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Recent developments in altering the fatty acid composition of ruminant-derived foods

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There is increasing evidence to indicate that nutrition is an important factor involved in the onset and development of several chronic human diseases including cancer, cardiovascular disease (CVD), type II diabetes and obesity. Clinical studies implicate excessive consumption of medium-chain saturated fatty acids (SFA) and trans-fatty acids (TFA) as risk factors for CVD, and in the aetiology of other chronic conditions. Ruminant-derived foods are significant sources of medium-chain SFA and TFA in the human diet, but also provide high-quality protein, essential micronutrients and several bioactive lipids. Altering the fatty acid composition of ruminant-derived foods offers the opportunity to align the consumption of fatty acids in human populations with public health policies without the need for substantial changes in eating habits. Replacing conserved forages with fresh grass or dietary plant oil and oilseed supplements can be used to lower medium-chain and total SFA content and increase cis-9 18:1, total conjugated linoleic acid (CLA), n-3 and n-6 polyunsaturated fatty acids (PUFA) to a variable extent in ruminant milk. However, inclusion of fish oil or marine algae in the ruminant diet results in marginal enrichment of 20- or 22-carbon PUFA in milk. Studies in growing ruminants have confirmed that the same nutritional strategies improve the balance of n-6/n-3 PUFA, and increase CLA and long-chain n-3 PUFA in ruminant meat, but the potential to lower medium-chain and total SFA is limited. Attempts to alter meat and milk fatty acid composition through changes in the diet fed to ruminants are often accompanied by several-fold increases in TFA concentrations. In extreme cases, the distribution of trans 18:1 and 18:2 isomers in ruminant foods may resemble that of partially hydrogenated plant oils. Changes in milk fat or muscle lipid composition in response to diet are now known to be accompanied by tissue-specific alterations in the expression of one or more lipogenic genes. Breed influences both milk and muscle fat content, although recent studies have confirmed the occurrence of genetic variability in transcript abundance and activity of enzymes involved in lipid synthesis and identified polymorphisms for several key lipogenic genes in lactating and growing cattle. Although nutrition is the major factor influencing the fatty acid composition of ruminant-derived foods, further progress can be expected through the use of genomic or marker-assisted selection to increase the frequency of favourable genotypes and the formulation of diets to exploit this genetic potential.

Keywords: milk, meat, saturated fatty acids, trans-fatty acids, conjugated linoleic acid

Implications

Public health policies recommend population-wide decreases in the consumption of fat, saturated and trans-fatty acids (TFA), and higher intakes of polyunsaturated fatty acids. Ruminant foods are a major source of medium-chain saturates and contribute to TFA consumption in human populations. Significant progress has been made in characterizing changes in milk and tissue fatty acid composition to diet, feeding system and genotype. Recent developments highlight the potential for

further progress to be made through genomic or marker-assisted selection of ruminant livestock and the formulation of diets to exploit this genetic potential.

Introduction

There is increasing evidence from clinical and biomedical studies that diet plays an important role in the onset and development of chronic disease in the human population including cancer, cardiovascular disease (CVD), insulin resistance and obesity (World Health Organization/Food

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Agricultural Organization (WHO/FAO), 2003). Both the direct and indirect costs of CVD have been estimated as €200 billion per annum within the European Union (Allender *et al.*, 2008) and \$403 billion per annum in the United States (Thom *et al.*, 2006). These costs are projected to increase because of people living longer and the rapid increase in obesity in developed and developing countries (Givens, 2010).

Studies in human subjects have indicated that saturated fatty acids (SFA), specifically 14:0 and 16:0, and *trans*-fatty acids (TFA) in the diet increase CVD risk, with the risk associated with TFA being higher than SFA (refer to Shingfield *et al.*, 2008b; Givens, 2010). Excessive intakes of SFA may also be associated with lowered insulin sensitivity, which is a key factor in the development of the metabolic syndrome and diabetes (Funaki, 2009; Kennedy *et al.*, 2009). In an attempt to lower the economic and social burden of chronic diseases, public health policies in most developed countries recommend population-wide decreases in the intake of total fat, SFA and TFA and an increase in the consumption of the long-chain n-3 polyunsaturated fatty acids (PUFA), 20:5n-3 and 22:6n-3.

Milk and dairy products are the main source of 12:0 and 14:0 in the human diet, although collectively ruminant-derived foods contribute significantly to total 16:0 and TFA consumption. The TRANSFAIR study on fat and fatty acid intake across 14 European countries (Hulshof *et al.*, 1999) reported that depending on country milk and dairy products provided 27.4% to 57.1% of total SFA, with that from meat and meat products ranging between 13.9% and 29.0% (Figure 1). Milk, milk products, cheese, butter, meat and meat products were found to make a significant but variable contribution to total TFA in the human diet (Figure 1). However, simply advocating a population-wide decrease in the consumption of ruminant meat and milk to lower SFA and TFA intakes ignores the value of these foods as a versatile source of high-quality protein, vitamins, minerals and bioactive lipids. Altering the fatty acid composition of ruminant meat and milk represents one means to lower SFA intakes and increase *cis* monounsaturated (MUFA) and PUFA in the human diet without requiring changes in consumer eating habits, while at the same time maintaining the potential benefits associated with the macro- and micronutrients in these foods.

The following review summarizes recent investigations of the physiological, biochemical and molecular mechanisms regulating fatty acid supply, lipogenesis and adipogenesis in growing and lactating ruminants and considers the potential to alter the fatty acid composition of ruminant meat and milk through diet and genetic selection.

Digestion of lipids in ruminants

Ruminal lipolysis and biohydrogenation

Tissue lipids and milk fat in ruminants contain much higher proportions of SFA compared with dietary intake, which is at least partly due to extensive lipolysis and subsequent biohydrogenation of unsaturated fatty acids in the rumen.

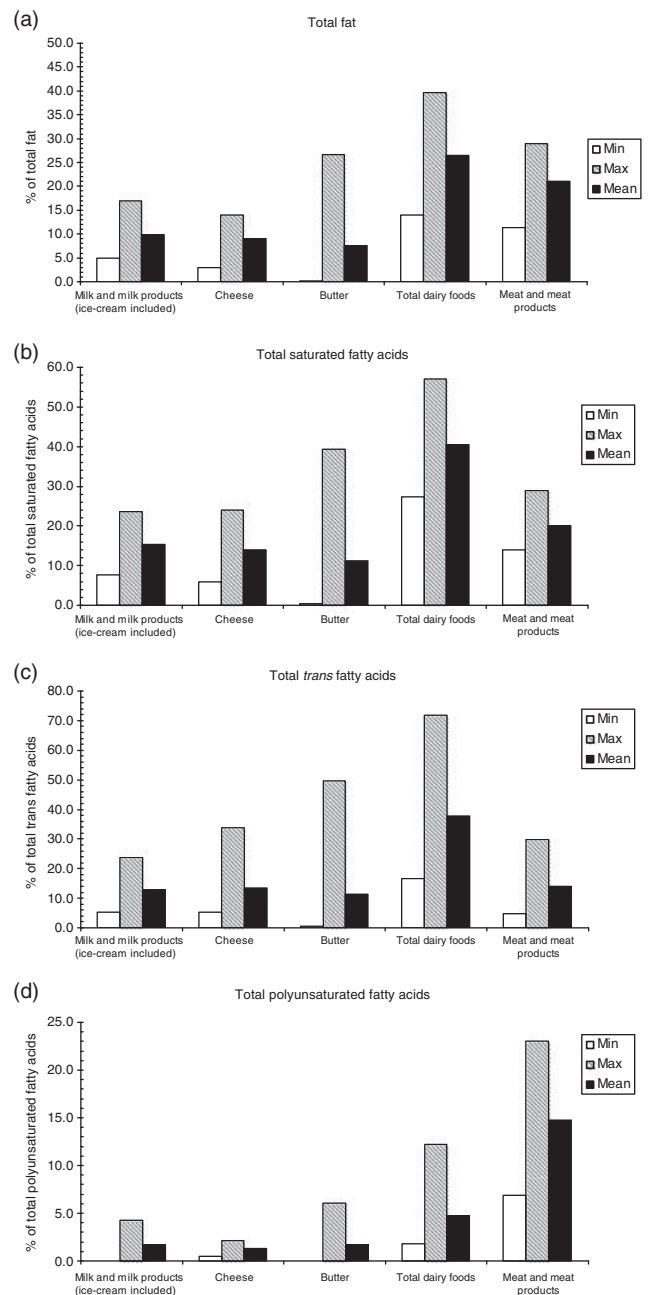


Figure 1 Contribution of animal-derived foods to the intake of total fat, saturated, *trans*- and polyunsaturated fatty acids as estimated in the TRANSFAIR study for 14 European Countries (Hulshof *et al.*, 1999).

Bacteria are thought to be primarily responsible, a process that serves to reduce the toxic effects of dietary unsaturated fatty acids on bacterial growth (Jenkins *et al.*, 2008; Lourenço *et al.*, 2010). Lipolysis represents the first step in the complete metabolism of dietary lipids, and under normal conditions more than 85% of esterified dietary lipids in the form of galactolipids, phospholipids (PL) and triacylglycerols (TAG) are hydrolysed (Palmquist *et al.*, 2005; Buccioni *et al.*, 2012).

Significant progress has been made in characterizing intermediates formed during ruminal biohydrogenation of unsaturated fatty acids, the mechanisms involved and some

of the bacterial species responsible (Jenkins *et al.*, 2008; Lourenço *et al.*, 2010; Shingfield *et al.*, 2010). Recent studies *in vitro* have demonstrated that a diverse range of intermediates are formed during incubations of pure fatty acid substrates with rumen fluid or pure strains of ruminal bacteria (Jenkins *et al.*, 2008; Lourenço *et al.*, 2010; Buccioni *et al.*, 2012; Table 1). For most diets, ruminal biohydrogenation of *cis*-9 18:1, 18:2n-6 and 18:3n-3 varies between 58% to 87%, 70% to 95% and 85% to 100%, respectively (Glasser *et al.*, 2008; Shingfield *et al.*, 2010), indicating that with the exception of diets containing fish oil or marine lipids 18:0 is the major fatty acid leaving the rumen.

Fatty acids available for absorption are also derived from rumen bacteria and protozoa. Microbial fatty acids, primarily in the form of structural membrane lipids, originate from biohydrogenation and utilization of dietary fatty acids and fatty acid synthesis *de novo*. *De novo* fatty acid synthesis is also responsible for the occurrence of odd- and branched-chain fatty acids in membrane lipids of rumen bacteria (Vlaeminck *et al.*, 2006).

Lipid absorption and transport

Mechanisms involved in the digestion and adsorption of fatty acids in the small intestine of ruminants are well documented (Vernon and Flint, 1988; Bauchart, 1993). On passage through intestinal epithelial cells, adsorbed fatty acids mainly in the form of non-esterified fatty acids (NEFA) are esterified to glycerol and used in conjunction with PL and cholesterol esters (CE) in the assembly of very-low-density lipoproteins (VLDL) and chylomicrons that enter the peripheral circulation via the thoracic duct (Vernon and Flint, 1988). Most of the fatty acids transported in plasma circulate as CE and PL within high-density lipoproteins (HDL), although TAG and NEFA typically account for less than 3% of total plasma lipids (Moore and Christie, 1979). The small amounts of absorbed PUFA are preferentially incorporated into CE and PL of circulating HDL, which is thought to arise from the action of acyltransferases during the synthesis of PL in enterocytes and the activity of lecithin:cholesterol acyltransferase in plasma (Vernon and Flint, 1988). Preferential incorporation into lipid fractions with a low affinity for lipoprotein lipase (LPL) represents a mechanism to limit the amount of essential fatty acids used for milk fat synthesis and oxidation.

Mammary lipogenesis in ruminants

Milk fat comprises TAG (96% to 98% of total milk lipids) with small amounts of 1,2-diacylglycerols and mono-acylglycerols (0.02%), NEFA (0.22%) and retinol esters. Ruminant milk fat contains more than 400 different fatty acids, but SFA of chain lengths from 4 to 18 carbon atoms, *cis*-9 16:1, *cis*-9 18:1, isomers of *trans* 18:1 and 18:2n-6 are the most abundant. Fatty acids incorporated into milk fat TAG are derived from the uptake of fatty acids from NEFA and TAG in arterial blood and synthesis *de novo* in the mammary gland (Chilliard *et al.*, 2007; Bernard *et al.*, 2008).

Several recent accounts have documented the biochemistry and molecular regulation of mammary lipogenesis in ruminants (Bernard *et al.*, 2008; Bionaz and Looor, 2008; Harvatine *et al.*, 2009; Shingfield *et al.*, 2010). Mammary epithelial cells synthesize short- and medium-chain fatty acids using acetate and 3-hydroxy-butyrate in the presence of two key enzymes, acetyl-CoA carboxylase (ACC) and fatty acid synthetase (FAS; Figure 2). Fatty acid synthesis *de novo* accounts for all 4:0 to 12:0, most of the 14:0 (ca. 95%) and about 50% of 16:0 secreted in milk, whereas all 18-carbon and longer-chain fatty acids originate from the absorption of fatty acids in the small intestine and body fat reserves. The activity of stearoyl-CoA desaturase (SCD) in mammary epithelial cells that catalyses the oxidation of fatty acyl CoA esters resulting in the introduction of a *cis* double bond between carbon atoms 9 and 10 is responsible for ca. 90%, 55%, 60% and 70% to 95% of *cis*-9 14:1, *cis*-9 16:1, *cis*-9 18:1 and *cis*-9, *trans*-11 conjugated linoleic acid (CLA), respectively, secreted in milk (Palmquist *et al.*, 2005; Shingfield *et al.*, 2010). *De novo* fatty acid synthesis, uptake of long-chain fatty acids and the formation of SCD products contribute to the fatty acid pool available for TAG synthesis (Figure 2).

Tissue adipogenesis in ruminants

The primary role of adipose tissue (AT) is to serve as an energy store. Mobilization of TAG from body fat stores results in the release of NEFA that can be used for fat synthesis in the mammary gland or muscles. The majority of TAG found in muscle is deposited in intramuscular adipocytes. Adipocyte numbers and the amount of lipid stored within adipocytes are determined by cellular adipogenesis, which involves the development of adipocytes from pre-adipocytes that originate from progenitor cells. Relatively little is known about the differentiation of progenitor cells into preadipocytes, whereas the transition of preadipocytes into mature adipocytes defined as permanently cell cycle-arrested, spherical, lipid-filled cells is well documented (Hausman *et al.*, 2009; Bonnet *et al.*, 2010; Du *et al.*, 2010). Studies with cell cultures models, murine 3T3-L1 and 3T3-F442A cell lines and immortalized brown preadipocyte cell lines have enabled the biochemical mechanisms involved in the termination of the mitotic phase and initiation of cell differentiation to be elucidated (Figure 3), a process orchestrated by a tightly regulated transcriptional cascade involving nuclear receptors. Although the temporal pattern of nuclear receptor appearance differs between species (Hausman *et al.*, 2009), CCAAT/enhancer-binding protein (primarily CEBP- α , but also CEBP- β and - δ) and peroxisome proliferator-activated receptor gamma (PPAR γ) are known to be central transcriptional regulators of adipogenesis in cattle (Bonnet *et al.*, 2010). Nuclear receptors induce the expression of numerous downstream target genes, including genes involved in the lipid metabolism and TAG deposition within adipocytes. The rate of TAG deposition and thereby adipocyte-lipid filling and hypertrophy depends on the relative rates of lipogenesis and lipolysis.

