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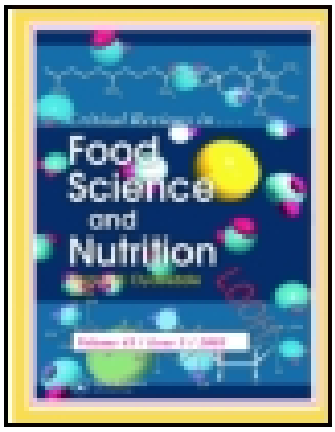

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The unresolved role of dietary fibers on mineral absorption

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The unresolved role of dietary fibers on mineral absorption

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Abstract

Dietary fiber is a complex nutritional concept whose definition and method of analysis has evolved over time. However, literature on the role of dietary fiber on mineral bioavailability has not followed pace. Although in-vitro studies revealed mineral binding properties, both animal and human studies failed to show negative effects on mineral absorption, and even in some cases reported absorption enhancing properties. The existing literature suggests that dietary fibers have negative effects on mineral absorption in the gastrointestinal tract largely due to mineral binding or physical entrapment. However, colonic fermentation of dietary fibers may offset this negative effect by liberating bound minerals and promoting colonic absorption. But existing studies are limited since they did not control for more potent mineral absorption inhibitors such as phytates and polyphenols. Animal studies have mostly been on rats and hence difficult to extrapolate to humans. Human studies have mostly been on healthy young men likely to have an adequate store of iron. The use of different types and amounts of fibers (isolated/added) with varying

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physiological and physicochemical properties makes it difficult to compare results. Future studies can make use of the opportunities offered by enzyme technologies to decipher the role of dietary fibers in mineral bioavailability.

Keywords: bioavailability, plant cell wall, carbohydrase, non-starch polysaccharides, carbohydrate

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1. Introduction

In the past, little attention was paid to fiber. It was simply referred to as roughage or bulk and was measured as crude fiber. However, in the last three to four decades, a great deal of research has brought new insights into the health benefits of dietary fiber. Epidemiological studies have correlated high consumption of dietary fiber (DF) with lower incidences of cardiovascular diseases and colorectal cancer (Park et al., 2005; Tungland & Meyer, 2002). Other benefits of higher fiber intake include decreased low-density lipoprotein (LDL)-cholesterol, lower insulin demand, laxative properties due to increased stool bulk and softening of fecal contents, and better body weight regulation (Gordon, 1989; Brown et al., 1999; Howarth et al., 2001; Slavin, 2008). Diseases like diabetes, atherosclerosis, breast cancer, diverticulitis, and hemorrhoids have also been associated with low intake of fiber (Anderson et al., 2009).

The mounting evidence for the health benefits and the knowledge that has accrued over the years has led to several revisions of the definition of dietary fiber (DeVries et al.,1999; DeVries, 2003). The way the definition has evolved over time is likely to influence our understanding and interpretation of the existing literature. This is particularly true of the literature regarding the effect of dietary fibers on mineral bioavailability, since much of the knowledge was generated in the 1980s and 1990s. In recognition of the different metabolic and physiological effects of different types of dietary fibers, the emphasis of research has evolved from concentrating mainly

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on the amount of fiber to the type of fiber. Hence, whether evidence for the effect of dietary fiber on mineral bioavailability holds true for all types of dietary fibers remains unclear.

Although several reviews of dietary fibers have been published in the last decade (Aleixandre & Miguel, 2008; Weickert & Pfeiffer, 2008; Anderson, et al., 2009), little emphasis was placed on the effects of dietary fibers on mineral bioavailability. The interaction between single components of dietary fibers such as non-digestible oligosaccharides and mineral bioavailability was reviewed (Scholz-Ahrens et al., 2007) but since then, the definition of dietary fiber itself has been subject to revision.

The aim of the present review is thus to give a brief description of the definition of dietary fiber and how it has evolved with time, followed by a synthesis of the literature regarding the effect of dietary fiber on mineral bioavailability to then highlight knowledge gaps. The potential role of emerging enzyme technologies in understanding mineral-fiber interactions as well as improving bioavailability is discussed.

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2. Definitions and classification of dietary fiber

The term dietary fiber was originally coined by Hipsley (1953) and referred to as the non-digestible components of the plant cell wall. Since then, the term has undergone several revisions **Fig. 1** (DeVries, 2003; Lupton et al., 2010) partly because of the considerable debate regarding the most appropriate definition and classification of dietary fibers (Lunn & Buttriss, 2007; Saura-Calixto & Díaz-Rubio, 2007). In the past, much of the debate focused on whether to use an analytically or physiologically appropriate definition, the latter being preferred from a nutritional

standpoint. However, accurate analytical measures are also important, especially for labeling and regulation purposes. In recent years, the nature of the debate has shifted and revolves around whether or not to consider synthetic fibers, oligosaccharides, and animal fibers as dietary fibers (Cummings et al.,2009).

After a decade-long debate on the definition of dietary fibers, a consensus has finally been reached, and a new and unifying definition was adopted by the commission of Codex Alimentarius in 2009.

The Codex definition defines dietary fiber as: ñ*carbohydrate polymers with ten or more monomeric units, which are not hydrolysed by the endogenous enzymes in the small intestine of humans and belong to one of the following categories:*

- Edible carbohydrate polymers naturally occurring in the food as consumed;

- Carbohydrate polymers, which have been obtained from food raw material by physical, enzymatic or chemical means and which have been shown to have a physiological effect of benefit to health as demonstrated by generally accepted scientific evidence to competent authorities;

- Synthetic carbohydrate polymers, which have been shown to have a physiological effect of benefit to health as demonstrated by generally accepted scientific evidence to competent authorities."

The definition leaves the decision to include oligomers with 3-9 degree of polymerization (DP) to national authorities.

Although we are closer than ever before to a long awaited unifying definition of dietary fibers, some unresolved issues remain. These include the decision to consider (or not) oligomers of 3-9

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DP as dietary fibers, a decision that is left to national authorities and thus may differ from one country to another, and the type of evidence of physiological health benefits required for synthetic and isolated polysaccharides to be considered as dietary fibers.

