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Food Matrix Effects for Modulating Starch Bioavailability

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Keywords

starch bioavailability, food matrix, interaction, glycemic response, production strategies

Abstract

As the prevalence of obesity and diabetes has continued to increase rapidly in recent years, dietary approaches to regulating glucose homeostasis have gained more attention. Starch is the major source of glucose in the human diet and can have diverse effects, depending on its rate and extent of digestion in the small intestine, on postprandial glycemic response, which over time is associated with blood glucose abnormalities, insulin sensitivity, and even appetitive response and food intake. The classification of starch bioavailability into rapidly digestible starch, slowly digestible starch, and resistant starch highlights the nutritional values of different starches. As starch is the main structure-building macroconstituent of foods, its bioavailability can be manipulated by selection of food matrices with varying degrees of susceptibility to amylolysis and food processing to retain or develop new matrices. In this review, the food factors that may modulate starch bioavailability, with a focus on food matrices, are assessed for a better understanding of their potential contribution to human health. Aspects affecting starch nutritional properties as well as production strategies for healthy foods are also reviewed, e.g., starch characteristics (different type, structure, and modification), food physical properties (food form, viscosity, and integrity), food matrix interactions (lipid, protein, nonstarch polysaccharide, phytochemicals, organic acid, and enzyme inhibitor), and food processing (milling, cooking, and storage).

1. INTRODUCTION

Obesity and diabetes have become major public health problems worldwide, with the number of new cases growing rapidly in recent years. Worldwide obesity has nearly tripled since 1975, with more than 1.9 billion adults who are overweight and over 650 million who are obese. In 2019, the global estimate of adults living with diabetes was 463 million, with health care costs of approximately $760 billion. These diet-related chronic diseases are associated with blood glucose abnormalities, including impaired glucose tolerance and impaired fasting glucose, which is linked to increased levels of digestible carbohydrate consumption according to epidemiologic evidence (Augustin et al. 2015, Miao et al. 2015a, Sun & Miao 2020, Zhang & Hamaker 2017). Current developments in food science and nutrition have led to advances in slowing down the rate of carbohydrate digestion as a nutritional intervention to regulate glucose homeostasis and energy metabolism balance for human well-being.

Starch is the most common polysaccharide in cereal grains, legumes, and tubers as well as some other plant foods. It is also the main structure-building macroconstituent in many widely consumed foods, such as bread, pasta, rice, breakfast cereals, and cookies, and is the principal glucose provider in human diets. Unlike the starchy foods our ancestors consumed, many thermally processed products have highly digestible and high-glycemic starches. The rate and location of digestion in the small intestine are important factors determining the nutritional quality of food and are influenced by food factors for modulating starch bioavailability (**Figure 1**), including the properties of the starch itself as well as by the food matrix and processing effects. Thus, starch is essential to the normal functioning of the body, and the liberated glucose not only provides energy but is a key signaling molecule regulating glucose and energy homeostasis, as well as

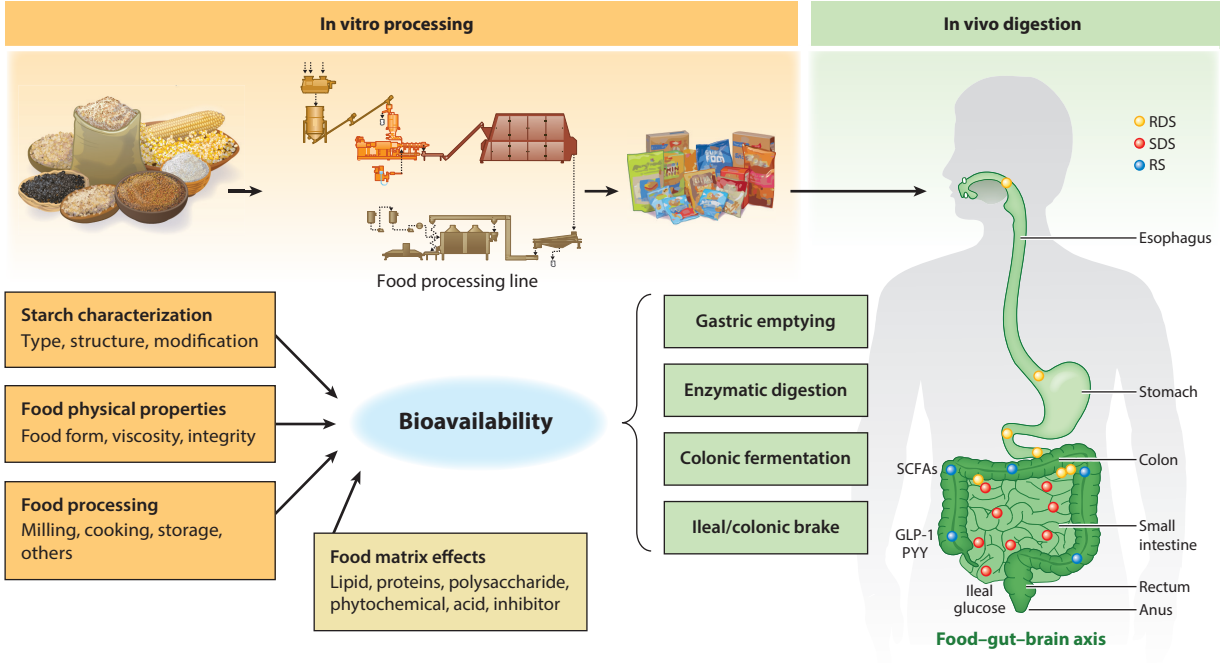

Figure 1

Food factors for modulating starch bioavailability. Abbreviations: RDS, rapidly digestible starch; RS, resistant starch; SDS, slowly digestible starch.

appetite, which are foundations of human health. This review focuses on the current knowledge of starch bioavailability in relation to native and processed product matrices and includes topics of classification and physiological benefits, determinants, and factors related to starch digestion rate, in vitro and in vivo measurements, and matrix interactions as well as the production strategies for both low-glycemic response and whole-grain foods.

2. STARCH BIOAVAILABILITY

2.1. Nutritional Classification of Dietary Starch

Starch is an important macronutrient providing biological fuel (45–65% of caloric intake) for the majority of the world's population. From the perspective of nutrition, starch can be classified as glycemic or nonglycemic depending on its bioavailability. Standardized measurements of the postprandial glycemic response of starchy foods are used to specify their glycemic index (GI) (Augustin et al. 2015, Englyst & Englyst 2005, Miao et al. 2015a). This approach has replaced the traditional method of classifying starches as either amylose or amylopectin. On the basis of the rate and extent of glucose liberation from starch digestion, starch is generally classified into three fractions using the standardized Englyst assay (Englyst et al. 1992, Hasek et al. 2018): rapidly digestible starch (RDS; fraction digested within 20 min), slowly digestible starch (SDS; fraction digested between 20 and 120 min), and resistant starch (RS; fraction undigested after 120 min) (**Table 1**). These categories are related to the utilization and biological function of starch after its consumption. Apparently, this nutritional classification is a measurement outcome–oriented concept, and there are no pure RDS, SDS, or RS materials (Zhang & Hamaker 2009). Also, the

Table 1 Starch bioavailability classification

Main category	Nutritional grouping	Digestion timeline (Englyst assay) and place	Examples	Physiological function
Glycemic starch	RDS	0–20 min, mouth and small intestine (duodenum and proximal region)	Freshly cooked starchy food	Rapid source of energy
	SDS	20–120 min, small intestine (jejunum and ileum)	Native cereal starch, pasta, parboiled rice, and biscuit	Slow and prolonged release of glucose
Nonglycemic starch	RS	>120 min, large intestine (colon)	RS1: physically inaccessible starch such as legumes, grains, and seeds RS2: RS granule from green banana, raw potato, and high-amylose maize starch RS3: retrograded starch, including commercial NOVELOSE and C☆Actistar RS4: chemically modified starch produced by dextrinization, etherification, esterification, oxidation, or cross-linking RS5: amylose–lipid complex	Fermentation that produces SCFAs for gut health

Abbreviations: RDS, rapidly digestible starch; RS, resistant starch; SCFAs, short-chain fatty acids; SDS, slowly digestible starch.

physiological effects of the three fractions are different. RDS, such as most thermally processed foods, is rapidly digested in the mouth as well as the duodenum and proximal regions of the small intestine, leading to postprandial hyperglycemia. SDS, as an intermediate starch fraction between RDS and RS, is digested slowly and possibly throughout the entire small intestine to provide sustained glucose release corresponding to the characteristic of low-GI foods. RS, which is not digested in the upper gastrointestinal tract, is typically fermented as a dietary fiber in the colon by microbiota to produce short-chain fatty acids (SCFAs) that are beneficial to gut health (Cantu-Jungles & Hamaker 2020, Miao et al. 2015a, Sun & Miao 2020, Zhang & Hamaker 2017).

2.2. Starch Digestion and Utilization

Starch digestion and utilization in the gastrointestinal tract are important physiological processes that together consist of three phases: the intraluminal phase, the brush border phase, and the glucose absorption phase, as depicted in **Figure 1**. After ingestion, starch is enzymatically digested by amylolytic α-amylases from saliva and the pancreas as well as the brush border glucogenic enzymes of glucogenic maltase-glucoamylase (MGAM) and sucrase-isomaltase (SI) (G. Zhang et al. 2015).

In humans, both salivary and pancreatic α-amylases [Enzyme Commission (EC) 3.2.1.1] are α-1,4 endo-glucosidases, which have five subsites to bind the starch substrate and then cleave the α-1,4 glycosidic linkages using a multiple-attack mechanism (Brayer et al. 2000, Miao et al. 2018). The human α-amylases exhibit optimum activity at pH 6.9 and 37°C as well as in the presence of chloride and calcium. It has been observed that pancreatic α-amylase is closely related to salivary α-amylase with a high identity (97%) based on the amino acid sequence homology. Starch is slightly hydrolyzed in the mouth by salivary α-amylase, and more extensive digestion of starch occurs in the small intestine because of the action of pancreatic α-amylase. α-Amylase efficiently cleaves adjacent and penultimate α-1,4 linkages toward the nonreducing side and the third linkage toward the reducing side at C-6 branched residue, leading to an increase in the products maltose, maltotriose (G3), maltotetraose (G4), and α-limit dextrin (Ao & Jane 2007). For the gluco-oligomers, the action patterns on G3 and G4 are concentration dependent. Differences in the substrate concentration lead to changes in the formation of α-limit dextrins, which can influence subsequent hydrolysis to release the glucose monomer by the brush border enzymes before absorption (G. Zhang et al. 2015).

