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A data analysis on the effect of acetic acid on dry matter intake in dairy cattle

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ABSTRACT

Silage is the main source of acetic acid in ruminant diets. In most silages, acetic acid is the fermentation product with the second highest concentration, after lactic acid. As it inhibits yeasts and therefore improves aerobic stability of silages, moderate concentrations of up to 30 g/kg dry matter (DM) are often recommended. However, acetic acid may impair the DM intake (DMI) by ruminants, most probably due to its sensory characteristics. The objective of this data-analysis was to evaluate the effect of the dietary content of acetic acid on the DMI in dairy cattle. Either rations containing silages inoculated with heterofermentative *Lactobacillus buchneri* or rations treated with pure acetic acid were included in the dataset. Data analysis was performed with a mixed model, including random effects of experiment (intercept and slope) and fixed effects of acetic acid concentration (intercept, linear and quadratic terms). A broken-line regression showed the best goodness of fit (the lowest corrected Akaike's information criterion and the largest R^2-adj = 0.77). Per 100 kg body weight (BW), an increase of 1 g acetic acid/kg DM led to a reduction of 1.2 g in DMI for acetic acid concentrations < 17.3 g/kg DM. From 17.3–60 g acetic acid/kg DM, DMI reduction was 5.6 g for each additional g of acetic acid in DM (per 100 kg BW). Therefore, dairy nutritionists should consider the content of acetic acid in fermented ingredients upon balancing the diet, to avoid DMI depression (< 17 g/kg DM). Considering typical proportions of silage in diet, current recommendations for the upper limit of acetic acid in silages might, from the perspective of maximizing DMI, be too high and therefore warranting reconsideration.

1. Introduction

Silage is an important ingredient in ruminant diets. During silage fermentation numerous volatile organic compounds (VOC) are formed. Due to their chemical structure and sensory characteristics several VOC, alone or in combination, may influence feed intake and metabolism of ruminants (Dulphy and Van Os, 1996; Kristensen et al., 2013; Gerlach et al., 2018) and may also be transferred into

Abbreviations: AICc, corrected Akaike's information criterion; BW, body weight; cfu, colony-forming unit; DM, dry matter; DMI, dry matter intake; LAB, lactic acid bacteria; VOC, volatile organic compound.

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their products (e.g., meat or milk) (Kalač, 2011). Different carboxylic acids are produced during silage fermentation with lactic acid being the most dominant and desired fermentation product as it efficiently reduces silage pH accompanied with only minimal dry matter (DM) and energy losses (McDonald et al., 1991). In most silages, acetic acid is the fermentation product with the second highest concentrations (Hafner et al., 2013; Kung et al., 2018). It is mainly produced by heterofermentative lactic acid bacteria (LAB), but can also be formed by enterobacteria, *Clostridium* spp., *Bacilluss* spp. and propionic acid bacteria under anaerobic conditions and by *Acetobacter* species and homofermentative LAB under the presence of oxygen (McDonald et al., 1991). The type of LAB and the type of substrates available in the feed do have an influence on the produced amount of acetic acid and therefore, especially in cases where fermentation relies on epiphytic microorganisms, the final acetic acid concentration in silages is hardly predictable (Mogodiniyai Kasmaei et al., 2013). Facultative heterofermentative LAB ferment hexoses almost exclusively to lactic acid but additionally, they are able to ferment pentoses to lactic and acetic acids using an inducible phosphoketolase (McDonald et al., 1991). Obligate heterofermenters ferment hexoses to lactic acid, acetic acid, ethanol and carbon dioxide (McDonald et al., 1991). Feed characteristics such as high moisture and buffering capacity, management problems such as low density and delayed sealing, and high environmental temperature often stimulate acetic acid formation in silage (Wang and Nishino, 2013; Kung et al., 2018).