According to the current definition of dietary fiber, the major components are non-starch polysaccharides (NSP), fructans (inulin and fructoligosaccharides), resistant starch and lignin. Along with lignin and resistant starch, NSPs are the major components of total dietary fiber.

Recently, proposals were made to include non-extractable polyphenols as components of dietary fibers (Goñi et al., 2009; Saura-Calixto, 2012). The proposal is based on the existence of a large proportion of polyphenols in foods that are non-digestible in the small intestine but partially fermentable in the colon (Goñi et al., 2009). The 2009 Codex definition recognized lignin and other minor non-carbohydrate components such as polyphenols, waxes, saponins, phytates, cutins and phytosterols as dietary fibers, but only when they are associated with plant cell wall components (McCleary et al., 2010).

The components of dietary fiber are often classified based on their solubility in water at a defined pH, or their fermentability in an in vitro system using aqueous human alimentary enzymes (Tungland & Meyer, 2002). Generally, easily fermentable fibers are soluble whereas poorly fermentable fibers are not (Asp, 1996). Accordingly, dietary fibers like pectin, guar gum, gum arabic, inulin, polydextrose, and oligosaccharides are soluble/ easily fermented, while cellulose, hemicelluloses, lignin and resistant starches are poorly soluble/fermentable (Chawla & Patil, 2010).

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3. Effect of dietary fibers on mineral bioavailability

3.1 Findings from in vitro studies

Several in vitro studies (table 1) have shown that semi-purified insoluble (cellulose, hemicelluloses and lignin) as well as soluble fibers (gums and pectin) have mineral-binding properties (Ismail-Beigi et al., 1977; Fernandez & Phillips, 1982; Debon & Tester, 2001; Bosscher et al., 2003; Miyada et al., 2011). The mineral-binding effect was found to depend on the type of fiber. For instance, in a study by Ismail-Beigi et al., (1977), 42.7 % of the zinc in solution was bound by carboxymethylcellulose, while only 14.5 % was bound by methylcellulose. The binding effect also depended on the concentrations of fiber (Fernandez & Phillips, 1982). In addition, pH and ionic strength determined the binding properties of several fibers, suggesting that ion exchange interactions, probably involving carboxyl and hydroxyl groups are partly responsible for binding (Debon & Tester, 2001; Miyada et al., 2011). At acidic pH, the binding properties of gums are minimal, whereas pectin bound iron is released in solution to varying extents depending on the ionic strength of the solution (Miyada et al., 2011). Among insoluble fibers, lignin was shown to have more mineral binding capacity than cellulose and hemicelluloses, probably because of its polyphenolic nature (Fernandez & Phillips, 1982). The mineral binding properties of both insoluble (cellulose, hemicellulose and lignin) and soluble (pectin) dietary fibers were inhibited by EDTA and citrates but not by ascorbic acid and cysteine (Fernandez & Phillips, 1982).

3.2 Findings from in-vivo studies

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Several animal and human studies (table 2) failed to confirm the negative effects of insoluble (cellulose, hemicelluloses and lignin) and soluble (pectins and gums) fibers on mineral absorption observed in vitro (Cook et al., 1983; Turnlund et al., 1984; Fly et al., 1996; Van den Heuvel et al., 1998; Catani et al., 2003). Although an earlier study on rats showed that the addition of 10% gum of various kinds in a semi-synthetic diet decreased absorption of minerals (i.e. Fe, Zn and Ca), the study was limited by the fact that the concentrations of other more potent absorption inhibitors (i.e. phytates) were not known (Harmuth-Hoene & Schelenz, 1980). A subsequent stable isotope study on young men by Turnlund et al., (1984) showed that Zn absorption was not affected by Ŭ-cellulose but was markedly reduced by phytate.

Studies by Fly et al., (1998) and Cook et al., (1983) also showed that while hemicelluloses and lignin had no negative effect on the absorption of supplemental or added (extrinsic) iron, the iron intrinsic to these fibers was not available for absorption, suggesting that minerals trapped in insoluble fibers are less likely to be available for absorption.

On the other hand, mineral absorption enhancing properties were observed for some soluble dietary fibers such as pectins and fructooligosaccharides while no such effect was observed for insoluble ones (Greger, 1999; Sakai et al., 2000). The absorption enhancing property of soluble fibers does not apply to all minerals but depends on the specific characteristics of the soluble fiber concerned. For instance, absorption enhancing properties were observed in low molecular weight pectins with a high degree of esterification while no such effects were observed in high molecular weight pectins with a low degree of esterification (Kim et al., 1996).

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4. Explaining disparities between in vitro and in vivo studies

Earlier in vitro/ in vivo studies lacked control over more potent absorption inhibitors and enhancers such as phytates, polyphenols, ascorbic acid (Cook et al., 1988, Van den Heuvel et al., 1998). Most of the animal studies were performed on rats, which may be a limiting factor given that iron is more easily absorbed by rats than by humans, especially from sources with low bioavailability mainly due to the presence of phytase in their intestinal tract (Reddy and Cook, 1991). The few existing human studies on the topic were mostly conducted on healthy young men, who likely have adequate stores of iron (Van den Heuvel et al., 1998). Differences in iron bioavailability among diets may be obscured when iron stores are adequate (Hulten et al., 1995). On the other hand, comparison of the results is also difficult because of the use of different types and amounts of fibers with varying physiological and physicochemical properties.

Notwithstanding these limitations, the existing literature suggests that both soluble and insoluble fibers may decrease gastrointestinal absorption due to mineral binding or physical entrapment of minerals. However, both physically and chemically bound minerals are likely to be available for absorption in the colon as a result of fiber fermentation, but this will depend on the fermentability of the fibers. Indeed, a recent study that compared the effect of pectin on iron absorption in ileorectomized, caectomized, and normal rats showed that absorption was reduced in the small intestine whereas it increased in the colon (Miyada et al., 2012). Iron absorption in the large intestine is less efficient than in the duodenum, but could nevertheless be significant in the case of iron deficiency (Yeung et al., 2005).

