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Ruminant milk: A source of vitamins in human nutrition

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Implications

- Meeting vitamin requirements is still a worldwide public health problem, especially when taking into account chronic suboptimal intakes. In contrast to what is generally believed, a large part of the population remains at risk, and this risk is primarily dependent on eating habits that, in turn, are dependent on age, physiology, season, geographical area, economic or social status, and cultural behavior.
- Bovine milk contains the 13 known vitamins, and as a common component in the human diet, it makes a significant contribution to the reference intake of adults for several vitamins such as retinol (vitamin A: 11 to 16%), calciferol (vitamin D: 17 to 50%), riboflavin (vitamin B2: 32 to 46%), pantothenic acid (vitamin B5: 17 to 21%), and cobalamin (vitamin B12: 42 to 56%), according to reference values for fresh milk from USDA.
- In Western societies, bovine milk and dairy products are among the primary contributors of retinol, calciferol, riboflavin, pantothenic acid, folic acid (B9), and cobalamin intakes in human nutrition. High nutritional density and the relatively low cost of milk and dairy products make them attractive sources of vitamins, especially for economically disadvantaged populations not having access to a diversified diet.
- Factors, especially from dietary origin, that may or may not act directly on vitamin concentrations in milk of dairy species should be elucidated in order to propose rearing systems that promote production of milk with an improved nutritional value; that is, an “ideal milk” according to its vitamin content.

Key words: consumer health, dairy products, micronutrients, ruminants, requirements

Introduction

Humankind will be facing a major challenge in future decades. The world population is increasing, especially in Asia, and the demand for food, markedly animal products, will increase simultaneously. At the same time, environmental concerns are increasing, and the negative role of livestock is often pointed out. The sustainability of agriculture, especially that of livestock, seems a difficult task. Among other challenges, agriculture must compete in the utilization of arable surfaces for the production of food for humans or for animals. To meet these challenges, the environmental impact of livestock and agriculture in general will have to decrease while the efficacy and efficiency of production will have to increase. Under these conditions, sharing dietary resources is important, but access to food with an optimal nutritional density is critical to meeting the nutritional requirements of the world population. Vitamin provision should be taken into account when discussing the nutritional density of food, and for several vitamins, consumption of animal products seems essential, as we will see in this paper. In the first part, vitamins and current knowledge of their nutritional value will be summarized. The role of ruminant milk, especially bovine milk, will then be discussed, with attention given to recommended daily intakes in human nutrition and observed natural variations in concentrations of vitamins in milk.

Nutritional Value of Vitamin Consumption

Biological activities of vitamins at the molecular and physiological levels

There are 13 known vitamins, divided in two groups according to their solubility; vitamin A (retinol), vitamin D (calciferols), vitamin E (tocopherols), and vitamin K (phylllo- and menaquiones) are lipophilic whereas the eight B vitamins and vitamin C (ascorbic acid) are water soluble (Table 1). Vitamins were first characterized as factors having essential biological properties, required in very low concentrations. They cannot be synthesized by humans, and consequently, must be provided by the diet. Vitamin deficiencies induce specific diseases; for example, the lack of vitamin C and scurvy. Vitamins were originally classified according to these characteristics rather than to their molecular nature (for detailed formula, see Graulet al., 2013), specific biological activities, or modes of action. In terms of modes of action, three main trends emerge.

Vitamins A and D have hormone-like activity regulating the expression of numerous genes through specific nuclear receptors (like steroid or thyroid hormones). Vitamin A (retinol and its related compounds, retinoic acid and 11-cis-retinaldehyde) has been and remains the focus of extensive investigation because nutritional deficiency in vitamin A is still a major public health problem all over the world (Blaner, 2013). Consequently, its biological properties, mechanisms of action (both at cellular and molecular levels), metabolism, and regulation are now well documented, and most of these aspects have been reviewed very recently (Al Tanoury et al., 2013; O’Byrne and Blaner, 2013). To summarize briefly, retinoids, as retinal, have essential and well-known roles in vision. Through the control of the expression of numerous target genes using nuclear receptor pathways, retinoic acid is involved in development and growth at the embryonic, fetal,
Table 1. Dietary reference intake for vitamins, main biological functions, consequences, and prevalence of deficiencies and at-risk human populations (Sources: Graulet et al., 2013; FAO/WHO, 2001).

