INTRODUCTION

Fat is an important energy component in the diet of ruminants and over the last decade fat supplementation has become a common practice to increase the energy density of the diet for high producing dairy cows. Recent advances have renewed the interest in dietary fats and lipid metabolism. One development is improved analytical procedures which have revealed the complex pattern of fatty acids that are produced in the rumen and incorporated into ruminant meat and milk fat. The old adage “what you eat is what you get” is clearly incorrect in the case of dietary lipids and ruminant animals, and this is of special importance given recent efforts to include lipid metabolism in dynamic models of ruminant digestion. Following absorption, a major fate of fatty acids is their oxidation for energy. However, a second recent development is the recognition that specific fatty acids produced in the rumen also play a critical role as signaling molecules involved in the expression of specific genes and the regulation of metabolic processes. Finally, recent discoveries in the functional foods area indicate that specific fatty acids produced in the rumen may have beneficial effects on human health, and there is a keen interest in the possibility of designing natural food products with enhanced levels of these fatty acids.

Given these recent advances, the CNC Organizing Committee asked us to review digestion and metabolism of lipids in the ruminant. This is a challenging task and a comprehensive review is well beyond the scope of our presentation. Thus, in the following sections we will provide an overview of lipid digestion and metabolism, giving special emphasis to recent developments that provide new insight and impact dairy cattle nutrition. We will also make a conscientious effort to refer readers to reviews where appropriate.

DIETARY SUPPLY

The diet of lactating dairy cows typically contains 4 to 5% fat. Higher levels may adversely effect rumen microbial fermentation so the general recommendation is that total dietary fat should not exceed 6 to 7% of dietary dry matter (Jenkins, 1993; Doreau et al., 1997; NRC, 2001). Primary sources of lipid in the ruminant diet are forages and concentrates, although the lipid content can be increased by the use of fat supplements. Forages typically contain 4 to 6% of the dry weight of the leaf tissue as lipid, of which the major lipid class is glycolipids (Harfoot, 1981). The lipid content of concentrates is usually higher than that of forages, and the majority is present in the form of triglycerides. Fat supplements that are by-products of rendering and vegetable oil
refining industries contain the lipid predominantly as triglycerides whereas rumen-protected supplements of Ca-salts are comprised of free fatty acids.

Determining the lipid content of the diet is one of the first requirements for diet formulation and this presents some challenges. Readers are referred to an excellent recent review by Palmquist and Jenkins (2003) that compares methods used to determine dietary lipid and discusses some of their practical limitations. The most common analytical procedure is the Soxhlet ether extraction (EE) method. However, EE methods also extract non-fatty acid material that has no nutritive value, and as a consequence EE overestimates the lipid content of the diet. The degree of overestimation depends on the type of feedstuff. Nutritive value is primarily associated with the fatty acids and their content can be as high as 80% of the EE for concentrates to less than 50% for forages (Palmquist, 1988). To account for this in feeding systems, Allen (2000) used the limited published literature and developed an equation to predict total fatty acid content from dietary values of ether extract. In turn, NRC (2001) adopted a modified version of this equation where: Total fatty acids = EE – 1. Clearly, the accuracy of predicting fatty acid content from EE values will vary by diet and dietary component.

The fatty acid profile of dietary components also varies, and this may affect the characteristics of the diet and can be important in assessing nutritional value. The fatty acid composition of representative feed components and fat supplements is provided in Table 1. Variation of the fatty acid composition within a specific dietary component is minor when compared to the variation among feedstuffs.

Table 1. Representative fatty acid composition of some typical feedstuffs and fat supplements

<table>
<thead>
<tr>
<th>Fatty acid, %</th>
<th>Feedstuff</th>
<th>Pasture grass</th>
<th>Corn</th>
<th>Tallow</th>
<th>RP Fatb</th>
<th>RP Fat/Reprob</th>
</tr>
</thead>
<tbody>
<tr>
<td>14:0</td>
<td></td>
<td>1</td>
<td>---</td>
<td>3</td>
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<td>16:1</td>
<td></td>
<td>2</td>
<td>---</td>
<td>6</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>18:0</td>
<td></td>
<td>2</td>
<td>2</td>
<td>18</td>
<td>4</td>
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<td>3</td>
<td>30</td>
<td>39</td>
<td>34</td>
<td>29</td>
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<td>18:2</td>
<td></td>
<td>13</td>
<td>47</td>
<td>5</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>18:3</td>
<td></td>
<td>61</td>
<td>2</td>
<td>1</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>20:5</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
</tr>
<tr>
<td>22:6</td>
<td></td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>2</td>
</tr>
</tbody>
</table>

Adapted in part from Palmquist 1988.

