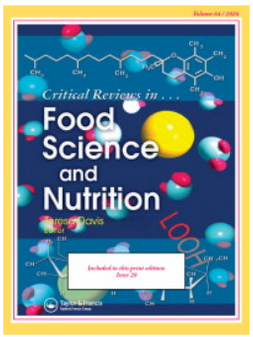

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REVIEW

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Comparative bioavailability of vitamins in human foods sourced from animals and plants

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ABSTRACT

Vitamins are essential components of enzyme systems involved in normal growth and function. The quantitative estimation of the proportion of dietary vitamins, that is in a form available for utilization by the human body, is limited and fragmentary. This review provides the current state of knowledge on the bioavailability of thirteen vitamins and choline, to evaluate whether there are differences in vitamin bioavailability when human foods are sourced from animals or plants. The bioavailability of naturally occurring choline, vitamin D, vitamin E, and vitamin K in food awaits further studies. Animal-sourced foods are the almost exclusive natural sources of dietary vitamin B-12 (65% bioavailable) and preformed vitamin A retinol (74% bioavailable), and contain highly bioavailable biotin (89%), folate (67%), niacin (67%), pantothenic acid (80%), riboflavin (61%), thiamin (82%), and vitamin B-6 (83%). Plant-based foods are the main natural sources of vitamin C (76% bioavailable), provitamin A carotenoid β-carotene (15.6% bioavailable), riboflavin (65% bioavailable), thiamin (81% bioavailable), and vitamin K (16.5% bioavailable). The overview of studies showed that in general, vitamins in foods originating from animals are more bioavailable than vitamins in foods sourced from plants.

KEYWORDS

bioavailability; vitamin; digestibility; absorption; availability; utilization

Introduction

Recent international reports suggest that some forms of animal food production may be environmentally unsustainable, and that the current consumption of animal-sourced foods should be lowered in favor of plant-based foods (Adesogan et al. 2020; Beal et al. 2023; FAO et al. 2020; Pimentel and Pimentel 2003; Springmann et al. 2018; WHO and FAO 2019; Willett et al. 2019). However, the nutritional quality of animal- and plant-sourced foods must be considered in the formulation of affordable, sustainable dietary patterns (Ambikapathi et al. 2022; FAO et al. 2020; Herforth et al. 2020; Hirvonen et al. 2020; Springmann et al. 2018). Our previously reported modeling studies, using Linear Programming, showed that dietary patterns that met the recommended minimum intake requirements for essential nutrients of an average adult in the United States of America or New Zealand, formulated at the lowest dietary cost, relied on foods sourced from both plants and animals (Chungchunlam et al. 2020, Chungchunlam, Garrick, and Moughan 2021). Modeled diets that included animal-sourced foods were relatively 30 to 45% cheaper than modeled diets that consisted exclusively of plant-based foods, and the prices of animal-sourced foods had to be increased by two to eleven times to be excluded from the least-cost dietary patterns. It was also highlighted that the first-limiting nutrients for adults in mixed modeled diets were not the macronutrients but rather mostly the vitamins and minerals, particularly vitamin A, B group vitamins, calcium, iron, potassium, and zinc (Chungchunlam et al. 2020, Chungchunlam, Garrick, and Moughan 2021). While the amount and form of essential nutrients may differ among their main dietary sources, their inherent bioavailability is often overlooked. These essential nutrients generally occur in animal-derived foods in higher concentrations and apparently with greater bioavailability, compared to plant-based foods (Adesogan et al. 2020; Murphy and Allen 2003). However, there is a paucity of published data on the comparison of the overall availability of vitamins and minerals between animal- and plant-sourced foods. The bioavailability of minerals and trace elements will be the subject of a future review from our research group. This review focuses on the bioavailability of vitamins.

Vitamins are essential components of enzyme systems that assist chemical reactions within the body, and are important for cell membrane integrity, nerve and muscle function, bone formation, and normal growth and overall good functioning of the human body (WHO and FAO 2004). The chemically active forms of vitamins are sometimes referred to as vitamers. There are two categories of vitamins, based on their solubility and the extraction method used to isolate them. The fat-soluble vitamins include vitamins A, D, E, and K. For the determination of the content

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of fat-soluble vitamins in food, an organic solvent is used to remove the vitamins dissolved in food fat. The extraction process for water-soluble vitamins in food involves the use of an aqueous solution. The water-soluble vitamins comprise vitamin C, and the B group vitamins, namely biotin (vitamin B-7), folate (vitamin B-9), niacin (vitamin B-3), pantothenic acid (vitamin B-5), riboflavin (vitamin B-2), thiamin (vitamin B-1), vitamin B-6, and vitamin B-12. The water-soluble compound choline is recognized strictly as not a vitamin, but is related to the B vitamins, and will be considered in this review. Animal-sourced foods are the almost exclusive natural sources of dietary vitamin B-12 (Scott 1997; Watanabe 2007) and choline (Zeisel et al. 2003; Zeisel and da Costa 2009), and plant-based foods are the main sources of natural dietary vitamin C (Bates 1997a; Olson and Hodges 1987). While most vitamins are widely distributed in foods (Ball 1998, 2006; WHO and FAO 2004), vitamin deficiencies are prevalent in human populations and may even occur with apparently sufficient dietary intakes (Bailey, West, and Black 2015; Beal et al. 2017; Beal and Ortenzi 2022; Passarelli et al. 2022; WHO and FAO 2004). This may in part be attributable to inadequate absorption and inadequate utilization of vitamins present in the human diet, which in turn may be dependent on food source (Ball 1998, 2006; Beal and Ortenzi 2022; Beal et al. 2023; Melse-Boonstra 2020; Passarelli et al. 2022; WHO and FAO 2004).

Bioavailability may be defined as the proportion of an ingested nutrient that is released during digestion, absorbed *via* the gastrointestinal tract (GIT), transported and distributed to target cells and tissues, in a form that is available for utilization in metabolic functions or for storage (Baker 1995; Ball 1998, 2006; Bates and Heseker 1994; Gibson 2007; Godber 1990; Heaney 2001; WHO and FAO 2004). However, the unifying term "bioavailability" has been employed generically and a clear consensus definition of bioavailability is needed. Various terms, such as absorbability, digestibility, availability, utilizability, and utilization, have been used when discussing the metabolic processes involved in transforming a specific nutrient present in food to a utilizable form (Table 1). Humans consume a combination of different foods, and digestion is the process that breaks down the food materials, releasing nutrients that can be absorbed by the human body (Singh and Gallier 2014). Mechanical action and saliva in the mouth, acid and enzymes released in the stomach, and bile and enzymes in the small intestine, all function together to break down the food macromolecules and release the nutrients (Singh and Gallier 2014). Absorption is the process by which the released nutrients pass from the GIT lumen, either passively or actively, through the intestinal epithelial cells, the enterocytes, into the systemic circulation or lymphatic system (Baker 1995; Baker and Stein 2013). Digestibility refers here to the disappearance of a nutrient during its passage through the GIT; this nutrient disappearance is sometimes assumed to equate with absorption (Baker 1995; Baker and Stein 2013; Bates and Heseker 1994). The bioavailability of dietary protein and amino acids is often expressed as digestibility and provides an indication of the quality of protein and amino acid supplied by a particular food (FAO 2013; Moughan 2021; Moughan and Wolfe 2019; Sarwar 1987). Availability refers to the proportion of absorbed nutrient that is physiologically available for anabolic utilization, mostly transported in the systemic circulation, and supplied to target body tissues (Baker 1995; Baker and Stein 2013; Gibson 2007; Godber 1990). Utilization is defined as the proportion of absorbed and available nutrient that has been used by the body for metabolic or physiological functions (Baker 1995; Baker and Stein 2013; Heaney 2001). Some of these terms are used interchangeably, but each has a precise meaning and this needs to be taken into account when comparing the biological availability of dietary nutrients.

Table 1. Terms used to define the processes pertaining to nutrient bioavailability.

	Definition
Digestion	The process during which food is broken down and nutrients released into the lumen of the gastrointestinal tract (GIT)
Absorption	The proportion of nutrient released in the GIT that is absorbed from the GIT
Digestibility	The amount of nutrient disappearing from the GIT during the transit of food
Availability	The proportion of nutrient that is absorbed in a form that can be used for anabolic processes
Utilization	The proportion of absorbed nutrient that is used by the body for metabolic or physiological functions

GIT, gastrointestinal tract

Several *in vitro* and *in vivo* approaches have been used to study digestibility and bioavailability. In the context of *in vitro* digestion approaches, the term bioaccessibility refers to the fraction of a nutrient found in food that has been converted by digestion into potentially accessible soluble forms for absorption, while the term bioactivity applies to the events that occur during transport, assimilation by the target tissue, interaction with other biomolecules, metabolism or biotransformation, and the physiological responses (Fernández-García, Carvajal-Lérida, and Pérez-Gálvez 2009; Marze 2017). Most *in vitro* methods are based on a simulated digestive process followed by measurement of the released test nutrient to assess bioaccessibility of nutrients. However, the bioactivity of nutrients is not adequately taken into account in *in vitro* studies and the responses are not as robust as those based on measures made in humans or animal models. In this review, "bioavailability" values were collected from *in vivo* studies conducted in humans or the pig as an animal model for the adult human (Baker 1995; Ball 1998, 2006; Bates and Heseker 1994; Godber 1990; WHO and FAO 2004). The gastrointestinal tract of humans and pigs has been shown to be similar (Guilloteau et al. 2010; Moughan et al. 1994). It should be recognized that bioavailability estimates are representative of the response of the human or animal model to a specific food or diet and therefore, may be dependent on the nutritional and health status of the subject (Gibson 2007; Godber 1990; WHO and FAO 2004). In addition to host-related factors, the quantification of bioavailability is influenced by dietary factors, such as the amount and form of the nutrients that are consumed in the diet, the dietary matrix, food processing and treatment, and the presence of other food components that may enhance or inhibit nutrient digestion, absorption, and utilization (Dave et al. 2023; Gibson 2007; Gibson, Perlas, and Hotz 2006; Godber 1990; Melse-Boonstra 2020; Murphy and Allen 2003; Platel and Srinivasan 2016).

The most common approach to measuring vitamin bioavailability is the balance study, whereby the difference between ingestion of a vitamin and its excretion is evaluated (Bates and Heseker 1994; Godber 1990; Heaney 2001; WHO and FAO 2004). Ileal digestibility is assessed by the difference between the ingested amount of vitamin and the amount of vitamin found in ileal effluent, and may be used as a robust proxy for apparent absorption (Baker 1995; Baker and Stein 2013; Bates and Heseker 1994). Fecal digestibility is assessed as the difference between vitamin intake and its fecal excretion, where the assumption is that unabsorbed vitamins are released in the feces (Baker 1995; Baker and Stein 2013; Bates and Heseker 1994). In some cases, this assumption is not valid, as large intestinal bacteria can both degrade and synthesize some vitamins (Baker 1995; Baker and Stein 2013; Bates and Heseker 1994; Said 2013; WHO and FAO 2004; Yoshii et al. 2019). Another potentially more accurate method involves the use of stable isotopes or radioactive isotopes to label foods either intrinsically or extrinsically, and monitoring the route and fate of the isotopically labeled dietary vitamin (Godber 1990; Heaney 2001). Other methods include the measurement of responses in blood, tissues, organs, body pools, or the urine (Godber 1990; Heaney 2001). Bioavailability values may also be obtained in relation to that of the test vitamin given in a purified form or in a standard ingredient. When the absorption efficiencies of the reference vitamin are known, the absolute apparent estimates of vitamin bioavailability may be calculated from the relative bioavailability values (Baker and Stein 2013). "True" bioavailability values are obtained either by correcting for endogenous losses with the balance method, or the comparison of the physiological response between oral doses of a dietary vitamin and the vitamin intravenously administered by injection (Baker 1995; Baker and Stein 2013; Bates and Heseker 1994; Dainty et al. 2007; WHO and FAO 2004). Nonetheless, the bioavailability data of most vitamins in human foods remain limited and fragmentary (Baker 1995; Ball 1998, 2006; Bates and Heseker 1994; Dave et al. 2023; Melse-Boonstra 2020; WHO and FAO 2004). There is an even wider knowledge gap when comparing vitamin bioavailability amongst human foods sourced from animals or plants. The objective of this conspectus was to provide a review of studies summarizing the multiple methodologies used to determine vitamin bioavailability and estimating the bioavailability of the fat-soluble vitamins A, D, E, and K, and the water-soluble biotin, folate, niacin, pantothenic acid, riboflavin, thiamin, vitamin B-6, vitamin B-12, vitamin C, and choline. Comparable relevant bioavailability data are brought together to allow a comparison of vitamin bioavailability in animal- and plant-sourced foods.

Bioavailability of vitamins in foods sourced from animals and plants

This section presents a general introduction of each specific vitamin, with a common description of biochemical forms, physiological functions, dietary sources, absorption and utilization, and the experimental approaches used to determine bioavailability of each vitamin in food. An important question remains as to what extent the bioavailability of vitamins differs amongst human foods sourced from animals or plants. It is difficult to provide such comparative assessment as bioavailability estimates have often been observed using different definitions of bioavailability, different methodologies to measure bioavailability and different study populations. Special care has been applied in this section, where these considerations are taken into account, to only use relevant and comparable data for comparisons of bioavailability of each vitamin in foods originating from animals or plants (Table 2 and Figure 1).

Vitamin A

Vitamin A absorption and utilization

Vitamin A (retinol) is a fat-soluble vitamin present in food as preformed vitamin A, primarily as retinol derivatives, and provitamin A carotenoids (carotenes) that are the precursors for retinol (Bates and Heseker 1994; IOM (Institute of Medicine, US) 2000, 2001; WHO and FAO 2004). In addition to its central role as a constituent of a visual pigment to maintain eye vision, vitamin A has many other roles in the human body, such as in growth and development, cell surface integrity, immune function, and reproduction (Biesalski 1997; de Pee and West 1996; Wolf 2002). Preformed vitamin A is found mostly in animal-sourced products, including meat, liver, milk, eggs, and fish (Biesalski 1997). Provitamin A carotenoids, mainly β-carotene and α-carotene, are commonly found in colored (orange, yellow, red, green, or purple) vegetables and fruits (Castenmiller and West 1998; de Pee and West 1996; Parker 1997; Parker et al. 1999; van Het Hof et al. 2000). The carotenoids exist mostly as the all-*trans* isomers, but can also occur as *cis* isomers (Castenmiller and West 1998; de Pee and West 1996; Parker 1997; Parker et al. 1999; van Het Hof et al. 2000). Some carotenoids, such as lycopene, do not exhibit vitamin A biological activity, but act as anti-oxidants (Castenmiller and West 1998; de Pee and West 1996; Parker 1997; Parker et al. 1999). Fatty acyl esters of retinol (retinyl palmitate, retinyl acetate), and β-carotene are often used as fortification agents of vitamin A to enrich milk, margarine, oils, condiments, and cereal products (Biesalski 1997; Castenmiller and West 1998; de Pee and West 1996; Parker 1997; Parker et al. 1999). On a cautionary note, vitamin A can be toxic when ingested in large amounts daily over a long period of time, with daily intake levels of more than 30 mg by pregnant women thought to have detrimental effects on the fetus (WHO and FAO 2004).

Ingested vitamin A is released from food by the action of gastric pepsin and intestinal proteolytic enzymes, as preformed vitamin A in the form of retinyl esters, and as provitamin A carotenoids (Biesalski 1997; Blomhoff et al. 1991; Goodman et al. 1966; Reboul 2013). In the duodenum, bile salts and pancreatic enzymes hydrolyze retinyl esters and free carotenoids, so that they may be solubilized into micelles and absorbed in the intestinal enterocyte. The presence of dietary fat is essential in forming these micelles and enhances the absorption of retinol and carotenoids (Blomhoff et al.

Table 2. Summary of results of studies in humans and pigs that estimated the bioavailability of vitamins in animal- and plant-based foods.

Nutrient	Food source	Food item	Intake	Study population	Process of bioavailability	Bioavailability	Reference
Vitamin A (retinol)	Animal	Beef liver, cooked	50 mg RE	10 female humans, mean age 26 y	Availability	84 %	Buss et al. 1994
		Beef liver, cooked	150 mg RE	10 female humans, mean age 26 y	Availability	75 %	Buss et al. 1994
		Liver paste	3.0 mg RE	35 female humans, mean age 27 y	Availability	43 %	van Vliet et al. 2001
		Liver paste	7.5 mg RE	35 female humans, mean age 27 y	Availability	62 %	van Vliet et al. 2001
		Liver paste	15.0 mg RE	35 female humans, mean age 27 y	Availability	98 %	van Vliet et al. 2001
Vitamin A (β-carotene)	Plant	Carrots, raw, chopped	2.50 mg RE	8 humans, age range 38–75 y	Availability	41 %	Livny et al. 2003
		Carrots, cooked, pureed	2.50 mg RE	8 humans, age range 38–75 y	Availability	65 %	Livny et al. 2003
		Carrots, cooked, shredded	2.00 mg RE	10 male humans, mean age 25 y	Availability	13.2 %	Huang et al. 2000
		Carrots, cooked from frozen	4.83 mg RE	30 male humans, age range 20–45 y	Availability	6.9 %	Brown et al. 1989
		Carrots, cooked from frozen	4.83 mg RE	30 male humans, age range 20–45 y	Availability	7.3 %	Micozzi et al. 1992
		Sweet potatoes, cooked, mashed	2.00 mg RE	10 male humans, mean age 25 y	Availability	14.8 %	Huang et al. 2000
		Spinach, cooked, whole leaf	1.67 mg RE	2 male and 5 female humans, mean age 51 y	Availability	26 %	Faulks et al. 2004
		Spinach, cooked, finely chopped	1.67 mg RE	2 male and 5 female humans, mean age 51 y	Availability	23 %	Faulks et al. 2004
		Spinach, cooked, whole leaf	3.97 mg RE	31 male and 38 female humans, mean age 42 y	Availability	7.3 %	van Het Hof et al. 1999b
		Spinach, cooked, minced	4.10 mg RE	31 male and 38 female humans, mean age 42 y	Availability	7.4 %	van Het Hof et al. 1999b
		Spinach, cooked, whole leaf	1.73 mg RE	5 male and 7 female humans, mean age 20 y	Availability	2.0 %	Castenmiller et al. 1999
		Spinach, cooked, minced	1.47 mg RE	5 male and 7 female humans, mean age 21 y	Availability	2.6 %	Castenmiller et al. 1999
		Spinach, cooked, liquefied	1.50 mg RE	5 male and 7 female humans, mean age 21 y	Availability	3.8 %	Castenmiller et al. 1999
		Spinach, cooked, liquefied, with added fiber	1.47 mg RE	5 male and 7 female humans, mean age 21 y	Availability	3.7 %	Castenmiller et al. 1999
		Water spinach, cooked, whole leaf	2.00 mg RE	10 male humans, mean age 25 y	Availability	10.4 %	Huang et al. 2000
Vitamin K (phylloquinone)	Plant	Kale, cooked, with added fat	119 µg per 2000 kcal (8.4 MJ)	4 male and 3 female humans, mean age 46 y	Availability	4.7 %	Novotny et al. 2010
		Spinach, raw	495 µg	11 humans, age range 22–30 y	Availability	13.9 %	Garber et al. 1999
		Spinach, cooked	1000 µg	3 male and 2 female humans, age range 25–45 y	Availability	3.3 %	Gijsbers, Jie, and Vermeer 1996
		Spinach, cooked with added fat	1000 µg	3 male and 2 female humans, age range 25–45 y	Availability	10.6 %	Gijsbers, Jie, and Vermeer 1996
		Broccoli, cooked	377 µg	36 humans, mean age 51 y	Availability	50 %	Booth, Lichtenstein, and Dallal 2002
Biotin	Animal	Meat meal	50 µg	6 male ileostomized pigs	Ileal Digestibility	82 %	Kopinski, Leiboholz, and Bryden 1989b
		Milk casein	22 µg	6 male ileostomized pigs	Ileal Digestibility	95 %	Kopinski, Leiboholz, and Bryden 1989b
Biotin	Plant	Soyabean meal	110 µg per kg dry matter	6 male ileostomized pigs	True (corrected) Ileal Digestibility	55 %	Sauer, Mosenthin, and Ozimek 1988
		Soyabean meal	130 µg	6 male ileostomized pigs	Ileal Digestibility (corrected)	25 %	Kopinski, Leiboholz, and Bryden 1989b
		Wheat	123 µg per kg dry matter	6 male ileostomized pigs	True (corrected) Ileal Digestibility	22 %	Sauer, Mosenthin, and Ozimek 1988
		Wheat (*var.* Banks)	144 µg	6 male ileostomized pigs	Ileal Digestibility (corrected)	18 %	Kopinski, Leiboholz, and Bryden 1989b
		Barley	121 µg per kg dry matter	6 male ileostomized pigs	True (corrected) Ileal Digestibility	4.8 %	Sauer, Mosenthin, and Ozimek 1988
		Barley	188 µg	6 male ileostomized pigs	Ileal Digestibility (corrected)	27 %	Kopinski, Leiboholz, and Bryden 1989b
		Maize	54 µg per kg dry matter	6 male ileostomized pigs	True (corrected) Ileal Digestibility	4.0 %	Sauer, Mosenthin, and Ozimek 1988
		Canola meal	513 µg per kg dry matter	6 male ileostomized pigs	True (corrected) Ileal Digestibility	3.9 %	Sauer, Mosenthin, and Ozimek 1988