Some soluble fibers like fructo-oligosaccharides, inulin, and pectin were also reported to have mineral absorption enhancing effects (Sakai et al., 2000). However, the enhancing properties of

inulin have been less consistent as recent human studies failed to show improvements in iron absorption (Coudray et al., 1997; Van den Heuvel et al., 1998; Petry et al., 2012). However, the effect of inulin might has been underestimated since the studies were either conducted on healthy young men (Coudray et al., 1997; Van den Heuvel et al., 1998) or compounds with potential absorption enhancing properties such as maltodextrins were used as a placebo (Miyazato et al., 2010; Petry et al., 2012).

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5. Plausible mechanism for the absorption inhibiting/enhancing effects of fibers

The components of fiber (NSP, lignin, etc.) can form insoluble and/or large complexes through the carboxyl group of uronic acid, the carboxyl and hydroxyl groups of phenolic compounds, and the surface hydroxyl of cellulose, thereby decreasing mineral bioavailability (Torre et al., 1995). NSP-induced digesta viscosity can also prevent contact with digestive enzymes and hence the availability of nutrients for absorption (Van der Klis et al., 1995, Guillon & Champ, 2000). Physical entrapment of minerals intrinsic to the fiber has also been suggested to be responsible for the decrease in absorption (Fly et al., 1996).

On the other hand, the enhancing effect of soluble/fermentable fibers could be related to fermentation products such as osmotically active sugars that may increase passive absorption and/or to the production of weak organic acids that may have absorption enhancing properties (Brommage et al., 1993). The lowering of pH is also likely to result in the reduction of ferric iron to its more bioavailable ferrous form. For instance, much of the iron bound to pectin was found

to be in the ferrous form, probably because of the reduction of ferric iron to ferrous iron by pectins (Miyada et al., 2011).

The fermentation of fibers in the colon often produces short chain fatty acids that can trigger increased proliferation of epithelial cells, which, in turn, increases the absorptive surface area and hence iron absorption (Yeung et al., 2005; Bauer et al., 2006). Indeed, a study on rats with diet-induced iron deficiency anemia (IDA) showed that synthetic xylanooligosaccharides (soluble fiber) promoted recovery from IDA and decreased the expression of divalent metal transporter1 (DMT1) and ferroportin mRNA (Kobayashi et al., 2011).

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6. Added versus dietary fibers

The chemical nature of fiber is complex as it is a mixture of chemical entities. However, in many of the *in vitro* and *in vivo* studies, the effects of fiber on mineral bioavailability were investigated using isolated, semi-purified or synthetic fibers. Due to difficulties in isolating plant cell walls in some plant materials, plant cell wall preparations usually contain different quantitities of non-wall materials that may affect mineral bioavailability. For example, both condensed (proanthocyanidins) and hydrolysable tannins occur in the vacuoles of plant cells (Strack, 1997), but are often associated with cell-wall preparations (Hall & Moore, 1983; Harris & Smith, 2006). In addition, plant cell walls vary enormously in their composition and physical properties depending on the type of cell and the plant species (Harris & Smith, 2006; Knox, 2008). Some of the processes used for isolating the fibers also alter the native composition and properties of the fiber (Elleuch et al., 2011). These plant and process specific differences in the composition and

properties of fibers have frequently been overlooked in studies investigating the role of fiber in mineral bioavailability. It is also likely that the effect of adding fiber to food may not be the same as the effect of the same amount of fiber already present in the food matrix.

7. Use of exogenous enzymes

In recent years, the emergence of enzyme technologies has led to the sale and use of carbohydrases primarily in animal feed but also in the food industry. For example, in the food industry, a combination of pectinase, cellulase, hemicellulase, collectively called macerating enzymes, is used to facilitate the extraction and clarification of fruit and vegetable juices (Bhat, 2000; Grassin & Fauquembergue, 1996). Other food applications include processing of beer, wine, bread and biscuits, and extraction of olive oil (Bhat, 2000). Thanks to the progress made in the past few years, the substrate specificities and efficacy of carbohydrases have increased tremendously. This provided the opportunity to develop better enzymatic methods for the determination of fiber in foods. The use of these enzymes enables *in situ* estimation of the effect of native dietary fibers on mineral bioavailability, and hence avoids the previously encountered limitations associated with the use of isolated fibers. However, only a few studies have taken advantage of this opportunity (Matuschek et al., 2001; Lestienne et al., 2005; Wang et al., 2008), and all were in vitro studies.

The application of carbohydrases along with, or subsequent to, treatments with phytases, tannase and, or polyphenol oxidases may also minimize the previously encountered cofounding effect of more potent mineral absorption inhibitors like phytates and polyphenols. With an appropriate

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experimental design involving several of these enzymes, the relative effects of each individual mineral absorption inhibitor could be evaluated as well as their combined effect. Lestienne et al., (2005) observed that treatment of pearl millet and sorghum with xylanase and phytase led to more soluble iron and zinc than phytase alone, suggesting that hemicelluloses native to foods could have a negative effect on the absorption of these minerals in the small intestine. Similarly, Wang et al., (2008) showed that treatment of rice with cellulase (1% U/g) increased *in vitro* zinc and calcium availability, but had no effect on iron availability. However, given the variability of the physicochemical properties of fibers between cereals and the changes brought about by different types of processing, more studies are needed. Several animal studies using exogenous enzymes (xylanase, cellulase, and phytase) have been conducted, but most focused on evaluating the digestibility of feed, or the growth performance of the animal (Cowieson & Bedford, 2009; Woyengo & Nyachoti, 2011), so further animal and human studies are needed in this regard. Although the safety and acceptability of the use of enzymes such as polyphenol oxidase may be questioned, enzymes such as xylanase have long been used as a bread improver (Polizeli et al., 2005). The use of phytase for bread making was reported to be approved by the former French Food Safety Agency (AFSA, presently ANSES) (Troesch et al., 2009). Tannase also has potential applications in wine, beer and ice tea processing, although its applications are currently limited by insufficient knowledge of its properties, optimal expression, and large-scale application (Polizeli et al., 2005).

