A Review of Nutritional and Physiological Factors Affecting Goat Milk Lipid Synthesis and Lipolysis

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ABSTRACT

Although the effect of lactation stage is similar, the responses of milk yield and composition (fat and protein contents) to different types of lipid supplements differ greatly between goats and cows. Milk fat content increases with almost all studied fat supplements in goats but not in cows. However, the response of milk fatty acid (FA) composition is similar, at least for major FA, including conjugated linoleic acid (CLA) in goats and cows supplemented with either protected or unprotected lipid supplements. Goat milk CLA content increases sharply after either vegetable oil supplementation or fresh grass feeding, but does not change markedly when goats receive whole untreated oilseeds. Important interactions are observed between the nature of forages and of oil supplements on trans-10 and trans-11 C18:1 and CLA.

Peculiarities of goat milk FA composition and lipolytic system play an important role in the development of either goat flavor (release of branched, medium-chain FA) or rancidity (excessive release of butyric acid). The lipoprotein lipase (LPL) activity, although lower in goat than in cow milk, is more bound to the fat globules and better correlated to spontaneous lipolysis in goat milk. The regulation of spontaneous lipolysis differs widely between goats and cows. Goat milk lipolysis and LPL activity vary considerably and in parallel across goat breeds or genotypes, and are low during early and late lactation, as well as when animals are underfed or receive a diet supplemented with protected or unprotected vegetable oils. This could contribute to decreases in the specific flavor of goat dairy products with diets rich in fat.

(Key words: goat milk fat, fatty acids, lipoprotein lipase, lipolysis)

INTRODUCTION

Lipid composition is one of the most important components of the technological and nutritional quality of goat milk. Lipids are involved in cheese yield (per kilogram of milk) and firmness, as well as in the color and flavor of caprine dairy products (Delacroix-Buchet and Lamberet, 2000). Besides their quantitative contribution to the amount of dietary energy, the different fatty acids (FA) (short- and medium-chain, saturated, branched, mono- and polyunsaturated, cis and trans, conjugated) are potentially involved as positive or negative predisposing factors for the health of human consumers (Parodi, 1999; Sébédio et al., 1999; Williams, 2000). Furthermore, the peculiarities of goat milk lipolytic system (Chilliard, 1982) and medium-chain FA (Ha and Lindsay, 1993) could greatly change the content in free FA, playing a major role in the occurrence of the characteristic goat flavor.

Fat supplementation of diets could improve goat milk composition for greater control of cheese processing and satisfaction of consumer demand. Dietary lipid supplementation may indeed change milk fat FA composition and result in positive or adverse changes in the physical characteristics and the nutritional or dietetic properties of goat dairy products, and/or modify the lipolytic system (Chilliard, 1982) and hence the flavor of these products. Furthermore, the expected positive effects of fat supplementation on goat milk fat content (Chilliard and Bocquier, 1993) could be useful in solving the technological problems of the goat cheese industry, which are linked to a low milk fat content, especially when fat content falls below protein content (the so-called “inversion of percentages syndrome”) (Morand-Fehr et al., 2000b). Although fat supplementation in dairy cows and ewes often decreases the milk protein content and the associated coagulation properties, this negative ef-
The aim of this paper is to review the main effects of physiological and nutritional factors, and more particularly recent studies on fat supplementation, on goat milk fat and protein contents, fatty acid composition, lipase activity and lipolysis.

Milk Fat Secretion and Composition

Goat Milk FA Composition

In comparison with cow milk, goat milk is higher in medium-chain FA (C8, caprylic acid and, more markedly, C10, capric acid). Conversely, cow milk is higher in butyric (C4) and, sometimes, palmitic (C16:0) acids (Glass et al., 1967). Thus, the regulation of mammary cells differs between caprine and bovine species, particularly in the elongation process of FA, which are synthesized de novo by the "fatty acid synthase" complex. A detailed comparison of the mechanisms between these two species would contribute to a better knowledge of the regulation of milk fat synthesis in ruminants (Knudsen and Grunnet, 1982), which is less well known than in rodent species (Barber et al., 1997).

Milk unsaturated FA may contain one or several trans double bonds. About 5 to 15% of total C18:1 are of trans configuration in goat (Bickerstaffe et al., 1972; Calderon et al., 1984; Alonso et al., 1999), cow (Storry and Rook, 1965; Selner and Schultz, 1980) and human species (Jensen, 1989; Guesnet et al., 1993). However, the proportion of different trans isomers varies between species: the main FA (35 to 40%) is trans-vaccenic acid (C18:1, n-7 or \( \Delta 11 \)) in goat and cow milk (Bicherstaffe et al., 1972; Alonso et al., 1999; LeDoux et al., 2002; Figure 1A and B), whereas human milk fat trans C18:1 contains larger percentages of FA with the double bond located on carbons 6 to 14 (Figure 1C). The profile of human milk fat is probably related to the consumption
Figure 2. Main pathways of milk trans fatty acids and conjugated linoleic acid synthesis (from Grininari and Bauman, 1999). (a) linolenic acid, (b) linoleic acid, (c) rumenic acid, (d) trans-vaccenic acid, (e) stearic acid, (f) oleic acid; SCD, stearoyl-CoA (delta-9) desaturase.

of a mixture of ruminant milk fat and of margarines, the latter being richer in Δ 6 to Δ 14 - trans C18:1, especially Δ 6 to Δ 10 (Figure 1 D). Quantitatively, the trans C16:1 isomers represent less than 0.2% of total FA, or 5% of all trans C16:1 and C18:1 isomers in ruminant milk fat. The distribution patterns of cis and trans C16:1 isomers are very similar for goat, cow, and ewe cheese fat (Destaillats et al., 2000).

The trans FA of margarines originate from industrial hydrogenation of polyunsaturated FA from vegetable oils, whereas ruminant trans FA originate from ruminal hydrogenation of polyunsaturated FA of forages and concentrates (Figure 2). Conjugated linoleic acid (CLA) is a precursor of trans-vaccenic acid in the rumen and a product of the delta-9 desaturation of this FA in the mammary gland (Figure 2). The major isomer (more than 90%) of bovine milk CLA (cis-9, trans-11 C18:2, or rumenic acid, RA) originates mainly from the latter pathway (Grininari and Bauman, 1999). It is interesting to emphasize that milk fat from monogastric farm animals such as mare or sow (that do not consume ruminant milk fat or margarines) is almost devoid of trans-vaccenic acid and RA, whereas human milk fat is of an intermediate composition (Jahreis et al., 1999). In that study, the trans-vaccenic and RA contents of goat milk fat were lower than those of milk fat from cow or ewe receiving similar diets. However, the mean milk RA values from three other goat studies were in the range 0.4 to 0.9% of total FA (Alonso et al., 1999; Gulati et al., 2000; Chilliard et al., 2002), i.e., similar to observations in dairy cows receiving diets without added lipids (Grininari and Bauman, 1999; Chilliard et al., 2000).

Effects of Changes in Lactation Stage and Energy Balance on Milk Fat Secretion and Composition

Milk fat content is high after parturition and then decreases during the major part of lactation in the goat (Chilliard et al., 1986; Sauvant et al., 1991) as in the cow (Jarrige et al., 1978). This is related to at least two phenomena: a dilution effect due to the increase in milk volume until the lactation peak, and a decrease in fat mobilization that decreases the availability of plasma NEFA, especially C18:0 and C18:1, for mammary lipid synthesis. Highly significant correlations were found between milk fat content and either energy balance, plasma NEFA content, r = -0.58; milk fat content versus energy balance, r = -0.77; milk fat content versus plasma NEFA content, r = +0.46; milk fat content versus milk C18:1 (%), r = +0.47.

