Role of K on Rumen Fermentation and Milk Fat Synthesis

Thomas C. Jenkins[1], Preston H. Morris[1], and Elliot Block[2]
[1]Department of Animal & Veterinary Sciences, Clemson University, Clemson, SC
[2]Arm & Hammer Animal Nutrition, Church and Dwight Co., Inc., Princeton, NJ

Introduction

Diet-induced milk fat depression (**MFD**) continues to have major economic impact in the dairy industry and a priority for finding solutions. Current thinking links MFD with the formation of bioactive *trans* fatty acid intermediates produced from biohydrogenation of unsaturated fatty acids by the rumen microbial population. The most potent biohydrogenation intermediates linked to MFD include several conjugated linoleic acid (**CLA**) isomers. Formation of these CLA isomers has been associated with several dietary risk factors including source and amount of grain, source and amount of fat, fiber source, and animal management factors. Solutions to solving MFD are complicated by interactions that often exist among two or more risk factors, making the process of reversing MFD often times slow and frustrating. Ideas and discussion has turned to the possibility of dietary supplements that might reverse accumulation of the undesirable CLA that are linked to MFD and speed return of milk fat % back to normal. Recent studies with lactating cows showed improvement in milk fat percentage following addition of K supplements to the diet, suggesting that K might act as a biohydrogenation normalizer. Results from several continuous culture experiments will be reviewed briefly to examine the role of K in influencing CLA formation and their possible role in alleviating MFD.

Effects of K on Milk Fat Synthesis

A study completed at the University of Georgia (Wildman et al. 2007) compared the effects of two levels of dietary cation-anion difference (**DCAD**) each at two different crude protein percentages on lactation performance. The two DCAD values were 25 and 50 mEq/100 g of diet DM and were adjusted using sodium bicarbonate at 0.97 and potassium carbonate at 0.97 percent of the diet DM. The two protein concentrations were 15% and 17%. Cows that were consuming the diet with increased DCAD showed a greater ($P< 0.05$) milk fat percentage than the cows in the low DCAD diet (2.92 vs. 2.44%). Increases in DM intake, yields of milk, energy-corrected milk, and milk fat, and milk fat percent were also observed. Recent research comparing alfalfa-corn silage diets with corn silage alone diets supplemented with potassium carbonate and calcium carbonate was completed at the University of Maryland (Erdman et al., 2011). In this study the diet supplemented with the extra minerals were meant to resemble the K and Ca values found in alfalfa. The alfalfa hay-corn silage diet tended ($P < 0.08$) to increase yields of milk fat yield (from 1,389 to 1,547 g/day) and fat-corrected milk (from 37.0 to 41.4 kg/d). The DCAD supplemented diet had increased ($P = 0.01$) feed efficiency 1.76

[1] Contact at: Clemson University, Department of Animal and Veterinary Sciences, Clemson, SC 29634; Phone: 864-656-2707; Email: tjnkns@clemson.edu

vs. 1.94, but DCAD had no effect on DM intake, milk yield, or fat percentage. In a study by Hu et al. (2007), the author assigned cow to three diets varying in DCAD (-3, 22, and 47 mEq/100 g) with two levels of crude protein (16 and 19%). The DCAD levels were adjusted with calcium chloride, sodium bicarbonate, and potassium carbonate. There was a positive linear ($P < 0.05$) response on DM intake, 4% fat-corrected milk yield, milk fat %, and milk fat yield with increasing dietary DCAD. Milk yield was not significantly different between the treatments.