Table 1 Intermediates formed during incubations of 18-carbon unsaturated fatty acids with strained ruminal fluid or pure cultures of ruminal bacteria

Substrate	Inoculum/bacterium	Intermediates and end products	References
<i>cis</i> -9 18:1	<i>Butyrivibrio proteoclasticus</i>	18:0	McKain <i>et al.</i> (2010)
<i>cis</i> -9 18:1	<i>Enterococcus faecali</i>	10-OH-18:0	Hudson <i>et al.</i> (1995)
<i>cis</i> -9 18:1	<i>Propionibacterium acnes</i>	10-OH-18:0, 10-0-18:0	McKain <i>et al.</i> (2010)
<i>cis</i> -9 18:1	<i>Selenomonas ruminantium</i>	10-OH-18:0	Hudson <i>et al.</i> (1995)
<i>cis</i> -9 18:1	Bovine ruminal fluid	<i>trans</i> -6, -7, -9, -10, -11, -12, -13, -14, -15, -16 18:1 18:0	Mosley <i>et al.</i> (2002)
<i>cis</i> -9 18:1	Bovine ruminal fluid	10-OH-18:0, 10-0-18:0, 18:0	Jenkins <i>et al.</i> (2006)
<i>trans</i> -9 18:1	Bovine ruminal fluid	<i>cis</i> -9, -11 18:1, <i>trans</i> -6, -7, -11 18:1 18:0	Proell <i>et al.</i> (2002)
<i>trans</i> -10 18:1	<i>B. proteoclasticus</i>	18:0	McKain <i>et al.</i> (2010)
<i>trans</i> -10 18:1	<i>P. acnes</i>	10-OH-18:0, 10-0-18:0	McKain <i>et al.</i> (2010)
<i>trans</i> -11 18:1	<i>B. proteoclasticus</i>	18:0	McKain <i>et al.</i> (2010)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Butyrivibrio fibrisolvens</i>	<i>trans</i> -11 18:1	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>B. fibrisolvens</i>	<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -9, <i>cis</i> -11 18:2, <i>trans</i> -9, <i>trans</i> -11 18:2	Wallace <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Butyrivibrio hungatei</i>	<i>trans</i> -11 18:1	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>B. proteoclasticus</i>	<i>cis</i> -9, <i>trans</i> -11 18:2 <i>trans</i> -11 18:1	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>B. proteoclasticus</i>	<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -9, <i>cis</i> -11 18:2, <i>trans</i> -9, <i>trans</i> -11 18:2	Wallace <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Clostridium aminophilum</i>	<i>cis</i> -9 18:1	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>E. faecalis</i>	10-OH-18:1, 13-OH-18:1	Hudson <i>et al.</i> (1998)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Fibrobacter succinogenes</i>	16:0	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Mitsuokella multiacidus</i>	<i>cis</i> -9 18:1	Maia <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>P. acnes</i>	<i>cis</i> -10, <i>trans</i> -12 18:2, <i>trans</i> -10, <i>cis</i> -12 18:2, <i>trans</i> -10, <i>trans</i> -12 18:2	Wallace <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	<i>Selenomonas bovis</i>	13-OH-18:1	Hudson <i>et al.</i> (1998)
<i>cis</i> -9, <i>cis</i> -12 18:2	Bovine ruminal fluid	<i>cis</i> -6, <i>cis</i> -12 18:2, <i>cis</i> -7, <i>cis</i> -12 18:2, <i>cis</i> -8, <i>cis</i> -12 18:2, <i>cis</i> -9, <i>cis</i> -11 18:2 <i>cis</i> -10, <i>cis</i> -12 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>cis</i> -9, <i>trans</i> -12 18:2, <i>trans</i> -8, <i>cis</i> -10 18:2 <i>trans</i> -8, <i>cis</i> -12 18:2, <i>trans</i> -9, <i>cis</i> -12 18:2, <i>trans</i> -10, <i>cis</i> -12 18:2 <i>trans</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -10, <i>trans</i> -12 18:2, <i>trans</i> -9, <i>trans</i> -12 18:2 <i>trans</i> -6-8, -9, -10, -11, -12, -13-14 18:1, <i>cis</i> -9, -11, -12 18:1 18:0	Honkanen <i>et al.</i> (2012)
<i>cis</i> -9, <i>cis</i> -12 18:2	Ovine ruminal fluid	<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -10, <i>cis</i> -12 18:2 <i>trans</i> -11 18:1	Wąsowska <i>et al.</i> (2006)
<i>cis</i> -9, <i>cis</i> -12 18:2	Ovine ruminal fluid	<i>cis</i> -10, <i>cis</i> -12 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>cis</i> -9, <i>trans</i> -12 18:2, <i>trans</i> -10, <i>cis</i> -12 18:2, <i>trans</i> -9, <i>trans</i> -11 18:2 <i>trans</i> -4, -5, 6-8, -9, -10, -12 18:1, <i>cis</i> -10, -12, -13 18:1 18:0	Jouany <i>et al.</i> (2007)
<i>cis</i> -9, <i>cis</i> -12 18:2	Ovine ruminal fluid	<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -10, <i>cis</i> -12 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -9, <i>cis</i> -11 18:2, <i>trans</i> -10, <i>cis</i> -12 18:2, <i>trans</i> -9, <i>trans</i> -11 18:2	Wallace <i>et al.</i> (2007)
<i>cis</i> -9, <i>trans</i> -11 18:2	<i>B. fibrisolvens</i>	<i>trans</i> -11 18:1	McKain <i>et al.</i> (2010)

Table 1 Continued

Substrate	Inoculum/bacterium	Intermediates and end products	References
<i>trans</i> -10, <i>cis</i> -12 18:2	<i>B. fibrisolvens</i>	<i>trans</i> -10, -12 18:1, <i>cis</i> -12 18:1	Mckain <i>et al.</i> (2010)
<i>trans</i> -9, <i>trans</i> -11 18:2	<i>B. fibrisolvens</i>	<i>trans</i> -11 18:1	Mckain <i>et al.</i> (2010)
<i>trans</i> -9, <i>trans</i> -11 18:2	<i>B. proteoclasticus</i>	<i>trans</i> -9, -11 18:1, <i>cis</i> -11 18:1	Mckain <i>et al.</i> (2010)
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	Ovine ruminal fluid	<i>cis</i> -9, <i>trans</i> -11, <i>cis</i> -15 18:3, <i>trans</i> -9, <i>trans</i> -11, <i>cis</i> -15 18:3	Wasowska <i>et al.</i> (2006)
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	Ovine ruminal fluid	<i>trans</i> -11, <i>cis</i> -15 18:2	Jouany <i>et al.</i> (2007)
		<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -9, <i>cis</i> -15 18:2, <i>cis</i> -11, <i>trans</i> -13 18:2	
		<i>trans</i> -9, <i>cis</i> -12 18:2, <i>trans</i> -11, <i>cis</i> -15 18:2, <i>trans</i> -9, <i>trans</i> -12 18:2, <i>trans</i> -11, <i>trans</i> -13 18:2	
		<i>trans</i> -6-8,-9, -11, -12, -13-14, -15, -16 18:1, <i>cis</i> -13, -15 18:1	
		18:0	
<i>cis</i> -9, <i>cis</i> -12, <i>cis</i> -15 18:3	Bovine ruminal contents ¹	<i>cis</i> -9, <i>cis</i> -11 18:2, <i>cis</i> -10, <i>cis</i> -12 18:2, <i>cis</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -9, <i>cis</i> -11 18:2	Lee and Jenkins (2011)
		<i>trans</i> -10, <i>cis</i> -12 18:2, <i>trans</i> -8, <i>trans</i> -10 18:2, <i>trans</i> -9, <i>trans</i> -11 18:2, <i>trans</i> -11, <i>trans</i> -13 18:2	

¹Following 48 h incubations of ¹³C-*cis*-9, *cis*-12, *cis*-15 18:3 with bovine ruminal contents, significant enrichment was detected for several unidentified fatty acids including two partially conjugated 18:3 isomers, 12 non-conjugated 18:3 and five non-conjugated 18:2 intermediates.

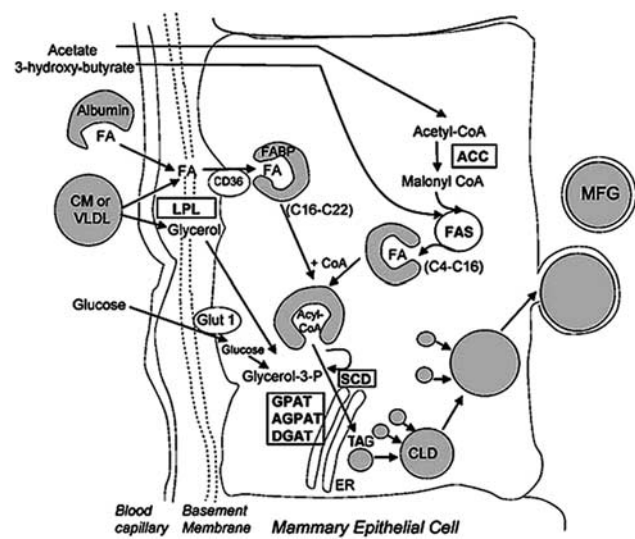


Figure 2 Synthesis of milk fat in the bovine mammary epithelial cell (adapted from Bernard *et al.*, 2008). ACC = acetyl-CoA carboxylase; AGPAT = 1-acylglycerol 3-phosphate acyltransferase; CD36 = cluster of differentiation 36; CLD = cytoplasmic lipid droplet; CoA = coenzyme A; CM = chylomicron; DGAT = diacylglycerol acyltransferase 1; ER = endoplasmic reticulum; FA = fatty acid; FABP = fatty acid-binding protein; FAS = fatty acid synthase; Glut 1 = glucose transporter 1; GPAT = glycerol-3 phosphate acyltransferase; LPL = lipoprotein lipase; MFG = milk fat globule; SCD = stearoyl-CoA desaturase; TAG = triacylglycerol; VLDL = very-low-density lipoprotein.

Three main lipogenic pathways are involved in TAG deposition in ruminants (Figure 3). Fatty acids are synthesized *de novo*, in the main, within adipocytes using acetate and to a lesser extent lactate as precursors, or are derived from LPL-mediated hydrolysis of plasma TAG. Synthesis *de novo* involves the coordinated activity of ACC and FAS and the involvement of glucose-6-phosphate dehydrogenase or malic enzyme (ME) (Figure 3). *De novo* fatty acid synthesis yields 16:0 as the final end product that can serve as a substrate for further elongation or desaturation. Fatty acid elongases 1, 3 and 6 use SFA and MUFA as substrates, whereas elongases 2, 4 and 5 act on PUFA (Cherfaoui *et al.*, 2012). Unsaturated fatty acids are synthesized via the activity of Δ-5, Δ-6 or Δ-9 desaturases. Within AT, stored TAG can be rapidly mobilized by the hydrolytic action of hormone-sensitive lipase (HSL) and adipose triglyceride lipase (ATGL), resulting in the release of NEFA.

Intramuscular fat (IMF) comprising PL and TAG varies between 1 and 5 g/100 g muscle. Accretion of TAG is directly related to body fatness, whereas the amount of PL in muscle is relatively constant. In both lipid fractions, 16:0, 18:0 and *cis*-9 18:1 are the major fatty acids, but PL contains higher proportions of PUFA. Typically, IMF contains 45 to 48, 35 to 45 and up to 5.0 g/100 g fatty acids as SFA, MUFA and PUFA, respectively (Scollan *et al.*, 2006).

Altering the fatty acid composition of ruminant milk

Potential to alter milk fat composition

The extent to which dietary unsaturated fatty acids are incorporated into milk is dependent on both biohydrogenation

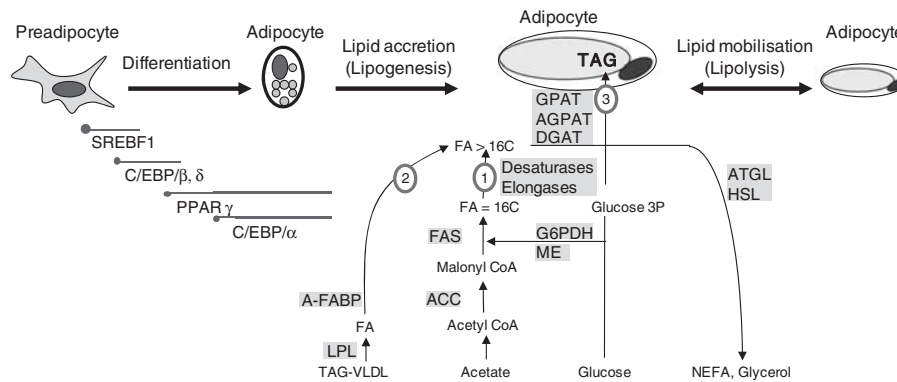


Figure 3 Cellular and biochemical pathways of terminal adipogenesis, lipid accretion and lipid mobilization. Numbers indicate *de novo* lipogenesis (1), lipolysis and uptake of circulating fatty acids (2) and esterification of fatty acids and synthesis of triacylglycerols (3). ACC = acetyl-CoA carboxylase; A-FABP = adipocyte fatty acidbinding protein; AGPAT = 1-acylglycerol 3-phosphate acyltransferase; ATGL = adipose triacylglyceride lipase; CEBP = CCAAT/enhancer-binding protein; CoA = coenzyme A; DGAT = diacylglycerol acyltransferase; FA = 16C = 16-carbon fatty acids; FA > 16C = fatty acids containing 16 or more carbon atoms; FAS = fatty acid synthase; G6PDH = glucose-6-phosphate dehydrogenase; GPAT = glycerol-3 phosphate acyltransferase; HSL = hormone-sensitive lipase; LPL = lipoprotein lipase; ME = malic enzyme; NEFA = non-esterified fatty acids; PPAR γ = peroxisome proliferator-activated receptor gamma; SREBF1/ADD1 = sterol regulatory element-binding protein 1; TAG-VLDL = triacylglycerols transported in the peripheral circulation as very-low-density lipoproteins.

in the rumen and the efficiency of transfer from the small intestine into milk fat. Transfer of 18-carbon or longer fatty acids into milk is regulated by the availability of fatty acids for absorption, with evidence that the supply of 4- to 16-carbon fatty acids synthesized *de novo* may also be important (Glasser *et al.*, 2008b). Infusions of oils or fatty acid preparations at the abomasum or duodenum have established the potential to increase the concentration of unsaturated fatty acids in milk in the absence of biohydrogenation in the rumen.

Infusions of rapeseed oil or high oleic sunflower oil fatty acids at the abomasum or duodenum increase *cis*-9 18:1 in milk of up to 57 g/100 g fatty acids (Table 2). Post-ruminal infusions of soya bean oil, linseed oil or linseed fatty acids indicate that bovine milk fat can be substantially enriched in 18:2n-6 and 18:3n-3 (16.6 and 25.4 g/100 g fatty acids, respectively; Table 2). Administration of linseed fatty acids also results in marginal increases in milk 20:5n-3 content (Table 2), confirming limited, but significant, elongation and desaturation of 18:3n-3 in ruminant tissues. Increases in the availability of 18-carbon unsaturated fatty acids in the small intestine also lower the concentration of 8- to 16-carbon fatty acids in milk fat (Table 2). Data from recent experiments, excluding studies where post-ruminal lipid infusions lowered intake and milk production, indicate that 18:2n-6 and 18:3n-3 are transferred from the small intestine into milk fat with a mean efficiency of 49% (Figure 4).

Even in the absence of biohydrogenation in the rumen, the potential to increase 20:5n-3 and 22:6n-3 in milk is extremely limited (Table 2). A lower transfer efficiency from the small intestine into milk for 20:5n-3 and 22:6n-3 (14.3% to 33.0% and 13.3% to 25.0%, respectively) than 18-carbon unsaturated fatty acids is thought to arise from the preferential incorporation of absorbed 20:5n-3 and 22:6n-3 into plasma PL and CE of HDL, rather than TAG of circulating VLDL and chylomicrons (Palmquist, 2009).

A number of methodologies have been developed to protect lipids from biohydrogenation in the rumen, but in most cases the technologies used do not substantially increase the amount of unsaturated fatty acids available for absorption (Jenkins and Bridges, 2007). Changes in milk fat and tissue lipid composition in sheep, goats and cattle confirm formaldehyde treatment of emulsions of oilseeds or casein with oil as the most effective (Palmquist, 2009; Doreau *et al.*, 2011). The use of such supplements has been reported to enrich 18:2n-6, 18:3n-3, 20:5n-3 and 22:6n-3 in ruminant milk up to concentrations of 7.6, 5.1, 1.4 and 2.2 g/100 g fatty acids, respectively (Gulati *et al.*, 2005).

Nutritional approaches to altering milk fat composition

Replacing grass silage with red clover silage consistently increases 18:2n-6 and 18:3n-3 in milk and often lowers 4- to 18-carbon SFA concentrations (Dewhurst *et al.*, 2006; Vanhatalo *et al.*, 2007; Lourenço *et al.*, 2008; Table 3). Replacing grass silage, grass hay or conserved lucerne with maize silage has variable effects on milk SFA content, but typically increases *trans* 18:1 and 18:2n-6 and lowers 18:3n-3 concentrations (Chilliard *et al.*, 2007; Kliem *et al.*, 2008; Bernard *et al.*, 2009c). Compared with lowland pastures, milk from cows fed botanical diverse pastures typically contains lower 4:0 to 16:0 and higher 18:2n-6 and 18:3n-3 concentrations (Table 3).

Milk from grazing ruminants contains lower proportions of SFA and higher *trans*-11 18:1, *cis*-9, *trans*-11 CLA, 18:2n-6 and 18:3n-3 concentrations compared with dried or ensiled forages (Table 3). Effects on milk fat composition occur in direct relation to the amount of dietary energy from pasture, with the extent of 18:2n-6 and 18:3n-3 enrichment being related to grass maturity and lipid content (Dewhurst *et al.*, 2006; Chilliard *et al.*, 2007). Comparisons of milk composition from cows at pasture or housed indoors and offered chopped grass harvested from the same sward (Leiber *et al.*, 2005; Mohammed *et al.*, 2009) highlight that the effects of pasture

Table 2 Effect of post-ruminal infusions of oils and fatty acid preparations on milk fatty acid composition in lactating cows

