

## RESISTANT STARCH IN POTATO

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### ABSTRACT

**Background.** Starch and dietary fibers as well as carbohydrates that are not digested and absorbed in the small intestine, are chemically heterogeneous components derived from plants consumed by humans. These chemical components undergo a full or partial fermentation process in the large intestine. Starch and other carbohydrates are the main sources of energy in all diets, while cell wall polysaccharides are the main components of dietary fiber.

**Aim of the study.** The role of starch and other carbohydrates in the human diet was analyzed in terms of structure and distribution in tissues, modification of these components during food processing and impact on functional properties in human nutrition and their behavior in the gastrointestinal tract.

**Conclusion.** Potato and other starch products can play a large role in the prevention of hyperglycemia if starch-derived glucose is released into the circulation in a very slow manner. Potato starch cultivars are therefore very important not only for the industry, but also in the human diet.

**Key words:** dietary fibre, health benefits, non-starch polysaccharides, nutrition, potato, resistant starch, slowly available starch

### INTRODUCTION

With extensive research in the area of nutrition and diet some important conclusion have been drawn, such as, all starches are not the same in their effects on blood glucose and lipids and all starches are not completely digested. We have learned that the indigestible carbohydrates by humans are not just neutral bulking agents in “foods”, but have important physiologic effects, and even contribute energy to the diet (Andre *et al.*, 2007; Bethke *et al.*, 2008). Starch is the main source of glucose in the diet for the rapid development of children. Starches from different crops naturally differ in their molecular structure and properties. Cooking, processing and storage can change their molecular properties and affect their digestibility and functionality. Starch digestion is affected by susceptibility to  $\alpha$ -amylase and  $\alpha$ -glucosidase

(maltase), and susceptibility is determined by the granular structure of starch and glucan structures, as well as the interaction between starch and other food ingredients. In addition, the starch is given as complementary feeding of young children in many cultures. Starch or modified starch is used in special formulas for baby foods or supplements. Although indigestible starch does not provide much energy, it can have a positive effect on the health (Lin, 2018; Tetlow, 2018). However, knowledge in all these areas is far from complete (Andre *et al.*, 2007). In addition, there is unresolved controversy about how to define and how to measure indigestible carbohydrates and starch (dietary fibre, DF), DF was defined in 1953 by Hipsley as non-digestible constituents of plant cell walls however, and later many modifications were brought out to satisfy their structure – function relationship (Tetlow, 2018). And

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finally, Codex Alimentarius Commission\* (The Codex Alimentarius is a collection of internationally recognized standards, codes of practice, guidelines, and other recommendations relating to foods, food production, and food safety) defined DF as Dietary fiber means carbohydrate polymers with  $\geq 10$  monomeric units, which are not hydrolyzed by the endogenous enzymes in the small intestine of humans (Englyst *et al.*, 1982, 1996; Lin, 2018). Understanding the relationships between the compositions of raw food materials, the effects of processing on their structures and interactions, and their behaviour in the gastrointestinal (GI) tract are crucial for elucidating the relationships between diet and health. The aim of the review is to discuss the importance of dietary fiber and starch and their role in the prevention and management of selected civilization diseases based on a review of the latest available literature.

## REVIEW OF LITERATURE

### Dietary fiber

Dietary fiber (DF) is chemically heterogeneous ingredients derived from plants consumed by man, as well as carbohydrates, which are not digested and absorbed in the small intestine, but undergo full or partial fermentation in the large intestine. Dietary fiber is subjected to bacterial fermentation in the gastrointestinal tract. The increase in fiber intake, in addition to physiological benefits, may reduce the risk of civilization diseases. Thus, fermentative end products are closely related to the intestinal microflora and can have a significant effect on the composition of the intestinal microflora (Keenan *et al.*, 2006; Zhou *et al.*, 2006; Figurska-Ciura *et al.*, 2007; Sawicka *et al.*, 2017). An indigestible part of food is always obtained from plants, and the majority of plant products contain a mixture of two ingredients:

1. Soluble fiber, which dissolves in water, occurs in peas, beans, apples, citrus fruits, carrot roots, in oat and barley grains, etc., can easily ferment in the colon in gases and physiologically active by-products (gel) that can act as a prebiotic. These products slow down digestion, which in turn helps to lower cholesterol and blood glucose (Burrowes and Ramer, 2008; Priebe *et al.*, 2010; Shimotoyodome *et al.*, 2010; Sawicka *et al.*, 2017).

2. Insoluble fiber. This type of fiber remains unchanged up to the large intestine, making the waste heavier and softer, allowing it to shimmy through the intestines more easily promotes the flow of material through the digestive system and increases the stool volume, so it can be of benefit to those who fight constipation or irregular stools (Regmi *et al.*, 2011; Keenan *et al.*, 2012a; Sawicka *et al.*, 2017; Lin, 2018).

### Digestion and absorption of starch

An adult person consumes in the usual Western diet from 300 to 350g of carbohydrate per day, of which 50% is starch, 30% – sucrose, 6% – lactose, and the others are maltose, trehalose, glucose, fructose, sorbitol, cellulose and pectin. Food starch is a polysaccharide consisting of long chains composed of glucose molecules. Amylose is about 20% starch in the diet and breaks down within  $\alpha$ -1,4 linkages through ptyalin contained in saliva and pancreatic amylase that converts amylose to maltotriosis and maltose. Amylopectin, about 80% of food starches, has branches of every 25 molecules of glucose in the main chain;  $\alpha$ -1,6 glucose bonds in amylopectin they form final digestion products by amylase: maltose, maltotriose and residual branched saccharides – dextrins. In general, starch is almost completely converted into maltose and other small glucose polymers before the passage to the duodenum and the proximal jejunum. The final digestion of carbohydrates is the result of the brush border enzymes on the luminal surface of enterocytes (Lin, 2018; Tetlow, 2018).

Starch products, including potato, may play an important role in the prevention of hyperglycaemia if starch-derived glucose is released into the circulation very slowly (slowly available starch). Mechanisms that work to maintain normal plasma glucose levels and the causes and consequences of hyperglycaemia are important. Secondly, potential targets for slowing down the rate at which starch derived glucose becomes available for absorption in the gastrointestinal tract. Also important are *in-vitro* and *in vivo* starch digestion monitoring and current (nutritional) strategies for preventing hyperglycaemia (Priebe *et al.*, 2010b; Lin, 2018). For example, the effect of

a night meal is caused by short-chain fatty acids (SCFA, acetate, propionate and butyrate) produced by the fermentation of indigestible carbohydrates by colonic microflora, although other, yet unknown, mechanisms can not be ruled out. These short-chain fatty acids are quickly absorbed from the colon lumen and metabolized by colon epithelial cells, but some of them also enter the portal and peripheral circulation (Shimotoyodome *et al.*, 2010). The effect of SCFA on liver metabolism (Priebe *et al.*, 2010) and associated with the influence on fat metabolism (Zhou *et al.*, 2006) has been reported. Although the liver extracts 75% of acetate, 90% propionate and 95% butyrate from the portal vein (Sawicka *et al.*, 2017), higher concentrations of short-chain fatty acids in the peripheral circulation were observed after ingestion of non-greasy carbohydrates (Zhou *et al.*, 2006; Priebe *et al.*, 2010; Sawicka *et al.*, 2017). SCFAs can delay gastric emptying (Priebe *et al.* 2007), have insulin-like properties (Zhou *et al.*, 2006), increase insulin sensitivity by decreasing the concentration of free fatty acids (FFA) (Shimotoyodome *et al.*, 2010), have anti-inflammatory effects or

promote insulin-independent glucose savings (Regmi *et al.*, 2011; Kennan *et al.*, 2012a).

The digestion of starch begins with salivary amylase; broken into polysaccharides and oligosaccharides end up with monosaccharide's by hydrolysis before being absorbed. Pancreatic amylase in the small intestine hydrolyzes starch, with the primary end products being maltose, maltotriose, and  $\alpha$ -dextrins, although some glucose is also produced. The products of  $\alpha$ -amylase digestion are hydrolyzed into their component monosaccharide's by enzymes expressed on the brush border of the small intestinal cells, the most important of which are maltase, sucrose, isomaltase and lactase (Table 1) (Englyst *et al.*, 1982; Lin, 2018). This is reflected by the presence of finger-like villi in the mucosa of the upper small intestine, with wider and shorter villi in the lower half of the small intestine. However, carbohydrate digestion and absorption can occur along the entire length of the small intestine, and is shifted toward the ileum when the diet contains less readily digested carbohydrates (Zhou *et al.*, 2006, 2008; Priebe *et al.*, 2010).

**Table 1.** Characteristics of the carbohydrase of the brush border

Enzyme	Substrat	Produkt
Lactase	Lactose	Glucose
Maltase (glucoamylase)	$\alpha$ -1, 4-oligosaccharydes down nine residues sugar	Glucose
Sucrase-isomaltase (Sukrozo- $\alpha$ -dextrinase)	Sucrose	Glucose
sucrase	$\alpha$ -dextrin	Fructose
isomaltase	$\alpha$ -dextrin	Glucose
Both enzymes	$\alpha$ -1,4 bonds at the end not reduction	Glucose
Trehalaza	Trehaloza	Glucose

Source: Marsh and Riley, 1998, Keenan *et al.*, 2015.

