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Food Structure and Carbohydrate Digestibility

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1. Introduction

Carbohydrate is almost universally the major dietary source of metabolic energy. Nearly all of it is obtained from plants, and nearly all of it requires digesting before it is available for metabolism. While digestion is aimed at breaking down molecular structure within carbohydrate molecules, there is a raft of further plant structural impediments to be overcome before most plant carbohydrates are available for digestion.

Starch, for instance, represents energy stored, not for animals, but for the plant that made the starch. It is a reserve available to carry a plant between seasons, to sustain it during periods when photosynthesis is limited, to prepare it for times of intense energy use such as flowering, and to support its progeny in seeds before autonomous growth. But so accessible is free starch as a form of energy that plants have taken special measures, many of them structural, to protect it physically from all sorts of opportunist consumers – animals, fungi and bacteria - and from the effects of existing in a hydrating entropic environment. All these structural barriers have to be overcome before the carbohydrate becomes available for digestion, and can be used as a source of food-derived energy.

In the human diet, lack of available carbohydrate is associated with under-nutrition and its attendant problems, while at the same time a surfeit of available carbohydrate is associated with obesity, metabolic syndrome, and diabetes – scourges of the developed world. Therefore, as food structure can have a critical role in determining the proportion of carbohydrate that is made available by food processing and digestion (Bjorck et al. 1994), it is of fundamental importance to nutrition and health.

This chapter discusses the importance of carbohydrate digestibility to human health, various forms of plant and food structure that have an impact on carbohydrate digestibility, and how food processing methods of various types overcome them.

2. The nutritional importance of carbohydrate digestion

Digestibility, energy and the glycemic response

The nutritional importance of available carbohydrate currently extends far beyond its role as a major source of sustenance for humans. Thanks to modern agriculture, transport and food technology, and to the market-driven economy in which appetite-driven food wants, rather than nutritional needs and survival, have come to determine the types of foods available to consumers, energy intakes have far exceeded energy requirements. As a result, the “developed” world is now facing an obesity crisis. Carbohydrate digestibility has gained new importance, not only because of its contribution to obesity, but also because a secondary consequence of obesity is the metabolic syndrome for which a defining feature is glucose intolerance – an impaired ability to control blood glucose concentrations after a carbohydrate meal.

It is now evident that the adipose tissue of obesity is not a passive fat storage tissue, but is physiologically active and intimately involved in glucose homeostasis. It plays a key role in glucose intolerance and Type 2 diabetes by producing factors, including free fatty acids, that induce insulin resistance (Saltiel & Kahn 2001). Resistance to insulin leads to a reduced rate of clearance of glucose from the blood, and the resulting increased concentration of glucose in the blood leads to generalized damage throughout the body, from chemical bonding (glycation) of proteins, increased oxidative stress, and damage to numerous biochemical processes (Brownlee 2001). In response to increased blood glucose and to the rate of blood glucose loading, insulin production increases, with its own damaging effects (Guigliano et al. 2008). Ultimately, exhaustion of the capacity of the pancreas to produce adequate insulin means that the insulin resistance of Type 2 diabetes evolves into the insulin insufficiency of Type 1 diabetes. The generalized, cumulative, systemic damage of prolonged and/or repeated exposure to high blood glucose concentrations manifests itself as a raft of disorders associated with long-term diabetes – kidney failure, circulatory problems, neuropathy, heart disease, blindness and so on – that are imposing enormous costs in suffering and resources (Zimmet et al. 2001).

In the context of the pandemic of obesity and glucose intolerance in the modern world, new ways of manipulating the rate and extent of digestibility of carbohydrate are being sought. The rate of starch digestion is important because the degree to which blood glucose loading exceeds blood glucose clearance determines the acuteness of the net increase in blood glucose concentrations, and consequently, the intensity of the insulin response required to remove the glucose overload and restore normal blood glucose concentrations. The rate of digestion also determines how sustained will be the supply of glucose by continued digestion in the gut, and therefore, how prolonged its contribution to delaying the urge to eat again will be.

Carbohydrate digestibility and colonic health

The extent of digestion during transit through the foregut is important because it determines the proportion of starch that is available to the colon as polysaccharide for fermentation,

which has a role in colonic health (Fuentes-Zaragoza et al. 2010) and probably also in appetite control through the colonic brake feedback mechanism (Brownlee 2011). Undigested food residues, including both food structures and the carbohydrates and other nutrients that they have protected from digestion, are now recognized as being not simply gastrointestinal refuse, but a valuable feedstock for the colonic ecosystem. Through both fermentation of the residues and through the ability of a proportion of them to survive colonic transit, they play an essential part in maintaining gut health and function, as well as good health in general (Buttriss & Stokes 2008).

It is increasingly recognized that events in the colon influence the body as a whole, through products of colonic fermentation, through effects on the immune system mediated by the colonic epithelium, and through neuronal and hormonal feedback from the colon to upstream regions of the digestive tract (Wikoff et al. 2009). Short chain fatty acid products of colonic fermentation, propionic acid in particular, may play a direct role in blood glucose control by suppressing the release of plasma triglycerides, which contribute to insulin resistance. Colonic fermentation also appears to have indirect effects on hormones from the pancreas and adipose tissue that are involved in the regulation of energy metabolism (Nilsson et al. 2008).

Recent research suggests that obesity is associated with a colonic microbiota that is more effective in scavenging energy from undigested food polysaccharides than the microbiota from lean individuals (Turnbaugh et al. 2006). Although the daily increments in energy gain may be small, over time they accumulate in expanding adipose tissue. Recovering undigested energy by colonic fermentation could make the important difference between starving and surviving in an energy-depleted environment where food is scarce and of poor quality, or under the precarious conditions in which we evolved. However, in the present developed world of plenty, it may contribute to the difference between remaining trim and being overtaken by creeping obesity.

3. Forms of food structure affecting carbohydrate digestion

Food structure can take a number of forms that can affect the availability of carbohydrate in a number of different ways and at a number of different levels – molecular, cellular, plant tissue and food.

3.1. Molecular level

In the case of short chain sugars, such as the disaccharides sucrose, maltose and lactose, the structural constraint on digestion to monosaccharides lies solely within the glycosidic linkage between monosaccharide units, and is easily overcome by disaccharidases of the gut brush border (Wright et al. 2006). But even then, the rate at which the monosaccharide units traverse the gut wall, and so the extent to which absorption is completed during small intestinal transit, depends on the ability of membrane-bound transporters to recognize the structure of monosaccharides. Glucose transporters (SGLT1, GLUT 2) achieve active ATP-driven facilitated transport against a gradient, whereas the transporters that recognize

fructose as a structure carry out less effective absorption by facilitated transport, which may result in overflow of fructose into the terminal ileum and colon, leading to intestinal discomfort from the resulting osmotic and fermentative effects (Gibson et al. 2004). Similarly, the structural specificity of lactase means that decline in lactase activity leads to the severe gastrointestinal problems of lactose intolerance.

Starch

Starch presents a different challenge for digestion from that of the common food disaccharides. Although it consists solely of α -D-glucose units, it may have a degree of polymerization of thousands or millions, and the glucose units may be α (1-4) linked into long linear amylose chains, or shorter amylose chains may be connected at α (1-6)-linked branch points. Most starch (~70%) is branched (amylopectin) and has a molecular weight of 50-500 million, and a degree of polymerization in the millions, depending on the plant species (French 1984; James et al. 2003; Thomas & Atwell 1998). The long regular string of glucose units in both amylose and amylopectin provides the opportunity for interactions between starch chains, leading to the buildup of pseudo-crystalline regions, which may sterically inhibit amylase access.

a. Native starch and Starch granules (RS2)

Above the scale of amylose and amylopectin molecules, the starch is organized during growth in plants into granules that impose further restrictions on enzyme access (Ayoub et al. 2006; Gallant et al. 1997). Starch granules characteristically consist of concentric rings of alternating amorphous and pseudo-crystalline structures laid down during granule growth (**Figure 1**). The amorphous starch corresponds to regions that are rich in branches at α (1-6) glycosidic bonds, while in the pseudo-crystalline regions the starch is highly organized as closely packed short branches, approximately 10-20 glucose subunits in length (Gallant et al. 1997; Ratnayake & Jackson 2007; Waigh et al. 2000). The high degree of organization of the pseudo-crystalline region is revealed by the typical Maltese cross birefringence pattern of

