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Dietary Fibers and Absorption of Nutrients[1] (42200)

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The increased intake of foods containing dietary fiber can generally be shown to result in increases in fecal volume and dry weight and in fecal energy content (1–3). These changes are in part directly attributable to increased consumption of undigestible plant cell wall material, but there is also evidence that the certain dietary fibers may also affect the digestion and absorption of other nutrients.

The effect of dietary fiber on increased fecal energy content can be expressed by fruit, vegetable, or cereal fiber (4, 5) and has been reported to vary between 58 and 321 kcal/day, depending on the type and amount of dietary fiber ingested (4–7). This energy loss is largely in the form of fat and protein (7) and has been suggested to be of both bacterial and metabolic origin (8, 9).

Generally, the effects of increasing intakes of fiber in the form of wheat bran have, at best, only a mild effect on fecal energy loss (10). A portion of this loss is due to fat which is closely associated with the bran and largely inaccessible to the lipases of the intestinal contents. However, increased intakes of fiber in the form of pectin, which, when pure, lacks endogenous fat, cause more apparent increases in fecal fat content (11, 12), and this loss is therefore of endogenous or metabolic origin.

Southgate (2) has pointed out the difficulties of assessing the effects of dietary fibers on the digestibility of dietary macronutrients. In many nutritional studies, assessment of nutrient digestibility is based on comparisons of nutrient intakes and fecal recoveries. This, however, only represents apparent digestibility (2), since even when the digestion and/or absorption of a nutrient is negligible, there is a finite fecal recovery. Thus, true digestibility must represent both the events in the small intestine plus the amount degraded or metabolized by the colonic microorganisms. Direct measurements on the effects of various fiber sources on losses of nutrients from the small intestine in man, and on subsequent bacterial utilization of these nutrients have yet to be reported. There is, however, direct and indirect evidence that certain dietary fibers sources may modify the digestion and absorption of macronutrients, and that this may affect energy balance in humans.

Potential Mechanisms for Modifying Nutrient Absorption. From current knowledge on the physiological responses to fiber-rich foods and to individual types of fiber components, there are several potentially important mechanisms by which fibers can alter the rate and/or efficiency of nutrient utilization. As shown in Fig. 1, these include, among others: Rates of gastric filling and emptying; altered pH and metabolic responses in the stomach; effects on intestinal motility and transit; modification of digestive enzyme activities; sequestration of lipid micellar components; bulk interference with nutrient diffusion and absorption, and interaction of the fiber with the intestinal surface.

Gastric filling and emptying. Intestinal absorption of nutrients can be influenced by modifying the rates at which food enters and/or leaves the stomach. High fiber, bulkier foods may require longer periods for ingestion and thereby modify rates of gastric filling (13, 14). Radiological studies in man suggest that stomach emptying after a meal containing wholemeal bread is slower that with white bread (13). In general, however, stomach emptying is measurably slowed in response to the water-soluble, viscous fiber derivatives, such as guar gum (cluster bean galactomannan) and pectins (polygalacturonic acid) (15–17). That this is largely, if not entirely, a response to the viscosity of the fiber preparation has been documented (18) and is shown in Fig. 2. As discussed below, these fiber types also blunt glucose tolerance curves and modify insulin responses in man.

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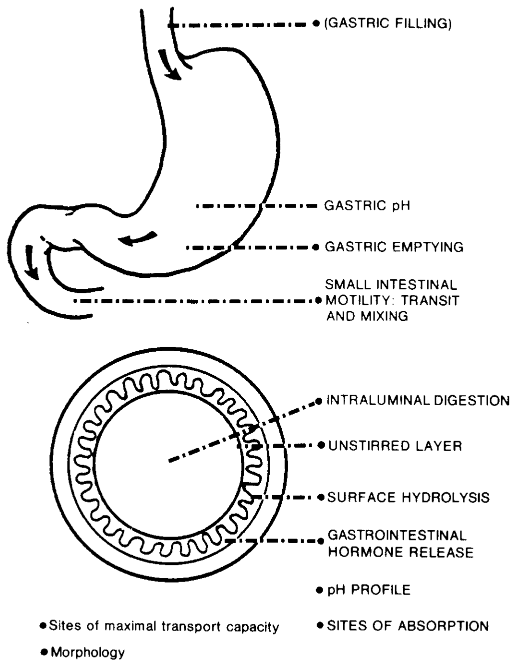

FIG. 1. Potential mechanisms by which dietary fiber may affect the rate and/or efficiency of nutrient absorption (18). Courtesy of A. K. Leeds.

Gastric acidity. There has not been sufficient attention given to the possibility that dietary fibers may influence the overall acidity and metabolic or digestive characteristic of the stomach. Early studies by Lennard-Jones *et al.* (19) demonstrated that the increase in gastric acidity was greater following ingestion of refined grain products, such as maize cornflower, that with whole maize meal (Fig. 3). Tovey (20) also reported that wheat bran, rice bran, and unrefined grains demonstrated greater buffering capacity that did polished rice or white flour. More recently, Rydning (21) reported that preparations containing wheat bran or guar gum modified gastric pH in healthy subjects given a standard meal of porridge and juice.

