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Do the Physical Structure and Physicochemical Characteristics of Dietary Fibers Influence their Health Effects?

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Studies on humans, animals, and *in vitro* have clearly shown that the way dietary fiber is degraded and fermented throughout the digestive tract depends on both its physical and chemical structure (intrinsic properties such as crystallinity and particle size) and its interaction with the closed environment of the gut (i.e., physical–chemical properties such as porosity, water-holding capacity, and solubility) (Guillon and Champ, 2000). For example, cellulose, which has a compact structure, is only partially fermented whereas soluble pectin is fully fermented, due to its much greater porosity (Fardet *et al.*, 1997; Salvador *et al.*, 1993). Thus, a greater porosity enables enzymes to access their substrate and degrade it more efficiently. This illustrates the interaction between factors such as porosity, solubility, and water-holding capacity.

Although much is known about factors influencing the fermentation of dietary fiber, less is known about the influence of a change in fiber structure, either isolated or within a complex food matrix, on human health. For example, is an increase in the porosity of fibers in a food beneficial? What are the consequences of higher fiber porosity on the short-chain fatty acid (SCFA) profiles generated during fermentation in colon? Increasing porosity probably increases the rate of fermentation within the colon, yielding a more rapid and massive arrival of SCFAs. But does the way the SCFAs are released have any effect on human physiology and health? Do the exact places where SCFAs are released (transverse, ascending, or descending colon) influence human health? These questions are of great interest in terms of the important physiological roles of the main SCFAs: butyric (Blouin *et al.*, 2011), propionic (Hosseini *et al.*, 2011), and acetic (Kondo *et al.*, 2009) acids.

Although today we cannot fully answer these questions, this review will attempt to discuss the physicochemical parameters of fiber that can be modified and their relationship with their effects on human physiology and/or health (e.g., glycemia, cholesterolemia, satiety, microbiota, and fecal bulking). In a recent publication, Monro notably reviewed and discussed the impact of polysaccharide-based structures on nutritional properties in the foregut, focusing on complex foods containing such fiber-based structures (Monro, 2014). This review is more

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focused on isolated fibers and their structural features; some of the best studied being crystallinity, particle size, solubility, porosity, water-holding capacity, and the ability to adsorb bile acids, complex minerals, and trace elements (Guillon and Champ, 2000).

1.1 Influence of the Chemical and Physical Structure on the Metabolic Effects of Fibers

The intrinsic properties of fibers, their chemical and physical structure, are fundamental to their biological actions. The chemical structure of a fiber greatly influences the rate and extent of its fermentation in the colon. Thus, pectins, hemicelluloses, cellulose, lignin, and resistant starch (all included in the definition of fiber) are not all fermented at the same speed and the same extent. Cellulose has a compact structure, whereas hemicellulose is much more porous and more accessible to bacterial enzymes. Hence, hemicelluloses are almost completely degraded in the colon, but cellulose is only partially fermented and is excreted in the feces. Lignins are almost undegraded in humans (Holloway *et al.*, 1978; Slavin *et al.*, 1981).

Interestingly, Eastwood *et al.* (1986) showed that there is no obvious correlation between the chemical composition, structure, molecular size, shape, and physical properties of a fiber and its physiological effects in humans. For example, wheat bran and gum tragacanth have very different chemical structures but they have similar physiological effects. However, these findings are only valid for the physiological properties tested: the weight of stool, serum cholesterol levels, and the excretion of hydrogen. From this study, other physiological parameters have been tested.

It is hardly surprising that the chemical structure of a fiber influences its physiological effects, as each type of fiber is a complex mixture of carbohydrates (including pentoses and hexoses). A recent review has focused on the relationships between the molecular structure of cereal fibers and their physiological effects in humans (Gemen *et al.*, 2011). There appears to be a clear link between the chemical structure of a fiber and blood glucose and insulin responses and satiety. However, the authors emphasize that information on the molecular structure are rarely given in the literature and there are no obvious trends in the relationship between the molecular structures of fibers and their fermentation profiles in humans (Gemen *et al.*, 2011). Indeed, conclusions are generally given for a particular type of fiber, rather than based on its structure, and interpretations are generally extrapolated from *in vitro* studies (Gemen *et al.*, 2011).

