

Crystallinity of starch, food composition, and digestibility of starch

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Citation: Šárka E., Smrčková P., Sluková M. (2025): Crystallinity of starch, food composition, and digestibility of starch. Czech J. Food Sci., 43: 90–104.

Abstract: Starch granules in their native state are insoluble and semi-crystalline. There are three forms of starch/amylopectin in nature: A, B, and C: in cereals (A), tubers and high amylose starches (B), and some varieties of peas and beans (C). Crystallinity and rate of starch hydrolysis depend on the plant species and growing conditions. The changes during food preparation include gelatinisation, the formation of amylose-lipids and amylose-protein complexes, and resistant starch (RS) origin. They are accompanied by changes from crystal to amorphous form and *vice versa*. Starch in human food is mostly rapidly or slowly digestible. Rapidly digestible starch is formed by gelatinisation, cooking extrusion, breaking down of starch granules, or hydrolysis to maltodextrins. By definition, RS is not digested in the small intestine. This review addresses the influences of biochemical processes in the human body on starch digestibility. It is strongly influenced by the degree of chewing, the activity of α -amylase in the intestine, and transit time through the stomach and small intestine. Resistant starch and endogenous intestinal mucus support the growth of specialist microbes in the large intestine that produce a variety of short-chain fatty acids, causing the perception of satiety, lowering pH, and inhibiting pathogens in the colon.

Keywords: human obesity; reduction of overweight; soluble fibre; plant polyphenols; gluten-free foods; type 2 diabetes mellitus

Obesity is a significant risk factor for many chronic diseases, in addition to diabetes also cardiovascular diseases, non-alcoholic fatty liver disease, dyslipidemia, hypertension, type 2 diabetes mellitus, and certain cancers, making it a significant public health concern (Tian et al. 2023). Overweight and obesity contribute to 3.4 million deaths annually worldwide. In the U.S., data from the National Health and Nutrition Examination Survey (2017–2018) indicates that 42.5% of adults are obese, 9.0% have severe obesity, and 31.1% are overweight (Anderson et al. 2024). In nearly every country in Europe, over half of adults were classed as overweight or obese in 2022. The highest rate was recorded in Romania, with 67% of adults self-reporting as overweight or obese. In Croatia and the United Kingdom, around 64% of adults have a body mass index of over 25 (Stuart 2024).

Starch granules in their native state are insoluble and semi-crystalline having characteristic size and shape according to biological origin. They are composed of two polysaccharides – mostly linear amylose and branched amylopectin. The relative proportion of amylose/amylopectin in starch can be influenced by choice of plant species or variety, growing conditions, the physical separation of one of the components, enzymatically, or the action of microorganisms (Wang et al. 2019a; Tian et al. 2023). Amylopectin has stabilising effects on starch gel and prevents retrogradation, whereas amylose forms a rigid gel. Amylose has a strong tendency to form complexes with lipids and other components in starch dispersions. The amylopectin molecule in the native starch contains crystalline laminates having a greater concentration of matter, in which the parallel chains form dou-

<https://doi.org/10.17221/33/2025-CJFS>

ble helices, and less dense layers (branching zone) have an amorphous character. The length and configuration of the chains in amylopectin influence many properties such as crystallinity, pasting and thermal properties, gelatinisation temperatures (Han et al. 2021), retrogradation and syneresis, resistant starch formation and digestibility (Mahajan et al. 2022; Narayanamoorthy et al. 2022; Vázquez-León et al. 2022). There are three crystal forms of starch/amylopectin in nature: A, B, and C. According to origin: cereals (A); tubers, and high amylose starch such as maize starch (B); and some varieties of peas and beans (C). Amylose can form inclusion complexes with small hydrophobic molecules; these complexes have a single helical structure stacked in a V-type crystalline structure. An example is complexes with fatty acids (Zhu et al. 2025).

In the food sector, starch is generally used as a thickener, water binder stabiliser, filler, and gelling agent (Sharma and Panesar 2018). Food processing changes starch granules and starch functional properties. Physicochemical changes during food preparation include gelatinisation, formation of complexes with fatty acid chains and starch-protein complexes, and origin of resistant starch. Therefore, they influence the digestibility. Slowing down starch digestibility requires e.g. changes in the production process so that gelatinisation of the starch granules does not occur or is limited, and the crystalline lamellae in amylopectin molecules are preserved.

All digestive compartments including the mouth, stomach, small intestine, and large intestine play key roles in regulating the overall starch digestion process. The main biological factors are oral mastication and salivation, gastric emptying and motility, small intestinal enzymes, and motility, resistant starch-large intestinal microbiota interactions, gut-brain feedback control, glucose adsorption, and hormonal feedback control (Li et al. 2023). The digestion of starch granules in the gut includes different phases: the diffusion of the enzyme towards the substrate with the impact of the porosity of the substrate, the adsorption of the enzyme to the starchy material, and the hydrolytic reaction (Colonna et al. 1992).