Effects of Changes in Lactation Stage and Energy Balance on Milk Fat Secretion and Composition

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The nutritional status of lactating animals can be estimated by their energy (or protein, mineral, etc.) balance, i.e., by the difference between ingested nutrients and requested nutrients for body maintenance and for milk secretion. This balance is highly variable, according to animal milk genetic potential and lactation stage, as well as to composition and nutrient density of the diet. When energy balance is negative, animals mobilize lipids stored in adipose tissues, mainly in the form of NEFA. As ruminant adipose tissues are very
Effects of Lipid Supplementation on Milk Fat Secretion

Dietary factor (forage-to-concentrate ratio, type of forages, etc.) effects on goat milk composition have been reviewed by Morand-Fehr et al. (2000a). Dietary lipid supplementation is a means for increasing both energy intake and efficiency in early lactation-high yielding cows, thereby increasing milk yield, but it did not limit the mobilization of body lipids (Chilliard, 1993). Effects of lipid supplementation on goat milk secretion have been reviewed by Morand-Fehr et al. (1982) and Polidori et al. (1991). Feeding diets very low in lipids decreased goat milk yield and fat content, and this was reversed by lipid supplementation (Delage and Fehr, 1967; Morand-Fehr et al., 1984a, Table 1).

In four early-lactation trials (Table 1), lipid supplementation tended to increase milk yield (+0.1 to +0.4 kg/d or more when the control diet was very low in fat) and fat content (+2 to +7 g/kg). Effects on protein content were highly variable. The calculated energy balance increased or decreased according to respective effects on intake of DM and energy, and milk fat secretion. In three other early-lactation trials, milk yield and protein content remained unchanged, and fat content increased, with either protected sunflower seeds (15% of concentrate; Morand-Fehr et al., 1984a), extruded soybeans (160 g/d; Morand-Fehr et al., 1984b) or calcium soaps of palm oil (100 g/d; Martin et al., 1999). There were no clear trends concerning effects of fat supplementation on goat BW changes or body fat mobilization during early lactation. Results from early-lactation experiments are limited by their lack of precision, linked to possible differences in milk potential of animals and limited use of covariates, when lipid supplementation begins before or immediately after parturition.

Contrary to what was observed in dairy cows (Chilliard et al., 2001), feeding fat supplements to mid- or late-lactation goats did not increase milk yield, whereas milk fat content always increased sharply (+5.7 g/kg in 23 supplemented groups in Table 2). The ranges of observed responses were similar with different types of fat supplements: saturated free FA, calcium salts or triglycerides; animal fat; vegetable oils (C18:1-, C18:2-, or C18:3-rich oils; free oils, encapsulated oils); oilseed (whole, crushed, extruded, or formaldehyde-treated oil seeds) (Table 2, and Schmidely and Sauvant, 2001). Remarkably, goat milk fat content did not decrease even when vegetable oils (rich in polyunsaturated FA) were added to a low-forage diet (e.g., footnote 8 in Table 2), contrary to what was very clearly observed in dairy cows (Bauman and Grinnari, 2001). As previously observed for early-lactation goats, response of milk protein content was highly variable in midlactation goats (Table 2). Body weight gain was either higher (Baldi et al., 1992), lower (Gelaye and Amoah, 1988), or unchanged (footnote 8 in Table 2) in fat supplemented vs. control goats.
The response of dairy goats to fish oil supplements is not well known but differs from the responses to other fat supplements. Feeding unprotected fish oil to goats sharply decreased DMI and milk yield without changing milk fat content (Kitessa et al., 2001). This differs markedly from cow responses, where milk yield increased (despite a significant decrease in dry matter intake) and milk fat content decreased sharply (Chilliard and Doreau, 1997). Feeding partially protected fish oil (20 g/d of EPA + DHA) to goats did not change intake, milk yield, or milk fat content (Kitessa et al., 2001). This contradicts the results of Léger et al. (1994), showing that a duodenal infusion of EPA + DHA (4 g/d) decreased goat milk fat content, as observed in cows (Chilliard et al., 2000, 2001).

The response of milk fat secretion to fat supplementation could be lower during midlactation than during early lactation (Figure 5). This could be related to the fact that goat adipose tissue anabolic enzymes involved in de novo lipogenesis, and lipoprotein lipase (the enzyme involved in the uptake of blood lipoproteins carrying dietary FA absorbed from the intestine), are more active after the lactation peak than before it (Chilliard et al., 1977, 1979a), because they are positively related to energy balance (Chilliard et al., 1987). Body lipid mobilization dominates during early lactation, and this would favor the partitioning of dietary FA towards the mammary gland (Chilliard, 1993). It results from these events that a greater part of the exogenous FA are taken up by the adipose tissue after the lactation peak (Chilliard et al., 1991). However, contrary to milk fat secretion, the highest milk fat content responses were observed in late-lactating or low-yielding goats (Table 2), probably because the dietary FA were less diluted in the milk of these animals.

Results available in dairy cattle (Chilliard et al., 2001), goat (Chilliard and Bocquier, 1993, and present review), and sheep (Chiofalo et al., 1993; Caja and Bocquier, 2000; Nudda et al., 2002) show that responses to fat supplementation differ considerably according to the species:

- milk yield increases in midlactation dairy cows, but not in goats and ewes;
- milk fat content (and fat secretion) sharply increases in dairy ewes and goats, but not always in dairy cows in which it could often either decrease or not change;
- milk protein content decreases in dairy cows and ewes, but not in goats. Milk protein secretion decreases in milking ewes, but does not change in dairy cows and goats.

The reasons for these differences in dairy performance response to fat supplementation between ruminant species are not easy to identify, as fewer trials and less information are available for ewes and goats than for dairy cows. The differences may be linked to complex digestive and metabolic interactions (as observed in dairy cows) between the basal diet (nature and proportion of forages and concentrates), fat supplementation (nature and technological treatment, dose and/or duration) and animal characteristics (species, breed, lactation stage, milk potential, etc.; see reviews from Chilliard et al., 2000; Bauman and Gruinari, 2001). It has been suggested that the rate of passage of digesta
is higher in goats than cows (Hart, 2000). This could decrease in goats the effects of dietary FA on the yield of some ruminal factors that reduce mammary lipogenesis in cows.

Effects on mammary metabolism of the balance and availability of glucogenic, lipogenic, and aminogenic nutrients (including related endocrine changes) are not completely understood, and may vary between species, thus changing their relative responses in lactose, fat, and protein secretions. Furthermore, the caprine α-s1 casein locus is remarkable for its high level of polymorphism and for the fact that important differences exist in milk protein content and, in some cases, in fat content between alleles or groups of alleles (Grosclaude et al., 1994; Tables 3 and 4). It is not known whether the response to dietary fat supplementation would be different between these genotypes.

Goat milk production is largely used for transformation into cheese. Fat supplementation changes goat milk composition in ways that allow a better control of cheese processing. Indeed, one problem encountered with fat supplementation in dairy cows and ewes is that the milk protein content is most of times reduced, thus altering coagulation properties. However, this negative effect does not exist in goats (Table 2). Furthermore, the clear positive effects of almost all types of fat supplementation on milk fat content could be useful to solve the technological problems of the goat cheese industry which are linked to the so-called “inversion of percentages syndrome” during the spring and summer.

Table 2. Effects of fat supplementation on dairy performance1 in mid- or late-lactation goats.