Because most studies evaluating DCAD fed a combination of mineral supplements, it is difficult to isolate the effects of K. A few studies examined the effects of K supplementation alone on lactation performance, but the impacts on milk fat % were variable. Holstein cows past the peak of lactation were fed 0.45, 0.55, and 0.66% of diet DM as KCl with no reported effects on milk yield, milk fat, or solids-not-fat content (Dennis et al. 1975). However, alternative K sources added at higher concentrations in the diet showed positive results. Cows fed 1.2% K_2CO_3 had greater ($P< 0.05$) milk fat % than cows fed 1.5% $NaHCO_3$ during the first half of a 7-week study, and produced milk with greater fat % than cows fed the control diet during the last half of the study. A recent study completed at Washington State University (Harrison et al. 2012), additional dietary K fed as potassium carbonate sesquihydrate in the form of DCAD Plus (Church & Dwight Co., Inc.) increased dietary K from 1.3 to 2.1% of diet DM from weeks 3 to 12 of lactation. The authors observed an increase in milk fat % from 3.8 to 4.3%. Cows fed potassium carbonate sesquihydrate also had increased DM intake, yields of milk and energy-corrected milk, and efficiency of milk production per unit of DM intake.

The Cause of Milk Fat Depression

The biohydrogenation theory links MFD with the formation of specific CLA isomers produced from the biohydrogenation of dietary polyunsaturated fatty acids. Formation of the CLA isomers causing MFD has been associated with several dietary risk factors including excessive fat intake, high grain diets, and low rumen pH. Solutions to solving MFD are complicated by interactions that often exist among two or more risk factors, making the process of reversing MFD often times slow and frustrating.

The CLA are produced as intermediates from the process of lipid biohydrogenation by the microbial population in the rumen. Substrates for biohydrogenation include both linoleic and linolenic acids (Figure 1, Lee and Jenkins 2011a,b) that are found in nearly all plant-based components of dairy diets. Biohydrogenation of linoleic acid begins with its conversion to CLA where the number of double bonds remains the same but one of the double bonds is shifted to a new position by microbial enzymes (Jenkins et al., 2008). Normally, the double bonds in linoleic acid are separated by two single bonds, but in CLA, the double bonds are only separated by one single bond. Many types of CLA are produced in the rumen of dairy cows, but a common CLA produced from biohydrogenation of linoleic acid is cis-9, *trans*-11 C18:2.

As biohydrogenation progresses, double bonds in the CLA intermediates are then hydrogenated further to *trans* fatty acids having only one double bond. A final

hydrogenation step by the ruminal microbes eliminates the last double bond yielding stearic acid (Figure 2) as the final end product. The *Trans* double bonds only differ from the *cis* double bonds in the placement of the hydrogen ions (Figure 3). The hydrogen ions are shown on opposite sides of the double bond for *trans* fatty acids, but on the same side of the double bond for *cis* fatty acids. Although the difference in structure between *trans* and *cis* fatty acids appears small, it causes significant differences in their physical and metabolic properties.

Changes in the ruminal environment initiated through the diet can lead to a microbial population shift that is accompanied by a change in the type of CLA produced (Figure 4). For example, low rumen pH can be a key factor contributing to a microbial shift and changes in the type of CLA produced. Dropping pH in continuous cultures of mixed ruminal microorganisms caused an increase ($P < 0.05$) in the concentration of *trans*-10, *cis*-12 CLA but no change in *cis*-9, *trans*-11 CLA (Fuentes et al., 2009). Qiu et al. (2004) reported that reduced ruminal pH can affect microbial populations, especially cellulolytic bacteria. Total cellulolytic bacteria numbers are reduced, accompanied by reduced acetate to propionate ratio and altered biohydrogenation when pH was low.

Accumulation of *trans*-10, *cis*-12 CLA in ruminal contents has been linked to MFD. According to a study conducted by Baumgard et al. (2002), *trans*-10 *cis*-12 CLA decreased the lipogenic rate and milk fat synthesis of dairy cows, showing a 42% decrease in milk fat content and a 48% reduction in milk fat yield. These researchers also found that lipogenic activity decreased 82% using a radio-labeled acetate, and the activity of acetate oxidation to carbon dioxide was reduced to 61% in dairy cows inoculated with *trans*-10 *cis*-12 CLA. Additionally, the mRNA expression of all measured enzymes decreased from 39 to 54% after a dosing with *trans*-10 *cis*-12 CLA. The results suggested that the *trans*-10 *cis*-12 CLA inhibited milk fat synthesis by decreasing the enzyme activity through the inhibition of gene expression affecting *de novo* fatty acid synthesis, uptake, and transport. *Trans*-9 *cis*-11 CLA and *cis*-10 *trans*-12 CLA have also been reported as potential inhibitors of milk fat synthesis (Sæbø et al., 2005; Perfield II et al., 2007) with the former being associated with a 15% reduction in milk fat yield.