### In the mouth

Carbohydrate digestion is a multi-stage, enzymatic

process that begins in the mouth – at the moment when the first bite of food is chewed. The purpose of

digestion is to break down macromolecular sugars into monosaccharides, which only in this form can be absorbed in the small intestine into the bloodstream. Saliva contains a significant digestive enzyme – salivary amylase that detaches from polysaccharides, e.g. starch (specifically referred to as 1,4  $\alpha$ -glycosidic bonds), gradually maltose molecules (disaccharides) to break this polysaccharide into smaller chains. In the mouth, of course, this process is preliminary and polysaccharides are made into smaller fragments. In the case of starch, these are so-called dextrans – that is polysaccharides, which originate from the decomposition (hydrolysis) of starch. As a result of salivary amylase, starch is "cut up" into smaller fragments composed of dextrin molecules (of different lengths) and maltose. Saliva contains many minerals and organic compounds, including some ions (electrolytes), enzymes, plasma proteins (e.g. gamma globulins that act as an immune protein (Marsh and Riley, 1998; Priebe *et al.*, 2010; Keenan *et al.*, 2015; Sawicka *et al.*, 2017).

### In the stomach

After the carbohydrate food is chewed into smaller pieces and mixed with salivary amylase and other salivary juices, it is swallowed and passed through the esophagus. The mixture enters the stomach where it is known as chyme. There is no further digestion of chyme, as the stomach produces acid which destroys bacteria in the food and stops the action of the salivary amylase (Sawicka *et al.*, 2017; Lin, 2018).

### In the pancreas and small intestine

After being in the stomach, the chyme enters the beginning portion of the small intestine, or the duodenum. In response to chyme being in the duodenum, the pancreas releases the enzyme pancreatic amylase, which breaks the polysaccharide down into a disaccharide, a chain of only two sugars linked together. The small intestine then produces enzymes called lactase, sucrase and maltase, which break down the disaccharides into monosaccharides. The monosaccharides are single sugars that are then absorbed in the small intestine (Marsh and Riley, 1998; Keenan *et al.*, 2012a, b).

The digestion of carbohydrates at this stage is resumed. The pancreatic juice produced by the

pancreas, through the drainage wires, goes to the duodenum. In man, the pancreatic duct connects to the bile duct and as a common duct it escapes to the so-called greater duodenum wart. The duodenum is a short (about 25 cm) initial fragment of the small intestine and the food pulp is mixed with pancreatic juice and bile at this point. Both of these juices are alkaline (about 7.8–8.8 pH) and thus neutralize acidic food content from the stomach, which ensures an optimal pH for enzyme action. In the further part of the duodenum, monosaccharides are absorbed. Pancreatic juice is responsible for the digestion of carbohydrates, proteins and fats, while bile is involved in the digestion of fats and absorption of vitamins A, D, E and K (i.e. fat-soluble vitamins). The most important pancreatic enzymes include: amylase – it is responsible for the digestion of carbohydrates; lipase – is responsible for the digestion of fats; trypsin and chymotrypsin – are responsible for the breakdown of proteins. Amylase and lipase are produced in an active form, trypsin and chymotrypsin are produced as inactive proenzymes (i.e. enzyme precursors), they become active only in the intestinal lumen (Saksena *et al.*, 2009; Lin, 2018).

**The small intestine** is characterized by a special structure – the mucosa forms the so-called intestinal villi on the surface of which enterocytes are found. Thanks to them, the small intestine performs the functions of absorption and digestion. From the intestinal lumen, their surface is additionally covered by microvilli (the so-called brush border), which increases the absorption surface up to 30 times. Pancreatic amylase brings the process of carbohydrate digestion almost to the end. The dextrans and other polysaccharides mentioned above are completely broken down to disaccharides (Neary *et al.*, 2005, Zhou *et al.*, 2008). Amylase, like saliva, slowly detaches maltose molecules from the end of the polysaccharide chain, until the whole sugar pool is distributed. In addition, a different enzyme is secreted – pancreatic maltase, which in turn "breaks down" maltose molecules into the final product – glucose, which is then absorbed. When most of the carbohydrate chains are already well "digested" into disaccharides or short dextrans, the function is taken over by the brush border of the intestinal villi. It contains enzymes that break down the disaccharides:

a lactase that breaks down lactose to glucose and galactose; maltase breaking down maltose to glucose monomers; the isopascase that breaks down any dextrin chains to glucose. Glucose accounts for over 80% of the final carbohydrate digest, fructose and galactose is not more than 10%. It should be added that carbohydrates are absorbed only in the form of monosaccharides (Marsh and Riley, 1998; Sawicka *et al.*, 2017; Lin, 2018). Glucose and galactose are absorbed by SGLT-1 by means of active transport with Na + Na + ions. When the sodium ion penetrates inside the enterocyte, it involves glucose and galactose. From the intracellular space to the extracellular glucose, it gets through GLUT-5, which is independent of Na + ions and goes to the bloodstream. Fructose enters from the intestinal lumen into the cell by facilitated diffusion, meaning that this process does not require any energy expenditure from the cell. The conveyor for fructose is GLUT-5, located on the enterocyte peak membrane. It leaves the cell through the GLUT-2 receptor also by facilitated diffusion, then goes into the bloodstream. The duration of the whole process is much longer than in the case of glucose, hence the thesis that fructose is absorbed from the intestine much slower than glucose. An interesting fact is that while the amount of SGLT1 in the cell membrane of enterocytes does not change the GLUT2 level increases in response to the high concentration of sugars in the intestine. In practice, this means faster absorption of sugars. There is a hypothesis that fructose causes an increase in the number of these receptors, such as sweeteners, which increase the glycemic index of foods assimilated with each other. Subsequently, the sugars are transported via the blood vessels from the intestinal villi to the portal vein (which first falls into the liver), then they are distributed throughout the body (Marsh and Riley, 1998; Neary *et al.*, 2005; Zhou *et al.* 2008; Priebe *et al.*, 2010; Shimotoyodome *et al.*, 2010).

### In the large intestine (Colon)

Carbohydrates that were not digested and absorbed by the small intestine reach the colon where they are partly broken down by intestinal bacteria. Fiber, which cannot be digested like other carbohydrates, is excreted with feces or partly digested by the

intestinal bacteria (Scharlau *et al.*, 2009; Cryan and Dinan, 2012; Lovegrove *et al.*, 2015; Lin, 2018). Starch polysaccharides and cell walls (or non-starch polysaccharides, NSP) are not digested, but are the main components of dietary fiber and are fermented by colonic microflora and are used to produce short-chain fatty acids (SCFA) (Ravussin *et al.*, 2012; Lovegrove *et al.*, 2015).

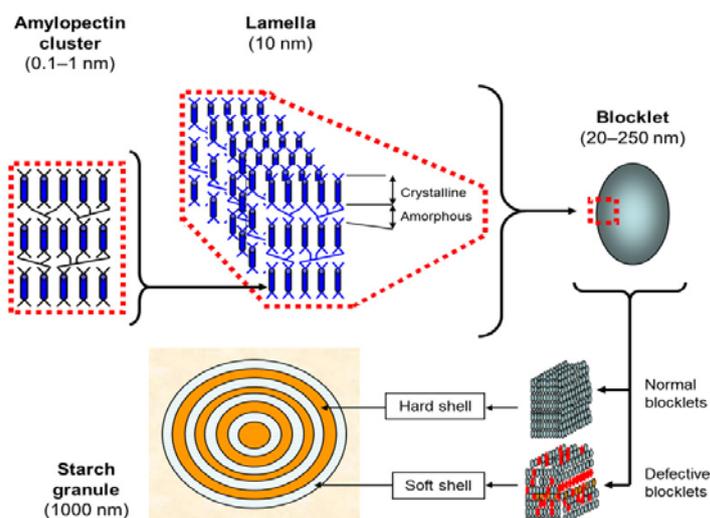
### Potato starch

Potato starch is starch extracted from potatoes. The cells of the root tubers of the potato plant contain starch grains (leucoplasts). Starch is a mixture of two glucose polymers: amylose, which comprises (1→4) α-linked chains of up to several thousand glucose units and amylopectin which is highly branched (with (1→6) α-linkages as well as (1→4) α-linkages) and may comprise over 100,000 glucose residues (Vilaplana *et al.*, 2012; Lovegrove *et al.*, 2015). Amylose is rather unbranched, but may contain several long branches, which are more common in tuber starch than in cereal and potato starch (Hoover, 2001). Most starches consist of 20-30% amylose and 70-80% amylopectin, although mutations in the biosynthetic pathway may result in a starch form with altered amylose: amylopectin ratios. Due to the presence of small amounts of branching in amylose, the exact determination of the amylose: amylopectin ratio is slightly misleading due to the presence of hybrid material (Vilaplana *et al.*, 2012). Amylose and amylopectin are deposited (complex) in specialized plastids, called amyloplasts, in highly organized granules that differ in size and shape between different species (Tester *et al.*, 2014; Lovegrove *et al.*, 2015). Starch granules can vary in size and shape from <1 μm to >100 μm depending upon the starch source. Examination of the starch granules by microscopy with polarised light reveals a birefringence pattern with a characteristic – Maltese cross – indicative of a high degree of molecular orientation within the starch granule. The starch granules have a semi-crystalline structure separated by amorphous growth rings (Fig. 1) (Lovegrove *et al.*, 2015).