The importance of food in the regulation of gastrin release in the stomach has been reviewed elsewhere (22). This has important implications in tissue growth responses to the hormone as well as secretory responses of this organ. Fiber-dependent modifications of gastric pH, whether indirect or direct, may alter the efficiency of peptic digestion of protein as well as subsequent proteolytic activities in the small intestine (23). These potential effects require additional experimental attention.

The possibility that various dietary fiber derivatives might differentially modify the se-

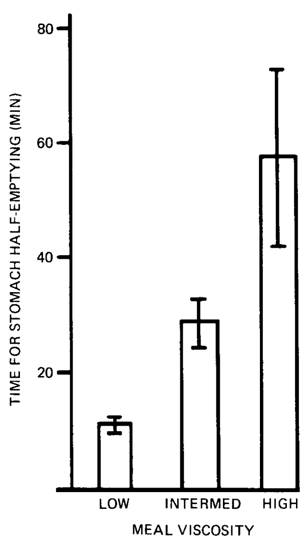

FIG. 2. Effect of dietary intakes of low, intermediate, and high viscosity guar gum on gastric emptying of glucose in the rat [modified from Ref. (18)].

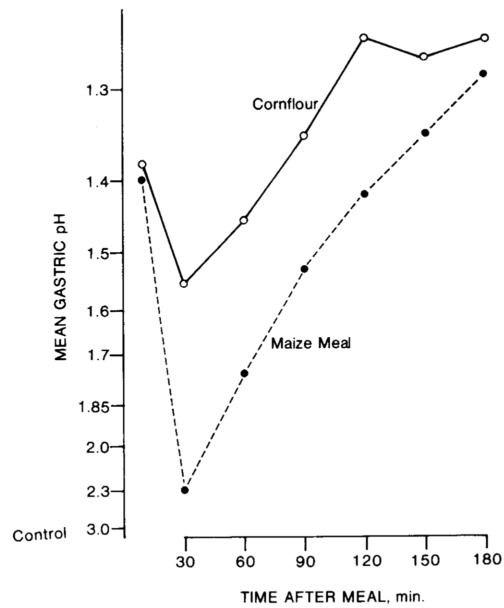

FIG. 3. Modification of gastric acidity in patients with duodenal ulcers after meals of maize and cornflour [modified from Ref. (19)].

cretion and/or responses to gastrin is not without precedent. Secretion of other gastrointestinal hormones, such as gastric inhibitory peptide (GIP) (24–26) and glucagon (26, 27) is significantly modified by dietary fiber. The delayed release of gastric contents and modified intestinal pH might also alter responses of intestinal secretin and cholesystokinin which regulate pancreatic and biliary secretions, and this can have major implications in the rates and efficiencies of nutrient digestion.

Small intestinal transit. The specific effects of dietary fiber on small intestinal transit has been difficult to determine as an independent variable, and there are only limited results in relation to dietary fiber content or types of fiber in the diet. Early radiological studies suggested that transit through the small intestine in man was more rapid with wholemeal bread that with white bread (28). In contrast, there is evidence in rats that high viscosity fibers, such as guar gum, result in a slower transit in the midintestine (18). Other studies, reviewed elsewhere (18, 29), have only considered mouth to cecal transit times and therefore also include effects of the fiber sources on gastric filling and emptying. Nevertheless, a more rapid overall transit in the intestine in response to insoluble fibers and slow transit with viscous fibers is predictable and could be expected to affect digestion and/or absorption of nutrients (e.g., contact time).

Pancreatic and intestinal digestive enzymes. As reviewed by Schneeman (23), another important aspect of nutrient bioavailability includes the effect of various fiber sources on the interaction of digestive enzymes and their substrates, and the limited diffusability of absorbable products in the intestinal lumen. The evidence from *in vitro* studies and from duodenal aspirates suggest that most of the fiber derivatives tested can alter the activities of pancreatic amylase, lipase, and the proteolytic enzymes (23). This may be a response to either a modification of the enzyme–substrate interaction or to the presence of proteolytic enzyme inhibitors associated with the fiber source (30). The inhibitory effects of fiber on pancreatic enzyme activities has been attributed to viscosity, pH changes, and adsorption (31).

Available evidence suggests that the fibers have little if any direct effect on pancreatic secretory activity or the pancreatic content of digestive enzymes (32–34), suggesting that the primary effect of the fiber on nutrient digestion resides in the intestinal lumen.

Effects of feeding various fiber preparations on the activities of the mucosal-associated digestive enzymes have not been consistent (see 34). Thus, pectin-containing diets have been reported to decrease the activities of mucosal alkaline phosphatase (35–37), and of lactase and invertase (36, 37), to have no effect on the intestinal disaccharidases (38), or to increase the activities of these villus enzymes (39). These differences may be due to the nutritional state of the animal at the time of study (40) and/or to the extent of tissue rinsing and preparation prior to enzyme measurement (see 34).

