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# THE PHYSIOLOGICAL EFFECT OF DIETARY FIBER: AN UPDATE

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## INTRODUCTION

Dietary fiber is a member of the family of dietary complex carbohydrates. These complex carbohydrates have individual and diverse actions. At present we cannot chemically identify or predict the biological action in the gastrointestinal tract of individual polymers. Each polymer is peculiar in its biological action and is modified by its physical format and processing (10). Dietary polysaccharide polymers that exceed 20 sugar residues can be classified as dietary complex carbohydrates (43). An alternative description is non-starch



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polysaccharides (NSP) and starch (21). Both of these are chemical descriptions, but they may not satisfy physiologists and consumers who want to know what is the best source of edible fiber, what is the nutritional benefit of a particular fiber, and how will cooking and processing modify the desired effect.

## PLANT STRUCTURE AND CHEMISTRY

Considerable anatomical differences exist between and within economically important plant groups (8). The variety of changes in the cell wall could be important in determining the diversity of actions of sundry dietary fibers in the gastrointestinal tract.

Cell wall structure not only differs among plant species but also during normal development within one species or even within a single cell. The composition of the cell wall is dependent not only on the plant species but also on the tissue type, the maturity of the plant organ at harvesting, and to some extent on the post-harvest storage conditions. Noncarbohydrate components of plant cell walls may influence physiology in the plant and the nutritional potential of the plant fibers, e.g. lignin, phenolic esters, cutin and waxy materials, and suberin. As the plant cell wall develops, it is constantly altered to confirm to a specific developmental pattern that results in the unique shape of any given species (3, 26, 47).

Parenchymatous tissues are the most important source of vegetable fiber. The vascular bundles and parchment layers of cabbage leaves, runner beans, pods, asparagus stems, and carrot roots are relatively immature and only slightly lignified on harvesting and digestion. The soft fruits such as strawberries contain very little dietary fiber but luxious amounts of water. Lignified tissues are of greater importance in cereal sources such as wheat bran and oat products. Cereals contain very little pectic substances, but there is substantial arabinoxylan in wheat or $\beta$-glucan in barley and oats. The distribution of polysaccharides within the plant tissue also varies. Much of the $\beta$-glucan in oats is concentrated in the cells of the outermost layer of the seeds, whereas the $\beta$-glucans in barley are more evenly distributed (3, 26, 47).

An important aspect of the plant cell wall is the interlocking of water-soluble polysaccharides to form biological barriers that are water resistant. Many of the constituents of the plant cell wall, hemicelluloses and pectins, are soluble in water after extraction. This solubility, unmasked by the extraction process, contrasts with the insolubility of the complex polysaccharide of the intact cell wall. The debate of the quantitative measurement of soluble and insoluble fiber is an analytical contrivance rather than an argument that has real significance either in regard to the physiology of the plant or to the recipient of the food fiber.

The backbone of the plant cell wall, cellulose, is a polymer of linear β-(1→4)-linked glucose molecules, several thousand molecules in length. Cellulose occurs largely in a crystalline form in microfibrils, coated with a monolayer of more complex hemicellulosic polymers held tightly by hydrogen bonds. These are embedded in a gel of pectin polysaccharides. The cellulose microfibrils are coated with a layer of xyloglucans bound by hydrogen bonds, and this enables the insoluble cellulose to be dispersed within the wall matrix. Substitution of the hydroxyl group at C6 with xylose, as in xyloglucans, renders cellulose more soluble in alkali and water. Hemicelluloses provide part of the true rigidity of the cell wall. The important hemicelluloses are xyloglucans, xylans, and β-glucans. Xyloglucan is a linear (1→4)β-D-glucan chain substituted with xylosyl units that may be further substituted to form galactosyl-(1→2)β-D-xylosyl or fucosyl-(1→2)α-D-galactosyl-(1→2)β-D-xylosyl units.

The pectins may act as biological glue, cementing cells together through ionic bonds. The precise function of pectins within the cell wall is unclear, but they are closely associated with calcium. Most pectins are probably derived from the primary cell wall and appear to be soluble only after calcium ions are removed. The principal cross-linkage is provided by the helical (1→4)α-D-galactosyluronic groups from adjacent polysaccharides, and condensation with calcium converts soluble pectin into rigid "egg-box" structures. The extent of calcium cross-bridging or esterification through aromatic linkages, and even degree of branching and size of neutral sugar side chains, influence gel flexibility, cell wall porosity, and interaction with hemicellulosic polymers.