<table>
<thead>
<tr>
<th>Food item</th>
<th>Dietary reference intake* (µg/day)</th>
<th>Main biological functions</th>
<th>Consequences of deficiencies</th>
<th>Prevalence of deficiencies and at-risk populations</th>
</tr>
</thead>
<tbody>
<tr>
<td>A: Retinol‡</td>
<td>300 to 500 600 to 900</td>
<td>Vision, immunity, organogenesis and tissue differentiation, epithelial cellular integrity, reproduction</td>
<td>Xerophthalmia, decreased reproductive efficiency, anemia, retarded growth</td>
<td>Several million preschool children and pregnant women per year, essentially in developing countries</td>
</tr>
<tr>
<td>B₆: Thiamin</td>
<td>200 to 600 900 to 1,200</td>
<td>Carbohydrates and branched-chain amino acids metabolism</td>
<td>Beri-beri, polyneuritis</td>
<td>Endemic in Asia</td>
</tr>
<tr>
<td>B₂: Riboflavin</td>
<td>300 to 600 900 to 1,300</td>
<td>Carbohydrates and fatty acid metabolism, energy production</td>
<td>Arabinoflavinosis, sore throat, hyperaemia, pharyngeal oedema, cheilosis, angular stomatitis</td>
<td>Persons with digestive problems: children in developing countries with gastrointestinal infections, patients with lactose intolerance, celiac disease, malignancy and resection of the small bowel, decreased gastrointestinal transit, severe alcoholism.</td>
</tr>
<tr>
<td>B₃: Niacin</td>
<td>2,000 to 8,000 12,000 to 16,000</td>
<td>Carbohydrates and fatty acid metabolism</td>
<td>Pellagra: dermatitis, dementia, diarrhoea</td>
<td>Endemic in the poorest areas of India, China and Africa</td>
</tr>
<tr>
<td>B₅: Pantothenic acid</td>
<td>1,700 to 3,000 4,000 to 5,000</td>
<td>Fatty acid and energy metabolism</td>
<td>Irrascibility, postural hypotension, rapid heart rate, epigastric distress, numbness and tingling of hands and feet, hyperactive tendon reflexes and weakness of finger muscles</td>
<td>Rarely encountered alone</td>
</tr>
<tr>
<td>Vitamin B₆</td>
<td>100 to 600 1,000 to 1,700</td>
<td>Aminotransferase metabolism and heme synthesis</td>
<td>Convulsions, skin changes, anemia, nervous system dysfunction, impairment of the immune system</td>
<td>At-risk subjects are infants, people with poor nutritional conditions or eating disorders</td>
</tr>
<tr>
<td>B₇: Biotin</td>
<td>5 to 12 20 to 30</td>
<td>Carrier of active bicarbonate for substrate carboxylation in fat, glycogen and amino acids synthesis</td>
<td>Dermatitis, conjunctivitis, alopecia, central nervous system abnormalities and developmental delay in infants, depression, hallucinations and paresthesia in adults</td>
<td>Mainly observed in normal subjects with high consumption of raw egg whites or in patients with short gut syndrome and other causes of malabsorption</td>
</tr>
<tr>
<td>B₈: Folic acid</td>
<td>65 to 200 300 to 400</td>
<td>Carrier of monocarbon functional units for the methylation cycle involved in nucleic acid, lipids, hormones, proteins, myelin synthesis</td>
<td>Megaloblastic anaemia</td>
<td>Common for people eating folate-poor diets, subjects with malabsorption syndrome, pregnant and lactating women (due to the increase in folates demand for conceptus growth or secretion in milk, respectively)</td>
</tr>
<tr>
<td>B₁₂: Cobalamines</td>
<td>0.4 to 1.2 1.8 to 2.4</td>
<td>Folate activation, oxidation of branched-chain aminotransfereases, odd-chain fatty acids, or propionate</td>
<td>Pernicious anemia, neuropathy and/or anemia</td>
<td>People eating diets without animal products, elderly patients suffering of pernicious anaemia or more commonly from atrophic gastritis</td>
</tr>
<tr>
<td>C: Ascorbic acid</td>
<td>15,000 to 50,000 45,000 to 90,000</td>
<td>Major water-soluble antioxidant or reducing agent participating also as cofactor for collagen hydroxylation, nor-epinephrine synthesis, peptide hormones amidation, tyrosine metabolism</td>
<td>Anemia, scurvy</td>
<td>People eating diets with very low vegetable and fruit</td>
</tr>
<tr>
<td>D: Cholecalciferol</td>
<td>5 5 to 15</td>
<td>Calcium and phosphate homeostasis, bone mineralization, muscle contraction, nerve conduction</td>
<td>Rickets due to deficiencies in childhood, hip fracture in elderly people</td>
<td>Infants have large vitamin D needs for skeletal growth but breastfed babies have low supply due to the low concentrations in human milk; reduced exposure to sun for proper biosynthesis depending of season, latitude, culture or social reasons can be an increasing factor; elderly persons are also at-risk</td>
</tr>
<tr>
<td>E: Tocopherol</td>
<td>4,000 to 7,000 11,000 to 15,000</td>
<td>Major liposoluble antioxidant whom role is to protect cell membrane components among which polyunsaturated fatty acids</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>K: Phylloquinone</td>
<td>2 to 55 60 to 120</td>
<td>Blood coagulation, cell cycle regulation</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