It would appear that, in general, viscous fiber preparations may modify the rates of enzymatic digestion of disaccharides and peptides at the mucosal surface (41), and that this effect may be reversed if the tissue is carefully washed free of the fiber (42).

Sequestration of lipid micellar components. Eastwood and Boyd (43) reported that appreciable quantities of bile acids were associated with the insoluble fraction of the small intestinal contents of rats. Since then, there have been repeated demonstrations of the binding of bile acids to various grains, food fiber sources, and isolated fiber components (44–49). This binding appears to be primarily an adsorption phenomenon, and is influenced by pH and osmolarity, bile acid structure, and the physical and chemical forms of the fiber (44). In general, binding of bile acids is greater at lower pH, where acidic groups are un-ionized, is probably hydrophobic (44), and appears to be reversible (50). Certain fiber sources appear to exhibit preferential binding of unconjugated bile acid, rather than the taurine or glycine conjugates, and may show a degree of specificity for di- or trihydroxylated bile acid analogs. However, this is not a uniform phenomenon among the various fibers tested *in vitro.*

Among the fibers and their individual components, the viscous or gelling fibers, and the lignins appear to have the greatest bile acid-sequestering ability (51, 52). With the viscous fibers, such as pectin, this ability to affect the normal partitioning in the intestine has been demonstrated indirectly by the ability of dietary fiber to increase fecal bile acid *in vivo* (51). With the insoluble fibers, the majority of studies have been conducted *in vitro* and generally have considered only individual or mixed bile acids at micellar concentrations. Other studies (49, 52), however, suggest that this sequestration phenomenon may be more complex than originally proposed.

The sequestration ability of commercial bile acid-binding resins and certain types of fibers does not appear to be confined to bile acids. The binding of cholesterol from bile acid micelles by cholestyramine, cereal fibers, and alfalfa has also been demonstrated, and at levels roughly proportional to bile acid-binding (47, 49, 50). In more recent studies (49, 52), the ability of various fiber preparations to sequester individual amphipaths and amphiphiles, which normally constitute mixed micelles in the intestinal lumen, was tested. With this complex mixture of bile salts, phospholipids, fatty acids, monoglycerides, and cholesterol, the apparent binding of all components of mixed micelles was roughly proportional. As expected, the ion-exchange resin, cholestyramine, completely sequestered the available micellar bile acid and also removed all other micellar components (Table I). Among the fiber material tested, the viscous guar gum and insoluble lignin were effective micelle sequestrants while cellulose was essentially inert in binding micelles. The importance of this bile acid-sequestering property of dietary fibers in altering lipid absorption and metabolism is discussed below.

Bulk interference with nutrient diffusion and absorption. There is evidence that viscous fibers, in particular, can influence accessibility of absorbable nutrients to the mucosal absorptive surface. Studies on the uptake of sugars and amino acids by rat intestinal segments suggest that nutrient flux is inversely related to the viscosity of the incubating solution (42, 53). This response is evident with various preparations of gums or with carboxymethylcellulose. These effects, however, are completely dependent upon the presence of the fiber preparation since the inhibition of nutrient uptake is completely reversed either by washing or reincubating the tissue in the absence of fiber (42) or by using rinsed intestinal segments from fiber-fed animals (54).

It has been proposed, based on both suggestive and direct evidence, that at least one acute effect of viscous fiber preparations is due to an increased resistance or thickness of the unstirred water layer barrier, at the intestinal surface, to nutrient absorption (42, 53–56). Thus, in addition to the possibility that certain dietary fibers may acutely interfere with bulk phase diffusion of nutrients in the intestinal lumen, they may also, when present, alter the transport characteristics of nutrients at the mucosal surface.

In addition to these reports suggesting that nutrient absorption is inversely related to the luminal fluid viscosity, there is a recent report (54) describing transport characteristics of water-soluble nutrients by rinsed intestinal segments from rats prefed either cellulose or pectin-containing diets for 4 weeks. Compared to segments from rats given fiber-free diets, both the apparent K_m and the maximal transport capacity for amino acid and glucose analogs were increased. These studies suggest that, in

TABLE I. IN VITRO BINDING OF MICELLAR COMPONENTS BY ION EXCHANGE RESINS AND CERTAIN DIETARY FIBER PREPARATIONS[a]

Test substance	Percentage bound				
	Bile salt[b]	Lecithin	Cholesterol	Monolein	Fatty acids[c]
Cholestyramine	82	92	95	96	96
DEAE-Sephadex	49	99	100	99	98
Guar gum	36	22	23	23	33
Lignin	20	9	5	13	13
Alfalfa	7	4	1	19	18
Wheat bran	4	6	0	11	12
Cellulose	2	1	8	4	4

[a] Modified from (49, 52).
[b] Sodium taurocholate.
[c] Equimolar mixture of palmitic, oleic, and linoleic acids.

addition to the acute effects of viscous fiber derivatives, there are chronic adaptive responses in the intestine to fiber-containing diets (54). Such adaptive responses to changing nutriture of the intestine are well recognized (57–60) and have been described for effects of dietary fibers on both morphological (e.g., 60) and functional (34, 54, 61) parameters of the small intestine.