Lipid infused	Amount (g/day)	Fatty acid composition (g/100 g fatty acids)															References
		4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ¹	18:3n-3	20:5n-3	22:6n-3	
Rapeseed oil ²	0	3.62	2.68	1.66	4.39	5.58	14.8	37.5	6.17	15.1	0.89	3.61	NR	1.29	NR	DePeters <i>et al.</i> (2001)	
	330	3.39	2.51	1.57	3.93	4.59	12.3	27.2	6.89	21.7	0.75	9.54	NR	3.79	NR		
Rapeseed oil ³	0		6.26		3.63	11.9	30.1	10.7	24.2	1.95	2.37	0.51	0.42	NR	Chelikani <i>et al.</i> (2004)		
	1000		5.59		3.68	8.07	18.3	8.75	34.6	2.15	8.69	0.51	3.36	NR			
High oleic sunflower Fatty acids ⁴	0	4.54	2.86	1.71	3.96	4.41	12.4	28.2	9.93	19.4	1.72	3.75	NR	0.72	NR	Drackley <i>et al.</i> (2007)	
	224	3.99	2.48	1.48	3.34	3.72	11.1	25.2	9.43	28.3	1.45	3.61	NR	0.68	NR		
	459	4.10	2.49	1.49	3.24	3.43	9.83	20.4	8.04	39.2	1.29	2.67	NR	0.55	NR		
	727	3.67	2.13	1.22	2.60	2.79	7.96	19.5	5.40	46.5	1.12	3.40	NR	0.44	NR		
Soya bean oil ⁵	856	3.34	1.48	0.75	1.37	1.19	4.32	15.8	7.26	57.4	1.23	3.35	NR	0.40	NR		
	0	3.65	1.64	1.60	3.36	4.12	11.2	30.6	9.35		21.3	2.68	NR	0.36	NR	Litherland <i>et al.</i> (2005)	
	200	3.74	2.23	1.47	3.37	3.79	10.1	26.3	10.9		21.6	6.96	NR	0.97	NR		
	400	3.59	2.05	1.22	2.66	2.86	8.33	23.6	10.6		23.2	12.7	NR	1.78	NR		
Soya bean oil ⁶	600	3.54	2.05	1.22	2.71	2.97	8.17	23.4	9.03		20.9	16.6	NR	2.36	NR		
	0		8.53		2.84	10.34	31.7	9.44	16.8	0.62	2.43	NR	0.40	NR	Ortiz-Gonzalez <i>et al.</i> (2007)		
Linseed oil	445		7.75		2.09	7.71	21.6	9.06	24.3	0.59	14.5	NR	1.48	NR			
	0	5.7	2.3	1.4	3.1	3.8	11.1	36.9	9.6		20.3	1.9	NR	1.0	0.14	NR	Petit <i>et al.</i> (2002)
Linseed oil ⁷	500	4.9	2.3	1.6	4.2	5.2	10.3	25.5	8.6		16.3	5.4	NR	13.9	0.15	NR	
	0	4.13	1.58	0.91	1.73	2.29	8.46	18.7	11.6	26.5	8.57	2.52	NR	2.33	0.09	NR	Kazama <i>et al.</i> (2010)
Linseed fatty acids ⁸	400	4.64	2.42	1.46	3.43	3.81	9.32	20.1	8.54	17.3	1.34	6.14	NR	14.4	0.22	NR	
	400	5.21	2.33	1.27	2.56	2.63	7.67	16.1	14.1	21.7	3.19	5.03	NR	11.6	0.16	NR	
	0	3.67	2.34	1.44	3.39	3.98	12.4	35.3	9.94	17.4	1.28	2.38	0.37	0.61	0.09	NR	Khas-Erdene <i>et al.</i> (2010)
	39	3.07	1.84	1.01	2.86	3.57	11.6	34.7	9.92	16.6	1.21	2.94	0.37	6.49	0.18	NR	
	75	3.16	1.20	1.28	3.25	3.82	10.9	31.1	9.26	13.7	1.15	3.19	0.28	12.4	0.22	NR	
	117	2.02	1.50	1.03	2.81	3.27	9.72	29.4	10.88	11.7	1.28	3.77	0.26	18.8	0.21	NR	
Fish oil	156	2.01	1.67	1.14	2.77	3.19	8.85	24.9	9.51	11.5	0.98	4.16	0.18	25.4	0.22	NR	
	0	3.58	2.40	1.54	3.91	5.09	13.5	30.3	14.0		18.9	1.63	NR	1.46	0.09	0.00	Hagemeister <i>et al.</i> (1988)
	220	2.88	2.28	1.75	5.15	6.29	13.7	21.8	8.12		16.8	2.21	NR	1.98	3.44	1.67	
Fish oil ⁹	420	2.75	2.18	1.67	4.84	6.16	13.7	25.0	7.43		16.9	2.24	NR	1.84	2.43	1.01	
	0	1.91	1.92	1.28	3.43	4.27	13.9	34.2	8.69	15.8	3.01	1.88	0.56	0.28	0.08	0.04	Loor <i>et al.</i> (2005)
	270	1.84	2.07	1.52	4.30	5.17	14.6	28.5	9.34	14.5	3.04	2.01	0.53	0.37	1.47	0.47	

¹ *Cis*-9, *trans*-11 conjugated linoleic acid.

² Rapeseed oil contained (g/100 g fat) 16:0 (5.57), 18:0 (2.41), *cis*-9 18:1 (43.0), 18:2n-6 (26.5) and 18:3n-3 (7.99) as major components. Milk fatty acid concentrations reported as g/100 g fat.

³ Rapeseed oil contained (g/100 g fatty acid methyl esters) 16:0 (4.21), 18:0 (2.08), *cis*-9 18:1 (62.4), 18:2n-6 (18.5) and 18:3n-3 (8.97) as major components. Milk fatty acid concentrations reported as g/100 g fatty acid methyl esters.

⁴ High oleic sunflower fatty acid preparations contained (g/100 g) 16:0 (2.45), 18:0 (1.80), *cis*-9 18:1 (91.4) and 18:2n-6 (2.35) as major components. Milk fatty acid concentrations reported as g/100 g fatty acid butyl esters.

⁵ Soya bean oil contained (g/100 g fatty acids) 16:0 (10.4), 18:0 (4.30), *cis*-9 18:1 (23.6), 18:2n-6 (52.4) and 18:3n-3 (7.71) as major components. Milk fatty acid concentrations reported as g/100 g fat.

⁶ Soya bean oil contained (g/100 g fatty acids) 16:0 (9.04), 18:0 (3.26), *cis*-9 18:1 (25.8), 18:2n-6 (54.1) and 18:3n-3 (6.37) as major components. Milk fatty acid concentrations reported as g/100 g fat.

⁷ Linseed oil contained (g/100 g fatty acid methyl esters) 16:0 (5.33), *cis*-9 18:1 (18.8), 18:2n-6 (16.1) and 18:3n-3 (53.7) as major components. Cows on the control diet received ruminal infusions of 400 g linseed oil/day.

⁸ Fatty acid preparations contained (g/100 g) *cis*-9 18:1 (2.8), 18:2n-6 (14.7) and 18:3n-3 (82.4). Milk fatty acid concentrations reported as g/100 g fatty acid methyl esters.

⁹ Fish oil contained (g/100 g fatty acids) 14:0 (7.60), 16:0 (9.20), *cis*-9 18:1 (8.00), 20:5n-3 (21.5) and 22:6n-3 (7.10) as major components.

NR, not reported.

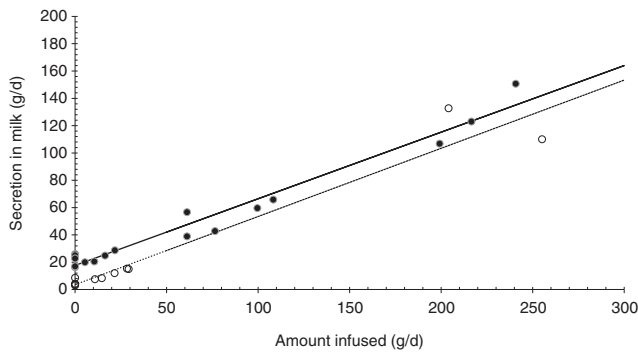


Figure 4 Relationship between the amount of 18:2n-6 (●) or 18:3n-3 (○) infused at the abomasum and mammary secretion of 18:2n-6 and 18:3n-3 in lactating cows. Data derived from experiments involving infusions of examining the effects of post-ruminal infusion of soya oil (Litherland *et al.*, 2005), soya fatty acids (Litherland *et al.*, 2005; Ortiz-Gonzalez *et al.*, 2007) and linseed oil (Petit *et al.*, 2002; Kazama *et al.*, 2010). Solid line indicates the relationship: $18:2n-6_{\text{milk}} = 0.488 \times 18:2n-6_{\text{infused}} + 17.67$ ($n = 11$, $R^2 = 0.968$, $P < 0.001$) and the dotted line indicates the relationship: $18:3n-3_{\text{milk}} = 0.499 \times 18:3n-3_{\text{infused}} + 3.55$ ($n = 11$, $R^2 = 0.942$, $P < 0.001$).

on milk fat composition are not explained solely by differences in PUFA intake. Comparisons of milk fat composition in cows fed diets based on grass hay or grass silages indicate that drying rather than ensiling has relatively minor effects on most fatty acids, but consistently increases 18:3n-3 concentrations (Shingfield *et al.*, 2005; Dewhurst *et al.*, 2006; Chilliard *et al.*, 2007).

Dietary plant oil or oilseed supplements are known to alter the fatty acid composition of ruminant milk (Chilliard *et al.*, 2007; Glasser *et al.*, 2008a; Shingfield *et al.*, 2008b). The extent to which plant oils or oilseeds alter milk fatty acid composition is dependent on several factors including the amount of oil included in the diet, fatty acid profile of the lipid supplement, form of lipid in the diet, and/or processing of oilseeds and the composition of the basal diet (Table 4). Plant oils or oilseeds in the diet result in dose-dependent decreases in the concentration and secretion of 10- to 16-carbon fatty acids, with no major differences in medium-chain SFA concentration responses to oils enriched in *cis*-9 18:1, 18:2n-6 or 18:3n-3 (Table 4). Such changes do not occur in isolation, but are also accompanied by increases in the relative abundance of 18:0, *cis*-9 18:1 and total *trans* 18:1 concentrations (Table 4).

On typical diets, concentrations of 18:2n-6 in bovine, caprine and ovine milk vary between 2.0 and 3.0 g/100 g fatty acids. Even when diets containing relatively high amounts of soya bean, sunflower or safflower oil are fed, enrichment of 18:2n-6 in ruminant milk is marginal and rarely exceeds 3.5 g/100 g fatty acids (Table 4). The potential to enrich 18:3n-3 in ruminant milk is also limited (mean responses 0.1 to 0.9 g/100 g fatty acids) even when oils or oilseeds enriched in 18:3n-3 are fed (Table 4).

Ruminant milk typically contains < 0.1 g of 20:5n-3/100 g fatty acids and trace amounts of 22:6n-3 (Table 5). Numerous experiments have examined the use of dietary fish oil, fishmeal or marine algae supplements to increase 20:5n-3

and 22:6n-3 in ruminant milk. Irrespective of the source of marine lipid, composition of basal diet or ruminant species studied, combined enrichment of 20:5n-3 and 22:6n-3 in milk fat rarely exceeds 1.2 g/100 g fatty acids (Table 5).

Genetic approaches to altering milk fat composition

It is well established that the milk fat content differs between cattle breeds. Selection for milk fat percentage typically increases the proportion of fatty acids synthesized *de novo* and 16:0 content and decreases 18-carbon fatty acid concentrations (Arnould and Soyeurt, 2009). Even within breed, prolonged genetic selection for milk yield in Holstein-Friesians has in certain populations been associated with a decrease in milk fat 6:0, 8:0, 10:0, 12:0, 14:0 and 16:0 content and higher *cis*-9 18:1 concentrations (Arnould and Soyeurt, 2009).

Developing effective breeding programmes for altering milk fat composition is dependent on the existence of genetic variation, estimation of genetic parameters, a mechanism for selection and sufficient economic incentives. Recent estimates of the heritability of milk fatty acid concentrations (Table 6) highlight the possibility to make further progress through breeding, although the impact of selection for milk fat composition on other economically important production, reproduction and health traits remains uncertain. More rapid progress towards the production of milk containing lower SFA and higher unsaturated fatty acid concentrations could be expected through the identification of polymorphisms of individual genes involved in milk fat synthesis. Consistent and significant associations have been reported between single-nucleotide polymorphisms (SNP) for diacylglycerol acyltransferase 1 (DGAT1) and SCD with milk fat composition traits, specifically the concentrations of medium-chain SFA and *cis*-9 containing unsaturated fatty acids in cattle (Arnould and Soyeurt, 2009; Conte *et al.*, 2010; Bouwman *et al.*, 2011) and goats (Zidi *et al.*, 2010). Available data suggest that polymorphism of the bovine SREBP1 gene is not significantly associated with milk fatty acid composition (Conte *et al.*, 2010).

Altering the fatty acid composition of ruminant meat

Potential to alter muscle lipid composition

The potential to alter the fatty acid composition of muscle lipids is to a large extent determined by the extent of lipolysis and biohydrogenation of dietary lipids in the rumen. Reports on the recovery of post-ruminal infusions of oil in ruminant tissues are scarce. Infusion of linseed oil at the duodenum was reported to increase 18:3n-3 concentrations in bovine muscle from 0.7 to 7.6 g/100 g fatty acids (Bauchart *et al.*, unpublished cited by Doreau *et al.*, 2011). More recently, the influence of continuous 42-day abomasal infusions of a control oil (3:2 w/w mixture of cotton seed oil and olive oil) or fish oil at a rate equivalent to 40 g/kg dry matter intake on muscle lipid composition was examined in growing crossbred steers (Fortin *et al.*, 2010). Compared

Table 3 Effect of forage species, conservation method and herbage maturity on the fatty acid composition of ruminant milk

Forage	Ruminant species	Fatty acid composition (g/100 g fatty acids)															References
		4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ¹	18:3n-3	20:5n-3	22:6n-3	
Ryegrass pasture	Bovine ²	3.55	2.55	1.53	3.54	3.85	11.5	25.3	10.1	18.3	4.76	0.94	1.71	0.70	0.08	0.01	Leiber <i>et al.</i> (2005)
Zero grazed ryegrass		3.48	2.55	1.52	3.46	4.04	12.1	29.3	9.30	16.4	4.03	0.84	1.37	0.62	0.07	0.01	
Conserved forage ³		3.48	2.37	1.31	2.74	3.14	10.7	34.0	10.2	18.8	1.70	1.38	0.53	0.50	0.06	<0.01	
Alpine pasture		3.55	2.04	1.02	1.95	2.09	8.5	25.4	11.8	24.1	4.08	1.57	1.34	1.15	0.08	0.01	
Zero grazed alpine pasture		3.89	2.17	1.06	1.91	2.23	9.5	29.5	10.4	21.6	3.25	1.42	1.16	0.95	0.08	0.01	
Conserved forage ³		3.26	2.19	1.21	2.53	3.00	10.8	33.7	9.4	20.2	1.56	1.31	0.55	0.54	0.07	<0.01	
Pasture – continuous grazing	Bovine	2.40	1.71	1.10	2.51	3.00	10.9	24.4	11.5	20.5	5.41	1.18	1.64	0.94	0.09	NR	Coppa <i>et al.</i> (2011)
Pasture – rotational grazing		2.32	1.72	1.14	2.75	3.39	11.6	25.5	9.45	19.8	5.85	0.83	2.22	0.73	0.07	NR	
Grass hay		2.20	1.84	1.25	3.19	4.06	13.4	32.4	7.67	17.6	1.98	1.26	0.62	0.72	0.08	NR	
Ryegrass pasture	Bovine	3.63	2.34	1.34	2.76	2.96	9.79	23.7	10.1	18.4	7.83	1.08	2.07	0.68	0.05	0.02	Mohammed <i>et al.</i> (2009)
Zero grazed ryegrass		3.87	2.57	1.45	3.02	3.16	10.4	26.3	10.6	16.5	6.18	1.03	1.38	0.82	0.07	0.02	
Ryegrass silage		3.94	2.57	1.39	2.95	3.29	11.2	37.9	7.26	13.2	2.67	0.82	0.54	0.34	0.05	0.02	
Grass hay	Bovine	2.51	2.16	1.47	3.41	3.97	13.3	34.5	9.17	15.2	3.78	1.21	0.45	0.50	0.26	<0.01	Shingfield <i>et al.</i> (2005)
Grass silage no additive		2.89	2.23	1.49	3.31	3.79	12.9	34.7	9.75	15.1	3.62	0.96	0.41	0.35	0.31	<0.01	
Grass silage inoculant		2.94	2.34	1.53	3.43	3.90	13.1	33.8	10.0	15.3	3.71	0.96	0.41	0.43	0.11	<0.01	
Grass silage formic acid		2.58	2.21	1.50	3.43	3.99	13.2	34.2	10.0	14.5	4.25	0.93	0.49	0.29	0.14	<0.01	
Perennial ryegrass silage	Bovine	4.91	2.69	1.36	2.95	3.52	11.7	32.5	11.0	20.7	1.13 ⁴	0.36	0.36	0.40	NR	Dewhurst <i>et al.</i> (2003)	
Red clover silage		5.78	2.98	1.43	2.83	3.31	11.3	30.6	11.6	20.2	1.25 ⁴	1.58	0.41	1.28	NR		
White clover silage		5.16	3.04	1.57	3.47	4.16	12.7	32.9	9.70	17.9	1.06 ⁴	1.54	0.34	0.96	NR		
Grass silage early cut	Bovine	5.60	2.79	1.51	3.20	3.60	12.0	29.4	10.4	16.9	3.63	1.24	0.38	0.41	0.05	0.005	Vanhatalo <i>et al.</i> (2007)
Red clover silage early cut		6.17	2.82	1.46	2.79	3.01	10.4	25.5	11.2	19.9	3.98	1.80	0.36	1.34	0.05	0.004	
Grass silage late cut		5.58	2.73	1.47	3.09	3.48	11.8	28.2	10.7	18.1	3.66	1.32	0.41	0.37	0.09	0.002	
Red clover silage late cut		5.91	2.75	1.42	2.79	3.05	10.7	27.0	10.5	19.3	4.10	1.65	0.42	0.88	0.08	0.004	
Italian ryegrass	Bovine			NR		3.13	8.99	29.4	11.7	22.6	4.34	1.32	1.03	0.81	NR	Lee <i>et al.</i> (2009b)	
Red clover				NR		2.99	12.1	27.2	11.0	23.9	5.10	2.38	1.09	1.47	NR		
Perennial ryegrass silage	Bovine			NR		3.67	12.3	38.5	8.88	17.7	2.24	1.00	0.45	0.56	NR	Moorby <i>et al.</i> (2009)	
Red clover silage				NR		3.11	11.3	36.5	8.74	19.9	2.28	1.63	0.39	1.49	NR		
Grass hay	Caprine	2.27	2.25	2.52	9.48	5.00	11.7	26.4	6.88	16.9	2.25	2.13	0.83	1.04	0.07	0.02	Bernard <i>et al.</i> (2009c)
Maize silage		2.38	2.47	2.74	10.6	5.72	12.1	29.9	4.88	13.7	2.41	2.41	0.82	0.19	0.03	0.01	
Burr medic ⁵ – winter	Ovine	4.55	2.65	1.88	8.75	4.03	10.6	23.9	9.15	21.5	3.24	2.35	2.30	2.19	NR	Addis <i>et al.</i> (2005)	
Burr medic ⁵ – spring		3.91	1.70	1.02	4.81	2.51	9.01	23.1	12.1	29.9	2.25	2.82	1.65	1.84	NR		
Daisy forb ⁶ – winter		5.06	2.43	1.59	6.90	3.40	10.1	20.9	10.8	25.4	4.00	2.74	2.35	1.62	NR		
Daisy forb ⁶ – spring		3.24	0.85	0.50	1.90	1.48	5.53	18.8	13.3	41.3	3.13	3.48	2.33	1.26	NR		
Ryegrass – winter		4.65	2.54	1.98	9.85	4.59	10.8	23.9	10.5	22.0	2.08	1.59	1.20	1.47	NR		
Ryegrass – spring		4.70	2.63	1.80	8.99	4.18	10.9	24.7	11.0	21.14	2.52	1.54	1.43	1.44	NR		

Table 3 Continued

Forage	Ruminant species	Fatty acid composition (g/100 g fatty acids)												References		
		4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	cis-9 18:1	trans 18:1	18:2n-6	CLA ¹		18:3n-3	20:5n-3
Sulla ⁷ – winter		4.91	3.16	2.55	13.9	6.52	11.7	22.5	9.61	13.3	3.18	1.58	1.25	2.98	NR	
Sulla ⁷ – spring		4.78	2.94	2.18	11.8	5.44	11.9	24.7	10.3	14.8	2.36	1.75	1.12	3.15	NR	
Pelleted lucerne	Ovine	3.20	2.63	2.70	11.0	8.97	16.4	30.5	2.06	6.76	5.58	3.43	0.17	1.05	0.05	0.03
Maize silage		3.22	2.90	3.04	10.3	7.18	11.7	22.7	6.48	14.1	6.71	4.97	0.82	0.42	0.03	0.07
Lucerne haylage		6.61	3.24	3.35	10.4	6.30	11.1	22.5	7.86	14.8	4.89	3.33	0.71	0.65	0.07	0.22
Maize silage		6.46	3.23	3.35	10.6	6.91	11.8	21.7	7.69	13.9	6.18	2.84	0.64	0.26	0.03	0.22

¹Cis-9, trans-11 conjugated linoleic acid.