1.1.1 Changing the Molecular Weight

Some of the results appear contradictory. Some studies have shown that reducing the molecular weight of a fiber, and hence its potential viscosity *in vivo*, has no significant effect on the glycemic response (Ellis *et al.*, 1991; Gatenby *et al.*, 1996). These authors concluded that low molecular weight guar gum can be used in

bread instead of a high molecular weight guar gum that is more viscous but less palatable (Ellis *et al.*, 1991). Another study showed that reducing the molecular weight of β -glucan in muffins tended to increase the blood glucose and insulin responses in humans (Tosh *et al.*, 2008). Immerstrand *et al.* (2010) showed that β -glucans with different molecular weights all had the same effect on the plasma cholesterol of mice. However, Kim and White (2010) found that low molecular weight β -glucan from oats produced more volatile fatty acids than did the β -glucan with a higher (4.4 times) molecular weight after fermentation for 24 hours *in vitro*.

An exhaustive review of the literature on cereal fiber suggests that the molecular weight of the fiber must be above a certain value to significantly increase the viscosity of the digestive effluents and to have a significant effect on postprandial glycemic and insulinemic responses. The authors even suggest that the thresholds value should be above 100 kDa for β -glucans and above 20 kDa for arabinoxylans. However, although low molecular weight fibers are more rapidly fermented, just how the molecular characteristics of a fiber influence its fermentation profile remains unclear (Gemen *et al.*, 2011). Nevertheless, viscosifying fibers with high molecular weights increase the viscosity of the digesta more than do lower molecular weights fibers that tend to be fermented faster (Gemen *et al.*, 2011). It has been shown that the molecular weights of fungal β -glucans significantly influence the secretion of interleukin-8 (IL-8) by HT29 cells *in vitro*, with lower molecular weight β -glucans producing more secretion than those of high molecular weight (Rieder *et al.*, 2011). Finally, the prebiotic effect of wheat arabinoxylans increases inversely with their molecular weight in the presence of human feces *in vitro* (Hughes *et al.*, 2007).

The fermentation and prebiotic properties of arabinoses from arabinoxyloligosaccharides (AXOS) have also been tested with respect to the degree of polymerization and substitution. Low molecular weight AXOS (average MW <3) produced more acetic and butyric acid and also stimulated an increase in the concentrations of bifidobacteria, whereas the fermentation of higher molecular weight (average MW = 61) AXOS resulted in a lack of the branched volatile fatty acids that are considered to be markers of protein fermentation and had no effect on the production of acetic and butyric acids or on bifidobacteria (Van Craeyveld *et al.*, 2008). The authors used an experimental design that varied both the molecular weight and degree of substitution of arabinose in AXOS and concluded that AXOS with an average molecular weight of 5 and a degree of substitution of 0.27 produces the best effects on intestinal health (Van Craeyveld *et al.*, 2008).

1.1.2 Changing the Degree of Crystallinity

Changes in the crystalline structure of a fiber are best illustrated in cellulose, the most abundant fibrous compounds on Earth. Indeed, like starch, cellulose has a crystalline structure, and by modifying it, it is possible to alter its digestibility/fermentation. This was clearly demonstrated in rats fed celluloses having degrees of crystallinity from 6 to 81%. As expected, the more crystalline the cellulose, the less it was fermented (about 20–9%) and the lower the fecal water content (Hsu and Penner, 1989). The degree of crystallinity influenced the

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accessibility of the cellulose to its cellulase enzyme because of the way it altered the porosity of the substrate (Jeoh *et al.*, 2007).

1.1.3 Modifying Particle Size

Intensive grinding of a fiber can influence the speed at which it passes through the gastrointestinal tract, and may promote hydrolysis of its constituent polysaccharides and, ultimately, their hydration and water-holding capacity (Lewis, 1978). Heller *et al.* (1980) showed that coarse wheat bran had a shorter transit time in humans, with more excreted daily in the feces, which had a higher water content, whereas the degradation/digestibility of the cellulose was low. In contrast, the fibrous components of fine bran were more digestible, probably due to its longer retention time in the colon. These results were later confirmed in humans by comparing coarse and fine wheat bran: the authors state that grinding the bran reduced the amount of feces excreted by reducing the water-holding capacity of the fibrous matrix (Wrick *et al.*, 1983). This effect was called the destruction of “the spongy action of fibrous matrix” by van Dokkum *et al.* (1983), who tested bread composed of fine and coarse brans in humans. The integrity of the fibrous matrix therefore appears to significantly influence the weight of the stool (van Dokkum *et al.*, 1983).