In recent years, some articles have appeared that focus on a detailed description of the mechanism of human digestion and the communication of the digestive organs with neurons and the brain. The topics are e.g. effects of chewing ability (Yang et al. 2023), effects on microbiome composition (Feng et al. 2023), the role of gut hormones in metabolic regulation (Bakar et al. 2023), biological factors controlling starch digestibility (Li et al. 2023), computer modelling of digestive

processes (van Aken 2024), and neuro-cognitive health via gut-microbiome-brain axis (Kadyan et al. 2024). Starch is successively hydrolysed by salivary and pancreatic α -amylase in the mouth and small intestine, respectively, to smaller oligomers eventually leading to mainly maltose and maltotriose as end-products as well as α -limit dextrins, which contain branch points resistant to α -amylase (Dhital et al. 2017). In terms of the arisen products to glucose, the key enzymes (α -amylase, maltase-glucoamylase, and sucrase-isomaltase) do appear to be inhibited by at least some polysaccharides within dietary fibre and some of the polysaccharides may hydrogen bond to α -glucans themselves (Qi et al. 2018). Then the glucose is absorbed by a sodium-dependent active process. A sodium pump, sodium/potassium adenosinetriphosphatase (ATPase), and sodium secreted in the alkaline pancreatic juice create a sodium gradient across the cell membrane. Then the sodium ions enter the cell together with glucose (Bender 2007). More explicitly glucose is transported into then through the intestinal cells to the bloodstream via the membrane-bound facilitative glucose transporter (GLUT2) and sodium-dependent glucose co-transporter (SGLT) (Wachters-Hagedoorn et al. 2004; Kellett and Brot-Laroche 2005; Sim et al. 2008). Adjacent to the brush border membrane lies the unstirred layer that acts as a diffusion barrier for high-permeability compounds and can affect the transport rate (Wachters-Hagedoorn et al. 2004).

This article is focused on the properties of starch that influence digestibility. Thus, the gastrointestinal tract is taken as 'a black box.'

Rapidly digestible starch, slowly digestible starch and resistant starch, glycemic index, glycemic load.

Englyst et al. (1983) divided starch into rapidly digestible starch (RDS), slowly digestible starch (SDS), and resistant starch (RS) as a consequence of susceptibility to α -amylase hydrolysis *in vitro*. This frequently used classification has been very simplistic, as this method assumes that starch hydrolysis takes place mainly in the intestinal tract, the reactions take the same delay time in the small intestine (for every meal and all individuals), and the dose of enzymes and their activities are also the same for any individual. Englyst set times for the events to divide into RDS, SDS and RS which do not match *in vivo*. On the other hand, the advantage of this method is that it allows researchers to easily categorise starch in food in terms of its digestibility.

RDS is rapidly (< 20 min) and completely digested in the small intestine. It is associated with elevated

plasma glucose and insulin; therefore, it is linked with diabetes, coronary heart disease, and aging. Insulin is a peptide hormone produced by beta cells of the pancreatic islets. It regulates the metabolism of carbohydrates by promoting glucose absorption from the blood into the liver, fat, skeletal, and muscle cells (Stryer 1995; Sylow et al. 2021).

SDS is completely but slowly digested in the small intestine. It is a desirable form of starch from a nutritional point of view (Soral-Smietana et al. 2001). The SDS fraction generally provides a slow and prolonged release of glucose into the bloodstream (Monsierra et al. 2024). Diets containing SDS improve the carbohydrate metabolism of diabetic patients (Golay et al. 1992; Goux et al. 2020). For example, it was shown that breakfast foods containing SDS reduced the insulin requirement of insulin-treated type 2 diabetic patients (Lehmann and Robin 2007). A very high SDS content was found in the thermally (80–100 °C) processed starch of gorgon nut (Zeng et al. 2022).

RS is not digested in the small intestine. The minimum energy content in RS has many positive effects on the human body. RS contains five groups now: the first group is physically encapsulated starch within the plant cells or food/polymer matrix (RS1), the second one is some native starch (RS2), the third one is recrystallised starch (RS3), the fourth one is some chemically modified starch (RS4), and the fifth one is starch-lipid complexes (RS5).

Type 1 resistant starch (RS1) is intact in plant tissue and is protected from enzymes by cell walls surrounding the starch. Also, intracellular components inside the cells (i.e. protein/lipid bodies, cytoplasmic matrices, enzyme inhibitors) have been reported to give an extra obstacle to the enzyme hydrolysis of starch (Kraithong et al. 2022).

RS2 represents for example raw potatoes, legumes, bananas, or high amylose starches (HASs). There are, e.g. the following HASs on the market: corn HASs produced by Ingredion (USA) (Serin and Sayar 2023) or Quanyinxiangyu Biotechnology Co., Ltd. (Beijing, China) (Han et al. 2024), having about 70% of amylose content. Besides, unripe plantain, pumpkin, and winter squash Yinli starch demonstrated the lowest RDS (< 3%) and the highest RS (> 90%) (Šárka et al. 2023).

RS3 is a crystalline form of gelatinised starch after retrogradation. Starch retrogradation is a process in which disaggregated amylose and amylopectin chains in a gelatinised starch paste reassociate to form more ordered structures (Wang et al. 2015). Before the retrogradation process, starch can be at first sub-

jected also by enzymatic (using debranching enzymes such as pullulanase or isoamylase) or by acid hydrolysis converting the amylopectin into amylose, or by partial hydrolysis with α -amylase to eradicate the amorphous regions and generate starch that is essentially free of amorphous parts and contains at least 90% crystalline material (Norul Nazilah and Tin 2020).