²Milk fatty acid concentrations reported as g/100 g fatty acid methyl esters.

³Conserved forage comprised a mixture of ryegrass silage, maize silage and grass hay fed in a ratio of 10:60:30 on a dry matter basis.

⁴Concentration of trans-11 18:1.

⁵*Medicago polymorpha* L.

⁶*Chrysanthemum coronarium* L.

⁷*Hedysarum coronarium* L.

NR, not reported.

with the control, administration of fish oil increased the concentration of 20:5n-3 and 22:6n-3 in muscle total membrane PL from 4.4 and 0.96 to 13.6 and 3.9 g/100 g fatty acids, respectively, and induce more than 8-fold increase in the sum of 20:5n-3, 22:5n-3 and 22:6n-3 of muscle TAG. As a result of the enrichment of both PL and TAG fractions, total long-chain n-3 PUFA content increased from 23.2 to 60.1 mg/100 g muscle. Responses to dietary rumen protected lipid supplements have also demonstrated the biological potential to alter meat fatty acid composition. In growing cattle, supplements of formaldehyde-treated soya bean and a mixture of sunflower oil and linseed oil (n-6 : n-3 ratio of 2.4 : 1) increased tissue 18:3n-3 content relative to unprotected linseed, but the incorporation of 18:2n-6 was much higher (Table 7). Feeding a similar type of supplement with a n-6 : n-3 PUFA ratio of 1 : 1 resulted in greater deposition of 18:3n-3 relative to 18:2n-6, leading to a relatively high 18:3n-3 content (ca. 130 mg/100 g muscle; refer to Scollan *et al.*, 2006). In both studies, no effects on the abundance of longer 20-carbon chain PUFA were observed. However, rumen-protected fish oil supplements can be used to increase 20:5n-3 and 22:6n-3 concentrations several-fold and lower the n-6 : n-3 ratio of lamb and beef (Gulati *et al.*, 2005; Dunne *et al.*, 2011).

Nutritional approaches to altering muscle fatty acid composition

Consistent with the nutritional strategies known to influence milk fat composition, the majority of studies in growing ruminants have examined the potential of forage species, forage conservation method and dietary plant oils, oilseeds, fish oil and marine algae supplements to alter muscle fatty acid composition (Table 7). However, in contrast to milk, it is possible to influence the abundance of 20-carbon PUFA in tissue PL by supplementing the diet with sources of 18:2n-6 and 18:3n-3, as well as dietary supplements containing 20-carbon PUFA (Table 7).

Rearing cattle or lambs on pasture rather than concentrate-based diets increases 18:3n-3 and the longer-chain derivatives 20:5n-3 and 22:6n-3 in the PL fraction of muscle (Arousseau *et al.*, 2004; Nuernberg *et al.*, 2005; Warren *et al.*, 2008), reflecting the opportunity for elongation and desaturation of 18:3n-3 in ruminant tissues. Recent investigations have identified mRNA encoding the elongase and desaturase responsible in bovine tissues (Cherfaoui *et al.*, 2012). Concentrates rich in 18:2n-6 result in higher concentrations of 18:2n-6 and associated longer-chain derivatives in the muscle of cattle (Warren *et al.*, 2008; Aldai *et al.*, 2011; Juárez *et al.*, 2011) and sheep (Nuernberg *et al.*, 2005; Radunz *et al.*, 2009; Turner *et al.*, 2012a).

Both the amount of grass and duration of rearing on pasture has been shown to influence the potential to enrich 18:3n-3, 20:5n-3 and 22:6n-3 in bovine muscle (French *et al.*, 2000; Noci *et al.*, 2005a; Alfaia *et al.*, 2009). Conversely, feeding concentrates for a 2-month finishing period was shown to lower the proportion of n-3 and increase the abundance of n-6 PUFA (Aldai *et al.*, 2011). Compared with

Table 4 Effect of dietary plant oil and oilseed supplements on the fatty acid composition of ruminant milk

Lipid supplement	Intake ¹ (g/day)	Ruminant species	Forage	F : C ²	Milk fatty acid composition (g/100 g total fatty acids)													References
					4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ³	18:3n-3	
Control	0	Bovine	LH/LS (55 : 45)	44 : 56	2.95	2.02	1.18	2.68	3.06	9.79	30.7	9.12	21.2	2.26	3.59	0.46	0.50	Mosley <i>et al.</i> (2007)
Palm oil by-product	476				3.09	1.88	0.99	2.12	2.42	8.63	39.1	6.83	19.3	1.79	3.17	0.40	0.41	
Palm oil by-product	887				3.09	1.77	0.89	1.85	2.11	7.96	44.0	5.79	17.9	1.54	2.99	0.34	0.36	
Palm oil by-product	1248				3.03	1.72	0.85	1.78	2.04	7.89	45.6	4.95	17.4	1.44	3.11	0.30	0.36	
Control	0	Bovine	LH/LS/BS (26 : 48 : 26)	53 : 47	3.29	2.13	1.30	3.25	4.08	12.3	32.6	9.22	14.8	2.83	2.26	0.23	0.40	Hristov <i>et al.</i> (2009)
Coconut oil	530				3.14	1.90	1.15	2.93	8.54	14.7	30.8	6.94	12.4	3.79	1.87	0.25	0.28	
Control	0	Bovine	Pasture (5)	(5)	1.87	1.40	0.97	2.33	2.83	10.2	24.1	14.3	22.1	4.95	1.12	1.19	0.60	Rego <i>et al.</i> (2009)
Rapeseed oil	500				1.58	0.99	0.59	1.29	1.63	6.90	18.0	17.3	30.6	7.51	0.98	1.14	0.38	
Sunflower oil	500				1.38	0.87	0.53	1.15	1.52	6.61	18.2	16.8	29.6	8.78	1.25	1.61	0.42	
Linseed oil	500				1.67	1.06	0.65	1.41	1.75	7.09	17.0	16.8	26.5	9.67	0.99	1.54	0.53	
Control	0	Bovine	RCS	55 : 45	3.35	1.76	1.23	3.19	3.91	13.0	32.4	7.63	13.2	4.02	2.08	0.44	1.1	Halmemies-Beauchet-Filleau <i>et al.</i> (2011)
Rapeseed oil	310				3.54	1.72	1.14	2.75	3.24	11.8	27.3	10.4	17.3	5.2	1.99	0.56	1.02	
Sunflower oil	280				3.58	1.71	1.14	2.76	3.24	11.7	26.5	10.9	16.6	5.55	2.55	0.64	0.99	
Camelina oil	300				3.57	1.69	1.14	2.72	3.20	11.6	27.1	9.86	16.5	4.91	2.10	0.57	1.17	
Camelina expeller	210				3.67	1.69	1.09	2.57	3.08	11.9	26.8	7.33	13.5	8.28	1.98	1.02	1.06	
Calcium salts of Palm oil	950				3.30	2.30	1.30	2.70	2.90	10.0	34.5	9.80	18.6	4.10	2.25	0.57	0.25	
Whole rapeseed	1186	3.30	2.50	1.50	3.30	3.60	11.7	31.1	10.8	17.0	3.20	1.76	0.44	0.23				
Milled rapeseed	1147	3.10	2.20	1.20	2.40	2.60	9.60	21.6	15.5	23.0	6.40	1.73	0.86	0.27				
Rapeseed oil	1044	2.70	1.80	0.90	1.90	2.20	8.70	19.8	14.6	24.3	10.0	1.78	1.31	0.22				
Ca salts of Palm oil	826	Bovine	MS/GS (75 : 25)	50 : 50	3.50	2.40	1.20	2.40	2.50	9.20	33.7	9.10	21.1	3.30	2.56	0.60	0.23	Kliem <i>et al.</i> (2011)
Milled rapeseeds	1345				3.20	2.20	1.10	2.10	2.30	8.80	20.2	16.1	26.9	5.70	1.82	0.71	0.28	
Milled oleic rapeseeds	1345				2.90	1.90	0.90	1.90	2.10	8.30	19.2	16.7	28.9	5.90	1.61	0.61	0.17	
Control	0	Bovine	MS/LH/GH (78 : 14 : 8)	57 : 43	2.76	1.64	0.99	2.39	2.93	10.5	24.9	11.2	20.7	6.64	2.79	0.67	0.36	Hristov <i>et al.</i> (2011)
Rapeseed expeller	609				2.58	1.46	0.84	1.93	2.38	9.26	23.4	12.5	22.7	8.17	2.58	0.68	0.36	
Oleic rapeseed expeller	515				2.71	1.50	0.86	1.94	2.40	9.13	22.9	11.9	23.5	8.34	2.45	0.91	0.30	
Erucic acid rapeseed expeller	648				2.56	1.47	0.86	1.94	2.39	8.96	21.0	11.6	23.1	6.43	2.52	0.49	0.36	
Control	0	Bovine	MS/GH (90 : 10)	65 : 35	3.13	2.24	1.41	3.37	4.22	12.6	29.1	8.32	17.4	3.49	1.69	0.77	0.67	Chilliard <i>et al.</i> (2009)
Whole linseed	559				3.11	2.14	1.24	2.74	3.22	10.8	25.0	13.7	23.5	2.13	1.28	0.44	0.65	
Extruded linseed	497				2.78	1.64	0.89	1.89	2.36	8.83	19.6	11.7	22.4	9.95	1.61	1.27	1.20	
Linseed oil	721				2.05	1.06	0.54	1.09	1.52	5.88	15.9	11.3	26.3	10.6	1.53	0.65	0.54	
Control	0	Caprine ⁴	GH	63 : 37	3.83	3.71	5.26	8.22	3.75	9.59	28.2	6.71	16.6	1.97	2.77	0.61	0.49	Mele <i>et al.</i> (2008)
Soya bean oil	100				3.81	3.50	4.58	6.36	2.65	7.81	24.0	8.19	18.8	9.98	3.25	3.79	0.34	
Control	0	Caprine	GH	35 : 65	3.80	3.79	5.04	8.69	4.02	10.0	30.0	6.70	16.6	2.11	2.97	0.80	0.39	Bernard <i>et al.</i> (2009c)
Soya bean oil	100				3.83	3.49	4.76	7.17	3.18	8.43	24.5	8.08	17.7	7.15	3.32	2.67	0.32	
Control	0	Caprine	GH	44 : 56	2.27	2.25	2.52	9.48	5.00	11.7	26.4	6.88	16.9	2.25	2.13	0.83	1.04	Bernard <i>et al.</i> (2009c)
Sunflower oil	130				2.58	2.08	2.01	6.13	2.65	7.42	16.7	12.5	20.6	11.0	2.24	3.69	0.57	

Table 4 Continued

Lipid supplement	Intake ¹ (g/day)	Ruminant species	Forage	F : C ²	Milk fatty acid composition (g/100 g total fatty acids)													References
					4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ³	18:3n-3	
Linseed oil	130			49 : 51	2.64	2.17	2.23	6.81	2.94	7.59	16.1	11.6	18.0	10.4	1.38	3.31	1.15	
Control	0		MS	39 : 61	2.38	2.47	2.74	10.6	5.72	12.1	29.9	4.88	13.7	2.41	2.41	0.82	0.19	
Sunflower oil	130			46 : 54	2.56	2.22	2.19	6.91	3.12	8.10	18.8	9.01	15.7	14.5	3.01	4.27	0.15	
Linseed oil	130			45 : 55	2.72	2.44	2.54	8.06	3.54	8.36	18.6	8.15	15.3	10.2	1.92	2.56	0.69	
Control	0	Caprine ⁵	LH	NR	NR	1.58	2.01	8.23	3.93	10.7	35.9	6.91	18.5	1.54	2.36	0.63	0.45	Nudda <i>et al.</i> (2006)
Extruded linseed	16			NR	NR	1.46	1.87	7.40	3.48	9.81	32.4	8.74	20.7	2.43	2.44	0.96	0.80	
Extruded linseed	32			NR	NR	1.59	2.05	7.77	3.67	9.46	27.5	10.0	23.5	2.44	2.44	1.05	0.99	
Control	0	Ovine ⁵	LH	20 : 80	4.37	3.34	2.78	9.00	4.90	11.2	26.0	6.45	15.0	4.44	2.26	0.87	0.22	Gómez-Cortès <i>et al.</i> (2008b)
Olive oil	148				4.59	3.14	2.77	6.64	3.22	8.48	23.0	8.32	23.6	9.85	1.46	0.39	0.15	
Control	0	Ovine ⁵	LH	20 : 80	3.51	3.27	2.90	9.64	5.09	12.4	28.0	4.86	12.1	6.19	2.70	1.04	0.35	Gómez-Cortès <i>et al.</i> (2008a)
Soya bean oil	140				4.27	2.28	1.98	5.15	2.95	8.48	22.3	7.60	15.3	15.6	3.46	3.44	0.46	
Control	0	Ovine ⁵	LH	20 : 80	4.21	3.55	3.44	10.9	6.12	11.4	27.4	5.46	11.7	4.62	2.49	0.66	0.38	Gómez-Cortès <i>et al.</i> (2011b)
Sunflower oil	60				4.28	3.58	3.42	10.1	5.31	10.6	23.9	6.90	12.4	7.92	2.63	1.17	0.31	
Sunflower oil	117				4.61	3.27	2.92	8.26	4.48	9.88	22.3	6.66	12.9	12.3	2.87	2.12	0.29	
Sunflower oil	165				4.69	2.76	2.29	6.35	3.63	9.26	21.6	6.90	14.0	15.6	2.95	2.59	0.28	

LH = lucerne hay; LS = lucerne silage; BS = barley silage; RCS = red clover silage; MS = maize silage; GS = grass silage; GH = grass hay.

¹Intake of oil from dietary lipid supplements.

²Dietary forage : concentrate ratio (on a dry matter basis). For studies in grazing cows, the amount of concentrate supplements fed (kg/day) is reported in parentheses.

³*Cis*-9, *trans*-11 conjugated linoleic acid.

⁴Fatty acid concentrations reported as g/100 g fat.

⁵Fatty acid concentrations reported as g/100 g fatty acid methyl esters.

NR, not reported.

