REVIEW

Dietary starch and fiber: potential benefits to body weight and glucose metabolism

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Practice Points

- Dietary interventions that promote weight loss can be highly effective in preventing and delaying the onset of Type 2 diabetes.
- The fermentable fiber content of the diet may have an important role in appetite regulation, weight loss and insulin sensitivity.
- Colonic fermentation of resistant starch and dietary fiber yields short chain fatty acids that have been shown to stimulate the release of appetite-inhibitory gut hormones.
- Short chain fatty acids have been shown to influence adipose tissue metabolism and insulin sensitivity.
- Increasing the fermentable fiber composition of the diet may be an effective strategy to support long-term weight loss and improve insulin sensitivity.
- Further studies are needed to fully assess the efficacy of dietary interventions with fermentable fibers in protecting against obesity and Type 2 diabetes.

SUMMARY Dietary starch and fiber, particularly the fermentable content, may be important for long-term weight loss and the prevention and management of Type 2 diabetes. Resistant starch and most dietary fibers are fermented in the colon producing short chain fatty acids. Free fatty acid receptors 2 and 3 are two recently discovered receptors. The main ligands for these receptors are short chain fatty acids. These receptors are found on enteroendocrine L-cells in the colon where they stimulate the release of anorectic hormones (glucagon-like peptide-1 and peptide tyrosine tyrosine) and on adipocytes where they can exert improvements to insulin sensitivity. Recent studies have shown that supplementing the diet with fermentable fiber can have a positive effect on weight loss and insulin sensitivity. Further investigations with high-risk populations are warranted to determine if long-term dietary interventions with fermentable fibers can protect against or delay the progression of Type 2 diabetes.

Epidemiological evidence suggests that changes in diet and levels of physical activity are the main contributory lifestyle factors responsible for the increased prevalence of Type 2 diabetes mellitus (T2DM) found in nearly all countries, ethnic groups, and across the age range [1].

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Large-scale intervention studies have demonstrated that dietary and/or exercise interventions can be highly effective in delaying the onset of T2DM [2,3]. Evidence from large-scale trials suggests that weight loss and reduced adiposity are key to T2DM prevention and amelioration of insulin resistance [2–5]. Recent epidemiological and experimental studies have highlighted an inverse correlation between dietary fiber intake and body weight [6,7] and adiposity [8,9] making high fiber diets an attractive strategy to reduce obesity and the incidence of T2DM. The aim of the present article is to review the scientific evidence for the potential benefits of dietary starch and fiber on metabolism and body weight. Specifically, the review focuses on the possibility that the fermentable content of starch and fiber may be important in long-term weight loss and preventing the development of T2DM.

Dietary carbohydrate & metabolism

In most societies carbohydrates are the principal source of energy in the diet. Dietary carbohydrates can generally be separated into simple and complex forms based on saccharide chain length. Simple sugars include monosaccharides (e.g., glucose and fructose) and disaccharides (e.g., sucrose and lactose), while complex carbohydrates comprise polysaccharides, with starch and fiber being the principal components. Historically, nutritional advice for the prevention and management of diabetes has often recommended a restriction of simple sugars and increased amounts of starchy foods, based on the assumption that sugars are more rapidly digested and absorbed, exerting a greater rise in blood glucose [101]. However, it has been demonstrated that the saccharide chain length of a carbohydrate poorly predicts the metabolic response [10].