*Data provided are Recommended Dietary Allowances (RDA) for vitamins A, B₁, B₂, B₃, B₅, B₆, B₉, B₁₂, C, and E and Adequate Intakes (AI) for vitamins B₁, B₃, D, and K. † Children are considered from birth to 8 years old, and adults are males or females (not pregnant and not lactating) aged from 9 years old to more than 70. ‡ Expressed in retinol equivalent.
and post-natal levels and in immunity and maintenance of epithelial barriers as well as recently identified roles related to energy metabolism and nervous system function (Al Tanoury et al., 2013). Like vitamin A, interest in vitamin D is driven by new knowledge on its modes of action, not only on mineral homeostasis (in bones, intestine, and kidneys), but also on its action through an endocrine system acting via the vitamin D receptor (VDR), present in all tissues. The term “vitamin D” includes more than 30 compounds of the calciferol family that has as its main precursors, ergocalciferol (D2-sub-family) and cholecalciferol (D3-sub-family). They are both produced under the action of solar irradiation by fungi, yeasts, and some plants for ergocalciferol or in animal skin for cholecalciferol. Ergocalciferol and cholecalciferol are pro-hormones that have to be converted by hydroxylation, first in the liver to 25-hydroxyvitamin D (its concentration in serum is considered as the marker of vitamin D status) and then in the kidneys, to become fully active as 1,25-dihydroxyvitamin D (Tripkovic et al., 2012). The active forms regulate the expression of numerous genes through the VDR, a nuclear transcription factor (DeLuca, 2004). The well-known target genes of vitamin D affect calcium (and phosphorus) homeostasis at the levels of intestinal absorption, bone mineralization, and renal reabsorption. However, it is now accepted that VDR is expressed in almost every cell and organ, taking part in many major functions like immunity, metabolism, cardiovascular function, reproduction, and musculo-skeletal strength (Pludowski et al., 2013).

Vitamins C and E are both major natural antioxidants in their respective matrices, due to their ability to trap radicals or exchange electrons or hydrogen atoms. Thus, they protect the other components in living cells or biological fluids from oxidation and peroxidation processes. Oxidative risks come from oxidants and radicals naturally produced by mitochondria, peroxisomes, cytochrome P450, and phagocytes that have a quantitatively important function in oxidation processes (Bramley et al., 2000). The most active form of vitamin E in animals is α-tocopherol (Traber, 2013). As a fat-soluble component, α-tocopherol is located in cell membranes and lipoprotein envelopes allowing it to protect surrounding poly-unsaturated fatty acids (PUFA) from oxidative damage. Vitamin E exerts its antioxidant property by scavenging lipid radicals and/or ending oxidative chain reactions. In doing so, it favors the proper functions of the body cells and lipoproteins, acting on membrane fluidity that is especially important for membranous signal transduction in numerous biological processes (Bramley et al., 2000). Vitamin C possesses a complementary action by favoring reduction of the oxidized form of α-tocopherol (Bramley et al., 2000; Getoff, 2013). It also exerts its antioxidant property by acting as an enzyme cofactor, mainly for some iron-dependent dioxygenases involved in collagen synthesis, angiogenesis, cell survival, glucose metabolism, iron homeostasis, and numerous other functions (Du et al., 2012). Vitamins E and C share a common property based on their ability to transfer electrons. Moreover, for these two vitamins, the compounds absorbed in the digestive tract are biologically active and do not require conversion(s), i.e., bioactivation, to fulfill their functions.

