Effect of silage characteristics on enteric methane emission from ruminants

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Abstract

This review evaluates the effects of silage characteristics on enteric methane (CH_4) emission from ruminants by performing a meta-analysis. A total of 17 studies were selected from the literature, and the relationship between CH_4 yield (g/kg dry matter [DM] intake) and silage characteristics was determined using a mixed model univariate regression procedure. For grass silage, organic matter digestibility (%; $R^2 = 0.74$) and crude protein content (g/kg DM; $R^2 = 0.36$) were negatively associated, and neutral detergent fibre (NDF) content (g/kg DM; $R^2 = 0.44$) was positively associated with CH_4 yield. This indicates that increased grass silage quality consistently decreases CH_4 yield and may be an effective enteric CH_4 mitigation strategy. Similarly, optimizing maize silage quality appears to be an effective enteric CH_4 mitigation strategy, because NDF content (g/kg DM; $R^2 = 0.60$) was positively associated with CH_4 yield. Upon replacing grass silage with maize silage, dietary starch content (g/kg DM; $R^2 = 0.62$) and silage replacement level (%; $R^2 = 0.33$) were negatively associated, and NDF content (g/kg DM; $R^2 = 0.34$) was positively associated with CH_4 yield. These results indicate that replacing grass silage with maize silage consistently decreases CH_4 yield and may be an effective enteric CH_4 mitigation strategy. In contrast, replacement of alfalfa silage with maize silage was not associated with CH_4 yield and does not appear to be an effective strategy to decrease CH_4 yield. In conclusion, management practices to improve silage quality are a potent mitigation strategy to reduce enteric CH_4 emission per unit of feed fed to ruminants, and implications of silage quality have to be addressed when assessing greenhouse gas emissions in ruminant production.

Keywords: Enteric methane production, Mitigation, Grass silage quality, Maize silage quality, Silage replacement, Ruminants

Review Methodology: The following databases were used for the literature search: Web of Science (Thomson Reuters Science, New York, NY) and Scopus (Elsevier, Amsterdam, the Netherlands). Keyword search terms used: methane emission, ruminant, silage quality and silage replacement. In addition, we used backward reference searching (i.e. identifying the references cited in the articles obtained by the method described above) and forward reference searching (i.e. identifying articles that cite the articles obtained by the method described above).

Introduction

Forages, either grazed or conserved, represent a significant portion of ruminant diets [1]. The main forage on many farms is often conserved forage, in particular silage. Silages as feedstock are fed in balanced rations and are often a main part of the diet [2]. There is a large variety in nutritional characteristics of silages fed to ruminants, both within silage type (e.g. differences in grass silage quality) and between silage types (e.g. grass silage versus maize silage). Given the importance and variability of silages in ruminant production systems, it is vital to reliably assess the impact of silage characteristics on greenhouse gas emission, including enteric methane (CH_4) emission. Methane is the second most abundant greenhouse gas, and CH_4 produced by enteric fermentation in ruminants plays an important role in global climate change. Several studies have investigated the effect of silage characteristics on enteric CH_4 emission in ruminant livestock (e.g. Gordon *et al.* [3] varying grass silage quality for dairy cattle, McGeough *et al.* [4] varying maize silage quality for beef cattle and Jonker *et al.* [5] replacing alfalfa silage with maize silage for sheep). Here, and throughout the review, with grass silage quality we refer to organic matter (OM) digestibility (%) and chemical components related to OM digestibility (including crude protein [CP] and neutral detergent fibre [NDF] content); with corn silage quality we refer to starch and NDF content (g/kg dry matter [DM]). The current review aims to synthesize evidence from multiple studies and to provide an overview of the effect of silage characteristics on enteric CH_4 emission from ruminants by performing a meta-analysis. The review focuses on CH_4 yield (g CH_4/kg dry matter intake [DMI]). Enteric CH_4 production (g CH_4/day) depends largely on the DMI level, and effects of silage characteristics on DMI were not the prime interest of the current review. Insufficient availability of data and heterogeneous products among ruminants hampers proper evaluation of CH_4 intensity (g CH_4/kg ruminant product; ruminant products include milk, meat and wool).