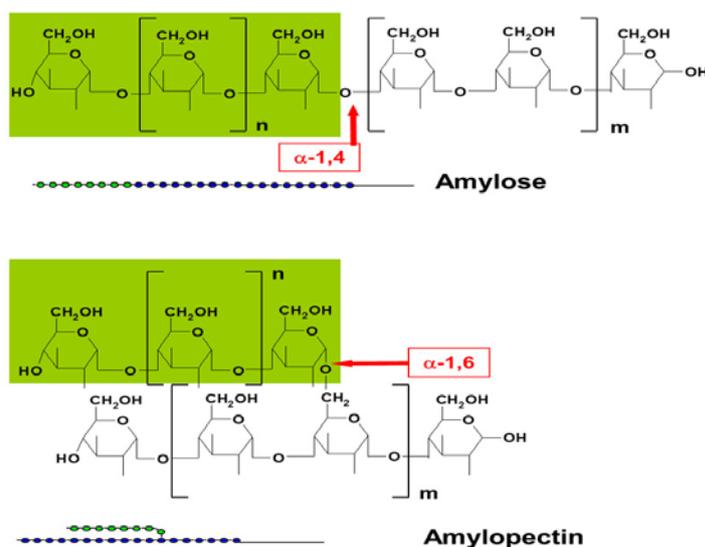
Four levels of organization make up the starch granule: the cluster of amylopectin molecules (0.1–1 nm), the lamella (~10 nm), the blocklet (20–250 nm) and the whole granule (>1 μm). Amylopectin

molecules are closely packed together to form clusters of double helices. The crystalline lamella is created by the association of amylopectin double helices interspersed with amorphous regions. The blocklet is the ordered aggregation of several crystalline-amorphous lamellae into an asymmetric structure with an axial ratio of 3:1 (named “normal

blocklets”). Amylose and other materials (e.g., water, lipids) disturb the regular formation of blocklets introducing “defects” (named “defective blocklets”). The ordered aggregation of normal and defective blocklets forms the concentric rings of hard (crystalline) and soft (semi-crystalline) shells in the starch granule (Fig. 2) (Taiz *et al.*, 2015 ).



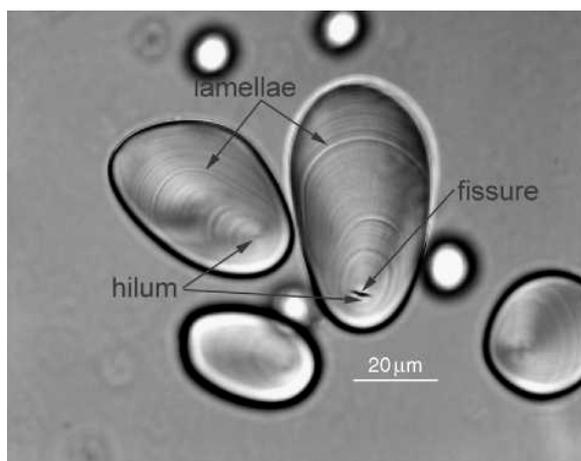
**Fig. 1.** A schematic illustration of levels of organization of the starch granule  
Adapted from: Taiz *et al.*, 2015



**Fig. 2.** The chemical composition of starch  
Adapted for: Taiz *et al.*, 2015

Starch is made up of amylose and amylopectin. Glucose units are linked almost exclusively through  $\alpha$ -D-1,4-glycosidic bonds in amylose. Amylopectin also contains  $\alpha$ -D-1,4-linked glucose chains (6 < nm < 100 glucose residues) but interspersed with  $\alpha$ -D-1,6-glycosidic bonds (branch points) that give a tree-like structure to the macromolecule (Taiz *et al.*, 2015).

Native starches vary widely among sources due to their content of different proportions of amylose (10–20%) and amylopectin (80–90%). But more importantly, the ratio of amylose to amylopectin defines the architecture of the regular semicrystalline arrays of amylopectin in the supermolecular complex called the starch granule (Fig. 3) (Maki *et al.*, 2012a; Taiz *et al.*, 2015).



**Fig. 3.** Concentric layers of the starch granule

Sources: <http://www.worldhistory.biz/prehistory/89036-what-is-starch.html>

In chloroplasts and amyoplasts (seed endosperm plastids), amylose and amylopectin are organized in relatively dense spheroidal granules (0.1 to > 50  $\mu$ m in diameter) that vary in shape and size (Taiz *et al.*, 2015). Non-starch polysaccharides (NSP) consist of hexose sugars: glucose, galactose and mannose, deoxy-hexosamino and fructose, glucuronic and galacturonic acids, as well as arabinose pentoses and xyloses (Bach Knudsen, 2001). NSP can be divided into classes (Waldron *et al.*, 2003). Cellulose is an unbranched chain containing up to about 15,000

(1 $\rightarrow$ 4) - $\beta$ -Diazotized glucose units. Glucose chains (1 $\rightarrow$ 4) - $\beta$ -D, in turn, bind via hydrogen bonding (both between and within the strand), thus giving strength to the cell wall. Linear polymers aggregate into amorphous or crystalline regions. Cellulose is insoluble in water and is indigestible to human enzymes, but is fermented, to varying degrees, by microorganisms in the large intestine. Arabinoxyans are usually found in single-chamber cell walls and consist of a (1-4) - $\beta$ -D-xylose backbone that is substituted for L-arabinose in position 3 or 2 and 3. There may be further modifications of these chains, including ferulation monosubstituted arabinose units that can lead to oxidative cross-linking of cell wall components. Cross-linked arabinoxylans can be important components of water-insoluble arabinoxylans. Substitution can also occur with p-coumaric acid, but at a lower frequency than ferulic acid. Xyloglucans consist of D-glucose units (1-4) linked by (3-substituted substituted (1 $\rightarrow$ 6) - $\alpha$ -D-xylose linkages, which may be further substituted (Cryan and Dinan, 2012, Lovegrove *et al.*, 2015). Glucomannans contain glucose and mannose units with  $\beta$ - (1 $\rightarrow$ 4) linkages and may also contain (1 $\rightarrow$ 6) - $\alpha$ -attached glucose substitutions. They are widely used in the food industry as thickeners and stabilizers. Galactan polysaccharides consisting of (1 $\rightarrow$ 3) - $\beta$ -D galactose and (1 $\rightarrow$ 4) -3, 6-anhydro- $\alpha$ -D-galactose. Mixed P-glucans are glucose units connected (1 $\rightarrow$ 4) - $\beta$  (as in cellulose), but interlaced with (1 $\rightarrow$ 3) - $\beta$  bonds. Connections (1 $\rightarrow$ 3) - $\beta$  generally occur after three or four  $\beta$ - (1 $\rightarrow$ 4) bonds. The irregular bonding structure prevents the formation of an ordered crystalline structure, which leads to the partial dissolution of  $\beta$ -glucans (Li *et al.*, 2006; Maki *et al.*, 2012b).

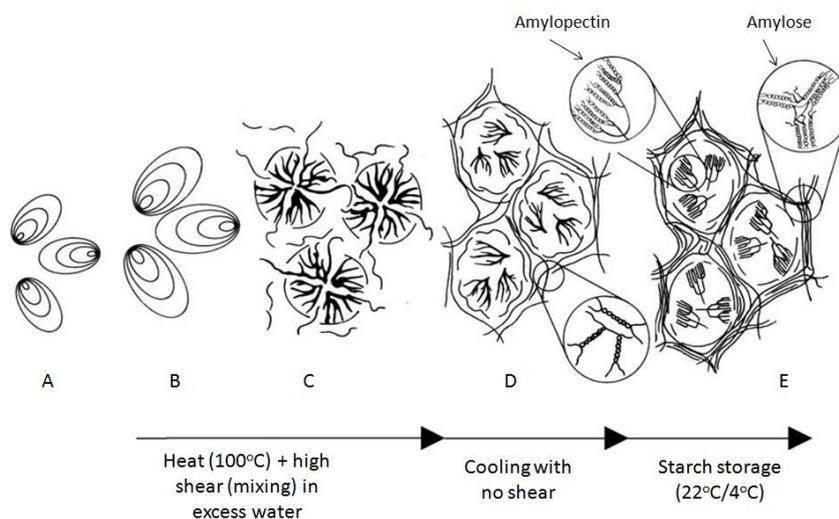
To extract the starch, the potatoes are crushed; the starch grains are released from the destroyed cells. The starch is then washed out and dried to powder. Potato starch contains typical large oval spherical granules ranging in size between 5 and 100  $\mu$ m. Potato starch is a very pure starch, containing minimal protein or fat. This gives the powder a clear white colour, and the cooked starch typical characteristics of neutral taste, good clarity, high binding strength, long texture and a minimal tendency to foaming or yellowing of the solution (Marsh and Riley, 1998; Keenan *et al.*, 2012a, 2015).