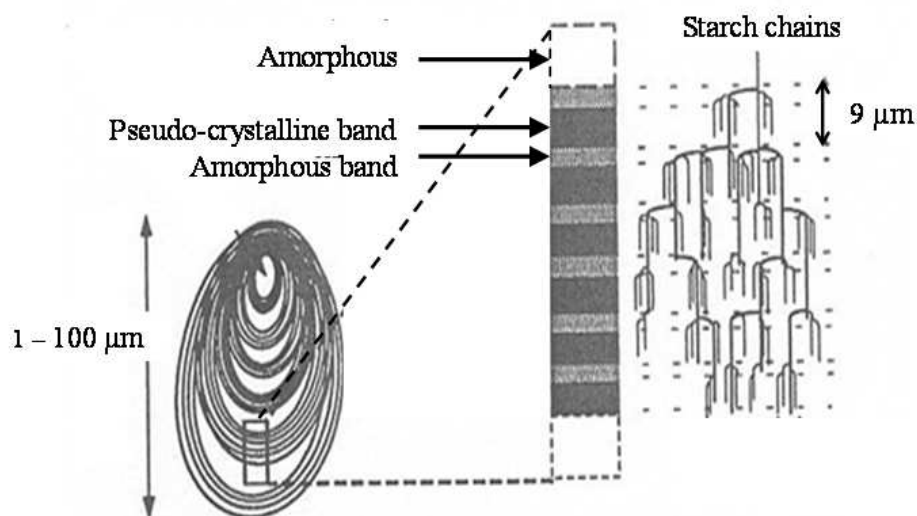


Figure 1. Schematic view of the organization of starch within a native starch granule

native starch when viewed in polarised light. The pseudo-crystalline regions are far more resistant to digestion by α -amylase than the amorphous regions (Donald 2004), and the highly organized starch granule as a whole may be relatively resistant to digestion, thanks to protein and lipid at the granule surface, which together form a coating resistant to water and digestive enzymes (Debet and Gidley, 2006).

Although covered with a resistant coating, almost all types of starch granules have been shown to bear surface pores that are entrances of channels that reach the near centre (hilum) of the granule (Huber & BeMiller 2000). The pores may be well developed in maize and nearly absent and much smaller in potato and tapioca (Juszczak et al. 2003). They may play an important role in digestion by allowing penetration of water and enzymes into the centre of the granules (Copeland et al. 2009) and leaching of glucose outwards, so the native starch granules often appear to be digested from the inside out (Gallant et al. 1997; Oates 1997; Planchot et al. 1995; Tester & Morrison 1990). However, digestion remains relatively slow while the starch is organized in its native (ungelatinized) state.

b. Gelatinized starch

Gelatinization is the loss of the pseudocrystalline structure of the starch granules and is characterised by a loss of the maltose cross pattern in polarised light and rapid water absorption and digestion in the presence of amylase. It involves a dramatic loss of structural organization of starch granules in response to temperatures above about 60°C in conjunction with excess moisture, or by processing at temperatures above 120°C at high shear, even at low moisture levels, such as during extrusion processing (**Figure 2**).

Various techniques used to study the gelatinization process suggest that the profound change in structure during gelatinization in moderate heat and in the presence of excess water is due principally to water invasion and swelling of the amorphous regions of the starch granule (Donald 2004). Because the molecules of the amorphous regions have connecting bonds with the semi-crystalline regions, as the amorphous regions swell they force the molecules of the pseudo-crystalline regions to dissociate. As the swelling and dispersion progresses, the starch becomes increasingly accessible to digestive enzymes, and the glycemic impact of the starch rises dramatically. Starch granule pores may assist by allowing water to invade deeply into the granule interior.

Starches differ in their susceptibility to gelatinization, and have been classified as those that swell rapidly, those that have restricted swelling associated with surface lipids and proteins (Debet & Gidley 2006), and a third group of granules that contain high amounts of amylose (high semi-crystalline content), which do not swell significantly at temperatures below 100°C.

c. Retrograded starch (RS3)

Retrogradation of starch is a form of structural change that has a large effect on digestibility. It occurs as the linear portions of starch molecules that have been dispersed during gelatinization randomly re-crystallize, without the organizing guidance of the living plant, when the gelatinized starch is cooled. Both amylose and amylopectin will retrograde.

However, amylose chains being less branched than amylopectin, will tend to re-crystallize almost irreversibly and again become nearly resistant to amylase digestion, while retrogradation of branched amylopectin is less complete and more reversible, and digestion by amylase is retarded less.

d. Modified starches (RS4)

As starch is a long digestible polymer covered in exposed hydroxyl groups, there are many ways that it may be modified. It may be partly depolymerized by enzymes or acid, substituent groups may be added (e.g. acetylated), it may be oxidized, cross-linked, pre-gelatinized and retrograded. Most modifications to starch are designed to change its functional properties as a food ingredient by altering its rheological characteristics (Taggart 2004; Whistler & BeMiller 1997). All the chemical/processing modifications involve structural change at the molecular level and many alter the digestion characteristics of the starch. Where chemical modification of starch causes resistance to digestion, type 4 resistant starch (RS4) is formed (Sajilata et al. 2006).

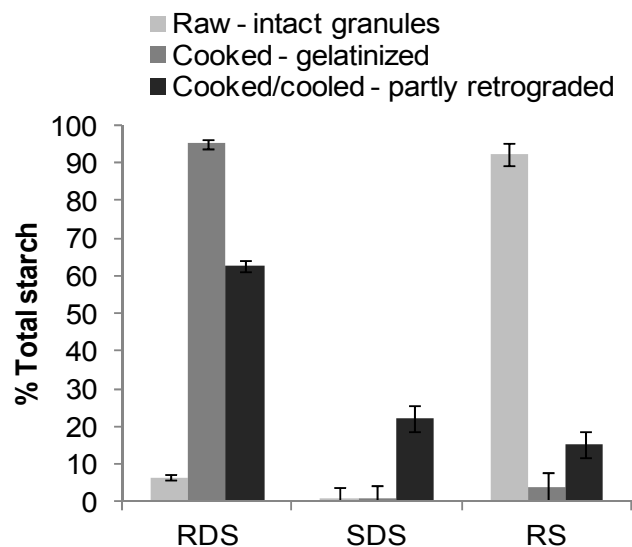


Figure 2. Effects of food structure at the molecular level - dependence of starch digestibility *in vitro* on its molecular form: rapidly digested (RDS), slowly digested (SDS) and digestion-resistant starch (RS) in potatoes digested raw (pseudo-crystalline, intact starch granules), freshly cooked (starch dispersed after gelatinizing), and cooked-cooled (starch partially recrystallized by retrogradation). (Mishra and Monro, unpublished)

e. Occluded starch (RS1)

In the mature endosperm of most cereals, the thin cell walls are largely obliterated and the endosperm becomes a protein matrix containing embedded starch granules (Eliasson & Wahlgren 2004; White & Johnson 2003). The density and occluding effect of the protein reduces water uptake during cooking by preventing the swelling of the starch granules and as a result reduces the rate of digestion. In species with hard endosperm, such as certain wheat and maize varieties and in rice, the protein matrix is almost continuous, whereas in

wheat and maize cultivars with soft endosperm, and in cereals such as oats, rye and sorghum (Earp et al. 2004), there are many discontinuities that create pathways for water and enzyme penetration into the endosperm. As a result, soft endosperm variants hydrate more quickly and present a greater internal surface area of starch for water absorption and digestion.

In pastas based on high-protein durum wheat, a relatively slow rate of digestion and low glycemic impact has been attributed to protein coating the starch granules, inhibiting both gelatinization and amylase access to starch (Colonna et al. 1990; Jenkins et al. 1987). Microscopy has revealed that protein-starch conglomerates survive in cooked pasta (Kim et al. 2007). Because of the protein occlusion of starch, carbohydrate digestion in pasta may be enhanced by cooperative protease activity (Holm & Bjorck 1988). In fatty or oily tissues such as nuts, the hydrophobic nature of the fat may also be a factor protecting the starch from hydration, gelatinization and subsequent digestion.

f. Complexed starch

Complexing of starch with other macromolecules may involve a change in structure that is associated with reduced digestibility. Amylo-lipid complexes, formed when starch is gelatinized in the presence of lipid, are regarded as crystalline (Eliasson & Wahlgren 2004). The rate of digestion of amylose-lipid complexes is less than digestion of amylose, but greater than digestion of retrograded amylose (Holm et al. 1983).