Meta-Analysis

A literature study was performed using Web of Science (Thomson Reuters Science, New York, NY) and Scopus (Elsevier, Amsterdam, the Netherlands), with the focus on silage characteristics (i.e. silage quality and silage replacement). Scientific studies had to fulfil each of the following criteria: (i) an *in vivo* experiment was conducted with ruminants, (ii) enteric CH_4 emissions were measured directly (i.e. not estimated), (iii) the composition of the silages as well as the basal diet were described and (iv) the results were available on DMI in combination with daily enteric CH_4 production or on CH_4 yield (g/kg DMI or % of gross energy intake [GEI]). A total of 17 papers met the selection criteria; five articles (representing eight studies) for grass silage quality (summarized in Table 1), three articles for maize silage quality (summarized in Table 2) and nine articles (representing 14 studies) for the replacement of grass silage or alfalfa silage with maize silage (summarized in Table 3). Enteric CH_4 emission was measured using the respiration chamber technique or the sulphur hexafluoride (SF_6) tracer technique. Usually, enteric CH_4 production was reported in grams per day and CH_4 yield in grams per kg DMI consumed. If reported in litres rather than grams, the values were converted assuming a molar weight of 16.04 g and a volume of 22.40 L [19]. If reported in MJ rather than grams, the values were converted assuming 55.65 kJ/g [20]. If the articles did not report CH_4 yield, this was calculated using the reported DMI and daily enteric CH_4 production.

To determine the relationship between CH_4 yield and silage characteristics, a mixed model univariate regression procedure (PROC MIXED of SAS; version 9.4, SAS Institute Inc., Cary, NC) was applied. This included a random experiment effect and silage characteristic variables as fixed effects. Silage characteristic variables included OM digestibility (%), NDF, starch and CP content (all in g/kg DM), as well as the silage replacement level (%). Having the experiment effect as a random effect resulted in the equation parameter estimates to be estimated first within study, and then averaged to obtain overall estimates. The covariance structure used was variance components. Adjusted independent variable values were subsequently calculated based on regression parameters of the developed model to determine the R^2 corrected for experiment effect, as described by St-Pierre [21].

Silage Characteristics and Enteric CH_4 Emission

Meta-analyses aim to synthesize evidence from many possible sources, by comparing and combining findings from several studies using statistical methods [22]. The meta-analysis in the current study summarizes the effects of grass silage quality, maize silage quality and the replacement of grass silage or alfalfa silage with maize silage, on CH_4 yield (g/kg of DMI) across ruminant livestock (i.e. dairy cattle, beef cattle and sheep). The studies included in the current analysis did not include type (genus, species or cultivar) differences within a study; interpretation of results with respect to type has to be done with care.

Grass silage quality

The results of the mixed model regressions and the corresponding R^2 are presented in Table 4 and visualized in Figure 1. For grass silage quality, both OM digestibility (%; $P = 0.001$, $R^2 = 0.74$) and CP content (g/kg DM; $P = 0.009$, $R^2 = 0.36$) were negatively associated with CH_4 yield, whereas NDF content (g/kg DM; $P = 0.004$, $R^2 = 0.44$) was positively associated with CH_4 yield.

Increased OM digestibility indicates that more OM has been digested in the total gastrointestinal tract, which also suggests that more OM has been fermented in the rumen. Enteric CH_4 emission is expected to increase upon a rise in OM fermentation in the rumen. However, increased OM digestibility of grass silage generally results in increased DMI [7] and an increased DMI depresses the amount of enteric CH_4 produced per unit of feed consumed [23, 24], because of the shorter residence time of the feed in the rumen [25]. Additionally, increased OM digestibility results in a faster fermentation and a trend towards greater proportion of propionate in volatile fatty acids produced [26, 27], which is associated with decreased enteric CH_4 emission given the adverse relationship between propionate formation and enteric CH_4 production. This together explains why OM digestibility was negatively associated with CH_4 yield.

A lower concentration of structural carbohydrates (NDF) generally accompanied by an increased OM

Table 1 Descriptive summary of the studies used to determine effect of grass silage quality on methane (CH_4) emissions