 Representative rumen protected (RP) fat supplements are Ca-salts of palm fatty acid dillillate (EnerGII and EnerGII Repro). Fatty acid values for these provided by D. Luchini (Bioproducts Inc.).

The double bonds in naturally occurring unsaturated fatty acids are almost exclusively in the cis configuration; generally, forage sources contain a higher
concentration of linolenic acid (18:3; cis-9, cis-12, cis-15), whereas linoleic acid (18:2; cis-9, cis-12) is the predominant fatty acid in cereal grains and seeds (Table 1). Unsaturated fatty acids such as these are susceptible to alteration during processing and storage. The lipids in forages can be altered during anaerobic fermentations that occur during ensiling, and unsaturated fatty acids present in forages as well as concentrates will also decline over time as a result of slow oxidation (Van Soest, 1982).

DIGESTION IN THE RUMEN

An extensive metabolism of lipid occurs in the rumen and this has a major impact on the profile of fatty acids available for absorption and tissue utilization. Davis (1990) provided an excellent schematic that illustrates the two major processes that occur in the rumen, hydrolysis of ester linkages in lipids and biohydrogenation of the unsaturated fatty acids (Figure 1).

Figure 1. Fat digestion in the rumen. Reproduced from Davis (1990).

Hydrolysis

When dietary lipids enter the rumen, the initial step in lipid metabolism is the hydrolysis of the ester linkages found in triglycerides, phospholipids, and glycolipids. Hydrolysis of dietary lipids is predominantly due to rumen bacteria with little evidence for a significant role by rumen protozoa and fungi, or salivary and plant lipases. The
hydrolysis of lipids is extracellular, and the glycerol and sugars that are liberated are readily metabolized by the rumen bacteria. Rumen hydrolysis has been most extensively characterized in Anaerovibrio lipolytica which hydrolyzes triglycerides and Butyrivibrio fibrisolvens which hydrolyzes phospholipids and glycolipids (Harfoot and Hazlewood, 1997). Although the extent of hydrolysis is generally high (>85%), a number of factors that affect the rate and extent of hydrolysis have been identified (see reviews by Harfoot, 1981 and Doreau et al., 1997). For example, the extent of hydrolysis is reduced as the dietary level of fat is increased (Beam et al., 2000) or when factors such as low rumen pH and ionophores inhibit the activity and growth of bacteria (Van Nevel and Demeyer, 1995; 1996b; Demeyer and Doreau, 1999).

Biohydrogenation

Biohydrogenation of unsaturated fatty acids is the second major transformation that dietary lipids can undergo in the rumen. It requires a free fatty acid to proceed and as a consequence rates are always less than those of hydrolysis, and factors that affect hydrolysis also impact biohydrogenation (Figure 1). Most biohydrogenation (>80%) occurs in association with the fine food particles and this has been attributed to extracellular enzymes of bacteria either associated with the feed or free in suspension (Harfoot and Hazlewood, 1997). The major substrates are linoleic and linolenic acids (Table 1) and the rate of rumen biohydrogenation of fatty acids is typically faster with increasing unsaturation. For most diets linoleic acid and linolenic acid are hydrogenated to the extent of 70-95% and 85-100%, respectively (Doreau and Ferlay, 1994; Beam et al., 2000). This extensive level of hydrogenation is reduced when diets high in concentrates are fed, which can be attributed to inhibition of lipolysis at the low pH that is typically observed on these diets (Van Nevel and Demeyer, 1995; 1996b). Hydrogenation is also adversely affected when excessive unprotected lipid is present in the diet. How fat interferes with microbial fermentation is not clear, but is believed to result from either the coating of feed particles or a direct toxic effect on the rumen microorganisms (Jenkins, 1993).