However, others found that the size of wheat bran particles (0.5 or 2 mm) had no effect on the morphology or function of the intestinal of rats (e.g., fat digestion, water content of feces, or cecum length), except that the fiber in the coarser bran was better digested (Kahlon *et al.*, 2001). In another study, the size of wheat bran particles had no effect on the fermentability of fiber in rats (Nyman and Asp, 1985). Similarly, there was no significant difference in the production of volatile fatty acids from coarse and fine wheat bran in the large intestine of pigs (Ehle *et al.*, 1982).

More recently, a Taiwanese team compared increasing intensity of micronization on some physicochemical properties of the fiber-rich fractions extracted from orange peel and cellulose, and showed that the micronized fibers were able to adsorb glucose and reduce the activities of α -amylase and lipase, which could slow down glucose uptake and reduce the serum concentration of glucose (Chau *et al.*, 2006). They tested the reduction of particle size of orange insoluble fiber in hamsters and concluded that micronized fibers would have a positive effect on the health of hamster intestines by decreasing the amount of harmful ammonia produced, increasing the dry weight of stools, and decreasing the activities of β -D-glucuronidase (associated with a lower incidence of colorectal tumors) and mucinase (leading to increased mucins that protect against bacterial invasion) (Wu *et al.*, 2007).

The apparent differences between the results of these studies may be due to differences in the particle sizes tested. Perhaps large differences in particle size (at least 10-fold) are needed to obtain significant differences in physiological effects. Controlling the size of the fiber particles could therefore help improve the health of the digestive tract, particularly the colon. But further studies are needed to confirm these results in humans.

1.2 Influence of the Physicochemical Properties of Fibers on their Metabolic Effects

The physicochemical properties of fibers determine the way they interact with their environment, in this context, the digestive tract, either the small intestine or the colon. But little is known about the long-term influence of changes in the physicochemical properties of fibers on human health. The most studied effect is probably the influence of the viscosity of fibers such as β -glucans and arabinoxylans on the digestion and metabolic fate of other nutrients (glucose or cholesterol). Viscosity is generally modified by changing the molecular weight of the fiber (Chillo *et al.*, 2011; Regand *et al.*, 2011; Wolever *et al.*, 2010). Thus, incorporating soluble, viscous fiber into starchy products significantly reduces their glycemic index (Fardet, 2015). The main actions of the added fiber are to encapsulate the starch (Brennan and Tudorica, 2008), slow the rate at which α -amylase diffuses to its substrate, and/or the movement of glucose to its intestinal absorption site due to increased viscosity and/or delayed transit (Hlebowicz *et al.*, 2008). Some fibers may also slow the rate of gastric emptying (Hlebowicz *et al.*, 2007; Mastropaolo *et al.*, 1986). In a previous recent review I also discussed the implication of pre-hydrolyzing fiber, either soluble or insoluble, on some physiological functions (e.g., cholesterolemia and glycemia) (Fardet, 2015).

1.2.1 Modifying the Degree of Solubility

The solubility of a fiber depends on the conformation of its polysaccharide components (linear or branched) and its crystallinity, and may be affected by grinding, cooking, and other processes (Lewis, 1978). Thus, increasing the proportion of insoluble fiber from wheat bran (0, 200, and 400 g/kg diet) decreases the retention times of both solid and liquid phases in the small intestine and colon of pigs (Wilfart *et al.*, 2007). Increasing the proportion of soluble fiber in the diet increases the viscosity of the digestive effluent, so slowing intestinal transit and the rates of diffusion and absorption of nutrients by the gastrointestinal mucosa.

In general, soluble fibers such as soluble arabinoxylans and β -glucans are rapidly fermented, whereas insoluble fibers such as cellulose and insoluble arabinoxylans are fermented more slowly (Williams *et al.*, 2011). Each type of fiber (e.g., insoluble barley fiber and soluble beet fiber; Fardet *et al.*, 1997) produces a specific profile of volatile fatty acids that may have different metabolic effects. However, the degree of polymerization of a soluble fiber such as the β -glucans or arabinoxylans, and thus their viscosity, does not significantly influence their rate of fermentation or the amounts of butyric, acetic, and propionic acids produced by fermentation (Williams *et al.*, 2011).