Folate	Animal	Beef liver	0.67–1.61 mg DFE	12 male humans, age range 20–35 y	Bioavailability	50 %	Tamura and Stokstad 1973
		Goat liver	1.00 mg DFE	5 male humans, age range 25–35 y	Bioavailability	70 %	Babu and Srikantia 1976
		Whole eggs, cooked	0.89–1.03 mg DFE	7 male humans, age range 25–35 y	Bioavailability	72 %	Babu and Srikantia 1976
		Egg yolks, hard-boiled	0.28 mg DFE	6 male humans, age range 20–35 y	Bioavailability	82 %	Tamura and Stokstad 1973
		Egg yolks, hard-boiled	1.03 mg DFE	6 male humans, age range 20–35 y	Bioavailability	59 %	Tamura and Stokstad 1973
Folate	Plant	Chickpea (Bengal gram)	0.99 mg DFE	6 humans, age range 20–22 y	Bioavailability	71 %	Devadas, Premakumari, and Moorthy 1979
		Chickpea (Bengal gram)	0.96 mg DFE	7 male humans, age range 25–35 y	Bioavailability	69 %	Babu and Srikantia 1976
		Mung bean (green gram)	0.98 mg DFE	6 humans, age range 20–22 y	Bioavailability	71 %	Devadas, Premakumari, and Moorthy 1979
		Mung bean (green gram)	0.99 mg DFE	7 male humans, age range 25–35 y	Bioavailability	55 %	Babu and Srikantia 1976
		Lima beans, green, cooked from frozen	1.02 mg DFE	6 male humans, age range 20–35 y	Bioavailability	96 %	Tamura and Stokstad 1973
		Lima beans, mature, dried, cooked	0.84 mg DFE	6 male humans, age range 20–35 y	Bioavailability	70 %	Tamura and Stokstad 1973
		Spinach	0.99 mg DFE	8 male humans, age range 25–35 y	Bioavailability	63 %	Babu and Srikantia 1976
		Spinach	0.36–0.44 mg DFE	12 humans, age range 48–56 y	Availability	69 %	Konings et al. 2002
		Spinach	0.36 mg DFE	10 male and 10 female humans, mean age 27 y	Availability	77 %	Prinz-Langenohl et al. 1999
		Spinach	0.20 mg DFE	74 male humans, mean age 31 y	Availability	31 %	Hannon-Fletcher et al. 2004
		Romaine lettuce	0.75 mg DFE	13 male humans, age range 20–35 y	Bioavailability	25 %	Tamura and Stokstad 1973
		Green cabbage, raw	0.83–1.09 mg DFE	6 male humans, age range 20–35 y	Bioavailability	47 %	Tamura and Stokstad 1973
		Green cabbage, cooked	0.67–1.03 mg DFE	6 male humans, age range 20–35 y	Bioavailability	47 %	Tamura and Stokstad 1973
		Tomatoes	0.98 mg DFE	7 male humans, age range 25–35 y	Bioavailability	37 %	Babu and Srikantia 1976
		Yeast	0.20 mg DFE	74 male humans, mean age 31 y	Availability	53 %	Hannon-Fletcher et al. 2004
		Brewer's yeast	0.98 mg DFE	8 male humans, age range 25–35 y	Bioavailability	10 %	Babu and Srikantia 1976
		Brewer's yeast	1.40 mg DFE	6 male humans, age range 20–35 y	Bioavailability	60 %	Tamura and Stokstad 1973
		Brewer's yeast extract	0.75 mg DFE	6 male humans, age range 20–35 y	Bioavailability	63 %	Tamura and Stokstad 1973
		Bananas	0.85 mg DFE	6 male humans, age range 20–35 y	Bioavailability	82 %	Tamura and Stokstad 1973
		Bananas	0.87–0.93 mg DFE	8 male humans, age range 25–35 y	Bioavailability	46 %	Babu and Srikantia 1976
		Orange juice	0.84 mg DFE	14 male humans, age range 20–35 y	Bioavailability	31 %	Tamura and Stokstad 1973
		Wheat germ	1.33 mg DFE	6 male humans, age range 20–35 y	Bioavailability	30 %	Tamura and Stokstad 1973
		Finger millet (Raji)	0.98 mg DFE	6 humans, age range 20–22 y	Bioavailability	50 %	Devadas, Premakumari, and Moorthy 1979
		Pearl millet (Bajra)	0.98 mg DFE	6 humans, age range 20–22 y	Bioavailability	54 %	Devadas, Premakumari, and Moorthy 1979
Niacin	Animal	Beef, cooked	45.2 mg	6 female EEV pigs	Ileal Digestibility	69 %	Roth-Maier et al. 2000
		Pork, cooked	66.5 mg	6 female EEV pigs	Ileal Digestibility	65 %	Roth-Maier et al. 2000
Niacin	Plant	Potatoes, boiled	39.5 mg	6 female EEV pigs	Ileal Digestibility	69 %	Roth-Maier et al. 2000
		Wheat	54.1 mg	6 female EEV pigs	Ileal Digestibility	59 %	Roth-Maier et al. 2000
		Wheat	54.1–54.4 mg	5 female EEV pigs	Ileal Digestibility	61 %	Wauer et al. 1999
		Whole-meal bread	20.6 mg	6 female EEV pigs	Ileal Digestibility	40 %	Roth-Maier et al. 2000
Pantothenic acid	Animal	Beef, cooked	3.25 mg	6 female EEV pigs	Ileal Digestibility	65 %	Roth-Maier et al. 2000
		Pork, cooked	5.05 mg	6 female EEV pigs	Ileal Digestibility	74 %	Roth-Maier et al. 2000
		Skimmed milk powder	24.8 mg	6 female ESV pigs	Ileal Digestibility	90 %	Roth-Maier and Kirchgessner 1996
Pantothenic acid	Plant	Potatoes, boiled	10.9 mg	6 female EEV pigs	Ileal Digestibility	70 %	Roth-Maier et al. 2000
		Wheat	14.1 mg	6 female EEV pigs	Ileal Digestibility	81 %	Roth-Maier et al. 2000
		Wheat	11.1–14.1 mg	5 female EEV pigs	Ileal Digestibility	78 %	Wauer et al. 1999
		Whole-meal bread	4.03 mg	6 female EEV pigs	Ileal Digestibility	28 %	Roth-Maier et al. 2000
		Wheat	10.7–15.0 mg	3 female ESV pigs	Ileal Digestibility	40 %	Wauer et al. 1999
		Wheat bran	9.92 mg	6 female ESV pigs	Ileal Digestibility	47 %	Roth-Maier and Kirchgessner 1996
		Maize	3.87 mg	6 female ESV pigs	Ileal Digestibility	20 %	Roth-Maier and Kirchgessner 1996
Riboflavin	Animal	Beef, roasted	1.25 mg	3 female ESV pigs	Ileal Digestibility	31 %	Roth-Maier et al. 1998
		Pork, roasted	1.86 mg	3 female ESV pigs	Ileal Digestibility	58 %	Roth-Maier et al. 1998
		Skimmed milk powder	12.0 mg	6 female ESV pigs	Ileal Digestibility	94 %	Roth-Maier and Kirchgessner 1996
Riboflavin	Plant	Wheat bran	1.43 mg	6 female ESV pigs	Ileal Digestibility	62 %	Roth-Maier and Kirchgessner 1996
		Maize	1.50 mg	6 female ESV pigs	Ileal Digestibility	67 %	Roth-Maier and Kirchgessner 1996

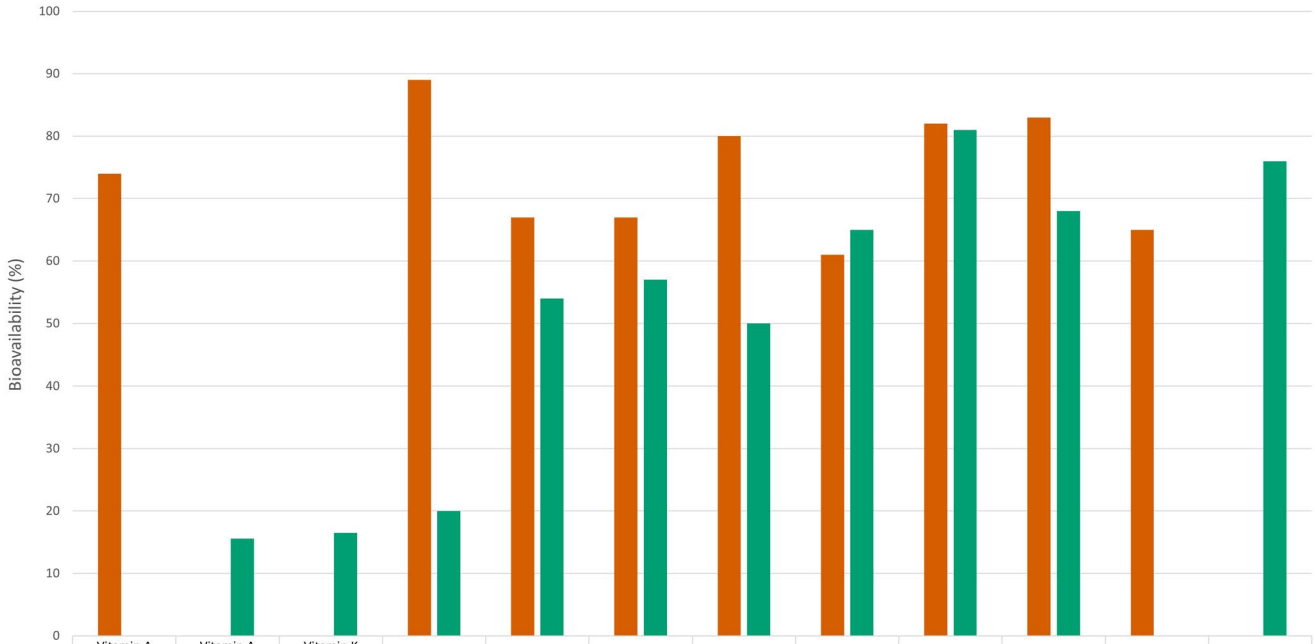
(*Continued*)

Table 2. Continued.

Nutrient	Food source	Food item	Intake	Study population	Process of bioavailability	Bioavailability	Reference
Thiamin	Animal	Beef, roasted	0.71 mg	3 female EEV pigs	Ileal Digestibility	79 %	Roth-Maier et al. 1998
		Pork, roasted	8.54 mg	5 female EEV pigs	Ileal Digestibility	96 %	Roth-Maier et al. 1998
		Milk powder	1.23 mg	6 male EEV pigs	Ileal Digestibility	88 %	Roth-Maier et al. 1999
		Whole eggs, boiled	1.40 mg	3 male EEV pigs	Ileal Digestibility	82 %	Roth-Maier et al. 1999
		Fish, stewed	0.97 mg	6 male EEV pigs	Ileal Digestibility	73 %	Roth-Maier et al. 1999
		Beef, roasted	0.93 mg	3 female ESV pigs	Ileal Digestibility	51 %	Roth-Maier et al. 1998
		Pork, roasted	7.56 mg	3 female ESV pigs	Ileal Digestibility	93 %	Roth-Maier et al. 1998
		Skimmed milk powder	2.60 mg	6 female ESV pigs	Ileal Digestibility	96 %	Roth-Maier and Kirchgessner 1996
Thiamin	Plant	Soyabeans, boiled	4.74 mg	6 male EEV pigs	Ileal Digestibility	94 %	Roth-Maier et al. 1999
		Potatoes, boiled	2.51 mg	4 female EEV pigs	Ileal Digestibility	84 %	Roth-Maier et al. 1998
		White cabbage	1.38 mg	6 male EEV pigs	Ileal Digestibility	81 %	Roth-Maier et al. 1999
		Brewer's yeast	2.54 mg	3 male EEV pigs	Ileal Digestibility	91 %	Roth-Maier et al. 1999
		Bananas	1.33 mg	6 male EEV pigs	Ileal Digestibility	77 %	Roth-Maier et al. 1999
		Wheat	5.18 mg	5 female EEV pigs	Ileal Digestibility	87 %	Roth-Maier et al. 1998
		Wheat	6.26 mg	5 female EEV pigs	Ileal Digestibility	87 %	Roth-Maier et al. 1998
		Wheat bran	2.88 mg	6 male EEV pigs	Ileal Digestibility	92 %	Roth-Maier et al. 1999
		Whole-wheat bread	2.59 mg	4 female EEV pigs	Ileal Digestibility	75 %	Roth-Maier et al. 1998
		Barley	4.72 mg	6 male EEV pigs	Ileal Digestibility	94 %	Roth-Maier et al. 1999
		Rye	4.17 mg	3 male EEV pigs	Ileal Digestibility	84 %	Roth-Maier et al. 1999
		Maize	3.47 mg	2 male EEV pigs	Ileal Digestibility	81 %	Roth-Maier et al. 1999
		Rice, boiled	2.88 mg	6 male EEV pigs	Ileal Digestibility	94 %	Roth-Maier et al. 1999
		Potatoes, boiled	2.51 mg	3 female ESV pigs	Ileal Digestibility	63 %	Roth-Maier et al. 1998
		Wheat	4.80 mg	3 female ESV pigs	Ileal Digestibility	75 %	Roth-Maier et al. 1998
		Wheat	4.95 mg	3 female ESV pigs	Ileal Digestibility	75 %	Roth-Maier et al. 1998
		Wheat bran	2.88 mg	6 female ESV pigs	Ileal Digestibility	91 %	Roth-Maier and Kirchgessner 1996
		Whole-wheat bread	2.59 mg	3 female ESV pigs	Ileal Digestibility	60 %	Roth-Maier et al. 1998
		Maize	3.96 mg	6 female ESV pigs	Ileal Digestibility	87 %	Roth-Maier and Kirchgessner 1996
Vitamin B-6	Animal	Beef, roasted	3.15 mg	5 female EEV pigs	Ileal Digestibility	89 %	Roth-Maier et al. 1998
		Pork, roasted	4.02 mg	5 female EEV pigs	Ileal Digestibility	89 %	Roth-Maier et al. 1998
		Milk powder	2.01 mg	6 male EEV pigs	Ileal Digestibility	84 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Whole eggs, boiled	1.71 mg	3 male EEV pigs	Ileal Digestibility	67 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Fish, stewed	2.61 mg	6 male EEV pigs	Ileal Digestibility	85 %	Roth-Maier, Kettler, and Kirchgessner 2002
Vitamin B-6	Plant	Soyabeans, boiled	3.34 mg	6 male EEV pigs	Ileal Digestibility	76 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Potatoes, boiled	5.60 mg	5 female EEV pigs	Ileal Digestibility	87 %	Roth-Maier et al. 1998
		White cabbage	6.23 mg	3 male EEV pigs	Ileal Digestibility	91 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Brewer's yeast	2.42 mg	3 male EEV pigs	Ileal Digestibility	78 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Bananas	9.10 mg	3 male EEV pigs	Ileal Digestibility	86 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Wheat	2.74 mg	6 female EEV pigs	Ileal Digestibility	69 %	Roth-Maier et al. 1998
		Wheat	2.77 mg	4 female EEV pigs	Ileal Digestibility	69 %	Roth-Maier et al. 1998
		Wheat bran	3.30 mg	6 male EEV pigs	Ileal Digestibility	56 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Whole-grain bread	2.18 mg	4 female EEV pigs	Ileal Digestibility	71 %	Roth-Maier et al. 1998
		Barley	3.91 mg	6 male EEV pigs	Ileal Digestibility	63 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Rye	1.81 mg	3 male EEV pigs	Ileal Digestibility	51 %	Roth-Maier, Kettler, and Kirchgessner 2002

		Maize	3.53 mg	2 male EEV pigs	Ileal Digestibility	67 %	Roth-Maier, Kettler, and Kirchgessner 2002
		Brown rice, boiled	1.62 mg	6 male EEV pigs	Ileal Digestibility	16 %	Roth-Maier, Kettler, and Kirchgessner 2002
Vitamin B-12	Animal	Chicken meat (100 g)	0.42–0.64 µg	3 humans	Fecal Digestibility	65 %	Doscherholmen, McMahon, and Ripley 1978
		Chicken meat (200 g)	0.84–1.28 µg	3 humans	Fecal Digestibility	62 %	Doscherholmen, McMahon, and Ripley 1978
		Chicken meat (300 g)	1.26–1.92 µg	3 humans	Fecal Digestibility	61 %	Doscherholmen, McMahon, and Ripley 1978
		Sheep mutton meat (100 g)	0.95 µg	7 male humans	Availability	65 %	Heyssel et al. 1966
		Whole eggs, fried	0.50–0.56 µg	18 humans	Fecal Digestibility	76 %	Doscherholmen, McMahon, and Ripley 1975
		Whole eggs, soft-boiled	0.50–0.56 µg	18 humans	Fecal Digestibility	76 %	Doscherholmen, McMahon, and Ripley 1975
		Whole eggs, scrambled	0.50–0.56 µg	18 humans	Fecal Digestibility	73 %	Doscherholmen, McMahon, and Ripley 1975
		Egg yolks, scrambled	0.50–0.56 µg	18 humans	Fecal Digestibility	64 %	Doscherholmen, McMahon, and Ripley 1975
		Fish fillets (50 g)	1.95–2.18 µg	3 humans	Fecal Digestibility	42 %	Doscherholmen, McMahon, and Economon 1981
Vitamin C	Plant	Mustard greens, cooked	57 mg	3 male and 9 female humans	Availability	73 %	Hollinger 1948
		Broccoli, raw	109 mg	23 male humans, mean age 40 y	Availability	58 %	Mangels et al. 1993
		Broccoli, cooked	108 mg	23 male humans, mean age 40 y	Availability	78 %	Mangels et al. 1993
		Green cabbage, raw	85 mg	3 male and 1 female humans	Availability	97 %	Clayton and Borden 1943
		Potatoes, baked	75 mg	3 male and 1 female humans	Availability	81 %	Clayton and Borden 1940
		Potatoes, mashed	50 mg	5 male humans, mean age 24 y	Availability	54 %	Kondo et al. 2012
		Potato chips	50 mg	5 male humans, mean age 24 y	Availability	53 %	Kondo et al. 2012
		Tomato juice	85 mg	3 male and 1 female humans	Availability	89 %	Clayton and Borden 1943
		Orange segments	109 mg	22 male humans, mean age 40 y	Availability	66 %	Mangels et al. 1993
		Orange juice	110 mg	22 male humans, mean age 40 y	Availability	74 %	Mangels et al. 1993
		Orange juice	50 mg	5 female humans	Availability	82 %	Todhunter, Robbins, and McIntosh 1942
		Strawberries	50 mg	5 female humans	Availability	86 %	Todhunter, Robbins, and McIntosh 1942
		Red raspberries	60 mg	7 female humans, mean age 31 y	Availability	77 %	Todhunter and Fatzer 1940
		Papayas	75 mg	3 male and 3 female humans, age range 29–34 y	Availability	86 %	Hartzler 1945
		Guava juice	75 mg	3 male and 3 female humans, age range 29–34 y	Availability	90 %	Hartzler 1945
		Gold kiwifruit	200 mg	9 male humans, mean age 24 y	Availability	78 %	Carr, Bozonet, and Vissers 2013

RE, Retinol Equivalent, whereby 1 mg of RE = 1 mg of retinol = 6 mg of β-carotene.
DFE, Dietary Folate Equivalent, whereby 1 mg DFE = 1 mg of food folate = 0.6 mg of folic acid from fortified food or as a dietary supplement consumed with food.
EEV, end-to-end ileo-rectal anastomosis.
ESV, end-to-side ileo-rectal anastomosis.



	Vitamin A (retinol)	Vitamin A (β-carotene)	Vitamin K (phylloquinone)	Biotin	Folate	Niacin	Pantothenic acid	Riboflavin	Thiamin	Vitamin B-6	Vitamin B-12	Vitamin C
Animal-based foods	74			89	67	67	80	61	82	83	65	
Plant-based foods		15.6	16.5	20	54	57	50	65	81	68		76

Figure 1. Estimated bioavailability (%) of vitamins in foods sourced from animals and plants.

1991; Goodman et al. 1966; Reboul 2013). Retinol absorption mainly occurs *via* a carrier-mediated, saturable transporter, and carotenoids are absorbed mostly by passive diffusion (Blomhoff et al. 1991; Goodman et al. 1966; Reboul 2013). Within the enterocyte, some of the absorbed β-carotene may be cleaved and converted to retinol and retinyl esters or β-apo-carotenals. Retinol, retinyl esters, β-apo-carotenals, and β-carotene, are incorporated into chylomicrons to be transported by the lymphatic system to the liver for retinol metabolism and storage (Blomhoff et al. 1991; Goodman et al. 1966; Reboul 2013). Retinol-binding proteins are involved in the release of free retinol from hepatic retinyl esters for distribution to target tissues (Blomhoff et al. 1991; Goodman et al. 1966; Reboul 2013). Vitamin A not absorbed from the gastrointestinal tract is eliminated in feces as biliary metabolites, and retinol metabolites are also excreted in the urine (Biesalski 1997; Blomhoff et al. 1991; Castenmiller and West 1998; de Pee and West 1996; Goodman et al. 1966; Parker 1997; Parker et al. 1999).