Dietary carbohydrate can affect metabolism in at least three ways: the rate of carbohydrate digestion; the rate of absorption across the small intestine; and fermentation in the colon. Based on these properties, the ingestion of different starches and fibers can have varying effects on metabolic responses. The rate and extent of carbohydrate digestion are determined by multiple factors, all of which affect the susceptibility of the polysaccharide to enzymatic digestion. These factors include the nature of the glycosidic bond, the structure of the starch granule, the amylose:amylopectin ratio, the degree of gelatinization and the integrity of the plant cell wall. For example, the branched amylopectin molecule has an open structure which is readily accessible to amylase. It is thus more rapidly digested and absorbed than the tightly packed amylose molecule [11,12]. If starch that is theoretically digestible is encased within a nondigestible cell wall (e.g., comprised of cellulose, lignin or pectin) it may be partially or totally resistant to digestion. At the end of the spectrum are the nonstarch polysaccharides and nondigestible oligosaccharides, which have glycosidic linkages that cannot be hydrolyzed by amylase. Examples include the β1–4 linkages in cellulose and the α-galactosidic linkages of raffinose. Resistant starch is not digested in the small intestine, but passes into the large intestine intact where along with some dietary fibers it may be fermented to produce short chain fatty acids (SCFA) [13]. The metabolic effects of SCFA will be discussed later in this article. Since resistant starch is not digested, studies have shown that the simple replacement of a digestible starch with a resistant starch in a meal will significantly reduce postprandial glucose and insulin responses [14]. In addition to the rate of digestion, certain physiochemical properties of dietary carbohydrate may affect the rate of absorption. For example, soluble fibers, such as pectin and β-glucan, have been shown to increase the viscosity of gastric contents, which is known to slow gastric emptying [15]. Insoluble fibers also alter gastric emptying via mechanisms dependent on their particle size. Changes in the physical characteristics of the gastric and intestinal contents may influence gastric emptying, dilute enzymes, prevent or delay polysaccharide hydrolysis, and slow the diffusion of products of digestion across the absorptive surface.

Glycemic index & weight loss

The issues outlined above make it difficult to understand the metabolic effects of carbohydrate from its simple saccharide chain length. Therefore, the glycemic index (GI) was proposed in 1981 as an alternative system of classifying carbohydrates based on postprandial glycemic response to improve the metabolic management of diabetes [16]. The GI corresponds to the incremental area under the blood response curve measured over 2 h to 50 g of available carbohydrate from a test food relative to that of a control food (either white bread or glucose) [17]. Due to the physical properties of resistant starch and fiber, many foods that are rich in these dietary components such as nuts, lentils, beans and oats have a low GI. The effect of different GI diets on

long-term glycemic control has been the subject of many scientific articles (for detailed review see [18,19]); however, the relationship between the GI of foods and their effects on long-term weight loss has received less attention. Investigations have examined the effect of GI on short-term satiety assessed either by a subjective method based on visual analogue scales or by an objective method using a preload test meal design. A recent systematic review article found that more than half the studies support an increased short-term satiety with low-GI compared with high-GI test meals [20]. For example, an investigation compared the effect of test breakfasts with low and high GI on appetite and food intake in children [21]. The results showed that low-GI foods eaten at breakfast significantly reduce food intake at an *ad libitum* lunch. Nevertheless, only a few studies have attempted to assess if the reduced hunger and subsequent energy intake from low-GI foods in the short-term has any effect on long-term body weight. A systematic review of six randomized controlled trials comparing the effects of low-GI with a higher GI or control diet suggest an overall positive effect of low-GI diets on weight loss [22]. However, the results from available studies have not shown consistent results. In a recent investigation, overweight and obese participants were provided with either a low- or high-GI diet for a 12-week treatment period. The study found no evidence to support the claims that a low GI will reduce body weight [23]. In comparison, a recent dietary intervention trial showed that subjects who were provided with a low-GI diet during an 8-week energy-restricted period experienced significantly greater weight loss than those who followed a conventional diet (7 vs 5% of the initial body weight) [24].

Dietary fiber & colonic fermentation

There are many factors that could be confounding the results of investigations assessing long-term effects of low-GI diets on weight loss. One important factor appears to be the diversity of foods utilized in the low-GI diets. Taken together, available studies would suggest that low-GI diets that have greater amounts of fiber from fruit, vegetables, legumes and cereal grains are effective at promoting weight loss [24–26]. Recent epidemiological and experimental studies have highlighted an inverse correlation between dietary fiber intake and body weight, BMI [6,7] and adiposity [8,9]. It has been shown that as obesity levels have steadily increased over the past 50 years the amount of fiber in the typical western diet has fallen. The current average American diet contains only 15 g of fiber per day, only half of the current recommended daily amount [27]. The term 'dietary fiber' can define a vast array of substances with different chemical properties and physiological effects and the type of fiber in the current western diet has also changed, with a lower proportion of fiber from fruit and vegetables and a greater amount from cereal grains [28]. Also, the fermentable fiber content in fruit and vegetables is greater than that of cereal grain. This is important as recent investigations would suggest that the products of colonic fermentation can influence appetite regulation, the control of body weight, and insulin sensitivity.