RS4 is chemically modified starch. Chemical modification of starch is done to alter the properties of the formed gel. Thus, a suitable functional group is inserted into the starch molecule. Used chemical reactions are cross-linking, partial hydrolysis, oxidation, esterification, and etherification. However, not every chemical reaction of starch forms RS4. Chung et al. (2008) found that (hydroxypropylation or acetylation) together with oxidation contribute to raising the amount of resistant starch (RS4) by decreasing SDS content in granular starch and decreasing RDS content in gelatinised starch. Additionally, Han and BeMiller (2007) stated that combinations of the crosslinking (CL) of waxy corn starch followed by stabilisation via hydroxypropylation (HP) or acetylation (AC) produced the highest content of SDS than did crosslinking alone, CL-AC produced the highest content of RS (~24%). Also, starch pyrodextrinisation products were classified by many authors as RS4 (Gałkowska et al. 2023).

RS5 is amylose-lipid complexes. The associated helical molecules of amylose form inclusion compounds with lipids (Polesi and Silveira Sarmento 2011).

The glycemic index (GI) is a common measurement of the rate of carbohydrate absorption after a meal (Lehmann and Robin 2007). Evidence from trials and observational studies suggests that this physiological classification may be relevant to chronic Western diseases associated with overconsumption and inactivity, leading to central obesity and insulin resistance. The glycemic index classification of foods has been used to assess potential prevention and treatment strategies for diseases where glycemic control is important, such as diabetes (Esfahani et al. 2009).

GI is generally defined as the quotient between the area under the blood glucose curve after the consumption of 50 g of carbohydrates from a test food and the area under the curve after the consumption of 50 g of carbohydrates from a reference food (white bread or glucose), multiplied by 100 (Ludwig 2000). The need to develop low GI products having a high fibre content and low energy is stressed by the FAO and WHO (Anon 1998). The recent situation in many countries is described in Barclay et al. (2021). The GI of many foods has been determined during the past

<https://doi.org/10.17221/33/2025-CJFS>

years, and summary tables of the GI of over 750 food items are available (Foster-Powell and Brand Miller 1995; Foster-Powell et al. 2002). E.g. whole wheat bread with a low glycemic index contains RS (Zeng et al. 2024) and dietary fibre components. The whole tissue structures originating from whole kernels or whole-wheat flour in bread decrease enzymatic hydrolysis due to limited accessibility (Autio et al. 2004). Interest in pseudocereals has grown because they contain proteins having better amino acid scores than cereals and a significant proportion of RS, thus having a lower glycemic index (Skřivan et al. 2023). Great differences in GI have been observed among different legume products. The botanical origin has an important effect and the processing, especially canning and mechanical disruption produces higher GI values. Also, in the case of legumes, the tissue integrity and softness of the product seem to be important factors

(Autio et al. 2004). The microphotographs of legume flours can be seen in Figure 1.

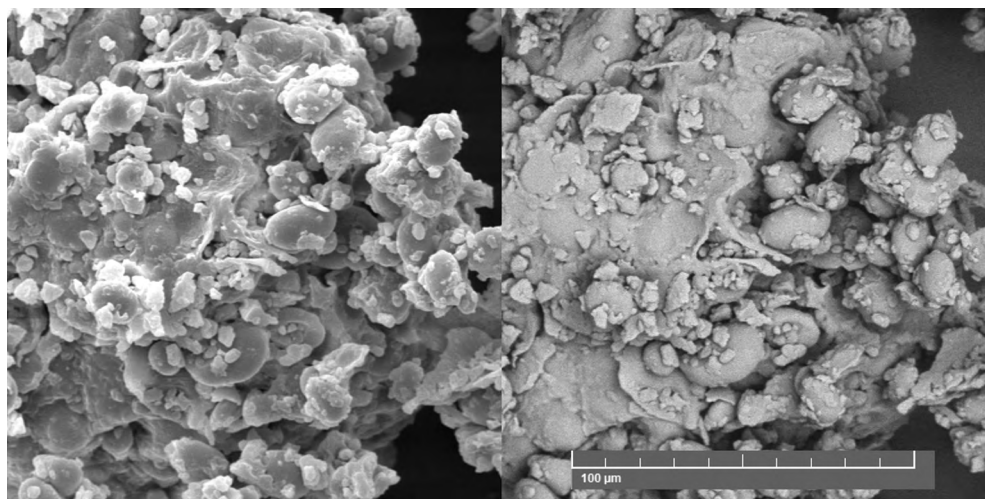
Nevertheless, some studies have shown a weak link between overall disease risk and GI (McClements 2021).

FAO's different term is glycemic load (GL), which describes the quality and quantity of carbohydrates in a food and is computed as the product of the glycemic index and the amount of carbohydrates available in a serving (Bao et al. 2011). Similarly to GI, the American Diabetes Association's dietary guidelines for diabetes prevention stated that there is insufficient, consistent information to conclude that low-GL diets reduce diabetes risk (Sluijs et al. 2010).

Effect of crystallinity on the digestibility of starch

Gelatinisation of starch, cooking extrusion, retrogradation. Starchy raw materials are usually modified by heat treatment such as cooking or baking,

(A)



(B)