Like ascorbic acid, B vitamins and vitamin K are enzyme cofactors, but unlike vitamin C, they have to be molecularly activated (except biotin) to fulfill their functions. After reduction into hydroquinone, vitamin K acts as a cofactor of the γ-glutamylcarboxylases, enzymes that perform the molecular conversion of specific glutamate residues into γ-carboxyglutamates in some proteins during their secretory process, allowing their post-translational activation. These proteins are mainly involved in blood hemostasis (coagulation factors) and calcium homeostasis (osteocalcin, matrix-Gla protein). However, some of them are factors regulating...
Table 2. Implication of B vitamins in the major metabolic pathways.*

<table>
<thead>
<tr>
<th></th>
<th>Thiamin (B₁)</th>
<th>Riboflavin (B₂)</th>
<th>Niacin (B₃)</th>
<th>Pantothenic acid (B₅)</th>
<th>Pyridoxine and its vitamers (B₆)</th>
<th>Biotin (B₇)</th>
<th>Folic acid (B₉)</th>
<th>Cobalamin (B₁₂)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lipids</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Proteins and amino acids</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Energy and carbohydrates</td>
<td>X</td>
<td>X</td>
<td>X</td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nucleic acid</td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
<td>X</td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oxido-reduction processes</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Heme synthesis</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>X</td>
<td></td>
</tr>
</tbody>
</table>

* X indicates a rather direct implication of the given B vitamin in the metabolic pathway considered.

Vitamin intakes and human health

For most of these vitamins, proposed Recommended Dietary Allowances (RDA; National Research Council, 1997, 1998, 2000, 2001) are considered to meet the needs of 97 to 98% of the population (according to age, gender, and for women, physiological status). Needs are very different among vitamins, ranging from several micrograms per day for vitamin B₁₂ and vitamin D to several tens of milligrams per day for vitamin C (Table 1). Recommendations vary with age and generally reach maximum values after puberty, when height tends to stabilize. Nevertheless, when reported according to body weight, requirements are markedly greater in infants, children, and teenagers than in adults.

Despite UNICEF programs, vitamin A deficiency remains a major concern. Its deficiency is by far the most common; it was estimated that 3 million children developed xerophthalmia annually whereas the estimation increased to 250 million when considering sub-clinical deficiencies detected by blood measurements (FAO/WHO, 2001). At-risk subjects are children under three years of age because this is a period of rapid growth, nutritional transition from breast feeding to other foods that may not be good sources of vitamin A, and severe infections. Non-negligible risk factors for vitamin A deficiency are the prevalent consumption of vitamin A as carotenoids from a diet with a low-fat content, which limits their absorption, or the seasonal shift between access to a diet rich in energy and macronutrients favoring child growth to a fruit-rich diet (like mangoes) containing increased concentrations of β-carotene (FAO/WHO, 2001).

Sub-clinical deficiencies of B vitamins are still a public health problem in several parts of the world (Asia and Africa mainly) due to poor-quality diets in terms of micronutrient supply. Similarly, vitamin C deficiency affects people consuming an insufficient amount of vegetables and fruits per day. Displaced populations and refugees living in camps are the most susceptible to developing vitamin deficiencies because of the consumption of cereal foods not fortified with micronutrients. B vitamin deficiencies affect especially breast-fed babies whose mothers consume deficient diets. Moreover, in spite of its wide distribution in foods, folate deficiency or suboptimal status is rather common due to relatively low intake combined with significant losses during harvesting, storage, processing, or cooking of foods. Similar to that of the other vitamins, pregnancy and lactation increase folate requirements; however, meeting folate requirements is especially important at the beginning of the pregnancy for adequate cell multiplication in the embryo and then tissue formation in the fetus. The increased need very early during the pregnancy has led to food fortification policies in 42 countries of America (USA, Canada, Mexico, almost all the countries of South America) and Arabia, but not Europe where the benefit:risk ratio of the folic acid fortification is still debated (Food Safety Authority of Ireland, 2006). However, recent studies conducted after many years of mandatory fortification of folic acid in food highlight the need for a more integrated approach to avoid detrimental effects due to cross-relationships between vitamins B₉, B₆, and B₁₂ in one carbon metabolism (Selhub and Paul, 2011).