3.2. Cell and tissue level

So far we have been discussing structural factors at the sub-cellular level that may affect carbohydrate digestibility. At the multicellular level, many sources of food carbohydrate are swallowed in the form of plant tissue fragments in which cell walls, and multiple overlying layers of cells, may act as partial barriers to both digestive enzyme penetration into, and carbohydrate diffusion out of the fragment or particle. In fruits, cereal kernels, nuts and pulses, tissue structure may influence the availability of carbohydrate and other nutrients (Mandalari et al. 2008; Palafox-Carlos et al. 2011; Tydeman et al. 2010a; Tydeman et al. 2010b).

Cereals

Seeds have evolved as dry, mechanically resistant structures that protect the embryo and the starchy endosperm from insect and animal attack until germination. In addition, in many mature grains such as rice, maize, the hard wheat varieties and some legumes, the molecular structural organization of starch and the protein that surrounds it results in a very hard endosperm that fragments into particles when crushed. Although the surface of such kernel particles is available for attack by digestive enzymes, penetration into the dense particles, especially when uncooked, is slow, and a high proportion of the starch may reach the colon. To obtain the digestible energy available in such grains, they must be subjected to processes such as grinding, flaking and cooking before being consumed. However, the dependence of digestibility on particle size provides a means by which the rate of starch availability, and

the amount escaping foregut digestion to act as a substrate for colonic bacteria, may be influenced. The progressive decrease in rapidly digestible starch and increase in inaccessible (resistant) starch with increasing particle size is a very clear trend (**Figure 3**).

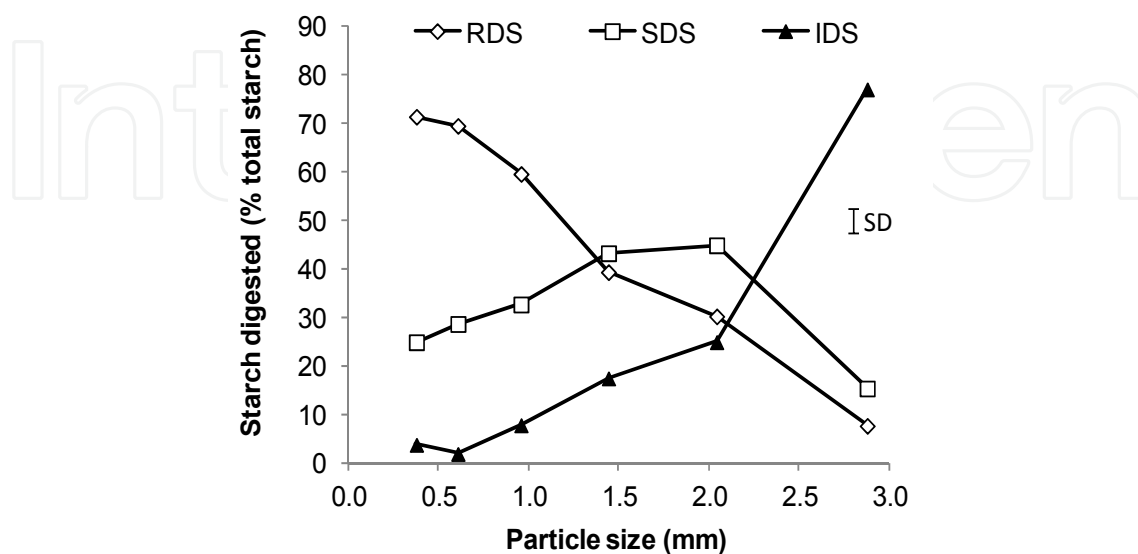


Figure 3. Effect of tissue structure on digestibility: Effect of particle size in chopped kernel fragments of the wheat cultivar 'Claire' on the *in vitro* digestibility of starch; RDS = rapidly digested (0-20 min), SDS = slowly digested (20-120 min), IDS = inaccessible digestible starch (undigested until residue homogenized) (Monro and Mishra, unpublished).

Pulses

In pulses, the starch-containing reserve tissues of the cotyledons differ in structure from the endosperm of cereals, in that the cells of the storage tissue are living and the walls retain an organized structure separating cells and contributing to tissue support in species in which the cotyledons become "seed leaves" after germination (Berg et al. 2012). In contrast, cereal endosperm cell walls are thin and usually disintegrated, and the structural integrity of the kernel is maintained by the starch/protein concretion of the endosperm, combined with the tough surrounding testa or seed coat (the bran in wheat). The differences in structure between the pulses and cereal products are reflected in the patterns of carbohydrate digestion from them (**Figure 4**).

The thick and resistant cell walls of pulses and may retard the gelatinization of starch by confining it within the cell lumen (Tovar et al. 1990; Tovar et al. 1992). When the starch is densely packed within resilient clusters of intact cells with robust cell walls, swelling is constrained. In addition, an encapsulating layer of gel from unconstrained starch in the outer cell layers of pulse fragments may create a barrier that impedes water penetration. However, partly because they are pectin rich compared with cereals, when processing is harsh or prolonged, the cell walls of pulses will degrade enough for the cells to separate. Then the starch becomes free to swell and disperse, and digestion is more rapid.

In domestic cooking, the robust cell walls of pulses are often able to survive moist heat enough to remain intact, so that cohesive plant cell clusters with encapsulated starch remain after cooking, making pulses some of the most slowly digested carbohydrate sources, with a typically low glycemic effect compared with other carbohydrate foods (Venn et al. 2006). Pulses such as kidney beans and chick peas are typical, and *in vitro* show a slow linear digestion that is usually incomplete (Figure 4). *In vivo* and particularly when cooking is incomplete or the food fragments are poorly comminuted before swallowing, they load the colon with fermentable starch (Type 1 resistant starch), which is largely responsible for the flatulence generated by pulses.

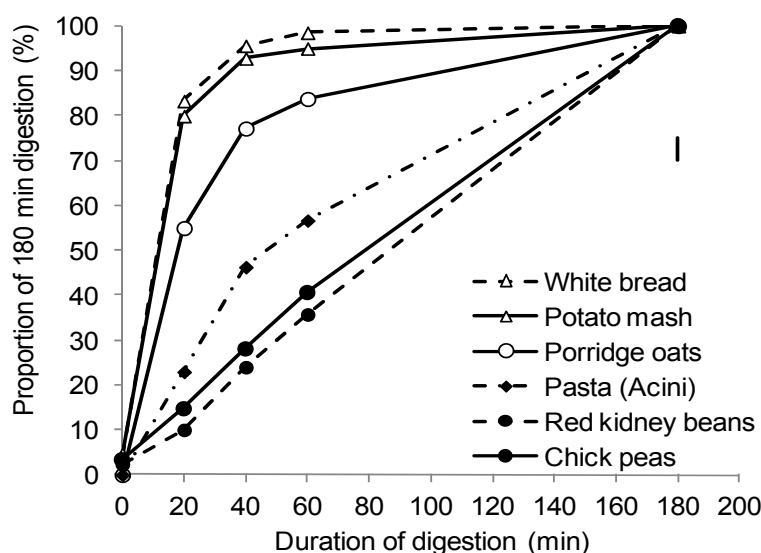


Figure 4. *In vitro* digestion patterns (% carbohydrate available after 180 min digestion) associated with different types of food structure: Porous, no intact cell walls (white bread), crushed and dispersed (mashed potato), crushed but partially intact native structure (porridge oats), dense non-porous structure (pasta; acini), robust and intact plant cell walls encapsulating starch (chick peas and red kidney beans). The bar represents the mean between duplicate ranges (5%). (Mishra and Monro, unpublished).

Fruits and vegetables

In most ripe fruits, available carbohydrates are in the form of soluble sugars – glucose, fructose and sucrose – which are highly soluble and mobile. Glucose and fructose are absorbed by specific transporters in the intestinal wall, while sucrose is hydrolyzed by a brush border invertase (Wright et al. 2006). Therefore, the only direct structural impediments to sugar availability from fruits are those that retard sugar diffusion. The parenchyma cell walls of fruits, even after mincing and digesting *in vitro*, can markedly retard sugar diffusion (Figure 5) and removing them from fruit puree increases its glycaemic impact (Haber et al. 1977). Such retardation can be regarded as a structural effect, as the presence of cell wall fragments with their enmeshed pectic polysaccharides increases the length of the diffusion pathways to a degree that would make a significant difference to blood glucose loading *in vivo*.