						Silage characteristics (g/kg DM, unless stated otherwise)						CH_4 emissions[3]		
Study	Ruminant type	CH_4 measurement technique[1]	F:C[2]	Feed allowance	Treatment	DM (g/kg)	OM	CP	NDF	OM digestibility (%)	DMI (kg/day)	Production	Yield	Energy
1. Gordon *et al.* [3]	Dairy cattle	RC	50:50[4]	Ad libitum	Low digestibility	199	n.d.[5]	123[6]	n.d.	67.7[7]	17.3	377	21.8	6.6
					High digestibility	203	n.d.	156[6]	n.d.	75.9[7]	19.0	341	18.0	5.4
2. Brask *et al.* [6]	Dairy cattle	RC	65:35	Ad libitum	Early, control	422	911	168	361	83.0	17.6	386	20.8	6.4
					Late, control	329	922	124	515	71.0	16.0	388	22.8	6.9
3. Brask *et al.* [6]	Dairy cattle	RC	65:35	Ad libitum	Early, fat supplementation	422	911	168	361	83.0	17.3	339	19.5	5.8
					Late, fat supplementation	329	922	124	515	71.0	16.1	362	22.2	6.5
4. Warner *et al.* [7]	Dairy cattle	RC	80:20	Restricted	28 day regrowth, 65 kg N/ha	436	903	149	476	80.6	15.8	361	23.0	6.8
					41 day regrowth, 65 kg N/ha	654	924	106	501	79.5	14.9	356	24.0	7.2
					62 day regrowth, 65 kg N/ha	762	934	78	561	73.9	14.9	347	23.4	7.1
5. Warner *et al.* [7]	Dairy cattle	RC	80:20	Restricted	28 day regrowth, 150 kg N/ha	430	895	197	459	80.3	16.0	347	21.7	6.4
					41 day regrowth, 150 kg N/ha	575	902	173	507	80.0	14.5	352	24.4	7.2
					62 day regrowth, 150 kg N/ha	540	914	120	603	72.1	13.3	322	24.6	7.3
6. Warner *et al.* [8]	Dairy cattle	RC	80:20	Low intake	Leafy	456	894	286	365	78.5	15.8	308	19.8	5.7
				(15.5 kg	Boot	510	898	209	469	78.6	15.7	353	22.6	6.6
				DM/day)	Early heading	407	909	145	518	75.2	16.0	357	22.2	6.6
					Late heading	431	921	124	546	68.4	14.5	345	24.3	6.9
7. Warner *et al.* [8]	Dairy cattle	RC	80:20	High intake	Leafy	456	894	286	365	76.8	16.8	321	19.3	5.5
				(16.6 kg	Boot	510	898	209	469	77.8	16.4	354	21.4	6.4
				DM/day)	Early heading	407	909	145	518	73.4	16.9	365	21.7	6.4
					Late heading	431	921	124	546	68.9	16.2	364	22.8	6.6
8. Dini *et al.* [9]	Dairy cattle	SF_6	100:0	Ad libitum	Low quality winter	482	890	94	704	31.1	5.5	109	23.6	7.9
					Low quality spring	279	886	116	549	56.8	10.1	164	16.8	5.2
					High quality winter	196	888	211	424	56.0	10.1	160	21.6	7.0
					High quality spring	183	902	228	409	64.0	12.8	177	14.3	4.2

[1]Respiratory chambers (RC) or SF_6-tracer technique (SF_6).
[2]Forage to concentrate ratio (DM basis).
[3]Methane production in g/day; methane yield in g/kg of DMI; methane energy as % of GEI.
[4]Forage was fed ad libitum, always supplemented with 10.0 kg concentrate/day. This resulted in forage content in diet ranging from 50 to 54%.
[5]Not determined.
[6]CP was not reported, but calculated assuming $CP = N \times 6.25$.
[7]OM digestibility not reported, DM digestibility values used instead.

Table 2 Descriptive summary of the studies used to determine the effect of maize silage quality on methane (CH_4) emissions

Study	Ruminant type	CH_4 measurement technique[1]	F:C[2]	Feed allowance	Treatment	Silage characteristics (g/kg DM, unless stated otherwise): DM (g/kg)	OM	CP	NDF	Starch	OM digestibility (%)	DMI (kg/day)	CH_4 emissions[3]: Production	Yield	Energy
1. Cammell *et al.* [10]	Dairy cattle	RC	56:44[4]	Ad libitum	23% DM	226	n.d.[5]	84	512	180	72.1	19.3	413	21.4	6.1
					28% DM	278	n.d.	76	436	263	71.2	20.0	395	19.8	5.7
					33% DM	319	n.d.	68	406	327	72.0	20.4	413	20.2	5.8
					38% DM	357	n.d.	66	413	401	71.5	20.2	413	20.5	5.9
2. Hatew *et al.* [11]	Dairy cattle	RC	80:20	Restricted	25% DM	283	961	83	407	275	72.5	18.0	390	21.7	6.3
					28% DM	292	963	83	394	305	73.7	17.5	400	23.0	6.7
					32% DM	318	963	80	359	356	71.2	18.5	386	21.0	6.3
					40% DM	396	965	79	349	385	69.0	18.0	361	20.1	6.0
3. McGeough *et al.* [4]	Beef cattle	SF_6	77:23[6]	Ad libitum	27.7% DM	277	964	88	485	315	70.8	10.9	301	29.4	8.4
					31.5% DM	315	964	89	447	362	72.6	12.0	304	25.8	7.7
					33.9% DM	339	967	92	437	381	73.6	11.1	301	27.7	8.1
					33.3% DM	333	966	93	434	386	71.8	11.1	284	26.2	7.3