Other risk factors for B vitamin deficiency are intestinal disorders leading to B vitamin malabsorption: hookworm infection (vitamins B₁ and B₂), Crohn’s disease (vitamin B₁₂), pernicious anemia (vitamin B₁₂), chronic

Table 3. Contribution of the bovine milk to the reference intake of vitamins.*

<table>
<thead>
<tr>
<th>Vitamins</th>
<th>Mean concentrations µg/L</th>
<th>Contribution to the RDI† %</th>
</tr>
</thead>
<tbody>
<tr>
<td>A†</td>
<td>385</td>
<td>11</td>
</tr>
<tr>
<td>D</td>
<td>10</td>
<td>17</td>
</tr>
<tr>
<td>E</td>
<td>700</td>
<td>1.2</td>
</tr>
<tr>
<td>K</td>
<td>3</td>
<td>0.6</td>
</tr>
<tr>
<td>B₁</td>
<td>420</td>
<td>9</td>
</tr>
<tr>
<td>B₂</td>
<td>1650</td>
<td>32</td>
</tr>
<tr>
<td>B₃</td>
<td>3430</td>
<td>17</td>
</tr>
<tr>
<td>B₆</td>
<td>390</td>
<td>6</td>
</tr>
<tr>
<td>B₉</td>
<td>50</td>
<td>3</td>
</tr>
<tr>
<td>B₁₂</td>
<td>4</td>
<td>42</td>
</tr>
<tr>
<td>C</td>
<td>7500</td>
<td>2</td>
</tr>
</tbody>
</table>

* Values estimated for the consumption of a cup (250 mL) of fresh unsupplemented bovine milk according to concentrations from USDA (2009) reference 01077, milk, whole, 3.25% fat (no data available on milk concentration of biotin). Please note that in the latest releases, this reference is for bovine milk with added vitamin D.
†RDI = required daily intake.
‡ Vitamin A was expressed in retinol equivalent (RAE).
§ Vitamin B₉ is given in niacin equivalents (NE).
¶ Vitamin B₁₂ is given in dietary folate equivalents (DFE).
alcoholism (vitamins B_1, B_2, B_3), or also age, as elderly people are more prone to develop deficiency of vitamins B_1, B_2, and B_12 (FAO/WHO, 2001).

**Increasing Vitamin Intakes through Milk Consumption**

Covering human vitamin requirements remains a huge worldwide public health problem. Several solutions have been proposed such as vitamin fortification in food or development of new food with an added value such as golden rice to provide supplementary provitamin A (carotenoids). A diversified diet with sufficient nutritional density is also a good way to supply vitamins, but access to a diet with an adequate nutritional quality is not always possible, depending on geographical location, season, economic considerations, socio-cultural behaviors, and age.

**Milk as a source of vitamins in human nutrition**

Milk and dairy products can be considered as reliable sources of vitamins because they contain the 13 vitamins (Table 3). Concentrations in bovine milk are one to several thousand micrograms per liter for vitamins C, B_2, and B_3; several hundred for vitamins A, E, and B_12; the low tens for vitamin B_6; and less than 10 µg/L for vitamins D and B_12. Moreover, milk is more or less available throughout the year, its cost is usually relatively low, and the general trend is that it enjoys a positive image across the world.

Milk is an essential component in the human diet especially after birth and during childhood. Even in adults, milk and dairy product consumption remains significant from 180 kg of milk consumed per capita per year in Iceland or Finland to 50 kg in China or Japan (Haug et al., 2007). In spite of the negative image linked to the presence of saturated fatty acids in milk and dairy products, several recent studies looking at micronutrient concentrations in food ingredients and eating habits of populations in France (Coudray, 2011), the Netherlands (Vissers et al., 2011), or the United States (Drewnowski, 2011) agree that milk and dairy products are good sources and are among the primary contributors of vitamins A, D, B_2, B_3, B_6, and B_12 intake in human nutrition. Moreover, the good nutritional value and relatively low cost of milk and dairy products make them very attractive sources of nutrients, including vitamins, for economically disadvantaged populations, either in Western societies or in developing countries as they “supplied the most nutrients for least money” (Drewnowski, 2011).