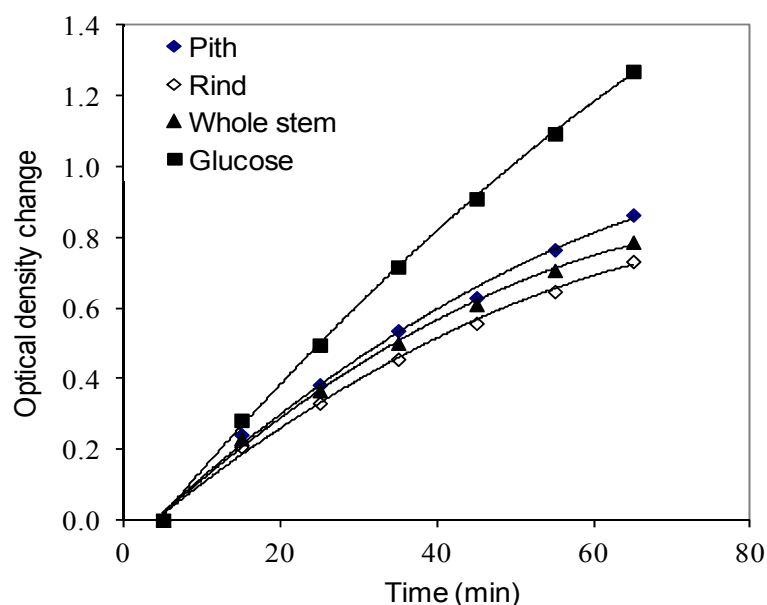


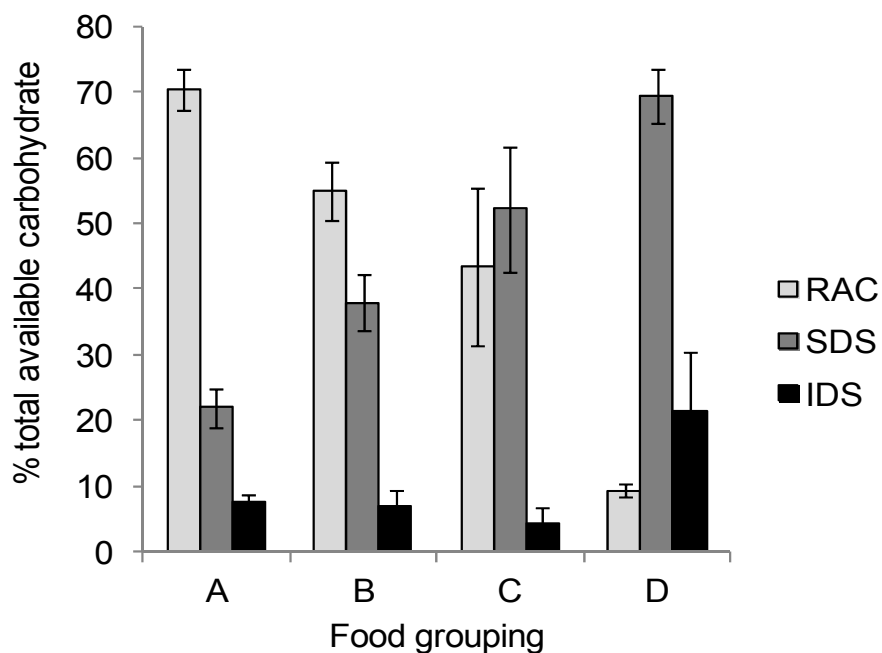
Figure 5. Effect of structure in digested plant tissue remnants on a process important to the digestive process - diffusion. Glucose diffusion was retarded about 40% by the presence of digestion-resistant remnants of broccoli tissue in an unstirred system. Pith – parenchyma cells. Rind (cortex) – parenchyma, fiber and vascular cells. The tissue remnants (cell walls) were at settled bed density, after they had been predigested *in vitro* and allowed to settle overnight by gravity. All the solutions contained 10% glucose (w/v) at the start of dialysis (Monro, unpublished). The mean between duplicate ranges was <0.1 OD units.

3.3. Food level - secondary structure established by processing

The characteristics of carbohydrate digestion in many carbohydrate foods are determined by the structure of the food matrix established during food processing involving cooking, with and without disruption of the original cellular structure of the plant source. Such secondary food structure exerts its influence largely by affecting the accessibility of the digestion medium to starch in the food. At the larger level, food particle geometry may create structures that have an enormous impact on digestibility through their influence on the surface area available for digestion (Monro et al. 2011).

a. Open porous structures

Foods with an open porous structure include leavened products such as breads and cakes, puffed products produced by steam expansion, including many snack foods, and breakfast cereals such as puffed rice. These structures have a high internal surface area that is almost immediately available for amylase attack, and as they are precooked to eliminate native starch granule structure, they typically digest very rapidly (Figure 4), causing an acute blood glucose response. Such foods are typified by a high rapidly digested starch (RDS) content, little slowly digested starch (SDS) and a small proportion of retrograded resistant starch (RS Type 3) (Figure 6, Group A).



- A: Little structure, starch gelatinized e.g. extruded, puffed and flaked precooked cereal products
 B: Some structure, minimally processed, incomplete starch gelatinization e.g. rolled oats
 C: Dense secondary structure, non-porous, surface digestion e.g. pasta
 D: Intact, robust cell walls encapsulating starch in native tissue structure e.g. pulses.

Figure 6. Effects of food structure typical of various food groupings on the content of rapidly digested (RDS), slowly digested (SDS) and resistant (inaccessible; IDS) starch that they contain. Error bars are SDs of food means within groups. (Mishra and Monro, unpublished).

b. Dense low porosity structures

Dense low porosity structures include products such as pastas, in which hydrated flour is force-molded into a dense configuration and then cooked under conditions such as boiling, and in which porosity as a result of gas formation in the food matrix does not occur. Foods such as pastas allow digestion only as fast as digestive enzymes can erode superficial layers of the food, to expose underlying carbohydrate, so their rate of digestion depends strongly on their surface area, and is therefore dependent on particle geometry. The dependence of digestion rate on particle geometry has been examined in detail using pastas of different shapes and gelatinized sago as models. As surface area of a sphere depends on the square of the radius, small increases in particle size can have a large influence on digestion rate (Monro et al. 2011).

The role of the dense structure of unexpanded starch in retarding digestion becomes clear during *in vitro* digestion of solid foods such as pasta and tapioca with and without homogenizing to eliminate the occlusive effect of the starch. After homogenizing the pasta and tapioca, starch was immediately digested, in contrast to the starch in the intact pasta and tapioca, which was gradually released as the starch was digested by superficial erosion (Figure 7). In dense low-porosity structures such as pastas made from durum wheat, the occlusive effects of protein will also retard starch digestion.

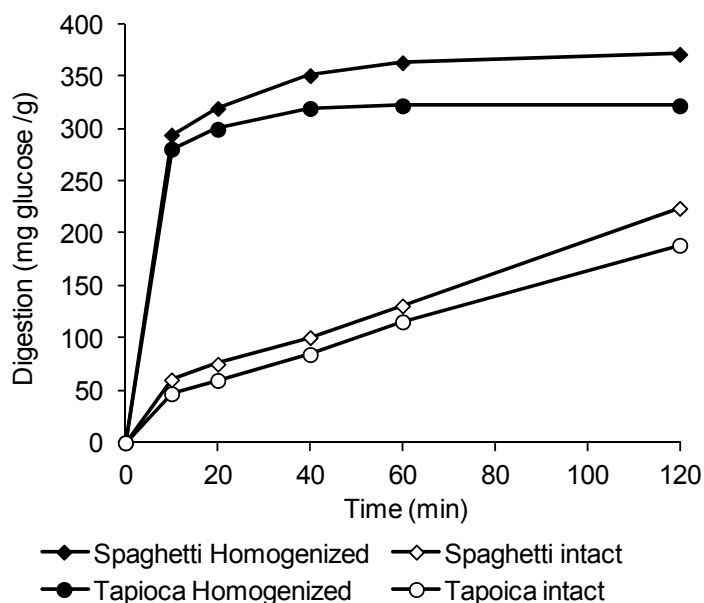


Figure 7. Effects of secondary structure on digestibility *in vitro*. Effect of occlusion by starch and dependence on surface area of food in dense non-porous foods revealed *in vitro* by the increased rate of digestion after homogenizing the foods to expose interior starch to digestive enzymes. The mean between duplicate range was < 5% (Mishra and Monro, unpublished).