The glycoproteins within the cell wall can provide extensive cross-linkages across the different polysaccharide components of the cell wall and may act to form a network with the cellulose microfibrils within a hemicellulose pectin gel (47).

Some plant polysaccharides are harvested from the plant and purified before inclusion as processed food components or therapeutic use. These are more often soluble polysaccharides and include the following.

Guar gum ($M_r = 0.25 \times 10^6$), linear nonionic galáctomannan.

Gum karaya ($M_r = 4.7 \times 10^6$), a cylindrical complex polysaccharide partially acetylated and highly branched with interior galacturonorhamnose chains to which are attached galactose and rhamnose end groups. Glucuronic acid is also present.

Gum arabic ($M_r = 0.5–1.5 \times 10^6$) with a complex acidic heteropolysaccharide based on a highly branched array of galactose, arabinose, rhamnose, and glucuronic acid. Uronic acid residues tend to occur on the periphery of an essentially globular structure.

Gum tragacanth ($M_r$ = 0.5–1 × $10^6$), a complex gum with two major components, bassorin and tragacanthin, is composed of arabinose, fucose, galactose, glucose, xylose, and galacturonic acid.

These gums and mucilages are used as additives by food manufacturers and therefore may contribute less than 2% of a food (16).

Starch, a ubiquitous storage polysaccharide, is an $\alpha$-linked glucan and is the major carbohydrate of foods such as cereal grains and potatoes. The majority of dietary starches are susceptible to hydrolysis by salivary and pancreatic $\alpha$-amylases, but, a proportion of dietary starch may escape digestion by human $\alpha$-amylase. This may be due either to physical inaccessibility or to the inhibition of amylase activity by a rigid stereochemical structure caused during food processing. This starch can pass undigested into the colon where it may act as a substrate for the bacteria and therefore have some of the biological properties of the undigestible plant cell wall (22).

In the plant, starch is contained within the granular structures in a closely packed, partly crystalline form. The actual crystalline structure of the starch granule is believed to depend on the chain length of amylopectin (6, 9).



## PHYSICAL PROPERTIES OF DIETARY FIBER

When considering the action of cooking on cell wall structure and comparing cooked and raw plant foods, the different solubility characteristics of cell wall polysaccharides should be considered. Cell wall structures are degradable to varying degrees, depending on the structure and the conditions used. An important function of insoluble fibers is to increase lumenal viscosity in the intestine. It is not yet clear whether the soluble fibers in food have the same effect. Other polymeric components of the diet (proteins, gelatinized starch) and mucus glycoproteins liberated from the epithelia contribute to viscosity in the same way. Particulate material present in chyme, such as insoluble fiber or hydrated plant tissues, also contribute to a lesser extent to overall viscosity. Digesta viscosity is highly sensitive to changes in ionic concentration that are due to intestinal secretion or absorption of aqueous fluids. Consequently, prediction of physiological action from viscosity measurements in vitro is difficult (23, 38, 39).

Raw apples undergo little sloughing of cells upon ingestion and mastication. Gastric hydrochloric acid only solubilizes a small proportion of the pectins. Cooking the apples results in cell sloughing, and hence significant proportions of the middle lamellae pectic polysaccharides are solubilized. These make the digesta more viscous.

Vegetables undergo structural change during cooking and mastication, e.g. cellular disintegration. The cells in the intact carrot are each bounded by an intact cell wall; after cooking most, if not all, the cell walls have been

ruptured and the cell contents lost. The grinding of foods before cooking and ingestion may also have pronounced effects on fiber action. Cell walls may be disrupted, and the reduced particle size of some fiber preparations such as wheat bran may be less biologically effective (27). The effect of other cooking processes, e.g. Maillard reactions, are not known.

Controlled drying of a heated starch gel can produce any of the different X-ray diffraction patterns, depending on the temperature. On cooling, gelatinized starchy foods will retrograde. During retrogradation, solubility of the starch molecule decreases and so does its susceptibility to hydrolysis by acid and enzymes. Chain length and linearity are important factors affecting retrogradation. The longer the starch chains, the greater the number of interchain hydrogen bonds formed (9).