Results cited above mainly concern bovine milk, but several differences seem to exist among dairy species. Bovine milk is by far the one for which the vitamin content has been the most studied, and data are “less incomplete” than for other dairy species. Dairy cows, goats, and ewes produce 87% of the milk in the world, but other dairy species can be of significance in some geographical areas like camelids in arid and semiarid regions (Medhammar et al., 2012). A compilation of the literature indicated that the overall pattern of milk vitamin concentrations would be similar for all these species (from concentration of vitamin C being the greatest to concentrations of vitamin B_12 and vitamin D being the lowest) even though differences exist for several vitamins between dairy species (Graulet et al., 2013). Indeed, milk of ewes and goats is richer in vitamin A than cow milk; ewe milk seems richer in vitamins than that of other ruminants (especially cows). Goat milk is especially poor in vitamin B_6, leading to the development of “goat milk anemia,” which is characterized by very low concentrations of plasma folates in infants fed a diet solely based on goat milk (Park et al., 2007). The milk of goats also seems poorer in vitamin D and vitamin E compared with the milk of other species. Dromedary milk is especially rich in vitamin C and vitamin A, which is of special interest for human nutrition in areas where vegetables and fruits are not easily available. By contrast, buffalo milk is reported to be 10-fold richer in vitamin B_6 and 2-fold richer in vitamin B_12 and vitamin E, but markedly poorer in vitamins B_2, B_3, and B_12 than cow milk (Medhammar et al., 2012). These comparisons should be considered with caution because of the low number of original data for most of these species. Moreover, in most studies, the dietary and physiological status of the lactating animals is not characterized, possibly leading to major bias when doing inter-species comparisons. Knowledge on the effects of diet composition or physiological status of dairy animals on milk concentrations of vitamins is essentially from studies performed in bovine and cannot be applied to other dairy species without supplementary studies.

**Increasing vitamin content in milk**

The importance of factors such as composition of the diet fed to the animal or physiological status of the animal on concentrations of vitamins in milk is still not very well defined. To reach the ultimate goal of offering a milk with natural and optimal vitamin concentrations to most people during the major part of the year would require identification of the major factors driving this variable. It is likely that a given rearing condition will not favor simultaneously all the vitamin concentrations. However, a consensus could be obtained to define the “ideal milk,” taking into consideration the major vitamin requirements in
human nutrition, the importance of milk and dairy products for vitamin supply, and the possibilities to modulate these vitamin concentrations in milk.

Increasing the vitamin content in bovine milk should likely be achievable mainly through changes in diet composition. Differences in milk concentrations of retinol, β-carotene, and α-tocopherol are mainly and directly explained by the dietary intakes of these vitamins by the animal and, to a lesser extent, indirectly by differences in milk fat content. Indeed, a relationship was observed between dietary intakes of β-carotene and vitamin E on the one hand and β-carotene, retinol, and α-tocopherol concentrations in plasma and/or secretion in milk fat on the other hand (Nozière et al., 2006; Calderón et al., 2007). The relationship was linear between β-carotene or α-tocopherol intakes and β-carotene, retinol, or α-tocopherol concentrations in milk; however, the relationship between intake and secretion of β-carotene in milk was linear only for dietary contents between 0 and 60 mg/kg DM; at greater dietary concentrations, milk concentrations of β-carotene reached a plateau, suggesting a saturation of the transfer from plasma to milk. Quantitative changes in dietary intake of carotenoids and vitamin E explain the differences in concentrations of these compounds in milk from cows fed different types of forages or different forage-to-concentrate ratios (Nozière et al., 2006), fresh grass being by far the richest forage in terms of carotenoids and vitamin E. However, under commercial farm practices, these effects of diet composition on milk vitamin concentrations are often masked by the use of vitamin supplements containing vitamins A and E (Hulshof et al., 2006; Agabriel et al., 2007). However, even if vitamin D supplementation is also becoming rather common, it does not induce an increase in milk vitamin D activity (McDermott et al., 1985).