Mucosal α-glucosidases (MGAM, EC 3.2.1.20 and 3.2.1.3 with a molecular weight of 210–289 kDa; SI, EC 3.2.1.48 and 3.2.1.10 with a molecular weight of 180–210 kDa) belong to the glucohydrolyase Family 31 with 60% amino acid sequence homology and are bound to the intestinal cell membrane (Diaz-Sotomayor et al. 2013, Nichols et al. 2009). Both enzymes have five distinct protein domains—an N-terminal cytoplasmic tail domain (26 amino acids), a transmembrane domain (anchoring domain, 21 amino acids), an *O*-glycosylated stalk domain (52 amino acids), and two similar catalytic domains (N-terminal subunit or C-terminal subunit, each ~900 residues)—and display α-1,4 exo-glucosidic activity from the nonreducing ends of linear chains in substrates as the final step of starch digestion (Chegeni et al. 2018). They also have complementary substrate specificity with a certain degree of substrate overlap. SI accounts for nearly all isomaltase activity, almost all sucrase activity, and 80% of maltase activity (Lee et al. 2016), whereas MGAM accounts for all glucoamylase activity, 20% of maltase activity, and 1% of sucrase activity (Quezada-Calvillo et al. 2008). MGAM hydrolyzes far larger and more complex glucans with longer chains compared to SI. The oligosaccharides, including G3, G4, and G5, displayed substrate inhibitory effects on MGAM activity, suggesting that MGAM can regulate the total digestion rate of starch (Quezada-Calvillo et al. 2008). Moreover, α-amylase hydrolysis

is not a requirement for native starch digestion in the small intestine, and mucosal MGAM is an alternative pathway for degradation of raw starch granules with a surface furrowed pattern in random, radial, or tree-like arrangements, which differ substantially from the erosion patterns of α-amylase (Ao et al. 2007). In addition, the indigestible starch fragments pass into the large bowel, where they are largely fermented into SCFAs that provide additional energy to the body along with a high proportion of butyrate as well as a prebiotic effect (Sajilata et al. 2006).

After gastrointestinal tract handling, glucose from glycemic starch digestion is transported into the small intestine enterocytes by the Na^+-K^+ cotransporter of sodium–glucose cotransporter 1 (SGLT-1) and into the blood system through glucose transporter 2 (GLUT2) for the assimilation of starchy food (Sun & Miao 2020). Glucose absorption is intimately associated with the activity and abundance of SGLT-1, which is hormonally regulated by incretin hormones in the digestive tract in response to distal glucose stimuli, such as glucose-dependent insulinotropic polypeptide (GIP) and glucagon-like peptide-1 (GLP-1) (Ma et al. 2009). These hormones, together with the vagus nerve, are the major regulators in the proximal–distal feedback loop (termed the gut–brain axis), controlling the coordination of gastrointestinal tract activity and internal metabolism, such as gastric emptying, blood glucose control, and insulin secretion for optimum health (G. Zhang et al. 2015). The released ileum glucose and SCFAs from gut fermentation have been shown to promote the ileal brake and colonic brake by stimulating the release of GLP-1 and peptide YY (PYY) through their ability to inhibit upper gut motility, slow the gastric-emptying rate, and decrease food intake–associated health benefits (Hasek et al. 2018, Pletsch & Hamaker 2018, G. Zhang et al. 2015). Thus, the location of digestion and colonic fermentation of dietary starch not only mediates brake effects but also improves the physiological processes via the maintenance of glucose homeostasis and energy balance to achieve a wide range of health benefits.

3. THE DETERMINANTS OF STARCH BIOAVAILABILITY

3.1. Starch Characteristics

It is known that starch is essentially composed of two glucose polymers: the mostly linear amylose ($\sim 10^6$ Da) with a few long-chain branches and the highly branched amylopectin ($\sim 10^8$ Da). These two types of molecule assemble into the semicrystalline granular structure in starch granules, which consists of concentric layers of amorphous and crystalline shells radiating from the hilum (BeMiller & Whistler 2009). The major intrinsic factors affecting starch digestibility include the botanical source, granule size, crystal architecture, ratio of amylose to amylopectin, amylopectin fine structure, and surface and interior characteristics of the starch granule (**Figure 1**). Investigators showed that the smaller granules of native starches have higher amylolysis rates than the larger counterparts, which is related to the increased surface-to-volume ratio of smaller granules for enzyme binding to the substrate, leading to a proportional increase in digestibility (Ao et al. 2007, Miao et al. 2015a, Warren et al. 2013). Dhital and coworkers (2010) also observed that the digestibility of size-fractionated native starch granules is well fitted with the surface area–controlled mechanism, depicting an inverse square relationship between the digestibility coefficient and granule size.

Most cereal starches that exhibit an A-type X-ray diffraction pattern in their native state are good representatives of SDS materials (>50%), whose digestion profiles are mainly determined by their physical structure. The layer-by-layer arrangement of crystalline and amorphous lamellae within the crystalline regions of these starches that are accessed through pores and channels, as well as their highly ordered crystalline structures, leads to the slow digestion profile of this type of raw starch granule (Zhang et al. 2006a,b). This unique structural mechanism is realized

by the inside-out layer-by-layer digestion pattern resulting from even digestion of crystalline and amorphous regions in a side-by-side manner. Regarding other types of starch, such as B-type potato starch, the granular surface does not have pores and channels and has a different arrangement of amorphous and crystalline regions, which makes enzyme binding more difficult and thereby the raw starch granule more resistant to digestion (Dhital et al. 2010). Moreover, structural features like surface pores and channels for most of the A-type cereal starches are believed to increase the effective surface area and thereby facilitate the direct and easier diffusion of enzymes through the channels, leading to an inside-out pattern of digestion (endo-corrosion), which has a higher enzyme susceptibility compared to B-type potato and banana starches because of their smooth surface and lack of channels for the outside-in pitting pattern (exo-corrosion) (Miao et al. 2011, Zhang et al. 2006a).

In fully gelatinized starch and at the molecular level, the amylolysis of starch is influenced by the ratio of amylose to amylopectin as well as the chain-length distribution and branching pattern of amylopectin. The higher RS levels in starches with a high ratio of amylose to amylopectin are mainly related to the reassociation of amylose and amylopectin molecules to form B-type crystalline structures with ordered hexagonally packed double helices, indicating that high-amylose starches are a source of RS (Szczodrak & Pomeranz 1991, Zhu et al. 2011). Also, branched amylopectin has been reported to be the structural basis for heat-stable SDS (Miao et al. 2011, Zhang & Hamaker 2009). There is a higher proportion of α-1,6 linkages in amylopectin molecules, which are less efficiently degraded by amylase, because the free energy of enzymatic digestion for an α-1,6 glycosidic bond (−7.1 KJ/mol) is greater than that of an α-1,4 glycosidic bond (−15.5 KJ/mol). A chain-length analysis of the fine structure of amylopectin reveals a parabolic relationship between SDS content and the weight ratio of short chains [degree of polymerization (DP) < 13] to long chains (DP ≥ 13), showing that amylopectin with a high amount of either short chains or long chains has a higher percentage of SDS compared to normally structured amylopectin (Zhang et al. 2008a,b). Enzymatic approaches to tailor the proportion of non-α-1,4 linkages and the branched-chain length using branching enzymes, such as amylosucrase, 4-α-glucanotransferase, maltogenic amylase, and glucansucrase, can improve the slow digestion property of regular amylopectin (Miao et al. 2018). Martinez et al. (2018) recently showed that amylopectin with long A and B1 chain lengths (DP ≥ 15.5) retrograde more rapidly to form SDS that was retained in a cake crumb. Other methods to improve the bioavailability of starch molecules have been the modification of the molecular structure using dextrinization, oxidation, cross-linking, esterification, and etherification (Miao et al. 2014, 2015a). The chemical groups were likely distributed near branching points of amylopectin molecules, which made starch resistant to amylase digestion because of the steric hindrance or hydrophobic microenvironments caused by the substituted groups (Han & BeMiller 2007, Miao et al. 2014, Ye et al. 2014).

3.2. Food Physical Properties

Food microstructure can affect the digestion and absorption of starch in several ways at the cellular tissue and food levels, including gastric emptying, glycemic response, and colonic fermentation. Starch granules are synthesized within amyloplasts in storage organs such as endosperm (cereals), cotyledons (legumes), and parenchyma (tubers), may be surrounded by a protein matrix, and are enclosed by thin and nonlignified cell walls (Dhital et al. 2016, Do et al. 2020, Zhou et al. 2018). This suggests that cereal kernels, grain legumes, and tuber tissues have mechanically resistant structures, which may influence starch bioavailability (Rovalino-Córdova et al. 2018). Cell wall entrapment acts as a physical barrier to digestive enzyme diffusion and hydrolysis of starches (Bhattarai et al. 2017, Do et al. 2020). Also, the cell walls provide an adsorptive surface for binding

the catalytic active site of amylase and further reducing the catalysis of entrapped starches (Dhital et al. 2016). Disruption of the tissue integrity by fine milling or other processing increases the susceptibility of starch to enzyme hydrolysis because of the increase in exposed surface area, thereby leading to higher glucose and insulin responses (Edwards et al. 2015a).

Many foods increase the viscosity of the gastrointestinal fluids because they contain water-soluble dietary fibers, such as arabinoxylan, β-glucan, guar gum, pectin, and psyllium as well as other nonstarch polysaccharides (Dikeman & Fahey 2006). In cereal-based products, viscosity can have a major effect on decreasing diffusion and accessibility of amylase toward starch, resulting in slow digestion and absorption of carbohydrates with lowered postprandial glycemic responses. The viscosity effect of dietary fiber slows gastric motility and emptying in simulated physiological conditions. An increase in the viscosity of the gastrointestinal fluids has been shown to flatten the glycemic response through delayed gastric emptying, extended satiety, and reduction of starch digestibility (Regand et al. 2011). However, relatively few commonly consumed foods have sufficiently high viscosity to generate such responses, with a notable exception being oat-based porridges. Moreover, soluble dietary fiber is fermented by bacteria in the human colon to produce SCFAs that trigger the release of the gut hormones PYY and GLP-1, affecting energy metabolism, insulin sensitivity, appetitive response, and food intake through the ileal and colonic brake feedback control systems (G. Zhang et al. 2015).

At the food level, the morphology of food particles influences the surface area accessible to enzyme digestion. Many porous foods, including leavened breads, puffed snack foods, and breakfast cereals, have a high internal surface area, which is favorable for amylase attack, causing an acute blood glucose response (Colonna et al. 1990, Wolever et al. 1986). Conversely, starches in foods with dense, low-porosity structures, such as pasta, are less accessible to amylases and therefore have a relatively low RDS content because of the presence of a physical barrier that retards starch digestion (Holm et al. 1992). Indeed, there is a continuous dense gluten network that entraps the starch granules in pastas (Granfeldt & Björck 1991). A starch granule ghost structure with enzyme-resistant properties originates from physical entanglements of larger-sized and more highly branched amylopectin molecules (Zhang et al. 2014). Moreover, in vitro and in vivo studies have shown that particle size is inversely related to starch digestibility (Guo et al. 2018). The reduction of particle size increases the surface area that is exposed to enzymes, which increases its digestion rate and elicits a higher glycemic response (Edwards et al. 2015a). For larger-sized particles of whole and cracked maize kernels, slower digestion rates and lower glycemic and insulinemic responses were observed compared with fine maize flour (Heaton et al. 1988).