Fish oil contains two longer chain fatty acids, eicosapentaenoic acid (EPA; 20:5) and docosahexaenoic acid (DHA; 22:6), that are often included in rumen-protected lipid supplements designed to improve reproductive performance. The degree to which EPA and DHA are biohydrogenated in the rumen is still not well understood. Studies conducted in vitro suggest that there is little biohydrogenation of these two omega-3 fatty acids (Ashes et al., 1992; Gulati et al., 1999). However, in vivo studies involving dietary supplements of fish oil indicate that much of the EPA and DHA is biohydrogenated, although to a lesser extent than typically observed for linoleic and linolenic acids (Chilliard et al., 2000; Wachira et al., 2000; Scollan et al., 2001).

Classical pathways of biohydrogenation were established using pure cultures of rumen organisms and these are presented in Figure 2. The rumen bacteria involved in biohydrogenation have been classified into two groups, A and B, based on their metabolic pathways (Kemp and Lander, 1984). To obtain complete biohydrogenation of polyunsaturated fatty acids (PUFA), bacteria from both groups are generally required.
(Figure 2). Although Group A contains many bacteria that can hydrogenate PUFA to trans 18:1 fatty acids, only a few species characterized as Group B can hydrogenate a trans 18:1 fatty acid to stearic acid (Harfoot and Hazlewood, 1997). This feature of biohydrogenation explains why increased feeding of PUFA simultaneously causes an increase in the rumen concentration of monounsaturated fatty acids and a decrease in the concentration of saturated fatty acids (Noble et al., 1974; Fellner et al., 1995).

The initial step in rumen biohydrogenation typically involves an isomerization of the cis-12 double bond to a trans-11 configuration resulting in a conjugated di- or trienoic fatty acid (Figure 2). Next is a reduction of the cis-9 double bond resulting in a trans-11 fatty acid. The final step is a further hydrogenation of the trans-11 double bond producing stearic acid (linoleic and linolenic acid pathways) or trans-15 18:1 (linolenic acid pathway). It is also possible to differentially affect steps in the biohydrogenation process. For example, dietary supplements of fish oil appear to inhibit the last step of biohydrogenation because they increase rumen outflow of trans 18:1 fatty acids and reduce the outflow of stearic acid (Wachira et al., 2000; Shingfield et al., 2003). Thus, supplements containing fish oils must primarily affect group B bacteria. Likewise, diets that cause a low rumen pH and the feeding of ionophores inhibit the final step in biohydrogenation resulting in an accumulation of trans 18:1 fatty acids. However, the extent of the inhibition is much lower than their inhibition of hydrolysis (Van Nevel and Demeyer, 1995, 1996b).

Figure 2. Biochemical pathways for the biohydrogenation of linoleic and linolenic acids in the rumen (adapted from Harfoot and Hazlewood, 1997).

Two key biohydrogenation intermediates are trans-11 18:1 (vaccenic acid; VA) formed from linoleic and linolenic acids and cis-9, trans-11 conjugated linoleic acid.
(CLA) formed in the biohydrogenation of linoleic acid. These intermediates are present in appreciable quantities in ruminant fat at a ratio of about 3:1, but in the rumen cis-9, trans-11 CLA is only a transitory intermediate and instead it is VA that accumulates. The difference is because most of the cis-9, trans-11 CLA found in ruminant fat originates in the mammary gland and adipose tissue from endogenous synthesis involving the enzyme delta-9 desaturase with rumen-derived VA as the substrate (see review by Bauman et al., 2003). This discovery is of special importance in considerations of “designing foods” because cis-9, trans-11 CLA is among the most potent naturally occurring anti-carcinogens (see discussion in Lock and Bauman, 2003).

As analytical techniques improved, we have gained an appreciation of the complexity of the biohydrogenation processes occurring in the rumen. In addition to major pathways involving trans-11 18:1 and cis-9, trans-11 CLA as intermediates, there must be many more pathways. A remarkable range of trans 18:1 and CLA isomers are present and Table 2 presents their outflow from the rumen based on limited data from growing cattle and lactating cows.