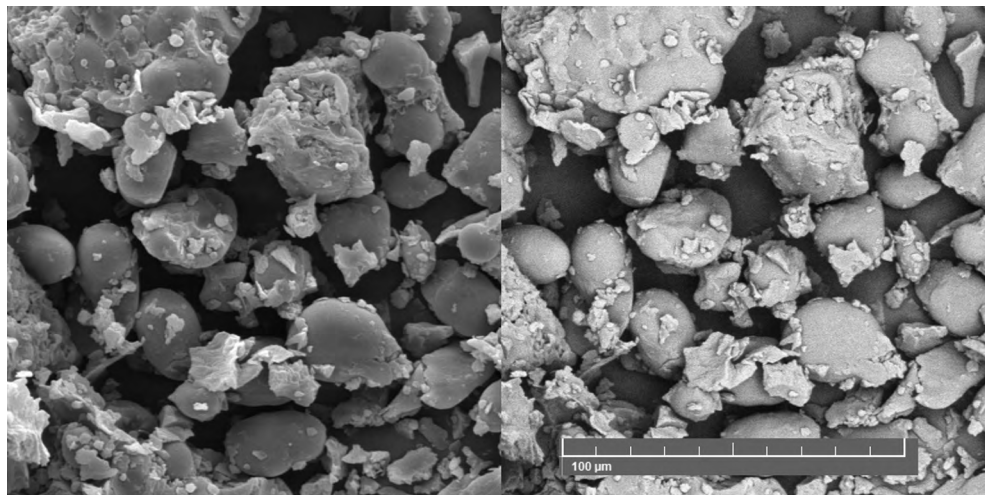


Figure 1. Microphotographs of the flour coming from (A) chick-pea and (B) lentil

e.g. in cooked potatoes or rice, bread, dumplings etc. Gelatinisation is a term describing an irreversible process occurring when starch is heated in the presence of water. The loss of crystalline order during heating sets in. As a result of gelatinisation, hydrogen bonds among starch molecules are destroyed. The *in vitro* and *in vivo* amylolysis rates increase dramatically. Therefore, gelatinisation leads to more digestible starch. Classically (Eliasson 1996), the starches from boiled corn, wheat, cassava, smooth pea, and raw potatoes have considerably higher postprandial responses in blood glucose than the corresponding raw ingredients. This heat treatment is crucial for people who need to speed up digestion.

In extruded cooked cereal products, e.g. breakfast cereals such as puffed rice and wheat, corn flakes, and corn chips, the thermal treatment, high pressure, and shear forces destroy the starch granular structure and increase its gelatinisation extent. This makes starch more available to amylolytic enzymes (Le François 1989; Teles et al. 2023) and causes higher glucose and insulin responses (Brand et al. 1985; Johnson et al. 2005).

Starch digestibility is influenced by starch molecular structure, especially by chain-length distributions (CLDs) of amylopectin. Chung et al. (2011) found that in indica long-grain rice, amylopectin intermediate chains ($DP < 40$) can contribute to a lower amount of RDS and a higher amount of SDS. It has also been found that RS content is positively correlated to the proportion of intermediate chains ($13 \leq DP \leq 24$) and negatively to short chains ($DP \leq 12$) (Wang et al. 2019b). Also, amylose's fine molecular structure is a significant factor in digestibility; short to medium amylose chains seem to have the most effect in this regard (Gong et al. 2019).

CLDs contribute not to only the digestibility but also the palatability of starch; normally these two attributes have opposing demands on starch structure. Zhu et al. (2023) focused on CLDs, the *in vitro* digestibility of 98 rice varieties, and the palatabilities of 9 market varieties, evaluated by human panellists. Simultaneous optimisation of two CLD features can secure acceptable palatability and healthy digestibility independently.

Sissons et al. (2022) suggested subtly manipulating the starch digestion of pasta through some processing procedures. The cooking time of pasta influences starch digestion; similarly, pasta with very high protein content (17%) reduces starch digestion extent. The semolina particle size distribution used to prepare pasta impacted pasta quality and starch digestion to a small extent indicating a finer semolina particle

size ($< 180 \mu\text{m}$) may promote a more compact structure and help to reduce starch digestion.

White wheat bread is very porous because gluten retains gases in the dough. Saliva easily penetrates through the pores inside the pieces and hydrolysis of starch begins in the mouth. Microstructural studies have shown that after mastication the pieces of white wheat bread are easily broken down by pepsin under conditions mimicking the stomach (Autio et al. 2004).

The digestibility of bread can be influenced by other factors such as the presence of grain husks (whole wheat bread), other grains, or damaged starch. The bread prepared from special finely ground whole grain flour with a lower proportion of damaged starch can have poorer digestibility and, conversely, fine passages of back flour with a high proportion of damaged starch may have very high digestibility.

As mentioned, during starch retrogradation amylose and amylopectin chains reassociate to form more ordered structures. This retrograded starch is more crystalline than native starch and the digestibility is worse. Additionally, retrogradation in many cases determines the quality, acceptability, nutritional value, and shelf-life of the finished foods (Wang and Copeland 2013). On the other hand, starch retrogradation has nutritional significance, due to the slower enzymatic digestion of retrograded starch and moderated release of glucose into the bloodstream (Copeland et al. 2009; Wang and Copeland 2013).

Consumption of native starches. Starch is usually not consumed in its native form, except in some fruits (e.g. bananas) or unfavourable situations such as hunger or high levels of diabetes.

The dimensions of native starch granules are critical to controlling digestion by amylase. Small starch granules (excluding the high amylose starches) are generally digested faster than large granules (Qi and Tester 2016). Besides, the hydrolysis of native starches depends on botanical origin, which determines morphology and crystalline organisation (Tester et al. 2004).

Some native starches are more digestible than others. The high content of SDS ($> 35\%$) is found in the native starch of annatto (Cortés-Viguri et al. 2022), *Euryale ferox* (Zhang et al. 2022) and parkia (Sankhon et al. 2013). The resistant starches R1 and R2 are examples of starch having considerably decreased digestibility. According to Du et al. (2014) and Yuan et al. (2022) native beans, winter squash, and pumpkin are the RS sources in formulations with desired fibre-like benefits such as lower digestibility.