Modifications of some properties of starch and NSPs may occur at the initial stage of mechanical processing. Damaged starch possesses a water absorption capacity ten times greater than native starch and it is more prone to gelatinisation with implications for end-use properties and digestion (Lovegrove *et al.*, 2015).

### Hydrothermal heating and gelatinization of starch

Different processing conditions have different effects on starch structure and availability, which in turn affects digestibility. Heating of natural starch (50–100°C) in excess of water causes gelation. During this process, the semi-crystalline starch granule is completely ruptured. Hydrogen bonds, which together hold the helical double structure of  $\alpha$ -glucan chains (amylopectin), are broken, resulting in a higher proportion of amorphous material (Dona *et al.*, 2010). Heat treatment thus changes the morphology of starch granules from the orderly to the disordered structure (Fig. 4). Gelatinization of starch requires both heat and moisture, and is the fastest when starch is heated in excess moisture (>70%) in

the range of 50–100°C (Mościcki *et al.*, 2009; Roder *et al.*, 2009). Gelatinization of high amylose starch may require temperatures above 120°C, which is much higher than normal (Roder *et al.*, 2009). The presence of a resilient food matrix (e.g., a cell wall structure or protein network) may also limit gelatinization of starch, limiting water, heat transfer or space, despite prolonged exposure to hydrothermal conditions (Lovegrove *et al.*, 2015; Taiz *et al.*, 2015). Potato starch contains approximately 800 ppm phosphate bound to the starch; this increases the viscosity and high swelling power (Keenan *et al.*, 2006). It gives the solution a slightly anionic character. Potato starch is gelatinized during hydrothermal treatment (78°C); in this form it is easily digested. This triggers a rapid increase in blood glucose. The measure of blood glucose accumulation as a result of carbohydrate digestion is the Glycemic Index (IG). IG higher than 70 is considered high and <55 too low (Figurska-Ciura *et al.*, 2007) but potato gives about 95, which means that after consuming 50 g of potato, the glucose level may increase by as much as 95%.



**Fig. 4.** Effects of processing on starch granules

A – Intact native starch granule; B – Heat treatment in excess water under high shear conditions results in granular swelling; C – Granule disruption occurs during starch gelatinisation with linear amylose chains leaching out of the granule; D – Upon cooling, amylose chains aggregate together to form an ordered gel network; E – Recrystallisation of amylopectin and amylose chains occurs upon storage of gelatinised starch

Source: Schematic representation adapted from Lovegrove *et al.*, 2015.

However, there are ways to lower this indicator. Namely, after cooking potato tubers put them in the refrigerator for 24 hours, and then reheat, then their IG should fall because the lower temperature transforms the starch contained therein into a more resistant one (Foster-Powell *et al.*, 2002). In addition, the IG of a potato can be reduced by adding fat to it (e.g. olive oil). As a result, potatoes will be digested slowly in the intestine, which means no sudden increase in blood sugar level (Ulmus *et al.*, 2012a). On the other hand, the positive effect is the fact that the consumption of potato with a high IG in a short time provides the body with the necessary glucose and energy. The size of the Glycemic Cargo is also significant, calculated on the basis of the IG and the amount of carbohydrates contained in the product consumed. It takes into account not only the amount of carbohydrates consumed, as well as the rate of their decomposition and absorption by the human body, and therefore its value also results in the potential level of glucose in the blood and the need for insulin (Foster-Powell *et al.*, 2002; Ulmus *et al.*, 2012b).

### Resistant starch in potato

Resistant starch (RS) is characterized into 4 categories: RS1–RS4 (Lin, 2018; Tetlow, 2018). RS1 is found in whole grains (WGs) and legumes and is entrapped in a non digestible matrix. Ungelatinized starch granules are found in foods such as raw potatoes and high amylose cornstarch and comprise the RS2 category. The RS3 category includes foods that have undergone “retrogradation,” which occurs when foods containing starches are cooked and then cooled. Examples of foods in this category include potatoes cooled after cooking and puddings. Chemically modifying starches with the addition of ester and ether groups and crosslinking amylose strands usually render them resistant to digestion. These starches are found in breads and cakes, and they are categorized as RS4. Much of the research with RS uses high-amylose products. The term “resistant starch” was first used by Englyst *et al.* (1982), as “a small fraction of starch that was resistant to hydrolysis by exhaustive amylase and pullulanase treatment in vitro.” Were confirmed later, that this same type of starch also resisted hydrolysis

in vivo using healthy ileostomy subjects (Englyst *et al.*, 1996). RS, by definition, is a starch that reaches the large intestine in which it is fermented by bacteria. The FDA does not allow the term “resistant starch” on food labels. Thus, RS is a type of fiber suitable for fermentation and can be considered as one kind of prebiotic, *i.e.* provides “food” for bacteria living in the large intestine. RS fermentation produces SCFA and reduces pH in the proximal large intestine. In addition, the weight of the blank gut and the empty blind angle increases in response to fermentation (Keenan *et al.*, 2006; Zhou *et al.*, 2006). RS is a type of starch that is not fully degraded and absorbed, but rather converted into short-chain fatty acids by intestinal bacteria. This can lead to exceptional health benefits. Potential benefits of RS: improved blood fats, better feeling of fullness, better insulin sensitivity, improved digestion, better body composition, keeping us hydrated, improved resistance (Englyst *et al.*, 1996; Keenan, 2006). The effect of the fermentation process is the formation of short-chain fatty acids, mainly butyric acid, which nourishes symbiotic intestinal bacteria. Nourished microbiome is important for maintaining the health of the digestive system, prevents the development of diseases of the small and large intestines, among others colon cancer, ulcerative colitis or Crohn's disease. It also affects the regularity of bowel movements and normal intestinal motility, prevents bloating and constipation. RS lowers the energy intake of a meal with a large portion, so it can be used in the treatment of overweight and obesity. People with type 2 diabetes and / or insulin resistance should also pay attention to RS. It increases the sensitivity of cells to insulin and lowers blood sugar. After a meal containing RS, there is no sudden increase in the level of glucose in the blood and the accompanying discharge of a large portion of insulin, thereby relieving the pancreas. In a rat study, it was found that eating meals with the addition of resistant starch by animals increased the absorption of minerals such as calcium and phosphorus (Lin, 2018).

### How to speed up and slow down the metabolism, or regulation of the metabolic rate?

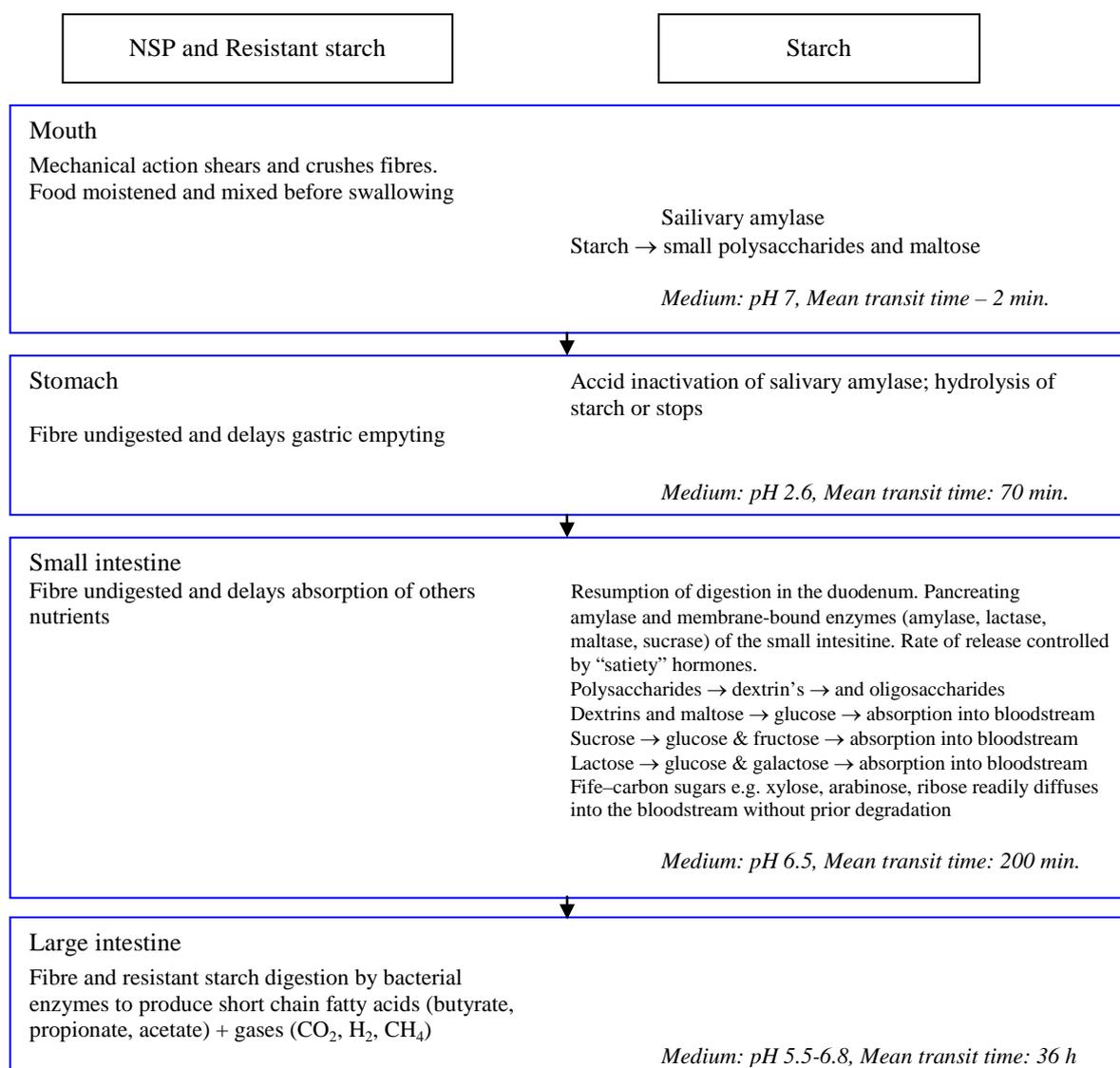
Metabolism is the whole of chemical and energy