All dietary fiber passes through the small intestine unaffected by digestive enzymes. Upon reaching the colon anaerobic bacteria are able to degrade some dietary fibers via a fermentation process yielding metabolizable energy (~2 kcal/g), gases (CO_2, H_2, and CH_4) and SCFA [13]. Over 80% of SCFA present in the human colonic lumen are in the form of acetate (C2), propionate (C3) and butyrate (C4) in the approximate molar ratio 60:20:20 [29]. The metabolic effects of SCFA are summarized in **Figure 1**. However, the production of SCFA is very difficult to predict due to large inter-individual differences in gut microbiota composition and gut transit time [13]. The fermentability of soluble fibers is also much greater than that of insoluble fibers, with pectin, resistant starch, gums and polyfructans being the most highly fermented substrates. In 2003 it was demonstrated that SCFA act as ligands for the previously orphaned G-protein coupled receptors GPR41 (now called free fatty acid receptor [FFAR]3) and GPR43 (now called FFAR2) [30,31]. It was found that FFAR2 and FFAR3 are activated by physiological doses of SCFA with similar micromolar activation potencies for acetate, propionate and butyrate. A possible role for these receptors in appetite regulation emerged with the identification of FFAR2 and FFAR3 mRNA expression in the rat colon [32]. These findings have since been confirmed in humans with FFAR2 and FFAR3 shown to be present on the luminal side of the L-cell [33]. The L-cell is the most abundant endocrine cell in the intestine and cosecretes the hormones peptide tyrosine tyrosine (PYY) and glucagon-like peptide (GLP)-1.

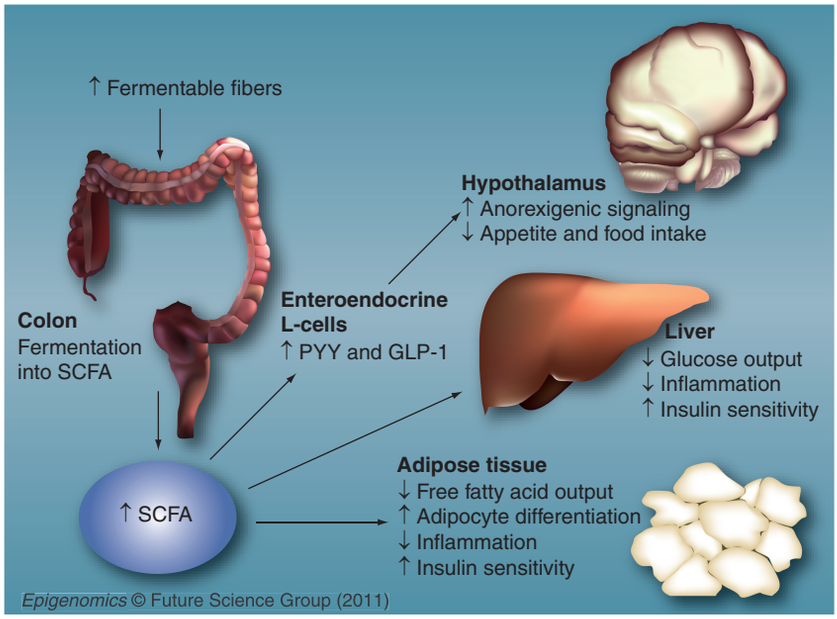

Figure 1. The potential effects of increasing the amount of dietary fermentable fiber on appetite regulation and metabolism.
GLP: Glucagon-like peptide; PYY: Peptide tyrosine tyrosine; SCFA: Short chain fatty acid.