Table 5 Effect of dietary fish oil and marine algae supplements on the fatty acid composition of ruminant milk

Lipid supplement	Intake ¹ (g/day)	Ruminant species	Milk fatty acid composition (g/100 g total fatty acids)															References
			4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ²	18:3n-3	20:5n-3	22:6n-3	
Control	0	Bovine ³	4.22	2.23	1.11	2.22	2.40	10.2	24.0	15.4	22.2	4.14	1.88	0.51	0.42	0.05	0.00	Shingfield <i>et al.</i> (2003)
Mackerel/herring oil	250		2.22	1.66	1.08	2.81	3.39	13.3	32.3	3.50	5.93	13.2	2.01	2.41	0.45	0.11	0.10	
Control	0	Bovine	1.91	1.92	1.28	3.43	4.27	13.9	34.2	8.69	15.8	3.01	1.88	0.56	0.28	0.08	0.04	Loor <i>et al.</i> (2005)
Menhaden fish oil	270		1.83	1.75	1.23	3.54	4.49	14.8	31.8	2.71	6.05	13.8	2.01	3.20	0.31	0.36	0.17	
Control	0	Bovine	2.00	1.31	1.66	4.14	5.08	13.3	30.7	7.04	17.8	1.68	2.83	0.52	0.54	0.12	0.03	Bharathan <i>et al.</i> (2008)
Menhaden fish oil	127		1.94	1.21	1.51	3.65	4.44	12.9	29.7	6.53	18.9	2.25	2.84	0.90	0.53	0.19	0.04	
Control	0	Bovine	4.29	2.53	1.48	3.41	4.07	11.4	34.4	6.86	14.9	2.44	1.68	0.44	0.21	0.03	0.00	Shingfield <i>et al.</i> (2006)
Mackerel/herring oil + sunflower oil	261 + 522		3.01	1.41	0.76	1.73	2.26	9.39	27.3	4.52	11.9	18.3	1.79	3.04	0.23	0.11	0.07	
Control	0	Bovine	2.57	2.14	1.34	3.14	3.61	10.8	31.0	8.49	17.3	5.10	2.34	0.44	0.44	0.05	0.03	Cruz-Hernandez <i>et al.</i> (2007)
Anchovy oil + sunflower oil	(5 + 45) ⁴		2.23	1.46	0.75	1.62	1.88	7.34	19.5	9.79	16.3	20.7	2.75	3.38	0.31	0.04	0.03	
Control	0	Bovine ⁵	4.65	2.80	1.35	2.71	2.49	9.35	28.8	10.2	22.1	2.04	1.89	0.48	0.50	NR	0.09	Boeckart <i>et al.</i> (2008)
Marine algae	201		4.69	1.94	1.09	1.98	2.07	8.01	27.7	3.59	17.6	11.6	1.37	1.00	0.42	NR	1.10	
Control	0	Caprine	NR	1.81	2.41	9.10	4.28	11.0	29.3	8.33	20.4	1.42	1.44	0.89	0.62	0.07	0.06	Gagliostro <i>et al.</i> (2006)
Fish oil ⁶	27		NR	1.70	2.79	11.2	6.90	11.5	27.2	1.15	8.40	7.02	1.44	6.16	0.34	0.27	0.52	
Control	0	Caprine	NR	1.68	2.10	8.13	3.89	11.0	31.0	8.02	20.8	1.38	1.48	1.03	0.61	0.09	0.06	
Fish oil ⁶ + sunflower oil	30 + 60		NR	1.55	2.42	8.41	3.86	8.50	21.7	1.93	9.98	19.3	1.89	9.89	0.20	0.10	0.20	
Control	0	Ovine ⁵	3.26	3.34	3.24	10.7	6.10	12.2	27.0	5.80	12.4	4.22 ⁷	2.64	0.64	0.33	0.03	0.02	Toral <i>et al.</i> (2010a)
Sardine and tuna oil	27.5		3.38	3.52	3.50	10.9	5.90	11.7	26.5	2.04	9.02	10.3 ⁷	2.47	1.66	0.34	0.15	0.38	
Control	0	Ovine	3.20	2.63	2.70	11.0	8.97	16.4	30.5	2.06	6.76	5.58	3.43	0.17	1.05	0.05	0.03	Reynolds <i>et al.</i> (2006)
Marine algae + soya bean oil	39 + 79		3.20	3.14	3.63	11.6	7.61	13.2	22.4	1.79	7.88	12.6	3.85	0.27	0.99	0.47	1.39	
Control	0		3.22	2.90	3.04	10.3	7.18	11.7	22.7	6.48	14.1	6.71	4.97	0.82	0.42	0.03	0.07	
Marine algae + soya bean oil	35 + 70		4.56	4.30	4.51	12.2	6.91	13.3	27.2	2.10	8.64	18.4	4.63	0.90	0.53	0.44	1.94	
Control	0	Ovine ⁵	3.71	3.49	3.47	10.9	5.99	11.8	25.9	6.57	13.2	2.55 ⁷	2.37	0.44	0.53	0.05	0.03	Toral <i>et al.</i> (2010b)
Marine algae + sunflower oil	0 + 86		4.00	3.34	3.08	8.80	4.70	10.8	22.4	8.84	16.0	5.56 ⁷	2.23	1.23	0.41	0.04	0.02	
Marine algae + sunflower oil	16 + 87		4.06	3.02	2.77	8.38	4.83	11.8	24.3	3.16	9.84	13.2 ⁷	2.03	2.78	0.37	0.05	0.17	
Marine algae + sunflower oil	29 + 82		4.00	3.29	3.02	8.73	4.61	11.4	24.8	2.37	9.34	13.7 ⁷	2.04	2.58	0.36	0.09	0.46	
Marine algae + sunflower oil	44 + 83		3.84	3.22	2.92	8.27	4.40	11.1	25.9	2.33	9.19	13.0 ⁷	1.86	3.22	0.34	0.10	0.57	

¹Intake of oil from dietary lipid supplements.²*Cis*-9, *trans*-11 conjugated linoleic acid.³Fatty acid concentrations corrected for the effects of ruminal infusions of the lithium salt of cobalt ethylenediaminetetraacetic acid (Shingfield *et al.*, 2008a).⁴Intake of lipid supplements not reported. Concentrations of oil in the diet (g/kg diet dry matter) indicated in parentheses.⁵Fatty acid concentrations reported as g/100 g fatty acid methyl esters.⁶Fish species not reported.⁷Under the specified conditions of analysis *cis*-11 18:1 co-elutes with *trans*-15 18:1 and *trans*-16 18:1 and *cis*-14 18:1 elute as a single peak.

NR, not reported.

Table 6 Heritability of individual fatty acids in bovine milk

Breed	Number of cows	Number of milk samples	Fatty acid (g/100 g fatty acids)											References			
			4:0	6:0	8:0	10:0	12:0	14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6		CLA ¹	18:3n-3	
Multiple ^{2,3}	NR	7700	NR	NR	NR	NR	NR	0.09	0.19	0.20	0.28	0.15	0.15	NR	NR	NR	Soyeurt <i>et al.</i> (2007)
Holstein	233	592	0.00	0.00	0.18	0.22	0.18	0.00	0.00	0.09	0.24	0.06	0.06	NR	NR	NR	Bobé <i>et al.</i> (2008)
Holstein-Friesian	1918	990	0.35	0.39	0.48	0.54	0.49	0.35	0.49	0.31	0.19	0.18	0.12	0.21	0.09	0.09	Stoop <i>et al.</i> (2008)
Holstein-Friesian ³	990	990	NR	NR	NR	NR	NR	NR	0.07	0.03	0.08	0.17	0.12	0.12	NR	NR	Mele <i>et al.</i> (2009)
Holstein-Friesian	2408	2408	0.10	0.27	0.27	0.20	0.13	0.09	0.06	0.06	0.04	0.12	0.08 ⁴	0.02	0.02	0.05	Garnsworthy <i>et al.</i> (2010)

¹ *Cis*-9, *trans*-11 conjugated linoleic acid.

² Population (%) included primiparous and multiparous cows of the Brown Swiss (2.90), Belgian Blue (12.3), Holstein-Friesian (45.4), Jersey (3.92), Montbeliarde (11.2), Normande (13.1), Meuse-Rhine-Yseel Red and White (4.31) breeds and those of unknown genetic origin (6.85).

³ Fatty acid concentrations expressed as g/100 g fat.

⁴ Heritability estimate of total *trans* fatty acid concentrations.

NR, not reported.

finishing on high-concentrate diets, rearing of cattle or lambs on forage-based systems is often associated with a decrease in muscle 16:0 and total SFA and higher *cis*-9 18:1 concentrations (Scollan *et al.*, 2006; Sinclair, 2007; Alfaia *et al.*, 2009; Aldai *et al.*, 2011). Replacing grass silage with whole-crop wheat silage (Noci *et al.*, 2005b) or maize silage (Smith *et al.*, 2009) increased in the n-6 : n-3 ratio of muscle, whereas wilting grass before ensiling decreased this ratio (Noci *et al.*, 2007b). Substituting grass silage with red clover silage increased 18:2n-6 and 18:3n-3 content of muscle (Sinclair, 2007; Lee *et al.*, 2009a), but the higher content of 18:3n-3 due to red clover or lucerne in the diet is not associated with higher 20:5n-3 and 22:6n-3 enrichment (Table 7). Rearing cattle on concentrate containing linseeds increases 18:3n-3 in muscle and the longer-chain derivative 20:5n-3, but not necessarily 22:6n-3 (Noci *et al.*, 2007a; Herdmann *et al.*, 2010a; Nassu *et al.*, 2011; Table 7). In several studies, linseeds also lowered the proportion of 16:0 in IMF (Noci *et al.*, 2007a; Herdmann *et al.*, 2010a; Nassu *et al.*, 2011). Dietary supplements of oils and oilseeds enriched in 18:3n-3 induce similar changes in muscle fatty acid composition of growing lambs (Bessa *et al.*, 2007; Sinclair, 2007; Turner *et al.*, 2012a).

A number of studies have examined the potential of feeding concentrates containing fish oil or marine algae to enrich 20:5n-3 and 22:6n-3 in muscle of growing cattle and lambs. Despite extensive biohydrogenation in the rumen changes in the abundance of long-chain PUFA in muscle reflects the fatty acid profile of dietary marine lipid supplements. Even though fish oil can be used to lower the n-6 : n-3 ratio, increases in the PUFA : SFA are often marginal (0.10 to 0.15). Given that 20-carbon n-3 fatty acids are incorporated mainly into PL rather than TAG, it is possible to enrich these PUFA in muscle without increases in fatness *per se*. Depending on the source and amount of fish oil supplement, concentrations of 20:5n-3 and 22:6n-3 in muscle can be increased by up to 2.33 and 2.55 g/100 g fatty acids, respectively (Scollan *et al.*, 2006; Sinclair, 2007; Noci *et al.*, 2007b).

Potential to alter ruminant muscle composition through genetic selection

Genetics have a much lower influence on muscle PUFA composition in growing ruminants compared with nutrition, whereas age of the animal and breed type specifically affect the concentration of MUFA in beef by affecting SCD gene expression and activity (Smith *et al.*, 2009). Nevertheless, in cattle or sheep fed the same diet and slaughtered at a similar proportion of mature live weight, differences in the abundance of n-3 and n-6 PUFA in muscle between breeds have been identified (Sinclair, 2007; Warren *et al.*, 2008), confirming the importance of genetic factors in regulating IMF composition. The use of high-throughput DNA sequencing techniques, microarray technologies and protein analysis has facilitated the discovery of single SNP for several candidate genes involved in adipogenesis in cattle.

Comparisons of the full-length bovine SCD complementary DNA sequences of Japanese Black cattle revealed the occurrence

Table 7 Effect of forage species, plant oils and rumen protected lipid supplements on the fatty acid composition of muscle (mg/100 g muscle) in growing cattle

Diet	Breed/sex	Fatty acid composition (mg/100 g muscle)											References	
		14:0	16:0	18:0	<i>cis</i> -9 18:1	<i>trans</i> 18:1	18:2n-6	CLA ¹	18:3n-3	20:5n-3	22:5n-3	22:6n-3		Total
Concentrate	Angus steers ²	76.7	808	405	987	88.4	210	14.9	8.1	2.6	8.6	0.6	3129	Warren <i>et al.</i> (2008)
Grass silage	Angus steers ²	218	1830	721	2204	59.7	84.0	12.7	48.3	19.7	27.2	5.1	6173	
Pasture	Asturiana bulls ³	3.30	86.5	86.7	103.1	24.5	76.5	1.9	18.2	5.6	7.1	0.5	547	Aldai <i>et al.</i> (2011)
1-month concentrate after pasture	Asturiana bulls ³	8.82	149	119	164	55.1	95.3	2.2	16.3	7.5	9.3	0.6	813	
2-month concentrate after pasture	Asturiana bulls ³	14.3	221	162	244	62.8	103	3.5	12.5	7.7	9.4	0.8	1055	
Grass silage	Charolais steers ⁴	NR	501	313	660	54.6	63.0	10.4	37.2	18.8	21.6	3.6	2115	Scollan <i>et al.</i> (2008)
Grass/red clover silage (50 : 50 DM basis)	Charolais steers ⁴	NR	644	412	845	57.9	63.6	10.7	42.5	17.5	19.6	3.1	2607	
Red clover silage	Charolais steers ⁴	NR	457	305	585	42.2	71.8	7.6	45.5	18.5	21.4	4.3	1945	
Grass silage	Holstein–Friesian cows	90.5	965.8	467	1351	32.4	66.6	7.8	25.3	11.0	19.6	1.8	3564	Lee <i>et al.</i> (2009a)
Red clover silage	Holstein–Friesian cows	66.5	753.2	432	944	25.5	73.1	4.7	42.6	12.2	20.5	1.7	2769	
Maize silage + n-6 concentrate	Holstein bulls	63.9	653	363	903	73.4	95.4	7.7	14.6	3.9	9.2	1.4	2451	Herdmann <i>et al.</i> (2010a)
Grass silage + n-3 concentrate restricted	Holstein bulls	40.5	422	251	535	70.2	96.9	6.7	22.8	8.2	13.4	2.3	1661	
Grass silage + n-3 concentrate unrestricted	Holstein bulls	31.6	380	233	496	56.8	92.1	5.6	21.0	6.5	11.6	2.1	1497	
Pea hay	Limousin steers	190	1339	511		1811	71	12.0	9.0	NR	NR	NR	4286	Mir <i>et al.</i> (2002)
Pea hay + sunflower oil	Limousin steers	238	1397	698		2150	111	59.0	8.4	NR	NR	NR	4958	
Pea hay	Wagyu steers	406	2959	918		4089	109	25.0	10.2	NR	NR	NR	9259	
Pea hay + sunflower oil	Wagyu steers	452	2998	1269		4701	198	134	5.2	NR	NR	NR	10388	
Barley	Crossbred steers	201	1620	773		2242	82.4	10.5	5.8	NR	NR	NR	5250	Mir <i>et al.</i> (2003)
Barley + sunflower oil	Crossbred steers	236	1622	864		2374	138	19.5	5.2	NR	NR	NR	5571	
Grass silage + palm oil concentrate	Charolais steers	116	953	493	1146	63	81	11.3	22	11	19	2.2	3529	Scollan <i>et al.</i> (2001)
Grass silage + linseed concentrate	Charolais steers	226	916	497	1246	147	78	35.6	43	16	20	2.4	4222	
Grass silage + fish oil concentrate	Charolais steers	267	1336	570	1258	184	66	24.3	26	23	24	4.6	4292	
Hay	Crossbred cows	275	2662	1127	3797	84.6	260	15.3	51	24	44	NR	5680	Nassu <i>et al.</i> (2011)
Hay + linseed	Crossbred cows	276	2339	1170	3465	337	240	30.7	122	27	40	NR	5875	
Barley silage	Crossbred cows	275	2596	1143	4057	73.8	210	11.4	31	13	30	NR	6772	
Barley silage + linseed	Crossbred cows	280	2361	1194	3858	204	212	16.2	106	23	36	NR	6413	
Control	Charolais steers	108	1007	518	1197	72.7	110	16.8	26	11.2	18.6	2.5	3607	Scollan <i>et al.</i> (2003)
Protected lipid (1000 g/day)	Charolais steers	70	642	352	923	39.0	243	10.7	50	9.8	14.4	2.0	2604	
Control	Crossbred heifers	86.6	730	283	937	NR	80.4	NR	13.3	13.0	NR	3.4	2870 ⁵	Dunne <i>et al.</i> (2011)
Protected fish oil (275 g/day)	Crossbred heifers	132	953	388	1083	NR	82.0	NR	27.9	52.3	NR	15.4	3890 ⁵	

DM = dry matter.

¹*Cis*-9, *trans*-11 conjugated linoleic acid.²Data for 19-month-old cattle.³Fatty acid content expressed as mg fatty acid methyl ester/100 g muscle.⁴Silage offered *ad libitum* for 120 days followed by 100 days grazing on perennial ryegrass pastures.⁵Chemical determinations of intramuscular fat.

NR, not reported.

of eight nucleotide substitutions, three in the protein coding region and five in the 3' untranslated region (Taniguchi *et al.*, 2004). Nucleotide substitutions at 878 bp in the protein coding region correspond to valine replacing alanine in the SCD1 protein (Taniguchi *et al.*, 2004). The three SNPs detected in the protein coding region were shown to be linked, constituting two variants of the SCD gene, type V and A. Genotyping of 1003 Japanese Black steers revealed significant differences in IMF total MUFA concentrations between SCD genotypes, with the average effect of substitution for the SCD type A gene being associated with 0.81 g/100 g higher MUFA concentration (Taniguchi *et al.*, 2004). Genotyping for three SNPs in the 3' untranslated region of the SCD gene for a reference Wagyu × Limousin F2 population also revealed that the high SCD alleles were associated with on average -1.76, +1.29 and 0.26 g/100 g differences in muscle SFA, MUFA and PUFA concentrations, respectively (Jiang *et al.*, 2008). Furthermore, there is increasing evidence of a positive association between muscle SCD mRNA abundance and MUFA concentrations (Smith *et al.*, 2009; Mannen, 2011), suggesting that differences in SCD expression contribute to the differences in muscle IMF composition between cattle breeds.

The bovine SREBP1 gene has also been sequenced. Although no mutation was identified in exon regions, a 84 bp insertion (long type, L) and a deletion (short type, S) in intron 5 of bovine SREBP1 was detected (Hoashi *et al.*, 2007). Genotyping of 606 Japanese Black cattle reported that the SS genotype exhibited on average 1.3 g/100 g higher muscle MUFA concentration compared with the LL genotype (Hoashi *et al.*, 2007). Sequencing of four exons that encode for the thioesterase domain located at the 3' end of the bovine FAS gene revealed three SNPs, one that was predicted to result in threonine being replaced with alanine in the FAS protein and the other two being silent (Zhang *et al.*, 2008). Among the three SNPs identified, two were significantly associated with the concentrations of PL, TAG and total lipid in muscle. Genotyping of 331 Angus bulls indicated that the SNP predicted to cause an amino acid substitution was associated with -0.40, -0.81, +1.89, -1.0 and +1.45 g/100 g differences in the concentration of 14:0, 16:0, total 18:1, SFA, MUFA concentrations in IMF, respectively (Zhang *et al.*, 2008).

Further investigations have reported several SNP in the bovine ACSL1 ($n = 3$), FABP4 ($n = 4$), LXR α ($n = 4$) and ACC ($n = 8$) genes, but none for ACSL4 and DGAT2 (Hoashi *et al.*, 2008; Zhang *et al.*, 2010). Genotyping of single or multiple breeds has provided evidence that polymorphisms of the ACC, FABP4 and LXR α gene are associated with alterations in bovine muscle fatty acid composition (Hoashi *et al.*, 2008; Zhang *et al.*, 2010).

Although the association between polymorphisms of single candidate genes on muscle lipid composition may appear small, most have been determined for highly controlled reference populations used for progeny testing. When extending these investigations on commercial Japanese Black populations, both the SCD and FAS genotype have

been significantly associated with 14:0, *cis*-9 14:1, 18:0 and *cis*-9 18:1 concentrations, whereas no effect of the SREBP1 genotype has been detected (Ohsaki *et al.*, 2009; Matsuhashi *et al.*, 2011). Elucidating the role of other genes involved in tissue lipogenesis can be expected leading to the possibility of developing DNA tests to select for muscle fatty acid composition and the identification of molecular markers for predicting the potential of individual animals to produce meat of a specific lipid composition.

