in genetic selection for low CH<sub>4</sub> emitters also depends on better understanding of the variables involved in the observed between-animal variation of this trait. The objective of the present study was to evaluate between-cow variation and repeatability in digestion and fermentation variables contributing to CH<sub>4</sub> emis-

sions using a large data set from physiological digestion studies using a meta-analytical approach.

## MATERIALS AND METHODS

### Data

A meta-analysis was conducted to evaluate repeatability and between-animal variation in digestion and fermentation variables related to CH<sub>4</sub> yield in dairy cows. The data were taken from studies on rumen-cannulated dairy cows, conducted using either a Latin square or switch-back design, in the Nordic countries: Finland (30 studies, 117 diets), Sweden (8 studies, 27 diets), and Norway (2 studies, 10 diets). The complete data set consisted of 637 cow/period observations, which were considered to be the experimental unit (Supplemental data file; <https://doi.org/10.3168/jds.2016-12206>). A minimum pre-condition for inclusion of a study in the meta-analysis was that feed intake, BW, milk production data, and rumen fermentation variables were reported. In addition, diet digestibility in the total tract was determined in 34 studies, omasal flow of nutrients in 26 studies, and ruminal pool sizes and digestion kinetics in 15 studies.

The mean forage-to-concentrate ratio of the diets was 59:41 on a DM basis. The concentrate supplements consisted principally of cereal grains, fibrous by-products from the food industry, and protein supplements, typically canola and soybean meal. Grass silage was the main forage source, but in 9 studies it was partly replaced with legume or whole-crop cereal silage. The diets were fed ad libitum either as TMR (30 studies) or fixed amounts of concentrate with forage ad libitum (10 studies). In omasal flow studies, the intake was usually restricted to 95% of ad libitum intake to avoid variations in daily intake during digesta sampling. When some chemical components (starch and fat in concentrate ingredients) were not reported in a specific study ( $n = 6$ ), the missing values were taken from Finnish feed table values (LUKE, 2016). Production measurements included BW, feed intake, diet chemical composition, milk yield, and milk composition (fat, protein, lactose, and MUN). Energy-corrected milk was calculated according to Sjaunja et al. (1991).

Diet digestibility was determined by total feces collection (27 studies) or by fecal spot sampling (7 studies) using acid-insoluble ash (Van Keulen and Young, 1977) or indigestible neutral detergent fiber (iNDF; Huhtanen et al., 1994) as internal markers. Digesta flow measurements were conducted in 26 studies using the omasal sampling technique (Ahvenjärvi et al., 2000) with the triple-marker system (France and Siddons, 1986). Microbial N synthesis was determined using <sup>15</sup>N

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