<table>
<thead>
<tr>
<th>Lipid sources (% of concentrate)</th>
<th>Milk yield (kg/d)</th>
<th>Fat content (g/kg)</th>
<th>Protein content (g/kg)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Palmitic acid, 14%</td>
<td>−0.06</td>
<td>+1.4</td>
<td></td>
<td>Astrup et al., 1985</td>
</tr>
<tr>
<td>Stearic acid, 14%</td>
<td>+0.10</td>
<td>+0.5</td>
<td></td>
<td>Astrup et al., 1985</td>
</tr>
<tr>
<td>Animal fat2</td>
<td>−0.38</td>
<td>+2.0</td>
<td>−1.0</td>
<td>Gelaye and Amoah, 1988</td>
</tr>
<tr>
<td>Animal fat2</td>
<td>−0.29</td>
<td>+7.0</td>
<td>+1.0</td>
<td>Lu, 1993</td>
</tr>
<tr>
<td>Animal fat, 4%</td>
<td>−0.09</td>
<td>+3.7</td>
<td>+1.4</td>
<td>Daccord, 1987</td>
</tr>
<tr>
<td>Calcium salts, 15%3</td>
<td>−0.02</td>
<td>+14.23</td>
<td>+1.5</td>
<td>De Maria Ghionna et al., 1987</td>
</tr>
<tr>
<td>Calcium salts4</td>
<td>+0.10</td>
<td>+3.7</td>
<td>−0.1</td>
<td>Teh et al., 1994</td>
</tr>
<tr>
<td>Calcium salts5</td>
<td>+0.21</td>
<td>+5.2</td>
<td>+0.3</td>
<td>Rousselot et al., 1995</td>
</tr>
<tr>
<td>Calcium salts, 6%6</td>
<td>+0.10</td>
<td>+3.0</td>
<td>0.0</td>
<td>Buldi et al., 1992</td>
</tr>
<tr>
<td>Canola oil, 4%</td>
<td>+0.19</td>
<td>+9.2</td>
<td>−0.3</td>
<td>Mir et al., 1999</td>
</tr>
<tr>
<td>Treated linseeds, 23%7</td>
<td>−0.20</td>
<td>+6.3</td>
<td>+1.4</td>
<td>Ferlay et al.7</td>
</tr>
<tr>
<td>Linseeds, 14%8</td>
<td>+0.27</td>
<td>+5.5</td>
<td>+2.5</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>Linseed oil, 5%8</td>
<td>+0.30</td>
<td>+4.2</td>
<td>+2.4</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>Sunflower seeds, 9%8</td>
<td>+0.42</td>
<td>+6.3</td>
<td>+2.1</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>Sunflower oil (SO), 5%8</td>
<td>+0.42</td>
<td>+4.9</td>
<td>+1.3</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>High-oleic SO, 8%7</td>
<td>−0.10</td>
<td>+7.2</td>
<td>+0.3</td>
<td>Ferlay et al.7</td>
</tr>
<tr>
<td>Lupine, 51%8</td>
<td>+0.23</td>
<td>+2.8</td>
<td>+1.9</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>Soybean, 26%5</td>
<td>+0.49</td>
<td>+3.9</td>
<td>+1.4</td>
<td>Rouel et al.8</td>
</tr>
<tr>
<td>Soybean, 49%9</td>
<td>−0.14</td>
<td>+9.34</td>
<td>+0.3</td>
<td>Bernard et al.9</td>
</tr>
<tr>
<td>Extruded soybean, 20%</td>
<td>−0.69</td>
<td>+4.5</td>
<td>+1.9</td>
<td>Daccord, 1987</td>
</tr>
<tr>
<td>Cottonseed, 18%</td>
<td>−0.02</td>
<td>+4.4</td>
<td></td>
<td>Bartocci et al., 1988</td>
</tr>
<tr>
<td>Protected oil, 7%10</td>
<td>−0.08</td>
<td>+2.9</td>
<td>−0.8</td>
<td>Lanzani et al., 1985</td>
</tr>
<tr>
<td>Olive cake silage11</td>
<td>−0.05</td>
<td>+3.1</td>
<td>−0.5</td>
<td>Hadjipanayotou, 1999</td>
</tr>
</tbody>
</table>

Mean response (±sd)          +0.07 (±0.27) | +5.74 (± 3.0) | +0.9 (±1.1) |

1Significant response (P < 0.01).
1Differences between fat supplemented and control groups.
25% of the ration.
2Calcium salts of palm oil, fed to low-yielding goats (1.6 kg milk/d).
3High response in late-lactation or low-yielding goats.
4Calcium salts of palm oil, 3–4% of the ration.
5Calcium salts of sunflower (50%), tallow and lard.
6Calcium salts of sunflower (50%), tallow and lard.
7Diet with 3.6% added fat from formaldehyde-treated crushed linseeds or high-oleic sunflower oil; five goats per group (A. Ferlay, J. Rouel, L. Bernard and Y. Chilliard, unpublished).
8Diet with 3.6% added fat, four late-lactation (280 d) goats per group (L. Bernard, J. Rouel and Y. Chilliard, unpublished).
9Low-forage (30% of total DM) diets with 3.4% added fat, 12 goats per group (J. Rouel, E. Bruneteau and Y. Chilliard, unpublished).
10Diets with 3.8% added fat, four late-lactation (280 d) goats per group (L. Bernard, J. Rouel and Y. Chilliard, unpublished).
11Protected oil was 25% soybean oil and 75% maize meal treated with formaldehyde. The supplemented group differed also from control group by receiving 30% of the concentrate DM as liquid feed (molasses, animal protein, etc.).
12Diet containing 16% DM as olive cake silage, corresponding to 1.4% added fat.
Figure 5. Response of milk fat secretion to fat intake in the goat, according to lactation stage: early (●), or mid-lactation (○) (from Sauvant et al., 1983).

Effects of Lipid Supplementation on Milk FA Composition

**Palmitic or stearic acid.** Feeding of palmitic acid increased goat milk C16:0 percentage considerably (Table 5). When stearic acid was fed instead, milk C18:0 and C18:1 percentages increased considerably, at the expense of C10:0 to C16:1 (Table 5). These results illustrate the important role of mammary delta-9 desaturase in regulating the monounsaturated:saturated FA ratio, especially for C18 FA.

**Calcium salts of palm oil.** In three trials, feeding calcium salts of palm oil (rich in palmitic and oleic acids) to lactating goats increased the percentage of C18:1 and/or C16:0 in milk fat (Table 6). Another goat trial also reported an increase in milk C16:0 percentage (Sleiman et al., 1998). These results are comparable to those observed in dairy cows, showing increases in both palmitic acid and C18:1 (Table 6), although the responses were more marked in goats.

**Encapsulated oils.** When vegetable oils or oilseeds are fed to ruminants, their polyunsaturated FA are largely hydrogenated in the rumen (Figure 2), unless these lipid supplements are efficiently protected by encapsulation in a formaldehyde-treated protein coat (McDonald and Scott, 1977). This is illustrated by data in Table 5 showing that feeding protected canola seeds to goats increased milk C18:1, C18:2, and C18:3 proportionally to the respective percentages of these FA in canola oil. On the other hand, feeding unprotected oil increased mainly C18:0 and C18:1, the latter increase probably being due, to a large extent, to unidentified *trans* isomers of C18:1 (cf. Griinari and Bauman, 1999; Chilliard et al., 2000, 2001, for data in cows). This illustrates that both total and partial hydrogenation of unsaturated FA take place in the rumen (Figure 2).

Feeding protected soybean oil sharply increased milk C18:2 percentage (Table 5). The increase in C18:0 (and probably part of the C18:1) could be because some soybean oil escaped protection and was hydrogenated to C18:0 and *trans*-C18:1. In this trial, the increase in milk C18-FA was compensated for by a sharp decrease in the C16:0 percentage, although there was a trend for increasing short- and medium-chain FA percentages.