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8. Summary and perspectives

The definition of fiber has evolved over time, making it difficult to interpret the existing literature. The few available human studies were on healthy young men with adequate iron status which might have led to the effects of fiber on iron absorption being underestimated. Most of these studies failed to characterize the type of fiber investigated, did not control for other absorption inhibitors/enhancers, and used isolated, semi-purified or synthetic fibers that are likely to behave differently from native fibers.

Interactions between dietary fibers and associated components are also likely. However, the use of carbohydrases may enable investigation of the effect of native dietary fibers *in situ*, while the application of enzymes targeting phytates, polyphenols and fibers either simultaneously or sequentially may enable better estimation of the effect of dietary fiber by limiting confounding factors.

If the polyphenols and phytates associated with plant cell walls are to be considered as components of dietary fiber as proposed by (Cummings et al., 2009), the role of dietary fibers on mineral absorption is likely to remain elusive, at least until the nature and type of association as well as the type of the associated polyphenol and phytate is determined.

Although soluble and insoluble fibers have been shown to hamper mineral absorption in the small intestine due to binding and/or physical entrapment, this is believed to be compensated for by liberation of trapped/bound minerals for colonic absorption as a result of fiber fermentation by gut microflora. Moreover, mineral absorption enhancing properties have been documented for soluble/ easily fermentable fibers. This suggests that some soluble dietary fibers can be considered as mineral absorption enhancers. Future studies should investigate whether

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solubilizing insoluble fibers by either application of exogenous enzymes or by activating endogenous ones could enhance mineral absorption.

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References

Afsana, K., Shiga, K., Ishizuka, S., & Hara, H. (2003). Ingestion of an indigestible saccharide, difructose anhydride III, partially prevents the tannic acid-induced suppression of iron absorption in rats. *J Nutr,* ***133***, 3553-3560.

Aleixandre, A., & Miguel, M. (2008). Dietary fiber in the prevention and treatment of metabolic syndrome: a review. *Crit. Rev. Food Sci. Nutr., 48*(10), 905-912.

Anderson, J. W., Baird, P., Davis Jr, R. H., Ferreri, S., Knudtson, M., Koraym, A., Waters, V., & Williams, C. L. (2009). Health benefits of dietary fiber. *Nutr Rev, 67*, 188-205.

Anon. (2000). AACC Board holds midyear meeting. *Cereal Foods World, 45,* 325.

Asp, N. G. (1996). Dietary carbohydrates: classification by chemistry and physiology. *Food Chem., 57*(1), 9-14.

Asp, N. G., Johansson, C. G., Hallmer, H., & Siljestroem, M. (1983). Rapid enzymic assay of insoluble and soluble dietary fiber. *J. Agric. Food Chem., 31*(3), 476-482.

Bauer, E., Williams, B., Verstegen, M., & Mosenthin, R. (2006). Fermentable carbohydrates: potential dietary modulators of intestinal physiology, microbiology and immunity in pigs. *Biology of Growing Animals, 4*, 33-63.

Bhat, M. (2000). Cellulases and related enzymes in biotechnology. *Biotechnol adv., 18*(5), 355-383.

Bosscher, D., Van Caillie-Bertrand, M., & Deelstra, H. (2001). Effect of thickening agents, based on soluble dietary fiber, on the availability of calcium, iron, and zinc from infant formulas. *Nutrition, 17*(7), 614-618.

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Bosscher, D., Van Caillie-Bertrand, M., Van Cauwenbergh, R., & Deelstra, H. (2003). Availabilities of calcium, iron, and zinc from dairy infant formulas is affected by soluble dietary fibers and modified starch fractions. *Nutrition, 19*(7), 641-645.

Brommage, R., Binacua, C., Antille, S. & Carrié, A. L. (1993) Intestinal calcium absorption in rats is stimulated by dietary lactulose and other resistant sugars. *J Nutr.* 123:2186-2194.

Brown, L., Rosner, B., Willett, W. W., & Sacks, F. M. (1999). Cholesterol-lowering effects of dietary fiber: a meta-analysis. *Am J Clin Nutr., 69*(1), 30-42.

Catani, M., Amâncio, O., Fagundes-Neto, U., & Morais, M. (2003). Dietary cellulose has no effect on the regeneration of hemoglobin in growing rats with iron deficiency anemia. *Braz J Med Biol Res., 36*(6), 693-697.

Chawla, R., & Patil, G. (2010). Soluble dietary fiber. *Compr Rev Food Sci F., 9*(2), 178-196.

Cook, J. D., Noble, N. L., Morck, T. A., Lynch, S. R., & Petersburg, S. J. (1983). Effect of fiber on nonheme iron absorption. *Gastroenterology, 85*(6), 1354-1358.

Coudray, C., Bellanger, J., Castiglia-Delavaud, C., Remesy, C., Vermorel, M., & Rayssignuier, Y. (1997). Effect of soluble or partly soluble dietary fibres supplementation on absorption and balance of calcium, magnesium, iron and zinc in healthy young men. *Eur J Clin Nutr., 51*(6), 375-380.

Cowieson, A., & Bedford, M. (2009). The effect of phytase and carbohydrase on ileal amino acid digestibility in monogastric diets: complimentary mode of action? *World Poultry Sci J., 65*(4), 609.

Cummings, J., Mann, J., Nishida, C., & Vorster, H. (2009). Dietary fibre: an agreed definition. *The Lancet, 373*(9661), 365-366.

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Debon, S. J. J., & Tester, R. F. (2001). In vitro binding of calcium, iron and zinc by non-starch polysaccharides. *Food Chem., 73*(4), 401-410.

DeVries, J., Prosky, L., Li, B., & Cho, S. (1999). A historical perspective on defining dietary fiber. *Cereal Foods World, 44*, 367-369.

DeVries, J. W. (2003). On defining dietary fibre. *Proc Nutr Soc., 62*(01), 37-43.

Dietary Reference Intakes*: Proposed Definition of Dietary Fiber*. (2001). The National Academies Press.

Elleuch, M., Bedigian, D., Roiseux, O., Besbes, S., Blecker, C., & Attia, H. (2011). Dietary fibre and fibre-rich by-products of food processing: Characterisation, technological functionality and commercial applications: A review. *Food Chem., 124*(2), 411-421.

