

CALORIC VERSUS NONCALORIC CONSIDERATIONS WHEN FEEDING FAT TO DAIRY CATTLE

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Summary

Fat supplements have traditionally been fed to dairy cattle to meet the energy demands of high milk yields without sacrificing fiber intake. Interest in the caloric value of fat continues to grow as cows are pushed to even higher levels of milk production. Recent studies have demonstrated several advantages to fat supplements that cannot be attributed to just energy. These include improved reproductive performance of cows fed certain types of fat supplements, and altered fatty acid composition of milk. Most of the noncaloric benefits of fat supplements are attributable to one or more unsaturated fatty acids comprising its complete fatty acid profile. A key factor affecting the delivery of beneficial unsaturated fatty acids to the tissues of the cow is the nature and extent of lipid transformations by the microbial population in the rumen. Ruminal microbes can destroy the majority of the dietary unsaturated fatty acids through a process called biohydrogenation. At the same time, biohydrogenation can produce a number of *trans* fatty acids that have unique and potent metabolic effects. The purpose of this paper is to examine the nature of these lipid transformations by the ruminal microbes, and how it can be controlled to deliver specific unsaturated fatty acids that are beneficial to the cow or to humans consuming dairy products.

Introduction

Adding fat to dairy rations can affect productive efficiency of dairy cows through a combination of caloric and noncaloric effects. Caloric effects are attributable to greater energy content and energetic efficiency for lipid compared to carbohydrate or protein with the overall benefit being increased milk production. Noncaloric effects are caused by benefits from added fat that are not directly attributable to its energy content or increased milk production. Examples of proposed noncaloric effects include improved reproductive performance, and altered fatty acid profile of milk.

Noncaloric benefits of lipid supplements are generally attributable to one or more unsaturated fatty acids making up the complete fatty acid profile of the supplement. Although these beneficial unsaturated fatty acids are abundant in the diet of dairy cows, they largely disappear as the feed

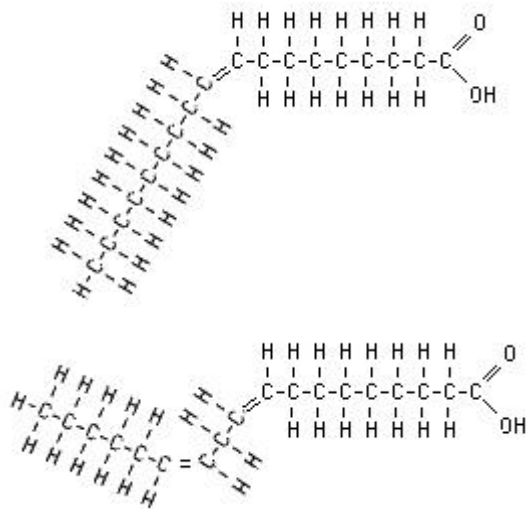
Table 1. Fatty acid composition of several fat supplements used in livestock rations.

Abbreviation ^a	Common Name	Tallow	Cottonseed	Canola	Poultry
C14:0	Myristic	3.0	1.0		1.0
C16:0	Palmitic	25.0	23.0	4.0	21.0
C18:0	Stearic	21.5	3.0	2.0	8.0
C18:1	Oleic	42.0	18.5	60.0	41.0
C18:2	Linoleic	3.0	52.5	20.0	19.0
C18:3	Linolenic			10.0	1.0

^aNumber of carbons:number of double bonds.
From Rouse (1996)

Oleic acid and linoleic acid are examples of unsaturated fatty acids containing one or more double bonds (Figure 2). Oleic acid has a single double bond between carbons 9 and 10, and is

Figure 2. The structures of oleic and linoleic acids.



referred to as a monounsaturated fatty acid. Linoleic acid is a polyunsaturated fatty acid (PUFA) containing two double bonds between carbons 9 and 10, and between carbons 12 and 13. Oleic acid is the predominant fatty acid in animal fats and some plant oils, such as canola oil (Table 1). Linoleic acid is the predominant fatty acid in many plant oils, including cottonseed oil, soybean oil, and corn oil.