3.3. Food Processing

A wide range of industrial-scale processing operations impact food microstructure and therefore starch bioavailability. As described in **Figure 1**, mechanical disruption of physical or botanical structures of foods is one of the most effective ways of increasing the rate of starch digestion and postprandial glycemic response (Björck et al. 1994). Thus, coarse particles of whole grain, compared to finely milled flour, are more slowly digested (Liljeberg et al. 1992). This indicates that grain milling increases starch susceptibility to digestibility because of both disruption of the surrounding plant tissue and damage to starch granules (Li et al. 2014). Regarding the milling for decreasing particle size, the RS fraction decreases, whereas the RDS fraction increases, with little change in the SDS fraction (Hallfrisch & Behall 2000). Moreover, internal changes of starch granules do not occur as a result of the mild shear forces generated in processes such as crushing, pounding, and cutting, resulting in the relatively slow rate of digestion and the related reduction of the glycemic impact of food products (Venn & Mann 2004).

When starch is cooked under hydrating conditions, the crystalline structure of the starch granules is disrupted by heat and moisture, which brings about a dramatic increase in starch digestibility due to gelatinization (Zhang et al. 2006a). As previously stated, starch digestibility depends on the water content, gelatinization temperature, and molecular structure, including the ratio of amylose to amylopectin and the fine structure of amylopectin, which therefore impact the nutritional properties of gelatinized starch (Zhang et al. 2008a). To retain a slow digestion profile, incomplete gelatinization can be achieved by decreasing the moisture level, lowering the cooking temperature, and shortening the cooking time (Miao et al. 2010). A controlled gelatinized starch with higher SDS occurred prior to the visible morphological changes and granular structure breakdown (before 60°C), which reveals a physical structure of SDS consisting of amorphous regions and a small portion of less perfect crystallites. For the partially gelatinized starch, the amount of RDS fraction was negatively correlated with the relative melting enthalpy of the starch samples (Chung et al. 2006). Moreover, two hydrothermal treatments of starch, heat-moisture treatment (at low moisture levels, $<35\%$ w/w) and annealing (at $\geq 40\%$ w/w water content and below gelatinization temperature), refer to molecular rearrangement for decreased digestibility as well as the retention of starch granular structure and birefringence (Jacobs & Delcour 1998). Heat-moisture treatment converts the crystalline packing of starch from B type into A or C type, whereas annealing alters the binding forces between crystallites and the amorphous region, which can be used to increase the formation of SDS and the moderate glycemic response (Anderson et al. 2002, Jacobs & Delcour 1998). When modified high-amylose starch, as the best representative of RS, was heated above 120°C for 4–5 min, the SDS fraction increased at the expense of the RS portion, which was produced as a sterilized liquid product with low-GI property (Severijnen et al. 2007).

During the storage of cooked starch, the amylose chain and linear section of amylopectin are apt to form double helices and crystalline structures as the result of retrogradation, which limits access by amylase and decreases susceptibility to starch hydrolysis (Miao et al. 2015a). The high proportion of RS fraction in starch is mostly related to the retrogradation of amylose, whereas the controlled retrogradation of partially debranched amylopectin is used to make rich SDS-state food (Miao et al. 2009, Shin et al. 2004). The maximum SDS is obtained using higher enzyme concentration, a shorter debranching time, and short-term storage at low temperature (Guraya et al. 2001), which favor the nucleation step of crystallization for SDS formation with imperfect crystals, whereas higher temperature and long-term retrogradation favor the propagation and maturation of crystals and become a way to generate RS (Miao et al. 2009, Robin et al. 2008). This time dependency of SDS indicates SDS is closer to RS in basic structure, and measures to stabilize the progress of retrogradation might be used industrially to produce starches with improved nutritional attributes.

Processing techniques offer the possibility of improving starch nutritional functionality in processed food and foodstuffs with various combinations of moisture, temperature, and time (Chanvrier et al. 2007). Among these processing strategies, extrusion, autoclaving, baking, pressure-cooking, flaking, and parboiling are known to influence starch availability and related physiological effects through controlling gelatinization and food matrix interactions between starch and other components (Bhattarai et al. 2018, Kingman & Englyst 1994). For instance, starch in flaked whole-grain wheat was less available and elicited lower blood glucose compared with starch in boiled, popped, and steam-cooked wheat (Holm et al. 1985). High-amylose maize starch after extrusion cooking was shown to generate noncrystalline dense packing of starch chains and provide high levels of the resistant fraction using a mechanism of enzyme resistance of granular high-amylose starches that was qualitatively different from that for processed high-amylose starches (Lopez-Rubio et al. 2008, Htoon et al. 2009, B. Zhang et al. 2015).

Table 2 Measurement methods for starch bioavailability

Model		Equation	Commentary	Reference(s)
In vitro	Starch fractions	RDS = (G20 − FG) × 0.9 SDS = (G120 − G20) × 0.9 RS = TS − RDS − SDS	The equations use two time points during hydrolysis without the digestion mechanism	Englyst et al. 1992
	First-order kinetics	$C = C_\infty (1 - e^{-kt})$	The k is a function of the fixed amylase and substrate concentrations during starch digestion and is pseudo–first order	Goñi et al. 1997
	Michaelis-Menten kinetics	$V = V_{max}S/(K_m + S)$ $V_{max} = k_{cat}\, E_0$	A linear relationship is found with a Freundlich plot, suggesting enzyme adsorption limits the rate of starch digestion	Slaughter et al. 2001
In vivo	Glycemic response	GI = ($IAUC_{test\ food}$/ $IAUC_{standard\ food}$) × 100 GL = (GI × amount of carbohydrate)/100 GGE = W_{food} × (%CHO/100) × ($GI_{food}/GI_{glucose}$) EGI = GCAS − GCAC GP = D/H	GI is only used to define the quality of carbohydrate foods, leaving the starch digestion and absorption for maintenance of plasma glucose unconsidered	Jenkins et al. 1981, Monro & Mishra 2010, Rosén et al. 2009, Salmerón et al. 1997, Zhang & Hamaker 2009

Abbreviations: %CHO, percent available carbohydrate content; C, quantity of digested starch at time t; C_∞, quantity of digested starch at infinite time; D, duration time of net glucose increment; E_0, the total enzyme concentration; EGI, extended glycemix index; FG, free glucose; GCAC, glycemic curve areas for control; GCAS, glycemic curve areas for sample; G20, amount of glucose after digestion for 20 min; G120, amount of glucose after digestion for 120 min; GGE, glycemic glucose equivalent; GI, glycemic index; k, rate constant; GL, glycemic load; GP, glycemic profile; H, blood glucose incremental peak; IAUC, incremental area under the blood glucose response curve; k_{cat}, catalytic constant; K_m, Michaelis-Menten constant; RDS, rapidly digestible starch; RS, resistant starch; S, substrate concentration; SDS, slowly digestible starch; t, digestion time; TS, total starch; V, rate of enzyme reaction; V_{max}, maximum reaction velocity; W_{food}, food weight.

4. STARCH BIOAVAILABILITY MEASUREMENT

4.1. In Vitro Methods

The Englyst method is most widely used to quantify starch fractions with different digestion profiles using a simulated human digestive system (Englyst et al. 1992). In this procedure, RDS, SDS, and RS fractions are calculated from the released glucose at different time points, using the controlled hydrolysis with pancreatic amylase, amyloglucosidase, and invertase at 37°C and pH 5.2 as well as a GOPOD assay kit (**Table 2**). When food products contain simple sugars (free glucose and the glucose moiety of sucrose), the glycemic starch fractions are divided into rapidly available glucose and slowly available glucose as the in vitro measures describing the rate of glucose release (Englyst et al. 1996, 2003). These in vitro classifications were used to measure the rate and extent of starch digestion and the amount of glucose likely to be absorbed in the human small intestine, which has been validated to influence blood glucose and insulin levels using in vivo data (Englyst et al. 2018). However, there are some drawbacks to the Englyst test, including the lengthy procedure, numerous enzymes involved, and poor reproducibility (Miao et al. 2015a). On the basis of this, Guraya and coworkers developed a simpler method to measure major starch fractions by monitoring the maltose from porcine α-amylase hydrolysis (1% w/v, pH 6.9) using a DNS colorimetric assay (Guraya et al. 2001).

When starchy foods are hydrolyzed with amylase or in combination with amyloglucosidase, the digestion rate decreases as the time is extended and plots of the digesta concentration against time are logarithmic (Butterworth et al. 2012). The decrease of the digestion rate at different time intervals is a natural feature of an exponential reaction and shows a simple decay curve with apparent first-order behavior, as described by Goñi et al. (1997). This starch substrate decay process fits a single exponential decay equation of $C = C_\infty (1 - e^{-kt})$ (**Table 2**), and the hydrolysis index is also calculated based on the area under the hydrolysis curves of given and reference samples, which is a good predictor of glycemic response. However, it is difficult to obtain an accurate equilibrium value for C_∞ without long-time digestion. To solve this problem, the Guggenheim method has been introduced to calculate the rate constant at which C_∞ is unavailable, and the equation is converted as follows: $\ln(dC/dt) = \ln(C_\infty\ k) - kt$ (Edwards et al. 2015b). Thus, a plot of $\ln(dC/dt)$ against t is linear with a slope of $-k$, which is also called a logarithm of the slope (LOS) plot and can identify and quantify nutritionally important starch fractions. In foods containing starch fractions that are digested at different rates, LOS plots reveal two or more distinct linear phases, including the initial stage (rapid phase) and over the entirety of the reaction (slower phase) (Al-Rabadi et al. 2009). This empirical model has been used for rapid and accurate predictions of amylolysis of both cooked and raw grain starch samples (Butterworth et al. 2012, Warren et al. 2013).

Michaelis-Menten kinetics is appropriate for describing a slow product-forming reaction following the rapid reversible formation of an enzyme-substrate complex when the amylase concentration is low relative to starch concentration. For the initial stages of starch digestion (typically up to 20 min), an approximately linear increase in product concentration with time is observed (Slaughter et al. 2001). As shown in **Table 2**, the kinetic parameters obtained from the Michaelis-Menten equation are used to compare the hydrolysis of different starch substrates (Sanromán et al. 1996). This kinetics equation also describes the velocity of the liberation of reducing sugars as a function of initial low substrate concentration because of the product inhibition and substrate exhaustion for reducing the velocity with prolonged time. The maximal velocity of reaction (V_{max}) decreases with decreasing molecular weight of starch, whereas the Michaelis-Menten constant (K_m) increases (Heitmann et al. 1997). Both molecular weight and branching density of starches have been reported to affect amylolysis because of steric hindrance or mass transfer limitation (Warren et al. 2013).