4. Manipulating food structure to control carbohydrate digestibility

Many of the properties of foods that retard carbohydrate digestion discussed in the previous section are the result of the carbohydrate being stored by the plant during biosynthesis in a stable, organized, semi-crystalline and protected form, until it is required by the plant. For animals and humans to use plant carbohydrate as an energy source, it is necessary to overcome or reverse the steps the plant has taken to protect its energy reserves. Thus, before the process of enzymatic depolymerization of the individual starch molecules in the gut can provide the minimized molecular forms in which starch is absorbed by the gut border – as glucose, maltose and dextrans – there are several obstructions to be removed: firstly, the protective tissues of the plant; secondly, the barrier function of the starch granule surface; and thirdly, the obstructive molecular packing of starch within the starch granule must be overcome.

The inaccessibility of starch due to plant tissue structure has been overcome in four main ways, by external mechanical disruption, by cooking, by chewing, and in the intestine by the weak shearing and abrasion of intestinal contractions acting on digesta. In practice, with most starchy foods all four processes are used sequentially to obtain available carbohydrate from food for absorption, but the contributions that each may play in determining the amount of carbohydrate digested have been demonstrated individually.

4.1. By mechanical disruption during ingredient preparation

Mechanical disruption of food structure is one of the most effective ways of increasing carbohydrate energy availability from foods, and milling, crushing, pounding and such

processes have been used for thousands of years to improve energy extraction from all types of plant tissue, but especially from the well protected form of seeds. On the other hand, reducing tissue disruption to lower carbohydrate digestibility of grain products has been found to be an effective strategy in reducing the glycemic impact of foods in populations with excessive energy intakes, obesity and diabetes (Venn & Mann 2004).

a. Milling

The most widely used procedures for milling of cereals such as wheat involve a combination of cutting and grinding, and applying strong shearing forces that break the seed coat and tear the endosperm tissue apart. More than any other process, milling can convert kernels of grain in which starch remains almost completely protected from digestion, even when cooked, to the finely divided form of flour, in which the same starch is rapidly digested because the inaccessibility of the starch to digestive enzymes caused by intact cell walls and protective plant structures has been eliminated. The effective protection of starch in cooked but intact plant tissue, and its susceptibility to digestion as soon as the tissue is disrupted by milling, is revealed by the changing distribution of starch between RDS (0-20 min), SDS (20-120 min), and RS (digestion-resistant) starch fractions measured by *in vitro* digestion (**Figure 2**). With decreasing particle size the RDS fraction increases and the RS fraction decreases, while there is very little change in SDS; the cooked starch is either inaccessible (“resistant”) or accessible, and if accessible, is rapidly digested - with the cell wall barrier removed starch is quickly degraded once gelatinized (Hallfrisch & Behall 2000).

The effects of milling do not result solely from the disruption of surrounding plant tissue, but damage to the starch granules, including cracking, fracturing, and internal changes to the granules occur that also increase their susceptibility to gelatinization and digestibility (Donald 2004).

b. Chopping/cutting

Cutting and chopping such as that occurring during the kibbling of grain does not cause the internal tissue disruption caused by the strong shearing force of grinding mills, and produce a more slowly digested product. Even simple crushing has an enormous influence on the availability of starch, because it involves forces strong enough to disrupt starch-protein conglomerates and cells containing encapsulated starch and other nutrients effectively, and creates pathways for ingress of digestive enzymes. Cutting and chopping without the shearing forces of grinding may increase digestibility much less because plant tissue damage is more restricted to the cut surfaces (**Figure 8**). Penetration of the effects of digestion through layers of intact cells underlying the cut surfaces may be a relatively slow process (Mandalari et al. 2008).

Recent detailed studies of the release of nutrients from nut fragments have shown that cell walls formed a very effective barrier against the intestinal environment (Mandalari et al. 2008; Palafox-Carlos et al. 2011; Tydeman et al. 2010a; Tydeman et al. 2010b). Mandalari et al. (2010) showed that after 3 h of simulated gastric plus duodenal digestion of almond fragments, the intracellular contents had been lost from only the first layer of the cells, at the

fracture surface. After 12 h of digestion, the loss of nutrients had extended to only three to five cell layers deep. In the zone of digestion the cell walls appeared to change in structure, in that they swelled, but without any detectable change in composition of the cell wall polysaccharides. There was no evidence of cell wall fracture, so any enzyme penetration into the food particles could occur only by diffusion through the cell walls.

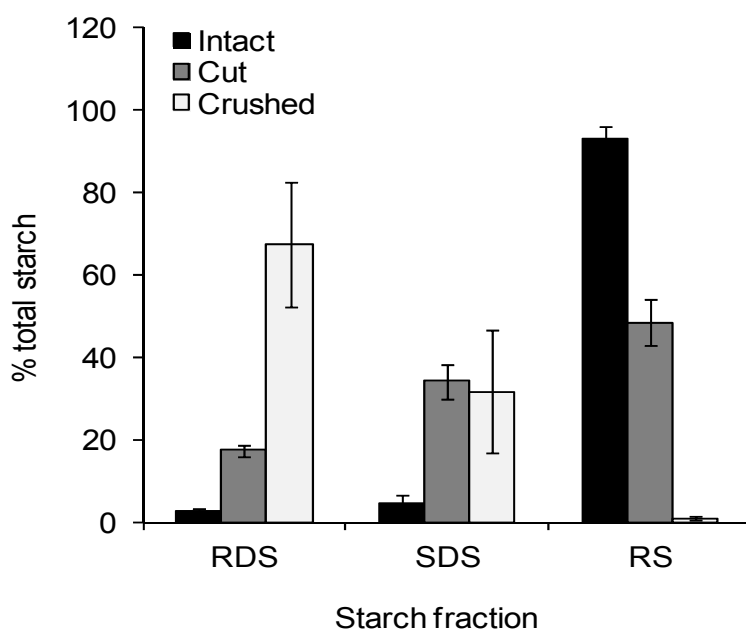


Figure 8. Influence of tissue structure on digestion revealed by the effect of cutting and crushing of cooked wheat kernels on *in vitro* digestion of starch. Individual whole hydrated kernels ($n = 5$ /treatment) were cooked and digested either intact (“Intact”), after they had been cut transversely in half (“Cut”) or crushed to 1 mm thickness (“Crushed”). RDS = rapidly digested, SDS = slowly digested, RS = resistant starch. Error bars are the standard deviations (Monro, unpublished).

4.2. By controlling gelatinization during cooking

Cooking starch under hydrating conditions brings about an often dramatic increase in starch digestibility as a result of gelatinization. In some plants, such as potato, the raw starch granules are virtually indigestible, but as soon as gelatinization occurs they are rapidly and totally digested (Figure 2). Between the extremes of raw starch and total gelatinization, the degree of gelatinization may be controlled by limiting the amount of water available for hydration and by carefully controlling the cooking temperature. Because starch gelatinization requires a combination of heat and water, the availability of water during cooking can substantially modulate the effects of cooking on digestibility. In food products in which the water content is not adequate to gelatinize starch fully, the glycemic impact may be correspondingly reduced. Rolled oats, for instance, are prepared under conditions in which incomplete gelatinization of starch occurs. If consumed directly in the form of muesli, the starch digestibility is relatively low, but if further cooked and hydrated to form porridge, starch digestion is greatly increased along with the glycemic impact of the oats (Figure 9).

The sensitivity of starch digestion to the degree of hydration during cooking of a number of starches for 10 minutes at 95°C – maize (normal starch, 27% amylose), Hi maize (70% amylose), Mazaca (waxy maize, 2% amylose), pea, potato, rice, tapioca and wheat – increased steadily as moisture content was increased in 5 or 10% intervals from 0% moisture, reaching a maximum digestibility at about 60% moisture (Figure 10), which corresponds approximately to the degree of gelatinization that occurs in water-unlimited conditions at 100°C. The dependence of digestion on hydration during cooking was very similar for all the starches, even though the starches (controls) cooked with no added water differed considerably in their susceptibility to digestion in the raw (granular) state, as indicated by different Y intercepts in Figure 10. The differences in the digestibility of uncooked starch (Fig 10 A) probably reflect the importance of granule morphology, including pore size and surface chemistry, rather than any intrinsic differences in the starch molecules in determining the initial rate at which raw starch is digested. In food products containing hydrating components other than starch, such as non-starch polysaccharides in cell wall remnants, intrinsic and added gums, and sugars, competition for water may reduce the gelatinization of starch during cooking (Pomeranz et al. 1977), allowing the digestion-inhibiting effect of native starch structure to persist. Even in white bread, which contains about 60% moisture, partially intact birefringent starch granules remain in the cooked product.