Table 2. Range of double bond positions of trans 18:1 and conjugated 18:2 fatty acids and their ruminal outflow (g/day) in growing and lactating cattlea

<table>
<thead>
<tr>
<th>Trans 18:1</th>
<th>Ruminal outflow</th>
<th>Conjugated 18:2</th>
<th>Ruminal outflow</th>
</tr>
</thead>
<tbody>
<tr>
<td>trans-4</td>
<td>0.5-0.7</td>
<td>trans-7, cis-9</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>trans-5</td>
<td>0.4-0.6</td>
<td>trans-7, trans-9</td>
<td>0.01-0.05</td>
</tr>
<tr>
<td>trans-6-8</td>
<td>0.4-6.7</td>
<td>trans-8, cis-10</td>
<td>0.01-0.12</td>
</tr>
<tr>
<td>trans-9</td>
<td>0.8-6.2</td>
<td>trans-8, trans-10</td>
<td>0.01-0.10</td>
</tr>
<tr>
<td>trans-10</td>
<td>1.7-29.1</td>
<td>cis-9, cis-11</td>
<td>0.01-0.01</td>
</tr>
<tr>
<td>trans-11</td>
<td>5.0-121.0</td>
<td>cis-9, trans-11</td>
<td>0.19-2.86</td>
</tr>
<tr>
<td>trans-12</td>
<td>0.5-9.5</td>
<td>trans-9, trans-11</td>
<td>0.22-0.55</td>
</tr>
<tr>
<td>trans-13 + 14</td>
<td>6.5-22.9</td>
<td>trans-10, cis-12</td>
<td>0.02-0.32</td>
</tr>
<tr>
<td>trans-15</td>
<td>3.2-8.5</td>
<td>trans-10, trans-12</td>
<td>0.05-0.06</td>
</tr>
<tr>
<td>trans-16</td>
<td>3.1-8.0</td>
<td>cis-11, trans-13</td>
<td>0.01-0.10</td>
</tr>
<tr>
<td></td>
<td></td>
<td>trans-11, cis-13</td>
<td>0.01-0.46</td>
</tr>
<tr>
<td></td>
<td></td>
<td>trans-11, trans-13</td>
<td>0.09-0.40</td>
</tr>
<tr>
<td></td>
<td></td>
<td>cis-12, trans-14</td>
<td>&lt;0.01-0.05</td>
</tr>
<tr>
<td></td>
<td></td>
<td>trans-12, trans-14</td>
<td>0.08-0.19</td>
</tr>
</tbody>
</table>

aData derived from three studies where samples were collected from the duodenum (Duckett et al., 2002; Piperova et al., 2002) or omasum (Shingfield et al., 2003).

Clearly, many intermediates are formed in the ruminal biohydrogenation of PUFA and these are absorbed and incorporated into ruminant fat. Some of the isomers may be formed by chemical bond migration (Griinari and Bauman, 1999) and a portion of the trans 18:1 isomers can be derived from oleic acid (cis-9 18:1; Mosley et al., 2002). We also know that diet and changes in the rumen environment can shift the pathways of biohydrogenation resulting in dramatic changes in the fatty acid intermediates. To date,
this has been best characterized for diets that cause milk fat depression where a marked increase in trans-10, cis-12 CLA and trans-10 18:1 content of rumen fluid and milk fat is generally observed (Bauman and Griinari, 2003). In fact, Kim et al. (2002) recently identified a rumen bacterium, Megasphaera elsdenii, that produces significant quantities of trans-10, cis-12 CLA. However, the extent to which the various pathways of biohydrogenation are associated with specific enzymes and species of bacteria or represent a lack of specificity of the enzymes involved in biohydrogenation is unknown.

Microbial Lipids

A portion of the fatty acids found in the rumen are phospholipid components of microbial membranes. The rumen microorganisms derive these from de novo synthesis (mainly 16:0 and 18:0) and the uptake of preformed fatty acids (mainly PUFA; Jenkins, 1993; Harfoot and Hazlewood, 1997). Thus, the level of fat supplementation and its composition can affect the fatty acid composition of the rumen microorganisms (Bauchart et al., 1990; O’Kelly and Spiers, 1991). Demeyer and Doreau (1999) pooled data from five studies and estimated that the bacteria may contribute up to 17% of the lipid flowing from the rumen when a corn silage diet is fed.