Effects of K on Biohydrogenation

Reports of increased milk fat yields following the addition of K to the diet raised questions if K altered ruminal biohydrogenation and the type of CLA produced. A series of continuous culture experiments were run at Clemson University to determine if increasing K concentration in the culture contents was associated with a decline in the production of the *trans*-10, *cis*-12 isomer linked to MFD. The first experiment (Jenkins et al., 2010) consisted of four dosage levels of a 10% K_2CO_3 (w/w) stock solution (0, 10.6, 21.2, and 32 mL) injected directly into the fermenters twice daily immediately after each feeding (fermenters were fed 60 g of 1:1 forage to concentrate in two equal portions at 0800 and 1630 h). Distilled water was also injected (32, 21.4, 10.8, and 0 mL, respectively) to maintain a total injection (K_2CO_3 + water) volume of 32 mL/d. The K added was 0, 0.6, 1.2, and 1.8 g/d or 0 (**K0**), 1% (**K1**), 2% (**K2**), or 3% (**K3**) of the daily feed. Because aqueous solutions of K_2CO_3 are strongly alkaline, pH was expected to

increase with increasing dosage of K_2CO_3. To determine if any changes in biohydrogenation and fermentation could be attributed to effects on pH, a fifth treatment (NaOH) consisted of injection of sufficient 10% NaOH (w/w) each day to match the K3 pH.

As expected, pH averaged over the three sampling days increased ($P < 0.05$) linearly with increasing K, but remained in the 6.0 to 6.4 range (Table 1). Culture pH were similar for the K3 and NaOH treatments. Increasing K had effects on VFA proportions but not total VFA concentrations. As K addition to the cultures increased, there were linear decreases ($P < 0.05$) in propionate but increases ($P < 0.05$) in acetate and acetate to propionate ratio. Addition of NaOH could not duplicate the VFA changes seen for K_2CO_3. K addition also affected the pattern of biohydrogenation intermediates. As K addition increased, the daily production in mg/d of *trans*-11 18:1 and *cis*-9, *trans*-11 CLA both increased ($P < 0.05$) linearly. Conversely, K addition decreased ($P < 0.05$) *trans*-10 C18:1 but had no effect on *trans*-10, *cis*-12 CLA. The addition of K caused a shift in biohydrogenation intermediates consistent with the improvement in milk fat % observed in previous lactation trials. Changes in biohydrogenation intermediates also were caused by the NaOH treatment suggesting K might shift biohydrogenation by elevating pH.

A second continuous culture experiment (Jenkins et al., 2011) was run to examine the effects of K in culture contents that had elevated *trans*-10, *cis*-12 CLA concentrations induced by feeding high fat. Six treatments were arranged as a 2 x 3 factorial with two levels of added soybean oil (0 and 4%) and 3 levels of added K (0, 1.5, and 3%). Potassium was introduced by injection of a 10% K_2CO_3 (w/w) stock solution (0, 16, and 32 ml/d) directly into the fermenters twice daily immediately after each feeding. Distilled water was also injected (32, 16, and 0 mL/d, respectively) to maintain a total injection (K_2CO_3 + water) volume of 32 mL/d. The K added was 0, 0.9, and 1.8 g/d or 0 (**K0**), 1.5% (**K1.5**), or 3% (**K3**) of the daily feed. Cultures on the low fat diet were fed 60 g basal diet per day. Cultures on the high fat diet were fed 60 g basal diet plus 2 g soybean oil (mixed as a complete diet) for a total of 62 g feed per day.

