

Potential Health Benefits of Potato Starch

Miquel Nofrarias^{1*} • Daniel Martínez-Puig² • José F. Pérez³

¹ Centre de Recerca en Sanitat Animal (CRESA), UAB-IRTA, Campus de la Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain

² Bioiberica S.A., Palafròls, Barcelona, Spain

³ Departament de Ciència Animal i dels Aliments, Universitat Autònoma de Barcelona, 08193 Bellaterra, Spain

Corresponding author: * miquel.nofrarias@cresa.uab.cat

ABSTRACT

Starch is considered a major source of available energy in the human diet. In potato, starch content varies from 70 to 90% on a dry matter basis depending on the botanical variety. The traditional view of starch digestion is that to a large extent starch is rapidly digested. However, a variable fraction of ingested starch can escape digestion in the foregut, and ferment later in the hindgut (RS, resistant starch). Raw potato starch is largely considered as a high RS ingredient. However, potato is mostly consumed processed, which gelatinizes starch at different extents, and this will have an effect on the composition and nutritional values (glycemic index and RS content). In general, processed potato has high levels of digestible starch, although the values may decrease with an increased time of storage after cooking. RS is becoming more desirable in the human diet because of its relevance to health, on the prevention and control of some digestive and metabolic disorders. RS intake, in substitution to digestible starch, seems to decrease postprandial glycemic and insulinemic responses, improve whole body insulin sensitivity, increase satiety, lower plasma cholesterol and triglyceride concentrations, and reduce fat storage. RS has also been associated with protective effects on chronic colonic diseases, including reduction of colon cancer risk and in the treatment of bowel inflammatory conditions. In summary, this review presents the current understanding of potato starch and potential health benefits which are likely to be associated with intake of resistant potato starch.

Keywords: bowel disease, dietary fiber, fermentation, gelatinization, glycemic index, resistant starch

Abbreviations: GI, glycemic index; NSP, non-starch polysaccharides; RDS, rapidly digestible starch; RS, resistant starch; SCFA, short-chain fatty acids; SDS, slowly digestible starch

CONTENTS

INTRODUCTION.....	1
POTATO STARCH COMPOSITION AND DIGESTIBILITY	1
GELATINIZATION OF STARCH.....	3
FERMENTATION OF POTATO RESISTANT STARCH.....	4
POTENTIAL HEALTH BENEFITS OF POTATO STARCH.....	5
REFERENCES.....	6

INTRODUCTION

Starch is considered a major source of available energy in the human diet (Noda *et al.* 2008). This is not only a consequence of its high abundance in cereals, some legume grains and potatoes (*Solanum tuberosum* L.), but also because of its high energy content and digestibility (Hizukuri 1996). In potatoes, the starch content varies from 70 to 90% based on dry matter, depending on the botanical variety.

The traditional view of starch digestion is that starch to a large extent is rapidly digested. However, the kinetics and extent to which starch is digested depends on its composition and physicochemical characteristics. Moreover, it is known that a variable fraction of ingested starch can escape digestion in the foregut, and ferment later in the hindgut. Thus, starch has been classified as rapidly digestible starch (RDS), slowly digestible starch (SDS), and resistant starch (RS) to specify the characteristics of starch and physiological relevance (Englyst *et al.* 1992). The glycemic index is related to the amount of RDS, while SDS and RS are becoming more desirable in the human diet because of their relevance to health and the prevention and control of some digestive and metabolic disorders, such as obesity, diabetes,

coronary heart disease and the colonic cancer (Cummings *et al.* 1996; Kendall *et al.* 2004). Raw potato starch is largely considered as a high RS ingredient. However, potato is mostly consumed processed in different ways: boiled, oven baked, or fried, alone as well as with other foods. Processing will gelatinize starch at different extents, and this will have an effect on the composition and nutritional values (glycemic index and RS content).

This review presents the current understanding of potato starch, its composition and nutritional characteristics in different ways of consumption, which will have an effect on the digestive processes and on potential health benefits which are likely to be associated.