4.2. In Vivo Methods

The concept of GI was developed more than 30 years ago to classify different sources of carbohydrate-rich foods on the basis of their ability to increase the blood glucose level and was used to make a relative ranking of individual foods according to their effect on postprandial glucose responses of available dietary carbohydrates (Foster-Powell et al. 2002, Jenkins et al. 1981). GI is determined by feeding 10 or more healthy people a portion of the food containing 50 g of digestible carbohydrates and then measuring the effect on their blood glucose levels over the next 120 min (**Table 2**). Numerous studies have demonstrated that GI has been associated with a reduced risk of cardiovascular diseases and diabetes (Ludwig 2002, Miao et al. 2015a, Sun et al. 2020, Zeevi et al. 2015). As not only the availability and absorption rate but also the carbohydrate content are important for the postprandial fluctuations of plasma glucose, glycemic load (GL) has been proposed and proved useful in epidemiological studies (Salmerón et al. 1997). GL is calculated by multiplying the GI of a food by the amount of total dietary carbohydrates per serving, as an indicator of the ability of carbohydrates to raise plasma glucose levels. To overcome the limitations of GI, glycemic glucose equivalent (GGE) has recently been proposed and is defined as the weight of glucose with the same glycemic impact as a given weight of food (Monro & Mishra

2010). For the consumption of SDS-rich foods, the postprandial glycemic curve shows a slow and prolonged release of glucose, suggesting a balanced energy release unlike the glycemic response of low-GI food (Gourineni et al. 2017). The new concepts of extended GI (EGI) and glycemic profile (GP) have been developed as in vivo evaluation tools for the physiological nature of SDS and as complementary to GI (Rosén et al. 2009, Zhang & Hamaker 2009).

5. FOOD MATRIX INTERACTIONS FOR MODULATING BIOAVAILABILITY

5.1. Impact of Lipids

It has been recognized that interactions between starch and lipids lead to the production of novel structures. Saturated monoacyl lipids or free fatty acids can form helical inclusion complexes with amylose, whereas di- or triglycerides do not form complexes because of their steric hindrance. The complexation of amylose with free fatty acids and monoglycerides results in significant changes in the physicochemical and nutritional properties of starch, including the change in X-ray diffraction pattern, reduced solubility, increased gelatinization temperature, retarded retrogradation, and lowered digestibility (Miao et al. 2015a, Tufvesson & Eliasson 2000). For the amylose inclusion complex formation, amylose exists as left-handed helices with a hydrophilic outer surface and a hydrophobic helical channel that interacts with a range of small guest hydrophobic molecules (Ai et al. 2013, Gelders et al. 2004). This complex is defined as V-type crystalline and has two crystalline polymorph forms, including the amorphous form VI from a random arrangement of the individual complex with a low melting temperature and the lamellar crystalline form VII from the ordered organization of the individual complex with the high melting temperature (Genkina et al. 2015). After heating at a temperature above the dissociation temperature, the amorphous form VI can further rearrange into the crystallite form VII, accompanied by greater resistance to digestive enzymes (Ai et al. 2013). Also, a higher preparation temperature and higher chain length of starch with a narrower distribution facilitated the formation of the VII complex (Luo et al. 2020). Molecular dynamics simulation showed that the amylose fragment complexes with linoleic acid to form a V-type structure in which linoleic acid is located in the cavity of the amylose helix with the hydrophobic tail inside it (Cheng et al. 2019). More glucose residues participated when the number of linoleic acid molecules increased, and the glucose rings changed from the $^{4}C1$ to $^{1}C4$ conformation with intramolecular hydrogen bonds during the complex formation.

A starch–lipid complex was developed as the new type of resistant starch, RS5, via processing high-amylose starch with free fatty acids (Hasjim et al. 2010). Using an in vivo animal model, an amylose–lipid complex–containing diet slightly lowered serum glucose and insulin more than a maltodextrin-containing control diet (Murray et al. 1998). Apart from the starch–lipid complex that could alter the glycemic response, several studies have shown that co-intake of fat reduces postprandial glucose by decreasing the gastric-emptying rate via increased stimulation of GIP and GLP-1 (Morgan 1998). Owen & Wolever (2003) showed that fat intake along with carbohydrates in normal healthy subjects could decrease the glycemic response in a dose-dependent relationship; however, fat consumption in the normal range (17–44% energy) did not significantly affect glycemic response. Thus, the type and amount of both fat and carbohydrates consumed in a meal, as well as the health status of the subjects, would need to be taken into account when evaluating postprandial glucose responses of the starch–lipid complex.

5.2. Impact of Proteins

In cereal or legume products, the protein matrix surrounding the starch granules appears to form a physical interaction inside the endosperm or cotyledon, which limits the accessibility

of amylolytic enzymes to starch and reduces the rate of α-amylolysis (Bhattarai et al. 2018, Dhital et al. 2016, Zhou et al. 2018). Several studies have demonstrated that pasta and spaghetti represent an example of the impact of protein in slowing starch digestion rate with low-glycemic responses (Colonna et al. 1990, Granfeldt & Björck 1991, Wolever et al. 1986). The gluten forms a viscoelastic and dense network entrapping starch granules as well as the compact structure, which restricts the swelling and leaching of starch granules during cooking, resulting in decreased enzyme accessibility and slow-release features (Fardet et al. 1998, Zou et al. 2016). Similarly, the cooked sorghum porridge has expanded protein networks around the gelatinized starch granules that hold the granules in dense packing to impede starch digestibility (Hamaker & Bugusu 2003). The 3-deoxyanthocyanidins present in sorghum are mainly responsible for creation of these web-like networks by mediating a sulfhydryl-disulfide exchange to build protein polymers for the slow digestion property (Schmidt 2019). Furthermore, the interaction between starch and protein in wheat bread reduced the availability of starch compared to gluten-free bread with higher glucose response (Jenkins et al. 1987). In addition to a protein barrier to restrict amylolysis, adsorption of α-amylase on proteins as a binding interaction can lead to reduced enzyme activity or availability for starch digestion in flour (Yu et al. 2018).

Biomimicking of starch–protein interactions has inspired researchers and industry to develop healthy foods with low-glycemic properties. Microencapsulation of corn starch by zein protein via low-temperature spray-drying was used to mimic the natural starch–protein matrices in corn grains (Xu & Zhang 2014). The zein matrix formed a hydrophobic physical barrier that could be effective in resisting water adsorption and restricting granular swelling, leading to a dense packing of encapsulated starches with high SDS and acceptable sensory properties, which could make it an ingredient for specialty food preparation and glycemic control. Zhang and coworkers discovered the self-assembly of a novel ternary nanoscale complex through heating and cooling of a mixture of starch, protein, and fatty acid, which was used as a nanocarrier for the controlled release of lipophilic ingredients to maintain their stability, bioactivity, water solubility, and slow digestion (Zhang et al. 2010). Molecular features of both amylose and fatty acid had a significant impact on the properties of the nanocomplex, whereas the negatively charged fatty acid was the bridge between amylose and protein in the ternary complexation. To gain insight into the process of macromolecule assembly, molecular dynamics simulation showed that the fatty acid was included in the amylose helix and the protein was associated with the carboxyl head of the fatty acid (Bhopatkar et al. 2015). Moreover, starch conjugated with protein or amino acids through the Maillard reaction has been shown to reduce the swelling and solubility of starch, thus lowering the rate of digestion (Yang et al. 1998); however, the potential side effects caused by consumption of glycated products need to be considered.

5.3. Impact of Nonstarch Polysaccharides

Besides interactions with lipids or proteins, as mentioned above, viscous-forming nonstarch polysaccharides such as guar gum and β-glucan decrease diffusion kinetics of enzymes and carbohydrate digestion rates, potentially leading to delayed gastric emptying and reduced glucose liberation and absorption in the small intestine (Dartois et al. 2010, Regand et al. 2011). The native-form β-glucans in oat grains also encapsulate protein and starch to decrease the enzyme accessibility, leading to reduced starch digestion and significantly decreased postprandial glycemia (Zhang et al. 2017). Moreover, cellulose as insoluble fiber can significantly inhibit α-amylase activity for in vitro starch digestion through a mixed-type inhibition mechanism (Dhital et al. 2015). The inhibition of α-amylase activity was positively correlated with cellulose concentration and α-amylase nonspecifically bound on the cellulose surface to attenuate starch hydrolysis. A similar

phenomenon was observed for interactions between pectin and digestive enzymes (Bai et al. 2017). Association between amyloglucosidase and pectin was likely because of a conformational change of enzyme that hindered access to the substrate and was consistent with a slower rate of digestion of longer amylopectin chains.

As stated above, encapsulation of starch granules in a fiber network as biomimicking of a plant cell or tissue decreases the enzyme accessibility and modulates the digestibility. An alginate-based encapsulation of corn starch generated a slowly digestible microsphere with digestion proceeding from the proximal to distal regions of the gastrointestinal tract (Venkatachalam et al. 2009). The amount of SDS can be modulated according to the biopolymer type and concentration, starch type, and microsphere size. These starch-entrapped microspheres have both a moderated glycemic response and the potential to implement physiological changes through ileal or colonic triggers that influence appetitive response and the sustained energy effect (Cisse et al. 2017, Hasek et al. 2018). Furthermore, starch-entrapped microspheres have been shown to have promising properties, such as slow and extended rate of fermentation, unusually high levels of butyrate production, and positive influence on the gut microbiota of inflammatory bowel disease patients (Kaur et al. 2019, Rasmussen et al. 2017, Rose et al. 2010). Recently, Luo & Zhang (2018) attempted to construct starch in a whole-grain-like structure form through calcium-induced alginate gelation in the presence of starch and β-glucan to biomimic the microstructure of endosperm tissue. Aside from exhibiting a considerable content of SDS and RS with reduced postprandial glycemia, the animal studies also showed that encapsulated starch in a cell wall–like physical structure significantly reduced the body weight gain and white adipose content as well as improved hepatic insulin sensitivity of obese mice (Luo et al. 2019).

5.4. Impact of Phytochemicals

Phytochemicals such as phenolic acids, polyphenols, flavonoids, and anthocyanidin are bioactive compounds present in plant-based foods and have numerous health benefits for stimulating the immune system and treating various metabolic diseases. Apart from antioxidant and anti-inflammatory activities, phenolic compound binding with starch has been shown to alter starch digestion and postprandial glucose response by interfering with either digestive enzymes or glucose transporter at the intestinal brush border (Bordenave et al. 2014, Simsek et al. 2017, Sun et al. 2018b). These phenolic compounds are believed to inhibit gastrointestinal enzymes by interacting with them through hydrophobic and hydrogen bonds (Miao et al. 2013, Sun et al. 2018b). The impact of noncovalent interactions on the physicochemical and nutritional properties of starchy foods has been reported to be dependent on both the type and structure of starch and phenolic compound as well as the processing method (Miao et al. 2015b, Sun & Miao 2020). Simsek et al. (2015) reported that dietary phenolic compounds selectively inhibit the individual C- and N-terminal subunits of MGAM and SI for a modulated glycemic carbohydrate digestion. They found that both chlorogenic acid and (−)-epigallocatechin gallate were potent, noncompetitive inhibitors of C-MGAM and C-SI with the highest activity. Also, the amylose–polyphenol complexation influenced the self-assembling process of amylose chains through a hydrogen bonding interaction, resulting in a low-ordered crystalline structure to modulate the digestion property and postprandial glycemic control (Chai et al. 2013). A similar slow digestion property was observed for the hydrophobic interaction–induced complexation between octenyl succinic anhydride starch and tea polyphenols, which led to a flattened and prolonged glycemic response and low-level oxidative stress for improved health (Peng et al. 2015).