Vitamin A content in food

Vitamin A is generally expressed as retinol equivalents (REs) to account for the different forms of vitamin A and the lower absorption efficacy of provitamin A carotenoids and their bioconversion to retinol (FAO 1998; WHO and FAO 1967). Based on rat growth bioassays, one unit of RE is defined as the equivalent amount of retinol that can be obtained from the provitamin A carotenoids, namely 6 units of retinol from β-carotene, or 12 units of retinol from α-carotene, γ-carotene, β-cryptoxanthin and other provitamin A carotenoids (Biesalski 1997; FAO 1988; Olson 1987a; WHO and FAO 1967, 2004). Vitamin A was previously expressed as International Units (IU) of retinol, whereby 1 IU retinol is equivalent to 0.3 unit of RE (Biesalski 1997; WHO and FAO 2004). In the United States of America, where the intake of provitamin A carotenoids is higher and where their biological activities are assumed to be two-fold lower, vitamin A is usually expressed as retinol activity equivalents (RAEs), whereby 1 unit of RAE is equivalent to 1 unit of retinol, 12 units of β-carotene, or 24 units of other provitamin A carotenoids (IOM (Institute of Medicine, US) 2001). In this review, the dietary intakes of vitamin A are expressed in terms of RE, using the conversion factors of 1:1 for retinol, 1:6 for β-carotene, and 1:12 for other provitamin A carotenoids. The retinol equivalence of different forms of carotenoids from different foods remains contentious.

Determination of the bioavailability of dietary vitamin A and supplementary vitamin A in purified form

The bioavailability of dietary vitamin A has been determined through the measurement of retinol, retinyl esters, β-carotene, α-carotene, and other provitamin A carotenoids in the blood, ileal effluent, and feces.

Several studies have compared the relative blood response of dietary vitamin A to synthetic vitamin A. Pure preformed vitamin A (retinol, retinyl esters) given with dietary oil to healthy human subjects, has been estimated to be 80% bioavailable (Edwards et al. 2001, 2002; Goodman et al. 1966; IOM (Institute of Medicine, US) 2001; Olson 1987a; WHO and FAO 1967, 2004; Wolf 2002), and this value is often used as a baseline to calculate absolute bioavailability. There was a wide variability (3 to 100%) reported for the bioavailability of purified provitamin A carotenoids, particularly β-carotene (Castenmiller and West 1998; de Pee and West 1996; Faulks et al. 1997; Haskell 2012; IOM (Institute of Medicine, US) 2001; Olson 1987a;

Parker 1997; Parker et al. 1999; van Lieshout, West, and van Breemen 2003; WHO and FAO 2004), which may possibly be attributable to the presence of dietary fat and intake doses (Blomhoff et al. 1991; Goodman et al. 1966; Reboul 2013). For a usual optimal intake of 1–4 mg of β-carotene per meal, 6 units of β-carotene are equivalent to 1 unit of retinol or RE. However, at lower intakes (<1 mg of β-carotene per meal) when β-carotene is absorbed more efficiently, 4 units of β-carotene may yield 1 unit of retinol, while at higher intakes (>4 mg of β-carotene per meal) when the system may be saturated, 10 units of β-carotene is needed to give 1 equivalent unit of retinol (de Pee and West 1996; FAO 1988). The bioavailability estimates for provitamin A carotenoids reflect both the absorption efficiency of carotenes and the proportion of carotenes converted to retinol or retinyl esters. Based on the assumption that the absorption and conversion efficiencies of pure all-*trans*-β-carotene consumed in oil, is half that of pure retinol (de Pee and West 1996; Goodman et al. 1966; IOM (Institute of Medicine, US) 2001; Olson 1987a; WHO and FAO 1967, 2004), pure β-carotene is considered to be 40% bioavailable.

The factors influencing the bioavailability of dietary provitamin A carotenoids have been identified under the acronym "SLAMANGHI" or "SLAMENGHI", where the letters stand for: Species of carotenoid, molecular Linkage, Amount of carotene consumed in a meal, dietary Matrix in which the carotenoid is incorporated, Absorption modifiers or Effectors of absorption and bioconversion, Nutrient status of the subject, Genetic factors, Host-related factors, and Interactions (de Pee and West 1996). Each factor of SLAMENGHI also affects the efficiency of absorption of vitamin D (Borel, Caillaud, and Cano 2015) and vitamin E (Borel, Preveraud, and Desmarchelier 2013). Data estimates of the bioavailability of vitamin A in food depend on the form of the vitamin A, the dietary matrix, food processing, and the experimental method used.

Bioavailability of vitamin A (β-carotene) in mixed diets

In a human study measuring β-carotene in plasma in response to ingested β-carotene, the availability of β-carotene in a mixed vegetable and fruit diet (5.10 mg β-carotene, 0.85 mg RE), relative to supplementary purified β-carotene, was 14% (van Het Hof et al. 1999a). Based on the assumption that purified β-carotene is 40% bioavailable, an absolute availability of β-carotene of 5.6% was calculated.

Bioavailability of vitamin A (retinol) in animal-sourced foods

Two human studies measured the amount of retinol and retinyl esters in blood plasma and determined the availability of vitamin A in food liver (3–150 mg RE), relative to that of supplementary vitamin A (Buss et al. 1994; van Vliet et al. 2001). The relative availability of vitamin A in 50 and 150 mg of fried beef calf liver (50–150 mg RE) was 105 and 94%, respectively (Buss et al. 1994). Consumption of 3.0, 7.5, and 15.0 mg of vitamin A in liver paste (3–15 mg RE) resulted in relative vitamin A availability of 54, 77, and 123%, respectively (van Vliet et al. 2001). Based on the assumption that purified preformed vitamin A retinol is 80% bioavailable, the absolute mean apparent availability of vitamin A was calculated to be 68% for liver paste and 80% for cooked beef liver (Table 2).

A human study showed that the absolute apparent bioavailability of retinol following the consumption of whole (3.6% fat) milk (0.14–0.26 mg RE) was 16.4% (Herrero-Barbudo et al. 2006). The data were highly variable and it is unclear from the study that all retinol in the triglyceride-rich lipoprotein fraction was determined. Nor did the study include an external control (pure retinol) and the values are thus likely to underestimate absolute availability. Consequently, the absorption values were considered to be more qualitative than quantitative. Interestingly, the plasma response of retinyl esters following consumption of whole (3.6% fat) milk fortified with vitamin A (0.63–1.19 mg RE) and skimmed (0.2% fat) milk fortified with vitamin A (0.31–0.57 mg RE) was lower than that for the non-fortified whole milk, despite the higher vitamin A content in the vitamin A-fortified milks (Herrero-Barbudo et al. 2006).

Bioavailability of vitamin A (β-carotene) in plant-based foods

Livny et al. (2003) determined the mass balance (food intake corrected for blood and ileal effluent excretion) of β-carotene in ileostomates, and found that the apparent availability of β-carotene in raw chopped carrots (15.00 mg β-carotene, 2.50 mg RE) was 41%, and 65% for cooked pureed carrots (15.00 mg β-carotene, 2.50 mg RE) (Table 2). In another study of similar design, Faulks et al. (2004) demonstrated that the apparent availability of β-carotene in cooked whole leaf spinach (10.00 mg β-carotene, 1.67 mg RE) and cooked finely chopped spinach (10.00 mg β-carotene, 1.67 mg RE) was 26 and 23%, respectively (Table 2).

Several studies compared the blood β-carotene response to dietary β-carotene with that following the consumption of similar doses of supplementary purified β-carotene (Brown et al. 1989; Castenmiller et al. 1999; Huang et al. 2000: Micozzi et al. 1992; van Het Hof et al. 1999b). The relative availability of β-carotene was found to be 17.2% for cooked from frozen carrots (29.00 mg β-carotene, 4.83 mg RE) (Brown et al. 1989), 18.2% for cooked from frozen carrots (29.00 mg β-carotene, 4.83 mg RE) (Micozzi et al. 1992), 33% for cooked stir-fried shredded carrots (12.01 mg β-carotene, 2.00 mg RE) (Huang et al. 2000), 37% for cooked deep-fried mashed sweet potato balls (12.01 mg β-carotene, 2.00 mg RE) (Huang et al. 2000), 26% for cooked stir-fried whole water spinach (water convolvulus) leaves (12.01 mg β-carotene, 2.00 mg RE) (Huang et al. 2000), 18.2% for cooked whole leaf spinach (23.80 mg β-carotene, 3.97 mg RE) (van Het Hof et al. 1999b), 18.5% for cooked chopped minced spinach (24.60 mg β-carotene, 4.10 mg RE) (van Het Hof et al. 1999b), 5.1% for cooked whole leaf spinach (10.40 mg β-carotene, 1.73 mg RE) (Castenmiller et al. 1999), 6.4% for cooked minced spinach (8.80 mg β-carotene, 1.47 mg RE) (Castenmiller et al. 1999), 9.5% for cooked liquefied spinach (9.00 mg β-carotene, 1.50 mg RE, 28.2 g dietary fiber)

(Castenmiller et al. 1999), and 9.3% when dietary fiber was added to cooked enzymatically liquefied spinach (8.80 mg β-carotene, 1.47 mg RE, 31.3 g dietary fiber) (Castenmiller et al. 1999). Based on the assumption that supplementary purified β-carotene is 40% bioavailable, the absolute apparent availability of β-carotene was estimated to be 9.1% for cooked carrots, 14.8% for sweet potatoes, 4.5% for spinach, and 10.4% for water spinach (Table 2).

Using the human oro-fecal balance of β-carotene, the apparent absorption of β-carotene was found to be 14% for a mixed vegetable and fruit diet (Van Loo-Bouwman et al. 2009, 2010), 46% for sweet potatoes (James and Hollinger 1954), 81% for carrots (Rao and Rao 1970), 76% for Amaranth green leafy vegetables (Rao and Rao 1970), and 90% for papaya fruit (Rao and Rao 1970). These absorption values based on fecal collection may be misleading and need to be interpreted with caution due to the potential interference from the microbial metabolism of carotenoids by intestinal bacteria.

Comparison of vitamin A bioavailability between animal- and plant-based foods

The bioavailability of vitamin A in animal- and plant-based foods is difficult to compare due to differences in the form of vitamin A found in animal- and plant-sourced foods. The mean bioavailability of preformed vitamin A retinol in liver was found to be 74%, and the mean bioavailability of provitamin A carotenoid β-carotene in vegetables was 15.6%, and ranged from 2.0 to 65%. In general, β-carotene in plant foods appears to be less bioavailable than retinol in animal foods (Figure 1), though the number of observations, especially in animal-sourced foods, is low. It has been recognized that there are differences in the efficiency of conversion from provitamin A carotenoids (carotenes) to preformed vitamin A retinol. An attempt to take this information into account is to express vitamin A in terms of retinol equivalent (RE), whereby the biological activity of β-carotene is one-sixth of that of retinol, and one-twelfth for the other provitamin A carotenoids. Using RE must be interpreted with caution. Using RE to interpret the bioavailability (absorption and bioconversion) of vitamin A in foods may be misleading. The bioavailability estimates of vitamin A in foods sourced from animals and plants cannot be directly compared and it may be more meaningful to use retinol and β-carotene values separately, to provide comparable bioavailability data in animal- and plant-based foods.

Vitamin D

Vitamin D absorption and utilization

Vitamin D is a fat-soluble vitamin and plays an important role in bone, muscle, and nervous functions, and modulates the absorption and re-absorption in the kidney of calcium and phosphorus (Bates and Heseker 1994; IOM (Institute of Medicine, US) 2011; van den Berg 1997d; WHO and FAO 2004). Cereal grains, vegetables, fungi (e.g., mushrooms), and fruits naturally contain ergosterol, that is converted to vitamin D2 (ergocalciferol), upon exposure to ultraviolet (UV) radiation (Borel, Caillaud, and Cano 2015; Cashman 2012; Holmes and Kummerow 1983; Jäpelt and Jakobsen 2013; van den Berg 1997d). The main form of vitamin D obtained from the diet is vitamin D3 (cholecalciferol), which is the irradiation product of the steroid 7-dehydrocholesterol and mostly occurs in animal-derived foods, such as fatty fish, meat, milk and dairy products, and eggs (Borel, Caillaud, and Cano 2015; Cashman 2012; Holmes and Kummerow 1983; Jäpelt and Jakobsen 2013; Schmid and Walther 2013; van den Berg 1997d). The amount of vitamin D naturally found in milk relies on the level of exposure of the animal to solar UV radiation and the content of vitamin D in the diet of the animal (Jakobsen and Saxholt 2009; Kurmann and Indyk 1994; Schmid and Walther 2013). Most vitamin D in milk is attributed to fortification. The amount of vitamin D naturally present in eggs may be influenced by the concentration of supplementary vitamin D consumed by the laying hens (Mattila, Valkonen, and Valaja 2011; Mattila et al. 1999). Vitamin D3 produced in the human skin following adequate sunlight exposure may sufficiently meet vitamin D requirements (Cashman 2012; Holmes and Kummerow 1983; Jäpelt and Jakobsen 2013; van den Berg 1997d). Under low exposure to UV sunlight, it has been recommended that humans consume at least 10 µg of vitamin D (Cashman 2012; Holmes and Kummerow 1983; IOM (Institute of Medicine, US) 2011; WHO and FAO 2004). However, natural food sources provide less than 1 µg of naturally occurring vitamin D, so dietary supplements or foods commonly fortified with vitamin D, such as milk and margarine, are common sources of vitamin D (Cashman 2012; Holmes and Kummerow 1983; van den Berg 1997d).

Dietary vitamin D is solubilized within mixed micelles in the duodenum and this process is stimulated by the presence of dietary fat. The micelles are absorbed in the jejunum into chylomicrons, which transport the vitamin D in the lymph to the systemic circulation (Borel, Caillaud, and Cano 2015; Holmes and Kummerow 1983; Reboul 2015). The major circulating form of vitamin D is the biologically active metabolite 25-hydroxy-vitamin D (25(OH)D), which can be stored in the adipose tissue, muscle, and liver (Borel, Caillaud, and Cano 2015; Holmes and Kummerow 1983; Jäpelt and Jakobsen 2013; Reboul 2015; Seamans and Cashman 2009; van den Berg 1997d; Whyte et al. 1979). It is unclear if vitamin D2 (ergocalciferol) is as effective as vitamin D3 (cholecalciferol) in increasing and maintaining circulating levels of the bioactive 25(OH)D (Cashman 2012; Heaney et al. 2011; Holick et al. 2008; Lehmann et al. 2013; Rapuri, Gallagher, and Haynatzki 2004; Seamans and Cashman 2009; Trang et al. 1998; Tripkovic et al. 2012; van den Berg 1997d; Whyte et al. 1979).

Vitamin D content in food

Vitamin D can be expressed in international units (IU), whereby 1 IU of vitamin D is 0.025 µg of vitamin D or 0.005 µg of 25(OH)D (IOM (Institute of Medicine, US) 2011; van den Berg 1997d; WHO and FAO 2004).

Determination of the bioavailability of dietary vitamin D and supplementary vitamin D in purified form and in food

The bioavailability of vitamin D in natural or fortified food sources has been determined by comparing the response of circulating vitamin D with that from a vitamin D supplement, which is assumed to be 75–85% bioavailable (Thompson, Lewis, and Booth 1966).

Studies have determined the uptake of supplementary vitamin D following the consumption of fortified cheese (Wagner et al. 2008), fortified breads (Natri et al. 2006), and fortified orange juice (Biancuzzo et al. 2010), relative to a vitamin D supplement. Wagner et al. (2008) found that the relative availability of supplementary vitamin D given with fortified regular-fat (33% fat) and low-fat (7% fat) Cheddar cheese (100 µg vitamin D3 cholecalciferol, 4000 IU vitamin D) was 114%. The mean relative availability of supplementary vitamin D in breads fortified with vitamin D, low-fiber (3 g per 100 g) wheat bread (10.8 µg vitamin D, 432 IU vitamin D) and high-fiber (12 g per 100 g) sour dough rye bread (12.3 µg vitamin D, 492 IU vitamin D), was 80% (Natri et al. 2006). In a human clinical trial over 11 wk, Biancuzzo et al. (2010) studied which form of supplementary vitamin D would be more bioavailable following the daily consumption of a glass of orange juice fortified with water-soluble vitamin D (25 µg, 1000 IU). When incorporated in orange juice, supplementary vitamin D3 (cholecalciferol) had a relative availability of 98%, and supplementary vitamin D2 (ergocalciferol) a relative availability of 108%, with an average estimated relative availability of supplementary vitamin D of 103% (Biancuzzo et al. 2010). Based on the assumption that supplementary purified vitamin D is 80% bioavailable (Thompson, Lewis, and Booth 1966), the absolute apparent availability of supplementary vitamin D in vitamin D-fortified foods was estimated to be 79%.

Bioavailability of vitamin D (ergocalciferol) in animal-sourced foods

In a review, van den Berg (1997d) reported that the relative availability of naturally occurring vitamin D2 (ergocalciferol) in pig meat (10 µg vitamin D2, 400 IU vitamin D) was 60% that of a vitamin D2 supplement, based on the increase in serum 25-hydroxy-vitamin D2 (25(OH)D2) over a 6 week period in human participants. Assuming that the bioavailability of 100 µg of supplementary vitamin D is 77% (Thompson, Lewis, and Booth 1966), the absolute apparent availability of vitamin D in pork was estimated to be 46%.

Bioavailability of vitamin D (ergocalciferol) in plant-based foods

Brown button mushrooms cultivated in the dark contain very low concentrations of naturally occurring vitamin D2 (ergocalciferol) (0.18 µg per 100 g fresh weight), and can be enriched with more vitamin D when irradiated with ultraviolet (UV) light (491 µg per 100 g fresh weight) (Urbain et al. 2011). When a soup (4.2% fat) containing the UV-irradiated vitamin D-enriched mushrooms (700 µg vitamin D2 ergocalciferol, 28000 IU vitamin D) was consumed, the serum concentrations of the biologically active form of ergocalciferol (25(OH)D2) increased to a similar extent to those associated with the ingestion of 700 µg of vitamin D2 supplement. The relative availability of vitamin D from mushrooms was determined to be 83%, and based on the assumption that 500–1000 µg doses of pure vitamin D are 80% bioavailable (Thompson, Lewis, and Booth 1966), the absolute apparent availability of vitamin D from UV-irradiated mushrooms was calculated to be 66%.

Comparison of vitamin D bioavailability between animal- and plant-based foods

Vitamin D is synthesized in the human skin upon exposure to sunlight and this synthesis may in some cases, under ample solar exposure, be sufficient to meet the daily requirements for vitamin D. Studies comparing the relative bioavailability of naturally occurring vitamin D in food to that of supplementary vitamin D are lacking. Although the bioavailability of vitamin D in pork was estimated to be 46% (van den Berg 1997d), this data needs to be interpreted with caution as the review provided few details of the clinical study. It was estimated that the bioavailability of vitamin D in vitamin D-enriched brown button mushrooms exposed to ultraviolet irradiation was 66% (Urbain et al. 2011). There are insufficient data to make a comparison of the bioavailability of naturally occurring vitamin D in animal- and plant-based foods.

Vitamin E

Vitamin E absorption and utilization

Vitamin E is a fat-soluble vitamin, that includes four tocopherols (α, β, γ, δ) and four tocotrienols (α, β, γ, δ) (Bates and Heseker 1994; Borel, Preveraud, and Desmarchelier 2013; Cohn 1997; IOM (Institute of Medicine, US) 2000; Jiang 2014; WHO and FAO 2004). Most can be converted to the most biologically active form of vitamin E, α-tocopherol, that has a methyl group attached to an asymmetric carbon atom at positions 2, 4, and 8 (Borel, Preveraud, and Desmarchelier 2013; Cohn 1997; Jiang 2014). This *d*-α-tocopherol or RRR-α-tocopherol is mostly found in the systemic circulation and stored in the body (Borel, Preveraud, and Desmarchelier 2013; Cohn 1997; Reboul 2017; Reboul et al. 2006). Vitamin E, as α-tocopherol, mainly functions as an anti-oxidant by protecting polyunsaturated fatty acids present in body cells from being broken down by oxidation (Borel, Preveraud, and Desmarchelier 2013; Cohn 1997; Jiang 2014). Food sources that are naturally rich in vitamin E include cereal grains, nuts, seeds, vegetable oils, and some vegetables and fruits (Bauernfeind 1977; Chun et al. 2006; Cohn 1997; Jiang 2014; McLaughlin and Weihrauch 1979; Piironen et al. 1986). Margarines that are high in polyunsaturated fats are often fortified with vitamin E. Vitamin E is also found in small amounts in meat, dairy products, eggs, and fatty fish, but this is mostly dependent on the amount of vitamin E or supplementary vitamin E in the animal's diet (Bauernfeind 1977; McLaughlin and Weihrauch 1979; Piironen et al. 1985).

The absorption of α-tocopherol requires the presence of dietary fat and involves emulsification with food fats in the stomach. Dietary α-tocopherol is incorporated in mixed micelles to be solubilized across the unstirred water layer coating the brush border membrane of the small intestine, and absorbed either by passive diffusion or with the help of cholesterol transporters in the small intestine. Absorbed α-tocopherol enters the blood *via* the lymphatic system incorporated with chylomicrons (Borel, Preveraud, and Desmarchelier 2013; Cohn 1997; Jiang 2014; Reboul 2017; Reboul et al. 2006).