Studies in man suggest that the mainly retrograded amylose fraction virtually resists digestion in the small intestine (22).

## QUANTITATIVE MEASUREMENT OF FIBER

Chemical analysis or quantitative measurement of the fiber content of specific foods does not allow prediction of their biological action, since the physiological effects of dietary fiber depend predominantly on physical properties that do not relate in any simple or direct way to chemical composition (10).

Gravimetric and gas liquid chromatography (GLC) can be used to analyze dietary fiber. Gravimetric methods weigh an insoluble residue after chemical and enzymic solubilization of non-fiber constituents. The remaining protein is assayed and subtracted from the weight. These methods include the AOAC accepted method (41). Gas liquid chromatography involves the enzymatic breakdown of starch and the separation of the low molecular weight sugars, acid hydrolysis to free sugars, derivatization to alditol acetates, and finally separation and quantitation of neutral monomers with GLC, together with determination of uronic acid and lignin. The GLC methods enable the nature of the carbohydrate to be determined in more detail (21, 52).

## ACTION OF FIBER ALONG THE GASTROINTESTINAL TRACT

Dietary fiber has major effects on (*a*) the rate of gastrointestinal absorption, (*b*) sterol metabolism, (*c*) cecal fermentation, and (*d*) stool weight (13).

### *Rate of Intestinal Absorption*

In the upper gastrointestinal tract dietary fiber prolongs gastric emptying time and retards the absorption of nutrients. Both of these processes are dependent on the physical form of the fiber, and particularly on viscosity.

The inclusion of viscous polysaccharides in carbohydrate meals reduces the

postprandial blood glucose level concentrations in humans. No correlation between the rate of gastric emptying and postprandial concentrations of blood glucose has been observed (19).

Diets that contain a substantial amount of complex carbohydrate content tend to be bulky and require longer times for ingestion. The consumption of whole apple takes longer (17 min) than that required for puree (6 min) or apple juice (1.5 min) in equicaloric amounts (25).

Gastric emptying studies are bedeviled by problems of methodology. The physical nature of the gastric contents is as important as the chemistry of the components (20). Isolated viscous fibers tend to slow the gastric emptying rate of liquids and disruptible solids. It is almost certain, however, that the gastric emptying rate for a fiber ingested alone will differ from that of a fiber ingested along with other dietary constituents such as fat and protein. Likewise, it has been shown that the gastric emptying time for different fiber sources is variable (13).

Rates of release of nutrients from dietary fiber in the intestine are influenced by factors such as the intactness of tissue histology, degree of ripeness, and the effects of processing and cooking (25, 27).

There is no evidence to suggest that viscous polysaccharides inhibit transport across the small intestinal epithelium. More likely, their viscous properties inhibit the access of nutrients to the epithelium. Two mechanisms bring nutrients into contact with the epithelium. Intestinal contractions create turbulence and convection currents that mix the luminal contents and bring material from the center of the lumen close to the epithelium. Nutrients have to diffuse across the thin, relatively unstirred layer of fluid lying adjacent to the epithelium. Increasing the viscosity of the luminal contents may impair both convection and diffusion of the nutrients across the unstirred layer. In the case of isolated polysaccharides such as guar gum, the slowing of nutrient absorption appears to be a function of viscosity (20). The reduction in absorption caused by guar gum is probably due to resistance by viscous solutions of the convective effects of intestinal contractions (20).

In the case of whole plant material, the influence on absorption appears to be due to the inaccessibility of nutrients within the cellular matrix of the plant. The effects on absorption can be decreased by grinding the food before cooking or by thorough chewing; both processes open the cellular structure (20).

Inadequate mixing of luminal contents due to increased viscosity by soluble polysaccharides may also slow the movement of digestive enzymes to their substrates (46).

Viscous polysaccharides tend to delay small bowel transit, possibly due to resistance to the propulsive contractions of the intestine (31). In rats most of this delay is secondary to alterations in ileal motility; transit through the upper small intestine is little affected (42).