POTATO STARCH COMPOSITION AND DIGESTIBILITY

Pure starch consists of α -glucan chains in the form of amylose and amylopectin. Amylose is essentially a linear molecule, with a molecular weight between $1 \times 10^5 - 1 \times 10^6$ kDa (Tester *et al.* 2004) in which D-glucose monomers (1000 on average) are mainly linked (~99%) by $\alpha(1-4)$ glucosidic bonds, except a small fraction (~1%) of $\alpha(1-6)$. Amylopectin is a much larger molecule (molecular weight $\sim 1 \times 10^7 -$

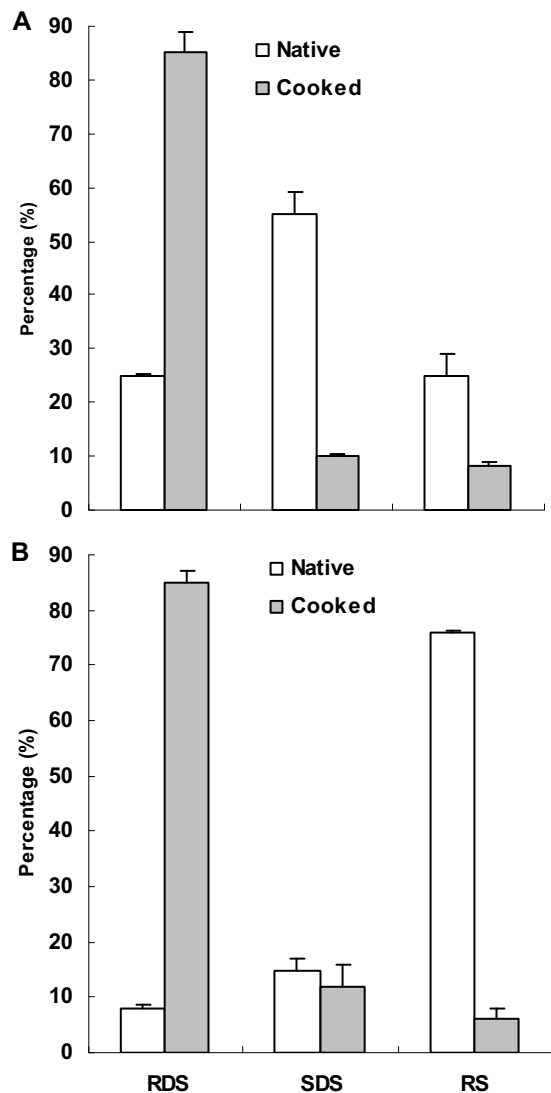


Fig. 1 Digestion profiles of native and cooked (A) normal maize and (B) potato starches. RDS, SDS, and RS, respectively, represent rapidly digestible starch, slowly digestible starch, and resistant starch based on the Englyst assay. Redrawn from Zhang G, Venkatachalam M, Hamaker BR (2006) Structural basis for the slow digestion property of native cereal starches. *Biomacromolecules* 7, 3259-3266, with kind permission of the American Chemical Society and authors, ©2006.

1×10^9) and with a higher ratio of branched bonds (~5%). Depending on the botanical origin of starch, differences in the amylose/amylopectin composition and levels of structure may govern the pattern and rate of the starch hydrolysis. While most native cereal starches are characterized by their slow digestion property (SDS >50%), raw potato starch shows a high resistance to α -amylase (Fig. 1, Zhang *et al.* 2006). In both cases, the disruption of the native starch organization by thermal processes leads to a loss of the slow digestion property and produces a huge increase in RDS.