Vitamin E content in food

Vitamin E is often described in terms of α-tocopherol equivalents (α-TEs), whereby 1 mg of α-TE equals 1 mg of RRR-α-tocopherol, 0.5 mg of β-tocopherol, 0.1 mg of γ-tocopherol, 0.3 mg of α-tocotrienol, or 0.74 mg of synthetic α-tocopherol from fortified foods and dietary supplements (IOM (Institute of Medicine, US) 2000; WHO and FAO 2004). It has been argued that vitamin E should be given in units of α-tocopherol only, and that 1 unit of α-TE can be converted to α-tocopherol using a factor of 0.8 (IOM (Institute of Medicine, US) 2000; WHO and FAO 2004).

Determination of the bioavailability of dietary vitamin E and supplementary vitamin E in purified form and in food

Isotope labeling was mostly used to determine the bioavailability of vitamin E, and most studies assessed the amount of α-tocopherol circulating in blood. Human studies have evaluated the uptake of supplementary vitamin E, when consumed with oil (Kelleher and Losowsky 1968; MacMahon and Neale 1970; Novotny et al. 2012) and when added to collard greens (Traber et al. 2015), apples (Bruno et al. 2006), and ready-to-eat wheat-based breakfast cereals (Leonard et al. 2004). The mean bioavailability of supplementary purified vitamin E, given with oil, was estimated to be 75%, based on a multi-compartmental kinetic study and two balance studies, involving normal human participants who provided blood, urine, and fecal samples (Kelleher and Losowsky 1968; McMahon and Neale 1970; Novotny et al. 2012). While consumption of vitamin E-fortified breakfast cereals (400 mg α-tocopherol or α-TE) resulted in a higher plasma response of isotopically labeled (d_9) α-tocopheryl acetate than that after ingestion of a purified vitamin E capsule, there was only a small amount of fat co-ingested with the supplement and fortified breakfast cereal, and the study did not report the percentage availability (Leonard et al. 2004). It was estimated that isotopically labeled (^2H) supplementary vitamin E (α-tocopheryl acetate) consumed in the presence of dietary fat (1.6 g) was 24% available from the ingestion of fortified collard greens (9.2 mg α-tocopherol or α-TE) (Traber et al. 2015). The estimated availability of supplementary deuterium labeled α-tocopherol added to apples increased from 10% when no fat was consumed with the α-tocopherol-enriched apples (8.0 mg α-tocopherol or α-TE), to 20% with 2.4 g of fat (7.3 mg α-tocopherol or α-TE), and 33% with 11 g of fat (6.5 mg α-tocopherol or α-TE) (Bruno et al. 2006). Supplementary vitamin E consumed in the presence of dietary fat with fortified collard greens (Traber et al. 2015) and fortified apples (Bruno et al. 2006), was about 26% bioavailable.

Bioavailability of vitamin E in plant-based foods

In a pilot ileal digestibility study involving two female human ileostomy patients, Mandalari et al. (2008) found that the apparent availability of naturally occurring vitamin E in almonds (5.4 mg of vitamin E) was 54%.

Comparison of vitamin E bioavailability between animal- and plant-based foods

In a human oro-ileal balance study, the bioavailability of naturally occurring vitamin E in almonds was estimated to be 54% (Mandalari et al. 2008), but this estimate was based on two female ileostomates only, and further studies are needed. The concentration of vitamin E in animal-sourced foods is dependent on the amount of vitamin E consumed by the animal (Bauernfeind 1977; McLaughlin and Weihrauch 1979; Piironen et al. 1985). To the best of our knowledge, there are no reported studies in human subjects or pig as an animal model for adult humans, on the bioavailability of vitamin E in animal-based foods. A paucity of clinical studies means that the bioavailability of naturally occurring vitamin E in food remains unknown, and it is not possible to provide a comparison of vitamin E bioavailability between animal- and plant-based foods.

Vitamin K

Vitamin K absorption and utilization

Vitamin K is a fat-soluble vitamin essential for its role in blood clotting and bone metabolism (Bates and Heseker 1994; IOM (Institute of Medicine, US) 2001; Olson 1987b; Shearer, Fu, and Booth 2012; WHO and FAO 2004). All forms of vitamin K comprise the 2-methyl-1,4-naphthoquinone nucleus attached at C-3 to a naturally occurring phytyl group for phylloquinone (vitamin K1), or a side chain composed of 6–10 unsaturated isoprene units for menaquinone (vitamin K2) (Basset et al. 2017; Beulens et al. 2013; Booth 2012; Shearer 1992; Shearer, Fu, and Booth 2012; Shearer, McBurney, and Barkhan 1974). Menadione (vitamin K3) is a fat-soluble synthetic compound that contains the 2-methyl-1,4-napthoquinone structure with no side chain, and can be converted to biologically active menaquinones in body tissues (Beulens et al. 2013; Booth 2012; Olson 1987b; Shearer 1992; Shearer, Fu, and Booth 2012). While most animal-sourced foods contain both phylloquinone and menaquinone, plant-based foods, mainly green leafy vegetables and vegetable oils, provide mainly phylloquinone, and bacteria in the human large intestine can also synthesize menaquinone (Basset et al. 2017; Beulens et al. 2013; Booth 2012; Booth and Suttie 1998; Hollander, Muralidhara, and Rim 1976; Olson 1987b; Parrish, Sheppard, and Sheppard 1980; Shearer 1992; Shearer, Fu, and Booth 2012).

The absorption of vitamin K requires the presence of dietary fat and the action of pancreatic juices in the duodenum for solubilization within mixed micelles (Hollander, Rim, and Muralidhara 1977; Olson 1987b; Shearer, Fu, and

Booth 2012; Shearer, McBurney, and Barkhan 1974). Following absorption mainly through the jejunum and ileum (Hollander, Rim, and Muralidhara 1977) and minimally from the colon (Hollander, Muralidhara, and Rim 1976), vitamin K is transported *via* the lymphatic route into the systemic circulation (Olson 1987b; Shearer, Fu, and Booth 2012; Shearer, McBurney, and Barkhan 1974). Vitamin K is mobilized in the liver before being distributed to body tissues or converted to water-soluble metabolites, which are either secreted into the bile for fecal excretion, or excreted in the urine (Olson 1987b; Shearer, Fu, and Booth 2012; Shearer, McBurney, and Barkhan 1974).

Determination of the bioavailability of dietary vitamin K and supplementary vitamin K in purified form

The bioavailability of vitamin K (phylloquinone) from food sources was assessed by determining the circulating levels of phylloquinone, based either on appearance in the blood of isotopically labeled phylloquinone or the plasma levels of ingested dietary phylloquinone relative to purified phylloquinone. Synthetic purified phylloquinone (vitamin K1) is considered to be 80% bioavailable (Shearer, McBurney, and Barkhan 1974).

Bioavailability of vitamin K (phylloquinone) in mixed diets

The availability of isotopically labeled (^{13}C) phylloquinone (vitamin K1) from three meals was measured from area under the plasma curve values over 8 h in twelve healthy human participants (Jones et al. 2009). The three test meals, representing the commonly consumed dietary patterns in the United Kingdom, were beef lasagna for an animal- and dairy-oriented meal (higher than average consumption of red meat and saturated fats, 33.0 µg phylloquinone), fish- and dairy-oriented pie meal for a cosmopolitan meal (higher than average consumption of vegetables, fruits, whole grains, fish, and dairy products, 26.3 µg phylloquinone), and chicken and dairy meal provided with baked beans and potato chips for a convenience meal (higher than average consumption of fast foods and refined cereals, and lower than average consumption of vegetables, fruits, and whole-grain cereals, 19.9 µg phylloquinone). The study showed statistically significant differences in the effects of meal food matrix and meal composition of the food material, on the uptake of phylloquinone, relative to the absorption of 20 µg of tracer phylloquinone consumed together with the three meals. The overall relative bioavailability of the meal and matrix effects was 20% for the animal-oriented meal (beef lasagna), 46% for the cosmopolitan meal (fish pie), and 100% for the convenience meal (chicken pie with beans and chips) (Jones et al. 2009).

Bioavailability of vitamin K (phylloquinone) in plant-based foods

Several studies have investigated the availability of phylloquinone (vitamin K1) in vegetables. In a kinetic study using a three-compartment (gastrointestinal tract, blood plasma, body tissue pool) model of the estimated fraction of labeled (^{13}C) phylloquinone, Novotny et al. (2010) found that the mean availability of phylloquinone in cooked kale (119 µg phylloquinone per 2000 kcal or 8.4 MJ) ingested with 30 g of peanut or safflower oil, was 4.7% (Table 2), and ranged from 1.0 to 14.0%. Comparing the blood response to food phylloquinone with that of supplementary purified phylloquinone, the relative availability of phylloquinone ranged from 4.1% for boiled spinach (1000 µg phylloquinone) (Gijsberg, Jie, and Vermeer 1996), 13.3% for boiled spinach consumed with 25 g of butter (1000 µg phylloquinone) (Gijsberg, Jie, and Vermeer 1996), 17.4% for raw spinach (495 µg phylloquinone, 25% of energy from fat) (Garber et al. 1999), and 63% for microwaved broccoli (377 µg phylloquinone) (Booth, Lichtenstein, and Dallal 2002). The higher relative availability of phylloquinone from cooked broccoli may be partly because of its higher extraction and loose association with the thylakoid membrane in chloroplasts (Booth, Lichtenstein, and Dallal 2002). With regards to the study of Garber et al. (1999), that used a reference dose of 500 µg of pure phylloquinone, the amounts of phylloquinone from raw spinach (50 g), raw Romaine lettuce (200 g), and raw and cooked broccoli (159 g) were too low (165–214 µg phylloquinone) to be considered for calculating the relative availability of phylloquinone from these test vegetables. Based on the assumption that the bioavailability of supplementary purified phylloquinone is 80% (Shearer, McBurney, and Barkhan 1974), the absolute apparent availability of vitamin K was determined to be 13.9% for raw spinach, 3.3% for cooked spinach, 10.6% for cooked spinach consumed with fat, and 50% for cooked broccoli (Table 2).

Comparison of vitamin K bioavailability between animal- and plant-based foods

The bioavailability of phylloquinone (vitamin K1) in dark green vegetables has been estimated (Figure 1), though the results that ranged from 3.3 to 50% were conflicting. Some vegetable oils are also rich sources of phylloquinone. Animal-sourced food products contain low levels of phylloquinone, but liver can supply great amounts of menaquinones (vitamin K2). Measures of bioavailability of vitamin K in vegetable oils and animal-sourced foods have not been reported. A comparison of the bioavailability of vitamin K in animal- and plant-based foods cannot be made.

Biotin

Biotin absorption and utilization

Biotin (vitamin B-7) is a water-soluble vitamin whose main essential function is as a coenzyme required for fat synthesis, branched-chain amino acid catabolism and gluconeogenesis (Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; van den Berg 1997a; WHO and FAO 2004). Biotin is found in various natural food sources, and most of the biotin obtained from meat, cereals, yeast, legumes, and nuts, is bound to protein, and biotin occurring in vegetables, fruits, rice bran, and milk, is in the free form (Bonjour 1977; van den Berg 1997a; Zempleni and Mock 1999). A glycoprotein present in raw egg white, avidin, has a high

binding affinity to biotin and prevents biotin from being absorbed. However, avidin has no effect on biotin when the egg is cooked (Bonjour 1977; van den Berg 1997a; Zempleni and Mock 1999).

Biotin is largely found bound to food protein. After its hydrolytic release from its protein-bound form, ingested free biotin is mainly absorbed in the jejunum through a saturable, sodium-dependent transporter (Said 1999, 2011). Absorbed biotin is transported in the blood to the liver, which is the major site of biotin utilization and metabolism (Said 1999, 2011). It has been suggested that free unbound biotin is also synthesized by microflora mainly in the colon, potentially by the stimulatory effect of fiber present in plant foods, and can be absorbed by the host (Bonjour 1977; Kopinski, Leiboholz, and Bryden 1989a; Said 1999, 2011, 2013; Scholtissek et al. 1990; Yoshii et al. 2019; Zempleni and Mock 1999). This is based on the observation that when biotin is directly injected into the colonic lumen, the plasma concentrations of biotin increase considerably (Kopinski, Leiboholz, and Bryden 1989a; van den Berg 1997a). Furthermore, the excretion of biotin in the urine and feces often exceeds the dietary intake of biotin by three to six times, indicating a significant degree of large intestinal microbial biotin synthesis (Bonjour 1977; Kopinski, Leiboholz, and Bryden 1989a, 1989b; Sauer, Mosenthin, and Ozimek 1988; Scholtissek et al. 1990).

Determination of the bioavailability of dietary biotin and supplementary biotin in purified form

The bioavailability of biotin from dietary sources has been mainly determined based on ileal digestibility measures using the growing pig as an animal model for adult humans. In a pig study involving cannulated growing pigs, Sauer, Mosenthin, and Ozimek (1988) determined the endogenous biotin present in ileal digesta, and found that the true (corrected) ileal digestibility of biotin for synthetic purified biotin was 94%.

Bioavailability of biotin in animal-sourced foods

A pig study conducted by Kopinski, Leiboholz, and Bryden (1989b) found that meat meal (50 µg biotin) had an apparent ileal digestibility of biotin of 82% (Table 2), and milk casein (22 µg biotin) an apparent biotin ileal digestibility of 95% (Table 2). It is likely that the digestibility of biotin in these animal-sourced foods would be higher if correction was made for the GIT endogenous biotin, but this has not been reported.

In the same study, based on the amount of biotin excreted in the urine and correcting for the 35 µg of biotin lost daily in the urine in biotin-deficient pigs of similar weight, the true utilization of biotin in meat meal was reported to be 92% (Kopinski, Leiboholz, and Bryden 1989b).

Bioavailability of biotin in plant-based foods

The apparent ileal digestibility of biotin in soyabean meal (130 µg biotin) was 12% in a pig digestibility study (Kopinski, Leiboholz, and Bryden 1989b). By accounting for an endogenous ileal biotin loss of 11 µg per kg dry matter, Sauer, Mosenthin, and Ozimek (1988) reported that the true (corrected) ileal digestibility of biotin in soyabean meal (110 µg biotin per kg dry matter) was 55% (Table 2). Misir and Blair (1988) used the regression method to relate doses of synthetic biotin to plasma responses in biotin-depleted newly-weaned pigs. Although plasma-based biotin values are difficult to interpret as they are confounded by the uptake of microbially synthesized biotin, the data do suggest that the biotin digestibility value for soyabean meal may also be applicable to soya protein isolate, commonly consumed by humans. Therefore, the ileal digestibility values for soyabean meal will be used in the current comparison of biotin bioavailability between animal and plant foods.

A pig digestibility study found that the apparent ileal digestibility of biotin was 6% for wheat (*var.* Banks, 144 µg biotin), −3% for wheat (*var.* Egret, 125 µg biotin), 18% for barley (188 µg biotin), and −123% for sorghum (355 µg biotin) (Kopinski, Leiboholz, and Bryden 1989b). These low or sometimes negative values for the apparent ileal digestibility of biotin in plant-based foods may indicate that there is little uptake of biotin from these plant foods, or that there are relatively large amounts of endogenous biotin present in ileal digesta. Similarly, in the pig digestibility study of Sauer, Mosenthin, and Ozimek (1988), generally low apparent ileal and true (corrected) ileal digestibilities of biotin were found for plant-based foods. Based on the assumption that 11 µg per kg dry matter of endogenous biotin is excreted in ileal digesta, the true (corrected) ileal digestibility of biotin was 22% for wheat (123 µg per kg dry matter), 4.8% for barley (121 µg per kg dry matter), 4% for maize (54 µg per kg dry matter), and 3.9% for canola meal (513 µg per kg dry matter) (Sauer, Mosenthin, and Ozimek 1988) (Table 2).

By accounting for the urinary excretion of 35 µg of endogenous biotin, the true utilization of biotin in soybean meal was 30%, and 12, 2, 20, and −1, for wheat (*var.* Banks), wheat (*var.* Egret), barley, and sorghum, respectively (Kopinski, Leiboholz, and Bryden 1989b).

Comparison of biotin bioavailability between animal- and plant-based foods

The bioavailability of biotin in food sources has not been studied directly in humans, but there is some evidence for the ileal digestibility of biotin in studies involving ileal cannulated pigs. By correcting the results of Kopinski, Leiboholz, and Bryden (1989b) for gut endogenous biotin (Table 2) and taking the data of Sauer, Mosenthin, and Ozimek (1988) (Table 2), together the ileal digestibility of biotin in meat and milk products appears high (82–95%), but in legumes, cereals and seed products much lower values (4–55%) are found. It is concluded that in general, biotin is more bioavailable in animal-based foods (89%) than in plant-based foods (20%) (Figure 1). Nonetheless, estimates of biotin digestibility determined in pigs should be interpreted with caution as the absorption of colonic microbial synthesized biotin may influence the amount of biotin measured in the ileal digesta.

Folate

Folate absorption and utilization

Folate (folacin, vitamin B-9) belongs to the water-soluble group of B vitamins and is mainly biologically active as the mono-glutamate, with the chemical name pteroyl mono-glutamic acid (PteGlu) (Bates and Heseker 1994; Gregory 1989; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004). Folate functions as a coenzyme involved in metabolic pathways associated with other B vitamins, particularly as a methyl donor substrate with vitamin B-12 (Gregory 1989, 1997a, 2001; Krishnaswamy and Nair 2001; McNulty and Pentieva 2004; Ohrivk and Witthoft 2011; Witthöft et al. 1999). Both vitamins are involved in the conversion of homocysteine to methionine (Gregory 1989, 1997a, 2001; Krishnaswamy and Nair 2001; McNulty and Pentieva 2004; Ohrivk and Witthoft 2011; Witthöft et al. 1999). Folate also plays a role in the formation and normal functioning of red blood cells, the methylation of nucleic acids and the metabolism of amino acids (Gregory 1989, 1997a, 2001; Krishnaswamy and Nair 2001; McNulty and Pentieva 2004; Ohrivk and Witthoft 2011; Witthöft et al. 1999). Folate, in the form of mono-glutamates or poly-glutamates, occurs naturally in a wide variety of foods, including meat, liver, milk, vegetables, and fruits (Gregory 1989, 1997a, 2001; Krishnaswamy and Nair 2001; McNulty and Pentieva 2004; Ohrivk and Witthoft 2011; Witthöft et al. 1999). Some folate is lost in the heat treatment of foods (Gregory 1989; Krishnaswamy and Nair 2001; Witthöft et al. 1999). As a public health measure aimed at children, girls and women of childbearing age, and pregnant women, who are more at risk of folate deficiency, cereals and grain food products are generally enriched with the synthetic form of folate, referred to as folic acid (IOM (Institute of Medicine, US) 1998; Krishnaswamy and Nair 2001; WHO and FAO 2004). The synthetic folic acid normally used in fortified foods and dietary supplements, occurs in the form of the chemically stable oxidized mono-glutamate.

When food folate is ingested in the form of poly-glutamates, it is hydrolyzed by intestinal conjugase enzymes to mono-glutamates (Said 2011; Witthöft et al. 1999). The presence of conjugase inhibitors and folate-binding proteins (FBP) in some foods may reduce the absorption of folate (Said 2011; Witthöft et al. 1999). Mono-glutamates are primarily actively absorbed by a pH-dependent saturable mechanism in the jejunum, and by passive diffusion in the ileum at higher intakes (Said 2011, 2013; Witthöft et al. 1999). It is also thought that bacteria in the large intestine synthesize mono-glutamates but these are incompletely absorbed (Gregory 1989, 2001; Ohrivk and Witthoft 2011; Said 2011, 2013; Witthöft et al. 1999; Yoshii et al. 2019). The major circulating form of folate is 5-methyl-tetrahydrofolate and the main metabolic product of folate is acylated mono-glutamate, which is excreted in the urine (Gregory 1997a; Said 2011, 2013).

Folate and folic acid content in food

Dietary folate equivalents (DFEs) have been established to adjust for the lower bioavailability of food folate compared with that of supplementary folic acid consumed as part of a mixed diet, whereby 1 mg of DFE equals 1 mg of food folate, or 0.6 mg of folic acid from fortified food or as a dietary supplement consumed with food (IOM (Institute of Medicine, US) 1998; WHO and FAO 2004).

Determination of the bioavailability of dietary folate and supplementary folate (folic acid) in purified form and in food

There is much uncertainty associated with the forms (mono-glutamates or poly-glutamates) of folate present in food, the presence and concentrations of dietary components that may inhibit intestinal absorption of folate (conjugase enzymes, folate-binding proteins), folate analysis methods (high performance liquid chromatography or microbiological folate assay), and the end-point criteria used to determine bioavailability (plasma or serum folate, folate in red blood cells, urinary folate). The bioavailability of food folate and the synthetic folic acid has been determined in human studies using isotopic labeling and the measurement of folate in the circulating blood and in the urine. Several human studies have determined the availability of food folate based on incremental folate excretion in the urine of human subjects who were in a folate saturated condition (Babu and Srikantia 1976; Devadas, Premakumari, and Moorthy 1979; Tamura and Stokstad 1973). It was assumed that for the folate-saturated individuals, absorbed incremental food folate would be completely excreted, and folate bioavailability values were given.