The effect of feeding protected cottonseeds differed from that of other vegetable oils, resulting in a large increase in the milk C18:2 percentage and in the C18:0 to C18:1 ratio, despite the fact that this oil is poor in C18:0 and contains only 16% of C18:1 (Table 5). This response is related to the fact that cottonseeds are rich in cyclopropenoic FA, which are strong inhibitors of mammary delta-9 desaturase activity. With unprotected cottonseeds, the increase in milk C18:2 did not occur, whereas the increase in milk C18:1 (Table 5) was probably due in part to unidentified *trans* isomers of C18:1 arising from C18:2 hydrogenation in the rumen.

Responses were different when linseeds were added to the diet. Milk C18:3 (n-3) percentage was signifi-
Table 4. Effects of casein α-s1 genotype and lactation stage on Alpine goat milk composition and lipolysis.1

<table>
<thead>
<tr>
<th>Casein α-s1 genotype</th>
<th>Lactation stage (mo)</th>
<th>High2</th>
<th>Low3</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td></td>
<td>6</td>
</tr>
<tr>
<td>Milk yield (kg/d)</td>
<td>3.3</td>
<td>2.9</td>
<td>3.5</td>
</tr>
<tr>
<td></td>
<td>3.2</td>
<td></td>
<td>3.2</td>
</tr>
<tr>
<td>Protein content (g/kg)</td>
<td>32.2</td>
<td>32.3</td>
<td>26.1b</td>
</tr>
<tr>
<td></td>
<td>28.1b</td>
<td></td>
<td>26.9b</td>
</tr>
<tr>
<td>Fat content (g/kg)</td>
<td>36.4</td>
<td>28.7a</td>
<td>29.5b</td>
</tr>
<tr>
<td></td>
<td>29.5b</td>
<td></td>
<td>22.6b</td>
</tr>
<tr>
<td>Lipolysis (mmol FFA/100 g fat)</td>
<td>0.78</td>
<td>1.56</td>
<td>0.64</td>
</tr>
<tr>
<td></td>
<td>2.30a</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Significantly different (P < 0.01) from previous lactation stage.
2Significantly different (P < 0.01) from “high casein α-s1 genotype”.
4Ten AA goats.
5Ten goats (6EF, 2EO and 2FF).

Cannily increased by 159 or 320% when goats received a diet with 4% added fat from either crushed linseeds or formaldehyde-treated crushed linseeds, respectively (Y. Chilliard, P. Capitan, J. Rouel, A. Ferlay, unpublished results). These results show that C18:3 was partially protected in crushed linseeds, and that formaldehyde treatment approximately doubled (P < 0.01) its degree of protection.

Unprotected oils or seeds. The response to feeding different kinds of unprotected lipid supplements consisted mainly of an increase in the percentages of milk C18:0 and C18:1, at the expense of mainly C8 to C14 (and C16:0 in most trials; Astrup et al., 1985; De Maria Ghionna et al., 1987; Bartocci et al., 1988; Baldi et al., 1992; Mir et al., 1999; Schmidely and Sauvant, 2001; Tables 7 and 8). This was probably due to the ruminal hydrogenation of polyunsaturated FA into C18:0 and trans-C18:1, which are inhibitors of the de novo FA synthesis, mainly C8 to C16. The final response of milk C16:0 percentage depended on the level of dietary intake, that is, the C16:0 percentage in the lipid supplement which was studied. The decreases of C12:0 to C16:0 resulted in a sharp decrease in the atherogenicity index of the milk fat (Tables 7 and 8). The responses to fat supplementation of C4 to C8 were less marked, or even opposite to those of C10 to C14 (Tables 5, 7, and 8), and this peculiarity is probably related to their origin from nonmalonyl CoA pathways (see above).

The responses to unprotected fish oil supplementation (3% of diet DM, Kitessa et al., 2001) consisted of an increase in milk fat trans-C18:1 percentage, a decrease in C18:0, small increases in C20:5 and C22:6, the appearance of 10-hydroxystearic acid, and a very sharp (+33%) increase in oleic acid, probably due to body fat mobilization since DMI decreased by 50%. The transfer rates to milk of C20:5 and C22:6 (about 4 to

Table 5. Effect of different lipid supplements1 on goat milk fatty acid composition.

<table>
<thead>
<tr>
<th>Supplement</th>
<th>Saturated FA2</th>
<th>Canola seeds3</th>
<th>Soybean oil4</th>
<th>Cotton seeds5</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C16:0</td>
<td>C18:0</td>
<td>Protected</td>
<td>Unprotected</td>
</tr>
<tr>
<td>C4:0 to C8:0</td>
<td>+1.5</td>
<td>+0.5</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>C10:0 to C14:0</td>
<td>−4.4</td>
<td>−4.2</td>
<td>−0.6</td>
<td>−2.0</td>
</tr>
<tr>
<td>C16:0</td>
<td>+6.4</td>
<td>−6.2</td>
<td>−8.2</td>
<td>−4.1</td>
</tr>
<tr>
<td>C16:1</td>
<td>+2.4</td>
<td>−2.0</td>
<td>nd</td>
<td>nd</td>
</tr>
<tr>
<td>C18:0</td>
<td>0.0</td>
<td>+7.0</td>
<td>−3.9</td>
<td>+5.8</td>
</tr>
<tr>
<td>C18:1</td>
<td>−2.0</td>
<td>+6.6</td>
<td>+7.9</td>
<td>+6.9(c/t ?)</td>
</tr>
<tr>
<td>C18:2</td>
<td>−0.5</td>
<td>−0.6</td>
<td>+5.9</td>
<td>+1.1</td>
</tr>
<tr>
<td>C18:3</td>
<td>+0.3</td>
<td>−0.6</td>
<td>+3.1</td>
<td>+0.5</td>
</tr>
</tbody>
</table>

1Effects expressed as the difference between fat supplemented and non-supplemented control groups. nd = not determined.
2C16:0 or C18:0 (14% of the concentrate); from Astrup et al. (1985).
3110 g oil/d (55% C18:1 + 25% C18:2 + 11% C18:3); from Gulati et al. (1997).
4Soybean oil (12% C16:0 + 20% C18:1 + 50% C18:2) at 1.8% of concentrate, in formaldehyde treated maize meal; from Lanzani et al. (1985).
5Cottonseed oil contains 22% C16:0 + 16% C18:1 + 57% C18:2.
6110 g lipids/d; from Gulati et al. (1997).
734 g lipids/d; from Bartocci et al. (1988).
8c/t = cis/trans.
milk (about 6 to 7%) (Kitessa et al., 2001).

slightly the transfer rate of C20:5 and C22:6 to goat C18:1 and 10-hydroxystearic acid, and increased C18:2). These four treatments sharply increased goat either linseed (rich in C18:3) or sunflower (rich in polyunsaturated FA, contrary to the other seeds, seeds and whole soybeans showed that all four seeds sharply increased milk stearic and oleic acids. However, the highest oleic:stearic ratio was observed with lupine seeds, probably because they did not increase the secretion of polyunsaturated FA, contrary to the other seeds, which increased either C18:3 (linseeds) or C18:2 (sunflower and soybean beans). Thus the mammary delta-9

5%), which escaped from ruminal biohydrogenation, were similar to those (about 3 to 4%) observed in dairy cows (Chilliard et al., 2001). The partial protection by a casein-formaldehyde coating, which avoided the increases in oleic acid, did not avoid the increases in fat content (+3 to 6 g/kg), but had very different effects on milk FA composition. Linseed oil had a greater effect on increasing the percentages of milk linoleic acid (+325%) and cis 9, trans 13 isomer of C18:2 (+350%), whereas sunflower oil had more effect on milk linoleic (+55%), trans-vaccenic (+290%) and rumenic (+283%) acids, probably undergoing the mechanisms indicated in Figure 2. trans-Vaccenic acid and RA and, surprisingly, polyunsaturated FA were more significantly increased by free oil than by oilseeds, whereas stearic and oleic acids were less affected. This suggests that biohydrogenation was less efficient when oil was added free than as part of the seeds, and that a low concentration of free oil (3 to 4% of diet DM) was sufficient to disturb rumen metabolism in a way that inhibited the biohydrogenation of its own FA, thus increasing the transfer of polyunsaturated and trans FA to milk.