1.2.2 Changing the Water-Holding Capacity

There have been very few studies in humans *in vivo* on the influence of changing the water-holding capacity of a fiber on its digestive and fermentative fate. An early study on potato fibers with different water-holding capacities found that the water-holding capacity had no effect on the stool weight, but that the type of fiber,

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potato or wheat bran, had a significant effect, with wheat bran producing heavier stools (Eastwood *et al.*, 1983). Another study in the same year found that 12 subjects produced significantly heavier stools after consuming a diet that included bread with coarse bran (>0.35 mm) than they did after eating bread containing fine bran. The authors ascribed this observation to the ability of the larger bran particles to retain water and suggested that the “spongy activity of fibrous matrix” is the main factor involved (van Dokkum *et al.*, 1983). A more recent study in rats fed insoluble fibers of tossa jute (*Corchorus capsularis*) and shiitake fungus (*Lentinula edodes*) found that the viscosity of the rat digesta was negatively correlated with its free water content, which was reduced by fibers that held water and swelled (Takahashi *et al.*, 2009). The authors suggested that insoluble fiber may increase the viscosity of the digesta. Similar changes in the colonic digesta of piglets were obtained when they were fed insoluble fiber such as wheat bran (Molist *et al.*, 2009). Such results are important for human nutrition because of the key influence of viscosity on the rate at which nutrients like glucose and cholesterol are absorbed in the intestine and on the physiology of satiety. For example, human subjects fed two liquid meals with identical compositions that differed only in their viscosities, containing oat bran β -glucans with different molecular weights, experienced different degrees of satiety and hormone-related responses (Juvonen *et al.*, 2009).

It is therefore possible to use the water-holding capacity of a fiber, and hence the rheological properties of ingested foods, to control the absorption of nutrients by the human gastrointestinal tract.

1.2.3 Changing Fiber Porosity

Porosity is another important physicochemical parameter of fibers that determines the surface area of a fiber that is accessible to the enzymes responsible for its fermentation (Chesson *et al.*, 1997). Clearly, the greater the porosity, the easier it will be for hydrolytic enzymes to access their substrate and degrade it, as was shown with cellulose under steam explosion (Wong *et al.*, 1988). Thus, digestion in the small intestine can also increase the porosity of a beet fiber matrix by causing a loss of pectin, resulting in faster fermentation *in vitro* (Fardet *et al.*, 1997). Another *in vitro* study found that fermentation was directly correlated with the porosity of beet fiber, indicating that the pore volume accessible to bacteria controlled fermentation (Guillon *et al.*, 1998). How more rapid fiber fermentation influences metabolism and the resulting effects on health remain to be explored.

1.2.4 Adsorption of Bile Acids

Another property of fibers that has been extensively studied is their ability to bind bile acids, and so influence cholesterol metabolism by reducing blood cholesterol. Thus, low molecular weight oat β -glucan binds more bile acids (4.4 times) than do higher molecular weight oat β -glucans (Kim and White, 2010). The ability of various cereal brans (rice, oats, wheat, and maize) to bind bile acids *in vitro* does not appear to be proportional to their soluble fiber content. This suggests that soluble fiber is probably not involved in this property (Kahlon and Chow, 2000). At first glance, these results seem to contradict the finding that viscosifying soluble fiber

can reduce plasma cholesterol. However, while soluble fibers bind less bile acid (precursors of cholesterol) than do insoluble fiber *in vitro*, it is possible that the two act in synergy *in vivo*, with insoluble fiber fixing bile acids and viscousifying soluble fiber decreasing the diffusion of ingested cholesterol.

A recent study tends to confirm these results. Zacherl *et al.* (2011) studied three types of fiber – cellulose, psyllium, and oat fiber – that had been digested to the same degree as when they arrived in the colon and found that the capacity to bind bile acid was mainly, but not solely, correlated with the viscosity of the digested chyme. Heat damage that caused oat fibers to lose their viscosity did not reduce their capacity to bind bile acids, which was higher than that of cellulose. Binding forces other than viscosity (e.g., hydrophobic interactions) are therefore involved. These other binding forces might be responsible for the capacity of insoluble fiber to bind bile acids, as discussed above.

There is therefore good evidence that the hypocholesterolemic capacity of a fiber can be modified by altering its structure.

1.2.5 The Ability to Complex Minerals and to Increase their Extent of Absorption

The properties of fibers are seemingly paradoxical vis-à-vis mineral absorption: they can both form complexes with them (Bergman *et al.*, 1997; Lopez *et al.*, 2002) and promote their absorption by the intestine. The fermented fibers increase the area for their absorption by causing hypertrophy of colon cells and increasing length of the small intestine (Faraldo Correa *et al.*, 2009; Lopez *et al.*, 2000, 2001a), or by promoting the hydrolysis of phytic acid via increased fermentation and stimulating bacterial enzymes (Lopez *et al.*, 2001b; Callegaro *et al.*, 2010). Phytic acid is well known for its ability to complex minerals (Lopez *et al.*, 2002).