Often, the bioavailability of naturally occurring folate in food sources is derived in relative terms to a reference dose of supplementary synthetic purified folic acid. It has been assumed that the bioavailability of folic acid ingested as a dietary supplement under fasting conditions is 100% (Gregory 1997a; IOM (Institute of Medicine, US) 1998). Witthöft et al. (2006) determined plasma concentrations of folate (5-methyl-tetrahydrofolate) and found that when a dose of the vitamin was given by intramuscular injection, plasma values were higher (but not statistically significantly so) than when the supplementary vitamin was given *per os via* a gelatin capsule after fasting. Based on measures of ileal folate excretion and plasma folate, the folate given in capsule form had an absorption of around 90% in healthy ileostomates, who were given folic acid supplements prior to the study and had optimal baseline levels of plasma folate (Witthöft et al. 2006). This may indicate that even when supplementary folate is administered on an empty stomach, that it is not fully absorbed. When the supplementary vitamin was given along with food, the uptake was considerably lower (Witthöft et al. 2006). When added to fermented milk, the plasma folate content was around 80% that of the supplement given after fasting (Witthöft et al. 2006). The bioavailability of a folic acid supplement consumed with a light meal (0.40 mg folic acid and 0.14–0.15 mg food folate) was estimated to be 85% (Pfeiffer et al. 1997). The relative bioavailability of folate in food (0.02–0.30 mg food folate) was found to be no more than 50% in a depletion-repletion human study (Sauberlich et al. 1987). It is assumed here that the bioavailability of synthetic folate (folic acid) added to a food is 85%.

Bioavailability of dietary folate in mixed diets

In a human study measuring folate in serum as a percentage of ingested folate, Winkels et al. (2007) determined the availability of folate following the consumption of a non-vegetarian mixed diet (0.37 mg food folate or DFE, with liver paste contributing 20%, boiled vegetables 29%, and fruits and fruit juices 38% of the total food folate content), relative to that of added synthetic folic acid. The relative availability of folate was 78% based on serum isotopically labeled ($^{13}C_{11}$) folate, and 85% based on changes in absolute serum folate concentrations. The overall availability of folate in the non-vegetarian mixed diet relative to that of folic acid from capsules taken with the meal, was around 82%. If it is assumed that the added folic acid was itself 85% bioavailable, an absolute value for folate availability in the non-vegetarian mixed diet of 70% can be calculated.

In a study by Brouwer et al. (1999), the availability of folate in human participants provided with a mixed diet rich in folate (0.56 mg food folate or DFE) from vegetables (spinach, green peas, broccoli, brussels sprouts, green beans) and citrus fruits (oranges, tangerines), was compared to folate availability from a supplementary folic acid capsule consumed with a low-folate diet. The relative availability of folate in the vegetable and fruit mixed diet was estimated to be 78% based on changes in plasma concentrations of folate, and 98% based on folate levels in red blood cells. If a mean overall value of 88% is taken, and it is assumed that the supplementary folic acid is 85% bioavailable, an absolute value for folate bioavailability in the vegetable and citrus fruit mixed diet of 75% can be calculated. In another human study, Vahteristo et al. (2002) found that the relative folate availabilities after consumption of a diet containing natural folates from rye-based products and orange juice (0.18 mg food folate or DFE) compared to a folic acid supplemented wheat diet, were 84% based on plasma folate, and 55% based on red blood cell folate. If a mean overall value of 70% is assumed, then an absolute value for bioavailability of folate in the rye and orange mixed diet of 60% can be calculated.

Bioavailability of dietary folate in animal-sourced foods

Using the measurement of folate in the urine of folate-saturated human subjects, Babu and Srikantia (1976) found that the bioavailability of folate in goat liver (0.32 mg food folate, 1.00 mg DFE) was 70% (Table 2), and 72% for cooked whole chicken eggs (0.21–0.35 mg food folate, 0.89–1.03 mg DFE) (Table 2). Tamura and Stokstad (1973), determining urinary folate excretion in folate-saturated human subjects, found that the bioavailability of folate in cooked beef liver (0.67–1.01 mg food folate, 0.67–1.61 mg DFE) was 50% (Table 2), and gave folate bioavailability values of 82% (range: 61–100%) and 59% (range: 23–129%) for hard-boiled egg yolks (0.28–0.35 mg food folate, 0.28–1.03 mg DFE) (Table 2).

Bioavailability of dietary folate in plant-based foods

Devadas, Premakumari, and Moorthy (1979), determining urinary folate excretion in folate-saturated humans, found folate bioavailability values for germinated chickpea (Bengal gram) (0.31 mg food folate, 0.99 mg DFE) and germinated mung bean (green gram) (0.30 mg food folate, 0.98 mg DFE) of 71% (Table 2). Devadas, Premakumari, and Moorthy (1979) also reported a folate bioavailability of 50% for germinated finger millet (Raji) (0.30 mg food folate, 0.98 mg DFE) and 54% for germinated pearl millet (Bajra) (0.30 mg food folate, 0.98 mg DFE) (Table 2). In another similar folate-saturated human study by Babu and Srikantia (1976), the bioavailability of folate in chickpea (Bengal gram) (0.28 mg food folate, 0.96 mg DFE) was 69%, 55% for mung bean (green gram) (0.31 mg food folate, 0.99 mg DFE), 63% for spinach (0.31 mg food folate, 0.99 mg DFE), 37% for tomatoes (0.30 mg food folate, 0.98 mg DFE), 10% for Brewer's yeast (0.30 mg food folate, 0.98 mg DFE), and 46% for bananas (0.19–0.25 mg food folate, 0.87–0.93 mg DFE) (Table 2). Using a similar folate-saturation urinary excretion model, Tamura and Stokstad (1973) showed that the bioavailabilities of folate were 96% for cooked frozen green Lima beans (0.42 mg food folate, 1.02 mg DFE), 70% for cooked dried mature Lima beans (0.24 mg food folate, 0.84 mg DFE), 25% for Romaine lettuce (0.75 mg food folate or DFE), 47% for raw and cooked green cabbage (0.33–0.49 mg food folate, 0.67–1.09 mg DFE), 60% for Brewer's yeast (1.40 mg food folate or DFE), 63% for Brewer's yeast extract (0.75 mg food folate or DFE), 82% for bananas (0.25 mg food folate, 0.85 mg DFE), 31% for orange juice (0.84 mg food folate or DFE), and 30% for wheat germ (0.73 mg food folate, 1.33 mg DFE) (Table 2).

In a clinical trial, Konings et al. (2002) studied which form of folate would be more bioavailable following the consumption of two spinach test meals in eleven ileostomates. Based on the amount of folate excreted in ileal digesta expressed as a percentage of folate intake, the apparent ileal digestibility of folate in spinach was 85% when folate was in the form of mono-glutamates (0.36 mg food folate or DFE), and 73% when folate was in the ratio of 40 mono-glutamates to 60 poly-glutamates (0.44 mg food folate or DFE). These values were not statistically significantly different and a mean overall ileal digestibility value for spinach of 79% was given. Based on the measurement of the area under the curve for serum folate following consumption of the spinach meals (0.36–0.44 mg food folate or DFE) relative to supplementary pure folic acid, the relative availability of folate in spinach was estimated to be 81% (Konings et al. 2002). In another human study by Prinz-Langenohl et al. (1999), consumption of spinach (0.36 mg food folate or DFE) resulted in a mean area under the plasma folate response curve that was 91% that for supplementary folic acid. Based on the assumption that supplementary folic acid is 85% bioavailable, an absolute bioavailability of folate in spinach of 69 and 77% can be calculated (Table 2). Based on serum folate responses, Hannon-Fletcher et al. (2004) reported that the relative availability of folate was 36% following consumption of spinach (folate in the ratio of 50 mono-glutamates to 50 poly-glutamates, 0.20 mg food folate or DFE) and 62% for yeast (folate as poly-glutamates, 0.20 mg food folate or DFE), giving absolute bioavailability values of 31 and 53% for spinach and yeast, respectively (Table 2). Using kinetic modeling of plasma folate, Witthöft et al. (2006) found that the

apparent availability of folate following consumption of yeast flakes in a lemon mousse dessert (0.07–0.08 mg food folate or DFE) ranged from 37 to 152%, with a median value of 80%.

Comparison of folate bioavailability between animal- and plant-based foods

The considerable variability in the mean estimates of folate bioavailability hampers making meaningful comparisons across food groups. Only five folate availability values were found for animal-sourced food products, and these ranged between 50 to 82% (Table 2). The overall animal mean ($n = 5$) folate bioavailability value was 67% (Figure 1). Published bioavailability values for plant-based foods are more numerous, with values ranging from 25 to 96% (Table 2). There are several published folate bioavailability values for yeast ranging from 53 to 80%, but there is one published value for Brewer's yeast of 10% (Table 2). It appears that there may be a greater range in the bioavailability of folate within plant-based foods, with bioavailability being quite low in some plant foods. The overall plant mean ($n = 24$) bioavailability value was 54% (Figure 1). Given the variability in the data and the low number of observations for animal-sourced foods, it is difficult to conclude as to whether animal- or plant-based foods are superior in terms of folate bioavailability (Figure 1), though the lowest value recorded for an animal-sourced food was 50%, whereas several of the plant-based foods ($n = 9$) had folate bioavailability values falling below 50%.

Niacin

Niacin absorption and utilization

Niacin (Vitamin B-3) is a water-soluble vitamin that is the generic term for nicotinic acid and nicotinamide (also called nicotinic acid amide or niacinamide) (Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004). Niacin is a constituent of nucleotide coenzymes (nicotinamide adenine dinucleotide, NAD) involved in several oxidation and reduction reactions, including hydrogen transfer, the respiratory system, synthesis of fatty acids and amino acids, and energy metabolism (van den Berg 1997b). The major dietary sources of niacin are meat, fish, cereal grains, and seeds, with some niacin also found in milk, green leafy vegetables, and coffee beans (van den Berg 1997b). In animal-sourced foods, niacin mostly occurs in the form of nucleotides (NAD), whereas niacin found in mature cereal grains can sometimes be bound to proteins or glycosides (Ghosh et al. 1963; van den Berg 1997b). Niacin is present in maize and some other cereals in an esterified form non-utilizable by humans. Bound niacin is liberated upon food treatment with an alkali or strong acid prior to ingestion (Ghosh et al. 1963).

Dietary nicotinamide nucleotides are hydrolyzed in the stomach and small intestine, and free niacin is readily absorbed through the jejunum, to be distributed to the liver (Melnick, Hochberg, and Oser 1945; Said 2011, 2013). While some niacin can be synthesized by colonic bacteria in the large intestine (Said 2013, Yoshii et al. 2019), most niacin is synthesized from the essential amino acid tryptophan in the liver, whereby 60 mg of dietary tryptophan can yield 1 mg of niacin (IOM (Institute of Medicine, US) 1998; van den Berg 1997b; WHO and FAO 2004). This conversion of tryptophan to niacin contributes to meet the bodily requirement for niacin, but is inhibited by inadequate body status of riboflavin (vitamin B-2), vitamin B-6 or iron. Under normal conditions, the amounts of nicotinic acid formed from tryptophan are inadequate to meet the total nicotinic acid requirement. Dietary supply of niacin is therefore essential (IOM (Institute of Medicine, US) 1998; van den Berg 1997b; WHO and FAO 2004). The major pathway for metabolism of excess niacin is by methylation in the liver, and excretion of the methylated niacin derivatives in the urine (van den Berg 1997b).

Niacin content in food

Dietary niacin is described by niacin equivalents (NEs), where 1 mg NE equals 1 mg of nicotinic acid or 1 mg of nicotinamide or 1/60 mg of tryptophan (Horwitt, Harper, and Henderson 1981; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004).

Determination of the bioavailability of dietary niacin

The utilization of niacin has been determined in human studies based on urinary excretion of niacin. These results need to be carefully interpreted, as dietary tryptophan can be used to generate niacin in the liver. The bioavailability of niacin has been determined using the oro-ileal balance method in ileostomized pigs, used as an animal model for adult humans.

Bioavailability of niacin in animal-sourced foods

In a digestibility study involving growing pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), Roth-Maier et al. (2000) found that the apparent ileal digestibility of niacin in cooked beef (45.2 mg niacin) and cooked pork (66.5 mg niacin), was 69 and 65%, respectively (Table 2).

Bioavailability of niacin in plant-based foods

A digestibility study involving growing pigs fitted with an end-to-end ileo-rectal anastomosis (EEV) by Roth-Maier et al. (2000), demonstrated that the apparent ileal digestibility of niacin was 69% for boiled potatoes (39.5 mg niacin), 59% for wheat (54.1 mg niacin), and 40% for rye-based whole-meal bread (20.6 mg niacin) (Table 2). When Wauer et al. (1999) compared pigs that underwent EEV surgery with those having end-to-side ileo-rectal anastomosis (ESV), the mean apparent ileal digestibility of niacin in wheat (53.7–54.4 mg niacin) was somewhat greater at 61% in EEV pigs (Table 2) than at 50% in ESV pigs.

Several human clinical trials have measured the urinary excretion of niacin following the consumption of plant-based foods. Girija, Sharada, and Pushpamma (1982) used human urinary excretion of niacin (as N-methyl-nicotinamide) and a response curve generated following consumption of graded doses of synthetic niacin, as a measure of the utilization of

niacin from curry dishes made with three commonly consumed green leafy vegetables in India. The relative utilization of niacin was 44% for Amaranth (28.2 mg niacin), 45% for Hisbiscus (Gogu) (30.7 mg niacin), and 40% for Moringa (Drumstick) leaves (33.9 mg niacin). The study also demonstrated that the mean urinary recovery of niacin following the consumption of these three green leafy vegetables was 10% of the ingested niacin. Using the urinary excretion of niacin as a percentage of ingested niacin, the urinary recovery of niacin in wheat-based bread (14.8 mg niacin) was 2.1% of the ingested dose and 1.7% of the ingested dose for the wheat bread supplemented with maize bran (15.3 mg niacin) (Yu and Kies 1993). Similarly, Edwards et al. (1971) showed that the urinary excretion of niacin was 3.6% of intake when wheat bread (6.9 mg niacin, 14.5 mg NE) was consumed, and 4.4, 3.3, and 3.8% upon ingestion with the wheat bread for rice (9.0 mg niacin, 16.7 mg NE), canned pinto beans (6.6 mg niacin, 14 mg NE), and peanut butter (10.3 mg niacin, 17.4 mg NE), respectively. In the same study, the urinary recovery of niacin metabolite (N-methyl-nicotinamide) as a percentage of dietary niacin intake was estimated to be 28% for the wheat bread diet, 26% for the rice and bread diet, 24% for the pinto beans and bread diet, and 22% for the peanut butter and bread diet (Edwards et al. 1971). However, these values reflect the utilization of niacin in plant-based foods, and the ileal digestibility data provide the most reliable indicators of niacin bioavailability in plant- and animal-based foods.

Comparison of niacin bioavailability between animal- and plant-based foods

The comparative bioavailability of niacin in animal- and plant-based foods has been determined in digestibility studies involving pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), by measuring the amount of niacin in ileal effluent as a proportion of intake. The apparent ileal digestibility of niacin in beef and pork was greater than the apparent ileal digestibility of niacin in potatoes, wheat, and bread (Table 2). Based on the limited ($n = 6$) data, the bioavailability of niacin in animal-sourced foods (67%) was generally greater than that in plant-based foods (57%) (Figure 1). It is important to note that the degree of conversion of niacin from dietary tryptophan is not known.

Pantothenic acid

Pantothenic acid absorption and utilization

Pantothenic acid (pantothenate, vitamin B-5) is a water-soluble vitamin that is part of the B group vitamins (Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004). Pantothenic acid is a constituent of coenzyme A, which is central to the release of energy from the metabolism of carbohydrates, fats, and proteins, and acyl-carrier proteins involved in the synthesis of fatty acids (Kelly 2011; Smith and Song 1996; Song 1990; Tahiliani and Beinlich 1991; van den Berg 1997c). Pantothenic acid is widely distributed in foods, and is commonly obtained from meat products, milk, eggs, whole-grain cereals, vegetables, and nuts (van den Berg 1997c).

Dietary pantothenic acid, mostly found in the bound form (as coenzyme A or phosphopantetheine), is first hydrolyzed by phosphatases to pantotheine, which is subsequently hydrolyzed by pantotheinases to free pantothenic acid in the intestinal lumen. Absorption of free pantothenic acid occurs through a saturable, sodium-dependent transport system mainly in the jejunum (Said 2011, 2013). Free pantothenic acid is also synthesized by bacteria in the large intestine (Said 2011, 2013; Yoshii et al. 2019). Free pantothenic acid is excreted in the urine, mainly as a metabolite of coenzyme A (Said 2011; van den Berg 1997c).

Determination of the bioavailability of dietary pantothenic acid

Urinary pantothenic acid excretion is commonly used as an indicator for human pantothenic acid nutritional status, and as a measure of pantothenic acid utilization in human studies (Smith and Song 1996; Tahiliani and Beinlich 1991; van den Berg 1997c). Using the growing pig as an animal model for humans, the bioavailability of pantothenic acid from food sources has been determined in pig ileal digestibility studies, where pantothenic acid is measured in ileal effluent and given as a percentage of pantothenic acid intake.

Bioavailability of pantothenic acid in mixed diets

Tarr, Tamura, and Stokstad (1981) reported a mean utilization of pantothenic acid, based on urinary pantothenic acid excretion in six male human subjects, given a non-vegetarian mixed average American diet (50% animal-sourced foods, 50% plant-based foods, 11.5 mg pantothenic acid) of 50%, relative to the consumption of supplementary pantothenic acid assumed to be 100% bioavailable.

Bioavailability of pantothenic acid in animal-sourced foods

Roth-Maier et al. (2000) conducted a study involving pigs fitted with an end-to-end ileo-rectal anastomosis (EEV) and found that the apparent ileal digestibility of pantothenic acid in cooked beef (3.25 mg pantothenic acid) was 65%, and 74% for cooked pork (5.05 mg pantothenic acid) (Table 2). In a digestibility study involving pigs fitted with an end-to-side ileo-rectal anastomosis (ESV), Roth-Maier and Kirchgessner (1996) showed that the apparent ileal digestibility of pantothenic acid in skimmed milk powder (24.8 mg pantothenic acid) was 90% (Table 2).

Bioavailability of pantothenic acid in plant-based foods

In a digestibility study involving pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), Roth-Maier et al. (2000) found that the apparent ileal digestibility of pantothenic acid was 70% for diets containing boiled potatoes (*var.* Agria, 10.9 mg pantothenic acid), 81% for wheat (14.1 mg pantothenic acid), and 28% for whole-meal rye bread (4.03 mg pantothenic acid) (Table 2). Wauer et al. (1999) compared the EEV with the end-to-side ileo-rectal anastomosis (ESV) technique for pigs consuming wheat-based diets (10.7–15.0 mg pantothenic acid), and reported that the mean

apparent ileal digestibility of pantothenic acid was 78% in EEV pigs and 40% in ESV pigs (Table 2). Using ESV pigs, Roth-Maier and Kirchgessner (1996) showed that the apparent ileal digestibility of pantothenic acid in wheat bran (9.92 mg pantothenic acid) and maize (3.87 mg pantothenic acid) was 47 and 20%, respectively (Table 2).

In a cross-over study involving nine human volunteers, Yu and Kies (1993) showed that the mean urinary recovery of pantothenic acid was 60% of the ingested dose following the consumption of wheat-based bread (3.24 mg pantothenic acid). When the wheat bread was supplemented with maize bran, urinary excretion of pantothenic acid was lowest following the consumption of coarsely ground maize bran produced by wet milling added to the wheat bread (3.28 mg pantothenic acid), than after ingestion of added dry-milled coarse maize bran (3.28 mg pantothenic acid), added wet-milled fine maize bran (3.28 mg pantothenic acid), or added dry-milled fine maize bran (3.28 mg pantothenic acid) (Yu and Kies 1993). A similar human study also showed that the urinary excretion of pantothenic acid was 59% of the ingested dose for wheat bread (3.50 mg pantothenic acid), and slightly differed when rice (3.50 mg pantothenic acid), canned pinto beans (3.50 mg pantothenic acid), and peanut butter (3.60 mg pantothenic acid) were added to the wheat bread diet (Edwards et al. 1971). Based on the recovered urinary excretion of pantothenic acid, the utilization of pantothenic acid was calculated to be 40% for wheat bread, and range between 38 and 51% when plant-based foods were added to the wheat bread diets (Edwards et al. 1971).

Comparison of pantothenic acid bioavailability between animal- and plant-based foods

Pantothenic acid bioavailability comparisons across food types need to be made within each ileostomy method used in pigs, either the end-to-end (EEV) or end-to-side (ESV) ileo-rectal anastomosis (EEV). Using EEV ileostomized pigs, the mean apparent ileal digestibility of pantothenic acid was 70% for meat and 64% for potatoes, wheat, and bread (Table 2). Using ESV ileostomized pigs, the mean apparent ileal digestibility of pantothenic acid in milk was 90%, and 36% for wheat, wheat bran, and maize (Table 2). It is concluded that in general, overall pantothenic acid is more bioavailable in animal-sourced foods (80%) than in plant-based foods (50%) (Figure 1).