Fat Supplements

Fat supplements are used as a means to increase the energy density of the diet and many of these are referred to as inert. In this case inertness simply means that the fat or fatty acid supplement has minimal effects on rumen fermentation. Although deemed inert at the level used, they can still be hydrolyzed, if a triglyceride, or hydrogenated, if unsaturated. Often fat supplements are “rumen-protected” as a means of avoiding the deleterious effects of a high fat diet on microbial fermentation. The requirement for these fat supplements is that the method has efficacy in providing both rumen protection and post-ruminal availability (Wu and Papas, 1997). Recent protection methods are pH-dependent and take advantage of the transition occurring between rumen pH (~5.8 to 6.7) and pH of the abomasum (~2 to 4). These methods include formaldehyde-treatment of a lipid-protein matrix (Ashes et al., 1979), microencapsulation with a water insoluble lipid coating (Putnam et al., 2003), preparation of fatty acid amides (Fotouhi and Jenkins, 1992), and formation of Ca salts of fatty acids (Jenkins and Palmquist, 1984). The first two methods can protect esterified or free fatty acids whereas the protected lipid in the later two methods has to be free fatty acids. Of these, Ca-fatty acid complexes are commercially used in the US and a typical fatty acid composition for these supplements is presented in Table 1. The mechanism whereby Ca-salts provide “protection” from rumen digestion is related to the inertness of the Ca-fatty acid complex in the typical rumen environment. However, factors such as low rumen pH and increased unsaturation of the fatty acid can lead to dissociation of the Ca-fatty acid complex allowing biohydrogenation to occur (Demeyer and Doreau, 1999). Van Nevel and Demeyer (1996a) found when free fatty acids derived from soybean oil or the Ca salts of the same fatty acids were incubated at different pH, the protection from hydrogenation (~30%) provided by the Ca-fatty acid complex at pH 6.9 was lost when pH was below 6.0. Furthermore, degree of fatty acid saturation appears to be important,
with PUFA more easily dissociated from the calcium salts as compared to monounsaturated fatty acids (Sukhija and Palmquist, 1990).

ABSORPTION IN THE SMALL INTESTINE

Biology of Absorption

Analysis of the lipid entering the small intestine has shown that it is virtually identical to that leaving the rumen. Thus, there is no significant absorption or modification of the long and medium chained fatty acids in the omasum or abomasum (Noble, 1981). As a consequence of rumen metabolism as detailed in the previous section, the lipid entering the small intestine consists of fatty acids that are highly saturated, mainly palmitic and stearic acids. The total amount of lipid entering the duodenum often exceeds lipid intake and the greatest increase typically occurs with high forage based diets. Dietary lipid supplements can result in higher, similar or lower post-ruminal flows relative to fatty acid intake, due to the range of effects they can have on microbial lipid synthesis (Demeyer and Doreau, 1999; Lock and Shingfield, 2003).

Approximately 80-90% of the lipid entering the small intestine is as free fatty acids attached to feed particles (Davis, 1990; Doreau and Chilliard, 1997). The remaining lipid components are microbial phospholipids plus small amounts of triglycerides and glycolipids from residual feed material, and these esterified fatty acids are hydrolyzed by intestinal and pancreatic lipases (Doreau and Ferlay, 1994). Even when protected fats are fed to dairy cows, increases in the flow of triglycerides will be observed only when encapsulated lipids are fed. Calcium salts of free fatty acids are the predominant source of protected lipids fed to ruminants and these dissociate to some extent in the rumen, but dissociation is much more extensive under the highly acidic conditions of the abomasum. Therefore, dietary lipid supplements protected by the use of Ca salts add to the pool of free fatty acids that enters the small intestine.