transformations taking place in a living organism. The speed of these reactions depends largely on age and health, however, our lifestyle has a significant impact on the metabolic rate (Shimtoyodome *et al.*, 2010; Tachon *et al.*, 2013; Bodinham *et al.*, 2014). Resistant starch – types Starch is a polycarbohydrate, made up of glucose molecules connected together, which when released from bonds is a source of energy for the body. In English, starch is referred to as the resist starch. Four types of starch can be distinguished, each with different characteristics and different uses. RS1 – starch which is not physically available to the body, is found in the cell walls of whole or partially crushed cereal and legume plants. RS2 – raw starch found in raw potatoes, lentils or immature bananas. RS3 – retrograded starch, that is, resistant, on which we can influence the production. RS3 is found in boiled potatoes and cereal products that are cooked, then cooled and eaten. The process of cooking and then cooling causes the starch to pass from the digestible form to the body into a form resistant to the action of digestive enzymes. So cold, boiled potatoes, rice or buckwheat for lunch or oat flakes flooded in the evening with water or milk and eaten for breakfast contain probiotic resistant starch! RS4 – modified starch, artificially obtained and added to a variety of highly processed products. They play the role of thickener in them. Not all resistant starches are the same. There are 4 different types (Andre *et al.*, 2013). Type 1: Is found in grains, seeds and legumes and resists digestion because it is bound within the fibrous cell walls. Type 2: Is found in some starchy foods, including raw potatoes and green, unripe bananas (Maki *et al.* 2012b; Bodinham *et al.*, 2014; Keenan *et al.*, 2013, 2015).

#### Method for the determination of RS

Of the many analytical procedures employed for RS, two have emerged as the leading candidates for approval. These are the methods described by Englyst *et al.*, (1982) and Shen *et al.* (2009). They both provide similar results. The first step is removal of digestible starch from the food sample using pancreatic  $\alpha$ -amylase (in cases where there may be inhibition of the pancreatic enzyme by products of digestion, amyloglucosidase is added). Sometimes the

amylolysis is preceded by a proteolysis step with pepsin and trypsin to mimic the action of the stomach and intestine. The RS is quantitated either directly in the residue or by difference between total starch and digestible starch, which are determined separately (Zhou *et al.*, 2009). A new procedure has been proposed which is derived from several RS analysis systems (Belobrajdic *et al.*, 2012). Its principle is that in-vitro RS is defined as that starch which is not hydrolyzed by incubation with  $\alpha$ -amylase. Amyloglucosidase is added to avoid inhibition by by-products of amylase digestion. Hydrolysis products are extracted with 80% ethanol and discarded. The RS is then solubilized with 2N potassium hydroxide and hydrolyzed with amyloglucosidase. RS is classified as a fraction of water-insoluble fiber. It is also defined as a starchy fraction resistant to digestive enzymes, but it is fermented in the large intestine by strains of beneficial bacteria that colonize it (Keenan *et al.*, 2006; Figurska-Ciura *et al.*, 2007). RS acts as prebiotic (Burrowes and Ramer, 2008). The health efficiency of RS has a wide range. Starch is the main source of glucose in the diet for the rapid development of children. Starches from different crops naturally differ in their molecular structure and properties. Cooking, processing and storage can change their molecular properties and affect their digestibility and functionality. Starch digestion is affected by susceptibility to  $\alpha$ -amylase and  $\alpha$ -glucosidase (maltase), and susceptibility is determined by the granular structure of starch and glucan structures, as well as the interaction between starch and other food ingredients. Starch is given as complementary feeding of young children in many cultures, and starch or modified starch is used in special formulas for baby foods or supplements. Although indigestible starch does not provide much energy, it can have a positive effect on the health of the colon (Lin, 2018). It is recognised that transit times are not very reliable and we have therefore quoted average times. Some foods reside in the stomach for longer or shorter periods of time. In ileostomy subjects the remaining part of the meal may reach the terminal ileum after >4 hours while the remaining parts of an almond meal came out of the stoma at 9-12 hours (Noah *et al.*, 1999; Charrier *et al.*, 2013).



**Fig. 5.** Schematic diagram of carbohydrate digestion through the digestive tract adapted from: Lovegrove *et al.*, 2015

The effect of the fermentation process is the formation of short-chain fatty acids, mainly butyric acid, which nourishes symbiotic intestinal bacteria, which are important for maintaining the health of the digestive system, prevents the development of diseases of the small intestine and colon, including: colon cancer, ulcerative colitis or Crohn's disease. It also affects the regularity and proper intestinal motility, prevents bloating and constipation (Sawicka *et al.*, 2017). RS lowers energy intake in a large

portion of a meal, so it can be used to treat overweight and obesity. People with type 2 diabetes or insulin resistance should also use RS. It increases the sensitivity of cells to insulin and lowers blood sugar. After a meal containing RS, there is no sudden increase in blood glucose levels and the accompanying outflow of a large amount of insulin, thereby releasing the pancreas (Shen *et al.*, 2011; Belobrajdic *et al.*, 2012). Eating meals with the addition of resistant starch increases the absorption of

minerals, such as calcium and phosphorus, which affects the metabolism or regulation of the metabolic rate. Four types of starch can be distinguished, each of which has different characteristics and uses. And so: RS1 is a starch that is not physically available to the body, because it is found in the cell walls of whole or partially crushed cereal and legume plants; RS2 is raw starch in raw potatoes, lentils or immature bananas; RS3 – retrogradated starch, i.e. resistant, which is found in boiled potatoes and cereal products that are cooked and then chilled and eaten (Keenan *et al.*, 2013). The process of cooking and then cooling causes the starch to go from the digestible form to the form resistant to the action of digestive enzymes. Thus, cold, boiled potatoes, rice, or buckwheat for breakfast contain probiotic resistant starch; RS4 is a modified starch, artificially obtained and added to many highly processed products. It plays the role of a thickener in them (Robertson *et al.*, 2005; Bodinham *et al.*, 2012).

After the cooling of the heat-treated products containing the gelatinized starch, its structure is changed (retrogradation), as a result of which the part undergoing is not digested. It consists of starch and its decomposition products not absorbed in the small intestine. RS in the large intestine is fermented by pre-biotic and /or probiotic bacteria from the genera *Bifidobacterium* and *Lactobacillus*. In tubers there are also so-called insoluble non-starch substances, primarily constituents of cell walls, such as: cellulose, hemicelluloses, lignins, etc. They form so-called dietary fiber. The content of dietary fiber in potato tubers is 2.0–2.3%. It is resistant to digestive enzymes and therefore has no energy value. However, it is necessary in food to "dilute" nutrients, thereby facilitating the access of digestive enzymes to them. Fiber improves intestinal peristalsis and also adsorbs bile acids and toxic heavy metals. Some of its components act as a prebiotic for probiotic microorganisms in the large intestine (Shen *et al.*, 2009; Zhou *et al.*, 2012). Eating too little fiber can make it difficult to control your blood sugar level because the fiber regulates the rate of digestion and contributes to the feeling of fullness. The fiber can move the food through the intestines too quickly, which means that fewer minerals are absorbed then with food. It can also cause flatulence and cramps,

especially when fiber intake increases overnight. The recommended amount of dietary fiber (DF) depends on age and gender. For men under 50, the DF intake is about 38 g fiber a day for women – 25 g (USDA, 2014). People who have recently undergone digestive surgery or suffer from digestive disorders, such as Leśniowski-Crohn's disease, diverticulitis or ulcerative colitis, may use a low-fiber diet. It limits the daily intake of fiber to 10–15 g, so much less than the recommended norm for healthy adults. Foods with low fiber content, including boiled potato pie, slow down the digestion rate, reduce the amount of stool in the intestines and allow the intestines to rest (Neary *et al.*, 2005). Potatoes boiled or baked until tender and then mixed, because they have low fiber content and can be accepted in a low-fiber diet (without skin). According to USDA (USDA, 2014), 1 serving of potatoes, without skin, contains 3.2 g of dietary fiber, slightly more than half of fiber, which is obtained from a large baked potato with intact skin (Bethke and Jansky, 2008; USDA, 2018).