Corn starch in uncooked form (UCCS) is very slowly digestible when ingested and thus it is used in patients

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with type 1 diabetes on intensive insulin therapy. This granular structural form is suitable after being digested in the gut to feed glucose into the bloodstream continuously. However, UCCS is not very palatable, which increases the risk of low dietary compliance. A conventional bedtime snack is a part of the therapy when glucose levels are below an arbitrary level ($4 \text{ mmol}\cdot\text{L}^{-1}$). Extending the range of slowly digestible products would increase dietary variety for patients with type 2 diabetes and improve the dietary treatment of glycogen storage disease type I (Bodamer et al. 2002).

On the other side, small granules of starch have high enzymatic hydrolysis rates when compared with large granules because of the 'outside-in' digestion pattern (Parada and Aguilera 2009), reduced amylose content (Lin et al. 2016), or higher number of amorphous growth rings in small starch granules (Blazek and Gilbert 2010). The digestion rate of starch granules by amylases has been reported to increase as their surface area increases (McClements 2021). The commercial sources of small starch granules include rice, wheat, and oat (Lindeboom et al. 2004).

The smallest granules ($< 5 \mu\text{m}$) having a high specific area are found in *Agriophyllum squarrosum*, amaranth, foxnut, and gorgon nut seeds and the leaves of *Arabidopsis thaliana* (Šárka et al. 2023). Additionally, Lindeboom et al. (2004) have discussed other potential sources of small granule starch e.g. quinoa (*Chenopodium quinoa* Wild), giant taro (*Alocasia macrorrhiza* L.), cow cockle (*Saponaria vaccaria* L.), canary grass (*Phalaris canariensis* L.), cat tail (*Typha latifolia* L.), dasheen (*Colocasia esculenta* L.), grain tef [*Eragrostis tef* (Zucc.) Trotter] and dropwort (*Filipendula vulgaris* Moench), all having granule sizes ranging from $0.5\text{--}10 \mu\text{m}$. On the other hand, Chávez-Salazar et al. (2022) and Puncha-arnon et al. (2007) found elongated particles of $65 \mu\text{m}$ in unripe plantains and granules of $47 \mu\text{m}$ in achira rhizomes, respectively. A bimodal size distribution of large and small granules is characteristic in wheat starches or those from rye and barley. The two populations are classified as A-granules ($> 10 \mu\text{m}$) and B-granules ($< 10 \mu\text{m}$) and differ somewhat in their physicochemical characteristics and end-use potential (Lindeboom et al. 2004).

The digestion patterns of starch granules include surface pitting and erosion, pores formation, and concentric layered shell structures. The α -amylolysis of waxy wheat starch is characterised by the formation of holes on the granular surface and the disruption of the core of the granule. Starch granules from

Diamondbird, Batavia, V306, and SM1046 (wheat lines with elevated amylose content) seemed to follow different patterns of α -amylolysis to that observed for waxy wheat starch. The granules from these starches were much less disrupted after 2 h than the waxy starch granules, and the layered structure corresponding to growth rings was not observed in any of the partly hydrolysed granules. Some fine pitting was noted on the surface and granules had a roughened appearance comparable to the waxy starch granules in the early stages of digestion (Blazek and Copeland 2010).

Other physical modifications. Recent studies indicate that the smaller particles increase solubility, influencing digestive functions (Tian et al. 2023). Some physical techniques, such as ultrasonic modification, nanotechnology, and microfluidisation, decrease the size of starch particles. The smaller particles improve their physical properties, e.g. water-holding, swelling, fat-binding, and cation-exchange capacity. Besides, they also enhance their biological activity thanks to associated bioactive substances such as polyphenols and phenolic acids.

Xie et al. (2023) dealt with the effect of high-pressure microfluidisation (HPM) on the microstructure, physicochemical properties, and digestibility of fractionated potato starch. The results show that the mechanical forces ($50\text{--}150 \text{ MPa}$) can break the molecules and enhance the digestion rate by increasing pressure. Authors suggested that HPM modifies potato starch resulting in different particle sizes. This method can expand industrial applications, such as an ingredient for infant food, energy food, functional beverages, or special medical food. Similarly, Augustin et al. (2008) dealt with the microfluidisation of RS. As to physiological functionality, these starches however couldn't hold moisture, thicken, or form gels.

Dynamic high-pressure microfluidisation can also be used for the preparation of starch-lipid complexes. Chen et al. (2018) prepared them from lotus seed starch and six saturated fatty acids of different carbon chain lengths and analysed their semi-crystalline structure and digestibility. Octanoic acid reduced the susceptibility to digestive enzymes significantly, increased SDS content (26%), and decreased digestion rate.