[1] Respiratory chambers (RC) or SF_6-tracer technique (SF_6).
[2] Forage to concentrate ratio (DM basis).
[3] Methane production in g/day; methane yield in g/kg of DMI; methane energy as % of GEI.
[4] Forage was fed ad libitum, always supplemented with 8.7 kg concentrate DM/day. This resulted in the forage content in the diet ranging from 55 to 57%.
[5] Not determined.
[6] Forage was fed ad libitum, always supplemented with 2.57 kg concentrate DM/day. This resulted in the forage content in the diet ranging from 76 to 79%.

digestibility of grass silage, because OM digestibility is negatively associated with growth and regrowth length of grass, and consequently the ratio stem to leaves of the grass harvested for ensiling. This appears to be valid for the studies used in the current meta-analysis as well; a decrease of 13 g NDF/kg of DM ($P < 0.001$) was accompanied by a 1% increase in OM digestibility. It is generally accepted that the fermentation of NDF favours the production of acetate in the rumen, which enhances hydrogen availability and activity of rumen methanogens [28, 29] and subsequently enteric CH_4 production. The negative association found in the current study between CH_4 yield and CP content is in agreement with Ellis *et al.* [30]. According to Bannink *et al.* [31], for each unit rumen-fermented protein a smaller amount of enteric CH_4 is produced compared with each unit of rumen-fermented sugar and fibre. This also appears to be valid in the current meta-analysis, where the increase in CP content (at the expense of the content of sugar and fibre) was positively associated with the OM digestibility of grass silage (i.e. an increase of 14 g CP/kg of DM [$P = 0.003$] was accompanied by a 1% increase in OM digestibility) and negatively associated with CH_4 yield. However, with increased OM digestibility of grass silage, an increase in CP content is often associated with a decrease in NDF content. The association between CP content and CH_4 yield may therefore be partially explained by the accompanied change in NDF content.

Overall, the results clearly indicate that increased grass silage quality (reflected in particular by increased OM digestibility and decreased NDF content) consistently decreases CH_4 yield, and may be a potent enteric CH_4 mitigation strategy. Only dairy cattle studies were included in the current analysis though. Similar research has been performed for beef cattle and sheep as well, but such studies [32, 33] included grass herbage rather than grass silage.

Maize silage quality

For maize silage quality, NDF content (g/kg DM; $P = 0.042$, $R^2 = 0.60$) was positively associated with CH_4 yield (Table 4 and visualized in Figure 2). CP content (g/kg DM; $P = 0.337$, regression not shown), starch content (g/kg DM) and OM digestibility (%) were not significantly associated with CH_4 yield ($P > 0.179$, see Table 4 for latter two regressions). The positive association between NDF content and CH_4 yield is according to expectations, assuming that the fermentation of NDF favours the production of acetate in the rumen, which enhances hydrogen availability and activity of rumen methanogens [28, 29]. Generally, when maize silage quality increases, NDF content decreases and starch content increases. This appears to be valid for the studies used in the current meta-analysis as well; an increase of 2 g starch/kg of DM ($P < 0.001$) was accompanied by a 1 g/kg of DM decrease in NDF content. Subsequently, ruminal fermentation shifts from NDF to starch as well.

Table 3 Descriptive summary of the studies used to determine effect of replacing grass silage or alfalfa silage with maize silage on methane (CH_4) emissions