Complex carbohydrates, particularly those that possess uronic and phenolic acid groups, or sulphated residues such as pectins and alginates may bind magnesium, calcium, zinc, and iron. However, other constituents of plant cells, e.g. phytates, silicates, and oxalates, also chelate divalent cations. The binding of minerals may be reduced by acid, protein, ascorbate, and citrate (13, 30).

The reduction in absorption of minerals and vitamins could, in theory, have adverse nutritional consequences, particularly in populations eating diets inherently deficient in these nutrients, i.e. in developing countries or fastidious, health food conscious communities where diets may be marginal in micronutrients but high in fiber. Children are particularly vulnerable to such conditions. Customary Western diets contain levels of minerals and vitamins in excess of daily requirements. Mineral balance studies have indicated that for people on nutritionally adequate diets, the ingestion of mixed high fiber diets or dietary supplementation with viscous polysaccharides is unlikely to cause mineral deficiencies (30).

The ingestion of dietary fiber may affect drug absorption in two ways: by reducing gastric emptying or inhibiting mixing in the small intestine. Viscous polysaccharides delay the absorption of paracetamol. Quite separately if a drug enters the enterohepatic circulation, any bacterial metabolism of the drug may be altered by coincidental fermentation of fiber and thus the half life of a drug may be increased or decreased. An example of this effect is digoxin. Digoxin has a narrow therapeutic range and is passively absorbed in the small intestine and so is affected by gastric emptying or decreased small intestinal absorption. Digoxin is also reduced to an inactive metabolite in the colon, so an inactive metabolite will be absorbed (33).

## *Alteration of Sterol Metabolism*

Dietary fiber has been shown to have an effect on sterol metabolism (12). This effect is not simple: Possibly dietary fiber displaces fat from the diet (49); polyunsaturated fats frequently eaten in conjunction with the fiber may also be important (51). The direct effect of fiber on sterol metabolism may be through one of several mechanisms: altered lipid absorption; altered bile acid metabolism in the cecum; reduced bile acid absorption in the cecum; indirectly via short chain fatty acids, especially propionic acid, resulting from fiber fermentation.

An important action of some fibers is to reduce the reabsorption of bile acids in the ileum and hence the amount and type of bile acid and fats reaching the colon. Bile acids may be trapped within the lumen of the ileum either because of a high luminal viscosity or because they bind to the polysaccharide structure. A reduction in the ileal reabsorption of bile acid has several direct effects. The enterohepatic circulation of bile acids may be affected. In the cecum, bile acids are deconjugated and 7$\alpha$-dehydroxylated. In this less

water-soluble form, bile acids are adsorbed to dietary fiber in a way that is affected by pH and is mediated through hydrophobic bonds, thereby increasing the loss of bile acid in the feces (17, 32).

Consequently, the enterohepatic pool is initially reduced. It may be renewed by increased synthesis of bile acids from cholesterol, thereby reducing body cholesterol. Other fibers, e.g. gum arabic, are associated with a significant decrease in serum cholesterol without increasing fecal bile acid excretion. The fibers that are most effective in influencing sterol metabolism (e.g. pectin) are fermented in the colon, as shown by increased breath hydrogen production. That the physiological effect is due entirely to adsorption to fiber in the colon is unlikely (14). In contrast, fiber has an important sequestrating effect in the ileum. Possibly, an alteration occurs in the end product of bile acid bacterial metabolism; these bile acids are absorbed from the colon and returned to the liver in the portal vein, thus modulating either the synthesis of cholesterol or its catabolism to bile acids (29). The precise relationship between the proportions of ileal and cecal absorption of bile acids is difficult to estimate. Clearly it is a variable and very diet dependent, especially in regard to the amount and type of fiber. In particular, some bacterial colonization of the ileum may simulate cecal bacterial activity. Approximately 25% of the body pool of cholic acid and 50% of chenodeoxycholic acid pass into the cecum either to be absorbed or excreted in feces (7, 37).

An alternative mechanism for the effect of fiber on serum cholesterol is the action of propionic acid, derived from fiber fermentation, on liver cholesterol synthesis. Initial in vitro experiments have indicated that cholesterol synthesis by isolated hepatocytes is inhibited by propionic acid. Whether this inhibition occurs in vivo at physiological concentrations is not clear (4).