### Starchy cultivars

Potato cultivars differ significantly in the content of starch in tubers. It is assessed in Poland by varietal experiments of the Central Research Center for Crop Plants (COBORU) and in the Post-registration Variety Experimentation System (PDO) (Gacek, 2018). In 2017, in registration experiments, on the 100 cultivars of registered 26 cultivars there were starch cultivars, of which in the early cultivar group there was only one cultivar, in the medium early group – 12 cultivars, in the medium late group – 3 cultivars and in the late group – 9 cultivars. The principle is therefore confirmed that the longer the growing season, the easier it is to obtain a large yield of starch. There is also a positive correlation between the content of starch and the length of the growing season, tuber yield, average tuber weight and weight, and negative – with early emergence of potato plants, tuber size and protein content (Leszczyński, 2002; Styszko and Kamasa, 2006). Nevertheless, the functioning of the early and very early starch cultivars in the world registers indicates the possibility of a significant shortening of the growing season in this breeding direction. Early cultivars are sought after by the potato industry. In 2017, in

Poland, according to the registration evaluations, only 5 cultivars had a starch content above 20% (Gacek, 2018). Cultivars with a higher resistance of leaves and tubers to potato late blight (*Phytophthora infestans* Mont. De Bary) and to the virus Y (PVY) and leaf roll virus (PLRV) usually have a higher content of starch. The content of this component in tubers is conditioned by several genes, predominantly dominant (Styszko and Kamasa, 2006; Gacek, 2018). Potato cultivars in this respect are heterozygous. When crossing of cultivars, a higher percentage of high starch forms are obtained in the offspring of parents with a higher starch content and greater ability to pass on. The use of one parent with a lower starch content for crossbreeding reduces the number of offspring with a higher content of starch. When crossing with wild species, with a high starch content, it inherits a lot of undesirable features for potato, such as: long stolons, shapeless tubers and late ripening (Styszko and Kamasa, 2006). The content of starch in potato tubers is affected not only by the genetic factor but also factors affecting the plant during its growth, such as: climatic and soil conditions, forecrop, date of potato planting, fertilization, applied plant protection products, deadline for harvesting tubers, etc. (Leszczyński, 2002; Gacek, 2018).

In further genetic-breeding work on the potato, enzymes of biosynthetic (Zhou *et al.*, 2006; Figurska-Ciura *et al.*, 2007). Studies on overexpression (McKibbin *et al.*, 2006; Zhang *et al.*, 2008) and silencing (Jobling *et al.*, 2002; Wischmann *et al.*, 2005) genes significantly expanded our knowledge of the functioning of the starch synthesis and degradation pathways in tubers. The GBSS enzyme (granule-bound starch synthase) proved to be particularly important. In 2006, a cultivar of Amflora was bred with a blocked expression of the GBSS gene (Wickramasinghe *et al.*, 2009). A potato variety was obtained which produced in the tubers amylose starch useful in the non-food industry. Genetic modification has been carried out to inhibit the production of one of the two starches naturally present in potatoes, so that it contains more than 99% of amylopectin, but very little amylose. This variety also contained an antibiotic resistance gene as a marker. Potato, derived from the "Prvalent" variety,

has been modified by the "antisense inhibition" of a gene that otherwise codes for starch synthase. Due to the absence of this enzyme, no amylose is formed, which usually constitutes 20-30% potato starch. The starch of the Amflora cultivar therefore contains more than 99% of amylopectin. In the case of industrial processing, this has the advantage that the starch fractions do not have to be separated in the production process. The Amflora cultivar also contains an antibiotic resistance marker that has been introduced to initially distinguish modified cells from unmodified, and which is not applicable, but nevertheless is present and actively produces the NptII protein that confers resistance to kanamycin, neomycin, gentamycin, paramomycin and framycetin. This event expresses the neomycin type II phosphotransferase protein (NptII) used as a selection marker during the transformation process. Neomycin is used in some countries in human and veterinary medicine, whereas kanamycin is listed by the WHO as a reserved antibiotic against many resistant strains of tuberculosis (Wischmann *et al.*, 2005; Wickramasinghe *et al.*, 2009; Moses and Brookes, 2013). Zhao *et al.* (2018) proved that the tubers of the genetically modified line with high amylose content T-2012 (30% DM) and its parental potato cultivar Dynamo, analyzed for starch resistance (RS) and dietary fiber (DF) after cooking and storage in cold, they had a significantly lower RS than the mother tubers (56% DM). However, after cooking, the high amylose tubers gave more RS (13% DM) than the parent (4% DM), and the RS level was further increased to about 20% DM after 1 day of storage in the cold store. The changed RS content can be attributed to changes in amylose content, starch granule structure and the structure of amylopectin induced by genetic modification. Tubers with high amylose also contain more DF (10-14% DM) than a parent (5–7% DM) (Moses and Brookes, 2013; Sawicka *et al.*, 2017; Zhao *et al.*, 2018).

## CONCLUSIONS

One of the most important plant products for the global society is starch synthesized in specialized organelles (chloroplasts, leaves, amyloplasts, tubers and others). Mainly vegetable tubers (eg potatoes),

but also grass seeds (eg wheat, rice) are by far the largest sources of starch for humanity and are an indispensable foodstuff, but also a very important intermediate in industrial processes, such as: adhesives or biodegradable plastics artificial. Starch is insoluble in cold water, because the crystalline areas of the granules do not allow the ingress of water. However, as the temperature rises, the crystalline regions begin to separate into swellable amorphous forms. Gelling properties are an important aspect in terms of processing requirements, especially when it comes to the production of raw materials for the food, chemical, pharmaceutical and textile industries. Therefore, two basic aspects should be implemented to improve these activities: enough to feed the world and the right quality for specific applications. The former is based on the farmer, but the responsibility of the farmer and production technologist, who is represented by the food and chemical industries, lies with the processing chain. Therefore, the challenge for the future will be to develop improved potato varieties, whose ultimate goal will be to feed the world and release chemical products that are less harmful to the environment. Some of the pro-health properties of dietary fiber were also discussed; some of them have already been well understood, while others require further research. The effect of using different fractions of the alimentary fiber is not always identical, although in most cases high repeatability can be observed. Providing fiber from various sources is important due to measurable health effects. Potato starch cultivars are therefore very important not only for the industry, but also in the human diet. Therefore, it is extremely important to constantly educate the public and remind you which food products should form the basis of a well-balanced diet.

## REFERENCES

- Andre, C.M., Ghislain, M., Bertin, P., Oufir, M., Herrera Mdel, R., Hoffmann, L., Hausman, J.F., Larondelle, Y., Evers, D.J. (2007). Andean potato cultivars (*Solanum tuberosum* L.) as a source of antioxidant and mineral micronutrients. *Agric. Food Chem.*, 55(2), 366–378.
- Bach Knudsen, K.E. (2001). The nutritional significance of dietary fibre analysis. *Animal Feed Science and Technology*, 90, 3–20.
- Belobrajdic, D.P., King, R.A., Christophersen, C.T., Bird, A.R. (2012). Dietary resistant starch dose-dependently reduces adiposity in obesity-prone and obesity-resistant male rats. *Nutr Metab (Lond)*, 9, 93.
- Bethke, P.C., Jansky, S.H. (2008). The effects of boiling and leaching on the content of potassium and other minerals in potatoes. *J. Food Sci.*, 73(5), 80–85.
- Bodinham C.L., Smith L., Wright J., Frost, G.S., Robertson, M.D. (2012). Dietary fibre improves first-phase insulin secretion in overweight individuals. *PLOS One*, 7, e40834.
- Bodinham, C.L., Smith, L., Thomas, E.L., Bell, J.D., Swann, J.R., Costabile, A., Russell-Jones, D., Umpleby, A.M., Robertson, M.D. (2014). Efficacy of increased resistant starch consumption in human type 2 diabetes. *Endocr Connect*, 3, 75–84.
- Burrowes, J.D., Ramer, N.J. (2008). Changes in potassium content of different potato varieties after cooking. *J. Ren. Natur.*, 18(6), 530–534.
- Charrier, J.A.M.R., McCutcheon, K.L., Raggio, A.M., Goldsmith, F., Goita, M., Senevirathne, R.N., Brown, I.L., Pelkman, C., Zhou, J., Finley, J., *et al.* (2013). High fat diet partially attenuates fermentation responses in rats fed resistant starch from high-amylose maize. *Obesity (Silver Spring)*, 21, 2350–2355.
- Cryan, J.F., Dinan, T.G. (2012). Mind-altering microorganisms: the impact of the gut microbiota on brain and behaviour. *Nat. Rev. Neurosci.*, 13, 701–712.
- Dona, A.C., Pages, G., Gilbert, R.G., Kuchel, P.W. (2010). Digestion of starch: In vivo and in vitro kinetic models used to characterize oligosaccharide or glucose release. *Carbohydr. Pol.*, 80, 599–617.
- Englyst, H., Wiggins, H.S.H.S., Cummings, J.H.J.H. (1982). Determination of the non starch polysaccharides in plant foods by gas-liquid chromatography of constituent sugars as alditol acetates. *Analyst.*, 107, 307–318.
- Englyst, H.N., Kingman, S.M., Hudson, G.J., Cummings, J.H. (1996). Measurement of resistant starch in vitro and in vivo. *Br. J. Nutr.*, 75, 749–755.
- Figurska-Ciura, D., Orzeł, M., Styczyńska, M., Leszczyński, W., Żechałko-Czajkowska, A. (2007). The influence of rs4 resistant starch on wistar rats metabolism. *Biochemical and lipid indices. Annals Nat. Inst. Hyg.*, 58(1), 61–66.