Effects of PYY & GLP-1 on appetite regulation

The consumption of food leads to the release of gastrointestinal hormones and the activation of neuronal pathways. These signals are integrated within the hypothalamus where they lead to changes in metabolic rate, regulation of gut motility and appetite [34]. PYY is released into the circulation after a meal, with levels rising to a plateau after 1–2 h and remaining elevated for up to 6 h [35]. The increase in PYY levels is proportional to dietary intake and it is preferentially secreted in response to fats compared with either carbohydrates or proteins [36]. Furthermore, decreased appetite following gastric bypass surgery is associated with increased basal and post-prandial levels of PYY [37]. Intravenous infusion of PYY to both lean and obese humans has been shown to significantly reduce *ad libitum* food intake [38,39], suggesting that sensitivity to the appetite-inhibitory action of peripheral PYY is preserved in obese individuals. Whilst GLP-1 is primarily recognized as an incretin, responsible for the increased secretion of insulin when glucose is given orally compared with intravenously, it also fulfills several criteria in order to be considered a satiety signal. Circulating levels of GLP-1 rise following a meal in proportion to energy intake and are low in the fasted state [40]. Across a range of studies, intravenous infusion of GLP-1 has also been demonstrated to acutely reduce food intake [41]. The discovery that FFAR2 and FFAR3 are colocalized with L-cells in the colon has therefore led to the suggestion that activation of these receptors by SCFA ligands may facilitate PYY and GLP-1 release. Subsequently, it has been proposed that increasing the fermentable fiber content of the diet could increase anorectic gut hormones, leading to reduced energy intake and long-term weight loss.

Fermentable fiber & body weight

In animal studies there appears to be clear evidence that increasing the fermentable fiber content of the diet will acutely increase PYY and GLP-1 release and lead to long-term improvements in body composition. Animals fed high doses of fermentable fibers (inulin and resistant starch) have increased endogenous secretions of PYY and GLP-1 [42,43], whilst a recent investigation reported that large amounts of dietary resistant starch in food-deprived animals result in a CNS neuronal activation pattern similar to that found in fully satiated animals [44]. However, it is questionable whether these consistent findings from animal investigations would be replicated in human studies. Investigations have shown that a relatively high concentration of SCFA in the colon is needed to trigger gut hormone release [45]. Consequently, animal studies that have reported increased anorectic hormones and improved body composition have provided a diet with substantial amounts of fermentable fiber (>7% of the total weight of food consumed). In human studies, levels are often <1% of total weight of food consumed and common side effects from increasing the amount of fermentable fiber in the diet include bloating, cramping, flatulence and soft stools. As a result, there are doubts whether humans can tolerate the amounts of fermentable fiber required to produce the colonic SCFA concentrations needed to modulate gut hormone release. Nevertheless, the current data concerning the effects of increasing the fermentable fiber composition of the diet on appetite responses and weight loss are encouraging. A recent investigation examined the effects of feeding 16 g/day of a fermentable fiber supplement (oligofructose) for 2 weeks on self-reported satiety and gut peptides during a test meal [46]. The study found that dietary supplementation was associated with increased GLP-1 and PYY and lower

hunger ratings. This finding is supported by an investigation that showed that adding 24 g of a fermentable fiber supplement (inulin) to a test meal significantly increases GLP-1 levels in the postprandial period [47]. Furthermore, a recent study attempted to examine the effects of a polyfructan supplement (oligofructose) in overweight and obese adults [48]. Volunteers were given 21 g/day of the fiber supplement or a placebo for 12 weeks. The fiber supplement group experienced significant body weight loss compared with the control group, which was associated with reduced self-reported energy intake during the treatment period. Enhanced PYY may have contributed to the reduced energy intake and weight loss. However, not all studies have demonstrated that high fiber meals/diets stimulate gut peptide secretion. An investigation reported that adding different cereal fibers to test meals had no effect on postprandial GLP-1 responses [49]. In addition, a recent investigation reported that it took 9–12 months for a high wheat fiber diet (24 g/day) to raise plasma GLP-1 concentrations [50]. Nevertheless, the failure to observe an effect on gut peptide secretion in these studies may be due to the poor fermentability of the fiber supplement.