The cation-exchange capacity of fiber is due to the presence of negative charges at their surface. These affect the viscosity of the digesta, but the exact mechanisms involved are still not known (Takahashi *et al.*, 2009).

Again, it is possible to manipulate the quality of dietary fiber to promote mineral absorption to a greater or lesser degree. However, the ability of some fibers to increase mineral absorption in humans remains to be demonstrated.

1.2.6 Fiber Structure and Hindgut Health

Monro and colleagues have extensively studied the influence of fiber structure on hindgut functions (Monro, 2014). They report that beyond providing essential fermentable substrates for bacteria,

from a physical viewpoint, polysaccharide-based structures that survive fermentation also make a major contribution to fermentation and large bowel function. They act as supports on which societies (“consortia”) of bacteria proliferate as biofilms, in which metabolic interactions between species of bacteria determine the metabolic products, such as the type of short-chain fatty acid produced from fermentable substrates (Macfarlane and Dillon, 2007). (Monro, 2014, p. 358)

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One of the most important effects of fiber within hindgut is notably its fecal bulking effect. In fact, “persistent plant structure in the form of robust cells occupies volume and provides water-bearing cavities” (Monro and Mishra, 2010), leading to removing of stagnant fecal water, reducing the chemical activity of toxins, promoting fecal softening, and distributing pressure (Monro, 2014). In other words, (insoluble) fiber with remaining unfermented structure keeps its ability to hold water, participating in very important health effects such as those described by Monro (i.e., potentially being able to protect from constipation, hemorrhoids, diverticular disease, colitis, and colorectal cancer) (Monro, 2014; Rose *et al.*, 2007). In contrast, fermentable fiber has other health benefits within hindgut more in association with fecal microbiota and production of SCFAs. According to my studies, these different behaviors of fiber, depending on their fermentability, illustrate well the dual characteristics of fiber (i.e., insoluble (that I call *lente* fiber)) and soluble (that I call *rapid* fiber) fibers with different health effects.

Interestingly, Monro and colleagues further developed a fecal bulking index in relation to the fecal bulking effect of fiber, and that they expressed in wheat bran equivalents (Monro, 2001). Briefly, “wheat bran equivalents for fecal bulking are defined as the gram quantity of wheat bran that would augment fecal bulk to the same extent as a given quantity of a specified food” (Monro, 2001).

Finally, authors showed that minimally processed fibers such as those of swede, broccoli head, broccoli rind, and asparagus exhibited a much higher fecal bulking effect (around 2- to 4-fold) than highly processed or unstructured fibers that are generally either added as isolated ingredients in foods or come from ultra-processed foods (Monro, 2014). These data showed that processed fiber have partially lost their ability to hold water via alteration of their original complex physical structure.

Consequent to the fecal bulking effect, there is also a relation between fiber physicochemical properties and transit time. Thus, Cherbut *et al.* (1991) showed that the fiber water-binding capacity of fibers from wheat bran, sugarbeet, maize, pea hulls, and roasted cocoa might affect the orofecal transit time in healthy volunteers. Fibers were found to act through a mechanical effect if they were not fermented, and the partly degradable fibers also changed the transit time via their products of fermentation (i.e., a large production of propionic and butyric acids).

1.3 The Effect of Fiber Structure on Fermentation Patterns and Microbiota Profiles: Slowly versus Rapidly Fermented Fiber

In vitro data from the literature clearly show that fibers impact SCFA fermentation patterns and microbiota profiles differently, depending on their type or origin and their structure. In addition,

dietary fiber fermentation profiles are important in determining optimal fibers for colonic health, and may be a function of structure, processing

conditions, and other food components. A greater understanding of the relationships between fermentation rate and dietary fiber structure would allow for development of dietary fibers for optimum colonic health. (Rose *et al.*, 2007)

1.3.1 Fiber Structure and Fermentation Patterns

In their review Rose *et al.* (2007) examined which parameters of the fiber chemical and physical structure may play a role on their fermentation rate and patterns. Briefly, they cited numerous studies emphasizing the importance of arabinoxylan cross-linking (through oxidative dimerization of ferulic acid moieties that are esterified to the arabinoxylan polymer), pectin degree of methylation or polymerization, fiber glycosidic linkages and molecular packing, native versus isolated fiber, resistant starch type, and particle size on fermentation patterns (Rose *et al.*, 2007). However, they underlined that the physical inaccessibility of colon renders such analyses difficult.