Fat absorption in the small intestine occurs in the jejunum and micelle formation is the key to efficient fatty acid absorption in all species (Davis, 1990). In non-ruminants, monoacylglycerols are required for micelle formation (Doreau and Chilliard, 1997). However, due to the nearly complete hydrolysis of dietary fatty acids in the rumen these are absent from digesta present in the small intestine of the ruminant. This is compensated for by the secretions of bile and pancreatic juice prior to the jejunum (Figure 3; Demeyer and Doreau, 1999). Bile supplies bile salts and lecithin, and pancreatic juice provides enzymes to convert lecithin to lysolecithins and bicarbonate to raise the pH (Davis, 1990). Lysolecithins, together with bile salts, desorb fatty acids from feed particles and bacteria, and this allows formation of the micelles. Once micelles are formed they are taken up by the epithelial cells of the jejunum where the fatty acids are re-esterified into triglycerides and then packaged into chylomicrons (Demeyer and Doreau, 1999).
Dynamics of Absorption

Doreau and Ferlay (1994) carried out an extensive review of the literature on lipid digestion using data obtained from fatty acid disappearance between the duodenum and ileum or between the duodenum and feces. Studies based on whole tract disappearance of lipid were not used because they typically underestimate fatty acid digestibility in the small intestine and lead to questionable results (Doreau and Ferlay, 1994). As discussed earlier, this is mainly due to inaccurate estimations of the dietary intake of fatty acids and because the flow of fatty acids to the duodenum is generally greater than dietary intake of fatty acids. Doreau and Ferley (1994) found a wide variation in the reported values for fatty acid digestibility, ranging from 55 to 92%, but this range was not related to fatty acid intake. In fact, the capacity of the dairy cow to absorb long-chain fatty acids is very high and can exceed 1 kg/day (Doreau and Chilliard, 1997).

In monogastrics, digestibility of individual fatty acids decreases when chain length increases, and increases as the number of double bonds increase (Lessire et al., 1992). Although similar patterns are observed in ruminants, the differences are modest (Ferlay et al., 1993). Digestibility does not differ significantly between 16 and 18 carbon saturated fatty acids and is lower for longer chain saturated fatty acids as compared to PUFA. The review by Doreau and Ferley (1994) reported that mean digestibilities were 0.77, 0.85, 0.83 and 0.76 for 18 carbon fatty acids with zero, one, two and three double bonds, respectively. Another approach to investigate fatty acid digestibility is abomasal infusion of fatty acids and these studies have generally given similar estimates of digestibility. The exception is the digestibility of linolenic acid where abomasal infusion studies observe a slightly higher value. This is probably related to inaccuracies of measuring 18:3 with unsupplemented diets because the flow of this fatty acid leaving the rumen is minimal.

Avila et al. (2000) evaluated the effects of supplemental fat from sources varying in proportions of unsaturated and saturated fatty acids on fatty acid digestibility. Increasing
the degree of unsaturation of abomasally infused fat source did not affect the fatty acid digestibility of cis-9 18:1, 18:2 or 18:3 fatty acids which averaged 0.67, 0.64 and 0.76 respectively. Interestingly, digestibility of trans 18:1 fatty acids was greater as compared to cis-9 18:1, a finding also reported by Enjalbert et al. (1997). Thus, there may also be small differences in the absorption of different 18:1 isomers, although data are limited. This may even be an evolutionary development since ruminants typically are exposed to very low amounts of cis 18:1 isomers entering the small intestine compared with the amount of trans 18:1 isomers. With the recent improvements in analytical techniques, differences in the digestibilities of individual fatty acids and fatty acid isomers can be more thoroughly examined, but application in feeding systems still requires accurate information on the profile of fatty acids leaving the rumen.

The overall conclusion is that differences in digestibility among individual fatty acids contribute very little to the extensive variation (~60-90%) in the digestibility of dietary lipids. Rather, the majority of this variation reflects differences among individual experiments, and thus relates to differences in diets and specific feed components (Demeyer and Doreau, 1999). Consequently, the composition of absorbed fatty acids is close to the composition of fatty acids leaving the rumen (Doreau et al., 1997).