The energy value of fat supplements is determined almost exclusively by the type and amount of fatty acid present in the supplement. Most fat supplements are comprised of different proportions of 5-8 common fatty acids all of which have similar energy values (approximately 9.4 kcal/g). Therefore, fatty acid content (g fatty acid/100 g fat supplement) is more important than fatty acid composition (g fatty acid/100 g total fatty acids) in determining the total energy value of the supplement.

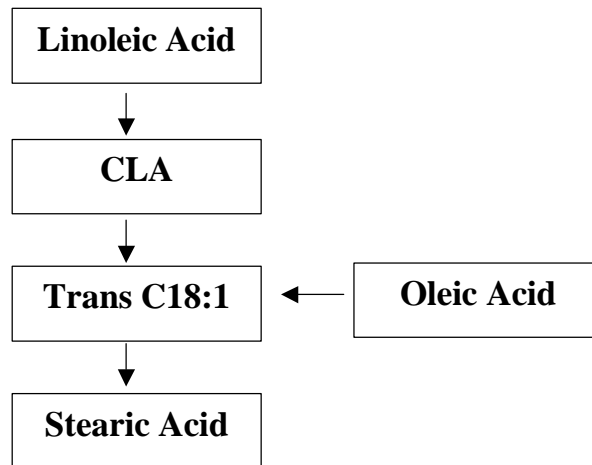
Fat supplements can be diluted by nonfatty acid components that have lower or no energy value. Fat content has traditionally been determined as the ether-extractable component of the feed. When defined in this manner, there can be considerable variation in lipid content among feed fats. Among the lowest is the ether extract in grains and forages. In addition to extracting fat, ether also extracts some carbohydrate, vitamins, and pigments. Therefore, fatty acids in corn grain are only 65% of the ether extract, and in alfalfa hay is only 40% of the ether extract (Palmquist and Jenkins, 1980). Because of the problems inherent with ether extract, many laboratories have moved to determining fatty acid content of feeds by gas chromatography instead of by ether extract.

With only a few exceptions, fats of plant and animal origin contain 100% ether extract with a high percentage (usually 90 to 100%) of fatty acids. The impurities extracted, such as water and pigments, are removed during refining leaving the commercial plant (soybean oil, canola oil, corn oil, etc) and animal (tallow, grease, etc) fats with mainly triglycerides consisting of 90-93% fatty acids. The remaining 7-10% is referred to as unsaponifiables and is mainly glycerol. Glycerol is readily utilized as an energy source, but only contains the energy of carbohydrates. Caution is advised when obtaining fats from unknown vendors to be sure that considerable impurities do not still remain in the product that lower the fatty acid and energy content. Rather than guessing, it pays to have a sample of the fat analyzed for fatty acid content and profile.

Fatty Acid Transformations by Ruminal Microbes

Food consumed by ruminants first passes through the largest of the four stomach compartments or rumen, which acts like a fermentation vat. Countless numbers of bacteria, protozoa, and fungi in the rumen ferment the feed releasing end products that are utilized by the host animal for maintenance and growth of body tissues. The microbial population in the rumen also is responsible for extensive transformation of dietary lipid (Figure 3). Lipid transformations include lipolysis to release free fatty acids from complex plant lipids, and biohydrogenation to convert unsaturated fatty acids in plant matter to more saturated lipid end products.

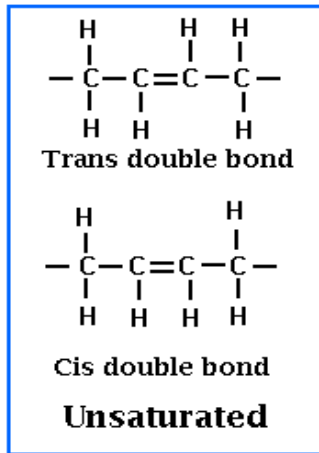
Figure 3. Major steps in the biohydrogenation of linoleic and oleic acids by ruminal microbes.



biohydrogenation to convert unsaturated fatty acids in plant matter to more saturated lipid end products.