In a recent study, Rumpagaporn *et al.* (2015) tried to elucidate the structural properties of cereal arabinoxylans that drive rate of fermentation. They used predigested residues of arabinoxylan isolates from corn, wheat, rice, and sorghum brans, and showed, using *in vitro* human fecal bacteria, that there was no relationship between molecular mass, arabinose/xylose ratio, or degree of substitution to fermentation rate patterns. However, interestingly,

slow fermenting wheat and corn arabinoxylans had much higher amount of terminal xylose in branches than fast fermenting rice and sorghum arabinoxylans. The slowest fermenting wheat arabinoxylan additionally contained a complex trisaccharide side chain with two arabinoses linked at the O-2 and O-3 positions of an arabinose that is O-2 linked to the xylan backbone. (Rumpagaporn *et al.*, 2015)

They concluded that the major structural factor that related to slow fermentation was type of linkage of the branch constituents, and large amounts of branches with single xylose units. Simpler structures were associated with a rapid initial rate of fermentation that was comparable to that of the fast fermenting fructooligosaccharides.

Similarly, with cereal arabinoxylans, Karppinen (2003) divided fiber polysaccharides of rye bran into three groups: (1) fermentable, soluble polysaccharides that are rapidly fermented, (2) fermentable cell wall-associated polysaccharides that are gradually released from the cell wall matrix and then fermented, and (3) polysaccharides and cell wall structures that are not fermented at all. However, in the study by Van Nevel *et al.* (2006) fiber water-holding capacity was surprisingly not correlated with fermentability within contents of pig cecum: it was highest for chicory roots, followed by wheat bran and sugar beet pulp; water-holding capacity was very high for sugar beet pulp (10.05 g H₂O/g dry matter), whereas the lowest value was obtained with wheat bran (3.00 g H₂O/g dry matter) (Van Nevel *et al.*, 2006). Similar results were obtained with oat hull fiber, gum arabic, carboxymethylcellulose, soy fiber, and psyllium. Similar results were

obtained with oat hull fiber, gum arabic, carboxymethylcellulose, soy fiber, and psyllium (Bourquin *et al.*, 1993a), and also with fibers from broccoli, carrot, cauliflower, celery, cucumber, lettuce, onion, and radish (Bourquin *et al.*, 1993b) for which their water-holding capacity – an indirect measure of fecal bulking potential – was not correlated with SCFA production and organic matter disappearance.

The results of these studies seems to show that water solubility is not a major, or at least not the only, determinant of fermentability and that structural characteristics at the molecular level of fiber would be particularly involved. Other physicochemical features have been shown to be involved in fiber fermentability such as gross porosity, microporosity, particle size, or crystallinity (Guillon *et al.*, 1998). Two sources of sugar beet fibers were submitted to various chemical and then dehydration treatments, resulting mainly in the removal of pectic polysaccharides (9–49% recovery) at the expense of cellulose (80–100% recovery). Following chemical extraction, harsh drying induced a noticeable decrease in the total pore volume (from 14.9 to 6.1 mL/g) and especially in the pore volume accessible to bacteria (from 10.4 to 3.2 mL/g). Drying following chemical extraction did not affect the crystallinity of cellulose in the fiber. Main results showed that neither the particle size, nor the crystallinity of cellulose were major determinant factors in degradability of sugar beet fibers, but that pore volume accessible to bacteria in sugar beet fibers was highly correlated ($r=0.88$) with its fermentability. Authors concluded that such results “illustrate the importance of matrix physical structure (especially porosity) in the control of the physicochemical behavior of fiber.” This conclusion was also supported by the results of the study by Mortensen and Nordgaardandersen (1993), showing with cellulose and dietary fiber in common clinical use that the amounts of soluble nonstarch polysaccharides in the fiber were closely associated with the mean productions of SCFAs after *in vitro* incubation with human fecal homogenates, but also that the mean production of ammonia was inversely related to the soluble fraction of the fiber. The authors concluded that their “findings support that the water solubility determines the degree of fermentability of dietary fiber and thereby the corresponding bacterial assimilation of ammonia.”