The common use of rumen-protected fat in the diets of dairy cows has raised an interest in the effects of Ca-salts of fatty acids on fat digestion and absorption. In an attempt to model ruminal metabolism and intestinal digestion of fatty acids in ruminants Chalupa et al. (2003) proposed that digestion coefficients for fatty acids derived from Ca-salts were "substantially greater" than coefficients for free fatty acids entering the small intestine. However, we find little support for this in published literature. The overall pattern is that the use of Ca-salts has little or no effect on the apparent digestibility of individual fatty acids in the small intestine (Moller, 1988; Wu et al., 1991; Ferlay et al., 1993; Enjalbert et al., 1997). Where minor differences exist, these are related to differences in the fatty acid profile of the supplements being compared, and the existence of small differences in digestibility among individual fatty acids as discussed above. As an example of the comparisons, Enjalbert et al. (1997) supplemented a control diet based on maize silage and concentrate with Ca-salts of either palm or rapeseed oil and found no differences from the control in the digestibility of total fatty acids in the small intestine (average 78.2% for all dietary treatments) and no significant differences in apparent digestibility for individual fatty acids across treatments (Table 3). Likewise, Ferlay et al. (1993) compared rapeseed oil supplied either as a Ca-salt (free fatty acids) or as the oil (fatty acids present in triglycerides) and observed no differences between treatments for fatty acid digestibility in the small intestine. The lack of any effect of Ca-salts is not surprising because the Ca-fatty acid complex would be dissociated to give free fatty acids in the abomasum (Grummer and Rabelo, 1999).
Table 3. Apparent digestibility in the small intestine (proportion of duodenal flow; adapted from Enjalbert et al., 1997)

<table>
<thead>
<tr>
<th>Ca-salts</th>
<th>Differences</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Control</td>
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<tr>
<td>16:0</td>
<td>0.69</td>
</tr>
<tr>
<td>18:0</td>
<td>0.79</td>
</tr>
<tr>
<td>cis-9 18:1</td>
<td>0.77</td>
</tr>
<tr>
<td>trans-11 18:1</td>
<td>0.84</td>
</tr>
<tr>
<td>18:2</td>
<td>0.60</td>
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<tr>
<td>18:3</td>
<td>0.67</td>
</tr>
<tr>
<td>Total 18</td>
<td>0.79</td>
</tr>
</tbody>
</table>

CONCLUSIONS

The increasing use of fats in dairy cattle diets and efforts to include lipid metabolism in nutrition models require an understanding of their fate. The digestion and metabolism of dietary fats and fatty acids in ruminants is complex and in this paper we have provided an overview that highlights current limitations and recent advances. Routine methods of dietary lipid analysis, specifically ether extract, provide an estimate of the fatty acid content that varies in accuracy among feedstuffs. Although lipid hydrolysis and classical pathways of fatty acid biohydrogenation are well established, analytical improvements have revealed the complexity of lipid metabolism in the rumen. Clearly, many pathways of biohydrogenation exist and many factors related to diet and rumen environment affect this process. As a consequence, there are numerous fatty acid intermediates produced during rumen biohydrogenation. Recent research has established that some of these unique fatty acids are signaling molecules that regulate metabolic processes in the cow and that others can have beneficial health effects when consumed in dairy products. The rumen outflow of lipids are predominantly free fatty acids and differences in the digestibility of individual fatty acids in the small intestine are negligible. Thus, the composition of fatty acids absorbed in the small intestine is similar to the composition of fatty acids leaving the rumen.

The post-absorptive metabolism of fatty acids is also a complex area where advances in understanding have occurred, and this will have to be the subject of a future paper. The post-absorptive use of fatty acids as a source of energy and for synthesis of milk fat and body fat has been extensively investigated. However, the role of fatty acids as signaling molecules involved in the expression of specific genes and their regulation of metabolic processes is an emerging area, especially as it applies to ruminants. This includes recent developments relating specific biohydrogenation intermediates to the regulation of fat synthesis and the role of polyunsaturated fatty acids in the signaling pathways involved in immune function and reproduction. There is also growing literature on the role of specific fatty acids in human health and the prevention of diseases, and this knowledge may offer an exciting opportunity to design
the fatty acid composition of ruminant-derived food products. Obviously, our knowledge of lipid digestion and metabolism is rapidly advancing and the opportunity and challenge is to effectively apply this knowledge in the feeding and management of today’s high producing dairy cows.

REFERENCES