Similar to the first experiment, increasing K caused an increase ($P < 0.05$) in culture pH regardless of diet fat content. Addition of K also affected VFA as in the first experiment, but differently depending on diet fat content. For the low fat diet, increasing K again increased ($P < 0.05$) acetate and acetate to propionate ratio, and reduced ($P < 0.05$) propionate concentration. However, K had little effect on VFA when diet fat content was high. As expected, the 4% added soybean oil increased ($P < 0.05$) *trans*-10, *cis*-12 CLA production from an average of 4.3 mg/d for the low fat diets to 53.8 mg/d for the high fat diets. Regardless of fat content in the diet, increasing K reduced ($P < 0.05$) *trans*-10, *cis*-12 CLA production supporting results from Experiment 1 that K enhances milk fat content by re-directing the pathways of biohydrogenation back to normal. As K decreased ($P < 0.01$) *trans*-10, *cis*-12 CLA, it also increased ($P < 0.05$) the production of *cis*-9, *trans*-11 CLA that is typical of normal biohydrogenation.

A third continuous culture experiment was run to determine if changes in biohydrogenation intermediates seen for K_2CO_3 in the first two experiments could be duplicated with KCl. The experiment again examined two fat levels with each of three K treatments, no added K or 3% added K from either K_2CO_3 or KCl. The results showed a number of differences between the two K sources. Although culture pH values were maintained between 6.3 and 6.6 on day 10, they were still increased ($P < 0.05$) by K_2CO_3 compared to KCl. As seem in the previous experiments, K_2CO_3 increased ($P< 0.05$) acetate and acetate to propionate ratio, but no VFA changes were seen for KCl. The high fat diet increased ($P < 0.05$) of *trans*-10, *cis*-12 CLA but there was no effect of K. However, addition of K_2CO_3 increased ($P < 0.05$) *cis*-9, *trans*-11 CLA and *trans*-11 18:1 but decreased ($P < 0.05$) *trans*-10 CLA, all of which are consistent with returning biohydrogenation pathways back to normal. The response to KCL was entirely different, with no changes in CLA or *trans* monenes following the addition of KCl. These results show that alleviation of MFD from added K is dependent on source of K.

Sources of Supplemental Dietary Potassium

There are several supplemental sources of K that can be used, namely, potassium carbonate in the sesquihydrate or anhydrous form, potassium bicarbonate, or potassium chloride. From a practical and economic standpoint use of potassium bicarbonate becomes economically problematic as it has half the amount of K as the carbonate forms at a price equal or greater than the carbonates.

Potassium carbonate is available in two distinct and separate forms, with different molecular weights, physical properties, and scientific designations (CAS numbers), potassium carbonate sesquihydrate and various forms of anhydrous potassium carbonate. The difference is primarily in the reactivity of the chemicals when they are in moist environments. Anhydrous potassium carbonate generates a lot of heat when it begins to hydrate (exothermic reaction), whereas the sesquihydrate form does not generate this heat. This exothermic heating of the anhydrous form can and has caused damage to feed mixes by heating the mixes and /or by setting up conditions (heat and moisture) for other chemical reactions to occur. Note that the research cited above used primarily the hydrated form of potassium carbonate.

Potassium chloride is another form of available K, however, from the research cited above there are two issues using this form of K. The chloride ion added reduces DCAD resulting in no net effect on DCAD when using this form of K. Also, from the research cited above, it appears that the chloride ion reverses or negates the beneficial effects of K on rumen biohydrogenation.

Finally, some forages, particularly legumes, can contribute high amounts of K to a ration. Potassium, which is a strong cation, in conserved forages is biologically available to animals but cannot exist without an accompanying anion. Usually this anion is an organic acid, a protein, or a bicarbonate ion. However, this anion can also be as chloride. As we are trying to avoid excessive dietary chloride in order to optimize DCAD and to maximize the positive effects of K on rumen biohydrogenation it is highly

recommended to test forages by wet chemical methods to determine their chloride and calculated DCAD values.