Biohydrogenation of linoleic acid in the rumen begins with its conversion to conjugated linoleic acid (CLA). In this initial step, the number of double bonds remains the same but one of the double bonds is shifted to a new position by microbial enzymes. 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.

Figure 4. Structural differences between *cis* and *trans* fatty acids.

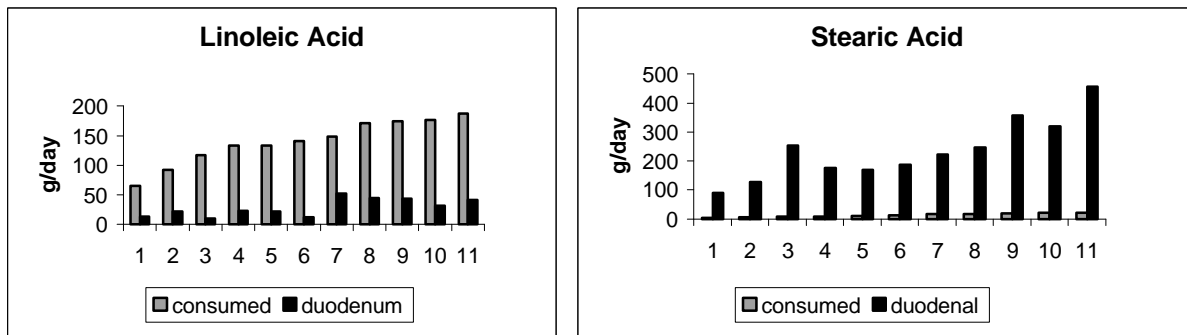


As biohydrogenation progresses, double bonds in the CLA intermediates are then hydrogenated further to *trans* fatty acids having only one double bond. A final hydrogenation step by the ruminal microbes eliminates the last double bond yielding stearic acid as the final end product. *Trans* double bonds only differ from *cis* double bonds in the placement of the hydrogens (Figure 4). The hydrogens 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.

In cows on a typical forage diet, the major *trans* C18:1 present in ruminal contents is *trans*-11 C18:1. Most of the remaining isomers have double bonds distributed equally among carbons 12 through 16 (Bickerstaffe et al., 1972). The exact pathways for the production of these positional isomers are not known. Linoleic and linolenic acids are converted to several *trans* C18:1 and C18:2 intermediates during biohydrogenation. Mosley et al. (2002) recently showed that the biohydrogenation of oleic acid by mixed ruminal microorganisms involves the formation of several positional isomers of *trans* C18:1 rather than only direct biohydrogenation to form stearic acid as previously described.

Biohydrogenation in the rumen greatly reduces the quantity of dietary unsaturated fatty acids reaching the small intestine of the cow. Intake of linoleic acid by dairy cows typically ranges from 70 to 200 g/day (Figure 5), with only 10 to 50 g of linoleic acid reaching the small intestine per

Figure 5. Daily intake vs duodenal flow of linoleic acid and stearic acid in lactating dairy cows fed typical diets without added fat. Taken from Jenkins (1999).



day. As much as 500 g of stearic acid reaches the small intestines of dairy cows each day, even though just a few grams of stearic acid are consumed. Therefore, stearic acid is the primary fatty acid absorbed in cows regardless of the quantity of unsaturated fatty acids consumed in the diet.

Noncaloric effects of unsaturated fatty acids

Milk Composition. Unsaturated oils cause milk fat depression (MFD) when fed to lactating dairy cows. Strong evidence in recent years points to their interference with fatty acid biohydrogenation as the likely cause of the MFD. Specifically, they block terminal steps of ruminal biohydrogenation which leads to the accumulation of trans fatty acid intermediates that were shown to cause MFD.