As described above, certain fiber preparations appear to acutely depress nutrient absorption by modifying the resistance of the mucosal surface barrier to transport (42, 53–56). This barrier has been described as an unstirred water layer associated with the mucosal surface. In addition, however, there is an extensive mucinous coat associated with the mucosal surface and these mucins are largely derived from the intestinal goblet cells which constitute about one of every eight cells on the villus column (62). Among the putative functions ascribed to these surface constituents are cytoprotection and antiviral and antibacterial activities (63). In addition, the mucins have been described as an important constituent of the unstirred water layer (64), and have been suggested to be a major rate-limiting diffusion barrier (64–66).

Morphological studies (60, 23) have suggested the possibility that prolonged intake of insoluble fiber constituents (e.g., cellulose or wheat bran) may alter the number and/or secretory activities of the goblet cells. More recently, the increased turnover of intestinal mucins in response to prolonged ingestion of insoluble fiber preparations (as assessed by isotope incorporation) has been reported (67). Thus, changes in mucin content or turnover in response to various fiber types requires consideration as a mechanism by which dietary fibers might modify the nutrient diffusion barrier at the intestinal surface.

Interaction of dietary fibers with the intestinal surface. Another potentially important action of dietary fibers on nutrient absorption involves the transient interaction of the fiber with the mucosal surface. Such an interaction is implied by findings that the acute effects of viscous fiber derivatives on nutrient absorption *in vitro* are not observed when tissues are rinsed prior to transport studies (42, 54).

The first direct evidence for this type of interaction has been obtained by studies with various fiber preparations covalently linked to the blue dye, Remazol (68). The covalent linkage is resistant to hydrolysis in the stomach and small intestine, and the physical properties of these preparations are similar to those of the unmodified fibers (unpublished studies). Mucosal homogenates prepared from the small intestine of rats given a single gastric dose of Remazol-labeled guar gum or wheat bran, or from intestinal segments incubated with the dye-labeled fibers, contain significant amounts of the dye. The viscosity of the homogenate is increased after incubations with guar but not after bran, which is a direct reflection of the properties of the two fiber types. Furthermore, the mucosa-associated fibers are largely recovered with a mucin fraction which is precipitated with cetyltrimethylammonium bromide, a reagent employed for isolation of gastric and intestinal mucins (69). These studies, albeit preliminary, suggest an additional mechanism whereby acute and chronic modification of intestinal nutrient absorption may occur.

In summary, there are various demonstrated and potential influences of dietary fibers on both intraluminal and mucosal aspects of gastrointestinal physiology, and any or all of these can influence the rate and extent of nutrient digestion and/or absorption. Available evidence for dietary fiber effects on individual macronutrients is summarized below.

Absorption of Carbohydrates. There are two major aspects of the relationship between dietary fibers and bioavailability of carbohydrates. The first deals with the availability of carbohydrates endogenous to various foods (e.g., legumes versus leafy vegetables) and this has been termed "biological equivalence" (70), or the glycemic index (71). The second involves the direct or indirect effects of individual fiber derivatives or fiber supplements on the rate and/or efficiency of utilization of other sources of dietary carbohydrates.

The glycemic index. The presence of intact cell walls in unrefined sources of dietary fibers in foods may limit the interaction of digestive enzymes with the plant nutrients, such as carbohydrates, fats, and proteins. A number of studies indicate that various foods are digested at different rates, as assessed largely by the glycemic responses (72–74). When selected carbohydrate foods were exposed to human digestive enzyme in dialysis bags, the rates of digestion varied markedly as assessed by rates of release of the digestion products (glucose, maltose, oligosaccharides) into the dialysate (71, 72). Thus, the starch in wholemeal bread was digested most rapidly and, in general, the slowest digestion occurred with legumes (Fig. 4). These *in vitro* results are consistent with glycemic responses in humans suggesting that rates of digestion *in vivo* may differ between various foods.

In order to allow comparisons of the glycemic responses to various food sources, a glycemic index is calculated as the percentage of the glycemic response to a particular food in comparison to the glycemic response to bread (71). These indices for some foods are shown in Fig. 5, and have had predictive value in designing diets for diabetic patients (71).

Although dietary fiber content and composition, and the assessibility of digestive enzymes to the cellular starch may be major factors involved in influencing the digestibility of food carbohydrates, other factors may also be involved (71). These include antinutrients, phytates (75), the physical form and gellation characteristics of the starch, and the effects of fats and proteins (76) on the glycemic responses to each food source. In any case, there is sufficient evidence to suggest that not only is the type of food important as a predictor of the glycemic response, but also that the form of the food ingested is important. Thus, apples eaten whole as opposed to in puree or juice form result in flattened glucose and insulin responses (14), as is the case with whole rice versus ground rice (77).

Influence of fiber supplements and fiber foods. As indicated earlier, Haber and colleagues (14) distinguished between the glycemic responses to a natural fiber-nutrient relationship and those of the fiber per se by comparing plasma glucose and insulin responses to whole apples, apple puree, and apple juice. The three preparations, given at equivalent carbohydrate levels and consumed at the same speed, resulted in discernible differences in the plasma glucose and insulin responses.