Research has shown that structural features of the raw starch granule have a major influence on the susceptibility of starch during bacterial or pancreatic α -amylolysis (Zhang *et al.* 2006). The enzymes involved in the solid-solution reaction first need to diffuse toward and bind the solid structure to cleave the glycosidic linkages. In plants, starch is compacted in spherical granules with a smooth surface constituted by final starch chains in a protein matrix. Differences in the granular structure of starches from different plant sources include shape, size and porosity (pores and channels within the starch granules). Potato granules are oval or spherical in shape and have a diameter of up to 75 μm , while cereal granules are smaller (5-35 μm) and polyhedral, and the legume ones (15-80 μm) are kidney shaped (Fig. 2, Robyt 1997). Potato starch granules are very large

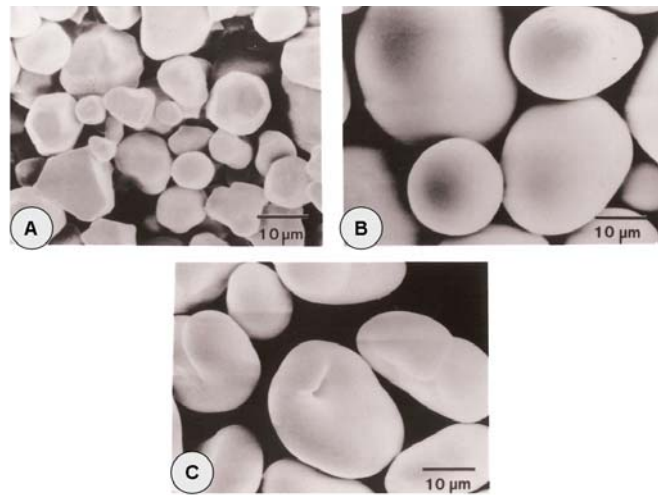


Fig. 2 Scanning micrographs of starch granules. (A) Corn, (B) potato, (C) pea. Reprinted from Robyt JF (1997) Polysaccharides I: Structure and Function. *Essentials of Carbohydrate Chemistry*, p 157-227, with kind permission of Springer-Verlag and author, ©1997.

and therefore have low surface areas relative to volume compared to cereal starch granules, resulting in a reduced area exposed to attacking enzymes. However there are important differences in starch potato granule size depending on cultivars and environmental factors. In general, it is accepted that tubers grown in regions with lower temperatures resulted in starches with larger granule sizes (Singh *et al.* 2008).

The properties of the starch granules are the result of a well organized structure. Starch granules are composed of a large number of small, randomly orientated crystalline regions in an amorphous matrix. The first level of organization is the arrangement of the side chains of amylopectin into clusters (French 1984). These clusters are part of the crystalline and amorphous lamellae. In the crystalline lamellae the long amylopectin chains form double helices, while the branching points and the shortest amylopectin chains are located in the amorphous lamellae (Fig. 3, Gallant *et al.* 1997). Crystalline and amorphous lamellae are organized into spherical structures termed blockets, which are proposed to be the next level of granule organization (Gallant *et al.* 1997). The blocket structures are in turn organized into growth rings, which are layers of semi-crystalline and crystalline shells visible by light microscopy. Finally, the starch polymers are arranged radially with their molecular axes aligned perpendicular to the growth rings and the granule surface (Baker *et al.* 2001).

X-ray diffraction analysis provides different types of spectral patterns depending on the origin of the starch: most cereal starches yield the A-type pattern, potato and part of the tuber starches the B-type, whereas most legume starches yield an intermediate C-type which is a mixture of A and B (Gernat *et al.* 1990). Starches with B- and C-type patterns are more resistant to digestion than A-type ones (Topping and Clifton 2001). Spectral patterns reflect the crystalline structures, because it is well known that amylopectin is the molecule that forms the crystallites in starch granules and that the length of their molecules is highly correlated with its fine structure. In a debranched profile of starch, different fractions can be identified, such as amylose, long chain amylopectin (degree of polymerization, dp ~50-60) and short chain (dp <25-30) amylopectin (Zhang *et al.* 2006). Large and small amounts of short chain fractions are associated with A- and B-type X-ray diffraction (Buléon *et al.* 1998). Ratios of ~3 and ~1.5 of short to long chain amylopectin fractions are described for cereal and potato starch, respectively.