Dietary phenolics have the ability to lower pasting properties and digestibility with RS formation and phenolic encapsulation (Li et al. 2018, Sun & Miao 2020). The formation of a V-type

amylose complex occurred in an amylopectin complex, in which phenolics might complex with starch through noncovalent CH-π bonds along α-1,4 glycosidic chains (Li et al. 2020). Relative glucose transport through a differentiated Caco-2 monolayer was reduced for an amylopectin–phenolic complex compared to native amylopectin but was higher for a potato starch–phenolic complex. Interestingly, the level of cellular phenolic uptake was lower for an amylopectin–phenolic complex and higher for a potato starch–phenolic complex. These observations suggest that physical phenolic–starch interactions might be a factor modulating functionality and nutritional values of both starch and phenolics (Li et al. 2019). In the cooked porridge model, phenolics were more degraded in the presence of starch and proteins than in the presence of starch only, which was linked to the ability of the phenolic compounds to form V-type inclusion complexes with starch and higher retention of phenolic compounds via the maximization of the starch:protein ratio in functional cereal-based foods (Ferruzzi et al. 2020). Moreover, soluble fiber polysaccharides reduced the inhibitory activity of tea polyphenols against pancreatic α-amylase because of the competitive interaction equilibrium among polysaccharides, polyphenols, and amylase (Sun et al. 2018a).

5.5. Impact of Organic Acids

The presence of organic acids or their corresponding salts, either formed during sourdough fermentation or added during food processing, was shown to reduce the postprandial responses of glucose and insulin (Liljeberg & Björck 1998, Liljeberg et al. 1995). Consumption of sourdough bread or breads with calcium lactate or sodium propionate lowered the postprandial blood glucose and insulin responses and prolonged the duration of satiety compared with wholemeal breads in the absence of these acids (Liljeberg et al. 1995). In vitro digestibility was significantly reduced in the presence of sodium propionate, suggesting its action as an enzyme inhibitor (Todesco et al. 1991). The incorporation of an SCFA (sodium propionate) into bread increased fecal bulk and anaerobic bifidobacteria and reduced blood glucose response in healthy subjects. Also, the lowered glycemic response to ingestion of bread with added sodium propionate was related to a lowered gastric-emptying rate (Darwiche et al. 2001). Addition of vinegar to a meal based on white wheat bread reduced the postprandial response of blood glucose and insulin and increased the subjective rating of satiety (Östman et al. 2005), whereas supplementation of high-GI meals with vinegar lowered postprandial hyperglycemia in patients with type II diabetes and adding vinegar had no effect on the low-GI meals (Liatis et al. 2010). A similar effect was observed with the addition of lactic acid or acetic acid to starch-based meals (Gustafsson et al. 1994, Mettler et al. 2009). Thus, food fermentation or food processing that incorporates organic acids has beneficial effects on the nutritional features of carbohydrates and related glucose metabolism.

5.6. Impact of Enzyme Inhibitors

Inhibitors of α-amylases and α-glucosidases may inhibit enzyme activity or bind to starch substrates and thereby modulate carbohydrate digestion and its associated glycemic response for the treatment of type II diabetes (Miao et al. 2015a, Zhang & Hamaker 2009). A wide variety of food crops such as legumes, rye, wheat, and oats contain, in varying quantities, phytic acid, lectins, tannins, saponins, hemagglutinin, and several enzyme inhibitors, which have the potential to interfere with starch digestion. For example, α-amylase inhibitors from kidney bean have high inhibitor activity and form a complex with amylase resulting in low postprandial glucose in healthy and diabetic subjects (Barrett & Udani 2011). These natural starch blockers have also shown promise in glucose homeostasis and are marketed as dietary supplements. Zou

et al. (2019) reported that the wheat gluten network contains the thermostable proteinaceous α-amylase inhibitors that interact and complex with α-amylase to inhibit starch digestion and linked slow pasta digestion to both the physical barrier of the gluten network and inhibition by endogenous enzyme inhibitors in the pasta. Moreover, commercial α-glucosidase inhibitors such as acarbose, voglibose, and miglitol retard carbohydrate digestion via competitive inhibition of the activity of brush border α-glucosidases and bind to these enzymes, preventing the breakdown of disaccharide and oligosaccharide substrates into absorbable monosaccharides (Dhameja & Gupta 2019). However, these fairly strong inhibitors have gastrointestinal side effects due to carbohydrate malabsorption. Although the use of enzyme inhibitors has shown promise, further studies are needed to evaluate the dose-response relationship, long-term tolerance, and side effects as well as the efficacy of these inhibitors incorporated into starchy foods.

6. PRODUCTION STRATEGIES FOR TAILOR-MADE HEALTH FOODS

6.1. Low Glycemic Index Foods

Low-GI (GI < 55) foods have been claimed to combat diabetes and cardiovascular disease through their ability to maintain glucose homeostasis without postprandial hyperglycemia (Ludwig 2002). Decreased postprandial glycemic response is certainly a property of low-GI foods, likely similar to SDS-induced glycemic response. Thus, SDS might be the material basis for a low-GI food. Indeed, the GI of starchy food can be explained by the levels of RDS and SDS, and there is a positive correlation between GI and the amount of RDS or rapidly available carbohydrates and a negative correlation between GI and SDS or slowly available carbohydrates (Englyst & Englyst 2005). From this aspect, the health benefit of low-GI foods can also be obtained from consuming SDS-rich food products. The European Food Safety Authority also validated the relationship between consumption of SDS and reduction of postprandial glycemic response: Foods are considered to have a high enough SDS content for health benefits if they contain at least 55% of their carbohydrates as available starch, of which at least 40% is SDS (EFSA 2011). However, there are many other factors affecting the GI, such as high fructose levels. Thus, SDS-based low-GI food might be preferred.

Although SDS generally produces a reduced postprandial glycemic response, the lower glycemia is not necessarily a property of SDS, as both RDS and SDS can still have a similar postprandial glycemia because of a slow glucose clearance rate when SDS is consumed (Eelderink et al. 2012). Other differences such as lower postprandial insulin and glucose-dependent insulinotropic polypeptide concentrations might also need to be considered, and certainly reduced insulin levels do not lead to plasma glucose fluctuation and the following cycles of hypoglycemia, hunger, and food intake.

6.2. Whole-Grain Foods

Whole-grain foods contain all the essential parts and naturally occurring nutrients of the entire grain seed in their original proportions, and endosperm starch is usually the major carbohydrate in whole-grain foods. Food structure is key to the starch digestion property of whole-grain foods, and any disruption of the physical or botanical structure of a cereal grain can considerably increase the rate of starch digestion and postprandial glycemic response (Björck et al. 1994). Thus, coarse particles of whole grain that include the cereal bran are more slowly digested compared to finely milled flour (Liljeberg et al. 1992), and the physical properties of cereal grains such as particle size play an important role in starch digestion (Heaton et al. 1988). Thus, the food processing–generated

physical structure of whole-grain foods can significantly influence starch digestion properties and related physiological effects.

The botanical structure of grain kernels provides a nature-produced physical barrier to protect the nutritive contents from environmental influences. As for starch, it is mainly located in the endosperm cellular compartment, which is embedded in a matrix formed by proteins and cell wall materials. Depending on the type of endosperm, dense packing of starch granules in the protein matrix of the vitreous endosperm significantly decreases the rate of starch digestion (Bhattarai et al. 2018, Dhital et al. 2016). The influence of the protein matrix, even after cooking, still reduces starch digestibility, as shown by the relatively high 20% SDS content in flour compared to 0–2% SDS in isolated starch (Zhang et al. 2008a). The endosperm cell wall also affects starch digestion, and different degrees of starch digestion were achieved to create different degrees of β-glucan solubilization from the cell wall material of oats by using cooking methods (Yiu et al. 1987). Whole-grain kernels also have fiber-rich multiple-layered bran that may decrease the accessibility of hydrolytic enzymes to some starch granules. The botanical structure of whole-grain kernels seems a natural way to produce a physical type of SDS.

The fact that a whole-grain botanical structure provides a physical barrier to starch hydrolytic enzymes indicates whole-grain food processing is an important factor in starch digestion, and retaining or minimizing the loss of physical barrier function is essential to the slow digestion property of starch (Vinoy et al. 2013). Food processing with high-temperature and high-shear conditions may completely disrupt grain structure and disperse gelatinized starch, leading to a higher RDS content. Such is the case in the processing of many snack foods and puffed cereal products. However, moderate processing, such as with rolled oats (Mishra & Monro 2009), with minimal disruption of the physical structure of the grain could lead to a reduced rate of starch digestion. Similarly, food processing to produce a dense packing of food components may generate a microenvironment restricting starch digestion, such as in pasta that may contain a high amount of SDS. Further development of novel food processing technologies to enhance carbohydrate quality will be important to realize whole-grain processed products with slow energy release (Vinoy et al. 2016).

7. FUTURE PERSPECTIVES AND CONCLUSION

Starch is not only quantitatively the most significant source of glycemic carbohydrates but also a vital source of nonglycemic carbohydrates in food, providing RS as food for colonic microbiota. The different bioavailability characteristics of various foods, which determine the location and digestion rate of starch in the small intestine, have important implications with regard to combating metabolic diseases. Food factors for modulating starch bioavailability are multiple and necessarily related to an interplay between intrinsic food characteristics and extrinsic processing factors. Important aspects, including starch molecular and physical structures, food matrix effects, and processing approaches, have been considered by investigators to manipulate the nutritional property of starchy foods to retain or maximize SDS and RS amounts for their potential health benefits. Attempts to develop production strategies as a means of modulating the nutritional attributes of foods related to starch bioavailability have been in progress for decades. However, the idea of bioavailability related to its nutritional property is still largely at a conceptual stage without many real applications in foods. Even so, there are some new products and prototypes of SDS- and RS-rich foods being developed by food companies. In comparison, increasing the consumption of whole-grain foods is now recommended by most governments in their dietary recommendations. Low-GI foods are recognized on the food label in Australia. Current knowledge of starch molecular and granular structures and matrices (i.e., interactions with nonstarch

constituents) now provides a path forward for plant breeders and the food industry to optimize the nutritional properties of starch in foods for health. Further studies are required to elucidate the relationship between the starch component and novel functional foods and to design healthy foods using modern food technologies that have moderated postprandial glycemic responses for health benefits and, potentially, appetite control. Finally, it is important to note that modifying the nutritional properties of starch may also alter its desirable physicochemical and sensory properties, thereby altering food quality, which should always be taken into account when formulating novel foods.