Feltrin, C., Batista de Morais, M., de Cássia Freitas, K., Beninga de Morais, T., Fagundes Neto, U., & Silvério Amancio, O. M. (2009). Effect of soluble fiber pectin on growth and intestinal iron absorption in rats during recovery from iron deficiency anemia. *Biol Trace Elem Res., 129*(1), 221-228.

Fernandez, R., & Phillips, S. (1982). Components of fiber bind iron in vitro. *Am J Clin Nutr, 35*(1), 100-106.

Fly, A. D., Czarnecki-Maulden, G. L., Fahey Jr, G. C., & Titgemeyer, E. C. (1996). Hemicellulose does not affect iron bioavailability in chicks. *J Nutr., 126*(1), 308.

Frölich, W. (1995). Bioavailability of micronutrients in a fibre-rich diet, especially related to minerals. *Eur J Clin Nutr., 49*, S116.

Gordon, D. T. (1989). Functional properties vs physiological action of total dietary fiber. *Cereal foods world., 34*(7), 517.

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Grassin, C., & Fauquembergue, P. (1996). Application of pectinases in beverages. *Prog Biotechnol, 14*, 453-462.

Greger, J. (1999). Nondigestible carbohydrates and mineral bioavailability. *J Nutr., 129*(7), 1434S-1435s.

Guillon, F., & Champ, M. (2000). Structural and physical properties of dietary fibres, and consequences of processing on human physiology. *Food Res Int., 33*(3), 233-245.

Hall, J. L., & Moore, A. L. (1983). *Isolation of membranes and organelles from plant cells*: Academic Press Inc.

Harmuth-Hoene, A. E., & Schelenz, R. (1980). Effect of dietary fiber on mineral absorption in growing rats. *J Nutr., 110*(9), 1774.

Harris, P. J., & Smith, B. G. (2006). Plant cell walls and cell-wall polysaccharides: structures, properties and uses in food products. *Int J Food Sci Technol., 41*(s2), 129-143.

Hipsley, E. H. (1953). Dietary ñfibreò and pregnancy toxaemia. *Br Med J., 2*(4833), 420-422.

Howarth, N. C., Saltzman, E., & Roberts, S. B. (2001). Dietary fiber and weight regulation. *Nutr Rev., 59*(5), 129-139.

Hulten, L., Gramatkovski, E., Gleerup, A., & Hallberg, L. (1995). Iron absorption from the whole diet. Relation to meal composition, iron requirements and iron stores. *Eur J Clin Nutr., 49*(11), 794-808.

Ismail-Beigi, F., Faraji, B., & Reinhold, J. (1977). Binding of zinc and iron to wheat bread, wheat bran, and their components. *Am J Clin Nutr, 30*(10), 1721-1725.

Kim, M., & Atallah, M. T. (1992). Structure of dietary pectin, iron bioavailability and hemoglobin repletion in anemic rats. *J Nutr., 122*(11), 2298.

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Kim, M., Atallah, M. T., Amarasiriwardena, C., & Barnes, R. (1996). Pectin with low molecular weight and high degree of esterification increases absorption of ^{58}Fe in growing rats. *J Nutr., 126*(7), 1883.

Knox, J. P. (2008). Revealing the structural and functional diversity of plant cell walls. *Curr Opin Plant Biol., 11*(3), 308-313.

Kobayashi, Y., Ohbuchi, T., Fukuda, T., Wakasugi, E., Yasui, R., Hamada, M., Yokoyama, M., Kuwahata, M., & Kido, Y. (2011). Acidic xylooligosaccharide preserves hepatic iron storage level in adult female rats fed a low-iron diet. *J Nutr Sci Vitaminol (Tokyo), 57*(4), 292-297.

Lestienne, I., Caporiccio, B., Besançon, P., Rochette, I., & Treche, S. (2005). Relative contribution of phytates, fibers, and tannins to low iron and zinc in vitro solubility in pearl millet (Pennisetum glaucum) flour and grain fractions. *J Agric Food Chem., 53*(21), 8342-8348.

Lopez, H. W., Levrat-Verny, M. A., Coudray, C., Besson, C., Krespine, V., Messager, A., Demigne, C., & Remesy, C. (2001). Class 2 resistant starches lower plasma and liver lipids and improve mineral retention in rats. *J Nutr, 131*(4), 1283-1289.

Lunn, J., & Buttriss, J. L. (2007). Carbohydrates and dietary fibre. *Nutr Bull., 32*(1), 21-64.

Lupton, J., Kamp, J., Jones, J., McCleary, B., & Topping, D. (2010). Codex definition of dietary fibre and issues requiring resolution. *Dietary Fibre: New Frontiers for Food and Health. JW van der Kamp, J. Jones, B. McCleary, and D. Topping, ed. Wageningen Academic Publishers, Wageningen, the Netherlands*, 15-24.

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ACCEPTED MANUSCRIPT

Matuschek, E., Towo, E., & Svanberg, U. (2001). Oxidation of polyphenols in phytate-reduced high-tannin cereals: effect on different phenolic groups and on in vitro accessible iron. *J Agric Food Chem., 49*(11), 5630-5638.

McCleary, B. V., De Vries, J. W., Rader, J. I., Cohen, G., Prosky, L., Mugford, D. C., Champ, M., & Okuma, K. (2010). Determination of total dietary fiber (CODEX definition) by enzymatic-gravimetric method and liquid chromatography: Collaborative study. *J AOAC Int., 93*(1), 221-233.

Miyada, T., Nakajima, A., & Ebihara, K. (2011). Iron bound to pectin is utilised by rats. *Br J Nutr., 106*(1), 73.

Miyada, T., Nakajima, A., & Ebihara, K. (2012). Degradation of pectin in the caecum contributes to bioavailability of iron in rats. *Br J Nutr., 107*(10), 1452.

Miyazato, S., Nakagawa, C., Kishimoto, Y., Tagami, H., & Hara, H. (2010). Promotive effects of resistant maltodextrin on apparent absorption of calcium, magnesium, iron and zinc in rats. *Eur J Nutr., 49*(3), 165-171.