Šárka et al. (2011) used the bead mill DYNO[®]-MILL type Research Lab (WAB Muttentz, Switzerland) to disintegrate potato starch granules in suspension with isopropanol. The granule shapes were changed to have radial pores on the surface (Figure 2). This starch damage was similar to that known for ground flour. The

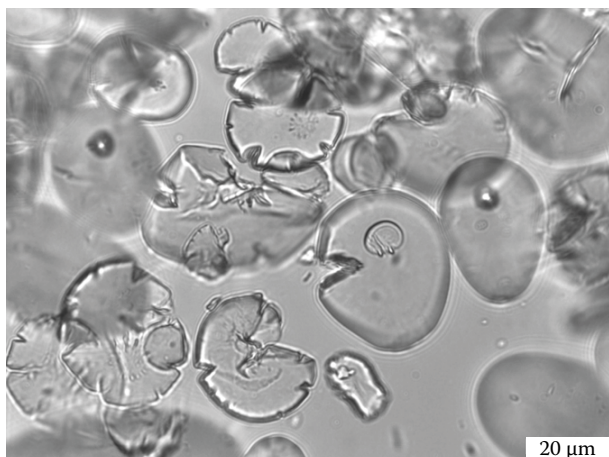


Figure 2. Microscopic observation of potato starch after ultrafine wet milling (action time 75 min)

crystallinity of starch was changed and after damage, the portion of the amorphous phase in the amylopectin molecule was much higher.

Annealing and heat moisture treatment. Later we also tested the annealing of these disintegrated particles at 0–4 °C. The crystallinity improved when we compared X-ray diffractograms of the native with ultrafine ground starch (Figure 3). The gelatinisation temperature was lower, and the gelatinisation enthalpy was similar to that of native potato starch.

Heat moisture treatment (HMT) or annealing can increase or modify the resistant starch level in RS2. Modifying RS using these two methods results in structural changes within the amorphous and crystalline regions of starch to different extents (Norul Nazilah and Tin 2020). According to Niba (2003), HMT caused higher digestibility for cocoyam, maize potato, and rice flours; on the other side, it fell in plantain flour.

New crystallites in the amorphous regions through amylose chain interactions or crystalline amylose-lipid complexes may cause a decrease in the enzyme sus-

ceptibility of HMT-treated corn starches (Hoover and Manuel 1996).

Role of dietetic fibre, gluten, fat, and phenolics in starch hydrolysis

The term dietary fibre (DF) describes indigestible carbohydrates associated with improving gut and general health (Mann and Cummings 2009). DF is a natural part of food or is added as a supplement, e.g. whole grains, legumes, vegetables, fruits (Gill et al. 2021), or bamboo culm flour (Vasques et al. 2022). It is well known that DF accelerates spontaneous peristaltic motion. Increasing the flow rate shortens the action time of amylases in the intestine, so the part of the slowly digestible starch analysed *in vitro* becomes RS.

The fermentation of substrates like dietary fibre (incl. RS) and endogenous intestinal mucus supports the growth of specialist microbes e.g. *Bacteroides* spp. that produce a variety of short-chain fatty acids (SCFAs) and gases, causing the lowering of the pH and inhibiting pathogens (Walker et al. 2011; Lamichhane et al. 2014; Gautier et al. 2022). However, some studies also indicate that major increases in DF can temporarily reduce the diversity of microbes, as those that digest fibre become specifically enriched, leading to a change in composition and, through competitive interactions, reduced diversity (Valdes et al. 2018). The type and concentration of SCFAs in the colon vary depending on the specific food consumed and the composition of the gut microbiome (Tian et al. 2023).

A sufficient intake of DF decreases mortality and provides several health benefits to humans, including reducing the risk of cardiovascular disease, coronary heart disease, stroke, hypertension, colorectal cancer, and type 2 diabetes (Shahidi and Chandrasekar 2017; McClements 2021). The researchers reported that the greatest reduction in risk from chronic disease could be achieved by consuming around 25–29 g of DF a day, which is much higher than the levels consumed

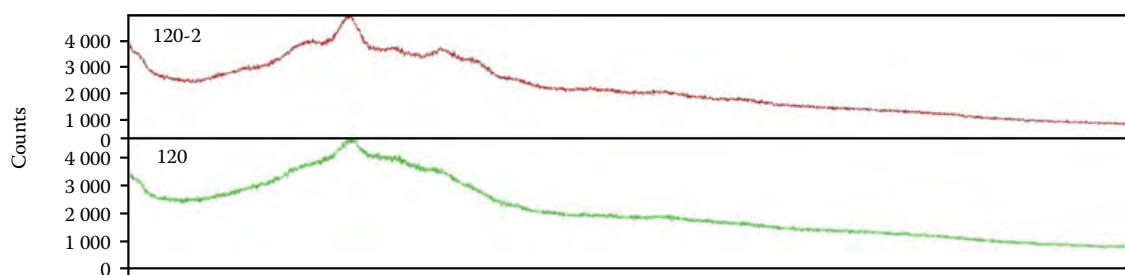


Figure 3. X-ray diffractograms of ultrafine wet ground (sample 120) and annealed ultrafine ground potato starch at 0–4 °C (sample 120-2)

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by most people, in both developed and developing countries (McClements 2021). Also, RS used as DF, reduces calorie intake (low glycemic index), prevents fat deposition and colon cancer, and enhances mineral absorption under the influence of lower pH (Yadav et al. 2024).

Most DF fermentation initiates in the proximal colon and terminates in the transverse colon, resulting in a limited number of metabolites that reach the distal colon, as evidenced by the decreasing concentrations of SCFAs, lactate, and succinate in the colon from proximal to distal regions (Tian et al. 2023).