A certain amount of acetic acid is desirable in silage, in order to minimize growth of yeasts and moulds during aerobic exposure (Wilkinson and Davies, 2013) such that target values of 10−30 g acetic acid/kg silage DM are often recommended (Bundesarbeitskreis Futterkonservierung, 2012; Kung et al., 2018). The obtained improvement in aerobic stability is the reason for inoculation of silages with obligate heterofermentative LAB (e.g., *Lactobacillus buchneri*). Driehuis et al. (2001) reported that inoculation with *L. buchneri* improves aerobic stability of silages by reducing growth and survival of yeasts during both the storage and the feed-out period. This can be mainly attributed to the ability of *L. buchneri* for anaerobic degradation of lactic acid to acetic acid and 1,2-propanediol (Oude Elferink et al., 2001).

Nevertheless, the effect of acetic acid in silages on feed intake remains debatable. Many studies found that high concentrations of acetic acid in ruminant diets have been associated with lower feed intake (e.g., Wilkins et al., 1971; Demarquilly et al., 1973; Huhtanen et al., 2002; Krizsan and Randby, 2007). A meta-analysis conducted by Eisner et al. (2006) showed that the concentration of acetic acid was closely and negatively related with silage intake. However, in wet silages or in silages with high buffering capacity, the negative effect of acetic acid on feed intake can be confounded with other compounds formed by a poor fermentation and not be caused by the content of acetic acid itself. Consequently, when investigating the effect of acetic acid on intake by ruminants it can be helpful to focus on forages where formation of acetic acid took place without remarkable changes in concentration of other fermentation products or proximal constituents. In silages inoculated with heterofermentative LAB or in diets treated with pure acetic acid (experimental conditions), the increase in acetic acid concentration occurs independently of a significant change in composition of proximate constituents, protein value or fibre fractions and without the concomitant production of undesirable compounds with hypophagic effects (e.g., proteolysis end products). Therefore, the objective of this meta-analysis was to evaluate the effect of the dietary content of acetic acid on DM intake (DMI) in dairy cattle fed rations containing silages that had been treated with *L. buchneri* or in cases where pure acetic acid was added to the ration.

2. Materials and methods

The database for the data analysis was created with publications that addressed the effects of acetic acid on DMI by dairy cattle

Table 1
Details of studies used for the data analysis to evaluate the effect of dietary acetic acid concentration on dry matter (DM) intake by ruminants.

Reference	Animal category	Range of diet DM content (g/kg)	Main source of acetic acid	Range of acetic acid in diet (g/kg DM)
Senel and Owen (1967)	Guernsey and Jersey cows (~ 17 kg/d of milk)	Not reported	Acetic acid supplementation	0 to 20
Dinius et al. (1968)	Holstein and Red Danish heifers	Not reported	Acetic acid supplementation	0 to 60
Driehuis et al. (1999)	Holstein-Friesian × Dutch-Friesian cows (~39 kg/d of milk)	Not reported	Maize silage treated with *L. buchneri* (1×10^5 cfu/g)	9.8 to 12
Taylor et al. (2002)	Holstein cows (~ 26 kg/d of milk)	490 to 521	Barley silage treated with *L. buchneri* (4×10^5 cfu/g)	18 to 24.7
Kendall et al. (2002)	Holstein cows (~ 31 kg/d of milk)	Not reported	Maize grain silage treated with *L. buchneri* (5×10^5 cfu/g)	10–11.2
Kung et al. (2003)	Holstein cows (~ 40 kg/d of milk)	566 to 596	Lucerne silage treated with *L. buchneri* (4×10^5 cfu/g)	13.3 to 20.7
Arriola et al. (2011)	Holstein cows (~ 32 kg/d of milk)	654 to 662	Maize silage treated with *L. buchneri* (4×10^5 cfu/g)	7.1 to 9.0
Kleinshmitt et al. (2013)	Holstein cows (~ 34 kg/d of milk)	443 to 448	Maize silage treated with *L. buchneri* (1 or 5 or 10×10^5 cfu/g)	17.3 to 26.9
Daniel et al. (2013)	Holstein cows (~ 36 kg/d of milk)	768 to 801	Acetic acid supplementation	0 to 42.6
Silva et al. (2017)	Holstein cows (~ 32 kg/d of milk)	432 to 433	Maize silage treated with *L. buchneri* (1×10^5 cfu/g)	6.9 to 7.3

cfu: colony-forming units.