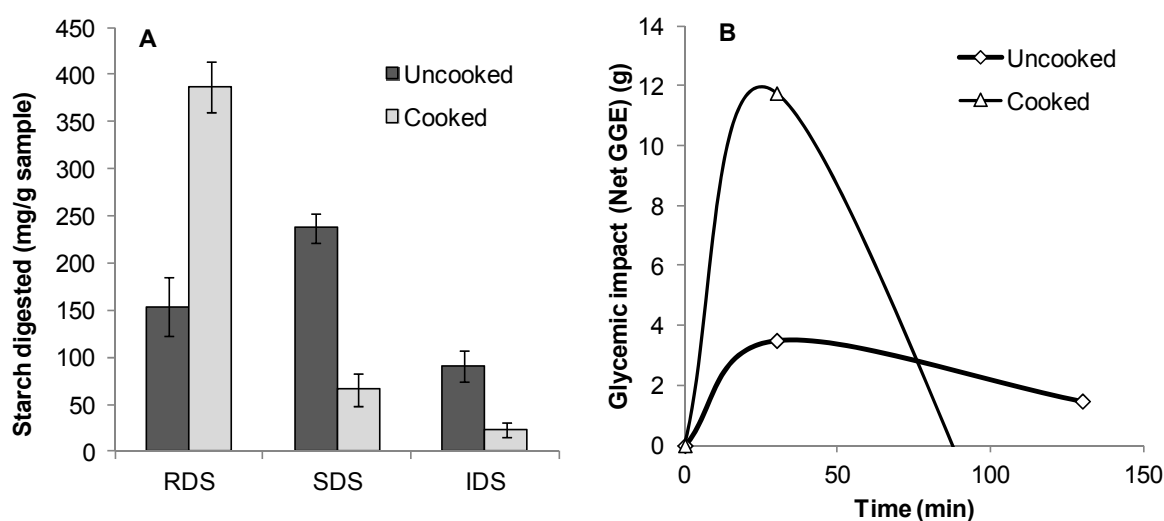


Figure 9. Effects on *in vitro* digestibility of further processing (boiling) of rolled oats (a minimally processed product) in preparing porridge, during which loss of starch structure (gelatinization) and extensive loss of oat grain structure occurs. **A** starch fractions of different digestibility defined in caption to Figure 3. **B** Theoretical blood glucose response curves based on RDS and SDS release with glucose disposal allowed for using the method of Monro et al. (2010). Error bars are standard deviations (Mishra and Monro, unpublished).

Two hydrothermal treatments of starch, annealing and heat-moisture treatment (HMT), cause changes in the structural and physicochemical properties and increase the digestibility of raw starch enough for it to qualify as slowly digested starch (digested between 20 and 120 min *in vitro*) (Lehmann & Robin 2007). In annealing, the starch is heated to below

gelatinization temperature but long enough for some molecular rearrangement of the starch to occur. In HMT, higher temperatures are used but water is restricted so that full gelatinization does not occur. Although structural change is sufficient to increase digestibility, the granular structure and birefringence of the starch granules remain.

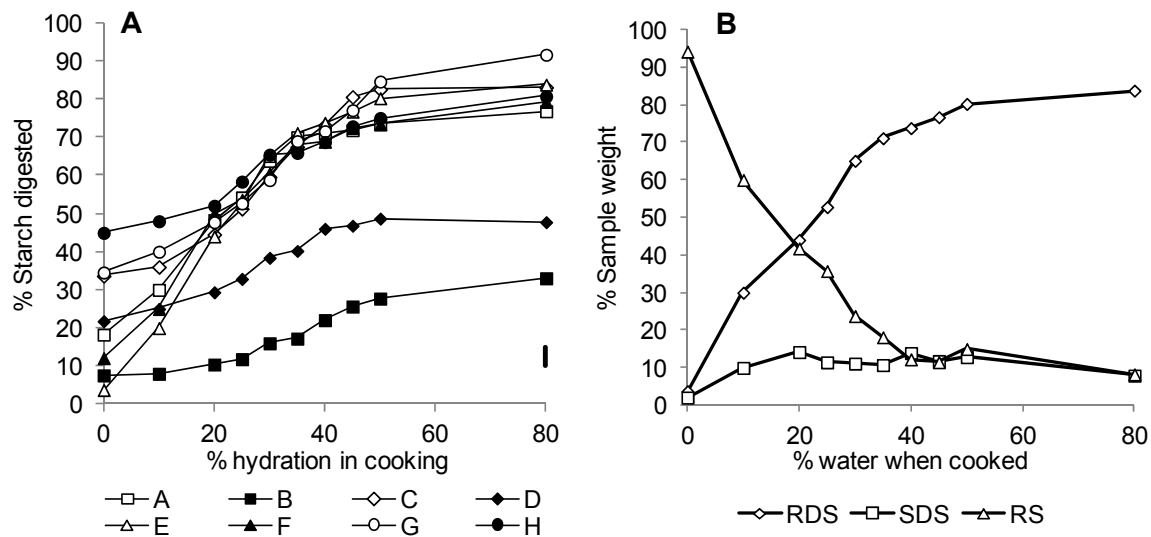


Figure 10. Effect of structural change in starch granules as a function of hydration during cooking, on *in vitro* digestion. Chart A. Rapidly digested starch as a % of total starch during cooking of seven starches at progressively increasing degrees of hydration: A. Maize; B. Hi Maize (high amylose); C. Mazaca (low amylose); D. Pea ('Sonata'); E. Potato; F. Rice; G. Tapioca; H. Wheaten cornflour. Chart B. Example of changes in starch fractions differing in digestibility: Potato starch showing that increased hydration caused the interconversion of resistant and rapidly digestible starch without substantially increasing slowly digested starch. The bar is the mean between-duplicate range.

4.3. By controlled retrogradation after cooking

During cooling of starch dispersed by gelatinization, the linear sections of amylopectin and amylose chains anneal to form hydrogen bonded alignments that limit access by digestive enzymes. The partial retrogradation of amylopectin in cooked potato to form slowly digested starch (SDS) is a good example of the effect of retrogradation (Figure 1; cooked-chilled), and has led to the suggestion that a way to reduce the glycemic impact of potatoes would be to consume them in the form of cold potato salad rather than as freshly cooked hot potato (Leeman et al. 2005; Monro & Mishra 2009).

Retrogradation is now used industrially to produce resistant starches (RS3). They have become widely used as bland low energy ingredients for which colonic benefits are claimed, in nutritionally enhanced bakery and other products.

4.4. By retaining tissue structure in whole foods – minimal processing

Tissue structure can be retained by consuming whole foods, in which the incomplete comminution achieved by chewing allows some survival and influence of food structure on

carbohydrate availability. The diffusion of sugars from fruit pieces, for instance, is much slower than from fruits consumed as a puree (Haber et al. 1977).

The use of retained tissue structure in cooked food is most widely used in the baking industries, when fragments of intact kernels are included in grain breads. Chopping and cutting (kibbling) of grain kernels that would otherwise be ground to flour has found a place in food processing for populations with high rates of obesity and glucose intolerance, where there is need to reduce both the rate and extent of carbohydrate digestion. By substituting partially intact kibbled kernels for flour in bread products, the rate of digestion and the resulting glycemic impact of foods can be significantly reduced, as is revealed by the increases in digestion rates and *in vitro* glycemic index estimates when kernel-rich breads are homogenized to remove grain structure (Figure 11). Pumpernickel is an extreme example, as it consists largely of a conglomerate of rye grains, and in line with its low digestibility, it has a much lower glycemic index than most other breads (Jenkins et al. 1986).