The comparison of these two whole seeds with lupine seeds and whole soybeans showed that all four seeds sharply increased milk stearic and oleic acids. However, the highest oleic:stearic ratio was observed with lupine seeds, probably because they did not increase the secretion of polyunsaturated FA, contrary to the other seeds, which increased either C18:3 (linseeds) or C18:2 (sunflower and soybean beans). Thus the mammary delta-9

5(C12 + C14 + C16 + C18 + C20 + C22 + C24)

Table 6. Effects of feeding calcium salts of palm oil on milk FA (%).

<table>
<thead>
<tr>
<th>Intake</th>
<th>C16:0</th>
<th>C18:0</th>
<th>C18:1</th>
<th>C18:2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Goat2</td>
<td>92</td>
<td>+0.46</td>
<td>+0.3</td>
<td>+6.4</td>
</tr>
<tr>
<td>Goat3</td>
<td>100</td>
<td>+3.4</td>
<td>+0.5</td>
<td>-1.1</td>
</tr>
<tr>
<td>Goat4</td>
<td>113</td>
<td>+4.1</td>
<td>+0.8</td>
<td>+5.8</td>
</tr>
<tr>
<td>Cow5</td>
<td>769</td>
<td>+2.1</td>
<td>+0.2</td>
<td>+2.2</td>
</tr>
</tbody>
</table>

1 Calcium salts of palm oil (g/d).
2 From De Maria Ghionna et al. (1987) (low-yielding goats).
3 From Martin et al. (1999) (early-lactation).
4 From Rapetti et al. (2002) (midlactation).
5 Six trials (review by Chilliard et al., 1993).
6 Difference between fat supplemented and control groups.

Table 7. Milk yield and composition in goats fed a low forage diet1 supplemented or not with oils or whole crude oilseeds2 (7 goats per group). (Y. Chilliard, J. Rouel, P. Capitan, E. Bruneteau, A. Ferlay, unpublished data).

<table>
<thead>
<tr>
<th>Diet</th>
<th>Control</th>
<th>Linseed oil</th>
<th>Sunflower oil</th>
<th>Sunflower seeds</th>
<th>Lupine seeds</th>
<th>Soybeans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Milk yield3 (kg/d)</td>
<td>2.86</td>
<td>3.12</td>
<td>2.91</td>
<td>3.15</td>
<td>3.11</td>
<td>3.16</td>
</tr>
<tr>
<td>Fat content (g/kg)</td>
<td>25.5a</td>
<td>28.6b</td>
<td>31.5c</td>
<td>30.7b</td>
<td>31.3b</td>
<td>29.2b</td>
</tr>
<tr>
<td>Protein content (g/kg)</td>
<td>27.2a</td>
<td>29.6bc</td>
<td>30.0c</td>
<td>28.2ab</td>
<td>29.1bc</td>
<td>29.0bc</td>
</tr>
<tr>
<td>Lactose content (g/kg)</td>
<td>43.2a</td>
<td>45.7b</td>
<td>45.4b</td>
<td>44.0ab</td>
<td>43.1a</td>
<td>44.6b</td>
</tr>
<tr>
<td>Fatty acids (w% of total FA)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C16:0</td>
<td>24.9a</td>
<td>16.3b</td>
<td>18.0b</td>
<td>17.3b</td>
<td>16.9b</td>
<td>18.6b</td>
</tr>
<tr>
<td>C18:1t 11</td>
<td>1.0a</td>
<td>2.9b</td>
<td>1.3c</td>
<td>3.9b</td>
<td>2.3d</td>
<td>0.7a</td>
</tr>
<tr>
<td>C18:1 c9</td>
<td>19.1b</td>
<td>22.6ab</td>
<td>24.7cd</td>
<td>20.8d</td>
<td>23.9bc</td>
<td>27.4d</td>
</tr>
<tr>
<td>C18:2 c9 t13</td>
<td>0.2a</td>
<td>0.9b</td>
<td>0.4c</td>
<td>0.4d</td>
<td>0.2a</td>
<td>0.2a</td>
</tr>
<tr>
<td>C18:2 c9 c12</td>
<td>2.2a</td>
<td>2.2ab</td>
<td>1.9b</td>
<td>3.4c</td>
<td>3.0d</td>
<td>1.6e</td>
</tr>
<tr>
<td>C18:3 c9 c12 c15</td>
<td>0.4b</td>
<td>1.7c</td>
<td>1.2d</td>
<td>0.5b</td>
<td>0.5c</td>
<td>0.6a</td>
</tr>
<tr>
<td>C18:2 c9 t11</td>
<td>0.6a</td>
<td>1.4b</td>
<td>0.6c</td>
<td>2.3b</td>
<td>0.8d</td>
<td>0.3c</td>
</tr>
<tr>
<td>Unidentified</td>
<td>3.6</td>
<td>10.1</td>
<td>6.1</td>
<td>8.5</td>
<td>6.7</td>
<td>4.8</td>
</tr>
<tr>
<td>Atherogenicity index5</td>
<td>2.9a</td>
<td>121b</td>
<td>1.61b</td>
<td>1.35c</td>
<td>1.48bc</td>
<td>1.7b</td>
</tr>
</tbody>
</table>

1 Natural grassland hay (30%) and concentrates with or without oils or oilseeds (70%).
2 3.4 ± 0.6% added lipid in DM intake (supplemented-control). Linseed oil contains 6% C16:0 + 17% C18:1 + 15% C18:2 + 57% C18:3; Sunflower oil contains 6% C16:0 + 22% C18:1 + 66% C18:2; Lupine seeds contain 8% C16:0 + 31% C18:1 + 48% C18:2 + 5% C18:3; Soybeans contain 12% C16:0 + 21% C18:1 + 52% C18:2 + 8% C18:3.
3 Data in same row with similar superscript letters do not differ at P < 0.05 level.
4 Odd and/or branched-chain FA (with 11 to 17 carbons).
interactions between forage nature and vegetable oil supplementation (5 to 6% of diet DM) on goat milk yield and composition (from Chilliard et al., 2002 and unpublished results).1