(cows and heifers). Our literature search used Google Scholar, PubMed, ScienceDirect, Scirus, CAB, investigation of references listed in papers and contact with other researchers. The search included the following keywords and their combinations: acetic acid, silage, intake, dairy, cow and heifer. Data were collected from publications where whole-crop silages from maize, lucerne or barley or high moisture maize silage were treated with *L. buchneri* or pure acetic acid was added to the ration. Data from trials with sugarcane silage inoculated with heterofermentative bacteria was not included in the dataset, since in that silage the inoculant changes the proximal composition significantly by preserving soluble sugars (Ávila et al., 2009; Daniel et al., 2015). The final dataset included seven full articles published in peer reviewed journals (six manuscripts with cows and one enrolling heifers) and three abstracts (all with cows) reported in proceedings of international events with scientific board, totalling 33 observations. Details of the used studies including animal category, main source of acetic acid in diet and range of acetic acid in diet are summarized in Table 1. The DMI is expressed as proportion of body weight (BW, kg/100 kg BW) to standardize this measurement across animal categories (i.e., cows and heifers). In Driehuis et al. (1999), the concentration of acetic acid in grass silage (second forage source) was not stated and then assumed to be 15.9 g/kg DM (Ward, 2000; grass silage with 340−360 g/kg DM). In Kung et al. (2003), the concentration of acetic acid in maize silage (second forage source) was not reported and then assumed to be 23.6 g/kg DM (Ward, 2000; maize silage with 360−400 g/kg DM). In four studies with lactating Holstein cows (Driehuis et al., 1999; Kendall et al., 2002; Taylor et al., 2002; Kung et al., 2003), BW was not reported and assumed to be 600 kg. Since the same BW was assumed for all treatments within a given study and the statistical model included a random study effect, it did not change the appraisal results.

Data analysis was performed with the MIXED procedure of SAS. The model included random effects of experiment (intercept and slope) and fixed effect of acetic acid concentration (intercept, linear and quadratic terms). Data adjusted for a random effect of experiment were also fitted with a broken-line regression with two linear segments, using the NLMIXED procedure of SAS (Robbins et al., 2006). In all models, the covariance structure was defined as unstructured (UN). Because experimental designs and accuracy varied across studies, observations were weighted by the number of experimental units using the Weight statement (St-Pierre, 2001; Sauvant et al., 2008). Model adjustments were assessed by the corrected-Akaike's information criterion (AICc; smaller is better) and adjusted-R^2 (larger is better).

3. Results

Dietary content of acetic acid ranged from 0 to 60 g/kg DM, where the highest level was achieved by adding acetic acid to the ration. The dataset was broad, representative and covered a large part of the practical range of acetic acid concentration in dairy diets, for both lactating cows and growing heifers.

The quadratic effect of acetic acid on DMI was not significant ($P = 0.57$). Although the linear model had a reasonable adjustment (AICc = -94.0, R^2-adj = 0.67, $P < 0.01$), a broken-line regression, with two linear segments, showed better goodness of fit (AICc = -102.1, R^2-adj = 0.77, $P < 0.01$). Per 100 kg BW, an increase of 1 g acetic acid/kg DM led to a reduction of 1.2 g in DMI for acetic acid concentrations < 17.3 g/kg DM. From 17.3–60 g acetic acid/kg DM, reduction was 5.6 g in DMI for each additional g of acetic acid in dietary DM (per 100 kg BW). For instance, increasing acetic acid from 10 to 30 g/kg DM will reduce DMI in a 600-kg cow by 0.48 kg/d. The effect of dietary acetic acid concentration on DMI is shown graphically in Fig. 1.