## *Substrate for Cecal Fermentation*

The colon may be regarded as two organs: The right side is a fermenter, the left side affects continence. The right side of the colon is involved in nutrient salvage so that dietary fiber, resistant starch, fat, and protein are utilized by bacteria and the end products absorbed and used by the body (11).

The colonic flora is a complex ecosystem largely consisting of anaerobic bacteria, which outnumber the facultative organisms at least 100:1. The colonic flora of a single individual consist of more than 400 bacterial species. The total bacterial count in feces is $10^{10}$ to $10^{12}$ colony-forming units per milliliter. Despite the complexity of the ecosystem, the microflora population is remarkably stable. Although wide variations in the microflora are found between individuals, studies in a single subject show that the microflora are stable over prolonged periods of time. The identification of individual bacteria is desirable. It is more profitable, however, for physiological and nutritional studies to regard the cecal bacterial complex as an important organ in its

own right that is complementary to the liver in the enterohepatic circulation (11).

The cecal bacterial flora are dependent upon dietary and endogenous sources for nutrition. The amounts of substances passing through the intestine from the ileum vary with an inverse relationship between cecal bacterial metabolism and upper intestinal nutrient absorption. Dietary fiber has an influence on bacterial mass and enzyme activity. The consensus view is that while the cecal bacterial mass may increase as a result of an increased fiber content in the diet, the types of bacteria do not alter (11).

The process whereby a compound is bacterially dissimilated in the cecum under anaerobic conditions is complex and varied, leading to partial or complete decomposition. The end products are absorbed from the colon and utilized as nutrients, absorbed and reexcreted in the enterohepatic circulation, and excreted in stool.

In addition, the colon is part of the excretion system provided by the liver and biliary tree, i.e. the enterohepatic circulation. Poorly water-soluble chemicals of a molecular weight or more than 300–400 are excreted in the bile with enhanced water-soluble properties through chemical conjugation with glucuronide, sulphate, acetate, etc, or are made physically soluble by the detergent properties of bile acid. These chemicals may be endogenous, e.g. bile acids, bilirubin, hormones, or exogenous, e.g. drugs, food additives, pesticides. They pass unabsorbed through the small intestine. In the cecum these biliary excretion products and also unabsorbed dietary constituents, e.g. resistant starch, fat and proteins, and mucopolysaccharides secreted by the intestinal mucosa, are fermented by the bacterial enzymes. The fermentation process of biliary excretion products removes substitutions that have enhanced water solubility and enabled biliary excretion to occur. The bacterial metabolic products are less water soluble. Some of the end products of the fermentation of biliary excretion compounds are reabsorbed, metabolically altered and reconjugated in the liver, and excreted in bile; an enterohepatic circulation is established (11).

The effects of dietary fiber in the colon may be summarized in terms of (*a*) susceptibility to bacterial fermentation, (*b*) ability to increase bacterial mass, (*c*) ability to increase bacterial saccharolytic enzyme activity, and (*d*) water-holding capacity of the fiber residue after fermentation.

Enlargement of the cecum is a common finding when some dietary fibers are fed, and this is now believed to be part of a normal physiological adjustment. Such an increase may be due to a number of factors such as prolonged cecal residence of the fiber, increased bacterial mass, or increased bacterial end products (11).

The fermentation of fiber yields hydrogen, methane, and short-chain fatty acids. Hydrogen is readily measured in the breath; it has a diurnal variation

with its nadir at midday, and it increases in the afternoon. Diverse sources of fiber influence the evolution of hydrogen in different ways. Disaccharides generate hydrogen more rapidly than trisaccharides, which in turn evolve hydrogen more quickly than oligosaccharides. More complex carbohydrates may not be fermented as rapidly and may require induction of specific enzymes before they can be utilized (13).

Methane-producing organisms are said to be strict anaerobes. The proportion of breath methane exhalers in different healthy adult populations vary widely, ranging from 33 to 80%. The breath methane status of an individual remains stable throughout the day and over prolonged periods. Yet feces from healthy individuals regardless of breath methane excretion status will always produce methane. This suggests that all individuals produce methane, but a certain amount must be produced to spill over into the breath (35).