Conclusions

A major breakthrough in the control of milk fat synthesis occurred with the discovery that a relatively minor CLA produced as an intermediate of lipid biohydrogenation, namely the *trans*-10, *cis*-12 isomer, was the cause of MFD. This led to the biohydrogenation theory of MFD that suggested feeding management was linked to an abnormal ruminal fermentation causing accumulation of the *trans*-10, *cis*-12 isomer. In general, no single dietary factor is responsible for MFD, and interactions among various dietary components can increase the rumen outflow of BH intermediates associated with MFD. Interest has turned to research findings that show increased milk fat % from some feed additives, suggesting these might act as biohydrogenation normalizers that shift pathways away from the *trans*-10, *cis*-12 CLA isomer to the more normal *cis*-9, *trans*-11 CLA isomer. Among the feed additives showing improvements in milk fat % are some K-based products. Research results from three continuous culture experiments at Clemson University have shown positive effects of K_2CO_3 on fermentation and patterns of biohydrogenation that were consistent with higher milk fat %. The positive results could not be duplicated by KCl. The mechanism of changes in biohydrogenation pathways caused by K_2CO_3 was not clear from the experiments, although maintenance of higher pH remains a contributing factor.

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Table 1. Changes in pH, VFA, and biohydrogenation intermediates in continuous cultures dosed with increasing amounts of K_2CO_3

	Treatment[1]					
	K0	K1	K2	K3	NaOH	SE
n	4	4	4	4	4	
pH d8-10[a]	6.01	6.22	6.25	6.38	6.29	0.12
VFA, mol/100 mol						
Acetate[ad]	48.2	48.7	52.0	52.1	48.7	1.0
Propionate[ad]	36.2	35.6	32.2	32.9	36.7	1.4
Acet/Prop[ad]	1.34	1.37	1.66	1.60	1.33	0.09
Total VFA, mM	103.5	95.2	98.4	95.1	95.4	6.0
BH intermediates, mg/d						
trans-18:1	537.6	499.8	461.1	538.2	575.8	38.4
t10c12 CLA	11.6	11.3	7.9	7.6	13.2	2.6
c9t11 CLA[a]	2.3	4.9	7.1	6.8	6.8	1.1

[a] Linear response of K0 through K3 ($P<0.05$).
[b] Quadratic response of K0 through K3 ($P<0.05$).
[c] Cubic response of K0 through K3 ($P<0.05$).
[d] K3 and NaOH differ ($P<0.05$).
[1] K_2CO_3 injected into culture flasks to provide the equivalent of 0, 1, 2, and 3% added K. The NaOH treatment used injections of NaOH into fermentation flasks to maintain the same pH as the K3 treatment.

Table 2. Changes in pH, VFA, and biohydrogenation intermediates in continuous cultures fed a low or high fat diet in combination with three concentrations of added K_2CO_3

	0% Fat			4% Fat			
Item	0	1.5	3	0	1.5	3	SEM
pH d8-10[ab]	5.99	6.32	6.36	5.91	6.13	6.17	0.10
VFA, mol/100 mol							
Acetate[bc]	46.6	56.1	57.2	50.7	52.1	50.3	2.5
Propionate[abc]	34.7	25.8	22.4	33.5	31.3	32.0	2.0
Acet/Prop[abc]	1.35	2.21	2.59	1.58	1.72	1.60	0.19
Total VFA, mM	76.7	69.7	71.6	79.9	85.8	79.1	7.1
BH intermediates, mg/d							
trans-18:1[abc]	320.9	140.0	132.3	883.9	773.7	444.7	69.0
t10c12 CLA [ab]	6.9	3.4	2.7	65.8	44.7	50.9	3.6
c9t11 CLA[b]	2.6	5.7	7.0	2.7	6.4	8.3	1.0

[a] Fat effect (P<0.05).
[b] K effect (P<0.05).
[c] Fat x K interaction (P<0.05).