However, most studies do not go as far as recording the physicochemical properties of fibers with fermentation profiles in the analysis, and they only describe SCFA production patterns according to fiber type. For example, in batch cultures of pig intestinal digesta, while β -glucan-grown cultures yielded the highest level of lactate, flaxseed or fenugreek gum-containing cultures generated a significant amount of acetate, propionate, and butyrate (Lin *et al.*, 2011). In another study, 20 soluble fibers (alginate, apple pectin, arabinogalactan, carrageenan, carboxymethylcellulose, citrus pectin, gellan gum, guar gum, gum arabic, gum ghatti, gum karaya, hydrolyzed guar gum, konjac flour, locust bean gum, methylcellulose, oat β -glucan, psyllium, tomato pectin, tragacanth gum, and xanthan gum) were tested *in vitro* for their fermentation profile using three human fecal inocula (Hussein *et al.*, 2008). Although all are soluble, and therefore supposed to be quite highly fermentable, significant differences were observed after 24 hours for dry matter disappearance (between 20% and more than 91%) and gas production, with some fiber having no gas produced. In the

same vein, Lu *et al.* (2000) examined the effects of an arabinoxylan-rich fiber extracted from a byproduct of wheat flour processing in the rat colon compared with well-characterized soluble/rapidly fermentable (i.e., guar gum) and insoluble/slowly fermentable (i.e., wheat bran) fibers. The SCFA pool was particularly high with arabinoxylan and guar gum fibers. Otherwise, arabinoxylans fiber was a good source for acetate, whereas guar gum and wheat bran favored propionate and butyrate production, respectively. Finally, fecal output was 7-, 6-, and 5-fold higher, respectively, in the arabinoxylan, guar gum, and wheat bran groups of rats than in the nonfiber groups ($p < 0.01$). Authors concluded that these results suggested that arabinoxylan fiber behaves like a rapidly fermentable, soluble fiber in the rat colon.

In another study, Monsma *et al.* (2000) used ileal digesta collected from swine fed oat or wheat bran fermented for 0–96 hours in an anaerobic *in vitro* system using inocula prepared from ceca of rats fed the same fiber sources. As in the studies described above, the authors distinguished between slow and rapid fiber. Fermentation of wheat bran digesta was significantly slower than fermentation of oat bran digesta, and oat bran digesta fermentation produced a significantly greater molar proportion of SCFAs as propionate, these latter being produced during fermentation of β -glucan. With regard to particle size, in rats coarse wheat bran gave significantly higher fecal butyrate concentrations than did the rice brans and fine wheat bran (Folino *et al.*, 1995).

More generally, Salvador *et al.* (1993) assessed the relationship between the disappearance of dietary fiber sugars and the production of individual SCFAs by studying *in vitro* using a human fecal inoculum the bacterial degradation of five dietary fibers whose sugars were quantified. Their results confirm that the nature and associations between the fiber sugars were key variables in the fermentability, and that the nature and the amounts of SCFAs produced were closely related to the *in vitro* fermentation of the main sugars available. Thus, as they concluded:

uronic acids seemed to be principally involved in the production of acetic acid whereas the production of propionic acid could be promoted by the fermentation of glucose and, to a lesser extent, by that of xylose and arabinose. Xylose tended to have a greater impact than uronic acids and glucose on the production of butyric acid.

Such results, together with those mentioned previously, suggest that one should be able to predict which SCFA would be specifically produced if the chemical composition and structure of the fiber are known (Salvador *et al.*, 1993).

1.3.2 Fiber Structure and Fecal Microbiota Profiles

Some studies showed that fibers differing in their structure may impact differently on the bacterial community structure. For example, using oat β -glucan, flaxseed gum, and fenugreek gum in batch cultures by pig intestinal digesta, Lin *et al.* showed that “the types of fiber had more significant influence on bacterial community structure than the origin of digesta used as an inoculum” (Lin *et al.*, 2011). Significant differences in bacterial species produced were also observed

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with fiber from chicory roots, sugar beet pulp, wheat bran, and corn cobs incubated with contents of pig cecum (Van Nevel *et al.*, 2006). In addition, bacterial mass increased more and was maintained longer during fermentation of oat bran digesta than the wheat bran digesta in an anaerobic *in vitro* system using inocula prepared from ceca of rats (Monsma *et al.*, 2000).

1.4 Conclusions

The results presented here clearly show that the intrinsic and physicochemical properties of fibers determine the rates at which they are fermented and their consequent health impacts (see brief summary in Figure 1.1). It is therefore no exaggeration to say that, there are *slow* and *rapid* (fermented) fibers, just as there are *slowly* and *rapidly* digested carbohydrates (Englyst *et al.*, 2003), fats (Keogh *et al.*, 2011), and proteins (Boirie *et al.*, 1997). What we do not know is how the kinetics of absorption of volatile fatty acids thus modified in the colon impacts the physiology and modifies the health effects over the long term. Nevertheless, the structure of a fiber can be modified to improve colon health, especially by altering the speed of fermentation, the site of fermentation and then butyrate production, which helps protect against carcinomas and colonic inflammation (Rose *et al.*, 2007). However, although many studies have compared the fermentative