Riboflavin

Riboflavin absorption and utilization

Riboflavin is a member of the water-soluble group of B vitamins (Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004). The main function of riboflavin is in the manufacture of the two main flavin nucleotide coenzymes mainly involved in energy metabolism and fatty acid oxidation (Bates 1997b). Vitamin B-2 is the generic term for three biologically active forms of flavin; riboflavin, flavin mononucleotide (FMN), and flavin adenine dinucleotide (FAD) (Bates 1997b). Milk, meat, liver, green vegetables, and yeast are major sources of vitamin B-2, with FMN and FAD the predominant flavin forms found in these foods (Bates 1997b). Vitamin B-2 occurs naturally in milk and eggs bound to food protein, and some vitamin B-2 in dairy milk is present as free riboflavin (Bates 1997b). Vitamin B-2 is easily destroyed by light and certain food storage methods. The storage of cow's milk stored in dark colored glass bottles has been shown to be effective to protect vitamin B-2 from sunlight-induced damage (Bates 1997b).

Following release from dietary flavin adenine dinucleotide (FAD), flavin mononucleotide (FMN), and protein-bound riboflavin, free riboflavin is mainly absorbed through a carrier-mediated, saturable transport system in the jejunum (Levy and Hewitt 1971; Melnick, Hochberg, and Oser 1945; Said 2011; Zempleni, Galloway, and McCormick 1996). It is also known that free riboflavin is synthesized by colonic bacteria and is directly absorbed in the large intestine (Bates 1997b; Melnick, Hochberg, and Oser 1945; Said 2011, 2013; Yoshii et al. 2019; Zempleni, Galloway, and McCormick 1996). Absorbed free riboflavin is converted to FAD and FMN in the blood to be distributed to body tissues (Levy and Hewitt 1971; Melnick, Hochberg, and Oser 1945; Said 2011, 2013; Zempleni, Galloway, and McCormick 1996). Excess vitamin B-2 is excreted in the urine (Said 2011, 2013; Zempleni, Galloway, and McCormick 1996).

Determination of the bioavailability of dietary riboflavin

The apparent availability or utilization of dietary riboflavin was determined in human studies using the measurement of riboflavin in blood or urine, respectively. The bioavailability of riboflavin has largely been determined using the balance between oral ingestion of dietary riboflavin and riboflavin found in ileal effluent, using the growing pig as an animal model for adult humans.

Bioavailability of riboflavin in animal-sourced foods

Roth-Maier et al. (1998) compared the apparent ileal digestibility of riboflavin in roast beef and roast pork, using growing pigs fitted with an end-to-end ileo-rectal anastomosis (EEV) or an end-to-side ileo-rectal anastomosis (ESV). With regards to EEV pigs, the apparent ileal digestibilities of riboflavin in roast beef (1.41 mg riboflavin) and roast pork (1.94 mg riboflavin), were 63 and 71%, respectively. Using ESV pigs, the apparent ileal digestibility of riboflavin in roast beef (1.25 mg riboflavin) was 31% and 58% for roast pork (1.86 mg riboflavin) (Table 2). In a digestibility study involving ESV ileostomized pigs, Roth-Maier and Kirchgessner (1996) found that the apparent ileal digestibility of riboflavin in skimmed milk powder (12.0 mg riboflavin) was 94% (Table 2).

Using kinetic modeling of plasma isotopically labeled (^{13}C) riboflavin in a human study involving twenty female participants who consumed semi-skimmed (1.7% fat) milk (0.40 mg riboflavin), Dainty et al. (2007) found that the apparent availability of riboflavin was 23%. Based on the measurement of urinary riboflavin following consumption of semi-skimmed milk and intravenously administered purified

riboflavin, Dainty et al. (2007) also reported a true utilization of riboflavin in milk of 67%. The relative utilization of riboflavin in ice cream (1.00 mg riboflavin), based on comparison with the urinary riboflavin response for pure riboflavin, was shown to be 90% (Everson et al. 1948).

Bioavailability of riboflavin in plant-based foods

In a study involving pigs fitted with an end-to-side ileo-rectal anastomosis (ESV), Roth-Maier and Kirchgessner (1996) showed that the apparent ileal digestibility of riboflavin was 62% for wheat bran (1.43 mg riboflavin) and 67% for maize (1.50 mg riboflavin) (Table 2).

In a human study measuring the plasma kinetics of isotopically labeled (^{13}C) riboflavin in cooked spinach (0.40 mg riboflavin), Dainty et al. (2007) reported an apparent availability of riboflavin of 20%. In the same study and based on the urinary recovery of riboflavin following consumption of riboflavin provided orally in spinach or administered intravenously, the true utilization of riboflavin was estimated to be 60%. In another human study determining the urinary riboflavin responses to doses of synthetic purified riboflavin, Girija, Sharada, and Pushpamma (1982) showed that the relative utilization of riboflavin from curry dishes, made from Amaranth (1.63 mg riboflavin), Hisbiscus (Gogu) (1.63 mg riboflavin), or Moringa (Drumstick) leaves (1.47 mg riboflavin), was 47, 46, or 52%, respectively. Another human study of similar design showed that the relative utilization of riboflavin in cooked frozen green peas (1.00 mg riboflavin) was 42%, and 39% following the consumption of roasted almonds (1.00 mg riboflavin) (Everson et al. 1948). When human participants consumed yeast and the amount of riboflavin excreted in the urine was compared with that found when purified riboflavin was fed, Price, Marquette, and Parsons (1947) showed that the relative utilization of riboflavin was 9% for fresh live yeast (2.60 mg riboflavin) and 24% for dried live yeast (3.00 mg riboflavin).

Comparison of riboflavin bioavailability between animal- and plant-based foods

The comparative bioavailability of riboflavin in animal- and plant-sourced foods has been determined using the oro-ileal balance method in pigs fitted with an end-to-side (ESV) ileo-rectal anastomosis. Based on the scarce ($n = 5$) data, the mean apparent ileal digestibility of riboflavin in roast beef, roast pork, and skimmed milk powder was similar to the mean apparent ileal digestibility of riboflavin in wheat bran and maize (Table 2). Further studies are needed to allow meaningful comparisons to be made for the comparative bioavailability of riboflavin between animal-sourced foods (61%) and plant-based foods (65%) presented in Figure 1.

Thiamin

Thiamin absorption and utilization

Thiamin (thiamin, aneurine, Vitamin B-1) is the first discovered water-soluble B vitamin (Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; WHO and FAO 2004). Thiamin plays a major role as the precursor for the coenzyme thiamin pyrophosphate (TPP), involved in energy-yielding reactions and the metabolism of carbohydrates and amino acids (Gregory 1997b). Thiamin is widely spread in plant and animal foods, and is found in particularly high amounts in meat, milk, eggs, vegetables, yeast and natural cereal grains (Gregory 1997b; Gregory and Kirk 1978). The husk, bran layers, and germ of cereals are rich sources of thiamin, but the process of milling and polishing of grains removes most of the thiamin (Gregory 1997b). Thiamin is also degraded upon the heating of foods and is inactivated in the presence of heavy metal salts, oxidizing agents, and sulfuric acid (Gregory 1997b).

The uptake of free thiamin, following breakdown from the dietary phosphorylated thiamin form (thiamin pyrophosphate, TPP) by phosphatases, occurs through a specific saturable transport system in the jejunum and ileum (Levy and Hewitt 1971; Melnick, Hochberg, and Oser 1945; Said 2011). Free thiamin and TPP are also produced by colonic microflora and absorbed in the large intestine, but while bacterially synthesized free thiamin is transported in the systemic circulation and distributed throughout the body, bacterially synthesized TPP is mainly used for energy metabolism within the local colonocytes (Gregory 1997b; Said 2011, 2013; Yoshii et al. 2019). Excess thiamin above the human bodily requirement is eliminated in the urine (Gregory 1997b; Levy and Hewitt 1971; Melnick, Hochberg, and Oser 1945).

Determination of the bioavailability of dietary thiamin

The utilization of thiamin, involving measures of urinary excretions of thiamin, has been determined in humans. However, this needs to be interpreted with caution, as the contribution of colonic bacterially synthesized free thiamin to the urinary recovery of thiamin is not known. The bioavailability of thiamin from food sources has been mostly determined in ileal digestibility studies involving end-to-end (EEV) or end-to-side (ESV) ileo-rectal anastomized pigs.

Bioavailability of thiamin in animal-sourced foods

A digestibility study involving growing pigs fitted with an end-to-end (EEV) or end-to-side (ESV) ileo-rectal anastomosis, showed that the apparent ileal digestibility of thiamin in roast beef (0.71–0.93 mg thiamin) using EEV and ESV pigs was 79 and 51%, respectively (Roth-Maier et al. 1998) (Table 2). The apparent ileal digestibilities of thiamin in roast pork (7.56–8.54 mg thiamin) were 96% in EEV pigs and 93% in ESV pigs (Roth-Maier et al. 1998) (Table 2). In a digestibility study involving EEV ileostomized pigs, the apparent ileal digestibility of thiamin was 88% for milk powder (1.23 mg thiamin), 82% for boiled whole eggs (1.40 mg thiamin), and 73% for stewed fish (Alaska pollack, 0.97 mg thiamin) (Roth-Maier et al. 1999) (Table 2). Using ESV ileostomized pigs, the apparent ileal digestibility of thiamin in skimmed milk powder (2.60 mg thiamin) was 96% (Roth-Maier and Kirchgessner 1996) (Table 2).

A human study found that the urinary excretion of thiamin was 22% of the ingested thiamin following consumption

of roast lamb (0.79 mg thiamin in 120 g roast lamb) and 19.8% of intake when a diet containing roast lamb (120 g) and baked potatoes (200 g) was consumed (0.85 mg thiamin) (Warnick et al. 1956).

Bioavailability of thiamin in plant-based foods

In a digestibility study involving male growing pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), Roth-Maier et al. (1999) found that the apparent ileal digestibility of thiamin in boiled soyabeans (4.74 mg thiamin) was 94%, 81% for white cabbage (1.38 mg thiamin), 91% for dried Brewer's yeast (2.54 mg thiamin), 77% for bananas (1.33 mg thiamin), 94% for barley (4.72 mg thiamin), 84% for rye (4.17 mg thiamin), and 94% for boiled rice (2.88 mg thiamin) (Table 2). The apparent ileal digestibility of thiamin using growing pigs fitted with an EEV and an end-to-side (ESV) ileo-rectal anastomosis was investigated by Roth-Maier and Kirchgessner (1996) and Roth-Maier et al. (1998, 1999). Using EEV and ESV ileostomized pigs, the respective apparent ileal digestibility of boiled potatoes (2.51 mg thiamin) was 84 and 63% (Roth-Maier et al. 1998) (Table 2). The consumption of wheat (4.80–6.26 mg thiamin) resulted in a mean apparent ileal digestibility of thiamin of 87% in EEV pigs and 75% in ESV pigs (Roth-Maier et al. 1998) (Table 2). The apparent ileal digestibility of thiamin in wheat bran (2.88–3.10 mg thiamin) was 92% in EEV pigs (Roth-Maier et al. 1999) and 91% in ESV pigs (Roth-Maier and Kirchgessner 1996) (Table 2). Whole-wheat bread (2.59 mg thiamin) had an apparent ileal digestibility of thiamin of 75 and 60%, in EEV and ESV pigs, respectively (Roth-Maier et al. 1998) (Table 2). The apparent ileal digestibility of thiamin in maize (3.47–3.96 mg thiamin) was 81% in EEV pigs (Roth-Maier et al. 1999) and 87% in ESV pigs (Roth-Maier and Kirchgessner 1996) (Table 2).

Parsons and Collord (1942) conducted a human study to investigate whether boiling would affect the availability and utilization of thiamin in yeast. Based on 66% of the ingested thiamin in dried live yeast (2.98 mg thiamin) and 22% of thiamin intake for boiled yeast (2.98 mg thiamin) excreted in the feces, the overall apparent availability of thiamin in yeast was estimated to be 56%. The urinary excretion of thiamin as a percentage of intake was 9.1% for dried yeast and 19% for boiled yeast (Parsons and Collord 1942). In a human dose-response study involving the measurement of urinary thiamin, the relative utilization of thiamin was 59% for Indian curry dishes made with Amaranth leaves (1.63 mg thiamin) and 62% for Moringa (Drumstick) leaves (1.46 mg thiamin) (Girija, Sharada, and Pushpamma 1982). The urinary excretion of thiamin following the consumption of baked potatoes (0.80–1.04 mg thiamin) by adult humans amounted to 15.2% of intake (Warnick et al. 1956). A human study reported that the percentage of thiamin excreted in the urine was 11% of the ingested thiamin in pinto beans (1.42 mg thiamin), 14.7% of intake for peanut butter (1.43 mg thiamin), and 16.9% of intake for cooked rice (1.83 mg thiamin) (Edwards et al. 1971). Human studies showed that the mean urinary excretion of thiamin ranged from 1.9% of ingested thiamin in wheat bread (1.00–1.77 mg thiamin) (Yu and Kies 1993) to 13.5% of intake for wheat (1.61 mg thiamin) (Edwards et al. 1971).

Comparison of thiamin bioavailability between animal- and plant-based foods

The bioavailability of thiamin in animal- and plant-based foods has been determined using pig ileal digestibility studies within each ileostomy method, either the end-to-end (EEV) or end-to-side (ESV) ileo-rectal anastomosis. Using EEV ileostomized pigs, the mean apparent ileal digestibility of thiamin was 84% for beef, pork, milk, eggs, and fish and 86% for soyabeans, potatoes, white cabbage, yeast, bananas, wheat, wheat bran, bread, barley, rye, maize, and rice (Table 2). Using ESV ileostomized pigs, the mean apparent ileal digestibilities of thiamin were 80% for beef, pork, and milk, and 75% for potatoes, wheat, wheat bran, bread, and maize (Table 2). In general, the overall bioavailability of thiamin in animal-based foods (82%) is comparable to that in plant-based foods (81%) (Figure 1).

Vitamin B-6

Vitamin B-6 absorption and utilization

The water-soluble vitamin B-6 mainly functions as a coenzyme involved in the metabolism of amino acids, glycogen, and carbohydrates, and niacin formation (Bates and Heseker 1994; Gregory 1997c; IOM (Institute of Medicine, US) 1998; Sebrell 1964; WHO and FAO 2004). The three main forms of vitamin B-6 naturally occurring in foods are pyridoxine, pyridoxal, and pyridoxamine, and their respective phosphorylated forms (Gregory 1997c; Sauberlich 1964; Sauberlich et al. 1972; Sebrell 1964). Plant-based foods predominantly contain pyridoxine, while pyridoxal is mainly obtained from animal-sourced foods, and pyridoxamine is found in both food groups (Gregory 1997c; Reynolds 1988; Reynolds and Leklem 1981; Sauberlich et al. 1972). Food sources rich in vitamin B-6 include cereal grains, rice, legumes, potatoes, peanuts, meat, milk, and eggs, and fish (Reynolds 1988; Reynolds and Leklem 1981; Sauberlich 1964; Sauberlich et al. 1972; Sebrell 1964).

In cereal grains, vitamin B-6 present in the bran components of wheat, maize, and rice, are poorly available to humans (Kies, Kan, and Fox 1984). Pyridoxine found in plant-based foods may also be glucosidically bound (PN-glucoside), and commonly undergoes deconjugation by a mucosal glucosidase in the small intestine, before absorption (Nakano, McMahon, and Gregory 1997; Reynolds 1988). Similarly, the phosphorylated forms of vitamin B-6 are hydrolyzed by alkaline phosphatase in the intestinal lumen before absorption (Said 2011, 2013). Free vitamin B-6 is readily absorbed by passive diffusion in the jejunum, to be transported to the liver (Said 2011, 2013). The liver is the major site where the different forms of B-6 vitamers are converted to pyridoxal phosphate (PLP), which is released as the predominant form of vitamin B-6 in the blood plasma, bound to albumin protein (Li, Lumeng, and Veitch 1974; Said 2011, 2013). Microbial vitamin B-6 is synthesized as PLP in the large

intestine (Said 2011, 2013; Yoshii et al. 2019) and a small amount of the dietary and microbial B-6 vitamers may be eliminated in feces (Linkswiler and Reynolds 1950; Said 2011, 2013; Shultz and Leklem 1981). While the three forms of vitamin B-6 can be metabolized to be released intact in urine, the major urinary excretory product of vitamin B-6 is 4-pyridoxic acid (4-PA) (Linkswiler and Reynolds 1950; Sauberlich et al. 1972; Shultz and Leklem 1981).

Determination of the bioavailability of dietary vitamin B-6

Methods commonly used to determine the bioavailability of vitamin B-6 in food include the measurement of B-6 vitamers and metabolites in the blood, urine, and feces of human participants. However, colonic microbially synthesized and absorbed vitamin B-6 may influence these estimates of the availability and utilization of vitamin B-6. The bioavailability of vitamin B-6 and its three main forms, from animal- and plant-based foods has been largely determined using the measurement of the oro-ileal thiamin balance in end-to-end (EEV) or end-to-side (ESV) ileo-rectal anastomized pigs, used as an animal model for adult humans.

Bioavailability of vitamin B-6 in mixed diets

Based on the assumption that vitamin B-6 from a purified vitamin B-6 supplement is 100% bioavailable, Tarr, Tamura, and Stokstad (1981) determined the relative availability and utilization of vitamin B-6 for an average American non-vegetarian mixed diet (2.30 mg vitamin B-6), comprising around half from animal-based foods and half from plant-based foods, in six male participants. The relative availability of vitamin B-6 for the non-vegetarian mixed diet was 71%, as determined by plasma levels of pyridoxal phosphate (PLP). The relative utilization of vitamin B-6 for the non-vegetarian mixed diet, based on the difference between vitamin B-6 ingested and that excreted in urine, was 79%.

Bioavailability of vitamin B-6 in animal-sourced foods

In a study involving growing pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), Roth-Maier et al. (1998) found that the apparent ileal digestibility of vitamin B-6 in roast beef (3.15 mg vitamin B-6) and roast pork (4.02 mg vitamin B-6) was 89% (Table 2). Roth-Maier et al. (1998) also reported that the apparent ileal digestibility of vitamin B-6 was 78% for roast beef (2.94 mg vitamin B-6) and 86% for roast pork (3.87 mg vitamin B-6), when determined using pigs fitted with an end-to-side ileo-rectal anastomosis (ESV). The apparent ileal digestibilities of the three forms of vitamin B-6 for roast beef were 75% for pyridoxine (0.18 mg), 76% for pyridoxal (0.75 mg), and 94% for pyridoxamine (2.22 mg), in EEV pigs, and 65% for pyridoxine (0.20 mg), 62% for pyridoxal (0.77 mg), and 84% for pyridoxamine (1.95 mg), in ESV pigs, respectively (Roth-Maier et al. 1998). The apparent ileal digestibilities of the three vitamers for roast pork were 90 and 77% for pyridoxine (0.31–0.43 mg), 85 and 84% for pyridoxal (1.58–1.71 mg), and 91 and 89% for pyridoxamine (1.86–2.01 mg), in EEV and ESV pigs, respectively (Roth-Maier et al. 1998).

In a pig digestibility study involving EEV ileostomized pigs, Roth-Maier, Kettler, and Kirchgessner (2002) showed that the apparent ileal digestibility of vitamin B-6 in milk powder (2.01 mg vitamin B-6) was 84%, 67% for boiled whole eggs (1.71 mg vitamin B-6), and 85% for stewed fish (Alaska pollack, 2.61 mg vitamin B-6) (Table 2). The apparent ileal digestibility of the two main forms of vitamin B-6 in milk powder (1.45 mg pyridoxal per kg dry matter and 0.78 mg pyridoxamine per kg dry matter) was 87% for pyridoxal and 75% for pyridoxamine. While the level of pyridoxine in milk powder was below the detection limit of 0.042 mg per kg dry matter, an apparent ileal digestibility value for pyridoxine of 85% was reported, but this value must be interpreted with caution (Roth-Maier, Kettler, and Kirchgessner 2002). The apparent ileal digestibilities of pyridoxal (2.19 mg pyridoxal per kg dry matter) and pyridoxamine (0.42 mg pyridoxamine per kg dry matter) in boiled whole eggs were observed to be 82 and 27%, respectively (Roth-Maier, Kettler, and Kirchgessner 2002). The apparent ileal digestibilities of the three dietary forms of vitamin B-6 in fish (0.26 mg pyridoxine per kg dry matter, 3.42 mg pyridoxal per kg dry matter, and 2.77 mg pyridoxamine per kg dry matter) were 22% for pyridoxine, 89% for pyridoxal, and 85% for pyridoxamine (Roth-Maier, Kettler, and Kirchgessner 2002).

In a human study involving nine male participants, Kabir, Leklem, and Miller (1983) showed that the consumption of canned tuna (1.52 mg vitamin B-6) resulted in 98% of ingested vitamin B-6 lost in urinary vitamin B-6 and urinary 4-pyridoxic acid (4-PA) and fecal vitamin B-6. Kabir, Leklem, and Miller (1983) also found that 53% of vitamin B-6 ingested from canned tuna was excreted as 4-PA in the urine.