Identification of factors affecting transfer of vitamin K and B vitamins in milk is more complex due to their multiple sources. For example, niacin in milk could come from the diet, be synthesized de novo by rumen microorganisms, or be derived from tryptophan in the cow liver. Moreover, in addition to the likely quantitative differences in their dietary intakes, the efficiency of synthesis of vitamin K and B vitamins in the rumen is probably modulated by rumen fermentation, but data are scarce. Milk concentrations of B vitamins seem generally poorly related to their dietary intakes (Haug et al., 2007) probably as the result of simultaneous processes of degradation and synthesis of these vitamins in the rumen. Indeed, duodenal flow and ruminal synthesis of B vitamins are modified by the composition of the diet but are poorly related to vitamin intake (Schwab et al., 2006; Seck et al., 2010a,b, 2011). Moreover, dietary supplements of synthetic B vitamins are extensively destroyed in the rumen (Santschi et al., 2005). Nevertheless, supplementation with pantothenic acid (vitamin B₉) in a form protected from bacterial degradation in the rumen increased its plasma concentration in dairy cows. However, when vitamin B₉ was provided in a unprotected form, it had only marginal effects, especially at the lesser doses, and transfer to milk was not affected, confirming that the vitamin was mostly destroyed by ruminal microflora (Ragaller et al., 2010, 2011). Conversely, high doses of folic acid and cobalamin (vitamin B₁₂) added in the total mixed ration of high-producing dairy cows increased milk concentrations of these vitamins (Graulet et al., 2007).

Interestingly, recent results observed on commercial farms showed that milk concentrations of vitamins B₂, B₃, and B₁₂ varied according to the feeding system. Indeed, the highest vitamin B₁₂ content (up to +32%) in bulk tank milk was observed in farms where cows were fed maize-rich diets whereas milk produced when diets were based on hay in winter or pasture during the grazing period were richer in vitamin B₆ (Chassaing et al., 2011) and vitamin B₂ (Vallet et al., 2013). Thus, if vitamin dietary intakes have a limited impact on their milk concentrations as stated by Haug et al. (2007), these results would be likely explained by the effects of diet composition on bacterial populations and/or fermentation. Indeed, diet composition would 1) alter bacterial synthesis of these vitamins; 2) alter vitamin bioavailability for the cow; and 3) possibly, because B vitamins act as cofactors in most major metabolic pathways, alter vitamin utilization by the animal due to changes in the metabolic demand linked to changes in milk production levels.

Like for dietary factors, knowledge on non-dietary factors affecting milk concentrations of vitamins is greater for vitamin A than for the other vitamins. The effects of breed, stage of lactation, health status of the udder, milk and fat yields, and genetic traits on milk concentrations of vitamin A have been reviewed by Nozière et al. (2006). For example, among dairy breeds, retinol concentrations are greater in milk of Holstein-Friesian than of Guernsey cows. Heritability of the milk concentrations of retinol, but also of vitamin B₁₂, as demonstrated recently (Rutten et al., 2013), has been reported, suggesting that genetic selection could be considered in a general strategy to improve milk vitamin composition. Variability among animals could be due to a genetically determined efficiency of transfer of the compounds from the digestive tract to the milk (at the level of the intestinal absorption, cellular conversion or bioactivation, plasma uptake, or secretion by the mammary gland). This variability could also be explained by factors related to animal performance such as different levels of metabolic utilization of the vitamins or also by a dilution/concentration effect in milk. More studies are needed to identify the factors responsible for changes in milk concentrations of vitamins according to physiological or metabolic status of cows in interaction with diet composition.

Conclusions

In spite of the importance of milk and dairy product consumption in human nutrition and vitamin requirements for human health, factors affecting concentrations of vitamins in milk have been relatively poorly studied with the exception of vitamin A. Access to a diversified diet to cover nutritional requirements will be an increasing concern in the future decades because of the increase of the world population. Optimizing nutritional values of food could be part of the solution, and research on the transfer of vitamins from the diet or rumen of the animal to milk could contribute to achieving this optimization.

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