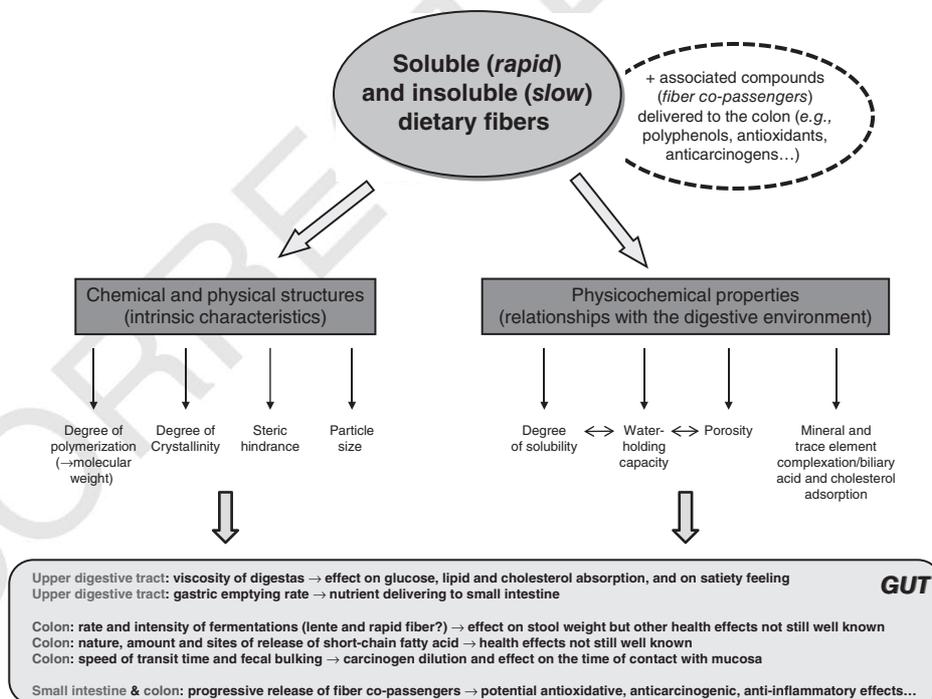


Figure 1.1 Chemical, physical, and physicochemical properties of dietary fiber, their digestive fate and potential health effects via the gut.

fate of different types of fibers, few have investigated the relationship between changes in physicochemical parameters of a single given fiber type (i.e., of equal chemical composition) and its implications for human physiology and health. Nevertheless, the development of the fecal bulking index is a promising step in this direction.

It is also worth emphasizing that fibers may act as vectors, delivering compounds associated with their structure in the gastrointestinal tract, notably at colonic level as shown *in vitro*; fruit and vegetable fibers release significantly more polyphenols than cereal fibers, for example (Taberner *et al.*, 2011). Thus, most of the antioxidants in the colon, such as cereal phenolic acids, are found bound to them (Vitaglione and Fogliano, 2010; Vitaglione *et al.*, 2008). Indeed, Vitaglione *et al.* (2008) suggest that fiber-bound antioxidants released at intestinal level by esterases and in the colon by microbiota – as natural free forms of polyphenols – are absorbed into the bloodstream, metabolized in the liver, and then, in conjugated form, exercise antioxidant power vis-à-vis oxidized LDL (low-density lipoproteins), and help to prevent cardiovascular disease. The authors point out that “It is generally accepted that a higher ratio of soluble fiber/insoluble in cereal products means a higher bioavailability of dietary fiber phenolic compounds complex” (Vitaglione and Fogliano, 2010). In addition to delivering antioxidants in the digestive tract, the fibers are also considered a free radical sponge (“A sponge for radicals”), free radicals participating in an increased oxidative stress that is damaging to numerous body metabolic functions (Vitaglione and Fogliano, 2010). Thus, the concept of “dietary fiber’s co-passengers” – they may exceed 200 000 – is now increasingly emphasized (Jones, 2010).

Therefore, beyond its mere chemical composition, dietary fiber may indirectly affect health through physical characteristics, the physicochemical structure of its matrix, and its ability to carry other compounds (e.g., as vectors of antioxidants), and to release them more or less quickly depending on their digestive and fermentative fate. Another research field of interest is undoubtedly the ability of fermentable fiber, notably as a result of changing their physicochemical properties, to modify gut microbiota and to further impact human health. Little is known about such an issue. Today, there is still a notable lack of studies in humans, probably because the intestine is difficult to access and still remain a “black box.”

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