<table>
<thead>
<tr>
<th></th>
<th>Corn silage</th>
<th>Alfalfa hay</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C</td>
<td>LO5</td>
</tr>
<tr>
<td>Milk yield (kg/d)</td>
<td>3.62$^{a}$</td>
<td>3.98$^{b}$</td>
</tr>
<tr>
<td>Fat content (g/kg)</td>
<td>34.4$^{a}$</td>
<td>34.6$^{a}$</td>
</tr>
<tr>
<td>Protein content (g/kg)</td>
<td>28.3$^{a}$</td>
<td>28.9$^{abc}$</td>
</tr>
<tr>
<td>Lactose content (g/kg)</td>
<td>45.6$^{a}$</td>
<td>47.1$^{b}$</td>
</tr>
<tr>
<td>Fatty acids (w% of total FA)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>C4:0</td>
<td>2.2$^{ac}$</td>
<td>2.9$^{b}$</td>
</tr>
<tr>
<td>C10:0</td>
<td>10.0$^{a}$</td>
<td>8.4$^{a}$</td>
</tr>
<tr>
<td>C14:0</td>
<td>11.6$^{a}$</td>
<td>8.7$^{a}$</td>
</tr>
<tr>
<td>C16:0</td>
<td>28.8$^{a}$</td>
<td>18.5$^{b}$</td>
</tr>
<tr>
<td>O &amp; BC</td>
<td>3.7$^{a}$</td>
<td>3.0$^{a}$</td>
</tr>
<tr>
<td>C18:0</td>
<td>7.5$^{a}$</td>
<td>9.2$^{b}$</td>
</tr>
<tr>
<td>C18:1 t10</td>
<td>0.2$^{a}$</td>
<td>3.0$^{a}$</td>
</tr>
<tr>
<td>C18:1 t11</td>
<td>1.3$^{a}$</td>
<td>6.8$^{a}$</td>
</tr>
<tr>
<td>C18:1 t9</td>
<td>15.7$^{a}$</td>
<td>14.8$^{a}$</td>
</tr>
<tr>
<td>C18:2 t9c12</td>
<td>2.0$^{a}$</td>
<td>1.5$^{a}$</td>
</tr>
<tr>
<td>C18:3 t9c12t15</td>
<td>0.32$^{a}$</td>
<td>0.68$^{a}$</td>
</tr>
<tr>
<td>C18:2 t9 t11</td>
<td>0.59$^{ad}$</td>
<td>2.25$^{b}$</td>
</tr>
<tr>
<td>Atherogenicity index$^7$</td>
<td>3.4$^{a}$</td>
<td>1.7$^{a}$</td>
</tr>
</tbody>
</table>

1C, LO, OSO, O, BC = control, linseed oil, oleic sunflower oil, odd-numbered FA, branched-chain FA, respectively; 12 goats per group, except hay-control group (n = 10); data in same row with similar superscript letters do not differ at $P < 0.05$ level.

2,3Probability for LO or OSO effect, respectively.

4Probability for forage-oil interaction (l or s indicates significant interaction for LO or OSO, respectively).

5Linseed oil contains 6% C16:0 + 17% C18:1 + 15% C18:2 + 57% C18:3.

6Oleic sunflower oil contains 4% C16:0 + 83% C18:1 + 7% C18:2.

7(C12:0 + 4 C14:0 + 16:0): (Sum of unsaturated FA).

Desaturase activity was probably higher with lupine seed, because desaturase activity is inhibited by polyunsaturated FA, and/or because lupine seeds tended to decrease trans-vaccenic acid (Table 7). This later decrease could also explain why lupine seeds decreased milk RA. Among the four seeds, only sunflower seeds increased trans-vaccenic acid and RA (Table 7). This suggests that when biohydrogenation occurred on the polyunsaturated FA released from linseeds or soya beans it occurred slowly but almost completely. These results on effects of soybeans are in agreement with observations in dairy cows by Morales et al. (2000) who suggested that polyunsaturated FA from roasted whole soybeans, compared to those from tallow, were, in part, protected against biohydrogenation and that the other part was slowly but completely hydrogenated, since both C18:2 and C18:0, but not trans-C18:1, increased in milk fat.

Lupine seeds FA were totally and completely hydrogenated and these seeds could even bring special (nitrogenous?) compounds, which could increase the biohydrogenation of polyunsaturated FA from the basal diet. Thus these three seeds (linseeds, soybeans, lupine seeds) would need to be physically treated (ground, heated, extruded,...) in order to specifically increase trans FA and RA in goat milk. On the contrary, oil from whole untreated sunflower seeds was probably more rapidly released and interacted with rumen microflora, in a way that significantly increased trans-vaccenic. However, the increase in RA was much lower than when free sunflower oil was used. Further research is needed to understand the mechanisms that could explain these differences.

The RA content of goat milk fat was lower during winter than during summer, when animals received fresh grass (Figure 6). The effect of grass feeding on milk RA is probably due to its high content in linolenic acid (cf. Figure 2). Furthermore, it is likely that different types of winter diets (hay vs. corn silage) are not equivalent for goat milk RA content, and that they could also interact differently with dietary fat supplements. We tested this possibility recently, comparing the effects of either linseed oil or high oleic sunflower oil, added to either hay or corn silage-based diets (Table 8).
Total DMI was higher for alfalfa hay-based diet (2.9 kg/d) than for corn silage (2.2 kg/d) and was not affected by oil addition. In the absence of added lipids, hay diet (compared to corn silage) lowered milk fat and lactose contents, C8:0, C10:0, and C18:0 percentages and increased C16:0, branched-chain and odd-numbered FA, C14:1, C16:1, C17:1, linoleic, and linolenic acid percentages (Table 8, and results not shown). Compared with control diets, linseed oil addition increased milk yield, and fat and lactose contents, C4:0, C18:0, trans-10 C18:1, trans-vaccenic, rumenic and linolenic acid percentages, and lowered C10:0 to C16:1, branched-chain and odd-numbered FA percentages, and the atherogenicity index. Effects of linseed oil addition on C4:0, C6:0 and trans-10 C18:1 were higher when combined with the corn silage diet, while effects on milk fat content and C14:0 to linolenic acid and RA (except trans-10 C18:1, oleic and linoleic acids) were higher with the hay diet. The effect on RA (+853% with hay diet) was spectacular. Compared with control diets, high oleic sunflower oil addition increased milk fat, protein and lactose contents, C4:0, C18:0, oleic, trans-vaccenic and RA percentages, and lowered C8:0 to C16:1, branched-chain and odd-numbered FA, linoleic and linolenic acid percentages, and the atherogenicity index. Effects of high oleic sunflower oil addition on C4:0 and trans-10 C18:1 were greater with the corn silage diet, while effects on C16:0, C16:1, oleic acid, branched-chain and odd-numbered FA and RA were higher with the hay diet. The trans-10 cis-12 CLA isomer was never present in significant amounts, whatever the diet used in Table 8.

Thus the differences between hay and corn silage diets were small. High oleic sunflower oil addition sharply increased stearic and oleic acid percentages. Linseed oil addition sharply increased trans-vaccenic and RA percentages, and the effects were higher with hay diet. Important interactions between forage and oil effects were observed. Furthermore, any increase in RA was systematically (for 38 different diets) accompanied by a 2.5-fold higher increase in trans-vaccenic acid (Figure 7), as in dairy cows (Griinari and Bauman, 1999). This implies that the potential effects on human health of both CLA and trans-C18:1 isomers have to be evaluated together with care (e.g., Jensen, 2002) in order to predict the putative effects of lipid supplementation on goat milk fat nutritional quality. A sharp decrease in the atherogenicity index of goat milk fat was observed for the two vegetable oils, whatever the forage. These results are an illustration of how dietary factors can broadly modify goat milk FA composition and have potential effects on its quality for human nutrition.

In other respects, the sensorial characteristics of goat milk and cheeses made from this trial were subject to several changes (Gaborit et al., 2002). Intensities of descriptors were generally higher for hay than for corn silage diets, and higher for hay + linseed oil and corn silage + high oleic sunflower oil, indicating several types of interaction between forages and oils used in this study. Lipid supplementation, especially linseed oil, de-
increased goat flavor (in agreement with data on milk lipase and lipolysis, see below) and increased negative flavors. Metallic/oxidized and fishy flavors could result from greater oxidation of free polyunsaturated FA following lipid supplementation, especially when using linseed oil (oxidation of C18:3). Thus, it could be difficult to simultaneously optimize goat milk sensorial and nutritional qualities, although the addition of antioxidants could be helpful in reducing unsaturated FA oxidation.