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LITERATURE CITED

Ai Y, Hasjim J, Jane J-L. 2013. Effects of lipids on enzymatic hydrolysis and physical properties of starch. *Carbohydr. Polym.* 92:120–27

Al-Rabadi GJS, Gilbert RG, Gidley MJ. 2009. Effect of particle size on kinetics of starch digestion in milled barley and sorghum grains by porcine α-amylase. *J. Cereal Sci.* 50:198–204

Anderson AK, Guraya HS, James C, Salvaggio L. 2002. Digestibility and pasting properties of rice starch heat-moisture treated at the melting temperature (T_m). *Starch* 54:401–9

Ao Z, Jane J-L. 2007. Characterization and modeling of the A- and B-granule starches of wheat, triticale, and barley. *Carbohydr. Polym.* 67:46–55

Ao Z, Quezada-Calvillob R, Simc L, Nichols BL, Rose DR, et al. 2007. Evidence of native starch degradation with human small intestinal maltase-glucoamylase (recombinant). *FEBS Lett.* 581:2381–88

Augustin LS, Kendall CW, Jenkins DJ, Willett WC, Astrup A, et al. 2015. Glycemic index, glycemic load and glycemic response: an International Scientific Consensus Summit from the International Carbohydrate Quality Consortium (ICQC). *Nutr. Metab. Cardiovasc.* 25:795–815

Bai Y, Wu P, Wang K, Li E, Gilbert RG. 2017. Effects of pectin on molecular structural changes in starch during digestion. *Food Hydrocoll.* 69:10–18

Barrett ML, Udani JK. 2011. A proprietary α-amylase inhibitor from white bean (Phaseolus vulgaris): a review of clinical studies on weight loss and glycemic control. *Nutr. J.* 10:24

BeMiller JN, Whistler RL. 2009. *Starch: Chemistry and Technology*. New York: Academic. 3rd ed.

Bhattarai RR, Dhital S, Mense A, Gidley MJ, Shi Y-C. 2018. Intact cellular structure in cereal endosperm limits starch digestion in vitro. *Food Hydrocoll.* 81:139–48

Bhattarai RR, Dhital S, Wu P, Chen XD, Gidley MJ. 2017. Digestion of isolated legume cells in a stomach-duodenum model: three mechanisms limit starch and protein hydrolysis. *Food Funct.* 8:2573–82

Bhopatkar D, Feng T, Chen F, Zhang G, Carignano M, et al. 2015. A self-assembled nanoparticle of common food constituents that carries a sparingly soluble small molecule. *J. Agric. Food Chem.* 63:4312–19

Björck I, Granfeldt Y, Liljeberg H, Tovar J, Asp NG. 1994. Food properties affecting the digestion and absorption of carbohydrates. *Am. J. Clin. Nutr.* 59:699S–705

Bordenave N, Hamaker BR, Ferruzzi MG. 2014. Nature and consequences of non-covalent interactions between flavonoids and macronutrients in foods. *Food Funct.* 5:18–34

Brayer GD, Sidhu G, Maurus R, Rydberg EH, Braun C, et al. 2000. Subsite mapping of the human pancreatic α-amylase active site through structural, kinetic, and mutagenesis techniques. *Biochemistry* 39:4778–91

Butterworth PJ, Warren FJ, Grassby T, Patel H, Ellis PR. 2012. Analysis of starch amylolysis using plots for first-order kinetics. *Carbohydr. Polym.* 87:2189–97

Cantu-Jungles TM, Hamaker BR. 2020. A new view on dietary fiber selection for predictable shifts in the gut microbiota. *mBio* 11:e02179-19

Chai Y, Wang M, Zhang G. 2013. Interaction between amylose and tea polyphenols modulates the postprandial glycemic response to high amylose maize starch. *J. Agric. Food Chem.* 61:8608–15

Chanvrier H, Uthayakumaran S, Appelqvist IAM, Gidley MJ, Gilbert EP, Lopez-Rubio A. 2007. Influence of storage conditions on the structure, thermal behavior, and formation of enzyme-resistant starch in extruded starches. *J. Agric. Food Chem.* 55:9883–90

Chegeni M, Amiri M, Nichols BL, Naim HY, Hamaker BR. 2018. Dietary starch breakdown product sensing mobilizes and apically activates α-glucosidases in small intestinal enterocytes. *FASEB J.* 32(7):3903–11

Cheng L, Zhu X, Hamaker BR, Zhang H, Campanella OH. 2019. Complexation process of amylose under different concentrations of linoleic acid using molecular dynamics simulation. *Carbohydr. Polym.* 216:157–66

Chung H-J, Lim HS, Lim S-T. 2006. Effect of partial gelatinization and retrogradation on the enzymatic digestion of waxy rice starch. *J. Cereal Sci.* 43:353–59

Cisse F, Pletsch EA, Erickson DP, Chegeni M, Hayes AMR, Hamaker BR. 2017. Preload of slowly digestible carbohydrate microspheres decreases gastric emptying rate of subsequent meal in humans. *Nutr. Res.* 45:46–51

Colonna P, Barry J-L, Cloarec D, Bornet F, Gouilloud S, Galmiche J-P. 1990. Enzymic susceptibility of starch from pasta. *J. Cereal Sci.* 11:59–70

Dartois A, Singh J, Kaur L, Singh H. 2010. The influence of guar gum on the in vitro starch digestibility: rheological and microstructural characteristics. *Food Biophys.* 5:149–60

Darwiche G, Östman EM, Liljeberg HG, Kallinen N, Björgell O, et al. 2001. Measurements of the gastric emptying rate by use of ultrasonography: studies in humans using bread with added sodium propionate. *Am. J. Clin. Nutr.* 74:254–58

Dhameja M, Gupta P. 2019. Synthetic heterocyclic candidates as promising α-glucosidase inhibitors: an overview. *Eur. J. Med. Chem.* 176:343–77

Dhital S, Bhattarai RR, Gorham J, Gidley MJ. 2016. Intactness of cell wall structure controls the in vitro digestion of starch in legumes. *Food Funct.* 7:1367–79

Dhital S, Gidley MJ, Warren FJ. 2015. Inhibition of α-amylase activity by cellulose: kinetic analysis and nutritional implications. *Carbohydr. Polym.* 123:305–12

Dhital S, Shrestha AK, Gidley MJ. 2010. Relationship between granule size and in vitro digestibility of maize and potato starches. *Carbohydr. Polym.* 82:480–88

Diaz-Sotomayor M, Quezada-Calvillo R, Avery SE, Chacko SK, Yan L, et al. 2013. Sucrase-isomaltase dominates mucosal maltase activity and early rate of ad libitum starch digestion. *J. Pediatr. Gastr. Nutr.* 57:704–12

Dikeman CL, Fahey GC. 2006. Viscosity as related to dietary fiber: a review. *Crit. Rev. Food Sci. Nutr.* 46:649–63

Do DT, Singh J, Oey I, Singh H, Frostad JM. 2020. A novel apparatus for time-lapse optical microscopy of gelatinisation and digestion of starch inside plant cells. *Food Hydrocoll.* 104:105551

Edwards CH, Grundy MML, Grassby T, Vasilopoulou D, Frost GS, et al. 2015a. Manipulation of starch bioaccessibility in wheat endosperm to regulate starch digestion, postprandial glycemia, insulinemia, and gut hormone responses: a randomized controlled trial in healthy ileostomy participants. *Am. J. Clin. Nutr.* 102:791–800

Edwards CH, Warren FJ, Campbell GM, Gaisford S, Royall PG, et al. 2015b. A study of starch gelatinization behaviour in hydrothermally-processed plant food tissues and implications for in vitro digestibility. *Food Funct.* 6:3634–41

Eelderink C, Schepers M, Preston T, Vonk RJ, Oudhuis L, Priebe MG. 2012. Slowly and rapidly digestible starchy foods can elicit a similar glycemic response because of differential tissue glucose uptake in healthy men. *Am. J. Clin. Nutr.* 96:1017–24

EFSA (Eur. Food Saf. Auth.). 2011. *Scientific opinion on the substantiation of a health claim related to "slowly digestible starch in starch-containing foods" and "reduction of postprandial glycaemic responses" pursuant to Article* 13(5) of Regulation (EC) No 1924/2006. Rep., EFSA Panel Diet. Prod. Nutr. Allerg., Parma, It.

Englyst HN, Kingman SM, Cummings JH. 1992. Classification and measurement of nutritionally important starch fractions. *Eur. J. Clin. Nutr.* 46:33–50

Englyst HN, Veenstra J, Hudson GJ. 1996. Measurement of rapidly available glucose (RAG) in plant foods: a potential in vitro predictor of the glycaemic response. *Br. J. Nutr.* 75:327–37

Englyst K, Goux A, Meynier A, Quigley M, Englyst H, et al. 2018. Inter-laboratory validation of the starch digestibility method for determination of rapidly digestible and slowly digestible starch. *Food Chem.* 245:1183–89

Englyst KN, Englyst HN. 2005. Carbohydrate bioavailability. *Br. J. Nutr.* 94:1–11

Englyst KN, Vinoy S, Englyst HN, Lang V. 2003. Glycaemic index of cereal products explained by their content of rapidly and slowly available glucose. *Br. J. Nutr.* 89:329–40

Fardet A, Hoebler C, Baldwint PM, Bouchet B, Gallant DJ, Barry JL. 1998. Involvement of the protein network in the in vitro degradation of starch from spaghetti and lasagne: a microscopic and enzymatic study. *J. Cereal Sci.* 27:133–45

Ferruzzi MG, Hamaker BR, Bordenave N. 2020. Phenolic compounds are less degraded in presence of starch than in presence of proteins through processing in model porridges. *Food Chem.* 309:125769

Foster-Powell K, Holt SHA, Brand-Miller JC. 2002. International table of glycemic index and glycemic load values: 2002. *Am. J. Clin. Nutr.* 76:5–56

Gelders GG, Vanderstukken TC, Goesaert H, Delcour JA. 2004. Amylose-lipid complexation: a new fractionation method. *Carbohydr. Polym.* 56:447–58

Genkina NK, Kiseleva VI, Martirosyan VV. 2015. Different types of V amylose-lipid inclusion complexes in maize extrudates revealed by DSC analysis. *Starch* 7:752–55

Goñi I, Garcia-Alonso A, Saura-Calixto F. 1997. A starch hydrolysis procedure to estimate glycemic index. *Nutr. Res.* 17:427–37

Gourineni V, Stewart ML, Skorge R, Sekula BC. 2017. Slowly digestible carbohydrate for balanced energy: in vitro and in vivo evidence. *Nutrients* 9:1230