Fermentable fiber, adipose tissue metabolism & insulin sensitivity

The SCFA produced through colonic fermentation are also absorbed into the circulation where they have been shown to influence adipose tissue metabolism and insulin sensitivity. FFAR2 and FFAR3 have been shown to be expressed on adipocytes [51,52], and evidence suggests that circulating SCFA reduce nonesterified fatty acid (NEFA) levels in plasma via inhibition of lipolysis in adipose tissue [52] and suppression of fatty acid production in the liver [53]. *In vitro*, both acetate and propionate have been shown to inhibit adipocyte lipolysis in a dose-dependent manner [52]. In mice, the infusion of sodium acetate to wild-type mice resulted in a reduced plasma NEFA level that coincided with a rise in plasma acetate concentration [52]. This effect was abolished in FFAR2 knock-out mice, suggesting that this effect was mediated by activation of FFAR2 by acetate. Studies have also shown that circulating SCFA also influence adipose tissue adipogenesis. Adipocyte size is strongly correlated with whole-body insulin sensitivity [54], and obesity is characterized by large adipocytes with impaired differentiation and a greater secretion of proinflammatory adipokines [55]. Evidence suggests that FFAR2 is involved in adipocyte development and differentiation [51], resulting in smaller adipocytes and lower secretion of proinflammatory adipokines. In view of the established role of circulating NEFA and inflammation on insulin sensitivity, recent investigations would suggest that elevating circulating SCFA by increasing the quantity of fermentable fiber in the diet could influence fat metabolism and lead to improved insulin sensitivity.

Data from animal studies supports the suggestion that fermentable fiber in the diet can have a major role in adipocyte metabolism and insulin sensitivity. In an investigation of rats fed a high resistant starch diet for 5 weeks, total body weight was found to be the same as that of the control group, but with smaller epididymal fat pads and adipocyte size [56]. Studies in mice have confirmed these observations and have demonstrated that increasing the fermentable fiber content of the diet leads to decreased hepatic cellular lipid content along with an increase in adipose tissue insulin-stimulated glucose uptake [57]. Investigations have also reported that increasing the amount of fermentable fiber in the diet improves insulin sensitivity in humans. Healthy volunteers fed 30 g/day of resistant starch for 4 weeks had improved insulin sensitivity compared with the control group, which was associated with a reduced NEFA flux from abdominal adipocytes and elevated concentrations of plasma acetate and propionate [58]. Intake of the resistant starch supplement also led to a small but significant increase in lean body mass. A recent investigation also revealed that providing a 40 g/day resistant starch supplement for 12 weeks to individuals at increased risk of T2DM improved insulin sensitivity [59]. The improvements in insulin sensitivity were significantly correlated with reductions in waist circumference and fat storage in the tibialis muscle.

Conclusion & future perspective

Diets rich in starch and fiber have been proposed to reduce adiposity and have a positive effect on weight loss. Specifically, the fermentable content of starch and fiber appears to play an important part in the control of food intake, body composition and insulin sensitivity. Recent investigations have provided a link between the products of colonic fermentation, FFAR2 and FFAR3 activation, anorectic

hormone release, and adipose tissue metabolism. Further investigations are warranted, particularly in high-risk populations, to determine if long-term dietary interventions with fermentable fibers can protect against obesity and the progression of T2DM.

Financial & competing interests disclosure

The Section of Investigative Medicine is funded by grants from the MRC, BBSRC, NIHR, an Integrative Mammalian Biology (IMB) Capacity Building Award, an FP7-HEALTH-2009-241592 EuroCHIP grant and is supported by the NIHR Imperial Biomedical Research Centre Funding Scheme. G Frost is supported by an NIHR Senior Investigator Award. E Chambers is supported by the BBSRC DRINC programme. N Guess is supported by a Diabetes UK Fellowship. A Viardot is supported by a fellowship from the Australian NHMRC. The authors have no other relevant affiliations or financial involvement with any organization or entity with a financial interest in or financial conflict with the subject matter or materials discussed in the manuscript apart from those disclosed.

No writing assistance was utilized in the production of this manuscript.

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