Mod, R., Ory, R., Morris, N., & Normand, F. (1982). In vitro interaction of rice hemicellulose with trace minerals and their release by digestive enzymes. *Cereal Chem., 59*.

Morais, M. B., Feste, A., Miller, R. G., & Lifschitz, C. H. (1996). Effect of resistant and digestible starch on intestinal absorption of calcium, iron, and zinc in infant pigs. *Pediatr Res., 39*(5), 872-876.

Park, Y., Hunter, D. J., Spiegelman, D., Bergkvist, L., Berrino, F., van den Brandt, P. A., Buring, J. E., Colditz, G. A., Freudenheim, J. L., & Fuchs, C. S. (2005). Dietary fiber intake and risk of colorectal cancer. *JAMA., 294*(22), 2849-2857.

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Petry, N., Egli, I., Chassard, C., Lacroix, C., & Hurrell, R. (2012). Inulin modifies the bifidobacteria population, fecal lactate concentration, and fecal pH but does not influence iron absorption in women with low iron status. *Am J Clin Nutr., 96*(2), 325-331.

Polizeli, M., Rizzatti, A., Monti, R., Terenzi, H., Jorge, J., & Amorim, D. (2005). Xylanases from fungi: properties and industrial applications. *Appl Microbiol Biotechnol., 67*(5), 577-591.

Prosky, L., Asp, N.-G., Furda, I., DeVries, J. W., Schweizer, T. F., & Harland, B. F. (1984). Determination of total dietary fiber in foods and food products: collaborative study. *J. AOAC Int, 68*(4), 677-679.

Reddy, M. B., & Cook, J. D. (1991). Assessment of dietary determinants of nonheme-iron absorption in humans and rats. *Am J Clin Nutr., 54*(4), 723-728.

Sakai, K., Ohta, A., Shiga, K., Takasaki, M., Tokunaga, T., & Hara, H. (2000). The cecum and dietary short-chain fructooligosaccharides are involved in preventing postgastrectomy anemia in rats. *J Nutr., 130*(6), 1608-1612.

Saura-Calixto, F. (2012). Concept and health related properties of non-extractable polyphenols: the missing dietary polyphenols. *J Agric Food Chem. 60* (45), 11195ï 11200.

Saura-Calixto, F., & Díaz-Rubio, M. E. (2007). Polyphenols associated with dietary fibre in wine: A wine Polyphenols gap? *Food Res Int., 40*(5), 613-619.

Scholz-Ahrens, K. E., Ade, P., Marten, B., Weber, P., Timm, W., Açil, Y., Glüer, C.-C., & Schrezenmeir, J. (2007). Prebiotics, probiotics, and synbiotics affect mineral absorption, bone mineral content, and bone structure. *J Nutr., 137*(3), 838S-846S.

Downloaded by [New York University] at 03:19 21 May 2015

Sinha, A. K., Kumar, V., Makkar, H. P. S., De Boeck, G., & Becker, K. (2011). Non-starch polysaccharides and their role in fish nutritionï A review. *Food Chem., 127*(4), 1409-1426.

Slavin, J. (2008). Position of the American Dietetic Association: health implications of dietary fiber. *J Am Diet Assoc, 108*(10), 1716-1731.

Strack, D. (1997). 10 Phenolic Metabolism. *Plant Biochem.*, 387.

Torre, M., Rodriguez, A. R., & Saura-Calixto, F. (1995). Interactions of Fe(II), Ca(II) and Fe(III) with high dietary fibre materials: A physicochemical approach. *Food Chem., 54*(1), 23-31.

Troesch, B., Egli, I., Zeder, C., Hurrell, R. F., de Pee, S., & Zimmermann, M. B. (2009). Optimization of a phytase-containing micronutrient powder with low amounts of highly bioavailable iron for in-home fortification of complementary foods. *Am J Clin Nutr., 89*(2), 539-544.

Trowell, H. (1985). Dietary fiber: a paradigm. *Dietary Fibre, Fibre-depleted Foods and Disease. Academic Press, New York*, 1-20.

Trowell, H. (1976). Definition of dietary fiber and hypotheses that it is a protective factor in certain diseases. *Am J Clin Nutr., 29*(4), 417-427.

Trowell, H., Southgate, D. T., Wolever, T. S., Leeds, A., Gassull, M., & Jenkins, D. A. (1976). Dietary fibre redefined. *The Lancet, 307*(7966), 967.

Tungland, B. C., & Meyer, D. (2002). Nondigestible Oligo- and Polysaccharides (Dietary Fiber): Their Physiology and Role in Human Health and Food. *Compr Rev Food Sci F., 1*(3), 90-109.

Downloaded by [New York University] at 03:19 21 May 2015

Turnlund, J., King, J., Keyes, W., Gong, B., & Michel, M. (1984). A stable isotope study of zinc absorption in young men: effects of phytate and alpha-cellulose. *Am J Clin Nutr., 40*(5), 1071-1077.

Van den Heuvel, E., Schaafsma, G., Muys, T., & van Dokkum, W. (1998). Nondigestible oligosaccharides do not interfere with calcium and nonheme-iron absorption in young, healthy men. *Am J Clin Nutr., 67*(3), 445-451.

Van der Klis, J., Kwakernaak, C., & De Wit, W. (1995). Effects of endoxylanase addition to wheat-based diets on physico-chemical chyme conditions and mineral absorption in broilers. *Anim Feed Sci Technol., 51*(1), 15-27.

Wang, Y., Cheng, Y., Ou, K., Lin, L., & Liang, J. (2008). In vitro solubility of calcium, iron, and zinc in rice bran treated with phytase, cellulase, and protease. *J Agric Food Chem., 56*(24), 11868-11874.

Weickert, M. O., & Pfeiffer, A. F. H. (2008). Metabolic effects of dietary fiber consumption and prevention of diabetes. *J Nutr., 138*(3), 439-442.

Woyengo, T., & Nyachoti, C. (2011). Review: Supplementation of phytase and carbohydrases to diets for poultry. *Can J Anim Sci., 91*(2), 177-192.