4. Discussion

Acetic acid is a natural and significant fermentation end product in silages. Typical concentrations of acetic acid in silages vary from < 5–30 g/kg DM (Kung et al., 2018), but sometimes silages present higher levels of acetic acid (> 40−60 g/kg DM), especially after the inoculation with heterofermentative LAB. Kleinschmit and Kung (2006) conducted a meta-analysis to evaluate the effect of inoculation with heterofermentative LAB on fermentation products and DM losses. Untreated maize silages contained 21.8 g acetic acid/kg DM and

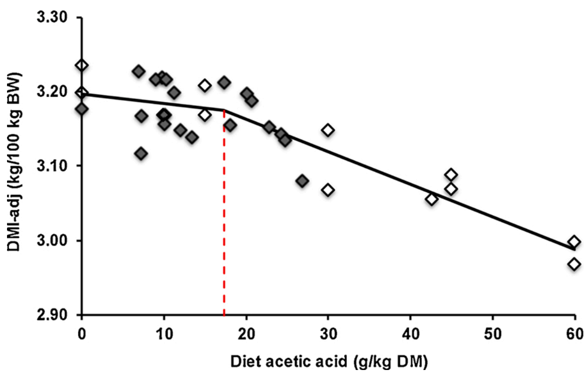

Fig. 1. Relationship between dietary content of acetic acid (g/kg dry matter (DM)) and DM intake (DMI) (kg/100 kg body weight (BW)) in dairy cattle (cows and heifers), adjusted with a random effect of study. If acetic acid < 17.3, then DMI = 3.20 – 0.0012 × acetic acid, else DMI = (3.20 – 0.0012 × acetic acid) – 0.0044 × (acetic acid – 17.3). Open diamonds: acetic acid was added onto the ration. Closed diamonds: silage was inoculated with *L. buchneri*.

the inoculation with *L. buchneri* significantly increased acetic acid concentrations to 26.3 g/kg DM (application rates < 100,000 colony-forming units (cfu)/g) and 38.9 g/kg DM (application rates > 100,000 cfu/g). A recent meta-analysis examining LAB inoculants for maize silage (Bernardi et al., 2019) reported acetic acid concentrations up to 68.2 g/kg DM. Especially in low DM silages, inoculation with heterofermentative LAB can lead to significantly increased acetic acid concentrations. This was shown by Gomes et al. (2019) with increased acetic acid concentrations of 69.7 and 44.4 g/kg DM in unwilted and wilted oat silages inoculated with *L. buchneri* compared to 15.1 and 14.3 g/kg DM in untreated control silages. Also without inoculation, increased acetic acid concentrations were reported, e.g. in low DM, soil contaminated red clover and lucerne silages (42 g/kg DM and 62 g acetic acid/kg DM, respectively; Scherer et al., 2019). The formation of acetic acid is typically associated with higher DM losses than lactic acid fermentation but due to the increased aerobic stability this is often accepted to avoid even higher losses caused by aerobic deterioration of the silages during the feed-out period (Holzer et al., 2003; Gerlach et al., 2013). Fermentation by heterofermentative LAB results in variable losses, depending on the substrate and pathway, with theoretical values of 5% and 24 % for fermentation of glucose and fructose, respectively (Alderman et al., 1971). The meta-analysis by Kleinschmit and Kung (2006) showed that the higher application rate drastically improved aerobic stability (number of hours before a 1–2 °C rise in temperature) from 25 h (untreated) and 35 h (application rates < 100,000 cfu/g) to 503 h. Concurrently, there was an only moderate increase in DM losses occurring during fermentation (4.5, 4.5 and 5.5 % of DM, respectively). However, Bernardi et al. (2019) showed that inoculation of maize silages with heterofermentative LAB resulted in higher DM losses in farm-scale silos as compared with that in laboratory silos (+56.6 vs. + 9.3 g/kg DM compared to the control). In their review, Holzer et al. (2003) stated that in some cases the amount of carbon dioxide formed by heterofermentative LAB might be negligible in comparison to that produced by aerobic spoilage microorganisms like yeasts and moulds. This was, for example shown by Weinberg et al. (2002) where inoculation of whole-crop wheat silages with heterofermentative LAB led to reduced DM losses during fermentation (under high ambient temperatures of 25−27 °C) in comparison to homofermentative LAB. In low DM oat silages, the use of *L. buchneri* caused significantly increased acetic acid concentrations and fermentation losses and can therefore not be recommended (Gomes et al., 2019). To avoid excessive formation of acetic acid in combination with increased DM losses during fermentation, the use of heterofermenters may only be advantageous for high DM silages.