Granfeldt Y, Björck I. 1991. Glycemic response to starch in pasta: a study of mechanisms of limited enzyme availability. *J. Cereal Sci.* 14:47–61

Guo P, Yu J, Wang S, Wang S, Copeland L. 2018. Effects of particle size and water content during cooking on the physicochemical properties and in vitro starch digestibility of milled durum wheat grains. *Food Hydrocoll.* 77:445–53

Guraya HS, James C, Champagne ET. 2001. Effect of enzyme concentration and storage temperature on the formation of slowly digestible starch from cooked debranched rice starch. *Starch* 53:131–39

Gustafsson K, Asp N-G, Hagander B, Nyman M. 1994. Dose-response of boiled carrots and effects of carrots in lactic acid in mixed meals on glycemic response and satiety. *Eur. J. Clin. Nutr.* 48:386–96

Hallfrisch J, Behall KM. 2000. Mechanisms of the effects of grain on insulin and glucose response. *J. Am. Coll. Nutr.* 19:320S–25

Hamaker BR, Bugusu BA. 2003. *Sorghum proteins and food quality*. Paper presented at the 2003 Afripro Conference, Pretoria, S. Afr. **http://www.afripro.org.uk/papers/Paper08Hamaker.pdf**

Han J, BeMiller JN. 2007. Preparation and physical characteristics of slowly digesting modified food starches. *Carbohydr. Polym.* 67:366–74

Hasek LY, Phillips RJ, Zhang G, Kinzig KP, Kim CY, et al. 2018. Dietary slowly digestible starch triggers the gut-brain axis in obese rats with accompanied reduced food intake. *Mol. Nutr. Food Res.* 62:1700117

Hasjim J, Lee S-O, Hendrich S, Setiawan S, Ai Y, Jane J-L. 2010. Characterization of a novel resistant-starch and its effects on postprandial plasma-glucose and insulin responses. *Cereal Chem.* 87:257–62

Heaton KW, Marcus SN, Emmett PM, Bolton CH. 1988. Particle size of wheat, maize, and oat test meals: effects on plasma glucose and insulin responses and on the rate of starch digestion in vitro. *Am. J. Clin. Nutr.* 47:675–82

Heitmann T, Wenzig E, Mersmann A. 1997. Characterisation of three different potato starches and kinetics of their enzymatic hydrolysis by an α-amylase. *Enzyme Microb. Technol.* 20:259–67

Holm J, Björck I, Asp N-G, Sjöberg L-B, Lundquist I. 1985. Starch availability in vitro and in vivo after flaking, steam-cooking and popping of wheat. *J. Cereal Sci.* 3:193–206

Holm J, Koellreutter B, Würsch P. 1992. Influence of sterilization, drying and oat bran enrichment of pasta on glucose and insulin responses in healthy subjects and on the rate and extent of in vitro starch digestion. *Eur. J. Clin. Nutr.* 46:629–40

Htoon A, Shrestha AK, Flanagan BM, Lopez-Rubio A, Bird AR, et al. 2009. Effects of processing high amylose maize starches under controlled conditions on structural organization and amylase digestibility. *Carbohydr. Polym.* 75:236–45

Jacobs H, Delcour JA. 1998. Hydrothermal modifications of granular starch, with retention of the granular structure: a review. *J. Agric. Food Chem.* 46:2895–905

Jenkins DJ, Thorne MJ, Wolever TM, Jenkins AL, Rao AV, Thompson LU. 1987. The effect of starch-protein interaction in wheat on the glycemic response and rate of in vitro digestion. *Am. J. Clin. Nutr.* 45:946–51

Jenkins DJA, Wolever TMS, Taylor RH, Barker H, Fielden H, et al. 1981. Glycemic index of foods: a physiological basis for carbohydrate exchange. *Am. J. Clin. Nutr.* 34:362–66

Kaur A, Chen T, Green S, Mutlu E, Martin B, et al. 2019. Physical inaccessibility of a resistant starch to Bacteroidetes shifts mouse gut microbiota to butyrogenic Firmicutes. *Mol. Nutr. Food Res.* 63:1081012

Kingman SM, Englyst HN. 1994. The influence of food preparation methods on the in-vitro digestibility of starch in potato. *Food Chem.* 49:181–86

Lee BH, Rose DR, Lin AHM, Quezada-Calvillo R, Nichols BL, Hamaker BR. 2016. Contribution of the individual small intestinal α-glucosidases to digestion of unusual α-linked glycemic disaccharides. *J. Agric. Food Chem.* 64:6487–94

Li E, Dhital S, Hasjim J. 2014. Effects of grain milling on starch structures and flour/starch properties. *Starch* 66:15–27

Li M, George J, Hunter S, Hamaker BR, Mattes RD, Ferruzzi MG. 2019. Potato product form impacts in vitro starch digestibility and glucose transport but only modestly impacts 24 h blood glucose response in humans. *Food Funct.* 10:1846–55

Li M, Ndiaye C, Corbin S, Foegeding EA, Ferruzzi MG. 2020. Starch-phenolic complexes are built on physical CH-π interactions and can persist after hydrothermal treatments altering hydrodynamic radius and digestibility of model starch-based foods. *Food Chem.* 308:125577

Li M, Pernell C, Ferruzzi M G. 2018. Complexation with phenolic acids affect rheological properties and digestibility of potato starch and maize amylopectin. *Food Hydrocoll.* 77:843–52

Liatis S, Grammatikou S, Poulia KA, Perrea D, Makrilakis K. 2010. Vinegar reduces postprandial hyperglycaemia in patients with type II diabetes when added to a high, but not to a low, glycaemic index meal. *Eur. J. Clin. Nutr.* 64:727–32

Liljeberg H, Björck I. 1998. Delayed gastric emptying rate may explain improved glycaemia in healthy subjects to a starchy meal with added vinegar. *Eur. J. Clin. Nutr.* 52:368–71

Liljeberg H, Granfeldt Y, Björck I. 1992. Metabolic responses to starch in bread containing intact kernels versus milled flour. *Eur. J. Clin. Nutr.* 46:561–75

Liljeberg HG, Lonner CH, Björck IM. 1995. Sourdough fermentation or addition of organic acids or corresponding salts to bread improves nutritional properties of starch in healthy humans. *J. Nutr.* 125:1503–11

Lopez-Rubio A, Flanagan BM, Shrestha AK, Gidley MJ, Gilbert EP. 2008. Molecular rearrangement of starch during in vitro digestion: toward a better understanding of enzyme resistant starch formation in processed starches. *Biomacromolecules* 9:1951–58

Ludwig DS. 2002. The glycemic index: physiological mechanisms relating to obesity, diabetes, and cardiovascular disease. *JAMA* 287:2414–23

Luo K, Wang X, Zhang G. 2019. Starch and β-glucan in a whole-grain-like structural form improve hepatic insulin sensitivity in diet-induced obese mice. *Food Funct.* 10:5091–101

Luo K, Zhang G. 2018. Nutritional property of starch in a whole-grain-like structural form. *J. Cereal Sci.* 79:113–17

Luo S, Zeng Z, Mei Y, Huang K, Wu J, et al. 2020. Improving ordered arrangement of the short-chain amylose-lipid complex by narrowing molecular weight distribution of short-chain amylose. *Carbohydr. Polym.* 240:116359

Ma J, Stevens JE, Cukier K, Maddox AF, Wishart JM, et al. 2009. Effects of a protein preload on gastric emptying, glycemia, and gut hormones after a carbohydrate meal in diet-controlled type 2 diabetes. *Diabetes Care* 32:1600–2

Martinez MM, Li C, Okoniewska M, Mukherjee I, Vellucci D, Hamaker B. 2018. Slowly digestible starch in fully gelatinized material is structurally driven by molecular size and A and B1 chain lengths. *Carbohydr. Polym.* 197:531–39

Mettler S, Schwarz I, Colombani PC. 2009. Additive postprandial blood glucose-attenuating and satiety-enhancing effect of cinnamon and acetic acid. *Nutr. Res.* 29:723–27

Miao M, Jiang B, Cui SW, Zhang T, Jin Z. 2015a. Slowly digestible starch: a review. *Crit. Rev. Food Sci. Nutr.* 55:1642–57

Miao M, Jiang B, Jiang H, Zhang T, Li X. 2015b. Interaction mechanism between green tea extract and human α-amylase for reducing starch digestion. *Food Chem.* 186:20–25

Miao M, Jiang B, Jin Z, BeMiller JN. 2018. Microbial starch-converting enzymes: recent insights and perspectives. *Compr. Revi. Food Sci.* 17:1238–60

Miao M, Jiang B, Zhang T. 2009. Effect of pullulanase debranching and recrystallization on structure and digestibility of waxy maize starch. *Carbohydr. Polym.* 112:214–21

Miao M, Jiang H, Jiang B, Li Y, Cui SW, Jin Z. 2013. Elucidation of structural difference in theaflavins for modulation of starch digestion. *J. Funct. Foods* 5:2024–29

Miao M, Li R, Jiang B, Cui SW, Zhang T, Jin Z. 2014. Structure and physicochemical properties of octenyl succinic esters of sugary maize soluble starch and waxy maize starch. *Food Chem.* 151:154–60

Miao M, Zhang T, Mu W, Jiang B. 2010. Effect of controlled gelatinization in excess water on digestibility of waxy maize starch. *Food Chem.* 119:41–48

Miao M, Zhang T, Mu W, Jiang B. 2011. Structural characterizations of waxy maize starch residue following in vitro pancreatin and amyloglucosidase synergistic hydrolysis. *Food Hydrocoll.* 25:214–20

Mishra S, Monro JA. 2009. Digestibility of starch fractions in wholegrain rolled oats. *J. Cereal Sci.* 50:61–66

Monro JA, Mishra S. 2010. Glycemic impact as a property of foods is accurately measured by an available carbohydrate method that mimics the glycemic response. *J. Nutr.* 140:1328–34

Morgan LM. 1998. The role of gastrointestinal hormones in carbohydrate and lipid metabolism and homeostasis: effects of gastric inhibitory polypeptide and glucagon-like peptide-1. *Biochem. Soc. Trans.* 26:216–22

Murray SM, Patil AR, Fahey GC Jr., Merchen NR, Wolf BW, et al. 1998. Apparent digestibility of a debranched amylopectin-lipid complex and resistant starch incorporated into enteral formulas fed to ileal-cannulated dogs. *J. Nutr.* 128:2032–35

Nichols BL, Quezada-Calvillo R, Robayo-Torres CC, Ao Z, Hamaker BR, et al. 2009. Mucosal maltase-glucoamylase plays a crucial role in starch digestion and prandial glucose homeostasis of mice. *J. Nutr.* 139:684–90

Östman E, Granfeldt Y, Persson L, Björck I. 2005. Vinegar supplementation lowers glucose and insulin responses and increases satiety after a bread meal in healthy subjects. *Eur. J. Clin. Nutr.* 59:983–88