Numerous studies have now shown that the plasma glucose and insulin responses to an oral carbohydrate load can be modified by addition of dietary fiber to the test meal (see 18, 78, 79, for reviews). Definitive studies concerning the effect of dietary fiber preparations on the rate and efficiency of sugar absorption have been conducted by Jenkins and colleagues, and include the importance of viscosity, the timing of fiber intake, and the possibility of malabsorption rather than delayed absorption of the sugar.

Glucose and insulin responses were determined in healthy volunteers given a 50-g glucose load alone or with addition of 12 g of one of several fiber sources or analogs (80). These included the galactomannans, guar gum, and gum tragacanth from the cluster bean; the methoxylated polygalacturonic acid, pectin;

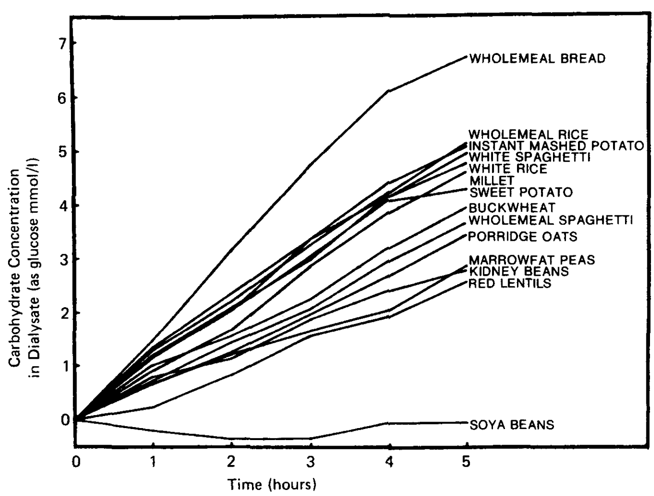

FIG. 4. Differences in starch digestibility following incubation of 2 g of available carbohydrate portions of foods with pooled human saliva and pancreatic juice. Courtesy of D. J. A. Jenkins (71).

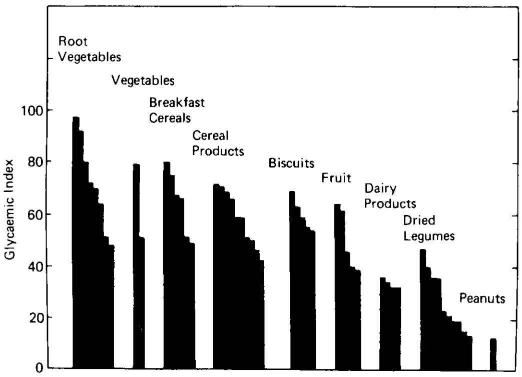

FIG. 5. The glycemic index of foods. Courtesy of D. J. A. Jenkins (71).

methyl cellulose; bran; and cholestyramine, the synthetic anion-exchange resin. In all cases, but especially with the viscous fiber preparations, there was a flattening of the glucose tolerance curves (Fig. 6). Insulin responses were also altered but not always in proportion to the glycemic responses.

The importance of viscosity of the fiber preparation in blunting the glycemic responses was also addressed in these studies (80). There was a direct correlation between the measured viscosity of 1% solutions of the preparations and the percentage difference in 2-hr blood glucose levels from control. Furthermore, mild acid hydrolysis of the guar preparation, which reduces its viscosity, also eliminated the effect of guar on the serum glucose and insulin responses.

That the effect of the fiber preparations was a result of delayed sugar absorption, rather than malabsorption, was tested using the unmetabolizable sugar, xylose. The urinary excretion of xylose from the guar meal was less than controls during the initial 2-hr collection period, but was thereafter (up to 8 hr) greater than controls, suggesting little if any impairment of overall absorption and excretion of the monosaccharide.

The importance of timing of ingestion of the fiber and its acute effect on glycemia after a glucose load has been emphasized (78). If

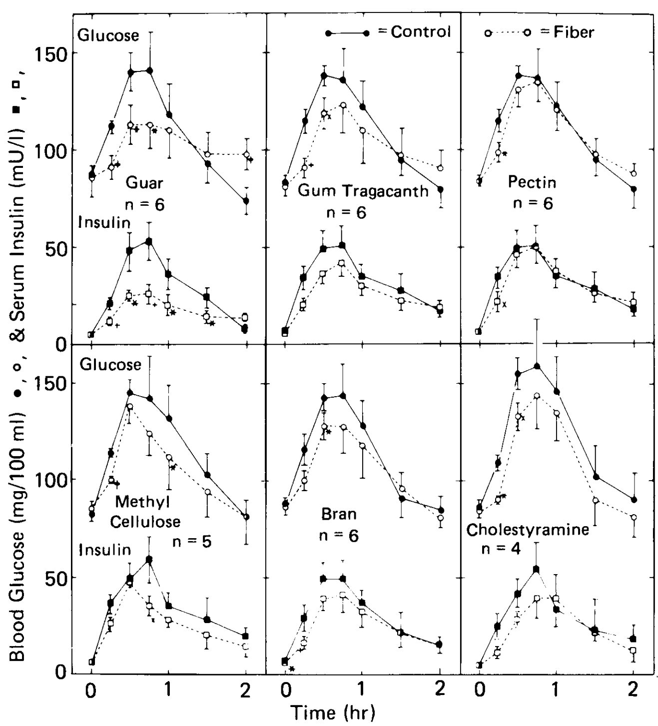

FIG. 6. Effect of adding 12 g various fibers (dry weights) on postprandial glucose and insulin responses. Courtesy of D. J. A. Jenkins (80).