							Diet composition (g/kg DM)						CH_4 emissions[4]		
Study	Ruminant type	CH_4 measurement technique[1]	F:C[2]	Feed allowance	Treatment[3]	Replacement level (%)	OM	CP	NDF	Starch	OM digestibility (%)	DMI (kg/day)	Production	Yield	Energy
1. Brask *et al.* [6]	Dairy cattle	RC	65:35	Ad libitum, control	100% early GS, 0% MS	0	908	209	304	43	76.4	17.6	386	20.8	6.4
					100% late GS, 0% MS	0	922	180	407	43	72.2	16.0	388	22.8	6.9
					0% early/late GS, 100% MS	100	948	164	355	141	71.3	17.6	354	19.0	5.6
2. Brask *et al.* [6]	Dairy cattle	RC	65:35	Ad libitum, fat supplementation	100% early GS, 0% MS	0	915	204	299	44	77.2	17.3	339	19.5	5.8
					100% late GS, 0% MS	0	924	178	391	44	70.4	16.1	362	22.2	6.5
					0% early/late GS, 100% MS	100	949	155	337	137	70.8	16.8	326	18.1	5.2
3. Doreau *et al.* [12]	Dairy cattle	SF_6	45:55	Restricted, beet pulp	100% GS, 0% MS	0	923	168	437	118	75.9	18.1	366	20.1	6.4
					0% GS, 100% MS	100	948	154	341	274	73.7	17.7	310	17.8	5.6
4. Doreau *et al.* [12]	Dairy cattle	SF_6	45:55	Restricted, dehydrated lucerne	100% GS, 0% MS	0	895	144	465	118	70.2	17.8	332	18.7	5.9
					0% GS, 100% MS	100	915	144	371	266	66.8	18.2	307	17.0	5.4
5. Van Gastelen *et al.* [13]	Dairy cattle	RC	80:20	Restricted	100% GS, 0% MS	0	924	192	431	5	n.d.[5]	16.2	399	24.6	7.0
					67% GS, 33% MS	33	931	182	396	91	n.d.	16.7	414	25.0	7.2
					33% GS, 67% MS	67	938	172	360	177	n.d.	16.6	411	24.5	7.1
					0% GS, 100% MS	100	945	163	325	262	n.d.	17.5	387	22.0	6.5
6. Günal *et al.* [14]	Dairy cattle	RC	74:16[6]	Ad libitum	100% GS, 0% MS	0	891	160	437	3	79.4	13.4	346	26.0	7.3
					0% GS, 100% MS	100	949	167	396	214	72.0	17.7	435	24.6	6.9
7. Staerfl *et al.* [15]	Beef cattle	RC	57:43[7]	Ad libitum, 5 months	100% GS, 0% MS	0	903	187	403	n.d.	n.d.	4.0	59	14.6	4.4
					0% GS, 100% MS	100	944	165	286	n.d.	n.d.	3.6	54	15.2	4.6
8. Staerfl *et al.* [15]	Beef cattle	RC	74:26[8]	Ad libitum, 9 months	100% GS, 0% MS	0	895	177	425	n.d.	n.d.	8.3	137	16.7	5.3
					0% GS, 100% MS	100	947	138	283	n.d.	n.d.	7.0	106	15.1	4.6
9. Staerfl *et al.* [15]	Beef cattle	RC	73:27[9]	Ad libitum, 11 months	100% GS, 0% MS	0	887	190	407	n.d.	n.d.	8.5	140	16.6	5.1
					0% GS, 100% MS	100	940	128	341	n.d.	n.d.	7.2	137	19.0	5.7
10. Waldo *et al.* [16]	Dairy heifer	RC	100:0	Low daily gain (725 g/day)	100% AS, 0% MS	0	923	225	410	n.d.	68.8	6.9	156	22.6	n.d.
					0% AS, 100% MS	100	947	146	419	n.d.	72.9	6.3	171	27.0	n.d.
11. Waldo *et al.* [16]	Dairy heifer	RC	100:0	High daily gain (950 g/day)	100% AS, 0% MS	0	923	225	409	n.d.	68.9	7.3	156	21.2	n.d.
					0% AS, 100% MS	100	946	149	418	n.d.	73.6	6.9	180	22.1	n.d.
12. Hassanat *et al.* [17]	Dairy cattle	RC	60:40	Ad libitum	100% AS, 0% MS	0	917	168	307	170	71.0	21.7	440	20.3	5.9
					50% AS, 50% MS	50	928	162	297	228	71.9	23.3	483	20.7	6.1
					0% AS, 100% MS	100	942	156	286	300	72.9	24.6	434	17.7	5.3
13. Arndt *et al.* [18]	Dairy cattle	RC	55:45	Ad libitum	80% AS, 20% MS	20	936	180	281	240	73.2	26.5	683	25.7	7.8
					60% AS, 40% MS	40	942	175	279	265	73.7	26.6	729	27.5	8.3
					40% AS, 60% MS	60	948	170	276	280	72.2	26.5	743	28.1	8.5
					20% AS, 80% MS	80	955	166	273	296	71.4	26.3	697	26.6	8.0
14. Jonker *et al.* [5]	Sheep	RC	100:0	2% of body weight	100% AS, 0% MS	0	908	177	439	5	n.d.	1.1	20.2	18.3	5.4
					75% AS, 25% MS	25	929	140	422	127	n.d.	1.2	23.7	20.6	6.2
					50% AS, 50% MS	50	943	113	434	190	n.d.	1.1	26.3	23.3	7.0
					25% AS, 75% MS	75	956	115	424	284	n.d.	1.2	25.5	22.1	6.7
					0% AS, 100% MS	100	966	116	423	330	n.d.	1.1	22.3	21.0	6.4