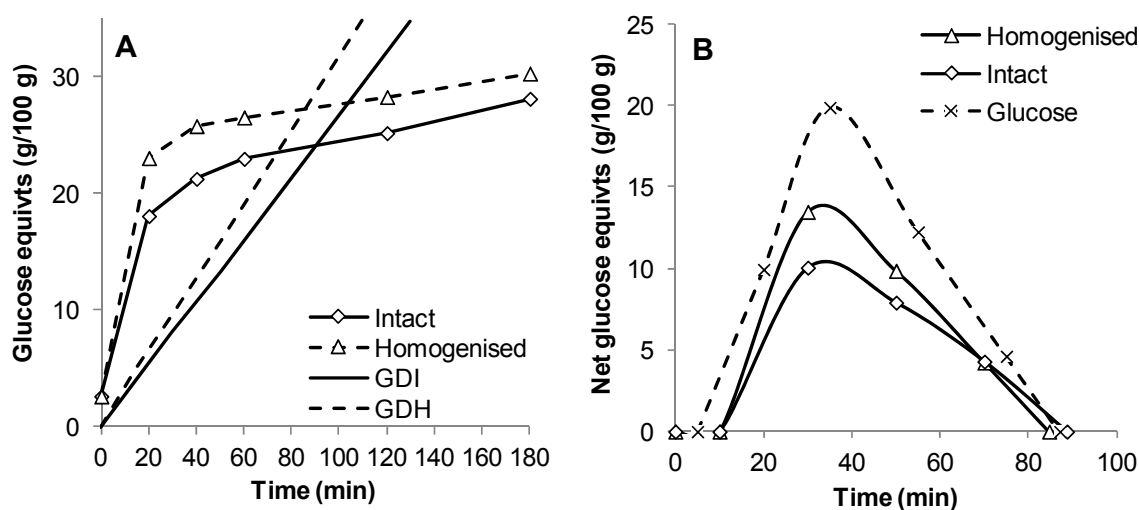


Figure 11. Effect of homogenizing to remove structure: A commercial wholegrain bread containing 25% kernel fragments > 2 mm in diameter was homogenized and the intact and homogenized breads digested *in vitro*. A. Digestion profiles (with markers) and lines of theoretical glucose disposal (GDI = glucose disposal for intact bread, GDH = glucose disposal for homogenized bread). Mean inter-duplicate range <5% at each time point. B. The curves after taking into account theoretical glucose disposal and response lag. The areas under the curves compared with the area under the glucose reference curve gave *in vitro* glycemic index values of 70 (high) for the homogenized bread compared with 55 (low) for the unhomogenized bread. Mean between-duplicate range was < 5% (Monro and Mishra, unpublished).

Minimal processing is not a term specific to any procedure, but it generally refers to processing that is the minimum required to make a product palatable, or saleable in a particular form for future cooking (Fellows 2000). The digestive advantages of minimal processing for nutrition are a reduced rate and extent of starch digestion, more resistant starch and non-starch polysaccharide for colonic function (as in bran), and greater nutrient retention than in a refined product from the same cereal source. The minimally processed category includes a range of cereal grains that have been steamed to partially precook and

then rolled or flaked to eliminate hardness, such as rolled oats and barley. Depending on how thinly they are rolled they may have a relatively low glycemic impact until further processed into the form of hot porridge (Granfeldt et al. 2000) (**Figure 9**).

One of the main points supporting the argument in favor of consuming a greater proportion of dietary carbohydrate as whole grains, in which native structure is partially retained, is that “wholeness”, in the sense of intactness, is associated with a reduced blood glucose loading, and increased colonic loading of resistant starch (Venn & Mann 2004). A significant association of increasing particle size with decreasing glycemic response (Fardet et al. 2006) and increased colonic fermentation (Bird et al. 2000) has been demonstrated and is consistent with results of *in vitro* analyses of grain starch digestibility.

4.5. By replacing native structure with secondary structure in food processing

a. Formation of open textures

Extrusion cooking under shear and pressure often at moisture contents of less than 15% is a means of producing highly digestible crisp, dry food products. The extrusion process involves high temperatures, extreme shearing forces, and release of hot product under high pressure, to yield expanded dry products that are gelatinized, porous and retain almost no native tissue or starch granule structure to resist amylase activity. Leavened products such as white bread are similar, except that tissue disruption is achieved by milling before cooking, and porosity is achieved by including a leavening agent such as yeast in the product formulation. The porosity of such products coupled with the absence of any integrated plant cell wall structures ensures rapid penetration of digestive enzymes and almost immediate collapse and digestion, so that the conversion of starch to sugar during digestion rapidly increases to a plateau where digestion is complete (**Figure 4**). Accordingly, such products are often of high glycemic impact (Foster-Powell et al. 2002).

b. Formation of dense low-porosity structures

Dense, low porosity food structures such as pasta are produced by extrusion at low temperatures with limited gelatinization and no puffing. In these foods, carbohydrate digestion is relatively slow and related to food geometry, because little enzyme penetration is possible, and any digestion is dependent on surface area (Monro et al. 2011). In such foods there is potential to use food shape to influence digestion rate as long as a proportion of the particles survive mastication. Dense foods that are soft enough to be swallowed partially intact, so that the influence of surface area on digestion rate is retained, may be useful in delivering available carbohydrate without an acute postprandial blood glucose response. Development of foods that use particle shape to determine digestion rate will therefore need also to consider the influence of food texture on the urge to chew.

4.6. By combinations of processes

Many food products are made using combinations of processes, each affecting food structure and carbohydrate digestibility in different ways. Some examples are given below (Table 1).

4.7. By changing the molecular structure of starch

Molecular modifications to starch that affect degree of branching or the ability of starch chains to interact or retrograde will affect digestibility, as already discussed. The feasibility of using starch modification at the point of biosynthesis in the plant is now being investigated, through genetic manipulation of the enzymes involved in establishing starch structure. Transgenic potato lines deficient in granule-bound starch synthase, and in two

Product type	Processes	Structure	Carbo-hydrate digestion	Relative Glycemic impact (GGE/g) ¹
Raw fruits	None	Plant tissue structure intact. Available carbohydrate as mono and disaccharides	High	Low
Pasta	Milling, cold low pressure, low shear extrusion, then time limited boiling	Dense, polymeric available carbohydrate (starch), incomplete starch gelatinization, protein occlusion of starch granules, superficial digestion	Slow but complete	Low-moderate
Biscuit	Milling then high temperature-low moisture cooking	Dense, friable, incomplete starch gelatinization. High fat levels coat starch	Moderate	Moderate
Bread, white	Milling then high temperature, high moisture cooking	Porous, more complete starch gelatinization than biscuits	High	High
Bread, kibbled grain	Milled flour plus cut grain, then high temperature, high moisture cooking	Porous gelatinized matrix containing intact kernel fragments with limited access of digestive enzymes	Moderate	Low-moderate ²
Extrusion cooked/puffed	Milling prior to high temperature, high shear, high pressure extrusion and puffing	All plant tissue structure and starch granule structure eliminated. Highly porous, readily accessible gelatinized starch	High	High
Muesli/rolled oats	Crushing, steaming, limited cutting	Plant tissue structure partially intact, starch partially gelatinized	Moderate	Low ³
Porridge	Crushing, steaming, then moist cooking	Plant tissue structure less intact than previous, starch gelatinized	High	Moderate - high

¹ Glycemic glucose equivalents/g sample

² Depends on inclusion rate of kibbled grain

³ Depends on degree of crushing and chopping

Table 1. Examples of the relationship between processing combinations, food structure, carbohydrate digestibility, and relative glycemic impact per equal food weight in several food types.

starch-branching enzymes have been produced. Lines in which more linear starch was produced showed a lowered susceptibility to *in vitro* digestion than the parent lines (Karlsson et al. 2007).

Traditional plant breeding and selection of mutant types has already produced varieties with alterations in starch structure that affect starch digestibility. A high amylose maize cultivar, for instance, is used as a source of commercially available resistant starch (HiMaize®, Figure 10).

4.8. By structural breakdown during food consumption and digestion

a. Chewing

As chewing is the natural way to increase carbohydrate availability by reducing food structure, it has been seriously suggested that a way of using structure to reduce carbohydrate digestion rate, to reduce glycemic impact, is to swallow food without chewing it (Read et al. 1986). However, chewing of food is such an important part of enjoying it and converting it into a lubricated form that can be swallowed, that not chewing food is not a practical option for controlling glycemic impact.

Evolution has equipped humans with an effective grinding mechanism in the form of teeth, and the sensitive and dexterous combination of cheek and tongue to sort and position food particles accurately between the molar grinding surfaces. The effectiveness of crushing in bringing about the conversion of inaccessible digestible (“resistant”; RS) to rapidly digested (RDS) starch (**Figure 8**) underscores the importance of mastication to the successful exploitation of starch in an omnivorous diet.

Chewing has three very important functions, all related to food structure. Firstly, chewing crushes foods to release nutrients; secondly, it reduces the size of food fragments so they may be comfortably swallowed; and thirdly, and most importantly, it churns and mixes the food with saliva to convert it into the form of a well-lubricated semi-solid bolus that may be easily swallowed. Not until the food is swallowed can effective digestion commence.