The fermentation of feces from herbivorous animals produces methane, whereas the fermentation of feces from carnivores does not. Differences also exist between the two feeding groups in the production of short-chain fatty acids. This suggests that methanogenic animals require a dietary fibrous residue (34).

It has been suggested that considerable methane excretion only takes place when sulphate-reducing bacteria are not active. The metabolic end product of dissimilatory sulphate reduction is thought to be toxic to methanogenic bacteria. When sulphate is present, sulphate-reducing bacteria have a higher substrate affinity for hydrogen than do methanogenic bacteria (24).

Some nonabsorbed carbohydrates, e.g. pectin, gum arabic, oligosaccharides, and resistant starch, are fermented to short-chain fatty acids (chiefly acetic, propionic and *n*-butyric), carbon dioxide, hydrogen, and methane. The molar ratio of acetate, propionate, and butyrate is of the order of 60:20:15, though small amounts of isobutyrate, valerate, and isovalerate are present; the latter originate from the breakdown of protein and in particular from the breakdown of branch-chained fatty acids. The production of short-chain fatty acids has several possible actions on the gut mucosa. All of the short-chain fatty acids are readily absorbed by the colonic mucosa, but only acetic acid reaches the systemic circulation in appreciable amounts. Butyric acid is metabolized before it reaches the portal blood; propionic acid is metabolized in the liver. Butyric acid appears to be used as a fuel by the colonic mucosa, and in vitro studies of isolated cells have indicated that the short-chain fatty acids and butyric acid in particular are the preferred energy sources of colonic cells. Short-chain fatty acids are potent stimulants of cellular proliferation not only in the colon but also in the small intestine (5).

Short-chain fatty acids are the predominant anions in the human feces (5). If the daily content of the diet is increased from 63 g of protein and 23 g of dietary fiber, type unspecified, to an isocaloric 136 g of of protein and 53 g of fiber, though the amount of ammonia in fecal water (1 mmol per liter) is

doubled, the short-chain fatty acids remain unchanged. Unless the dietary intake of fermentable carbohydrate is severely restricted or antibiotics are given, fecal short-chain fatty acid concentrations and molar ratios remain relatively constant in man. Cummings & Branch have estimated that 40–50 g of carbohydrate will yield 400–500 mmol total short-chain fatty acids, 240–300 mmol acetate, and 80–100 mmol of both propionate and butyrate (5). Almost all of these short-chain fatty acids will be absorbed from the colon. This means that fecal short-chain fatty acid estimations do not reflect cecal and colonic fermentation but rather reflect only the efficiency of absorption, the ability of the fiber residue to sequestrate short-chain fatty acids, and the continued fermentation of fiber around the colon, which presumably will continue until the substrate is exhausted. The absorption of short-chain fatty acids from the colon in man is concentration dependent and is associated with bicarbonate secretion. Bicarbonate appears consistently in the colonic lumen during short-chain fatty acid absorption, a process independent of the chloride-bicarbonate exchange. Possibly, an acetate-bicarbonate exchange takes place at the cell surface, but the precise mechanism is not understood. Short-chain fatty acids have a stimulatory effect on sodium absorption from the colonic lumen. This may be related to the recycling of hydrogen ions. The unionized short-chain fatty acid crosses into the cell where it dissociates and hydrogen ion is moved back into the lumen in exchange for sodium. Thus short-chain fatty acids provide a powerful stimulant to sodium and water absorption (5).

The bacteria in the colon produce an "organ" of intense metabolic activity. This activity in the colon is mainly reductive, in contrast to the activity in the liver, which is oxidative. The intestinal flora perform a wide range of metabolic transformations on ingested compounds. The major enzymes involved in these activities include azoreductase, nitrate reductase, nitroreductase, $\beta$-glucosidase, $\beta$-glucuronidase, and methylmercury-demethylase. The action of fiber on the activity of these enzymes may be species-dependent, and animal studies do not always indicate what happens in man (45).

## *Stool Weight*

Feces are complex and consist of 75% water. Bacteria make a large contribution to the dry weight; the residue is unfermented fiber and excreted compounds. There is a wide range of individual and mean stool weights. In a study in Edinburgh the variation in stool weight was between 19 and 280 g during a 24-hr period. The amount of stool excreted by an individual varies quite markedly from individual to individual and by that individual over a period of time. Of the dietary constituents, only dietary fiber influenced stool weight (15). It is not known why there is such individual variation in stool weight.