TFA content of ruminant-derived foods

The impact of TFA from ruminant-derived foods on the development of human chronic diseases is uncertain (Shingfield *et al.*, 2008b; Gebauer *et al.*, 2011). However, understanding the changes in TFA abundance and isomer distribution on diets formulated to lower SFA and/or increase PUFA in meat and milk remains an important research priority, allowing the ruminant livestock industry to respond once more biomedical and clinical data become available.

Trans-monoenoic fatty acids

Ruminant-derived foods contain a diverse range of unsaturated fatty acids containing a single *trans* double bond that originate from ruminal biohydrogenation of unsaturated fatty acids. *Trans* 18:1 isomers are quantitatively the most important in ruminant meat and milk fat. Although numerous isomers with double bonds in positions $\Delta 4$ to $\Delta 16$ are present, *trans*-11 18:1 is typically the most abundant in milk and meat of grazing ruminants or on diets containing high proportions of grass silage or ensiled forage legumes (Nuernberg *et al.*, 2005; Bessa *et al.*, 2007; Vanhatalo *et al.*, 2007; Table 8). Concentrations of *trans*-18:1 are higher in milk from pasture compared with conserved forages (Table 3) and tend to be increased on high-concentrate diets (Chilliard *et al.*, 2007; Table 4).

Dietary plant oil, oilseed and marine lipid supplements increase the content of *trans* 18:1 in milk (Tables 4 and 5) and muscle (Table 7), and alter the abundance of specific isomers in lamb (Bessa *et al.*, 2007; Radunz *et al.*, 2009; Turner *et al.*, 2012a), beef (Juárez *et al.*, 2011; Nassu *et al.*, 2011; Mapiye *et al.*, 2012) and milk (Rego *et al.*, 2009; Halmemies-Beauchet-Filleau *et al.*, 2011; Hristov *et al.*, 2011; Table 8). Dietary supplements enriched in *cis*-9 18:1, 18:2n-6 and 18:3n-3 can be expected to alter the distribution of 18:1 isomers and result in the specific enrichment of *trans* 6-8, *trans* 10-12, and *trans*-11-16, respectively (Chilliard *et al.*, 2007; Shingfield *et al.*, 2008b; Table 8). Increases in *trans* 18:1 in response to fish oil and marine lipid supplements are associated with elevated *trans*-6 to -15 18:1 concentrations and decrease in *trans*-16 18:1 abundance (Table 8). On low-forage diets or high-concentrate diets containing plant oils or marine lipids, *trans*-10 18:1 often replaces *trans*-11 18:1 as the major TFA in muscle (Shingfield and Griinari, 2007; Radunz *et al.*, 2009; Turner *et al.*, 2012a) and milk fat (Table 8).

Table 8 Effect of diet composition on trans 18:1 isomer concentrations in ruminant milk

Forage	F : C ¹	Lipid	Intake ² (g/day)	Ruminant species	Trans 18:1 isomer (g/100 g total fatty acids)										References
					Δ4	Δ5	Δ6 to 8 ³	Δ9	Δ10	Δ11	Δ12	Δ13/14 ³	Δ15	Δ16	
Ryegrass pasture	86 : 14	–	–	Bovine	0.03	0.03	0.34	0.30	0.51	4.73	0.41	0.85	0.23	0.39	Mohammed <i>et al.</i> (2009)
Zero grazed ryegrass	85 : 15	–	–		0.04	0.03	0.31	0.26	0.39	3.49	0.34	0.76	0.22	0.35	
Ryegrass silage	83 : 17	–	–		0.02	0.02	0.20	0.17	0.20	0.99	0.20	0.44	0.13	0.22	
Grass silage early cut	62 : 38	–	–	Bovine	0.03	0.02	0.25	0.27	0.29	0.99	0.26	0.60	0.61	0.33 ⁴	Vanhatalo <i>et al.</i> (2007)
Red clover silage early cut	60 : 40	–	–		0.04	0.03	0.31	0.34	0.39	0.97	0.33	0.68	0.65	0.37 ⁴	
Grass silage late cut	60 : 40	–	–		0.03	0.03	0.27	0.30	0.31	1.04	0.29	0.64	0.61	0.36 ⁴	
Red clover silage late cut	60 : 40	–	–		0.03	0.03	0.27	0.30	0.31	1.00	0.27	0.56	0.58	0.30 ⁴	
Maize silage/grass silage	50 : 50	Calcium salts of palm oil	950	Bovine	0.03	0.03	0.33	0.33	0.37	1.40	0.41	1.10	0.21	0.03 ⁴	Givens <i>et al.</i> (2009)
Maize silage/grass silage	50 : 50	Whole rapeseed	1186		0.05	0.08	0.77	0.73	0.84	4.90	0.93	1.50	0.39	0.05 ⁴	
Maize silage/grass silage	50 : 50	Milled rapeseed	1147		0.02	0.03	0.24	0.24	0.26	1.10	0.37	0.79	0.26	0.02 ⁴	
Maize silage/grass silage	50 : 50	Rapeseed oil	1044		0.05	0.08	0.56	0.50	0.62	2.20	0.68	1.60	0.40	0.05 ⁴	
Maize silage/grass silage	27 : 73	Control	0	Bovine	0.01	0.01	0.23	0.22	0.43	1.27	0.34	0.30	NR	NR	Roy <i>et al.</i> (2006)
Maize silage/grass silage	27 : 73	Sunflower oil	957		0.06	0.05	0.95	0.46	7.22	1.44	0.86	0.43	NR	NR	
Maize silage	65 : 35	Control	0		0.02	0.01	0.27	0.18	2.96	1.04	0.33	0.37	NR	NR	
Maize silage	65 : 35	Sunflower oil	755		0.05	0.09	1.43	0.59	18.62	1.36	0.74	0.80	NR	NR	
Pasture	NR	Control	0	Bovine	NR	NR	0.23	0.20	0.28	2.70	0.21	0.65	0.31	0.37 ⁴	Rego <i>et al.</i> (2009)
Pasture	NR	Rapeseed oil	500		NR	NR	0.72	0.49	0.74	2.54	0.49	1.26	0.61	0.66 ⁴	
Pasture	NR	Sunflower oil	500		NR	NR	0.68	0.47	1.21	3.32	0.58	1.17	0.63	0.71 ⁴	
Pasture	NR	Linseed oil	500		NR	NR	0.54	0.41	0.58	3.70	0.60	2.04	0.89	0.92 ⁴	
Red clover silage	50 : 50	Control	0	Bovine	0.02	0.05	0.24	0.22	0.36	0.96	0.43	0.74	0.48	0.52 ⁴	Halmemies-Beauchet-Filleau <i>et al.</i> (2011)
Red clover silage	50 : 50	Rapeseed oil	310		0.04	0.08	0.46	0.36	0.51	1.28	0.55	0.82	0.53	0.57 ⁴	
Red clover silage	50 : 50	Sunflower oil	280		0.04	0.16	0.39	0.33	0.56	1.42	0.57	0.82	0.53	0.58 ⁴	
Red clover silage	50 : 50	Camelina oil	300		0.03	0.06	0.34	0.30	0.42	1.21	0.53	0.84	0.57	0.60 ⁴	
Red clover silage	50 : 50	Camelina expeller	210		0.04	0.06	0.61	0.53	0.96	2.18	0.92	1.71	0.79	0.48 ⁴	
Maize silage/grass silage	74 : 26	Rapeseed oil	408	Bovine	0.03	0.03	0.57	0.40	3.34		0.53	0.95	–	0.46 ⁴	Jacobs <i>et al.</i> (2011)
Maize silage/grass silage	74 : 26	Soya bean oil	389		0.04	0.03	0.49	0.35	3.54		0.59	0.97	–	0.52 ⁴	
Maize silage/grass silage	74 : 26	Linseed	392		0.04	0.03	0.53	0.36	3.36		0.64	1.39	–	0.68 ⁴	
Maize silage	65 : 35	Control	0	Bovine	0.03	0.02	0.23	0.19	0.27	1.08	0.27	0.42	0.23	0.24 ⁴	Loor <i>et al.</i> (2005)
Maize silage	65 : 35	Menhaden fish oil	270		0.04	0.05	0.44	0.48	1.76	9.17	0.70	0.82	0.23	0.10 ⁴	
Grass hay	35 : 65	Control	0	Caprine ⁵		NR	0.13	0.23	0.34	1.01	0.20		NR		Mele <i>et al.</i> (2008)
Grass hay	35 : 65	Soya bean oil	100			NR	0.39	0.54	0.65	7.54	0.50		NR		
Grass hay	60 : 40	Control	0			NR	0.11	0.21	0.50	1.09	0.16		NR		
Grass hay	60 : 40	Soya bean oil	100			NR	0.34	0.47	1.06	4.87	0.47		NR		
Grass hay	44 : 56	Control		Caprine	<0.01	<0.01	0.12	0.19	0.15	1.51	0.15	0.22	0.17	0.00	Bernard <i>et al.</i> (2009c)
Grass hay	48 : 52	Sunflower oil	130		0.03	0.03	0.53	0.59	0.08	9.02	0.62	0.59	0.43	0.03 ⁴	
Grass hay	49 : 51	Linseed oil	130		0.02	0.02	0.51	0.54	0.05	8.14	0.57	0.91	0.55	0.02 ⁴	
Maize silage	39 : 61	Control	0		<0.01	0.01	0.14	0.21	0.44	1.17	0.16	0.29	0.13	0.00	

Table 8 Continued

Forage	F : C ¹	Lipid	Intake ² (g/day)	Ruminant species	<i>Trans</i> 18:1 isomer (g/100 g total fatty acids)										References
					Δ4	Δ5	Δ6 to 8 ³	Δ9	Δ10	Δ11	Δ12	Δ13/14 ³	Δ15	Δ16	
Maize silage	46 : 54	Sunflower oil	130		0.03	0.04	0.56	0.58	3.23	8.50	0.67	0.87	0.30	0.03 ⁴	
Maize silage	45 : 55	Linseed oil	130		0.03	0.04	0.56	0.58	3.23	8.50	0.67	0.87	0.30	0.03 ⁴	
Lucerne hay	20 : 80	Control	0	Ovine	NR		0.33	0.29	0.78	1.71	0.40	0.58	0.35 ⁵	0.33 ⁴	Gómez-Cortès <i>et al.</i> (2008b)
Lucerne hay	19 : 81	Olive oil	148		NR		1.39	1.19	3.90	1.42	0.84	0.84	0.27 ⁵	1.39 ⁴	
Lucerne hay	20 : 80	Control	0	Ovine ⁶	NR		0.30	0.30	0.78	1.88	0.48	NR	0.58 ⁵	0.30 ⁴	Gómez-Cortès <i>et al.</i> (2011b)
Lucerne hay	20 : 80	Sunflower oil	60		NR		0.45	0.45	1.40	3.87	0.74	NR	0.65 ⁵	0.36 ⁴	
Lucerne hay	19 : 81	Sunflower oil	117		NR		0.58	0.58	2.31	6.94	0.87	NR	0.67 ⁵	0.36 ⁴	
Lucerne hay	19 : 81	Sunflower oil	165		NR		0.68	0.64	3.74	8.50	0.95	NR	0.73 ⁵	0.37 ⁴	
Lucerne hay	70 : 30	Control	0	Ovine ⁷	NR		0.17	0.17	0.27	1.16	0.2	NR	0.37	0.30	Gómez-Cortès <i>et al.</i> (2011a)
Lucerne hay	70 : 30	Sunflower oil	73		NR		0.45	0.34	1.97	2.69	0.37	NR	0.36	0.27	
Lucerne hay	50 : 50	Control	0		NR		0.22	0.19	0.39	1.16	0.27	NR	0.33	0.32	
Lucerne hay	50 : 50	Sunflower oil	76		NR		0.37	0.33	0.76	2.5	0.43	NR	0.42	0.42	
Lucerne hay	30 : 70	Control	0		NR		0.29	0.23	0.83	1.54	0.28	NR	0.34	0.27	
Lucerne hay	30 : 70	Sunflower oil	69		NR		0.36	0.32	0.47	2.67	0.38	NR	0.39	0.42	
Lucerne hay	60 : 40	Control	0	Ovine ⁷	NR		0.36	0.33	0.53	1.55	0.34	NR	0.34 ⁵	0.35 ⁴	Gómez-Cortès <i>et al.</i> (2009)
Lucerne hay	60 : 40	Extruded linseed ⁸	(60)		NR		0.45	0.40	0.53	3.70	0.40	NR	0.46 ⁵	0.54 ⁴	
Lucerne hay	60 : 40	Extruded linseed ⁸	(120)		NR		0.53	0.49	0.50	5.76	0.52	NR	0.56 ⁵	0.67 ⁴	
Lucerne hay	20 : 80	Control	0	Ovine ⁷	NR		0.30	0.27	0.88	1.58	0.33	NR	0.52 ⁵	0.34 ⁴	Toral <i>et al.</i> (2010a)
Lucerne hay	20 : 80	Sardine and tuna oil	27.5		NR		0.18	0.25	4.34	4.47	0.32	NR	0.65 ⁵	0.11 ⁴	

¹Forage : concentrate ratio of the diet (on a dry matter basis).

²Intake of oil from dietary lipid supplements.

³Individual isomers unable to be resolved during gas chromatography analysis.

⁴Includes *cis*-14 18:1 as a minor isomer.

⁵Also contains unresolved *cis*-11 18:1.

⁶Fatty acid concentrations reported as g/100 g fat.

⁷Fatty acid concentrations reported as g/100 g fatty acid methyl esters.

⁸Amount of lipid supplementation (g/kg diet dry matter) indicated in parenthesis.

NR, not reported.

Trans-polyenoic fatty acids

Ruminant milk and meat contains several non-conjugated *trans* 18:2 fatty acids, but the concentration and isomer distribution differs compared with hydrogenated plant oils, margarines and edible oils (Shingfield *et al.*, 2008b; Table 9). On typical diets containing no additional lipid supplements, total *trans* 18:2 in ruminant milk varies between 0.32 to 0.91 g/100 g fatty acids, but concentrations can approach or exceed 2.0 g/100 g fatty acids when plant oil or oilseeds are fed (Bernard *et al.*, 2009c; Gómez-Cortès *et al.*, 2009; Rego *et al.*, 2009; Table 9). *Trans*-11, *cis*-15 18:2 is the major *trans* 18:2 isomer in milk from diets based on grass silage, grass hay or red clover silage (Bernard *et al.*, 2009c; Mohammed *et al.*, 2009; Halmemies-Beauchet-Filleau *et al.*, 2011), whereas *cis*-9, *trans*-13 18:2 is the most abundant isomer on diets based on maize silage, a mixture of barley silage, lucerne silage and lucerne hay or containing high proportions of concentrates (Shingfield *et al.*, 2008b; Bernard *et al.*, 2009c; Hristov *et al.*, 2011).

Collectively, *trans* 18:2 typically account for ca. 0.51 to 0.70 g/100 g total fatty acids in ruminant muscle with an isomer distribution similar to milk fat (Bessa *et al.*, 2007; Aldai *et al.*, 2011; Juárez *et al.*, 2011; Nassu *et al.*, 2011). Supplementing the diet of growing lambs or cattle with oilseeds or plant oils increases total *trans* 18:2 to concentrations of ca. 3.0 g/100 g total fatty acids (Bessa *et al.*, 2007; Juárez *et al.*, 2011; Nassu *et al.*, 2011). Most *trans* 18:2 in milk and meat originate from ruminal biohydrogenation of 18-carbon PUFA, but there is evidence that *cis*-9, *trans*-12 18:2 and *cis*-9, *trans*-13 18:2 are also synthesized endogenously in ruminant tissues (Shingfield *et al.*, 2008b).

Conjugated fatty acids

The effects of diet composition on the concentration and relative abundance of CLA isomers in ruminant milk and meat are well documented (Chilliard *et al.*, 2007; Martins *et al.*, 2007; Shingfield *et al.*, 2008b). Although ruminant foods contain numerous positional and geometric isomers with a conjugated bond system located between $\Delta 6,8$ and $\Delta 13,15$, *cis*-9, *trans*-11 is the major isomer due, in most part, to endogenous synthesis via the action of SCD on *trans*-11 18:1 (Palmquist *et al.*, 2005).

Nutritional strategies to increase *cis*-9, *trans*-11 CLA in ruminant meat and milk include replacing conserved forages with fresh grass or dietary supplements of oils and oilseeds enriched in 18:2n-6 and 18:3n-3, fish oil or marine algae (Tables 3 to 5 and 7). Supplements of marine algal lipids or fish oil in the diet are more effective than plant oils or oilseeds for enhancing *cis*-9, *trans*-11 CLA concentrations in milk fat. Enrichment of CLA in milk in ruminants fed fish oil or marine algae can be increased yet further when diets contain plant oils rich in 18:2n-6 (Table 5). Although the combined use of marine lipids and plant oils is an effective means for increasing milk fat *cis*-9, *trans*-11 CLA content, there is considerable variation in the response, owing to a number of factors, including breed, composition of the basal ration, relative proportions of oil sources and time on diet. Supplementing

a wheat pasture-based diet with fish oil (30 ml/day) and sunflower oil (150 ml/day) was reported to increase milk *cis*-9, *trans*-11 CLA concentrations in goats from 1.03 to 9.89 g/100 g fatty acids after 14 days on diet (Gagliostro *et al.*, 2006), which represents the highest enrichment reported in ruminant milk. Studies with growing lambs and cattle have shown that dietary lipid supplements can be used to enrich *cis*-9, *trans*-11 CLA in muscle up to 2.40 g/100 g fatty acids (Sinclair, 2007), whereas feeding Wagyu cattle diets supplemented with 60 g sunflower oil/kg diet dry matter cattle resulted in the highest reported *cis*-9, *trans*-11 CLA content of 134 mg/100 g muscle (Mir *et al.*, 2002).