Table 3. Changes in pH, VFA, and biohydrogenation intermediates in continuous cultures fed a low or high fat diet in combination with two sources of added K

	0% Fat			3% Fat			
Item	0% K	3% K_2CO_3	3% KCl	0% K	3% K_2CO_3	3% KCl	SE
pH d 10[b]	6.36[abc]	6.57[a]	6.35[bc]	6.33[bc]	6.47[ab]	6.21[c]	0.071
4 h VFA, mol/100 mol							
Acetate[ab]	52.6[ab]	54.2[a]	51.8[b]	49.4[c]	53.1[ab]	51.2[bc]	0.635
Propionate[ab]	29.9[bc]	26.5[d]	30.0[bc]	32.2[a]	28.5[c]	31.4[ab]	0.613
Ac/Pr[ab]	1.77[bc]	2.06[a]	1.73[bc]	1.54[d]	1.86[b]	1.64[cd]	0.054
Total VFA, mM	87.5[a]	78.9[a]	88.5[a]	90.7[a]	78.9[a]	90.7[a]	4.14
BH intermediates, mg/d							
t10-18:1[ab]	25.6[c]	17.8[c]	24.3[c]	221.2[a]	143.6[b]	196.5[a]	15.9
t11-18:1 [abc]	69.4[c]	104.5[bc]	65.4[c]	130.8[b]	272.3[a]	148.6[b]	16.9
t10c12 CLA [a]	2.14[b]	2.21[b]	2.08[b]	37.3[a]	36.4[a]	41.7[a]	2.34
c9t11 CLA[abc]	3.09[d]	5.80[cd]	3.60[d]	7.25[bc]	16.00[a]	8.97[b]	1.00

[a] Fat effect ($P < 0.05$).
[b] K effect ($P < 0.05$).
[c] Fat x K interaction ($P < 0.05$).

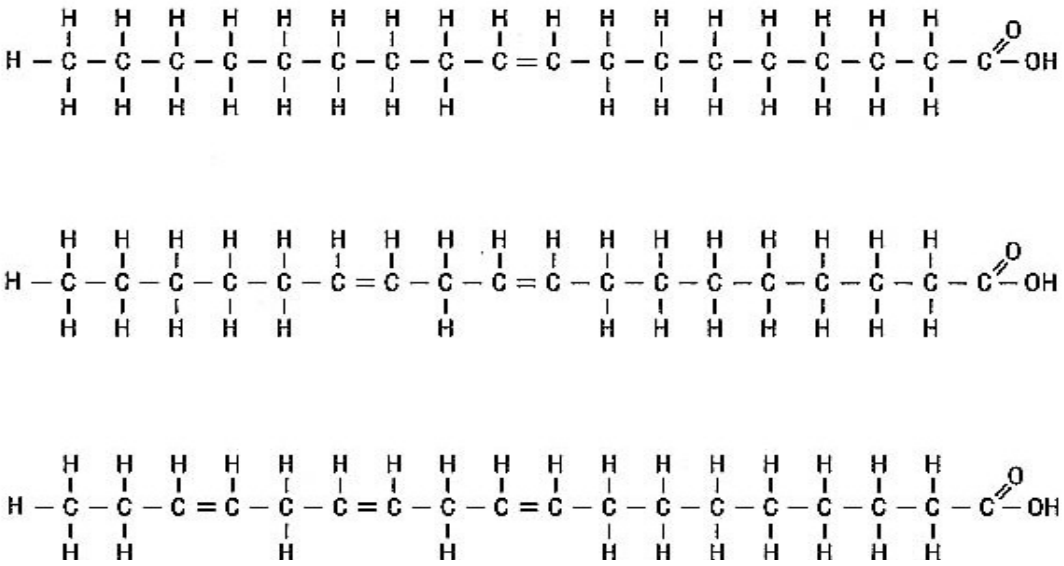

Figure 1. Structures of the three primary unsaturated fatty acids consumed by cattle, oleic acid (top), linoleic acid (middle), and linolenic acid (bottom).

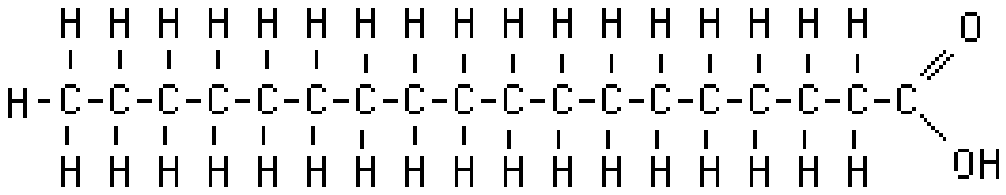

Figure 2. The structure of stearic acid, a saturated long-chain fatty acid.