Owen B, Wolever TMS. 2003. Effect of fat on glycaemic responses in normal subjects: a dose-response study. *Nutr. Res.* 23:1341–47

Peng S, Xue L, Leng X, Yang R, Zhang G, Hamaker BR. 2015. Slow digestion property of octenyl succinic anhydride modified waxy maize starch in the presence of tea polyphenols. *J. Agric. Food Chem.* 63:2810–19

Pletsch EA, Hamaker BR. 2018. Brown rice compared to white rice slows gastric emptying in humans. *Eur. J. Clin. Nutr.* 72:367–73

Quezada-Calvillo R, Sim L, Ao Z, Hamaker BR, Quaroni A, et al. 2008. Localization of luminal starch substrate "brake" on maltase-glucoamylase activity within the glucoamylase subunit. *J. Nutr.* 138:685–92

Rasmussen HE, Hamaker B, Rajan KB, Mutlu E, Greene SJ, et al. 2017. Starch-entrapped microsphere fibers improve bowel habit and gastrointestinal symptoms in those with unsatisfactory bowel movements in a randomized, double-blind, controlled, dose-ranging human trial. *Nutr. Res.* 44:27–37

Regand A, Chowdhury Z, Tosh SM, Wolever TM, Wood P. 2011. The molecular weight, solubility and viscosity of oat β-glucan affect human glycemic response by modifying starch digestibility. *Food Chem.* 129:297–304

Robin F, Mérinat S, Simon A, Lehmann U. 2008. Influence of chain length on α-1,4-D-glucan recrystallization and slowly digestible starch formation. *Starch* 60:551–58

Rose DJ, Venema K, Keshavarzian A, Hamaker BR. 2010. Starch-entrapped microspheres show a beneficial fermentation profile and decrease in potentially harmful bacteria during in vitro fermentation in fecal microbiota obtained from patients with inflammatory bowel disease. *Br. J. Nutr.* 103:1514–24

Rosén LAH, Silva LOB, Andersson UK, Holm C, Östman EM, Björck IME. 2009. Endosperm and whole grain rye breads are characterized by low post-prandial insulin response and a beneficial blood glucose profile. *Nutr. J.* 8:42

Rovalino-Córdova AM, Fogliano V, Capuano E. 2018. A closer look to cell structural barriers affecting starch digestibility in beans. *Carbohydr. Polym.* 181:994–1002

Sajilata MG, Shinghal RS, Kulkarni PK. 2006. Resistant starch: a review. *Comp. Rev. Food Sci. F* 5:1–17

Salmerón J, Manson JE, Stampfer MJ, Colditz GA, Wing AL, Willett WC. 1997. Dietary fiber, glycemic load, and risk of non-insulin-dependent diabetes mellitus in women. *JAMA* 277:472–77

Sanromán A, Murado MA, Lema JM. 1996. The influence of substrate structure on the kinetics of the hydrolysis of starch by glucoamylase. *Appl. Biochem. Biotechnol.* 59:329–36

Schmidt LCR. 2019. *Investigating phenolic-mediated protein matrix development for potential control of cereal starch digestion*. PhD Thesis, Purdue Univ., West Lafayette, IN

Severijnen C, Abrahamse E, van der Beek EM, Buco A, van de Heijning BJM, et al. 2007. Sterilization in a liquid of a specific starch makes it slowly digestible in vitro and low glycemic in rats. *J. Nutr.* 137:2202–7

Shin SI, Choi HJ, Chung KM, Hamaker BR, Park KH, Moon TW. 2004. Slowly digestible starch from debranched waxy sorghum starch: preparation and properties. *Cereal Chem.* 81:404–8

Simsek M, Quezada-Calvillo R, Ferruzi MG, Nichols BL, Hamaker BR. 2015. Dietary phenolic compounds selectively inhibit the individual subunits of maltase-glucoamylase and sucrase-isomaltase with the potential of modulating glucose release. *J. Agric. Food Chem.* 63:3873–79

Simsek M, Quezada-Calvillo R, Nichols BL, Hamaker BR. 2017. Phenolic compounds increase the transcription of mouse intestinal maltase-glucoamylase and sucrase-isomaltase. *Food Funct.* 8:1915–24

Slaughter SL, Ellis PR, Butterworth PJ. 2001. An investigation of the action of porcine pancreatic α-amylase on native and gelatinized starches. *Biochim. Biophys. Acta* 1525:29–36

Sun L, Miao M. 2020. Dietary polyphenols modulate starch digestion and glycaemic level: a review. *Crit. Rev. Food Sci. Nutr.* 60:541–55

Sun L, Warren FJ, Gidley MJ. 2018a. Soluble polysaccharides reduce binding and inhibitory activity of tea polyphenols against porcine pancreatic α-amylase. *Food Hydrocoll.* 79:63–70

Sun L, Warren FJ, Gidley MJ, Guo Y, Miao M. 2018b. Mechanism of binding interactions between young apple polyphenols and porcine pancreatic α-amylase. *Food Chem.* 283:468–74

Szczodrak J, Pomeranz Y. 1991. Starch and enzyme-resistant starch from high-amylose barley. *Cereal Chem.* 68:589–96

Todesco T, Rao AV, Bosello O, Jenkins DJ. 1991. Propionate lowers blood glucose and alters lipid metabolism in healthy subjects. *Am. J. Clin. Nutr.* 54:860–65

Tufvesson F, Eliasson AC. 2000. Formation and crystallization of amylose-monoglyceride complex in a starch matrix. *Carbohydr. Polym.* 43:359–65

Venkatachalam M, Kushnick MR, Zhang G, Hamaker BR. 2009. Starch-entrapped biopolymer microspheres as a novel approach to vary blood glucose profiles. *J. Am. Coll. Nutr.* 28:583–90

Venn BJ, Mann JI. 2004. Cereal grains, legumes and diabetes. *Eur. J. Clin. Nutr.* 58:1443–61

Vinoy S, Laville M, Feskens EJ. 2016. Slow-release carbohydrates: growing evidence on metabolic responses and public health interest. Summary of the symposium held at the 12th European Nutrition Conference (FENS 2015). *Food Nutr. Res.* 60:31662

Vinoy S, Normand S, Meynier A, Sothier M, Louche-Pelissier C, et al. 2013. Cereal processing influences postprandial glucose metabolism as well as the GI effect. *J. Am. Coll. Nutr.* 32:79–91

Warren FJ, Butterworth PJ, Ellis PR. 2013. The surface structure of a complex substrate revealed by enzyme kinetics and Freundlich constants for α-amylase interaction with the surface of starch. *Biochim. Biophys. Acta* 1830:3095–101

Wolever TMS, Jenkins DJA, Kalmusky J, Giordano C, Giudici S, et al. 1986. Glycemic response to pasta: effect of surface area, degree of cooking, and protein enrichment. *Diab. Care* 9:401–4

Xu H, Zhang G. 2014. Slow digestion property of microencapsulated normal corn starch. *J. Cereal Sci.* 60:99–104

Yang W, Hattori M, Kawaguchi T, Takahashi K. 1998. Properties of starches conjugated with lysine and poly(lysine) by the Maillard reaction. *J. Agric. Food Chem.* 46:442–45

Ye F, Miao M, Huang C, Lu K, Jiang B, Zhang T. 2014. Elucidation of substituted ester group position in octenylsuccinic anhydride modified sugary maize soluble starch. *J. Agric. Food Chem.* 62:11696–705

Yiu SH, Wood PJ, Weisz J. 1987. Effects of cooking on starch and β-glucan of rolled oats. *Cereal Chem*. 64:373–79

Yu W, Zou W, Dhital S, Wu P, Gidley MJ, et al. 2018. The adsorption of α-amylase on barley proteins affects the in vitro digestion of starch in barley flour. *Food Chem*. 241:493–501

Zhang B, Dhital S, Flanagan FM, Gidley MJ. 2014. Mechanism for starch granule ghost formation deduced from structural and enzyme digestion properties. *J Agric. Food Chem.* 62:760–71

Zhang B, Dhital S, Flanagan BM, Luckman P, Halley PJ, Gidley MJ. 2015. Extrusion induced low-order starch matrices: enzymic hydrolysis and structure. *Carbohydr. Polym.* 134:485–96

Zhang G, Ao Z, Hamaker BR. 2006a. Slow digestion property of native cereal starches. *Biomacromolecules* 7:3252–58

Zhang G, Ao Z, Hamaker BR. 2008a. Nutritional property of endosperm starches from maize mutants: a parabolic relationship between slowly digestible starch and amylopectin fine structure. *J. Agric. Food Chem.* 56:4686–94

Zhang G, Hamaker BR. 2009. Slowly digestible starch: concept, mechanism, and proposed extended glycemic index. *Crit. Rev. Food Sci. Nutr.* 49:852–67

Zhang G, Hamaker BR. 2017. The nutritional property of endosperm starch and its contribution to the health benefits of whole grain foods. *Crit. Rev. Food Sci. Nutr.* 57:3807–17

Zhang G, Hasek LY, Lee BH, Hamaker BR. 2015. Gut feedback mechanisms and food intake: a physiological approach to slow carbohydrate bioavailability. *Food Funct*. 6:1072–89

Zhang G, Maladen M, Campanella OH, Hamaker BR. 2010. Free fatty acids electronically bridge the self-assembly of a three-component nanocomplex consisting of amylose, protein, and free fatty acids. *J. Agric. Food Chem.* 58:9164–70

Zhang G, Sofyan M, Hamaker BR. 2008b. Slowly digestible state of starch: mechanism of slow digestion property of gelatinized maize starch. *J. Agric. Food Chem.* 56:4695–702

Zhang G, Venkatachalam M, Hamaker BR. 2006b. Structural basis for the slow digestion property of native cereal starch. *Biomacromolecules* 7:3259–66

Zhang J, Luo K, Zhang G. 2017. Impact of native form oat β-glucan on starch digestion and postprandial glycemia. *J. Cereal Sci.* 73:84–90

Zhou X, Ying YN, Hu BL, Pang YH, Bao JS. 2018. Physicochemical properties and digestibility of endosperm starches in four indica rice mutants. *Carbohydr. Polym.* 195:1–8

Zhu LJ, Liu QQ, Wilson JD, Gu MH, Shi YC. 2011. Digestibility and physicochemical properties of rice (Oryza sativa L.) flours and starches differing in amylose content. *Carbohydr. Polym*. 86:1751–59

Zou W, Schulz BL, Tan X, Sissons M, Warren FJ, et al. 2019. The role of thermostable proteinaceous α-amylase inhibitors in slowing starch digestion in pasta. *Food Hydrocoll*. 90:241–47

Zou W, Sissons M, Warren FJ, Gidley MJ, Gilbert RG. 2016. Compact structure and proteins of pasta retard in vitro digestive evolution of branched starch molecular structure. *Carbohydr. Polym.* 152:441–49