Detailed measurements of the CLA isomer distribution in ruminant milk indicate that supplementing the diet with sources of *cis*-9 18:1 increases *trans*-7, *cis*-9 CLA concentrations, 18:2n-6 results in higher *trans*-8, *cis*-10 CLA, *trans*-10, *cis*-12 CLA, *trans*-9, *trans*-11 CLA, and *trans*-10, *trans*-12 CLA abundance, whereas 18:3n-3 leads to *cis*-11, *trans*-13 CLA, *cis*-12, *trans*-14 CLA, *trans*-11, *cis*-13 CLA, *trans*-9, *trans*-11 CLA, *trans*-11, *trans*-13 CLA and *trans*-12, *trans*-14 CLA enrichment (Chilliard *et al.*, 2007; Martins *et al.*, 2007; Shingfield *et al.*, 2008b; Table 10).

Ruminant milk and meat also contain trace amounts of several conjugated linolenic acids (CLNA) that contain at least one conjugated bond (Destailats *et al.*, 2005; Plourde *et al.*, 2007; Gómez-Cortès *et al.*, 2009). Concentrations of *cis*-9, *trans*-11, *cis*-15 18:3 and *cis*-9, *trans*-11, *trans*-15 18:3 in milk for most diets are extremely low (6 to 30 and 10 to 14 mg/100 g total fatty acids, respectively), but increased several-fold when diets containing 18:3n-3 rich oils and oilseeds are fed (Gómez-Cortès *et al.*, 2009; Halmemies-Beauchet-Filleau *et al.*, 2011; Hristov *et al.*, 2011). Muscle of growing lambs was reported to contain negligible amounts of *cis*-9, *trans*-11, *cis*-15 18:3, whereas supplementing the diet with linseed oil over a 42-day finishing period resulted in concentrations of 329 mg/100 g total fatty acids (Bessa *et al.*, 2007). Bovine muscle contains between 50 to 239 and 105 mg/100 g total fatty acid methyl esters of *cis*-9, *trans*-11, *cis*-15 18:3 and *cis*-9, *trans*-13, *cis*-15 18:3, respectively, and trace amounts (20 mg/100 g total fatty acid methyl esters) of *cis*-9, *trans*-11, *trans*-15 18:3 (Plourde *et al.*, 2007; Aldai *et al.*, 2011; Nassu *et al.*, 2011). Feeding diets containing ground linseed over a 140-day finishing period was shown to increase CLNA content of LT in beef cows by between 30 and 70 mg/100 g total fatty acid methyl esters, with evidence that enrichment of specific CLNA isomers is dependent on the composition of the basal diet (Nassu *et al.*, 2011).

Molecular mechanisms and alterations of fatty acid composition of ruminant-derived foods

Synthesis of fatty acids in ruminant tissues and milk fat in the mammary gland requires efficient transcriptional, translation and secretory mechanisms that involve the coordinated and concerted action of multiple genes. Studies on the nutritional regulation of mammary lipogenesis in the bovine have almost exclusively been directed towards characterizing changes in the expression of a few candidate genes during

Table 9 Effect of dietary lipid supplements on the concentration of non-conjugated trans octadecadienoic fatty acids in ruminant milk

Lipid ¹	Ruminant species	Trans octadecadienoic isomer (mg/100 g total fatty acids)										Total	References	
		cis, trans			trans, cis			trans, trans						
		9,12	9,13	9,14	8,13	9,12	11,15	12,15	9,12	9,13	9,14			11,15
Control	Bovine	91 ²	314 ³	–	–	42	213	–	–	–	–	49	709	Rego <i>et al.</i> (2009)
Rapeseed oil		189 ²	458 ³	–	–	39	139	–	–	–	–	43	868	
SFO		224 ²	502 ³	–	–	43	109	–	–	–	–	37	915	
LO		285 ²	718 ³	–	–	85	619	–	–	–	–	181	1888	
Control	Bovine	30	276	141	–	29	153	71	–	36	–	34	770	Halmemies-Beauchet-Filleau <i>et al.</i> (2011)
Rapeseed oil		45	303	141	–	36	161	70	–	59	–	39	854	
SFO		50	293	145	–	52	109	63	–	57	–	37	806	
Camelina oil		50	339	152	–	39	226	83	–	50	–	50	989	
Camelina expeller		67	650	267	–	69	618	128	–	79	–	102	1980	
Control	Bovine	114 ⁴	344	147	–	36	114	42	26	65	–	22	910	Hristov <i>et al.</i> 2011
Rapeseed expeller		124 ⁴	403	169	–	35	171	47	31	76	–	28	1084	
High oleic rapeseed expeller		119 ⁴	378	151	–	34	157	43	28	85	–	26	1021	
High erucic acid rapeseed expeller		120 ⁴	370	160	–	29	112	45	22	54	–	22	934	
Control	Bovine	110	250 ³	–	120	40	120	–	30	–	–	–	670	Cruz-Hernandez <i>et al.</i> (2007)
Fish oil and SFO		200	520 ³	–	210	130	390	–	70	–	–	–	1520	
GH-Control	Caprine	80	172	–	–	3	125	–	6	–	14	24	424	Bernard <i>et al.</i> (2009c)
GH-SFO		142	325	–	–	5	92	–	10	–	51	38	663	
GH-LO		211	606	–	–	185	1485	–	21	–	24	458	2990	
MS-Control		59	150	–	–	2	73	–	12	–	28	< 0.1	324	
MS-SFO		86	282	–	–	25	135	–	9	–	66	6	609	
MS-LO		305	725	–	–	90	2748	–	94	–	15	296	4273	
Control	Ovine ⁵	70	60 ³	–	210	210	70	–	50	–	–	–	670	Gómez-Cortès <i>et al.</i> (2011b)
SFO		90	50 ³	–	230	260	100	–	90	–	–	–	820	
Control (70:30)	Ovine ⁵	30	100 ³	–	80	20	–	–	40	–	–	100	370	Gómez-Cortès <i>et al.</i> (2011a)
SFO		40	120 ³	–	90	30	–	–	50	–	–	90	420	
Control (50:50)		30	140 ³	–	80	20	–	–	40	–	–	60	370	
SFO		40	110 ³	–	90	30	–	–	60	–	–	70	400	
Control (30:70)		30	110 ³	–	60	20	–	–	40	–	–	60	320	
SFO		30	140 ³	–	60	30	–	–	30	–	–	80	370	
Control		Ovine ⁵	40	120	–	80	40	50	–	60	–	–	–	
Extruded linseed	60		240	–	140	70	1560	–	110	–	–	–	2180	
Control	Ovine ⁵	80	160	–	90	30	50	–	–	–	–	–	410	Toral <i>et al.</i> (2010a)
Fish oil		50	80	–	40	60	460	–	–	–	–	–	690	

SFO = sunflower oil; LO = linseed oil; GH = grass hay; MS = maize silage.

¹Details of diet composition and intake of lipid supplements are listed in Tables 4 and 5.

²Detected as a mixture with *trans*-8, *cis*-12 18:2.

³Co-elutes with *trans*-8, *cis*-13 18:2.

⁴Detected as a mixture with *cis*-16 18:1 and *trans*-8, *cis*-12 18:2.

⁵Concentrations reported as g/100 g fatty acid methyl esters.

Table 10 Effect of dietary lipid supplements on the concentration of conjugated linoleic acid isomers in ruminant milk

Supplement ¹	Ruminant species	CLA isomer (mg/100 g total fatty acids) ²														References	
		<i>cis, trans</i>			<i>trans, cis</i>					<i>trans, trans</i>							
		9,11	11,13	12,14	7,9	8,10	9,11	10,12	11,13	12,14	7,9	8,10	9,11	10,12	11,13		12,14
Control	Bovine	1186	0	6	44	0	NR	4	27	NR	7	4	11	8	32	17	Rego <i>et al.</i> (2009)
RO		1140	0	9	114	0	NR	6	12	NR	6	4	10	8	32	17	
SFO		1605	0	7	70	32	NR	1	13	NR	6	6	13	27	23	14	
LO		1544	1	30	89	0	NR	5	49	NR	7	3	23	9	81	77	
Control	Bovine	441	2	1	47	12	11	3	6	5	2	3	25	4	18	9	Halmemies-Beauchet-Filleau <i>et al.</i> (2011)
RO		560	1	1	78	15	12	4	11	6	2	4	25	6	24	12	
SFO		636	1	1	64	15	13	7	10	5	2	6	26	12	20	11	
CO		567	2	2	60	13	12	4	21	11	1	4	24	7	36	18	
CE		1020	3	1	125	18	21	7	6	12	2	4	27	9	51	16	
GH-Control	Caprine	828	NR	< 0.1	28	16	7	0.0	28	0.1	0.3	0.2	21	0.1	0.4	0.4	Bernard <i>et al.</i> 2009c
GH-SFO		3694	NR	< 0.1	93	74	< 0.1	5.0	63	0.2	11	8.0	51	18	15	14	
GH-LO		3313	NR	9	87	64	< 0.1	0.1	470	18	16	0.2	66	7	46	62	
MS-Control		816	NR	< 0.1	40	19	2	4	0.3	2.0	0.2	0.1	15	0.1	0.1	0.3	
MS-SFO		4266	NR	< 0.1	106	107	< 0.1	64	0.4	0.2	20	10	59	24	0.3	0.4	
MS-LO		2555	NR	14.0	94	50	< 0.1	16	102	16	13	6	38	0.3	28	42	
Control	Ovine	960	NR	NR	NR	NR	10	10	20	NR	NR		10		20	NR	
Olive oil		610	NR	NR	NR	NR	50	20	10	NR	NR		20		10	NR	
HF-Control	Ovine ³	386	NR	1	26	NR	NR	2	12	NR	9	11	9	6	18	NR	Mele <i>et al.</i> (2006)
HF-SBO		2224	NR	2	83	NR	NR	7	28	NR	13	18	32	22	27	NR	
LF-Control		582	NR	1	34	NR	NR	6	13	NR	8	10	11	5	13	NR	
LF-SBO		1806	NR	2	103	NR	NR	11	15	NR	14	19	28	19	24	NR	
Control	Ovine ⁴	730	NR	NR	NR	NR	10	10	10	NR	NR		10		10	10	Gómez-Cortès <i>et al.</i> (2009)
Linseed		2330	NR	NR	NR	NR	10	10	220	NR	NR		20		70	24	
Control	Ovine ⁴	440	NR	NR	40	20	20	< 1	10	NR	NR	NR	NR	NR	30	10	Toral <i>et al.</i> (2010a)
STO		3220	NR	NR	40	30	100	10	20	NR	NR	NR	NR	NR	20	10	
Control	Ovine ⁴	440	NR	NR	40	20	20	< 1	10	NR	NR	NR	NR	NR	30	10	Toral <i>et al.</i> (2010b)
SFOMA		3220	NR	NR	40	30	100	10	20	NR	NR	NR	NR	NR	20	10	

CLA = conjugated linoleic acid; RO = rapeseed oil; SFO = sunflower oil; LO = linseed oil; CO = camelina oil; CE = camelina expeller; GH = grass hay; MS = maize silage; HF = high forage diet (75:25); SBO = soya bean oil; LF = low forage diet (60:40); STO = sardine and tuna oil; SFOMA = a mixture of marine algae and SFO fed at an inclusion rate of 24 and 25 g/kg diet dry matter.

¹Details of diet composition and intake of lipid supplements are listed in Tables 4 and 5.

²Ruminant milk fat may also contain trace amounts of *cis*-9, *cis*-11 CLA, *cis*-10, *cis*-12 CLA, *cis*-11, *cis*-13 CLA, *cis*-8, *trans*-10 CLA, *cis*-13, *trans*-15 CLA, *trans*-6, *trans*-8 CLA and *trans*-13, *trans*-15 CLA.

³Concentrations reported as mg/100 g fat.

⁴Concentrations reported as g/100 g fatty acid methyl esters.

NR, not reported.

Table 11 Effect of dietary lipid supplements on mammary lipogenic gene expression and enzyme activity in ruminants

Biochemical process	Transcript/protein ¹	Species	Response (%) ²	Lipid supplement	Inclusion rate (g/kg dry matter)	Change in milk fat secretion (%) ²	References
Nuclear receptors							
SREBF1/S14	mRNA	Bovine	-32.1/-41.1	Soya bean oil ³	30	-38.0	Harvatine and Bauman, 2006
SREBF1	mRNA	Bovine	-29.9	Sunflower oil + marine algae	27 + 4.0	-29.9	Angulo <i>et al.</i> (2012)
	mRNA	Bovine	-30.8	Linseed oil + marine algae	27 + 4.0	-30.8	Angulo <i>et al.</i> (2012)
De novo lipogenesis and desaturation							
ACC/SCD	mRNA	Bovine	No change	Rapeseed	33	No change	Delbecchi <i>et al.</i> (2001)
ACC	mRNA	Bovine	-68.2	Soya bean oil ³	50	-43.3	Piperova <i>et al.</i> (2000)
FAS	Activity	Caprine	+67.8	Sunflower oil	61	No change	Bernard <i>et al.</i> (2009a)
SCD	mRNA	Caprine	-42.6	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005b)
	mRNA	Caprine	-54.4	Formaldehyde-treated linseed	112	+7.5	Bernard <i>et al.</i> (2005b)
	Activity	Caprine	-30.1	Sunflower oil	55	+17.4	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	-21.7	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005b)
	Activity	Caprine	-27.2	Linseed oil	55	+14.7	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	-34.8	Formaldehyde-treated linseed	112	+7.5	Bernard <i>et al.</i> (2005b)
ACC/FAS	mRNA	Bovine	-45.9/-63.8	Fish oil	37	-43.9	Ahnadi <i>et al.</i> (2002)
	Activity	Bovine	-61.2/-43.9	Soya bean oil ³	50	-43.3	Piperova <i>et al.</i> (2000)
	mRNA	Caprine	No change	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005a)
	mRNA	Caprine	No change	Formaldehyde-treated linseed	112	+7.5	Bernard <i>et al.</i> (2005a)
	Activity	Caprine	No change	Sunflower oil	55	+17.4	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	No change	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005b)
	Activity	Caprine	No change	Linseed oil	55	+14.7	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	No change	Formaldehyde-treated linseed	112	+7.5	Bernard <i>et al.</i> (2005b)
FAS/SCD	mRNA	Bovine	-26.2/No change	Soya bean oil ³	30	-38.0	Harvatine and Bauman, 2006
	mRNA	Bovine	-30.8/-34.5	Sunflower oil + marine algae	27 + 4.0	-29.9	Angulo <i>et al.</i> (2012)
	mRNA	Bovine	-33.3/-45.5	Linseed oil + marine algae	27 + 4.0	-30.8	Angulo <i>et al.</i> (2012)
ACC/SCD	Activity	Caprine	No change	Sunflower oil	61	No change	Bernard <i>et al.</i> (2009a)
ACC/FAS/SCD	mRNA	Caprine	No change	Rapeseed	146	No change	Ollier <i>et al.</i> (2009)
	mRNA	Bovine	No change	Safflower seed	135	NR	Murrieta <i>et al.</i> (2006)
	mRNA	Caprine	+72.1/+74.1/+166	Safflower oil	50	+26.1	Li <i>et al.</i> (2012)
	mRNA	Bovine	-28.1/-40.6/-35.0	Sunflower oil ³	10	-27.2	Peterson <i>et al.</i> (2003)
	mRNA	Caprine	No change	Sunflower oil	61	No change	Bernard <i>et al.</i> (2009a)
	mRNA	Caprine	No change	Sunflower oil	44	+20.0	Ollier <i>et al.</i> (2009)
	mRNA	Caprine	No change	Sunflower oil	55	+17.4	Bernard <i>et al.</i> (2009b)
	mRNA	Caprine	No change	Linseed oil	55	+14.7	Bernard <i>et al.</i> (2009b)
	mRNA	Caprine	No change	Linseed oil	62	+14.0	Bernard <i>et al.</i> (2009a)
	mRNA	Caprine	-25.6/+51.9/+121	Linseed oil	50	+34.0	Li <i>et al.</i> (2012)
	Activity	Caprine	No change	Linseed oil	62	+14.0	Bernard <i>et al.</i> (2009a)

Altering meat and milk fatty acid composition

Table 11 Continued

Biochemical process	Transcript/protein ¹	Species	Response (%) ²	Lipid supplement	Inclusion rate (g/kg dry matter)	Change in milk fat secretion (%) ²	References
Fatty acid uptake/processing							
LPL	mRNA	Caprine	No change	Rapeseed	146	No change	Ollier <i>et al.</i> (2009)
	mRNA	Bovine	+50	Safflower seed	135	NR	Murrieta <i>et al.</i> (2006)
	mRNA	Caprine	+43.2	Safflower oil	50	+26.1	Li <i>et al.</i> (2012)
	mRNA	Bovine	-23.4	Soya bean oil ³	30	-38.0	Harvatine and Bauman, 2006
	mRNA	Bovine	-29.7	Sunflower oil ³	10	-27.2	Peterson <i>et al.</i> (2003)
	mRNA	Caprine	No change	Sunflower oil	61	No change	Bernard <i>et al.</i> (2009a)
	mRNA	Caprine	No change	Sunflower oil	44	+20.0	Ollier <i>et al.</i> (2009)
	mRNA	Caprine	No change	Sunflower oil	55	+17.4	Bernard <i>et al.</i> (2009b)
	mRNA	Caprine	+50.9	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005b)
	mRNA	Caprine	No change	Linseed oil	55	+14.7	Bernard <i>et al.</i> (2009b)
	mRNA	Caprine	No change	Formaldehyde-treated linseed	112	+7.5	Bernard <i>et al.</i> (2005b)
	mRNA	Caprine	No change	Linseed oil	62	+14.0	Bernard <i>et al.</i> (2009a)
	mRNA	Caprine	+53.6	Linseed oil	50	+34.0	Li <i>et al.</i> (2012)
	mRNA	Bovine	-33.4	Sunflower oil + marine algae	27 + 4.0	-29.9	Angulo <i>et al.</i> (2012)
	mRNA	Bovine	-44.8	Linseed oil + marine algae	27 + 4.0	-30.8	Angulo <i>et al.</i> (2012)
	Activity	Caprine	No change	Sunflower oil	61	No change	Bernard <i>et al.</i> (2009a)
	Activity	Caprine	No change	Sunflower oil	55	+17.4	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	No change	Oleic acid rich sunflower oil	35	+16.3	Bernard <i>et al.</i> (2005b)
	Activity	Caprine	No change	Linseed oil	55	+14.7	Bernard <i>et al.</i> (2009b)
	Activity	Caprine	No change	Linseed oil	62	+14.0	Bernard <i>et al.</i> (2009a)
FACL	mRNA	Bovine	-34.4	Sunflower oil ³	10	-27.2	Peterson <i>et al.</i> (2003)
Esterification							
AGPAT/GPAT	mRNA	Bovine	-26.6/-51.6	Sunflower oil ³	10	-27.2	Peterson <i>et al.</i> (2003)
GPAM	mRNA	Bovine	-9.5	Sunflower oil + marine algae	27 + 4.0	-29.9	Angulo <i>et al.</i> (2012)
	mRNA	Bovine	-25.9	Linseed oil + marine algae	27 + 4.0	-30.8	Angulo <i>et al.</i> (2012)
FA transport							
FABP	mRNA	Bovine	No change	Sunflower oil ³	10	-27.2	Peterson <i>et al.</i> (2003)
FABP3/FABP4	mRNA	Caprine	No change/+36.0	Sunflower oil	44	+20.0	Ollier <i>et al.</i> (2009)
	mRNA	Caprine	No change	Rapeseed	146	No change	Ollier <i>et al.</i> (2009)

SREBF1 = sterol response element binding protein; S14 = thyroid hormone responsive spot 14; ACC = acetyl-CoA carboxylase; SCD = stearoyl-CoA desaturase; FAS = fatty acid synthase; LPL = lipoprotein lipase; FACL = fatty acyl CoA ligase; AGPAT = acylglycerol phosphate acyltransferase; GPAT = glycerol phosphate acyltransferase; GPAM = glycerol-3-phosphate acyltransferase 1; FABP = fatty acid binding protein.