the fiber preparation is not adequately mixed with the carbohydrate portion of the meal (81), or if guar is taken before the glucose tolerance test rather than with the glucose load (82), there is no effect on flattening of the glycemic responses.

The studies described above largely address aspects of sugar absorption in humans in response to acute effects of a single fiber dose. It has been suggested that these acute responses can largely be explained by effects of the viscous fibers, in particular, on delayed gastric emptying. However, there is also evidence that dietary fibers can also directly influence small intestinal absorption of sugars. Guar and pectin can delay glucose diffusion from dialysis bags in proportion to their relative viscosities (78). This type of bulk phase inhibition of diffusion has also been demonstrated in studies on glucose and amino acid transport by segments of rat jejunum (42, 53, 55, 56). The possible mechanisms by which dietary fiber could influence luminal and mucosal surface phenomena with respect to absorption of water-soluble nutrients (e.g., glucose, amino acids) has been reviewed above.

In addition to these acute responses, largely demonstrated by viscous fiber preparations, it is also apparent that similar responses may also be expressed by prolonged intake of insoluble fiber mixtures, such as wheat bran (83) and high-fiber foods. Miranda and Horwitz (27) clearly demonstrated the overall reduction in mean plasma glucose levels and insulin requirements in diabetics given fiber-supplemented diets. Munoz *et al.* (84) have also reported that dietary supplementation with an insoluble fiber preparation for up to 30 days improved glucose tolerance, despite the absence of the fiber in the glucose load. These findings together with those of Anderson (79), using high carbohydrate, high fiber diets, suggest the possibility of adaptive responses in the gastrointestinal tract to long-term fiber intakes (85).

Effects on gastrointestinal hormones. It now appears clear that at least one major gastrointestinal response to increased intake of high fiber foods or specific fiber derivatives is a modification of the secretion of intestinal hormones associated with carbohydrate metabolism. As shown in Fig. 7, the acute effects of pectin included with the glucose load on serum

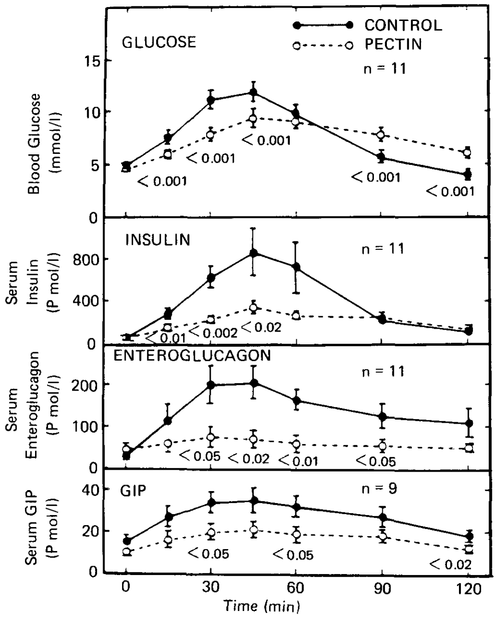

FIG. 7. Responses of blood glucose and specific hormones to 60-g doses of glucose given with and without pectin. Courtesy of D. J. A. Jenkins.

glucose and insulin responses, were also associated with a blunting in serum levels of enteroglucagon and GIP (26), which regulate insulin secretion (86). Similar responses in plasma GIP, but not glucagon, have been observed with guar gum (25), and in both GIP and glucagon-like immunoreactivity with increases in high fiber foods (27). These types of intestinal hormone responses, whether acute or adaptive have major implications in the efficient metabolism and disposition of dietary carbohydrate and likely of dietary fat.

Digestion and Absorption of Protein. Many studies have demonstrated that increasing intakes of dietary fiber are associated with increased levels of fecal nitrogen (e.g., 7, 87, 88). It has been suggested (88) that this may, at least in part, represent protein associated with plant cells and cell wall material, which is effectively part of the dietary fiber and therefore intrinsically less available for digestion.

Studies in which fecal nitrogen has been fractionated suggest that this is largely associated with the bacterial mass, either as bacterial products, mucosal cell debris, or unabsorbed intestinal secretions (8). This is likely, since interference with nutrient bioavailability by dietary fiber in the small intestine would result in increased flow of bacterial nutrients (fibers, fat, and protein) into the large bowel. This in turn results in increased bacterial growth and fecal elimination. Thus, increases in fecal nitrogen in response in increasing intakes of dietary fiber is likely a reflection of events in the colon rather than in the small intestine (8).

