Biochimie 141 (2017) 107–120

Contents lists available at ScienceDirect

Biochimie

journal homepage: www.elsevier.com/locate/biochi

Review

Production of *trans* and conjugated fatty acids in dairy ruminants and their putative effects on human health: A review

Anne Ferlay [a,*], Laurence Bernard [a], Annabelle Meynadier [b], Corinne Malpuech-Brugère [c,d]

[a] *Université Clermont Auvergne, INRA, VetAgro Sup, UMR Herbivores, F-63122, Saint-Genès-Champanelle, France*
[b] *GenPhySE, Université de Toulouse, INRA, INPT, ENVT, Toulouse, France*
[c] *Université Clermont Auvergne, INRA, UNH, Unité de Nutrition Humaine, F-63000, Clermont-Ferrand, France*
[d] *CRNH Auvergne, F-63009, Clermont-Ferrand, France*

A R T I C L E I N F O

Article history:
Received 31 March 2017
Accepted 8 August 2017
Available online 10 August 2017

Keywords:
Rumen
Bacteria
Biohydrogenation
Trans fatty acids
Conjugated fatty acids
Milk

A B S T R A C T

Consumption of milk and dairy products is important in Western industrialised countries. Fat content is an important constituent contributing to the nutritional quality of milk and dairy products. In order to improve the health of consumers, there is high interest in improving their fatty acid (FA) composition, which depends principally on rumen and mammary metabolism. This paper reviews the lipid metabolism in ruminants, with a particular focus on the production of *trans* and conjugated linoleic acids (CLA) and conjugated linolenic acids (CLnA) in the rumen. After the lipolysis of dietary lipids, an extensive biohydrogenation of unsaturated FA occurs by rumen bacteria, leading to numerous *cis* and *trans* isomers of 18:1, non-conjugated of 18:2, CLA and CLnA. The paper examines the different putative pathways of ruminal biohydrogenation of *cis*9-18:1, 18:2n-6, 18:3n-3 and long-chain FA and the bacteria implicated. Then mechanisms relative to the *de novo* mammary synthesis are presented. Ruminant diet is the main factor regulating the content and the composition of milk fat. Effects of nature of forage and lipid supplementation are analysed in cows and small ruminants species. Finally, the paper briefly presents the effects of these FA on animal models and human cell lines. We describe the properties of ruminant *trans* 18:1, when compared to industrial *trans* 18:1, CLA and CLnA on human health from meta-analyses of intervention studies and then explore the underlying mechanisms.

Contents

Abbreviations: CHD, coronary heart disease; CLA, conjugated linoleic acids; CLnA, conjugated linolenic acids; CVD, cardiovascular diseases; DM, dry matter; EI, energy intake; FA, fatty acids; F: C, forage: concentrate ratio; FO, fish oil; HDLc, high-density lipoprotein cholestrol; iTFA, industrial *trans* fatty acids; LAB, liquid-associated bacteria; LDLc, low-density lipoprotein cholesterol; MFD, milk fat depression; OBCFA, odd and branched fatty acids; OM, organic matter; PUFA, polyunsaturated fatty acids; RBH, ruminal biohydrogenation; rTFA, ruminant *trans* fatty acids; SAB, solid- attached bacteria; SCD, stearoyl-CoA desaturase; SFA, saturated fatty acids; SO, sunflower oil.

* Corresponding author.
E-mail address: anne.ferlay@inra.fr (A. Ferlay).

http://dx.doi.org/10.1016/j.biochi.2017.08.006
0300-9084/

1. Introduction

Human diets in Western industrialised countries are generally characterized by high levels of saturated fatty acids (**FA**) and n-6 FA and low levels of n-3 FA [1]. The World Health Organisation [2] has recommended that total fat, saturated FA (**SFA**) and *trans* FA should contribute up to 15–30%, <10%, and <1% of the total energy intake (**EI**), respectively. Moreover, the European Food Safety Authority [3] has recommended that total fat represent 20–35% of EI, and for SFA and *trans* FA, the intake should be as low as possible, whereas Anses [4] has recommended total fat be 35–40% of EI, SFA ≤12% of EI and 2% of EI for *trans* FA, respectively. These recommendations were created based on the fact that SFA consumption increases the risk of cardiovascular diseases (**CVD**) in humans [1]. Similarly, excessive consumption of *trans* FA has been linked to a substantially increased risk of CVD [1,5]. Nevertheless, recent published studies report that industrial and ruminant *trans* FA (**rTFA**), the two major sources of *trans* FA, have different effects on CVD risk factors [6].