[1]Respiratory chambers (RC) or SF_6-tracer technique (SF_6).
[2]Forage to concentrate ratio (DM basis).
[3]GS = grass silage, MS = maize silage and AS = alfalfa silage.
[4]Methane production in g/day; methane yield in g/kg of DMI; methane energy as % of GEI.
[5]Not determined.
[6]Forage was fed ad libitum, always supplemented with 5.5 kg concentrate per day. This resulted in the forage content in dietary DM ranging from 70 to 77%.
[7]Bulls received grass silage or maize silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg DM per bull per day during fattening. This resulted in the forage content in the dietary DM ranging from 56 to 60%.
[8]Bulls received grass silage or maize silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg DM per bull per day during fattening. This resulted in the forage content in the dietary DM ranging from 72 to 77%.
[9]Bulls received grass silage or maize silage ad libitum, but the daily amounts of concentrate increased from 1.6 to 2.2 kg DM per bull per day during fattening. This resulted in the forage content in the dietary DM ranging from 70 to 75%.

Table 4 Prediction equations developed for methane yield (g/kg DMI) based on grass silage quality characteristics, maize silage quality characteristics and silage replacement

Item	Intercept	SE	*P*-value	Slope	SE	*P*-value	R^2
Grass silage quality[1]							
OM digestibility (%)	35.4	3.53	<0.001	−0.188	0.0461	0.001	0.74
NDF content (g/kg DM)	14.3	2.33	<0.001	0.016	0.0046	0.004	0.44
CP content (g/kg DM)	25.4	1.35	<0.001	−0.023	0.0077	0.009	0.36
Maize silage quality[2]							
NDF content (g/kg DM)	13.3	4.49	0.098	0.023	0.0096	0.042	0.60
Starch content (g/kg DM)	26.0	3.01	0.013	−0.0088	0.00599	0.179	0.25
OM digestibility (%)	−0.3	21.72	0.989	0.326	0.3010	0.311	0.13
Replacement grass silage with maize silage[3]							
Starch content (g/kg DM)	22.8	1.20	<0.001	−0.013	0.0037	0.008	0.62
NDF content (g/kg DM)	14.1	2.64	<0.001	0.015	0.0064	0.043	0.34
Replacement level (%)	20.2	1.18	<0.001	−0.015	0.0059	0.030	0.33
Replacement alfalfa silage with maize silage[3]							
Starch content (g/kg DM)	21.0	2.50	0.014	0.0069	0.00560	0.256	0.18
Replacement level (%)	22.0	1.71	0.001	0.0147	0.01213	0.253	0.11
NDF content (g/kg DM)	24.8	9.30	0.076	−0.0059	0.02572	0.823	0.06

[1]Grass silage characteristics used for regression analysis.
[2]Maize silage characteristics used for regression analysis.
[3]Complete diet composition used for regression analysis.

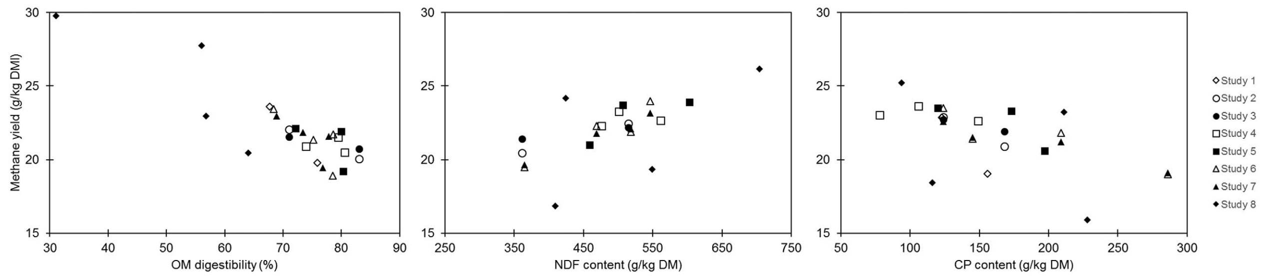

Figure 1. The relationship between methane yield (g/kg DMI) and grass silage quality characteristics; OM digestibility (%) in the left panel, NDF content (g/kg DM) in the middle panel and CP content (g/kg DM) in the right panel. Methane yield has been corrected for study effect. The different symbols identify the eight individual studies as described in Table 1.