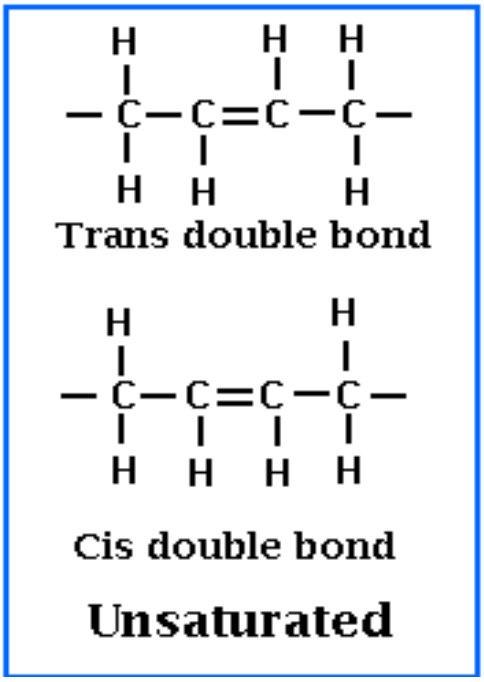

Figure 3. Structural differences between *cis* and *trans* fatty acids.

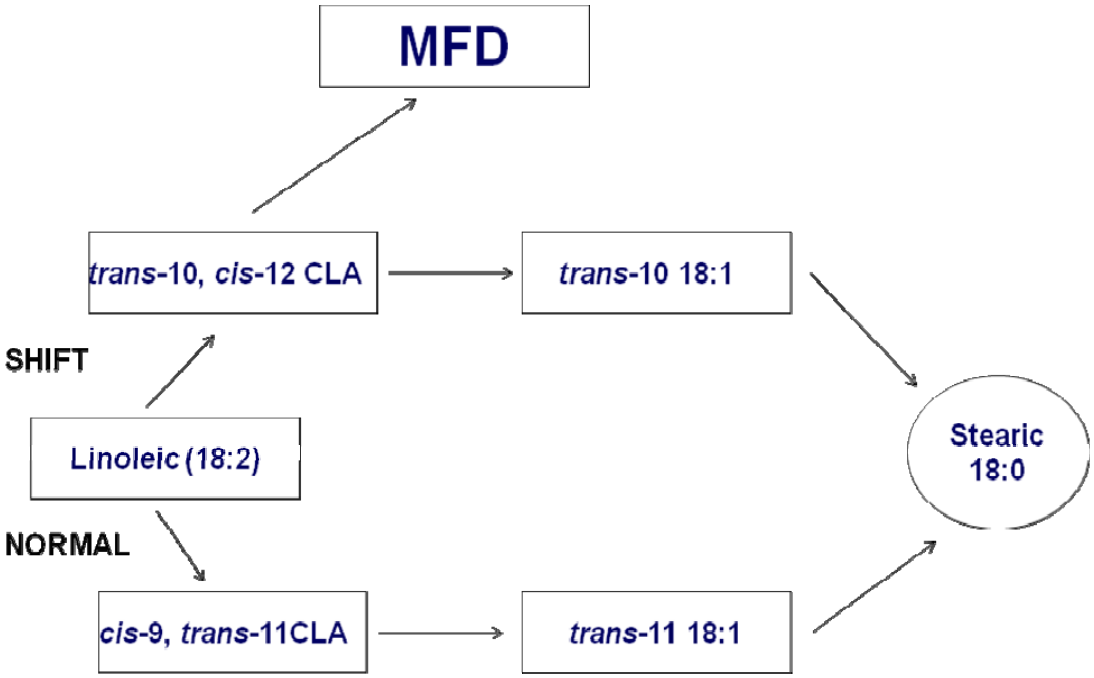

Figure 4. The shift in intermediates produced from biohydrogenation of linoleic acid in ruminal contents as a result of a diet-induced microbial shift.

SESSION NOTES