¹Measurement of tissue transcript abundance (mRNA) or protein activity (Activity).

²Response reported when treatment effects were significant ($P < 0.10$) and calculated as ((Treatment - Control)/Control × 100).

³Lipid supplementation also accompanied by decreases in dietary forage : concentrate ratio.

NR, not reported.

Table 12 Effects of dietary lipid supplements on the expression of lipogenic genes, enzyme abundance and activity in adipose tissue and muscle of growing cattle

Biochemical process	Transcript/ protein ¹	Tissue	Variation (%) ²	Lipid supplement	Intake (g/day)/inclusion rate [g/kg dry matter]	Treatment duration (days)	Breed ³	Initial age (months)/[Live weight]	References
Nuclear receptors									
PPAR γ	mRNA	LM	+150	Linseed	907	107	Angus steers	16	Kronberg <i>et al.</i> (2006)
PPAR α	mRNA	LM	No change	Linseed	907	107	Angus steers	16	Kronberg <i>et al.</i> (2006)
	mRNA	LM	No change	Fish oil	[18]	100	Crossbred bulls	NR	Waters <i>et al.</i> (2009)
SREBF1	mRNA	LM	-50	Fish oil	[18]	100	Crossbred bulls	NR	Waters <i>et al.</i> (2009)
Lipogenesis									
<i>De novo</i> lipogenesis ³		SC	-29	Whole cottonseed	[300]	21	Brangus steers	11	Page <i>et al.</i> (1997)
		SC	+74	Linseed	[100]	107	Angus steers	[358]	Archibeque <i>et al.</i> (2005)
		IM	No change	Linseed	[100]	107	Angus steers	[358]	Archibeque <i>et al.</i> (2005)
		PR	-47	Formaldehyde-treated sunflower seed + soya bean	[210 + 90]	112	Hereford steers	[250]	Yang <i>et al.</i> (1978)
G6PDH	Activity	PR	-72	Formaldehyde-treated sunflower seed + soya bean	[210 + 90]	112	Hereford steers	[250]	Yang <i>et al.</i> (1978)
ACC	Protein	SC/LM	No change	Rapeseed expeller + linseed oil	[120 + 30]	209 to 216	Holstein bulls	NR	Herdmann <i>et al.</i> (2010b)
LPL	Activity	PR	+112	Formaldehyde-treated sunflower seed + soya bean	[210 + 90]	112	Hereford steers	[250]	Yang <i>et al.</i> (1978)
SCD	Activity	SC	No change	Whole cottonseed	[300]	21	Brangus steers	11	Page <i>et al.</i> (1997)
	Activity	SC/IM	No change	Linseed	[100]	107	Angus steers	[358]	Archibeque <i>et al.</i> (2005)
	Activity	PR	No change	Oleic acid rich sunflower seed	[200]	180	Simmental cows	8	Chang <i>et al.</i> (1992)
	Activity	LM	+633	Oleic acid rich sunflower seed	[200]	180	Simmental cows	8	Chang <i>et al.</i> (1992)
	Protein	SC	-29	Rapeseed expeller + linseed oil	[120 + 30]	209 to 216	Holstein bulls	NR	Herdmann <i>et al.</i> (2010b)
	Protein	LM	-37	Rapeseed expeller + linseed oil	[120 + 30]	209 to 216	Holstein bulls	NR	Herdmann <i>et al.</i> (2010b)
	mRNA	LM	-40	Linseed	907	107	Angus steers	16	Deiullis <i>et al.</i> (2010)
	mRNA	LM	-80	Fish oil	[18]	100	Crossbred bulls	NR	Waters <i>et al.</i> (2009)
FADS2	Protein	SC	No change	Rapeseed expeller + linseed oil	[120 + 30]	209 to 216	Hereford bulls	NR	Herdmann <i>et al.</i> (2010b)
	Protein	LM	-33	Rapeseed expeller + linseed oil	[120 + 30]	209 to 216	Holstein bulls	NR	Herdmann <i>et al.</i> (2010b)
FACE	Activity	PR/LM	No change	Oleic acid rich sunflower seed	[200]	180	Simmental cows	8	Chang <i>et al.</i> (1992)
Lipolysis									
HSL	mRNA	LM	No change	Linseed	907	107	Angus steers	16	Deiullis <i>et al.</i> (2010)
ATGL	mRNA	LM	No change	Linseed	907	107	Angus steers	16	Deiullis <i>et al.</i> (2010)
FA transport									
A-FABP	mRNA	LM	+500	Linseed	907	107	Angus steers	16	Deiullis <i>et al.</i> (2010)
H-FABP	mRNA	LM	No change	Linseed	907	107	Angus steers	16	Kronberg <i>et al.</i> (2006)

PPAR γ = peroxisome proliferator-activated receptor gamma; LM = *longissimus* muscle; PPAR α = peroxisome proliferator-activated receptor alpha; SREBF1 = sterol response element binding protein; SC = subcutaneous adipose tissue; IM = intramuscular adipose tissue; PR = perirenal adipose tissue; G6PDH = glucose-6-phosphate dehydrogenase; ACC = acetyl-CoA carboxylase; LPL = lipoprotein lipase; SCD = stearoyl-CoA desaturase; FADS2 = fatty acid desaturase 2 (Δ -6 desaturase); FACE = fatty acid elongase; HSL = hormone-sensitive lipase; ATGL = adipose triacylglyceride lipase; A-FABP = adipose fatty acid binding protein; H-FABP = heart-type fatty acid binding protein.

¹Measurement of tissue transcript abundance (mRNA), protein abundance (Protein) or protein activity (Activity).

²Response reported when treatment effects were significant ($P < 0.10$) and calculated as ((Treatment - Control)/Control \times 100).

³*In vitro de novo* lipogenesis from acetate.

NR, not reported.

Table 13 Effects of dietary lipid supplements on the expression of lipogenic genes in adipose tissue of lactating goats

Biochemical process	Transcript/Activity ¹	Tissue	Variation (%) ²	Lipid supplement	Inclusion rate (g/kg dry matter)	Treatment duration (days)	DIM	References
Lipogenesis								
FAS/LPL	mRNA/Activity	SC/PR	No change	Soya bean	220	21	294	Bernard <i>et al.</i> (2005a)
	Activity	PR	No change	Formaldehyde-treated linseed	112	21	168	Bernard <i>et al.</i> (2005b)
	Activity	PR	No change	Oleic acid rich sunflower oil	36	21	168	Bernard <i>et al.</i> (2005b)
	mRNA/Activity	PR	No change	Sunflower-seed oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA/Activity	PR	No change	Sunflower-seed oil	61	21	137	Bernard <i>et al.</i> (2009a)
	mRNA/Activity	PR	No change	Linseed oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA/Activity	PR	No change	Linseed oil	62	21	137	Bernard <i>et al.</i> (2009c)
ME	Activity	SC/PR	No change	Soya bean	220	21	294	Bernard <i>et al.</i> (2005a)
	Activity	PR	+114	Formaldehyde-treated linseed	112	21	168	Bernard <i>et al.</i> (2005b)
	Activity	PR	No change	Oleic acid rich sunflower oil	36	21	168	Bernard <i>et al.</i> (2005b)
G3PDH/G6PDH	Activity	SC/PR	No change	Soya bean	220	21	294	Bernard <i>et al.</i> (2005a)
	Activity	PR	No change	Formaldehyde-treated linseed	112	21	168	Bernard <i>et al.</i> (2005b)
	Activity	PR	No change	Oleic acid rich sunflower oil	36	21	168	Bernard <i>et al.</i> (2005b)
	Activity	PR	No change	Sunflower oil	55	21	144	Bernard <i>et al.</i> (2009b)
	Activity	PR	No change	Sunflower oil	61	21	137	Bernard <i>et al.</i> (2009c)
	Activity	PR	No change	Linseed oil	55	21	144	Bernard <i>et al.</i> (2009b)
	Activity	PR	No change	Linseed oil	62	21	137	Bernard <i>et al.</i> (2009c)
SCD	mRNA	SC/PR	-66/No change	Soya bean	220	21	294	Bernard <i>et al.</i> (2005a)
	mRNA	PR	No change	Sunflower oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA	PR	No change	Sunflower oil	61	21	137	Bernard <i>et al.</i> (2009c)
	mRNA	PR	No change	Linseed oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA	PR	No change	Linseed oil	62	21	137	Bernard <i>et al.</i> (2009c)
Adipokines								
Leptin	mRNA/Plasma	SC/PR	No change	Soya bean	220	21	294	Bonnet <i>et al.</i> (2009)
	mRNA/Plasma	PR	No change	Formaldehyde-treated linseed	112	21	168	Bernard <i>et al.</i> (2005b)
	mRNA/Plasma	PR	No change	Oleic acid rich sunflower oil	36	21	168	Bernard <i>et al.</i> (2005b)
	mRNA/Plasma	PR	+22/+140	Sunflower oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA/Plasma	PR	No change	Sunflower oil	61	21	137	Bernard <i>et al.</i> (2009a)
	mRNA/Plasma	PR	No change	Linseed oil	55	21	144	Bernard <i>et al.</i> (2009b)
	mRNA/Plasma	PR	No change	Linseed oil	62	21	137	Bernard <i>et al.</i> (2009a)

DIM = days in milk; FAS = fatty acid synthase; LPL = lipoprotein lipase; SC = subcutaneous adipose tissue; PR = perirenal adipose tissue; ME = malic enzyme; G3PDH = glucose-6-phosphate dehydrogenase; G6PDH = glucose-6-phosphate dehydrogenase; SCD = stearoyl-CoA desaturase.

¹Measurement of tissue transcript abundance (mRNA), protein activity (Activity) or concentration in plasma (Plasma).

²Response calculated as ((Treatment - Control)/Control × 100).

diet-induced milk fat depression, rather than alterations in milk fat composition *per se*. Decreases in the proportion of milk fatty acids synthesized *de novo* and milk fat secretion on high-concentrate diets containing plant oils are known to be accompanied by a coordinate downregulation of mammary lipogenic gene expression (Table 11), which is thought to be partly mediated via the involvement of SREBP1c, S14 and PPAR γ transcription factors (Bernard *et al.*, 2008; Harvatine *et al.*, 2009; Shingfield *et al.*, 2010). However, in the absence of changes in milk fat synthesis, decreases in milk 8:0 to 16:0 content (-10.6%) and increases in 18:0 ($+14.7\%$) and *cis*-9 18:1 ($+16.6\%$) to dietary rapeseed supplements in cattle were not associated with changes in mammary ACC and SCD transcript abundance (Delbecchi *et al.*, 2001). Further studies are required to characterize mammary expression of lipogenic genes and gene networks for diets causing changes in milk fatty acid composition without altering milk fat synthesis.

In goats, dietary plant oil and oilseed supplements typically stimulate milk fat synthesis lower milk fat 12:0 to 16:0 content and increase mammary 18-carbon unsaturated fatty acid secretion in milk (Chilliard *et al.*, 2007). Over a range of diets, changes in caprine milk fat composition are generally not accompanied by significant changes in mammary ACC, FAS and LPL mRNA abundance or activity (Table 11). However, high oleic or conventional sunflower oil, linseed oil and formaldehyde have in some, but not all cases, been reported to decrease mammary SCD mRNA and/or activity in goats fed grass hay-based diets (Table 11).

Fatty acids supplied by dietary lipid supplements are known to regulate gene expression in adipocytes in carcass and intramuscular adipose of growing and lactating ruminants (Hausman *et al.*, 2009). In AT of growing cattle, lipogenesis from acetate *de novo* is decreased by oils rich in *cis*-9 18:1 and 18:2n-6, but increased by lipid supplements containing high proportions of 18:3n-3 (Table 12). These responses appear to be in direct contrast with the lipogenic and anti-lipogenic effects of 18:2n-6 and 18:3n-3, respectively, in rodents (Ailhaud *et al.*, 2008; Flachs *et al.*, 2009). However, ruminal biohydrogenation of PUFA results in the formation of numerous intermediates, including *trans* 18:1 and isomers of CLA capable of influencing adipocyte lipid metabolism. For example, *trans*-11 18:1 lowers lipogenesis *de novo* in rodent adipocytes (Cromer *et al.*, 1995), whereas *trans*-10, *cis*-12 CLA was recently shown to decrease ACC protein abundance in differentiating primary bovine adipocytes (Lengi and Corl, 2010).

The stimulatory effect of ground linseeds on *de novo* lipogenesis in subcutaneous, but not intramuscular AT (Archibeque *et al.*, 2005) differs to the decrease in TAG accumulation within AT of rodents fed diets containing 18:3n-3 (Ailhaud *et al.*, 2008; Flachs *et al.*, 2009). In rodent AT, the inhibitory effects of 18:3n-3 arise because of the induction of PPAR α -mediated FA oxidation and lipolysis. Thus far, PPAR α expression has not been reported for bovine AT, and the effect of n-3 PUFA on lipolysis remains to be determined. Given its important role on converting SFA to

unsaturated fatty acids, the role of diet on SCD mRNA and activity in ruminant AT has been an obvious candidate for investigation. In bovine AT, SCD mRNA is not altered by dietary supplements enriched in *cis*-9 18:1 and 18:2n-6, whereas oils and oilseeds abundant in 18:3n-3 generally lower SCD transcript abundance in AT and muscle (Table 12) possibly because of downregulation of SREBP-1c expression (Waters *et al.*, 2009). In growing cattle, linseed oil was reported to lower the expression of Δ 6 desaturase protein in *m. longissimus* (Herdmann *et al.*, 2010b), whereas inclusion of extruded or roasted rapeseeds, soya beans or linseeds oilseed had no effect on Δ 5 desaturase or Δ 6 desaturase protein expression in *m. masseter* and *pars costalis diaphragmatic* (Turner *et al.*, 2012b).

Data on the role of diet composition on the expression of genes and gene networks related to adipogenesis in AT of dairy ruminants in mid-lactation are scarce. Available data suggest that dietary lipid supplements that do not lower milk fat synthesis have few effects on the expression of genes related to adipogenesis in AT of goats and cows (Table 13). There are indications that more profound effects can be expected when rumen-protected lipids are fed. Daily infusions of 1.1 kg of rapeseed at the duodenum were shown to induce 26% decreases in FAS activity of perirenal AT of lactating cows (Chilliard *et al.*, 1991), whereas formaldehyde-treated linseeds increased ME activity in perirenal AT of lactating goats (Bernard *et al.*, 2005b). More recent studies indicate that dietary lipid supplements inducing milk fat depression in mid-lactation cows increase the transcription of genes or gene networks involved in adipogenesis in subcutaneous AT, with evidence that these changes are regulated via upregulation of the expression of genes encoding for adipogenesis-related nuclear receptors (Thering *et al.*, 2009). There is no substantial evidence that these effects are mediated via changes in leptin, a key adipose-derived signal of energy balance, as the expression of the leptin gene is generally not altered in response to diets containing plant oils or oilseeds (Chilliard *et al.*, 2005) even when upregulation by *trans*-biohydrogenation intermediates has been suggested to occur in lactating cows and goats (Bonnet *et al.*, 2009). Further studies are required to elucidate the mechanisms and genes involved in the repartitioning of energy from the mammary gland towards body fat stores.

Conclusions

Significant progress has been made in characterizing the influence of diet on the fatty acid composition of ruminant meat and milk, abundance of specific TFA in particular. Although it is possible to substantially alter the fatty acid composition of milk and meat under commercial conditions, the extent of changes do not allow nutritional claims to be made unless effective rumen-protected lipid supplements are fed. Identification of SNPs for several key lipogenic genes in growing and lactating ruminants and heritability estimates for certain fatty acids in milk highlight the potential of animal breeding to further alter meat and milk fatty acid

composition. However, the impact of selection for product nutritional quality on other traits of economic importance remains uncertain. Application of genomic tools combined with a more complete understanding of the molecular mechanisms underlying changes in tissue and mammary lipogenesis offer the opportunity to breed genetic resources inherently suited to the production of meat and milk containing lower proportions of saturates and higher concentrations of unsaturated fatty acids. Elucidating interactions between diet and animal genetics, changes in the expression of key genes and gene networks regulating nutrient partitioning, lipogenesis–lipolysis and oxidation in ruminant tissues and milk fat synthesis can be expected to facilitate further progress in altering the fatty acid composition of ruminant foods.

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