Increased concentrations of acetic acid have shown to negatively affect feed acceptance by ruminants such that some extension recommendations propose an upper limit of 30 g acetic acid/kg DM for dairy and beef cattle rations to avoid negative effects on total DMI (Bundesarbeitskreis Futterkonservierung, 2012). Though, Eisner et al. (2006) showed that already at lower concentrations of acetic acid, feed intake of dairy cows might be impaired. In their meta-analysis, an increase of 1 g acetic acid/kg DM led to a reduction of 81 g DM in silage intake and when analysing wilted grass silages only, reduction was 129 g DM for each additional g of acetic acid in DM. In our meta-analysis, DM content did not vary significantly within a given study, because the treatments were 1) addition of acetic acid or 2) inoculation with heterolactic LAB, on a same crop or diet. Moreover, a random effect of study was included in the statistical model. Therefore, the effect of diet DM was controlled in our meta-analysis. Yet, in our dataset the effect of acetic acid was not confounded with malfermentation.

Also in goats, acetic acid (9−17 g/kg DM) decreased preference for maize silages offered pairwise (Gerlach et al., 2013, correlation coefficient -0.73, $P < 0.05$) and in sheep, concentrations of acetic acid (0, 22, 44, 66 and 88 g/kg DM) were responsible for a linear decrease in DMI (Buchanan-Smith, 1990). Gherardi and Black (1991) investigated the effect of different chemical compounds on the palatability of wheaten hay in short-term preference tests where sheep simultaneously were offered treated and untreated hay. They identified acetic acid as one of two compounds that significantly decreased the preference for the offered forages, already in as low concentrations as 5 g/kg hay. Addition of acetic acid to wilted grass silages reduced silage DMI by growing steers, the reduction, however, equalled the amount provided by the added substances such that total DMI remained unaffected (Krizsan et al., 2012). Based on their results authors defined an upper limit of 54 g/kg DM of acetic acid in silage to avoid negative influence on silage intake. Miettinen et al. (1991) evaluated data from Finnish dairy farms and tried to identify intake reducing substances in silages (wet grass silages preserved with formic acid). Besides low pH as most common individual factor acetic acid also reduced intake when exceeding concentrations of 20 g/kg DM. This limit is close to the results obtained in the present data analysis which showed that with acetic acid concentrations in rations up to 17.3 g/kg DM, DMI of cows and heifers was slightly depressed, and with concentrations from 17.3–60 g/kg DM, intake was markedly impaired. For instance, increasing acetic acid from 10 to 30 g/kg DM will reduce DMI in a 600-kg cow by 0.48 kg/d. Assuming a feed efficiency of 1.5 (milk/DMI) such depression in DMI would represent a loss of 0.72 kg of milk per cow per day.

As discussed before, especially low DM silages and silages inoculated with heterofermenters can contain increased acetic acid concentrations (> 40 g/kg DM). Using those silages as main ingredients in (forage-based) total-mixed rations can therefore easily lead to diets with acetic acid concentrations > 17.3 g/kg DM and consequently, to reduced dietary intake potential.

The DMI and feed preference by ruminants are affected by the chemical composition of the feedstuff (including sensory characteristics like taste and smell) and the post-ingestive feedback the animal receives (Provenza, 1995). For the case of silages with elevated concentrations of acetic acid it is not yet clarified whether the intake reducing effect relies mainly on sensory or physiological aspects. Frederiksen and Ochia (1970) reported that acetic acid supplementation above 400 mL/d made the ration very unpalatable for lactating dairy cows, probably because of its pungent smell. Brown and Radcliffe (1972) assumed that digestive processes might not be affected by increased acetic acid concentrations such that reduced palatability due to the sensory characteristics of acetic acid seems to be the main triggering factor. For instance, considering the theoretical yield of acetate in the rumen from a dairy ration (approximately 3.5 mol/kg DMI; Resende et al., 2006), the level of acetic acid at the breakpoint found in the current data analysis (17.3 g/kg DM) would represent only 8% of the acetate absorbed daily, which is expectedly within the daily variation in acetic acid flux from the rumen.