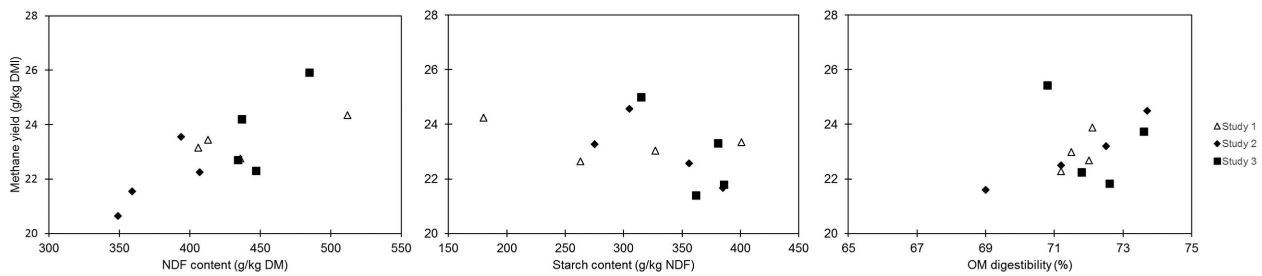

Figure 2. The relationship between methane yield (g/kg DMI) and maize silage quality characteristics; NDF content (g/kg DM) in the left panel, starch content (g/kg DM) in the middle panel and OM digestibility (%) in the right panel. Methane yield has been corrected for study effect. The different symbols identify the three individual studies as described in Table 2.

Fermentation of starch lowers ruminal pH and favours the production of propionate at the expense of acetate in the rumen [31], resulting in a decrease in enteric CH_4 emission. Besides, in contrast to NDF, starch not fermented in the rumen may be digested (rather than fermented) in the intestines, contributing to digestion of OM without any enteric CH_4 production. A shift in NDF and starch content is observed with increased maize silage quality in the studies used in the current meta-analysis. However, no significant association between starch content of maize silage and CH_4 yield is observed. This would suggest that the decrease in NDF content (and subsequent decrease in ruminal acetate) is more related to CH_4 yield than the increase in starch content (and subsequent increase in ruminal propionate or digestion in the small intestine). However, the decrease in NDF content (ranging from 51 g/kg DM in McGeough *et al.*

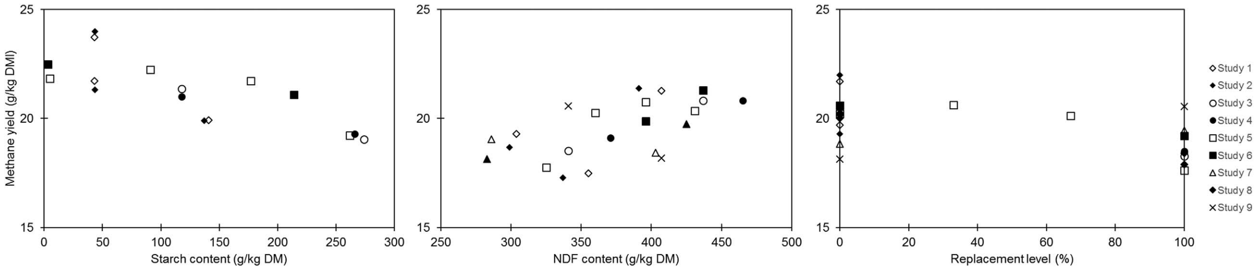

Figure 3. The relationship between methane yield (g/kg DMI) and characteristics reflecting replacement of grass silage with maize silage; starch content (g/kg DM) in the left panel, NDF content (g/kg DM) in the middle panel and replacement level (%) in the right panel. Methane yield has been corrected for study effect. The different symbols identify the nine individual studies as described in Table 3.

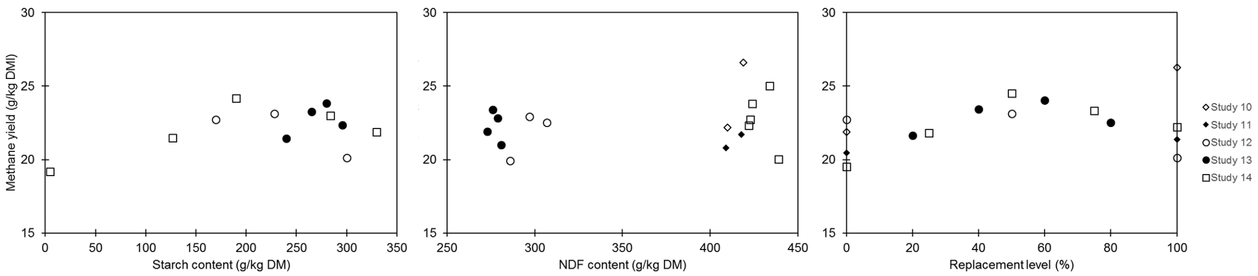

Figure 4. The relationship between methane yield (g/kg DMI) and characteristics reflecting replacement of alfalfa silage with maize silage; starch content (g/kg DM) in the left panel, NDF content (g/kg DM) in the middle panel and replacement level (%) in the right panel. Methane yield has been corrected for study effect. The different symbols identify the six individual studies as described in Table 3.