A particularly health-beneficial form of DF in food products is viscous fibre, so-called soluble fibre (SF, e.g. β -glucan, guar gum, pectin). Soluble DF shows a higher water absorption compared to insoluble fibre. Up to now, SF has been proven to lower the glycemic response of bread, oat-bran breakfast cereals, and bars (Bender 2007). SF slows down the passage through the intestine by an increase in the viscosity of boluses due to macromolecular substances, which increases the time delay in the small intestine. The absorption rate of nutrients could increase when intestinal transit is slowed down since a delay in small bowel transit increases the time of contact between the luminal contents and the absorptive epithelium. Only a few studies investigated the relationship between transit time and the digestion and absorption of carbohydrates (Wachters-Hagedoorn et al. 2004). In ileostomy patients, Chapman et al. (1985) and Edwards et al. (2015) showed that the absorption of starch is directly related to the small intestinal transit time. The fall in digestibility of SF is thought to be due to delayed gastric emptying and delayed glucose absorption in the small intestine, which is caused by a reduction in diffusion rate through the intraluminal bulk phase of the small intestine (Wachters-Hagedoorn et al. 2004).

Wheat gluten is an elastic and cohesive protein. It is the major factor affecting the amount of digested starch in bread. It is known that starch encapsulated in a gluten matrix or network could lead to a low digestion rate and extent (Zou et al. 2015). Zeng et al. (2024) found that adding wheat gluten (but also oat or barley protein) and/or β -glucan reduced starch digestion to a certain extent, and their synergistic effect was greater. Similarly, sorghum starch digestion is hindered by a complex protein network called prolamins, known to reduce enzymatic starch breakdown (Ezeogu et al. 2005). However, this action of gluten can be reduced by a contemporary action of some polyphenols, e.g. (-)-epigallocatechin-3-gallate (EGCG). On the

other hand, EGCG significantly reduces the digestion extent of wheat starch by 25–30% in the absence of gluten. Both gluten and starch can bind with EGCG in the ternary blends via hydrogen bonding and/or hydrophobic interaction and decrease the amount of unbound EGCG by competitive inhibitory characteristics in the system (Xie et al. 2019).

Animal and *in vitro* studies indicate that gluten-free bread reduces microbiota dysbiosis in people with gluten sensitivity or coeliac disease. However, a recent large observational study showed, that most people who avoid gluten and have no coeliac disease or proven intolerance, have an increased risk of heart disease, potentially because of the reduced consumption of whole grains (Valdes et al. 2018). Bonder et al. (2016) showed that 21 healthy people had substantially different gut microbiota profiles after four weeks on a gluten-free diet. Most people showed a lower abundance of several key beneficial microbe species.

The inhibition of α -amylase activity to limit the rise in postprandial glucose is one of the most notable effects of dietary plant polyphenols. The rate and extent of inhibition depend on many factors, including the structure of polyphenols and the substrate used (Le et al. 2024). Phenolic compounds are postulated to bind to active or secondary sites of digestive enzymes (Zhu 2015) and/or bind to substrate thus reducing starch hydrolysis. They also regulate gut microbiota composition and slow the fermentation of RS *in vitro*. On the other hand, a simultaneous supplement of RS and tannic acid could promote the later production of acetate and butyrate and the enrichment of beneficial bacteria. Co-supplement of RS and polyphenols may deliver RS to the distal colon *in vivo*, which keeps the distal colon healthy and will be investigated (Liu et al. 2024).

Phenolic compounds bind to active or secondary sites of digestive enzymes and/or bind to substrate, thus reducing starch hydrolysis (Barrett et al. 2013). Cattivelli et al. (2024) observed that phenolic-rich vegetable foods slow down starch hydrolysis during *in vitro* co-digestion with pasta, mimicking a real-life scenario as closely as possible. The most active foods were flavonoid-rich vegetables rather than phenolic acid-rich vegetables such as cherry tomatoes and dark purple eggplant (*Solanum melongena*). According to Lachowicz et al. (2020), the flowers and leaves of *Sanguisorba officinalis* L. are a good source of polyphenols, including hydrolysable tannins, phenolic acids, flavanols, and anthocyanins, and exhibit a significant antiradical and reducing potential. In turn, the roots and stalks are a valuable source of flavan-3-ols. The most effective inhibition of α -amy-

lase, α -glucosidase, and pancreatic lipase and antiproliferative activities, reflected in the inhibition of viability of pancreatic ductal adenocarcinoma, colorectal adenocarcinoma, and bladder cancer as well as T-cell leukemia cell, was shown by the flowers and leaves of *Sanguisorba officinalis* L. Similarly, whole grain brown rice has potential health benefits due to its high content of phenolics (Zeng et al. 2019). Also, pomelo contains carotenoids, anthocyanins, and other phenolics (Shi et al. 2017). Mung bean husk polyphenols facilitated the synthesis of SCFAs in the colon (Liu et al. 2023).

To elucidate mechanisms of interactions between a polyphenol and the enzyme, Le et al. (2024) compared the inhibition of porcine pancreatic α -amylase (PPA) by three differently structured polyphenols: p-coumaric acid (p-CA), quercetin (QUER), and cyanidin-3-glucoside (C3G), using solid corn starch as a substrate, which limits the formation of starch-polyphenol complexes due to the compact structure of starch granules. QUER exhibited the strongest inhibitory effect, followed by C3G, and p-CA. The corresponding inhibition modes were determined to be mixed, mixed and competitive, respectively.

Kan et al. (2020) proved that gluten had little influence on the inhibitory efficacy of monomeric polyphenols on starch digestibility but reduced the inhibitory efficacy of polymeric polyphenols on starch digestibility. The co-digestion of bread with black or green tea polyphenols significantly reduced the kinetic rate and extent of starch digestion. Green tea extract caused a similar reduction in the starch digestibility of both wheat and gluten-free bread. However, black tea extract caused a larger reduction in the starch digestibility of gluten-free bread compared to wheat bread.