In Europe, milk and dairy products provide from 27 to 57% of all SFA intake [1]. Moreover, these dietary products also contribute significantly to *trans* FA intake in human diets (from 17% to 72% for The Netherlands and Germany, respectively, TRANSFAIR study [7]). In France, the INCA study [8] indicated that adults consumed on average 168, 33 and 11 g/d of milk and dairy products, cheese and butter, respectively. These ingredients are important in human diets. Consequently, it becomes attractive to modify the milk FA composition to respond to consumer' concerns.

Ruminant dairy products contain high levels of SFA (67% of total FA), low levels (3%) of polyunsaturated FA (**PUFA**) (n-3 FA, conjugated linoleic acids (**CLA**), mainly *cis*9, *trans*11 isomer or rumenic acid, and conjugated linolenic acids (**CLnA**)) and a subsequent level (4%) of *trans* FA [5,9,10]. Milk fat is abundant in a large range of CLA isomers with double bonds located from Δ7,9 to Δ12,14 and isomers of Δ9,11,15-CLnA [11,12]. Adipose tissue and meat lipids, and milk fat in ruminants present much higher concentrations of SFA and lower concentrations of PUFA than dietary intake. This is mainly due to ruminal metabolism (complete lipolysis and subsequent biohydrogenation in the rumen) and mammary gland metabolism. The FA composition of dairy products could be changed by nutritional factors. Among them, the major changes that have been observed are due to the nature of forage (particularly grazing) and oilseed supplementation of diets [13].

First, this review describes the ruminal metabolism of PUFA and second, mammary lipid metabolism is presented with a particular focus on *trans* and conjugated FA. Then, the studied nutritional factors for modulating milk FA composition are presented, with an update on recent research on oilseed supplementation. The last part presents the consequences of *trans* 18:1 and conjugated FA on human health.

2. Ruminant diets and characteristics of the rumen

The reticulo-rumen is the first digestive compartment in ruminants, in which feeds are fermented by rumen microbes [14]. The reticulo-rumen leads to the omasum, the abomasum, and then the small intestine and the large intestine. The rumen represents almost 70–75% of the total content as well as 50–60% of the volume of the digestive tract [15]. It contains 85–90% of water. Its physicochemical characteristics are a constant temperature (39–40 °C), a negative redox potential (−250 to −400 mV), and pH values ranging from 6 to 7. The rumen with these properties can be compared to an anaerobic fermenter [15].

The main members of the rumen microbial community are anaerobic bacteria, archaea, ciliate protozoa and anaerobic fungi [16]. Bacteria are the most abundant (from 8×10^9 to 4×10^{10}/mL), followed by archaea (the CH4 producers) and ciliate protozoa ($2–5 \times 10^6$/mL) contributing up to half of the rumen microbial biomass, and then, in lower proportions, anaerobic fungi [15]. The bacteria are genetically varied, whereas the protozoa are monophyletic. The fungi have several morphotypes [16]. These different species play different roles that interact together and are essential for sustaining the microbial community and its cooperative activity. The rumen microorganisms rapidly colonise ingested feed particles and degrade them, which allows for the release of available nutrients [17]. Bacteria, thanks to their enzymes, convert fermentescible carbohydrate to volatile FA (mainly acetic, propionic and butyric acids), which represent the main energy substrates for ruminants [14]. On the one hand, ciliate protozoa are able to degrade cell-wall carbohydrates and N to nutrients for host animals. On the other hand, anaerobic fungi present a high cellulolytic activity [16].

Ruminant diets commonly contain forages and concentrates, such as cereals, oilseed meals and by-products. These feedstuffs