The purpose of chewing has been revealed in studies of individual differences in chewing. Although individuals differ markedly in the mechanical details of how they go about their oral comminution of foods, they all arrive at a remarkably similar endpoint in terms of the particle size reduction in the mouth (**Figure 12**). It is apparent that the urge to stop chewing and swallow is determined more by the physical properties of the bolus that results from chewing, than by details of the mastication process that lead to the bolus. Dentition, the number of chews, the rate of chewing and so on are less important than the final result (Peyron et al. 2004).

In many processed foods produced nowadays, digestibility is not very dependent on structural degradation due to crushing by chewing, because the foods are based on ingredients, such as flour, that have been thoroughly comminuted by milling before cooking. Foods for which chewing makes a difference are usually those consisting of, or containing intact grains, such as rice and kibbled grains, and those consisting of dense, non-

porous starch matrices. For many starchy processed foods the combination of mastication and salivary α -amylase activity reduces the adhesiveness of starch, and the structural cohesion of food in the form of a bolus, allowing the stomach to separate available carbohydrate from more fibrous components quite rapidly for transfer to the duodenum, which is the primary site of carbohydrate digestion in the gut.

The combination of salivary α -amylase with chewing, and the fact that starch is usually gelatinized and not intrinsically fibrous, means that most of the starch component is quickly reduced to a small particle-containing slurry that can be separated in the stomach and moved on to the ileum for digestion with little delay. The rapid dispersion of starch in most foods explains why, despite the tendency of the stomach to retain large particles, blood glucose responses to foods almost invariably commence after a lag of only about 10 min from ingestion and almost always reach a peak between 30 and 40 minutes from ingestion (Brand-Miller et al. 2009).

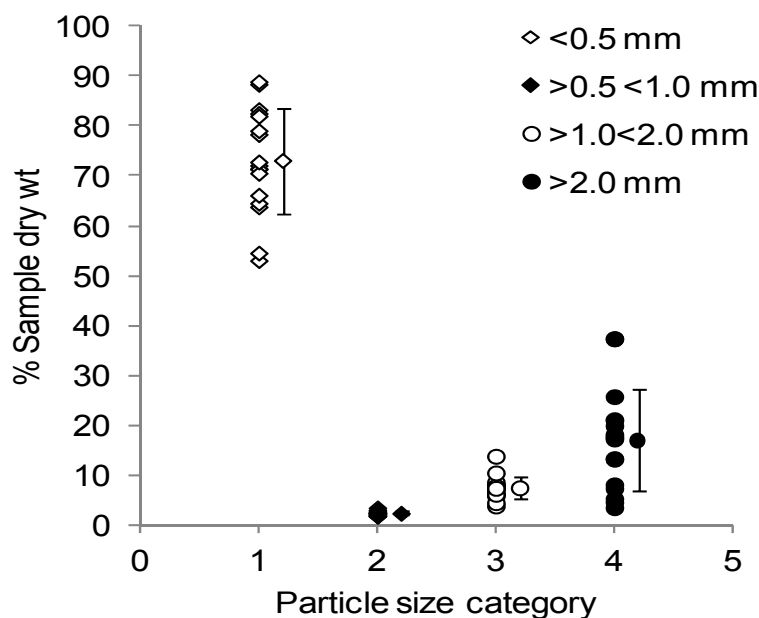


Figure 12. Effect of chewing on reduction of structure in a carbohydrate food – rice. Range of particle sizes in within size categories from cooked white rice chewed by 20 subjects. The subjects chewed intact whole rice grains in quantities they would normally consume and expectorated them when they felt the urge to swallow. For all subjects, most of the chewed sample was less than 0.5 mm in diameter. Means \pm SD shown for each size category. Based on data used in Ranawana et. al. (2010).

b. Gastric and small intestinal digestion

The stomach and intestine are not passive reservoirs, but are motile reactors in which food, while undergoing enzymatic dismemberment, is also continually subjected to shearing and abrasion from circumferential, longitudinally migrating contractions of the gut wall (Lentle & Janssen 2008). Compared with the concentrated forces exerted at the molar surfaces by jaw muscles in chewing, the forces on food particles in the stomach and intestine due to peristalsis are very small (Lentle & Janssen 2008). However, in combination with digestive

enzyme action they have the important role of reducing food structure by sloughing off the hydrated and digestively weakened surface layers of food particles, to improve access of digestive enzymes to the interior.

When the mechanical and processing steps of food preparation and mastication have reduced food structure to the extent that the food can be swallowed, and the stomach has then separated a starchy slurry from the large particles remaining, the starch is ready for digestion in the ileum by α -amylase from the pancreas working in concert with enzymes in the gut wall.

The rate of starch digestion depends partly on the rate of gastric emptying (Darwiche et al. 2001), but also the structural form in which it arrives in the ileum, as intact starch granules, as disorganized or dispersed gelatinized starch, or as once-disorganized starch that has re-aggregated to form retrograded starch. Digestion of intact food particles or starch granules is relatively slow in the gut, as it is *in vitro*, and the digestion pattern depends very much on the botanical origin of the granules (Donald 2004; Oates 1997).

a. Colonic digestion

In the colon, carbohydrate digestibility is governed by a completely different set of parameters than in the foregut, to which the discussion has referred so far. Carbohydrates entering the colon are those that were unable to be digested and/or absorbed during gastric/ileal transit. They include starch that has survived digestion for the reasons of structure and chemistry already discussed, including crystallinity in ungelatinized and retrograded starch, encapsulation by plant tissue cell walls, and occlusion by fat. However the main carbohydrate source entering the colon consists of the non-starch polysaccharides that constitute the plant cell wall and in the colonic ecosystem into which they pass they are exposed to a myriad of bacterial enzymes that are absent from the foregut. The colonic bacteria disassemble the cell walls to provide carbohydrate substrate for bacterial fermentation. The products of colonic fermentation are short chain fatty acids that are absorbed and enter intermediary metabolism, where they may provide as much as 10% of dietary energy requirements for humans.

The physical/structural constraints that modulate colonic fermentation of polysaccharide residues involve molecular structure, occlusion and particle size, which may all affect availability of substrate for bacterial enzymes and the ability of bacteria to colonize and invade fragments of plant tissue and cell walls. In the bacterial ecosystem that consists of thousands of species of bacteria that can adapt rapidly to changes in available substrates, there are few natural plant polysaccharides that on their own can resist the multipronged and coordinated attack of the diverse colonic microflora. However, some, such as psyllium gum, which is a complex and highly branched polysaccharide, are fermented so slowly that much of their molecular structure, and the hydration capacity that depends on it, remains intact after passage through the colon. Such polysaccharides make very effective faecal bulking agents but may lead to problems such as reduced mixing and fermentation in the colon when present at high concentrations. Cellulose, which exists as highly crystalline fibrils, is also slowly fermented, and is a major component of the dietary fiber that survives and contributes faecal bulk in plant-containing diets (Monro & Mishra 2010).

Plant residues are often non-fermentable because of the occlusive effects of secondary thickening of the tissues, initially by cellulose but followed in many cases by the deposition of lignin, resulting from phenolic condensation within pre-existing cell walls, usually when they have already undergone secondary thickening by cellulose deposition (Esau 1967). The combined effects of increasing amounts of crystalline cellulose and lignin is clearly seen in the contrast between fermentation of parenchymatous pith cells and of secondarily thickened rind (cortex) cells of broccoli stem in the hind gut. Although derived from the same parenchymatous ground tissue, the pith remains as parenchyma, while the rind differentiates to contain a high proportion of secondarily thickened and lignified xylem tissue. The parenchyma cells are almost completely consumed by the bacterial flora in the hind gut, while the cells of the rind remain apparently intact and recognizable in the feces (Monro & Mishra 2010).

Even within tissues consisting entirely of parenchyma cells, the rate of fermentation can be modulated by structure. Paradoxically, multicellular clumps of carrot cells were found to be more rapidly fermented than cell wall fragments, probably because the intercellular spaces and angles between cells in multicellular clusters provided colonization sites for colonic bacteria (Day et al. 2012). There is, however, likely to be an optimal size at which increased colonization sites are counterbalanced by inaccessibility in large particles.

5. Conclusion

Food structure can affect carbohydrate digestibility in a range of ways. From the level of molecular conformation to plant anatomy, structure plays an important role in carbohydrate digestion. Attempts to manipulate structure as a means of controlling nutritional attributes of foods related to carbohydrate digestion have been in progress for thousands of years. They remain an important focus of modern food technology aimed at addressing the health problems associated with both inadequate energy intakes in developing countries, and excessive energy consumption in the developed world.

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