For instance, Gaynor et al. (1994) infused *cis* fat, composed of 65% high oleic sunflower oil and 35% cocoa butter, or *trans* fat, composed of 93% shortening and 7% corn oil, into the abomasum of lactating dairy cows. Milk yield was not changed, however, milk fat percentage and milk fat yield were lower for the *trans* treatment. Similarly, Romo et al. (1996) infused into the intestines of cattle either a fat mixture high in *cis*-C18:1 isomers or a mixture high in *trans*-C18:1 isomers. Only the *trans*-C_{18:1} treatment resulted in reduced milk fat content. Others followed with similar dairy cattle studies showing marked depressions in milk fat content during abomasal infusion of *trans* fatty acids (Chouinard et al., 1999; Looor and Herbein, 1998).

Recent studies have reported that not all *trans* fatty acid isomers are responsible for the MFD noted previously. When various combinations of fat and fiber were fed to dairy cattle to cause MFD, the treatments causing the greatest decline in milk fat were accompanied by larger increases in *trans*-10 than any other positional isomers (Griinari et al., 1998). Baumgard et al. (2000) provided more direct evidence that *trans*-10 fatty acids were the positional isomers most responsible for MFD in dairy cows. When they infused *cis*-9, *trans*-11 or *trans*-10, *cis* 12 CLA postruminally into dairy cows, only the *trans*-10, *cis*-12 isomer led to significant MFD. With the recent discovery that *trans* fatty acids, and particularly the *trans*-10 positional isomers, have the greatest potency as fat inhibitors, comes questions about the source of *trans*-10 fatty acids and the prospects of enhancing their production in ruminants.

Manufacturing properties of milk. The hardness of milk fat has long been a concern of the dairy industry. Some applications require reducing hardness such as improving the spreadability of butter. Other applications are geared toward increasing hardness such as producing cheeses more desirable for grating. Hardness is determined by fatty acid composition of the milk fat and the molecular distribution of fatty acids on the triglyceride (Ashes et al., 1997). Processing technologies to alter milk fatty acid composition and distribution are currently being examined, but are hampered by high cost and sometimes complicated, lengthy procedures. An alternative to processing strategies is to utilize feeding, breeding, and environmental factors that influence the composition of milk.

Reproductive performance. In a few studies, feeding fat to lactating dairy cows has improved reproductive performance implying possible benefits on lifetime production potential.

Reported improvements of reproductive performance from added fat include higher conception rates (Schneider et al., 1988; Sklan et al., 1989; Ferguson et al., 1990), increased pregnancy rates (Schneider et al., 1988; Sklan et al., 1991), and reduced open days (Sklan et al., 1991). However, supplemental fat has had little or no benefit on reproductive efficiency in other studies (Carroll et al., 1990; Schingoethe and Casper, 1991).

The mechanism of how fat supplements alter reproductive performance is not clear. Fat may function in one capacity by providing additional energy during early lactation to support improved productive functions, including reproduction. Negative energy balance delays ovulation and the initiation of the first normal luteal phase (Butler et al., 1981). However, recent studies also suggest that the mechanism involves an energy independent response to fat.

When an equal quantity of energy from glucose, saturated animal fat (tallow), or unsaturated fat (yellow grease) were infused into lactating dairy cows via the abomasum, the fat but not carbohydrate decreased plasma estradiol and increased progesterone (Oldick et al., 1997). The study by Oldick et al. (1997) also demonstrated the potential to decrease $\text{PGF}_{2\alpha}$ synthesis by supplying elevated concentrations of PUFA. These results were similar to previous reports that intravenous infusion of unsaturated fatty acids from a soy oil emulsion increased plasma $\text{F}_{2\alpha}$, and number and size of follicles (Lucy et al., 1990, 1991). Ovarian follicular growth was also stimulated more in Brahman x Hereford cattle by fat compared to equal energy from carbohydrate, with a greater effect observed for fats with higher PUFA (Thomas et al., 1997). Hinckley et al. (1996) provided further support of the role of PUFA on reproductive function in ruminants. In their study, dispersed bovine luteal cells had a dose-dependent decline in progesterone production and an increase in production of prostaglandin as PUFA in the media increased. More recently, Staples et al. (2000) showed that size of the dominant follicle was greater for Holstein cows fed Ca salts of linoleic acid or fish oil fatty acids compared to those fed calcium salts of oleic acid. Results such as these continue to demonstrate a reproductive advantage from increased absorption of PUFA compared to other fat sources, such as monounsaturated fats.