**Conclusion.** Despite differences in the quantitative responses (milk yield and milk fat content), the changes in milk FA composition after lipid supplementation are very similar in goats (see above) and cows (reviews by Palmquist et al., 1993; Grinari and Bauman, 1999; Chilliard et al., 1993, 2001). It is likely that specific changes in minor FA that play an important role in the inhibition of mammary lipogenesis (such as trans-10 C18:1 or trans-10 cis-12 CLA in cows, Bauman and Grinari, 2001), and that are not well-known in goats, could partially explain between-species differences. However, the sharp increase in trans-10 C18:1 due to corn silage-vegetable oil interactions (Table 8) did not result in a decrease in goat milk fat content, contrary to observations in cows. Nevertheless, the trans-10 C18:1 could be involved in the lack of positive effect of oil supplementation on goat milk fat content when corn silage was used, whereas oil supplementation increased sharply milk fat content when hay was used (Table 8). Changing diet composition can allow rapid and efficient changes in goat milk FA composition, but potential effects on other aspects of the quality of caprine dairy products, such as taste, flavor, nutritive and health value for consumers, warrant further investigations.

**LIPASE AND LIPOLYSIS**

**The Lipolytic System**

Milk fat lipolysis is the hydrolysis of fat globule triglycerides into free FA. “Spontaneous lipolysis” in cold, stored milk is due to the action of milk lipoprotein lipase (LPL), which can be stimulated (“induced lipolysis”) by agitation, foaming or temperature changes. During long-term storage of dairy products, there could also be a significant contribution of microbial lipolysis, whereas milk endogenous LPL is easily destroyed by mild heat treatment (Chilliard and Lamberet, 1984).

Milk fat lipolysis and lipase (or LPL) activity are two distinct phenomena, although both result in the hydrolysis of triglycerides. Milk fat lipolysis generally takes place at 4°C, at natural milk pH, in the presence of biochemical factors naturally occurring in milk. It is generally lower than 1.0 mmol released FA/24 h/L of goat milk (Chilliard, 1982). Milk LPL activity is measured as maximal potential activity on an artificial lipid emulsion, at 37 or 39°C, at alkaline pH, in the presence of apoprotein activators from blood serum. It is generally higher than 20 μmol/h/ml of goat milk (Chilliard, 1982). Thus potential LPL activity is more than 500 times higher than spontaneous lipolysis in goat milk.

The lipolytic system differs considerably between goat (Bjorke and Castberg, 1976; Chilliard et al., 1984; Azzara and Dimick, 1989), cow (Cartier and Chilliard, 1990, 1994) and human (Castberg and Hernell, 1975; Neville et al., 1991) milks. Spontaneous lipolysis is not correlated to LPL activity in bovine milk, and lipolysis remains generally low despite the very high LPL activity of this milk. This could be due to the presence of inhibitors in bovine milk (Cartier et al., 1990), as well as to the fact that bovine milk LPL is largely bound to casein micelles, thus decreasing enzyme-fat substrate interactions. On the contrary, large proportions of human and goat milk LPL are bound to cream, which could explain that milk lipolysis is well correlated to milk LPL activity in these two species. This can be related to the lack of effect of heparin addition on goat milk lipolysis, contrary to its strong positive effect on cow milk lipolysis due to the release of casein-bound LPL by heparin (Chilliard et al., 1984). Furthermore, blood serum (a specific activator of LPL) increased lipolysis more in goat than in cow milk, except when goat milk total LPL activity was extremely low and became limiting (Chilliard et al., 1984). Goat milk serum proteose peptone fraction inhibited spontaneous (Chilliard et al., 1984) and induced (Arora and Joshi, 1994) lipolysis of goat milk, as was similarly observed for cow milk (Anderson, 1981; Cartier et al., 1990).

The development of goat flavor in cold, stored fresh milk is due to free FA, especially free C6:0 to C9:0 and more specifically volatile branched-chain C9 and C10 as 4-methyl- and 4-ethyl-C8, which are more abundant in small ruminant than in bovine milk fat (Ha and Lindsay, 1993; Lamberet et al., 2001). The high concentrations of total branched-chain FA in the milk fat of ruminant species results mainly from microbial metabolism of branched-chain amino acids in the rumen, since leucine and isoleucine give rise to iso-valeric and 2-methyl butyric acids; the corresponding acyl-CoA could be used as a primer in the elongating process to form the iso and anteiso series up to C17. Furthermore, goat milk contains minor volatile branched-chain FA with one methyl or ethyl group on carbon 4 (Ha and Lindsay, 1990a; Lamberet et al., 1996; Alonzo et al., 1999). These FA probably arise from tissue metabolism of propionate and butyrate absorbed from the rumen, such metabolism probably differing between bovine and caprine species. Interestingly, two of these minor FA (4-methyloctanoic acid which was first found with 4-methylnonan-
oic acid in mutton meat (Wong et al., 1975), and 4-ethylctanoic acid) are involved in goat flavor. Ha and Lindsay (1990b) proposed pathways for their formation in ruminant fat, by analogy with descriptions of fat from uropygial glands in waterfowl (e.g., Rainwater and Kolattukudy, 1982). But nothing is known of the way in which such a synthesis is regulated within the different tissues in ruminants. For example, according to Sugiyama et al. (1986), a homologous series of 4-ethyl branched-chain FA, in free and bound forms, is the main fat component from neck sebaceous glands of adult buck. 4-Ethyloctanoic acid, which can be considered as a pheromone, represents less than 5% of this series while 4-ethyldodecanoic acid accounts for about half the total amount. The presence of such a series leads to suppose that addition of ethylmalonyl-CoA at different stages of the FA elongation process takes place in the sebaceous gland cells. In goat milk, only the presence of 4-ethylctanoic acid was reported, and this FA has the lowest flavor threshold value determined until now for FA (Brennand et al., 1989; Karl et al., 1994).

Thus, the combination of goat milk FA composition, triglyceride structure (i.e., high proportion of C6-C10 FA esterified on carbon 3) and LPL characteristics could explain the link between LPL, lipolysis and goat flavor in caprine milk (Figure 8). Furthermore, it should be pointed out that goat flavor, which is regarded sometimes as a positive, sometimes as a negative feature in cheeses or milk, appears at lipolysis levels much lower than those responsible for the rancid-butyric flavor (Lamberet et al., 1996, 2001 and unpublished results).

Genetic Factors

There are large differences between caprine Norwegian (Bjoerke and Castberg, 1976; Skjevdal, 1979), Alpine (Chilliard, 1982; Chilliard et al., 1984), and Saanen

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Figure 8. Fatty acids, lipolysis, and goat flavor (from Chilliard, 1982; Ha and Lindsay, 1993; Lamberet et al., 1996).

Physiological Factors

Goat milk flavor (reviews by Skjevdal, 1979; Delacroix-Buchet and Lamberet, 2000), lipolysis and LPL activity (Table 4 and Figure 9) were at their highest after the lactation peak, and were low before wk 4 and after wk 30 of lactation. This confirms that the latter two parameters are well correlated in goats, unlike in cows in which milk LPL activity decreased as lipolysis increased during late lactation (Chazal and Chilliard, 1986). This effect of lactation stage in cows was in fact an effect of pregnancy stage (Chazal and Chilliard, 1986) linked to estrogens (Cartier and Chilliard, 1994) and/or progesterone (Chilliard et al., 1997). One reason for the lack of increase in milk lipolysis during late
lactation in goats could be that fecundation occurs later, due to the shorter pregnancy in this species. The involvement of sex steroid hormones in the maturation of the milk lipolytic system is also suggested by the fact that the normal increase of milk LPL activity during early lactation was delayed in goats hormonally induced into lactation without being previously pregnant (Figure 10). In other respects, there is an interaction between lactation stage and α-s1 casein genotype: the increase of lipolysis as lactation advances was more pronounced and significant in goats with E, F, or O alleles (Table 4).