The most important mechanism whereby dietary fiber increases stool

weight is through the water-holding capacity of unfermented fiber, e.g. wheat bran. The greater the water-holding capacity of the bran, the greater the effect on stool weight (44, 48).

Fiber may influence fecal output by another mechanism. Colonic microbial growth may be stimulated by ingestion of fermentable fiber sources such as apple, guar, or pectin. However, an increase in stool weight does not always result from eating these fibers (50). An osmotic effect of products of bacterial fermentation on stool mass may also occur, though this as yet is not a well-defined contribution (19).

One of the major functions of the colon is to absorb water and produce a plasticine-type of stool that can be readily voided at will from the rectum. The ileum contains a viscous fluid; the viscosity is created by mucus and water-soluble fibers whose molecular weight, degree of cross-linkages, and aggregation will affect the viscosity. If the viscosity increases to a certain point, peculiar to the constituent macromolecules, then a sol or hydrated carbohydrate complex will result. The sol will be coherent and homogeneous.

The concentration of ileal effluent in the cecum and colon is the result of the absorption of water. This might be expected to create a gel. Feces are not a gel, however, but a plasticine-like material, heterogeneous without viscosity, and made up of water, bacteria, lipids, sterols, mucus, and fiber. In the cecum, therefore, a marked physical change occurs, in part as a result of bacterial activity, in part by the presence of bacteria themselves. Such a plasticine structure is lost in watery diarrhea. The mechanism of this change, physiological or pathological, is unknown but some of the steps involved are described below (13).

In the colon water is distributed in three ways: (*a*) free water, which can be absorbed from the colon; (*b*) water that is incorporated into bacterial mass; (*c*) water that is bound by fiber. Stool weight is dictated by (*a*) the time available for water absorption to take place through the colonic mucosa, (*b*) the incorporation of water into the residue of fiber after the fermentation of fiber, and (*c*) the bacterial mass.

Wheat bran added to the diet increases stool weight in a predictable linear manner and decreases intestinal transit time. The increment in stool weight is independent of the initial stool weight. Wholemeal bread, unless it is of a very coarse nature, has little or no effect on stool weight. The particle size of the fiber is all important. Coarse wheat bran is more effective than fine wheat bran (48). The greater the water-holding capacity of the bran, the greater the effect on stool weight. The effect of the water-binding by wheat bran is such that in addition to an increase in stool weight, other fecal constituents such as bile acids, which in absolute amounts do not increase, are diluted by fecal water and hence their concentration decreases (13). The increment in stool weight per gram of wheat bran varies in different populations. For control subjects, an increase in stool weight, while being dependent on the particle

size of the bran, is generally of the order of 3 to 5 g wet stool weight per gram fiber. However in individuals with the irritable bowel syndrome and symptomatic diverticulosis the increment is of the order of 1 to 2 g wet weight per gram fiber. This suggests a difference in the handling of the fiber in the intestine in these situations (40).

Bacteria are an important component of the fecal mass (50). What percentage are living and what percentage are dead and as such are being voided is not known. The fermentation of some fibers results in an increase in the bacterial content and hence in the weight of stool. Other fibers (e.g. pectin) are fermented without any effect on stool weight. Possibly some fibers that increase stool weight in association with an increased bacterial mass do so because of an increase in excreted bacteria adherent to unfermented fiber (50).

The degree to which free water is absorbed from the colon is affected by a number of factors that are poorly understood (2). In the rat a comparison of cecal and fecal contents has shown that the fermentation of some complex carbohydrates, e.g. ispaghula and gellan, has a significant effect on the content of luminal short-chain fatty acids in the more distal colon. This effect appears to be related to continued fermentation along the colon (19). An increase in the short-chain fatty acid concentration of feces appears to be related to an increased output of fecal water. Thus under some circumstances short-chain fatty acid absorption may be less efficient, which may play a role in determining fecal output. This observation supports the view of Hellendoorn who suggested that fiber fermentation products play an important role in determining stool weight and transit time (28). The demonstration that short-chain fatty acids were rapidly absorbed in the colon suggested that short-chain fatty acids play no part in determining fecal output (36). However, it would appear that there is continued fermentation of some complex carbohydrates, e.g. ispaghula, in the distal colon. Under these circumstances the fecal short-chain fatty acids may influence fecal water osmolality, absorption, and stool weight (2).