Fatty acid nutraceuticals. Diet-conscience consumers continue to make food selections that are driven by concerns about fat content and quality. Preference is usually given to foods that are low in fat, cholesterol, and saturated fatty acids. While the relationship between saturated fatty acid intake and human health risks are unresolved, medical and nutritional advice to consumers is to limit their intake of saturated fatty acids from dairy products. Choices are now available for milk products that vary widely in fat content, but commercial products with reduced saturation have not been developed.

A typical fatty acid composition of milk fat is 70-80% saturated and 20-30% unsaturated. Of the unsaturated fatty acids, the majority (>70%) is oleic acid, which is monounsaturated. The ideal milk fatty acid composition according to members of a Milk Fat Round Table discussion sponsored by the Wisconsin Milk Marketing Board (O'Donnell, 1989) was less than 10% PUFA, up to 8% saturated fatty acids, and the remainder (82%) monounsaturated fatty acids.

Conjugated linoleic acid is a group of fatty acid isomers that were identified in the last 5 to 10 years as potent antioxidants, anticarcinogens, modulators in the immune system, anti-atherosclerosis agents, and body weight protectors. Meat and dairy products from cattle and sheep are important dietary sources of CLA. Isomerization of linoleic and linolenic acids to CLA occurs through a biohydrogenation process carried on by gut microorganisms within the rumen of the cow. Most attempts to increase CLA in meat and milk are focused on interrupting the completion of biohydrogenation, which leads to accumulation of *trans* fatty acid intermediates including CLA. Feeding high grain diets or diets with added fat will increase CLA content of meat and milk, but are limited in their use because of their potential to reduce production and cause metabolic disease when fed in high quantity.

Protected Fats

Probably the most widely known fat developed to resist biohydrogenation and increase milk PUFA levels was formaldehyde-treated lipid. This product consisted of polyunsaturated lipid droplets encapsulated with a formaldehyde protected protein source, such as casein. Polyunsaturated fatty acid levels in tissues of cattle and sheep were significantly elevated by feeding formaldehyde-treated lipid (Faichney et al., 1972; Cook et al., 1972; Faichney et al., 1973). Milk unsaturated fatty acids also increased when formaldehyde-treated lipid was fed to lactating cows. Milk linoleic acid content increased from 3 to 30% of total fatty acids during feeding of the protected supplement, and then quickly returned to normal when the supplement was withdrawn (Cook et al., 1972). Formaldehyde-protected canola seed increased yield of monounsaturated and PUFA in milk by 54% in a study by Ashes et al. (1992). However, the protected canola in the Ashes et al. (1992) study was compared to a control diet with no added fat and not a diet containing an equal amount of unprotected canola oil or whole canola seed. Commercial application of formaldehyde-protected lipids was never achieved in the United States, undoubtedly due in large part to health risks associated with the use of formaldehyde.

Feeding whole oilseeds (i.e. whole soybeans, whole cottonseeds, whole sunflower seeds, etc) to cows increases tissue and milk unsaturation according to some reports. When diets containing 0, 10, 15, or 20% whole cottonseed were fed to cows, 18:1 in milk steadily increased from 23.5 to 32.0% of total fatty acids (DePeters et al., 1985). However, there were no changes in milk 18:2 or 18:3 as cottonseed increased in the ration. Processing of the seed can affect the degree of protection from ruminal biohydrogenation and the extent that milk fatty acids are altered. Whole seeds provide some protection from biohydrogenation because of the nature of their hard outer seed coat. Disruption of the seed coat exposes the oil to the microbial population and the potential for fermentation problems and biohydrogenation. The seed coat can be sufficiently broken by chewing and rumination, or through a variety of processing techniques such as extrusion or grinding. Roasting of cottonseed was reported to reduce biohydrogenation (Pires et al., 1997).