Yeung, C. K., Glahn, R. E., Welch, R. M., & Miller, D. D. (2005). Prebiotics and Iron Bioavailabilityð Is There a Connection? *J Food Sci., 70*(5), R88-R92.

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Table 1: In vitro studies on the effect of fiber on mineral availability

Type of fiber	Source	Type of study	Effect on mineral	Remark	References
Cellulose	Modified cellulose	Binding	Zn binding		(Ismail-Beigi et al., 1977)
	Rice bran	Solubility	ŷ Ca and Zn solubility due to cellulase treatment but no ŷin Fe		(Wang et al., 2008)
Hemicellulose	Wheat bran	Binding	Fe, Zn binding	Dephytinized	(Ismail-Beigi et al., 1977)
Water soluble hemicellulose	Rice (isolated/purified)	Binding	Ca, Mg binding Liberation upon		(Mod et al., 1982)

Alkali soluble hemicellulose			hemicellulase treatment		
Hemicellulose	Pearl millet		ŷ in Fe with xylanase treatment No effect on Zn		(Lestienne et al., 2005)
Pectin	Semi-purified mostly galacturonic acid	^{59}FeSO4 binding/ solubility-dialysis	Minimal binding		(Fernandez & Phillips, 1982)
Highly esterified	Low methoxylpectin	Binding	Strong Fe^{3+}, Ca, Zn		(Debon & Tester, 2001)

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pectin	(citrus)		binding		
Low esterified pectin	Citrus	Dialysis	Ź10% Ca availability Ź37% Fe No effect on Zn	Binding of highly esterified > low esterified	(Bosscher et al., 2003)
Gums & mucilages					
Psyllium		$^{59}FeSO_4$ binding/ solubility-dialysis	High Fe binding		(Fernandez & Phillips, 1982)

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Alginic acid Locust-bean gum	Dialysis	ŹCa while ŷFe &Zn availability	(Bosscher et al., 2001)

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			ŹFe &Zn		
Guar gum	Purified fiber		availability		
					(Debon &
Agar		Dialysis		Mostly	Tester, 2001)
			No binding	electrostatic	
K-karrageenan			in acidic conditions except for Fe^{3+}	interaction	
Gum xanthan					
Gum arabic					
Gum karaya					
Gum tragacanth		Dialysis			
					(Bosscher et
Guar gum					al., 2003)
			ŹCa & Zn		
Locust bean gum			availability		

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Lignin					
Neutral lignin Acid lignin	Semi-purified lignin	Binding in $FeSO_4$ sol.	High iron binding	Counteracted by citrate and EDTA	(Fernandez & Phillips, 1982)
Inulin	Purified lignin	Dialysis	27% ŷ Ca availability No effect on Fe & Zn		(Bosscher et al., 2003)
Resistant starch Modified starch+ maltodextrin	Rice starch	Dialysis	ŷ in Fe, Ca Ź Zn		(Bosscher et al., 2003)

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Table 2: In vivo (animal/human) studies on the effect of fiber on mineral bioavailability

Type of fiber	Source	Type of study	Effect on mineral	Remark	Reference s
		Animal studies			
Cellulose	Diet with 100g/kg cellulose	Regeneration of rat hemoglobin	No effect on Fe	No effect on the control, probably due to the use of elemental iron which is poorly bioavailable	(Catani et al., 2003)
Hemicellulose	Synthetic psyllium	Chicks	No effect on Fe No effect on extrinsic Fe		(Fly et al., 1996)

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			but Źintrinsic Fe absorption		
	Synthetic - acidic xylo-oligosaccharide	Iron deficient adult female rats	Led to recovery from ID Źhepatic hepcidin mRNA ŷFe absorption ŹFe excretion		(Kobayashi et al., 2011)
Pectin (Different MW & DE)	Citrus	Hemoglobin regeneration in anemic rats	ŷHb regeneration efficiency ŷhematocrite ŷSerum Fe ŷtransferrin saturation Ź unsaturated	Effect was dependent on MW and DE No improvement in bioavailability for high MW	(Kim & Atallah, 1992; Kim et al., 1996)

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		and total Fe-	and low DE	
	Hemoglobin	binding	pectin	
50g/Kg diet high	regeneration	capacity	+ effect for	
DE	in anemic rats		low MW and	
Control: corn			high DE	(Feltrin et
starch		No effect on	pectins	al., 2009)
	Hemoglobin	Fe absorption		
	regeneration			
	in anemic rats			
DE: 72%				
		ŷHb		
	Hemoglobin	regeneration		(Miyada
	regeneration			et al.,
	in anemic		High degree of	2011)
DE: 38ï 40%	ileorectomise		esterification	
	d/		but no	
	caecectomised	Ź absorption in	information	
	rats	the SI	regarding MW	(Miyada
				et al.,
				2012)
	Caecectomise		Pectin bound	
	d rats		Fe is utilized	

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			Caecectomy ŹHb gain and regeneration efýciency. Bioavailability of Fe from the FeIIï OGA complex -not affected	by rats ŷrelease of Fe bound to pectin by microbial degradation, this ŷ bioavailability in the large intestine	
Gum & mucilage Carrageenan	Synthetic 10% added	Mineral balance of growing rats	Źabsorption of Fe, Zn, Ca, Cu, Co	Other absorption inhibitors not known	(Harmuth-Hoene & Schelenz, 1980)
Agar, agar			Źabsorption of Fe, Zn, Ca,		

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			Cu, Co		
Sodium alginate Carob bam gum Guar gum			Ź Fe Ź Zn Ź Zn		
FOS	DFA- III 30 g FOS	Prevention of tannic acid induced anemia in rats	ŷin Fe absorption	DFA partially prevented tannic acid induced anemia whereas FOS had no effect	(Afsana et al., 2003)
Resistant starch	Corn (16%)	Apparent absorption in piglets	ŷ Fe and Ca absorption		(Morais et al., 1996)
	RS-II	Mineral retention in rats	ŷ Ca, Mg, Zn, Fe and Cu absorptions		(Lopez et al., 2001)
	Maltodextrins		ŷ Ca, Mg, Zn,	Fe & Zn absorption	