There is also evidence to suggest that increased fiber intakes do not alter urinary nitrogen levels under conditions where fecal nitrogen output is increased (5). The implication is that there may not be an imbalance in metabolic nitrogen under these conditions.

Direct *in vivo* evidence for altered protein digestibility and amino acid absorption by dietary fiber is lacking. As reviewed above, certain dietary fibers may contain antinutrients or inhibitors of proteolytic enzymes which may alter protein utilization (89). Analysis of effects of various fiber derivatives on proteolytic enzyme activities *in vitro* (23, 30, 31), also suggest the possibility that dietary fiber may express effects on protein bioavailability *in vivo*.

The most definitive evidence that certain dietary fiber derivatives may influence the diffusibility and/or intestinal transport of peptides and amino acids has been obtained from *in vitro* studies with intestinal segments. Using everted segments of rat jejunum, Elsenhans *et al.* (40), found that high levels of guar gum (5 g/liter) inhibited the hydrolysis of L-phenylalanylglycine in a competitive manner. However, inhibitory effects on hydrolytic rates were not observed when intestinal homogenates rather than intestinal segments were studied.

Similar studies with free amino acids (leucine and phenylalanine) suggest that a variety of viscous fiber preparations, including guar, pectin, gum tragacanth, carubin and carrageenan can all inhibit intestinal uptake in relation to the viscosity of the solution (42). These effects, like those observed with monosaccharides (42, 53), were completely dependent on the presence of the fiber in the incubating medium. Similar findings on inhibition of leucine absorption by guar gum have been reported during single-pass perfusions in anesthetized rats (55). Potential mechanisms of these effects have been discussed earlier.

Absorption of Lipids. *General.* As indicated earlier, many studies in which dietary fiber intake is increased either by qualitative changes in diet or by supplementation with isolated fiber sources, demonstrate significant increases in fecal fat (7, 12, 90). This could be, in part, attributed to difficulties in the digestibility of lipids associated with the fiber source, especially with high fiber foods. However, Southgate *et al.* (7) were not able to associate the increase in fecal lipids with increased excretion of bran lipids, and studies with pectin or cellulose supplementation of diets (12, 90) suggest that the increase in fecal lipids is largely of endogenous or metabolic origin. Furthermore, apparent digestibility values correlated poorly with the increases in fecal fat (3), suggesting a limited utility of making deductions by analyses of fecal fat excretion (3).

There is also considerable literature on the overall effects of high fiber foods and fiber supplementation on general aspects of lipid metabolism, including circulating lipids and lipoproteins (91–96). These analytical approaches, albeit important, do not distinguish between primary or indirect effects on absorption of lipids from secondary responses due to modified hormonal levels or altered metabolism of carbohydrates.

In general, however, data from human studies suggest that dietary fibers, and particularly the viscous polysaccharides, may interfere with certain aspects of the emulsification and lipolysis of dietary fat, and most likely at the level of micellar solubilization and absorption of fat digestion products and cholesterol. As shown in Fig. 8, the emulsification of dietary fat for efficient lipolysis and the solubilization of lipolytic products and cholesterol is in part dependent on the concentration and composition of the biliary bile acid and phospholipid pools.

Cholesterol absorption. A prolonged increase in fecal excretion of bile acids (acidic steroids) has been taken to represent a potential reduction in the overall enterohepatic bile acid pool and to predict a reduction in the efficiency of lipid bioavailability (94, 95). Furthermore, an increase in fecal neutral sterols (cholesterol and its bacterial metabolites) can be taken to represent decreased cholesterol absorption or increased biliary output of sterols. Thus, the analyses of fecal acidic and neutral steroid outputs has indicated that in-

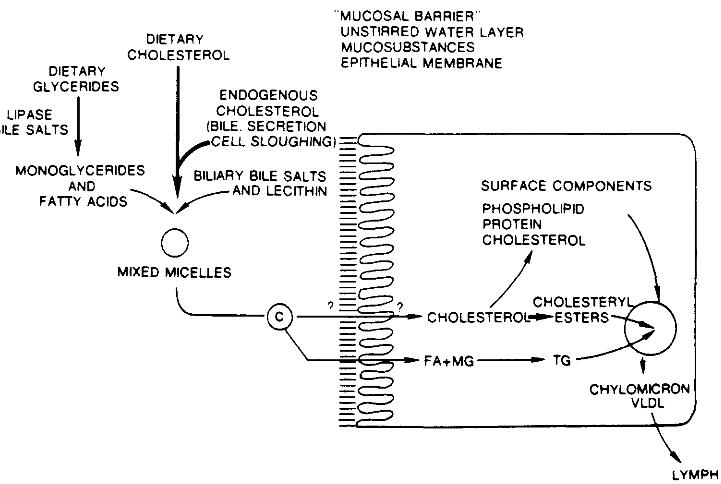

FIG. 8. Overview of the intestinal absorption and cellular transport of lipids. Adapted from (96).

creased intake of dietary fiber and particularly of the viscous fiber preparations, may modify the enterohepatic circulation of bile acids, and this presumably can affect aspects of lipid absorption (91–95).