Buchanan-Smith (1990) used sham-fed animals equipped with oesophageal fistulae to remove forages after ingestion. He aimed to to separate ingestive factors involving palatability from post-ingestive factors responsible for forage intake being depressed by ensiling. From a great number of silage fermentation products, acetic acid was identified as a product causing reduced palatability. This was a result of the product itself rather than acidity in general, since the same level of total acids in a combination of lactic and acetic acids (1.5:1) did not depress intake (Buchanan-Smith, 1990). Anil et al. (1993) and Mbanya et al. (1993) used intraruminal infusion of sodium acetate and studied the effect on voluntary intake of hay and silage. When given in physiological amounts, sodium acetate did not influence DMI by rumen-fistulated lactating dairy cows. Therefore, it is possible that elevation of acetic acid in forages decreased feed intake through an effect on palatability. Only few authors mentioned physiological aspects as intake-regulating factors after ingestion of acetic acid. An elevated osmotic pressure of the ruminal content after intraruminal infusion of sodium acetate was discussed (Forbes et al., 1992) but not pursued further. Chiofalo et al. (1992) suggested a direct action on chemical receptors, but also discussed the possibility that end products of silage fermentation may elicit a signal which does not permit the rumen to fill to the same level as with hay. Also Dulphy and Van Os (1996) summarized from literature that the detection of high acetic acid concentrations by the chemo-receptors in the rumen may limit intake such that especially with high intakes rates, acetic acid may act negatively on DMI during meals. However, changes in eating pattern reported in studies where pure acetic acid was supplied (Hutchinson and Wilkins, 1971; Daniel et al., 2013) suggest a negative effect of acetic acid on DMI mainly through sensory characteristics.

The negative effects of acetic acid found in different studies may not always be due to acetic acid alone. Some authors rather claim that the overall silage quality will also play a role. For example, high acetic acid contents often correlate with sub-optimal fermentation quality, which in turn can have a negative effect on feed intake (Driehuis et al., 2001). Also Dulphy and Van Os (1996) mentioned the complexity of silage studies with possible cumulative effects of single products that impede interpretation of results. This can be neglected for the current analysis as only silages where acetic acid arose from addition of heterofermentative LAB or pure acetic acid were considered. Therefore, a reduction in DMI may be observed in silages with elevated acetic acid concentrations without any signs of malfermentation or protein degradation. In consequence, the negative effect of silage acetic acid on DMI will depend on the concentration of acetic acid in silage and the proportion of silage in the ration. Current recommendations for the upper limit of acetic acid in ruminant rations might, from the perspective of maximizing DMI, still be too high and therefore warranting reconsideration. Dairy nutritionists should consider the content of acetic acid in fermented ingredients upon balancing the diet, to avoid DMI depression. However, it has to be considered that reductions in feed acceptance due to aerobically spoiled silages can be high (e.g., Whitlock et al., 2000; Gerlach et al., 2013; Brüning et al., 2018) and exceed losses in DMI due to elevated acetic acid concentrations. Nevertheless, results of the present study show that acetic acid in silages can reduce the voluntary feed intake such that maximum productivity cannot be reached. With good silage management that avoids aerobic deterioration (high compaction, high feed-out rate) farmers should aim to produce silages with low acetic acid concentrations as it affects DMI in ruminants negatively, especially at higher concentrations.

5. Conclusions

Although a higher content of acetic acid will protect the silage and total mixed ration against aerobic deterioration, dairy nutritionists should consider the content of acetic acid in fermented ingredients upon balancing the diet (maximum of 17 g/kg of diet DM), to avoid its negative effect on feed intake. Reliable and rapid methods are needed for determination of acetic acid concentrations also under commercial conditions.

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CRediT authorship contribution statement

Katrin Gerlach: Methodology, Visualization, Writing - original draft, Writing - review & editing. **João Luiz Pratti Daniel:** Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing - review & editing. **Clóves Cabreira Jobim:** Conceptualization, Methodology, Visualization. **Luiz Gustavo Nussio:** Conceptualization, Methodology, Visualization.

Declaration of Competing Interest

The authors report no declarations of interest.

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