## MATHEMATICAL EQUATIONS TO DESCRIBE THE INTRALUMENAL EFFECTS OF FIBER

In the gastrointestinal tract, fiber will interact with (*i*) one-phase miscible mixtures or (*ii*) binary mixtures (multiphase system). These include (*a*) two-phase systems with one continuous phase and one dispersed phase, and (*b*) two-phase systems with two continuous phases. There are equations for defining each of these classes of mixtures.

Fiber and other constituents of the intestinal luminal and mural phases may be involved in single-phase systems in which the components are completely miscible or soluble in each other. The properties that then become important

are the density of the liquid mixtures and the dielectric thermodynamic properties.

Alternatively, there can be two-phase or multiphase systems in which the components are insoluble or only partially soluble in each other. For two-phase systems, the shape and physical characteristics of the particles, the rate of diffusion through mixtures, the viscosity of the suspension, and the character and physical properties of the two phases become important.

Soluble fiber components can be regarded as forming a continuous sol phase within which insoluble and hydrated components are dispersed as a discontinuous, particulate phase. Other dietary components that do not form part of the homogeneous continuous phase (e.g. unmicellized fat) can be regarded as separate phases. In such two-phase or multiphase systems, certain physical properties, such as density, obey a simple rule of mixing:

$$P = P_1\phi_1 + P_2\phi_2 \ldots + Pn\phi n$$

where $P$ is the overall physical property of the entire system, $P_1, P_2, \ldots Pn$ represent the corresponding physical property in the individual phases, and $\phi_1 + \phi_2 + \ldots + \phi n = 1$.

Other physical properties, such as viscosity, however, combine in a much more complex way and may be difficult or impossible to predict from the behavior of the individual phases in isolation.

The principal physiological effect of dietary fiber in the small intestine is to reduce the rate or the extent of release of nutrients.

The rate of release of nutrients from fibrous particles into the surrounding intestinal fluid will be inversely proportional to particle size and directly proportional to solute gradient. It will also be affected, for example, by the physical state of the solute (e.g. whether it is present in solid form or is already dissolved in water trapped within the particle), so that dissolved solids can be squeezed out by peristaltic contractions or diffuse out. The surface properties of the particle, e.g. the suface tension effects, are also important. The concentration of nutrients within the continuous aqueous phase will be constantly depleted by enteric absorption, and will be replenished, as outlined above, by release of material from food particles. The progress of these sequential release processes will, of course, also be influenced by transit time (i.e. the duration of exposure to a particular absorptive surface or digestive environment).

These processes may be expressed as

$$R = k'\mathrm{cf/w}.$$

The rate of release of nutrients from a polymeric system in the intestine is in direct proportion to the concentration within the particle (*cf*) and decreases with increasing particle size (*w*).

The effect of fiber in the colon may be summarized as

$$\text{stool weight} = W_f(1 + H_f) + W_b(1 + H_b) + W_m(1 + H_m)$$

where $W_f$, $W_b$, and $W_m$ are, respectively, the dry weights of fiber remaining after fermentation in the colon, bacteria present in the feces, and osmotically active metabolites and other substances in the colonic contents that could reduce the amount of free water absorbed, and $H_f$, $H_b$, and $H_m$ denote their respective "water-holding capacities" (i.e. the weight of water resistant to absorption from the colon, per unit dry weight of each fecal constituent) (18).

Simple methods are being developed to anticipate the four major biological functions of dietary fiber whereby fiber affects absorption and metabolism in the intestine. This approach has been successful in comparing dietary fibers used in human experiments with those studied in vitro (1). The importance of measuring fiber in absolute amounts cannot be underestimated. Nevertheless, the measurement of fiber in terms that reflect function is of primary importance. The understanding of enzyme activity grew immeasurably after the establishment of Michaelis-Menten equations. Such functional classifications are an important model for the development of an understanding of the action of dietary complex carbohydrates and dietary fiber.

New methods need to be developed to determine the precise fate and disposition of the products of fiber fermentation. This is an unexplored and important field.



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