		Rats	Fe absorption	not affected by cacectomy	(Miyazato et al., 2010)
		Human studies			
Cellulose	Wheat muffin+cellulose	Multiple radioiron absorption (male +female)	No effect on Fe absorption	Phytate, polyphenols not assessed	(Cook et al.,1983)
	Diet with Ŭ-cellulose	Zn stable isotope study in young men	No effect on Zn, Phytate was inhibitory	Phytate was controlled	(Turnlund et al., 1984)

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Inulin	20 g/d	Isotope study in women with low Fe status	No increase in Fe absorption	Limitation: use of maltodextrin as a placebo. ŷ in Fe absorption observed for resistant maltodextrins	(Petry et al., 2012)
		Chemical balance inhealthy young men	ŷCa absorption		(Coudray et al., 1997)
	15 g/d	Double isotope study in healthy men	No change in Fe, Zn, Mg		(Van den Heuvel et al, 1998)
			No effect		

mRNA : messenger ribonucleic acid; ID: iron deficiency

MW: molecular weight; DE: degree of esterification; SI: small intestine; OGA: oligogalacturonic acid

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DFA: di-fructose anhydride; FOS: fructose oligo-saccharide; RS: resistant starch

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Table 3: Enzymes degrading non-starch polysaccharides and associated substances

NSP and associated substances	Monomers	Linkage	Enzymes
Cellulose	Glucose	ɓ -(1-4)	Cellulase
		Non-cellulosic polymers	
Arabinoxylans	Arabinose & xylose	ɓ -(1-4) linked xylose units	Xylanase/ hemicellulase
Mixed-linked ɓ-glucans	Glucose	ɓ -(1-3) & ɓ-(1-4)	Cellulase;ɓ-glucanasexyloglucan-specific ɓ-1,4-glucanase
Mannans	Mannose	ɓ-(1-4)	ɓ-D-mannosidase
Galactomannans	Galactose & mannans	ɓ-(1-4) linked mannans with Ŭ-(1-6) linked galactosyl side groups	ɓ-D-mannosidase
Glucomannans	Glucose & mannans	ɓ-(1-4) linked mannans with interspersed glucose residues	ɓ-D-mannosidase
Arabinans	Arabinose	Ŭ-(1-5)	Arabinan endo-1,5- Ŭ-L-

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			arabinanase
		Pectic polysaccharides	
Galactans	Galactose	ß-(1-4)	ß-galactosidase
Arabinogalactan type I	Arabinose & galactose	ß-(1-4) galactan backbone with 5ï linked and terminal arabinose residues	Arabinogalactan endo-1,4-ß-galactosidase
Arabinogalactan type II	Arabinose & galactose	ß-(1-3,6) linked galactose polymers associated with 3-/5-arabinose residues	ß-1- 3,6-galactosidase
		Plant cell- wall associated substances	
Phytate	Inositol & phosphates	-	Phytase (phytic acid hydrolase)
Polyphenols			
Tannic acid	Gallic acid & glucose	Depside bonds	Tannase (tannin acyl hydrolase)
Phenolic acids		-	
Fe-binding polyphenols	-	-	
	Monophenols & catechols		Polyphenol oxidase/ Laccase

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Sources: (Sinha et al., 2011); Brenda comprehensive enzyme information system (http://www.brenda-enzymes.org)

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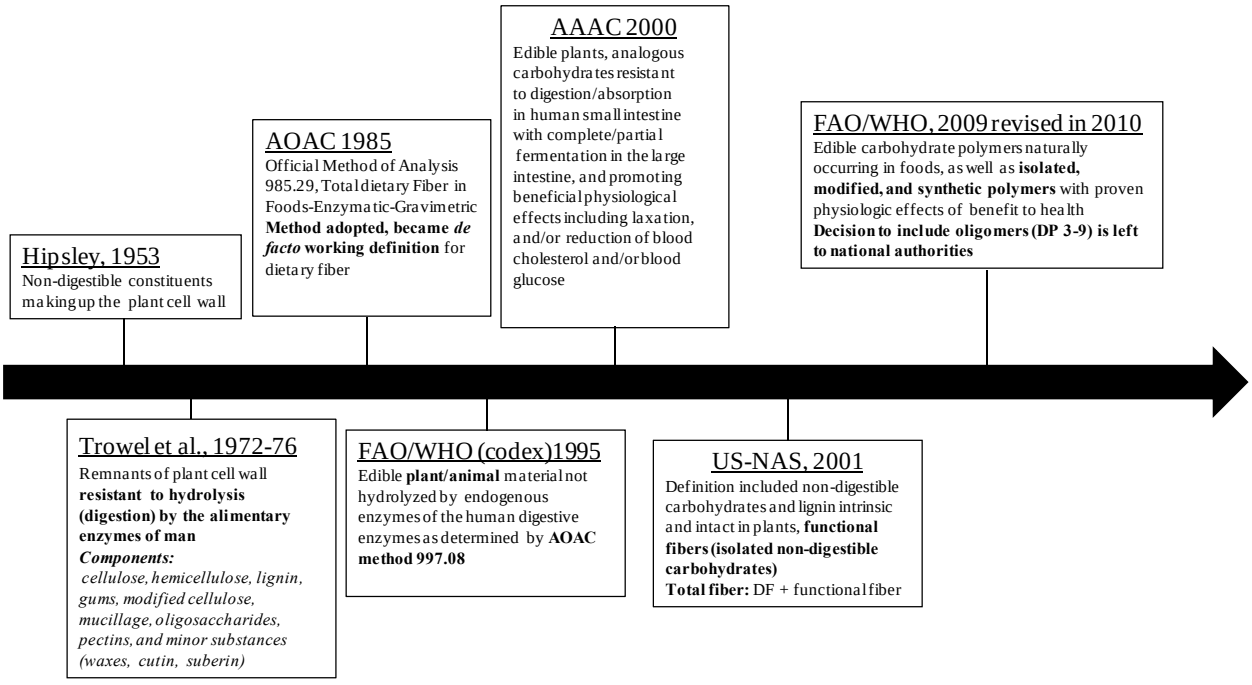

Fig. 1: Some of the major milestones in dietary fiber definition

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