Earlier studies on the effects of dietary fiber supplements on cholesterol absorption in experimental animals and humans, employed either balance techniques or the fecal recovery of isotopic tracers. Studies in rats (Table II) indicated that dietary supplementation with alfalfa, pectin, gum arabic, or agar resulted in increased output of fecal acidic steroids and diminished absorption of cholesterol. Similar results have been obtained with rabbits fed alfalfa (103), but not in humans given labeled cholesterol in a formula diet containing 60 g of neutral detergent fiber (104). In general, these and other studies (see 91–96) suggest that the greatest effects of dietary fibers on cholesterol absorption and plasma cholesterol levels are observed when cholesterol is included in the diet or the administered test preparation. Fiber-induced modifications of bile salt availability for solubilization of luminal cholesterol have been considered as a primary mechanism for the acute effects of viscous fiber preparations.

Additional mechanisms of dietary fiber influences on cholesterol absorption have been proposed. Gee *et al.* (105) reported that the uptake of micellar cholesterol by everted intestinal sacs or perfused intestine was markedly decreased in the presence of 0.5% guar gum,

TABLE II. EFFECT OF FIBER SUPPLEMENTATION ON FECAL STEROIDS AND CHOLESTEROL ABSORPTION IN THE RAT

Fiber supplement	Measured response	Reference
Alfalfa (rat chow)	Increased fecal bile acids	(97)
Alfalfa	Increased fecal neutral sterols; decreased cholesterol absorption	(98)
Pectin (500 mg/day)	Increased fecal acidic and neutrol steroids	(99)
Pectin (5%)	Increased fecal acidic steroids; decreased cholesterol absorption by fecal isotope recovery	(100)
Pectin (250 mg)	Decreased lymphatic absorption of cholesterol	(101)
Pectin (5%)	Decreased cholesterol absorption	(102)
Gum arabic (5%)	Decreased cholesterol absorption	(102)
Agar (5%)	Decreased cholesterol absorption	(102)

and was delayed in sacs preincubated with the guar. Fasting of rats, previously fed a 2% guar-containing diet for 30 days prior to study, however, eliminated the effect observed in the presence of guar. These studies, as with studies on glucose and amino acid absorption, suggested the requirement for the presence of the fiber in order to observe effects on sterol transport. The results, however, are inconsistent with others (61, 106–108) demonstrating that prolonged intake of fiber-supplemented diets result in a depressed absorption of lipids in animals which are fasted before study.

Vahouny and co-workers (61, 106, 107) have reported studies in which rats were fed for short and long periods on defined diets containing various insoluble and viscous fiber preparations, and fasted overnight prior to study. Whether the cholesterol was administered gastrically (106, 107) or duodenally (61), lymphatic recovery was depressed in all fiber-fed groups as well as in rats prefed 2% cholestyramine. These effects have been attributed to a variety of morphofunctional changes in the gastrointestinal tract in response to dietary fiber intake (e.g., 35, 39, 54, 60, 61), including modification of the intestinal surface-associated mucins (63, 67). This interpretation is further supported by the findings (39) that ingestion of either cellulose or pectin-containing diets result in decreased synthesis of intestinal phospholipids, which are required for chylomicron synthesis during cholesterol and glyceride absorption.

Glyceride and fatty acid absorption. In addition to impaired cholesterol absorbability in fasted animals prefed various fiber-containing diets, a similar response (correlation coefficient = 0.962) has been observed with lymphatic recovery of triolein in these same animals (107). In studies by Imaizumi *et al.* (108), the appearance of chylomicron triglycerides in mesenteric lymph was followed during intestinal infusions of triolein in animals prefed diets containing cellulose or guar gum. The delayed appearance of lymph triglycerides in the fiber-fed groups was not attributable to effects on gastric emptying. Based on studies in which the triglyceride was infused into either proximal or distal intestine, it was concluded that the fiber-related responses were due largely to delayed digestion and/or absorption of the lipolytic products of triolein.

Recent studies have been designed to circumvent possible effects of prefeeding fiber-containing diets on gastric emptying or on lipolysis of the administered triglyceride (61). Rats fed various fiber supplements, and fasted overnight were administered free oleic acid (and cholesterol) intraduodenally. In these animals, prefeeding the viscous fiber preparations, but not cellulose or alfalfa, reduced the rate of fatty acid absorption. None of the fiber supplements affected the overall extent of fatty acid recovery in lymph, in contrast to the findings with cholesterol.

The current evidence suggests that, in addition to direct effects of dietary fiber in the gastrointestinal tract, there are also fiber-dependent adaptations in the luminal availability of lipids. It appears that fatty acid absorption may be delayed but not impaired, particularly in response to direct or indirect effects of viscous fiber preparations. This is in contrast to the apparent impairment of cholesterol absorption, and of triglyceride bioavailability observed in the rat models. Whether these responses are due to interference with bulk phase diffusion of lipids, to persistent effects on biliary bile acids and micellar composition, to modifications in surface transport barriers, and/or to altered intestinal production of lipoproteins remains to be determined.

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