Fat may reduce postprandial glycemia by slowing down gastric emptying (Cecil et al. 1999) and in sufficient quantity, stimulates the secretion of insulin (Normand et al. 2001). Insulin resistance is the status of the cells, especially in muscle, fat, and liver tissue, that do not respond properly to the hormone insulin. This causes reduced glucose uptake, causing elevated blood sugar levels (hyperglycemia). This state can have serious health consequences, including an increased risk of developing type 2 diabetes and other metabolic disorders. Long-term high-fat feeding results in intramyocellular lipid accumulation, leading to insulin resistance. Intramyocellular lipid accumulation is related to an energy imbalance between excess fat intake and fatty acid consumption (Nakanishi et al. 2023).

On the other hand, in a significant proof-of-concept study examining real-world applicability, indi-

viduals with type 2 diabetes who consumed high-fat and high-protein foods (e.g. meat, cheese, fish) before consuming high-carbohydrate foods (e.g. bread, pasta, potatoes) for 8 weeks showed a marked improvement in postprandial glucose control. The strategic intake of these nutrients significantly influences oral carbohydrate tolerance. It operates through multiple physiological mechanisms, including the activation of neuronal and hormonal responses, alterations in plasma substrate levels, and subsequent influences on gastric emptying, insulin secretion, and excretion (Gulati and Misra 2025).

Effect of other parameters on digestibility

Food oral processing is the first step of digestion, where chewing ability strongly affects food digestion. This processing produces boluses with pieces of different particle sizes that may affect the digestion rate of nutrients (i.e. the starch digestion rate and glycemic response) and is characterised by a large inter-individual variability. Food matrix breakdown plays a pivotal role in how nutrients and bioactive compounds are available for absorption in the human body, therefore it regulates their concentration in the blood and utilisation in peripheral tissues (Suo et al. 2024).

Suo et al. (2024) studied factors influencing *in vitro* starch digestion of pasta. Mastication effort, shape, and their interaction mainly affected the starch digestion rate and the predicted glycemic index. The results suggested that small pasta like risoni, or less mastication effort, could be a strategy to have a relatively lower expected glycemic index. This is because the size reduction of food pieces, which leave the mouth into the stomach and have the form of coherent and large particles, will take longer, and the blood sugar values will be increased gradually.

In the stomach, food pieces are subjected to pepsin, acid conditions, and the vigorous grinding action of gastric motility. Some salivary amylase activity survives in the stomach as well. The gastric emptying rate is tightly linked to the rate of food digestion and nutrient absorption, and it is regulated so that the stomach only empties at a rate that mirrors the capacity of the small intestine to digest and absorb the received nutrients. Gastric emptying at half-time correlates with blood glucose and insulin values. The only exit from the stomach to the small intestine is the pylorus, which allows food pieces less than 2 mm in diameter to exit. Liquid phases of a meal are emptied faster from the stomach than solid phases (Autio et al. 2004).

The content of the intestine is gradually pushed in a direction from the stomach by peristaltic movements. One of the important influences on the digest-

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ibility of starch is the velocity of progress (flow rate) through the intestine. Generally, the flow character can be characterised as a piston flow. The time delay in both the small and large intestine depends on the volumetric flow rate according to the equation:

$$\tau = \frac{V}{V} \quad (1)$$

where: τ – time delay; V – intestinal volume; V – volume flow.

As mentioned, increasing the high flow rate shortens the action time of amylases in the intestine, so part of the slowly digestible starch analysed *in vitro* becomes non-digestible. It is known that DF accelerates peristaltic motion. Suggested DF ingredients are insoluble DF cellulose and soluble DF guar gum (Atzler et al. 2024). Similarly, a study by Tharakan et al. (2010) using an *in vitro* gastrointestinal tract (GIT) model, which included segmentation forces in the small intestine, showed that adding a thickening agent (guar gum) to the simulated intestinal fluids reduced the rate of glucose release after starch hydrolysis.

CONCLUSION

Starch is an important source of energy in food. The texture of food plays an important role. In the analytical methods simulating the activity of the digestive tract (e.g. according to Englyst et al. 1983), digestive enzymes are strictly dosed, and their effect is limited to a defined time. These methods are useful for sorting food by digestibility in the intestine into rapidly digestible, slowly digestible, and resistant starch. However, the *in vivo* digestibility can differ significantly for some individuals from the laboratory-determined value.

The main biological factors of starch digestion are oral mastication and salivation, gastric emptying and motility, small intestinal enzymes and motility, large intestinal resistant starch microbiota interactions, gut-brain feedback control, glucose adsorption, and hormonal feedback control.

The main factors of starch digestion in terms of food processing are gelatinisation, microfluidisation, cooking extrusion, heat moisture treatment, and annealing. Nevertheless, the origin of starch and the presence of other substances such as polyphenols, fat, gluten, and fibre also play a role.

Increasing the flow rate shortens the action time of amylases in the intestine, so the part of the slowly digestible

starch analysed *in vitro* becomes non-digestible. It is well known that dietary fibre accelerates peristaltic motion.

For healthy individuals, it is not recommended to consume regular gluten-free foods in which the proportion of the grain's coating layers is practically zero. These layers contain polyphenols that slow down hydrolysis. This inappropriate use of gluten-free foods increases the risk of heart disease, potentially because of the reduced consumption of whole grains.

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Received: February 21, 2025

Accepted: April 10, 2025

Published online: April 25, 2025