Hourly milking sharply increased goat milk LPL activity and sodium concentration, but only in some animals (Azzara and Dimick, 1989). Massage of the mammary gland or oxytocin injection was necessary to cause increased milk LPL activity in nonresponding goats. This suggests that paracellular leakage across mammary epithelium of LPL circulating in the blood (Figure 11) was increased. Furthermore, hourly milking compared with twice daily milking increased the percentage of milk LPL distributed in the serum fraction (Azzara and Dimick, 1989), thus suggesting that this milk fraction could contain mainly LPL from blood origin in goats (Figure 11). A similar effect of milking frequency was observed recently in dairy cows in which once daily milking decreased milk LPL activity compared with twice daily milking (Rémont et al., 2002).

**Nutritional Factors**

The distribution of protected sunflower oil (C18:2-rich) decreased goat milk LPL activity and the level of spontaneous lipolysis (Figure 12). This result was recently confirmed with unprotected C18:1-, C18:2-, and C18:3-rich oils: milk LPL activity and spontaneous lipolysis decreased sharply in goats fed hay- or corn silage-based diets when fat was added (5 to 6% of DMI from either regular or high-oleic sunflower oil or linseed oil, Figure 13). This matches with the negative correlation observed between goat milk flavor and polyunsaturated FA content (Skjevdal, 1979), and with the decrease in goat flavor in milk and cheeses from animals of Table 8 receiving lipid supplements (Gaborit et al., 1989).
It can be observed in Figure 13 that the effect of lipid supplementation was less important on milk spontaneous lipolysis than on milk LPL activity, and it can be predicted that milk lipolysis would only increase when milk LPL activity is higher than 15 to 18 μmol/h per milliliter. It could be hypothesized that milk LPL activity decreased when supplemental lipids were fed because mammary LPL was directed towards the basal membrane of secretory cells, where it is needed to allow the uptake of blood triglycerides (Figure 11). Conversely, the higher LPL activity in milk of animals with the FF genotype (Table 3) could be related to the lower flow of fat secretion, thus decreasing the need for LPL at the basal membrane and increasing the availability of LPL for secretion into milk for a given level (constitutive of the lactating status) of mammary LPL synthesis.

Goat milk LPL activity decreased sharply during fasting and rebounded at the beginning of the refeeding period (Figure 14). Milk spontaneous lipolysis did not change markedly and was poorly correlated to milk LPL activity during fasting-refeeding, whereas the free FA content of freshly drawn milk increased during fasting (Figure 14), probably due to a direct passage of blood NEFA to the milk when their concentration was increased by body fat mobilization. As the mammary gland LPL activity did not significantly change during fasting-refeeding (Figure 15), it may be thought either that mammary LPL was partitioned differently between basal membrane and milk when the nutritional status changed, or that blood LPL arising from adipose tissues contributed less to milk LPL secretion because it was decreased in adipose tissues during fasting (Figures 11 and 15). These observations can be related to the negative effect of fasting and to the positive effect of insulin on human milk LPL activity (Neville et al., 1991).

A putative link between adipose tissue LPL and milk LPL activity is also suggested by the positive correlation (r = +0.61) observed in lactating goats (Table 9).
This relationship was mainly due to intra-goat and between-lactation stage correlation. Indeed, adipose tissue LPL and other lipogenic activities were low in high-yielding goats at the beginning of lactation, and then increased when animals returned to a positive energy balance, after 3 or 4 mo of lactation (Figure 16). Simultaneously, milk LPL activity followed a similar pattern (Figures 9 and 10), whereas mammary LPL activity did not change significantly (Chilliard et al., 1986). In other respects, the strongest correlation ($r = -0.70$) was between milk LPL activity and milk fat C16:0 percentage (Table 9). It can be hypothesized that there is a mechanistic link between the physiological or nutritional regulation of the chain-length of synthesized FA and the synthesis and secretion of mammary LPL. This observation is also in agreement with the fact that feeding C16:0 to goats tended to decrease milk lipolysis and goat flavor, whereas there was surprisingly a positive interindividual correlation between C16:0 and goat flavor (Astrup et al., 1985).

The results reviewed here on physiological and nutritional variations of goat milk LPL activity are similar to what was observed in cow milk (Table 10). On the contrary, lipolysis in bovine milk was not correlated to LPL activity, and responded differently to physiological factors compared with observations in goat milk (Table

**Table 9.** Correlations between goat milk lipoprotein lipase (LPL) activity and production or metabolic traits.$^{1}$

<table>
<thead>
<tr>
<th>Parameter</th>
<th>$r$ ($n = 27$)$^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>DMI</td>
<td>+0.55</td>
</tr>
<tr>
<td>Milk yield</td>
<td>+0.44</td>
</tr>
<tr>
<td>Milk fat content</td>
<td>−0.33</td>
</tr>
<tr>
<td>Milk C16:0 (% of total FA)</td>
<td>−0.70</td>
</tr>
<tr>
<td>Mammary RNA/DNA</td>
<td>+0.41</td>
</tr>
<tr>
<td>Mammary LPL</td>
<td>NS</td>
</tr>
<tr>
<td>Adipose tissue LPL</td>
<td>+0.61</td>
</tr>
</tbody>
</table>

$^1$From Chilliard (1985).

$^2$goats at 3, 9, and 18 wk of lactation (4 normal and 5 hormonally-induced).

**Table 10.** Physiological and nutritional variations of milk lipoprotein lipase (LPL) activity and spontaneous lipolysis.$^{1}$

<table>
<thead>
<tr>
<th>LPL</th>
<th>Lipolysis</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cow</td>
<td>Goat</td>
</tr>
<tr>
<td>Cow</td>
<td>Goat</td>
</tr>
</tbody>
</table>

- Early lactation
- Late lactation
- Late pregnancy
- Milking frequency
- Underfeeding
- Protected lipid feeding

$^1$From Chilliard (1982 and present review) for goats, Chilliard and Lamberet (1984), Chazal and Chilliard (1986 and unpublished results), Azzara et al. (1987), Rémond et al. (2002 and unpublished results) for cows. (+/-) = increase/decrease (respectively).
10. Thus, important differences exist between goat and cow lipolytic systems as well as in the physiological regulation of milk lipolysis, even though the regulation of milk LPL activity was similar in the two species.

CONCLUSIONS

The responses of milk yield and fat content to lipid supplementation differ widely between the goat and the cow, even though the response of milk FA composition is similar, at least for major FA, including trans-vaccenic RA. Although the physiological and nutritional regulation of milk LPL activity is similar between the goat and the cow, their lipolytic systems differ. This probably explains why the physiological regulation and the husbandry factors of spontaneous lipolysis differ significantly between the two species. Peculiarities of goat milk FA composition and lipolytic system play an important role in the development of goat flavor.

Quantitative and qualitative aspects of milk quality cannot always be increased simultaneously. For example, lipid supplementation could improve the efficiency of goat cheese yield and its FA profile but decrease its sensorial quality. In other respects, the polymorphism of the casein α-s1 gene in goats presents an interesting model to study the mechanistic links between mammary protein and fat secretions, as well as the opposite regulations of goat milk fat and LPL secretion and their relationships with the development of goat flavor. The present and future knowledge on genetic, physiological, and nutritional factors regulating goat milk FA composition and lipolytic system will be helpful in the management procedures of goat husbandry to optimize the quantitative and qualitative (nutritional, sensorial, technological, etc.) aspects of goat dairy products.

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