Calcium salts of fatty acids have received some attention for partially escaping biohydrogenation. Wu et al. (1991) reported 49% biohydrogenation of fatty acids from calcium salts of palm oil compared to 80% for animal-vegetable fat and 62% for control diet fatty acids.

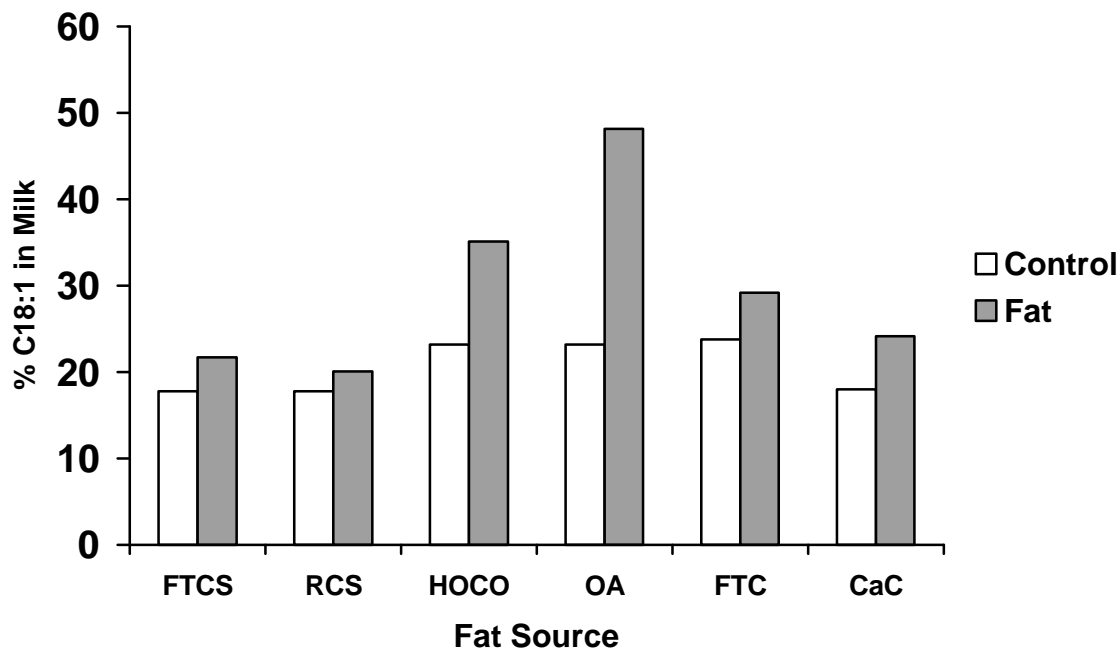
Klusmeyer et al. (1991) similarly found lower biohydrogenation for diets supplemented with calcium salts compared to a control diet. Feeding calcium salts of soybean oil (high in 18:2) or linseed oil (high in 18:3) to lactating cows had only minor effects on the proportions of 18:2 and 18:3 in milk fat (Chouinard et al., 1998). Calcium linoleate fed to sheep failed to increase flow of unsaturated fatty acids to the duodenum (Fotouhi and Jenkins, 1992). They proposed that calcium salts of unsaturated fatty acids were protected from dissociation in the rumen when encapsulated inside an insoluble matrix of saturated calcium salts. If so, protection is only possible if unsaturated fatty acid content is low, which greatly limits the extent that unsaturation of meat or milk can be altered. This was supported by observations of Enjalbert et al. (1997) showing that duodenal flow of 18:2 was greater for calcium salts of palm fatty acids than for calcium salts of rapeseed fatty acid. Intake of unsaturated fatty acids was higher for cows fed the rapeseed calcium salts.