Bioavailability of vitamin B-6 in plant-based foods

In a pig digestibility study involving pigs fitted with an end-to-end ileo-rectal anastomosis (EEV), the apparent ileal digestibility of vitamin B-6 in boiled soyabeans (3.34 mg vitamin B-6) was 76% (Roth-Maier, Kettler, and Kirchgessner 2002) (Table 2). The apparent ileal digestibility of the pyridoxine (3.90 mg per kg dry matter), pyridoxal (0.31 mg per kg dry matter), and pyridoxamine (4.83 mg per kg dry matter) forms of vitamin B-6 in boiled soyabeans were 98, 46, and 32%, respectively (Roth-Maier, Kettler, and Kirchgessner 2002). Soyabean meal (2.29 mg vitamin B-6) had an apparent ileal digestibility of vitamin B-6 of 75%, based on the oro-ileal vitamin B-6 difference in EEV ileostomized pigs (Roth-Maier, Kettler, and Kirchgessner 2002), but soyabean meal is generally not consumed by humans and this bioavailability value will not be considered further.

In a pig digestibility study using EEV ileostomized pigs, Roth-Maier, Kettler, and Kirchgessner (2002) found that the apparent ileal digestibility of vitamin B-6 in raw white cabbage (6.23 mg vitamin B-6) was 91% (Table 2), with the apparent ileal digestibilities of the three B-6 vitamers reported as 98% for pyridoxine (12.11 mg per kg dry matter), 69% for pyridoxal (1.66 mg per dry matter), and 76%

for pyridoxamine (1.47 mg per kg dry matter). In the same pig study (EEV ileostomized pigs), the apparent ileal digestibility of vitamin B-6 in Brewer's yeast (2.42 mg vitamin B-6) was 78% (Table 2), and the apparent ileal digestibility of pyridoxine (6.28 mg per kg dry matter) was 78%, and 80% for pyridoxamine (16.08 mg per dry matter) (Roth-Maier, Kettler, and Kirchgessner 2002). The consumption of bananas (9.10 mg vitamin B-6) by EEV ileostomized pigs resulted in an apparent ileal digestibility of vitamin B-6 of 86% (Table 2), with apparent ileal digestibilities of 95% for pyridoxine (3.90 mg per kg dry matter) and 91% for pyridoxamine (4.83 mg per kg dry matter) (Roth-Maier, Kettler, and Kirchgessner 2002). When wheat bran was consumed by EEV ileostomized pigs, the apparent ileal digestibility of vitamin B-6 in wheat bran (3.30 mg vitamin B-6) was 56% (Table 2), with apparent ileal digestibility values of 69% for pyridoxine (5.97 mg per kg dry matter) and 26% for pyridoxamine (0.50 mg per kg dry matter) (Roth-Maier, Kettler, and Kirchgessner 2002). Using EEV ileostomized pigs, the apparent ileal digestibilities of vitamin B-6 in barley (3.91 mg vitamin B-6), rye (1.81 mg vitamin B-6), and maize (3.53 mg vitamin B-6), were 63, 51, and 67%, respectively (Table 2). The apparent ileal digestibility of pyridoxine from these three cereal grains products (0.18–2.01 mg pyridoxine per kg dry matter) ranged from 14 to 91%, and the apparent ileal digestibility of pyridoxamine (0.36–1.12 mg per kg dry matter) varied from 29 to 64%. Intake of the B-6 vitamer pyridoxal was low, and Roth-Maier, Kettler, and Kirchgessner (2002) observed an ileal digestibility of pyridoxal of 41% for rye (0.22 mg pyridoxal per kg dry matter) and 79% for maize (1.73 mg pyridoxal per kg dry matter). In the same EEV pig digestibility study (Roth-Maier, Kettler, and Kirchgessner 2002), the apparent ileal digestibility of vitamin B-6 in boiled brown rice (1.62 mg vitamin B-6, 1.33 mg pyridoxine per kg dry matter), that had the hulls removed but the bran left, was 16% (43% in the form of pyridoxine) (Table 2).

In an oro-ileal balance study using EEV ileostomized pigs and pigs fitted with an end-to-side (ESV) ileo-rectal anastomosis, Roth-Maier et al. (1998) found that the apparent ileal digestibility of vitamin B-6 in boiled potatoes with skin (5.60 mg vitamin B-6) was 87% in EEV pigs (Table 2) and 81% in ESV pigs. Using EEV ileostomized pigs, the apparent ileal digestibility of pyridoxine (4.11 mg) was 98%, 46% for pyridoxal (0.53 mg), and 66% for pyridoxamine (0.94 mg), and using ESV ileostomized pigs, the apparent ileal digestibility of pyridoxine (4.10 mg) was 96%, 42% for pyridoxal (0.51 mg), and 41% for pyridoxamine (0.94 mg) (Roth-Maier et al. 1998). Roth-Maier et al. (1998) also reported that the mean apparent ileal digestibility of vitamin B-6 in wheat (2.74–2.89 mg vitamin B-6) was 69% in EEV pigs (Table 2) and 63% in ESV pigs. The mean apparent ileal digestibility of pyridoxine (1.84–1.90 mg) was 86% in EEV pigs and 89% in ESV pigs, and for pyridoxal (0.52–0.60 mg), 61% in EEV pigs and 50% in ESV pigs (Roth-Maier et al. 1998). Using EEV ileostomized pigs, the B-6 vitamer pyridoxamine in wheat (0.41 mg pyridoxamine) had an ileal digestibility of 0 and 8%, and the excretion of pyridoxamine in ileal effluent was found to be higher than intake in some EEV pigs and most ESV pigs (Roth-Maier et al. 1998). The consumption of wheat- and rye-based bread (2.16–2.18 mg vitamin B-6) gave a higher apparent ileal digestibility of vitamin B-6 of 71% in EEV pigs (Table 2) compared to that of 47% in ESV pigs (Roth-Maier et al. 1998). Using EEV ileostomized pigs, the apparent ileal digestibility of pyridoxine in whole-grain bread (0.96 mg pyridoxine) was 92%, 53% for pyridoxal (0.47 mg), and 24% for pyridoxamine (0.48 mg) (Roth-Maier et al. 1998). Using ESV ileostomized pigs, the apparent ileal digestibilities of pyridoxine and pyridoxal in whole-grain bread (1.24 mg pyridoxine and 0.45 mg pyridoxal) were 89 and 36%, respectively, but the ileal excretion of pyridoxal was higher than intake from whole-grain bread (0.37 mg pyridoxamine) (Roth-Maier et al. 1998).

In a human study evaluating the utilization of vitamin B-6 from a diet supplemented with wheat bran (1.69 mg vitamin B-6), Lindberg, Leklem, and Miller (1983) reported that 37% of the consumed vitamin B-6 was excreted in feces, suggesting that the fecal digestibility of vitamin B-6 was 63% for the mixed diet with added wheat bran. It was also reported by Lindberg, Leklem, and Miller (1983) that urinary total vitamin B-6 losses ranged from 7.4% to 7.9% of intake, 36% of vitamin B-6 intake was excreted in the urine as 4-pyridoxic acid (4-PA), and a mean of 81% of dietary vitamin B-6 intake was released as urinary total vitamin B-6, urinary 4-PA, and fecal total vitamin B-6. Similarly, 89% (Kabir, Leklem, and Miller 1983) and 90% (Leklem et al. 1980) of vitamin B-6 in whole-wheat bread (1.20–1.56 mg vitamin B-6) was excreted as urinary and fecal vitamin B-6 and urinary 4-PA. It was also found that the excretion of 4-PA in the urine as a percentage of dietary vitamin B-6 intake was 39, 75, 93, and 94%, when whole-wheat bread (1.56 mg vitamin B-6, Kabir, Leklem, and Miller 1983), whole-wheat bread (1.20 mg vitamin B-6, Leklem et al. 1980), white bread (0.35 mg vitamin B-6, Leklem et al. 1980), and white bread fortified with vitamin B-6 (1.18 mg vitamin B-6, Leklem et al. 1980), were respectively consumed. A study by Kabir, Leklem, and Miller (1983) showed that 86% of the vitamin B-6 ingested from peanut butter (1.56 mg vitamin B-6) was excreted as vitamin B-6 and 4-PA in the urine and fecal vitamin B-6 in nine male human participants, and 30% of ingested vitamin B-6 was excreted as 4-PA.

Comparison of vitamin B-6 bioavailability between animal- and plant-based foods

The mean estimates of the bioavailability of vitamin B-6 for animal-sourced foods and for plant-based foods are based on oro-ileal digestibility studies conducted in pigs that underwent end-to-end anastomosis (EEV) with a preserved ileo-caeco-colic valve (Figure 1). Foods of animal origin that were rich in vitamin B-6 included beef, pork, milk, eggs, and fish (Table 2). The overall apparent ileal digestibility of vitamin B-6 in these animal-sourced foods was 83% (Figure 1). Pyridoxal as the predominant form of vitamin B-6 present in animal-based foods had an average apparent ileal digestibility of 84%, while the B-6 vitamer pyridoxamine had an average ileal digestibility of 74%.

Plant-based foods that contained vitamin B-6 included soybeans, potatoes, white cabbage, yeast, bananas, wheat, wheat bran, bread, barley, rye, maize, and rice (Table 2). The overall apparent ileal digestibility of vitamin B-6 in these plant-based foods was 68% (Figure 1). Pyridoxine as the main form of vitamin B-6 found in plant-based foods had a mean apparent ileal digestibility of 78%, and the average apparent ileal digestibility of pyridoxamine was 48%. The bioavailability of vitamin B-6 was also evaluated in pigs that were fitted with an end-to-side ileo-rectal anastomosis (ESV) (Roth-Maier et al. 1998), and this resulted in a mean apparent ileal digestibility of 82% for beef and pork, and 63% for potatoes, wheat, and bread. Based on the comparative data within each anastomosis method (end-to-end or end-to-side) in growing pigs, it can be concluded that in general vitamin B-6 is more bioavailable in animal-based foods than in plant-based foods.

Vitamin B-12

Vitamin B-12 absorption and utilization

Vitamin B-12 (cobalamin) is a water-soluble B vitamin, essential for blood formation and plays an important role in the metabolism of fatty acids and nervous function (Allen 2010; Bates and Heseker 1994; IOM (Institute of Medicine, US) 1998; Scott 1997; WHO and FAO 2004). Naturally occurring vitamin B-12 is predominantly found in foods of animal origin, as vitamin B-12 is mostly produced from microbial synthesis and derived from the absorption of vitamin B-12 synthesized in the rumen and intestinal tract of animals, and the ingestion of vitamin B-12-containing animal tissue by animals (Allen 2010; Doets et al. 2013; Gille and Schmid 2015; Scott 1997; Watanabe 2007; Watanabe et al. 2002). Certain plant foods, such as green and purple lavers (Nori), contain vitamin B-12, while other edible algae and cyanobacteria contain only traces of biologically active vitamin B-12 (Watanabe 2007; Watanabe et al. 2002).

The absorption of dietary vitamin B-12 includes its release from food proteins in the stomach, its binding to a protein known as the R protein or a protein- and carbohydrate-containing intrinsic factor in the stomach, and the entry of that R protein-vitamin B-12 complex along with free intrinsic factor into the duodenum (Reizenstein, Cronkite, and Cohn 1961; Reizenstein, Ek, and Matthews 1966). In the jejunum, pancreatic proteases degrade both free R protein and complexes of R protein and vitamin B-12, so that the released vitamin B-12 binds to the intrinsic factor (Holdsworth and Coates 1961; Reizenstein, Cronkite, and Cohn 1961; Reizenstein, Ek, and Matthews 1966). That intrinsic factor-vitamin B-12 complex is mainly absorbed in the ileum and it is considered that vitamin B-12 is not absorbed in the large intestine (Armstrong 1968; Henderickx et al. 1964; Holdsworth and Coates 1961; Reizenstein, Cronkite, and Cohn 1961; Reizenstein, Ek, and Matthews 1966). The intrinsic factor-mediated intestinal absorption system is estimated to be saturated at about 1.5 to 3.0 µg of vitamin B-12 per meal (Watanabe 2007).

Determination of the bioavailability of dietary vitamin B-12 and supplementary vitamin B-12 in purified form and in food

The bioavailability of naturally occurring vitamin B-12 from food sources is generally determined using isotopes, but is sometimes assessed using the difference between food intake and ileal or fecal excretion measurements.

Studies have determined the availability of supplementary vitamin B-12 in purified form and in different food matrices in adult humans and pigs, used as an animal model for adult humans. Based on the measurement of the net flux of blood plasma vitamin B-12 in the portal drained viscera in pigs fitted with a catheter in the portal vein, Dalto et al. (2018) found that the apparent bioavailability of supplementary vitamin B-12 in its synthetic purified form (25.0 µg) was 17.5%. This low value likely reflects saturation of the uptake system. Using the whole body counting measurement of isotopically labeled (^{58}Co) vitamin B-12 in adult human participants over the age of 60 years, Russell, Baik, and Kehayias (2001) reported an apparent availability of supplementary vitamin B-12 in its purified form dissolved in water (0.25 µg vitamin B-12) of 55%, from enriched (2% fat) milk (0.45 µg vitamin B-12) of 65%, and from enriched white bread (0.35 µg vitamin B-12) of 55%. A review by Melse-Boonstra (2020) suggested that the bioavailability of vitamin B-12 in milk products was 65%, but that value is an estimate of the availability of supplementary vitamin B-12 added to enrich milk (Russell, Baik, and Kehayias 2001).

In a human study involving healthy human participants over the age of 60 years and based on the measurement of isotopically labeled (^{14}C) vitamin B-12 ingested and excreted in feces and urine, Garrod et al. (2019a) showed that the apparent utilization of supplementary vitamin B-12 added to enrich white bread dinner rolls (0.80 µg vitamin B-12) was 48%.

Bioavailability of vitamin B-12 in animal-sourced foods

Doscherholmen, McMahon, and Ripley (1978) found that the apparent availability of vitamin B-12 was 63% following consumption of chicken meat, by measuring the amount of isotopically labeled (^{57}Co) vitamin B-12 excreted in fecal samples as a percentage of intake, in three human participants with normal pre-study serum vitamin B-12 concentrations. It was observed that the apparent fecal digestibility of vitamin B-12 was 65% when 100 g of chicken meat (0.42–0.64 µg vitamin B-12) was consumed, 62% when 200 g of chicken meat (0.84–1.28 µg vitamin B-12) was ingested, and 61% when the intake was 300 g of chicken meat (1.26–1.92 µg vitamin B-12) (Table 2). Similarly, using whole body counting of isotopically labeled (^{60}Co) vitamin B-12, Heyssel et al. (1966) found that when seven healthy young men consumed 100, 200, and 300 g of sheep mutton meat patties, the apparent availability of vitamin B-12 was 65%, 83%, and 52%, respectively. The best estimate of the apparent availability of vitamin B-12 from sheep mutton meat within the intake levels of saturation would be that of 65% from 100 g of sheep mutton meat (0.95 µg vitamin B-12) (Table 2), rather than from 200 g (3.03 µg vitamin B-12) and 300 g (5.11 µg vitamin B-12) of sheep mutton meat.

Using a whole body counting of isotopically labeled (^{60}Co) vitamin B-12, Heyssel et al. (1966) reported that the consumption of sheep liver paste (38.0 µg vitamin B-12) resulted in an apparent availability of vitamin B-12 of 9.1% in six healthy young men, 4.5% in four healthy older adults, and 1.8% in five patients with pernicious anemia. Using the oro-fecal balance method, the apparent fecal digestibility of vitamin B-12 in beef or pig liver (20.0–24.0 µg vitamin B-12) was 30% in eleven healthy human subjects and 36% in ten pernicious anemia patients (Reizenstein and Nyberg 1959). However, these relatively low availability values reflect the saturated and low uptake of vitamin B-12 given the large amounts of vitamin B-12 ingested from sheep liver (38.0 µg vitamin B-12) (Heyssel et al. 1966) and beef or pig liver (20.0–24.0 µg vitamin B-12) (Reizenstein and Nyberg 1959).

The apparent availability of vitamin B-12 following the consumption of cooked fish fillets (rainbow trout) was assessed by measuring the amount of isotopically labeled (^{57}Co) vitamin B-12 excreted in fecal samples as a percentage of that ingested (Doscherholmen, McMahon, and Economon 1981). In three healthy adults, increasing the intake doses of vitamin B-12 from 50 g (1.95–2.18 µg vitamin B-12), 100 g (3.90–4.50 µg vitamin B-12), 200 g (7.80–10.90 µg vitamin B-12), to 300 g (11.7–15.6 µg vitamin B-12) of fish resulted in an apparent fecal digestibility of vitamin B-12 of 42, 38, 43, and 30%, respectively. As the uptake of vitamin B-12 may have been saturated at higher intakes of fish (3.90–15.6 µg vitamin B-12), only the apparent fecal digestibility of vitamin B-12 of 42% from 50 g of fish (1.95–2.18 µg vitamin B-12) will be considered (Table 2).

Doscherholmen, McMahon, and Ripley (1975) demonstrated that the method of cooking and form of eggs did not significantly influence the apparent availability of vitamin B-12 using the fecal excretion method, or the apparent utilization of vitamin B-12 using the urinary excretion technique, after giving isotopically labeled (^{57}Co) vitamin B-12 to eighteen healthy human participants with normal serum vitamin B-12 concentrations. When 0.50 to 0.56 µg of vitamin B-12 was ingested from the consumption of fried whole eggs with liquid egg yolks, soft-boiled whole eggs, scrambled whole eggs, and scrambled egg yolks, the apparent fecal digestibility of vitamin B-12 was 76, 76, 73, and 64% respectively (Table 2).

Using the urinary excretion method, the apparent utilization of vitamin B-12 was 9.2% when fried whole eggs were consumed, 8.9% for boiled whole eggs, 3.7% for scrambled whole eggs, and 8.0% for scrambled egg yolks (Doscherholmen, McMahon, and Ripley 1975). Using the difference between the intake of isotopically labeled (^{14}C) vitamin B-12 and excretion in both feces and urine, Garrod et al. (2019b) showed that the mean apparent utilization of vitamin B-12 in scrambled whole eggs was 30%, and the apparent utilization of vitamin B-12 was statistically significantly greater when lower doses of vitamin B-12 (1.40–1.66 µg) in eggs were consumed compared to higher doses (2.38–2.65 µg).

Two pig studies assessed the apparent availability of vitamin B-12, by measuring the net flux of blood plasma vitamin B-12 across the portal drained viscera following consumption of milk and cheese, using growing pigs fitted with a catheter in the portal vein (Dalto et al. 2018; Matte, Guay, and Girard 2012). An availability value of vitamin B-12 ranging between 8 and 10% for raw skimmed milk, pasteurized (temperature of 73 °C) skimmed milk, and microfiltrated and cold pasteurized (temperature of 35 °C) milk was observed by Matte, Guay, and Girard (2012), but the vitamin B-12 system was saturated with an intake of vitamin B-12 ranging from 47.7 to 86.7 µg per meal. Similarly, the uptake of vitamin B-12 was also saturated when Dalto et al. (2018) provided 24.8 µg of vitamin B-12 in Cheddar cheese and 25.1 µg of vitamin B-12 in Swiss cheese. The apparent availability of vitamin B-12 was 33 and 12% following the consumption of Cheddar cheese and Swiss cheese, respectively. Given that these measures of availability were made under conditions of saturation of the uptake system, the values obtained imply that vitamin B-12 is highly available from milk and milk products.

Comparison of vitamin B-12 bioavailability between animal- and plant-based foods

The bioavailability of naturally occurring vitamin B-12 in animal-sourced foods was 65% (Figure 1), and was based on suitable intake levels ranging from 0.42 to 2.18 µg of vitamin B-12, from the consumption of chicken, sheep mutton, eggs, and fish (Table 2). Vitamin B-12 is generally not found in plant-sourced foods unless it has been added as a supplement. It was reported that the bioavailability of supplementary pure vitamin B-12 (0.25 µg vitamin B-12) was 55%, and when synthetic vitamin B-12 was added to food (0.35–0.45 µg vitamin B-12), the availability of supplementary vitamin B-12 ranged from 55% for enriched white bread to 65% for enriched milk. However, these availability estimates for supplementary vitamin B-12 are significantly lower than the reported bioavailability values of naturally occurring vitamin B-12 found in animal-sourced foods (Table 2). It is important to interpret with caution the bioavailability estimates of naturally occurring vitamin B-12, based on appropriate physiological intake levels that do not saturate the uptake system.

Vitamin C

Vitamin C absorption and utilization

Vitamin C (ascorbic acid, ascorbate, cevitamic acid) is a water-soluble vitamin which is the least stable of all of the vitamins (Bates and Heseker 1994; IOM (Institute of Medicine, US) 2000; WHO and FAO 2004). Vitamin C is easily lost from foods with water, and destroyed during heat treatment of foods, such as home cooking, and in industrial canning and processing methods (Bates 1997a; Levine et al. 1999). Vitamin C is essential for the maintenance of cartilage, bone, and tooth structure, collagen synthesis, and the metabolism of cholesterol to bile acids (Bates 1997a; Levine et al. 1995, 1999). Vitamin C also functions as an anti-oxidant by readily scavenging reactive oxygen and nitrogen species (Bates 1997a; Levine et al. 1995, 1999). Symptoms that present with a deficiency of vitamin C, called scurvy, include lesions in the mouth, bleeding gums, and weak bones and

joints (Bates 1997a; IOM (Institute of Medicine, US) 2000; Levine et al. 1996; Sauberlich 1975; WHO and FAO 2004). Vitamin C is found mostly in vegetables and fruits, with orange juice and kiwifruit being common sources (Bates 1997a; Levine et al. 1995, 1999).