- Foster-Powell, K., Holt, S.H.A., Brand-Mill, J.C. (2002). International table of glycemic index and glycemic load values. *Am. J. Clin. Nutr.*, 76, 5–56.
- Gacek, E. (2018). Lista opisowa odmian roślin rolniczych. Burak Ziemniak Oleiste Pastewne. Wyd.: Centralny Ośrodek Badania Odmian Roślin Uprawnych, Słupia Wielka, 171.
- Hoover, R. (2001). Composition, molecular structure, and physicochemical properties of tuber and root starches: a review. *Carbohydr. Polym.*, 45, 253–267.
- Jobling, S.A., Westcott, R.J., Tayal, A., Jeffcoat, R., Schwall, G.P. (2002). Production of a freeze-thaw-stable potato starch by antisense inhibition of three starch synthase genes. *Nat. Biotechnol.*, 20, 295–299.
- Keenan, M., Zhou, J., McCutcheon, K.L., Raggio, A.M., Bateman, H.G., Todd, E., Jones, C.K., Tulley, R.T., Melton, S., Martin, R.J. (2006). Effects of resistant starch, a non-digestible fermentable fiber, on reducing body fat. *Obesity (Silver Spring)*, 14, 1523–1534.
- Keenan, M., Zhou, J., Raggio, A.M., McCutcheon, K.L., Senevirathne, R., Goldsmith, F., Janes, M., Tulley, R.T., Shen, L., Vidrine, K., *et al.* (2012b). Mechanisms by which resistant starch produces gut hormones and reduces body fat. In: Cho, S., Almeida, N. (eds), *Dietary fiber and health*. Boca Raton (FL): CRC Press: Taylor and Francis Group, 453–466.
- Keenan, M.J., Janes, M., Robert, J., Martin, R.J., Raggio, A.M., McCutcheon, K.L., Pelkman, C., Tulley, R., Goita, M., Durham, H.A., *et al.* (2013). Resistant starch from high amylose maize (HAM-RS2) reduces body fat and increases gut bacteria in ovariectomized (OVX) rats. *Obesity (Silver Spring)*, 21, 981–984.
- Keenan, M.J., Martin, R.J., Raggio, A.M., McCutcheon, K.L., Brown, I.L., Birkett, A., Newman, S.S., Skaf, J., Hegsted, M., Tulley, R.T. *et al.* (2012a). High-amylose resistant starch increases hormones and improves structure and function of the gastrointestinal tract: a microarray study. *J. Nutrigenet. Nutrigenomics*, 5, 26–44.
- Keenan, M.J., Zhou, J., Hegsted, M., Pelkman, Ch., Durham, H.A., Coulon, D.B., Martin, R.J. (2015). Role of Resistant Starch in Improving Gut Health, Adiposity, and Insulin Resistance1–4. *Reviews From Asn Eb 2014 Symposia*. American Society for Nutrition. *Adv. Nutr.*, 6, 198–205.
- Leszczyński, W. (2002). Czynniki kształtujące jakość surowca do przetwórstwa na skrobię. W: Chodkowski J. (red.) *Ekonomika i technologia produkcji ziemniaków skrobiowych*. Wieś Jutra, Warszawa, 145–152.
- Li, Y.H., Lee, K.K., Walsh, S., Smith, C., Hadingham, S., Sorefan, K., Cawley, G., Michael, W. (2006). Establishing glucose- and ABA-regulated transcription networks in Arabidopsis by microarray analysis and promoter classification using a Relevance Vector Machine. *Genome Res.*, 16, 414–427.
- Lin, A.H. (2018). Structure and Digestion of Common Complementary Food Starches. *J Pediatr Gastroenterol Nutr.*, 66 Suppl 3, 35–38.
- Lovegrove, A., Edwards, C.H., De Noni, I., Patel, H., Grassby, S.N.El.T., Zielke, C., Ulmius, M., Nilsson, M., Butterworth, P.J., Ellis, P.R., Shewry, P.R. (2015). Role of Polysaccharides in Food, Digestion and Health. *Crit. Rev. Food Sci. Nutr.*, 237–253.
- Maki, K.C., Gibson, G.R., Dickmann, R.S., Kendall, C.W., Chen, C.Y., Costabile, A., Comelli, E.M., McKay, D.L., Almeida, N.G., Jenkins, D., *et al.* (2012a). Digestive and physiologic effects of a wheat bran extract, arabino-xylan-oligosaccharide, in breakfast cereal. *Nutrition*, 28, 1115–1121.
- Maki, K.C., Pelkman, C.L., Finocchiaro, E.T., Kelley, K.M., Lawless, A.L., Schild, A.L., Rains, T.M. (2012b). Resistant starch from high-amylose maize increases insulin sensitivity in overweight and obese men. *J. Nutr.*, 142, 717–23.
- Marsh, M.N., Riley, S.A. (1998). Digestion and absorption of nutrients and vitamins. [in:] Feldman, M., Scharshmidt, B.F., Sleisenger, M.H. (Ed.): *Sleisenger & Fordtran's Gastrointestinal and Liver Disease: Pathology/Diagnosis/Management*. Philadelphia, WB Saunders, pp. 1480.
- McKibbin, R.S., Muttucumar, N., Paul, M.J., Powers, S.J., Burrell, M.M., Coates, S., Purcell, P.C., Tiessen, A., Geigenberger, P., Halford, N.G. (2006). Production of high-starch, low-glucose potatoes through over-expression of the metabolic regulator SnRK1. *Plant. Biotech. J.*, 4, 409–418.
- Moses, V., Brookes, G. (2013). The world of "free from GMOs". *GM Crops & Food*, 4(3) Special Issue on Consumer Affairs. <https://www.tandfonline.com/doi/abs/10.4161/gmcr.25992>.
- Mościcki, L., Mitrus, M., Wojtowicz, A., Oniszczyk, T., Rejak, A. (2009). Extrusion-Cooking of Starch. Chapter 13 in: *Advances in Agrophysical Research*. Grundas, S., Stępniewski, A. (ed.), 319–346.
- Neary, N.M., Small, C.J., Druce, M.R., Park, A.J., Ellis, S.M., Semjonous, N.M., Dakin, C.L., Filipsson, K., Wang, F., Kent, A.S., *et al.* (2005). Peptide YY3–36