More recently, oleamide has been investigated as a possible source of monounsaturated fatty acid resistant to ruminal biohydrogenation. Reeves et al. (1998) reported that biohydrogenation of *cis*18:1 was reduced 61% by adding it to microbial cultures as oleamide rather than adding it as the free acid (oleic acid). Oleamide added to the microbial cultures maintained higher concentrations of *cis*18:1 and lower 18:0 at 24 and 48 h incubation compared to cultures with added oleic acid. Also, when sheep were fed a diet with added oleamide, fatty acid and energy digestibilities were higher than either the control diet or a diet with added oleic acid.

Oleamide was examined in a dairy study in which nine first lactation Holstein cows were fed three diets in a 3 x 3 Latin square replicated three times (Jenkins, 1998). Each period lasted 3 weeks. The TMR consisted of 42% corn silage and 58% concentrate (DM basis) with either no added fat (control), 3.5% added high oleic canola oil, or 3.5% added oleamide. Dry matter intake was reduced by oleamide, but not by canola oil. Milk yields were the same for all treatments. Canola oil reduced FCM and milk fat concentration but these were not affected by oleamide. Milk protein concentration was lower for oleamide compared to canola oil, but neither fat supplement differed from the control diet.

Milk *cis*18:1 averaged 22 % of the total fatty acids for the control diet, and increased to 35 % by feeding canola oil. Feeding oleamide further increased *cis*18:1 to 47 % of milk total fatty acids. All fatty acids with ≤ 16 C were reduced by oleamide. Oleamide was more effective than canola oil in this study at increasing the oleic acid content in milk of lactating dairy cows. Oleamide ranked high when compared to other protected fat sources for its ability to enhance oleic acid concentration in milk (Figure 6).

Figure 6. Changes in milk oleic acid concentration when lactating dairy cows were fed protected fat supplements.



Protected fat sources included;

- FTCS = formaldehyde-treated canola seed (Tymchuk et al., 1998)
- RCS = rolled canola seed (Tymchuk et al., 1998)
- HOCO = high-oleic canola oil (Jenkins, 1998)
- OA = oleamide (Jenkins, 1998)
- FTC = formaldehyde-treated canola (Ashes et al., 1992)
- CaC = calcium salts of canola fatty acids (Bayourthe et al., 2000)

Conclusions

In some situations, fat supplements may provide benefits to dairy cows that cannot be explained simply by their high energy content. These benefits may be attributed to the manner in which the fat supplement affects the outflow of unsaturated fatty acids from the rumen. Beneficial unsaturated fatty acids reaching the intestines of the dairy cow are combinations of dietary fatty acids that escape biohydrogenation and *trans* fatty acid isomers that are intermediates in biohydrogenation. Feeding high amounts of unsaturated plant oils to cows will increase *trans* fatty acid outflow from the rumen more than it will increase outflow of dietary unsaturated fatty acids.

Reducing biohydrogenation and loss of dietary unsaturated fatty acids can be accomplished by feeding protected fat sources to cows. Once absorbed, unsaturated fatty acids can regulate lipid synthesis in the animal (including causing MFD), alter the production of prostaglandins and eicosenoids that are linked to reproductive performance of the animal, and be deposited in milk where they can affect milk manufacturing properties or be available as nutraceuticals for the human population.

Areas of Needed Information

Most of the information lacking about the benefits of unsaturated fatty acids in dairy cows relates to the basic question of supply and demand. On the demand side, the most critical questions relate to establishing when dairy cows may be stressed for unsaturated fatty acids, what body functions are affected, and what types of unsaturated fatty acids are needed to satisfy the additional need. This paper dealt mostly with the supply side, which is affected as much by ruminal biohydrogenation as it is by the concentration of unsaturated fatty acids in the diet. Although much is known about biohydrogenation, many of the accepted pathways fail to account for all the *trans* intermediates that are known to accumulate in ruminal contents. Also, more information is needed on regulation of biohydrogenation including how it can be stopped at intermediate points to allow for increased accumulation of beneficial *trans* intermediates, and how protected fats can be improved to deliver specific unsaturated fatty acids to body tissues.

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