Dietary vitamin C is actively absorbed in the ileum to enter the systemic circulation for distribution to target cells and tissues (Carr and Vissers 2013; Melnick, Hochberg, and Oser 1945; Said 2011; Sauberlich 1975). When intake levels of vitamin C are greater than 200 mg, vitamin C is absorbed by passive diffusion through the small intestine, and the kidney contributes to vitamin C homeostasis by excreting excess vitamin C in the urine (Carr and Vissers 2013; Levine et al. 1996, 1999; Melnick, Hochberg, and Oser 1945; Olson and Hodges 1987; Said 2011; Sauberlich 1975).

Determination of the bioavailability of dietary vitamin C and supplementary vitamin C in purified form

The bioavailability of vitamin C from food sources is generally determined by measuring the amount of vitamin C in the blood and relating this to food intake, to reflect availability (%), and in the urine, to reflect utilization (%), in normal replete adult humans. The results are usually expressed in relative terms to the responses to the ingestion of vitamin C consumed in its purified form. The bioavailability of synthetic purified vitamin C is considered to be 70–90% (Levine et al. 1999; Melse-Boonstra 2020), and therefore absolute availability measures can be derived by relating relative bioavailability to this baseline.

Bioavailability of vitamin C in plant-based foods

Several studies have estimated the availability and utilization of vitamin C in vegetables and fruits. Hollinger (1948) demonstrated that the relative availability of vitamin C was 91% from the consumption of blanched mustard greens (57 mg vitamin C). Mangels et al. (1993) found that raw broccoli (109 mg vitamin C) had a relative vitamin C availability of 73%, and 97% for cooked broccoli (108 mg vitamin C). Kondo et al. (2012) found that the consumption of mashed potatoes (50 mg vitamin C) had a relative availability of vitamin C of 68%, and the ingestion of potato chips (50 mg vitamin C) had a relative vitamin C availability of 66%. In one study, Clayton and Borden (1940) showed that the consumption of baked potatoes (50 mg food vitamin C, supplemented with a 25 mg vitamin C dose) had a relative availability of vitamin C of 101%. In another study by the same group (Clayton and Borden 1943), the relative availability of vitamin C in raw green cabbage (60 mg food vitamin C, supplemented with a 25 mg vitamin C dose) was found to be 121%, and 111% for tomato juice (60 mg food vitamin C, supplemented with a 25 mg vitamin C dose). The above relative availability values can be transformed to absolute availability values based on the assumption that 80% of synthetic pure vitamin C (100 mg dose) is available (Levine et al. 1999). The absolute apparent availabilities of vitamin C were 73% for mustard greens, 58% for raw broccoli, 78% for cooked broccoli, 97% for raw green cabbage, 89% for tomato juice, 81% for baked potatoes, 54% for mashed potatoes, and 53% for potato chips (Table 2).

In a human study by Kondo et al. (2012), the urinary response to the ingestion of mashed potatoes (50 mg vitamin C) and potato chips (50 mg vitamin C) was 99 and 102% of that of pure crystalline vitamin C, respectively. In another study by Clayton and Borden (1943), the relative utilization of vitamin C in raw green cabbage (60 mg vitamin C, supplemented with a 25 mg vitamin C dose) and tomato juice (60 mg vitamin C, supplemented with a 25 mg vitamin C dose) was 92 and 94%, respectively. Assuming that 75% of ingested synthetic pure vitamin C (100 mg dose) is utilized in healthy humans (Levine et al. 1999), the absolute apparent utilization of vitamin C in raw green cabbage was 69%, 74% for mashed potatoes, 77% for potato chips, and 71% for tomato juice.

Mangels et al. (1993) found that the relative availability of vitamin C was 83% from the consumption of orange segments (109 mg vitamin C) and 93% from the ingestion of reconstituted frozen orange juice (110 mg vitamin C). The relative availabilities of vitamin C in orange juice (50 mg vitamin C) and strawberries (50 mg vitamin C) were 103 and 107%, respectively (Todhunter, Robbins, and McIntosh 1942). Todhunter and Fatzer (1940) found that the relative availability of vitamin C in red raspberries (60 mg vitamin C) was 96%. The relative availability of vitamin C in papayas (75 mg vitamin C) was 108%, and with guava juice freshly made from cooked guavas (75 mg vitamin C), the relative vitamin C availability was 112% (Hartzler 1945). Based on the assumption that the ingestion of a dose of 100 mg of pure vitamin C is 80% available (Levine et al. 1999), the absolute apparent availability of vitamin C was found to be 66% for oranges, 78% for orange juice, 86% for strawberries, 77% for red raspberries, 86% for papayas, and 90% for guava juice (Table 2). In a randomized cross-over human study, Carr, Bozonet, and Vissers (2013) found that the relative availability of vitamin C in gold kiwifruit (200 mg vitamin C) was 108%. Based on the assumption that a 200 mg dose of purified vitamin C had a vitamin C availability of 72% (Levine et al. 1999), the absolute apparent availability of vitamin C was calculated as being 78% for gold kiwifruit (Table 2).

Using the urinary excretion method, Carr, Bozonet, and Vissers (2013) found a relative utilization of vitamin C in gold kiwifruit (200 mg vitamin C) of 138%, and when adjusted for the 50% utilization value of the reference dose of 200 mg of pure vitamin C (Levine et al. 1999), an apparent utilization of vitamin C in gold kiwifruit of 69% was calculated. The relative utilization of vitamin C in orange juice (100 mg vitamin C) was 101% (Hawley, Stephens, and Anderson 1936), 118% for red raspberries (60 mg vitamin C) (Todhunter and Fatzer 1940), 105% for papayas (75 mg vitamin C) (Hartzler 1945), and 101% for guava juice (75 mg vitamin C) (Hartzler 1945). Assuming that at 100 mg doses, purified vitamin C was 75% utilized in the human body (Levine et al. 1999), the absolute apparent utilization of vitamin C was calculated to be 76% for orange juice, 89% for red raspberries, 79% for papayas, and 76% for guava juice.

Comparison of vitamin C bioavailability between animal- and plant-based foods

The bioavailability of naturally occurring vitamin C in plant-based foods was 76% (Figure 1), and was based on the apparent bioavailability of vitamin C in vegetables and vegetable products of 73% (Table 2), and 80% for fruits and fruit products (Table 2). These absolute apparent availability values (Table 2) were calculated from the relative measurements of vitamin C in the blood that were 91 and 101% following the ingestion of vegetables and fruits, respectively, and relative to the response following the consumption of purified vitamin C. The vegetable sources studied were mustard greens, broccoli, green cabbage, potatoes, and tomato juice, and the fruit sources studied were oranges, gold kiwifruit, strawberries, red raspberries, papayas, and guava juice (Table 2). Animal-sourced foods are generally not important sources of vitamin C. Some beverages may be enriched with vitamin C. The bioavailability of supplementary synthetic purified vitamin C ranges from 70 to 90%. Therefore, supplementary vitamin C added to animal-based foods may be as bioavailable as naturally occurring vitamin C found in plant-based foods.

Choline

Choline absorption and utilization

Although choline is recognized strictly as not a true vitamin, choline is an essential water-soluble compound that is related to the B vitamins (Arias et al. 2020; Goh, Cheam, and Wang 2021; IOM (Institute of Medicine, US) 1998). Choline is required in higher daily amounts (400–600 mg for adult humans) compared with the vitamins (< 100 mg) (IOM (Institute of Medicine, US) 1998; Zeisel 2000; Zeisel and da Costa 2009; Zeisel et al. 2003). In a depletion-repletion human study, Fischer et al. (2007) showed that a daily intake of at least 400 mg choline per 70 kg body weight is sufficient to replete about 60% of the depleted state in human adults who displayed signs of organ dysfunction. The essential functions of choline include protection against oxidative damage, formation of the neurotransmitter acetylcholine, as precursor for the biosynthesis of phospholipids involved in lipid transport (phosphatidylcholine) and cell membrane structure and signaling (sphingomyelin), and methyl-group metabolism of homocysteine to methionine (betaine) (Goh, Cheam, and Wang 2021; IOM (Institute of Medicine, US) 1998; Zeisel and Blusztajn 1994; Zeisel and da Costa 2009; Zeisel et al. 2003). Animal-sourced foods provide more choline per unit weight than plant-sourced foods (Zeisel et al. 2003). The major animal-based food sources of choline include eggs, liver, meat, milk, and fish, while foods of plant origin containing appreciable amounts of choline include the cruciferous vegetables (Brassica genus), legumes, and some cereal grains (Arias et al. 2020; Zeisel et al. 2003; Zeisel and Blusztajn 1994; Zeisel and da Costa 2009). Choline is found in foods as water-soluble choline (free choline, phosphocholine, and glycerophosphocholine) and fat-soluble choline (phosphatidylcholine, and sphingomyelin) (Arias et al. 2020; Goh, Cheam, and Wang 2021; Zeisel and Blusztajn 1994; Zeisel and da Costa 2009). Lecithins added during food processing increase the level of phosphatidylcholine in foods (IOM (Institute of Medicine, US) 1998; Zeisel and Blusztajn 1994; Zeisel and da Costa 2009).

Absorption of dietary choline in the jejunum and ileum mainly occurs through choline-specific transporters in the enterocyte (Goh, Cheam, and Wang 2021). Water-soluble forms of choline enter the portal circulation to be distributed to the liver, while fat-soluble choline is incorporated into chylomicrons, and transported in the lymphatic circulation (Arias et al. 2020; Goh, Cheam, and Wang 2021). Some choline is metabolized by gut bacteria to betaine or trimethylamine, which are then absorbed in the small intestine (Arias et al. 2020; Goh, Cheam, and Wang 2021). Betaine is also found in foods but as it is synthesized from choline by irreversible reactions, dietary betaine does not contain choline nor can it be converted back to choline, and therefore should not be considered in total food choline content (Zeisel et al. 2003; Zeisel and da Costa 2009). A small amount of choline can be generated by intestinal microflora, and this endogenous bacterial synthesis of choline is stimulated by the ingestion of excess methionine, which serves as a methyl substrate for the biosynthesis of phosphatidylcholine (Goh, Cheam, and Wang 2021; Zeisel 2000; Zeisel and Blusztajn 1994; Zeisel and da Costa 2009).

Determination of the bioavailability of dietary choline

The bioavailability of choline from food sources has been determined in human studies using the measurement of choline and its derivatives in the circulating blood.

Bioavailability of choline in animal-sourced foods

In a randomized cross-over human study involving eighteen healthy adults, Smolders et al. (2019) found that natural choline in egg yolks (3000 mg) increased postprandial plasma responses of choline over six hours more than synthetic pure choline (choline bitartrate, 3000 mg choline) by about three times. However, Lemos et al. (2018) did not observe such an increase in plasma choline responses over four weeks following the consumption of whole eggs (400 mg choline) in thirty healthy human participants, with an estimated relative availability of choline of 101% in comparison with the consumption of supplementary choline (choline bitartrate, 400 mg choline). In a human study involving six healthy adult men, Böckmann et al. (2022) showed that the consumption of eggs (550 mg choline) increased the plasma concentrations of choline over twenty-four hours similarly to that following the intake of a supplement of choline chloride (550 mg choline) or choline bitartrate (550 mg choline). The relative availability of choline in eggs was 104% in comparison with supplementary choline chloride, and 105% in comparison with supplementary choline bitartrate.

Comparison of choline bioavailability between animal- and plant-based foods

There is little information on the bioavailability of choline, the vitamin-like essential nutrient, from food sources. Although the apparent availability of choline in eggs gave

conflicting results, the outcomes suggested that choline naturally occurring in this animal-based food source was as bioavailable as choline given as a supplement. The amount of dietary surplus methionine that may influence choline bioavailability estimates is unclear. More studies are needed to have reliable comparative data estimates of the bioavailability of naturally occurring choline in animal- and plant-based foods.

Discussion

The demand for safe, affordable, and nutritionally adequate plant-based dietary sources of protein, amino acids, minerals, trace elements, and vitamins, to replace animal-sourced foods, necessitates the crucial determination of the comparative amount and bioavailability of these essential nutrients between plant- and animal-based foods. Bioavailability may be defined as the proportion of an ingested nutrient that is released during digestion, intestinally absorbed, transported in biochemical active forms that is available to be utilized in metabolic functions (Baker 1995; Ball 1998, 2006; Bates and Heseker 1994; Gibson 2007; Godber 1990; WHO and FAO 2004). However, the unifying term of bioavailability has been employed generically, and in practice, quantitative measures of the digestibility, absorption, availability and utilization of nutrients have been encompassed to provide "bioavailability" values.

Although *in vitro* digestion models have been used to determine bioaccessibility, which refers to the fraction of a dietary nutrient that has been converted into potentially accessible soluble forms for absorption (Fernández-García, Carvajal-Lérida, and Pérez-Gálvez 2009; Marze 2017), *in vivo* methods in humans or the pig as an animal model for adult humans (Guilloteau et al. 2010; Moughan et al. 1994), are more appropriate approaches to determine bioavailability (Ball 1998, 2006; Bates and Heseker 1994; Godber 1990). It is important to note that bioavailability determined in *in vivo* studies is influenced by the nutritional and health status of the subject. In addition to host-related factors, the quantification of bioavailability is also subject to a number of dietary factors and differences in study methodologies (Gibson 2007; Godber 1990). The measurement of urinary nutrient metabolites, to reflect utilization, may be an inadequate method to determine bioavailability, particularly when the uptake system has reached saturation. Moreover, when studies use oro-fecal balance or measure fecal digestibility, the measurement of nutrient loss in feces needs to be interpreted with caution, as there may be some interference from nutrients synthesized and metabolized by the intestinal microflora mainly in the large intestine (colon) (Said 2013; Yoshii et al. 2019). The oro-ileal balance method (Ileal Digestibility) or experimental methods to determine the fraction of a dietary nutrient that is available in the systemic circulation are better common quantitative tools for bioavailability determination (Bates and Heseker 1994). Isotope labeling has also been employed in bioavailability studies, but may come at a high cost and a potential methodological limitation is in achieving sufficient nutrient labeling (Godber 1990; Heaney 2001). Careful regulation of the different approaches used to determine bioavailability, and appropriate comparative data are necessary to obtain meaningful bioavailability values of essential nutrients in foods. The main objective of this conspectus was to provide a critical review of published studies on the overall bioavailability of vitamins (and choline) in global human foods, in order to allow, wherever possible, a comparison to be made for vitamin bioavailability amongst foods sourced from animals and plants.

There is a lack of studies to estimate the bioavailability of naturally occurring choline, vitamin E, vitamin K, and vitamin D, from food sources. The bioavailability of choline may be confounded by the consumption of excess dietary methionine used to generate choline and endogenously synthesized gut choline, but a relatively high choline intake level is needed, and animal-based foods provide more choline per unit weight than plant-based foods. Based on the measurement of choline in the circulating blood, the limited data indicate that choline found in eggs is as bioavailable as supplementary synthetic pure choline (Böckmann et al. 2022; Lemos et al. 2018; Smolders et al. 2019). There is scarce data on the bioavailability of vitamin E (α-tocopherol), with the bioavailability of vitamin E in nuts estimated to be 54%, in a human oro-ileal balance study involving only two female ileostomy patients (Mandalari et al. 2008). The bioavailability of vitamin K in dark green vegetables has been estimated to be quite low at 16.5% (Figure 1), by measuring the relationship between ingested dose and amount circulating in blood of phylloquinone (vitamin K1) (Booth, Lichtenstein, and Dallal 2002; Garber et al. 1999; Gijsbers, Jie, and Vermeer 1996; Novotny et al. 2010). It is difficult to estimate the bioavailability of dietary vitamin D, as natural food sources of vitamin D provide less than 1 µg of naturally occurring vitamin D. For instance, brown button mushrooms contain 0.18 µg of vitamin D2 (ergocalciferol) per 100 g fresh weight, when cultivated in the dark, but when irradiated with ultraviolet light, brown button mushrooms can contain 491 µg of vitamin D2 (ergocalciferol) per 100 g fresh weight (Urbain et al. 2011). The bioavailability of vitamin D in irradiated brown button mushrooms was estimated to be 66%, based on the measurement of blood serum vitamin D2 (ergocalciferol) in a human study (Urbain et al. 2011). Nowadays, foods are commonly fortified with vitamin D, and it has been found that the mean bioavailability of supplementary vitamin D in fortified foods was 78%, and the responses of circulating vitamin D were similar to that following consumption of vitamin D supplements (Biancuzzo et al. 2010; Natri et al. 2006; Thompson, Lewis, and Booth 1966; Wagner et al. 2008). Similarly, the question remains as to whether synthetic folate (folic acid) added to foods is more bioavailable than natural folate in foods. Cereals and grain food products are usually fortified with folic acid and consumed regularly in the daily diet of humans around the world. It was shown that the bioavailability of folic acid in fortified foods was 85% (Pfeiffer et al. 1997). In comparison, the bioavailability of naturally occurring food folate was found to be slightly greater at 67% for animal-sourced foods than that of 54% for plant-based foods (Figure 1).

Furthermore, ileal digestibility studies involving ileostomized pigs as an animal model for adult humans, showed that the bioavailability of biotin, niacin (vitamin B-3), pantothenic acid, and vitamin B-6, was higher for animal-sourced foods compared with plant-based foods (Figure 1). Based on pig ileal digestibility studies, the bioavailability estimates for thiamin (vitamin B-1) were similar among animal- and plant-based foods (Figure 1). While the bioavailability of riboflavin (vitamin B-2) was found to be slightly lower in animal-sourced foods than in plant-based foods (Figure 1), this may be attributable to the low pig ileal digestibility observations based on only five food sources. Animal-sourced foods are widely recognized as rich natural sources of vitamin B-12 and preformed vitamin A (retinol) in the human diet. The bioavailability of vitamin B-12 (pig ileal digestibility studies) and preformed vitamin A (using the measurement of circulating retinol in human studies) in animal-sourced foods was high at 65 and 74%, respectively (Figure 1). Plant-based foods are the main sources of natural vitamin C and provitamin A carotenoids (β-carotene), and were found to have an estimated bioavailability (using the measurement of circulating vitamin C or β-carotene in human studies) of vitamin C in vegetables and fruits of 76% (Figure 1), and of β-carotene in vegetables of 15.6% (Figure 1). It is important to note that differences in food matrices, and food preparation, processing, and treatment, known to impact vitamin bioavailability, were also addressed. To the best of our knowledge, this is the first review comparing the bioavailability of these thirteen vitamins and choline in their main dietary sources, and presenting comprehensive comparable reliable results (Figure 1).

Many meals and diets are combinations of plant- and animal-sourced foods, and it is plausible that the bioavailability of mixed meals may be estimated from the bioavailability values of individual plant- and animal-based foods. There is some limited evidence for vitamin bioavailability in the context of mixed diets. Human studies have found that natural pantothenic acid and vitamin B-6 were highly available and utilized (50 and 75%, respectively) when consumed in mixed diets comprising half from animal-based foods and half from plant-based foods (Tarr, Tamura, and Stokstad 1981). Moreover, the bioavailability of natural food folate in a non-vegetarian mixed diet that comprise liver paste, vegetables, and fruits, was found to be 70% (Winkels et al. 2007), in comparison with 68% found in plant-based only mixed diets, containing vegetables, fruits, and rye-based foods (Brouwer et al. 1999; Vahteristo et al. 2002). Furthermore, it was estimated that the bioavailability of provitamin A carotenoid β-carotene in a mixed vegetable and fruit diet was 5.6% (van Het Hof et al. 1999a). It is possible that dietary factors, such as food processing and treatment, absorption effectors or inhibitors, and interactions among different food components, may affect vitamin bioavailability in mixed meals, and this requires further investigation.

While vitamin bioavailability was highly variable amongst dietary sources, in general, most vitamins in animal-based foods were found to be more bioavailable than vitamins in plant-based foods. Further studies are needed to determine the bioavailability of some vital vitamins in food, such as vitamin E and vitamin K. Vitamin bioavailability in the context of mixed meals or whole diets is also an important consideration, but data on the bioavailability of vitamins in mixed diets are limited. The considerable experimental evidence for the varying bioavailability of vitamins in animal- and plant-based foods presented here may be reliably employed to characterize the true nutritional value of different foods. Given that most dietary intake requirements for vitamins are described as bioavailable, nutritional adequacy depends on the amount and form and the bioavailability of vitamin in food. The knowledge and application of the vitamin bioavailability estimates are crucial for diet formulation, adequate nutrition, diet-related health outcomes, sustainable food production, and food and nutrient security.

Author contributions

S.M.S.C. was responsible for the study design, conducted the collection of data, analyzed the data, and prepared the manuscript. P.J.M. assisted with the study design, contributed to data analysis, and had primary responsibility for the final content of the manuscript. All authors have read and approved the final manuscript.

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Data availability statement

The data that support the findings of this study are available within the article.

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