[4] to 106 g/kg DM in Cammell *et al.* [10]) is considerably smaller than the increase in starch content (ranging from 71 g/kg DM in McGeough *et al.* [4] to 221 g/kg DM in Cammell *et al.* [10]). This means that the change in CH_4 yield per unit change in starch content is substantially smaller than the change in CH_4 yield per unit change in NDF content. This, together with the limited number of studies included in the meta-analysis and the relatively large variation in the slope per study, may explain the absence of a significant relationship between starch content of maize silage and CH_4 yield. Similar to grass silage quality, the current analysis indicates that optimizing maize silage quality is a potent enteric CH_4 mitigation strategy.

Replacement with maize silage

There are in total 14 studies that investigated the effect of replacing grass silage or alfalfa silage with maize silage on enteric CH_4 emission (Table 3). In total, nine studies replaced grass silage and five studies replaced alfalfa silage. Initially, all studies were combined to evaluate the effect of replacing one of these two silages with maize silage on CH_4 yield. This resulted in no significant associations with silage characteristics, which may be related to the differences in nutritional characteristics among the different silage types (Table 3). For example, upon replacing grass silage with maize silage, CH_4 yield usually declined, with the exception of the studies using beef cattle of 5 month and 11 month old in Staerfl *et al.* [15]. When replacing alfalfa silage with maize silage, CH_4 yield generally increased, with the exception of Hassanat *et al.* [17]. When combining all studies, such variation in change in enteric CH_4 might be too large to obtain significant associations between silage characteristic parameters and CH_4 yield. Therefore, it was decided to separate the grass silage studies from the alfalfa studies.

Upon replacing grass silage with maize silage, both OM digestibility of the diet (%) and dietary CP content (g/kg DM) were not associated with CH_4 yield ($P > 0.192$), whereas both starch content (g/kg DM, $P = 0.008$, $R^2 = 0.62$) and silage replacement level (%; $P = 0.030$, $R^2 = 0.33$) were negatively associated with CH_4 yield, and NDF content (g/kg DM; $P = 0.043$, $R^2 = 0.34$) was positively associated with CH_4 yield. These relationships (Table 4) are visualized in Figure 3. Replacing fibre-rich grass silage with starch-rich maize silage results in a decrease in NDF content and increase in starch content of the diet. As stated above, fermentation of starch favours the ruminal production of propionate at the expense of acetate, reducing hydrogen availability and activity of rumen methanogens [28, 29]. This is confirmed by results of the current meta-analysis, with CH_4 yield being positively associated with the NDF content and negatively associated with the starch content of the complete diet. This shift from NDF to starch is also reflected by the replacement level (%). With a higher replacement level, more fibre-rich grass silage is replaced with starch-rich maize silage, resulting in a lower CH_4 yield.

No diet characteristic (i.e. starch content, replacement level and NDF content) was associated with CH_4 yield upon replacing alfalfa silage with maize silage ($P > 0.05$; Table 4 and Figure 4). This is in contrast to the results found for replacing grass silage with maize silage. There are several reasons to explain this difference. Firstly, alfalfa silage has a relatively high CP content. As mentioned previously, according to Bannink *et al.* [31], for each unit rumen-fermented protein less enteric CH_4 is produced compared with each unit of rumen-fermented sugar, starch or fibre. Secondly, alfalfa silage has a relatively low and relatively rapidly degradable NDF content which is comparable with that of highly digestible grass silage. A greater digestibility of grass silage is generally associated with a decrease in CH_4 yield (Table 4), which is closer to the generally lower CH_4 yield of maize silage. Overall, the results clearly indicate that replacing grass silage with maize silage consistently decreases CH_4 yield, and may be a potent enteric CH_4 mitigation strategy. In contrast, replacing alfalfa silage with maize silage does not appear to be an effective strategy to decrease CH_4 yield.

Conclusions

In conclusion, the current meta-analysis indicates that silage characteristics (i.e. silage chemical composition, digestibility and type of silage) are associated with enteric CH_4 emission from ruminants. Improved grass silage quality, reflected by an increased OM digestibility and a decreased NDF content, is associated with a lower CH_4 yield. Similarly, improved maize silage quality, reflected by a decreased NDF content, is associated with a lower CH_4 yield. Replacing grass silage with maize silage, reflected by an increased replacement level as well as by an increased starch content and decreased NDF content, is associated with a lower CH_4 yield. Replacement of alfalfa silage with maize silage could not consistently be associated with a change in CH_4 yield. Overall, the current meta-analysis indicates that management practices to improve silage quality are potent mitigation strategies to reduce the emission of enteric CH_4 per unit of feed fed to ruminants, and that the implications of silage quality have to be addressed when assessing greenhouse gas emissions in ruminant production systems.

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