- and glucagon-like peptide-17–36 inhibit food intake additively. *Endocrinology*, 146, 5120–5127.
- Noah, L., Lecannu, G., David, A., Kozłowski, F., Champ, M. (1999). *Reproduction Nutrition Development, EDP Sciences*, 39(2), 245–254.
- Priebe, M.G., Wang, H., Weening, D., Weening, D., Scheppers, M., Preston, T., Vong R.J. (2010). Factors related to colonic fermentation of no digestible carbohydrates of a previous evening meal increase tissue glucose uptake and moderate glucose-associated inflammation. *Am. J. Clin. Nutr.*, 91, 90–97.
- Ravussin, Y., Koren, O., Spor, A., LeDuc, C., Gutman, R., Stombaugh, J., Knight, R., Ley, R.E., Leibel, R.L. (2012). Responses of gut microbiota to diet composition and weight loss in lean and obese mice. *Obesity (Silver Spring)*, 20, 738–747.
- Regmi, P.R., van Kempen, T.A., Matte, J.J., Zijlstra, R.T. (2011). Starch with high amylose and low in vitro digestibility increases short-chain fatty acid absorption, reduces peak insulin secretion, and modulates insulin secretion in pigs. *J. Nutr.*, 141, 398–405.
- Robertson, M.D., Bickerton, A.S., Dennis, A.L., Vidal, H., Frayn, K.N. (2005). Insulin-sensitizing effects of dietary resistant starch and effects on skeletal muscle and adipose tissue metabolism. *Am. J. Clin. Nutr.*, 82, 559–670.
- Roder, N., Gerard, C., Verel, A., Bogracheva, T.Y., Hedley, C.L., Ellis, P.R., Butterworth, P.J. (2009). Factors affecting the action of alpha-amylase on wheat starch: Effects of water availability. An enzymic and structural study. *Food Chem.*, 113, 471–478.
- Saksena, S., Dwivedi, A., Gill, R.K., Singla, A., Alrefai, W.A., Malakooti, J., Ramaswamy, K., Dudeja, P.K. (2009). PKC-dependent stimulation of the human MCT1 promoter involves transcription factor AP2. *Am. J. Physiol. Gastrointest Liver Physiol.*, 296, 275–283.
- Sawicka, B., Johar, K., Sood, P.P., Gupta, P.D. (2017). Imbalance of gut microbiota induces cancer: A Review. *J. Cell Tissue Res.*, 17(2), 6073–6084.
- Scharlau, D., Borowicki, A., Habermann, N., Hofmann, T., Klenow, S., Miene, C., Munjal, U., Stein, K., Gleib, M. (2009). Mechanisms of primary cancer prevention by butyrate and other products formed during gut flora-mediated fermentation of dietary fibre. *Mutat. Res.*, 682, 39–53.
- Shen, L., Keenan, M.J., Martin, R.J., Tulley, R.T., Raggio, A.M., McCutcheon, K.L., Zhou, J. (2009). Dietary resistant starch increases hypothalamic POMC expression in rats. *Obesity (Silver Spring)*, 17, 40–45.
- Shen, L., Keenan, M.J., Raggio, A., Williams, C., Martin, R.J. (2011). Dietary-resistant starch improves maternal glycemic control in Goto-Kakazaki rat. *Mol. Nutr. Food Res.*, 55, 1499–1508.
- Shimotoyodome, A., Suzuki, J., Fukuoka, D., Tokimitsu, I., Hase, T. (2010). RS4-type resistant starch prevents high-fat diet-induced obesity via increased hepatic fatty acid oxidation and decreased postprandial GIP in C57BL/6J mice. *Am. J. Physiol. Endocrinol. Metab.*, 298, 652–662.
- Styszko, L., Kamasa, J. (2006). Relacje pomiędzy odpornością odmian ziemniaka na patogeny a plonem skrobi w latach o różnym poziomie plonowania. *Progress in Plant Protection / Postępy w Ochronie Roślin*, 46(2), 512–516.
- Tachon, S., Zhou, J., Keenan, M., Martin, R., Marco, M.L. (2013). The intestinal microbiota in aged mice is modulated by dietary resistant starch and correlated with improvements in host responses. *FEMS Microbiol. Ecol.*, 83, 299–309.
- Taiz, L., Zeiger, E., Møller, I.M., Murphy, A. (2015). *Starch Architecture*. Topic 8.13. [in:] *Plant Physiology and Development*, Six<sup>th</sup> Edition, L. Taiz, E. Zeiger, I.M. Møller, A. Murphy (eds.), *Plant Physiology and development 3.html*.
- Tester, R.F., Karkalas, J., Qi, X. (2014). Starch – composition, fine structure and architecture. *J. Cereal Sci.*, 39, 151–165.
- Tetlow, I.J. (2018). *Starch Biosynthesis in Crop Plants*. *Agronomy*, 8(81), 1–4.
- Ulmus, M., Adapa, S., Önning, G., Nilsson, L. (2012b). Gastrointestinal conditions influence the solution behaviour of cereal  $\beta$ -glucans in vitro. *Food Chem.*, 130, 536–540.
- Ulmus, M., Önning, G., Nilsson, L. (2012a). Solution behavior of barley  $\beta$ -glucan as studied with asymmetrical flow field-flow fractionation. *Food Hydrocoll.*, 26, 175–180.
- USDA (2014). *Composition of Foods Raw, Processed, Prepared USDA National Nutrient Database for Standard Reference, Release 27. Documentation and User Guide*, August 2014, Revised, May 2015 [https://www.ars.usda.gov/ARUserFiles/80400525/Data/SR27/sr27\\_doc.pdf](https://www.ars.usda.gov/ARUserFiles/80400525/Data/SR27/sr27_doc.pdf) (accessed: 11.07.2018)
- USDA (2018). *USDA Food Composition Databases*. <https://ndb.nal.usda.gov/ndb/>.
- Vilaplana, F., Hasjim, J., Gilbert, R.G. (2012). Amylose content in starches: Toward optimal definition and

- validating experimental methods. *Carbohydr. Polym.*, 88, 103–111.
- Waldron, M., Nonnecke, B.J., Nishida, T., Horst, R.L., Overton, T.R. (2003). Effect of lipopolysaccharide infusion on serum macromineral and vitamin D concentrations in dairy cows. *J. Dairy Sci.*, 86, 3440–3446.
- Wickramasinghe, H.A.M., Blennow, A., Noda, T. (2009). Physico-chemical and degradative properties of in-planta restructured potato starch. *Carbohydr. Polym.*, 77, 118–124.
- Wischnmann, B., Blennow, A., Madsen, F., Jørgensen, K., Poulsen, P., Bandsholm, O. (2005). Functional characterization of potato starch modified by specific in planta alteration of the amylopectin branching and phosphate substitution. *Food Hydrocoll.*, 19, 1016–1024.
- Zhang, L., Häusler, R.E., Greiten, C., Hajirezaei, M.R., Haferkamp, I., Neuhaus, H.E., Flügge, U.I., Ludewig, F. (2008). Overriding the co-limiting import of carbon and energy into tuber amyloplasts increases the starch content and yield of transgenic potato plants. *Plant Biotech. J.*, 6, 453–464.
- Zhao, X., Andersson, M., Andersson, R. (2018). Resistant starch and other dietary fiber components in tubers from a high amylose potato. *Food Chem.*, 251, 58–63.
- Zhou, J., Hegsted, M., McCutcheon, K.L., Keenan, M.J., Xi, X., Raggio, A.M., Martin, R.J. (2006). Peptide YY and proglucagon mRNA expression patterns and regulation in the gut. *Obesity (Silver Spring)*, 14, 683–693.
- Zhou, J., Keenan, M.J., Keller, J., Fernandez-Kim, S.O., Pistell, P.J., Tulley, R.T., Raggio, A.M., Shen, L., Zhang, H., Martin, R.J., *et al.* (2012). Tolerance, fermentation, and cytokine expression in healthy aged male C57BL/6J mice fed resistant starch. *Mol. Nutr. Food Res.*, 56, 515–518.
- Zhou, J., Martin, R.J., Tulley, R.T., Raggio, A.M., McCutcheon, K.L., Shen, L., Danna, S.C., Tripathy, S., Hegsted, M., Keenan, M.J. (2008). Dietary resistant starch upregulates total GLP-1 and PYY in a sustained day-long manner through fermentation in rodents. *Am. J. Physiol. Endocrinol. Metab.*, 295, 1160–1166.
- Zhou, J., Martin, R.J., Tulley, R.T., Raggio, A.M., Shen, L., Lissy, E., McCutcheon, K., Keenan, M.J. (2009). Failure to ferment dietary resistant starch in specific mouse models of obesity results in no body fat loss. *J. Agric. Food. Chem.*, 57, 8844–8851.

## SKROBIA OPORNA W ZIEMNIAKU

### ARTYKUŁ PRZEGLĄDOWY

#### Streszczenie

Skrobia i włókna dietetyczne, a także węglowodany, które nie są trawione i wchłaniane w jelicie cienkim, są chemicznie niejednorodnymi składnikami pochodzącymi z roślin spożywanych przez ludzi. Te składniki chemiczne przechodzą pełny lub częściowy proces fermentacji w jelicie grubym. Skrobia i inne węglowodany są głównymi źródłami energii we wszystkich dietach, podczas gdy polisacharydy ściany komórkowej są głównymi składnikami błonnika pokarmowego. W pracy przeanalizowano rolę skrobi i innych węglowodanów w diecie człowieka pod względem struktury i rozmieszczenia w tkankach, modyfikacji tych składników podczas przetwarzania żywności oraz wpływu na właściwości funkcjonalne w żywieniu człowieka oraz ich zachowania w przewodzie pokarmowym. Ziemniaki i inne produkty skrobiowe mogą odgrywać dużą rolę w zapobieganiu hiperglikemii, jeśli glukoza pochodząca od skrobi jest uwalniana do krążenia w bardzo powolny sposób. Odmiany skrobiowe ziemniaka są zatem ważne nie tylko dla przemysłu skrobiowego, ale również w diecie człowieka.

**Słowa kluczowe:** błonnik pokarmowy, korzyści zdrowotne, polisacharydy nieskrobiowe, skrobia oporna, wartości odżywcze, wolno dostępna skrobia, ziemniak