The shortest chains with a degree of polymerisation of 5-10 cannot form stable double helices, and may disrupt the

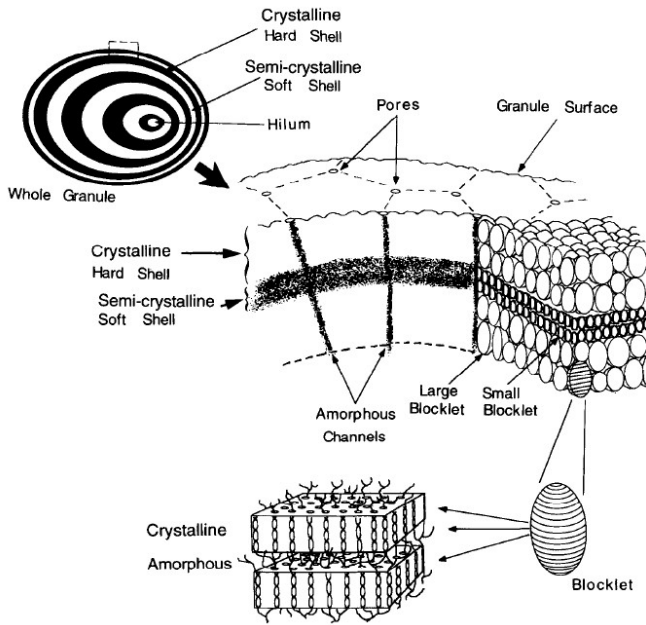


Fig. 3 Overview of starch granule organization. Reprinted from Gallant DJ, Bouchet B, Baldwin PM (1997) Microscopy of starch: evidence of a new level of granule organization. *Carbohydrate Polymers* 32, 177-191, with kind permission of Elsevier and authors, ©1997.

formation of an ordered crystalline structure. On the other hand, long chains which are used to connect adjacent clusters are considered a quantitative indicator of crystalline perfection (Gerard *et al.* 2001). As described above, potato starch is characterized by a higher proportion of long chain amylopectin with longer chains in comparison with cereals. These long chains allow a fine crystalline structure with shorter flexible spacers than the A-type starch. Shorter flexible spacers decrease the mobility of starch and lead to lower α -amylase accessibility and higher RS content of the potato starch granule.

Another factor that helps explain the low digestibility of

raw potato starch is its high concentration of covalently bound phosphate compared to other starches (Hizukuri *et al.* 1970). Amylolytic enzymes are incapable of bypassing the phosphorylated glucosyl residue, so phosphoryl-oligosaccharides are released from the digestion of potato starch with amylase (Kamasaka *et al.* 1995). For all these reasons, raw potato starch is classified as RS type 2 (RS granules) according to the classification published in 1992 by Englyst.

GELATINIZATION OF STARCH

Potato for human consumption is processed in different ways, boiled, oven-baked or fried. The main result of these processes is gelatinization of starch and the disruption of the starch granules. It is well known that when native starches are heated at low or moderate levels of moisture, the crystalline structures within the starch granule lose order. This process is referred to as melting and occurs at temperatures that vary depending on the moisture and origin of the starch. In the absence of water, melting temperatures exceed 150°C but fall to 100-120°C at 20% moisture (Annisson and Topping 1994). When starch is heated in excess water the granules undergo a characteristic structural reorganization, which occurs as a two stage process. The first stage involves the swelling of the granule that leads to the loss of organized structure (loss of A and B patterns). Ultimately granule structure is completely lost and a thin paste or gel is formed. At the molecular level the process is explained by hydrating double helices as a consequence of elevated temperatures. Scanning electron microscopy studies of potato starch have revealed a honeycombed-like structure that appears in the granules as they gelatinize (Tester *et al.* 2004). Above 90°C, a marked loss of granular structure occurs, although the starch granules may remain as fragments comprised of amylopectin suspended in a solution of amylose (Liu and Zhao 1990). This process makes the starch completely digestible by starch hydrolyzing enzymes (Fig. 1). The binding step of amylase is of kinetic significance when the enzyme is acting on a particular granular or supra-molecular structure, but when acting on soluble starch fragments, the reaction can be described by conventional Michaelis-Menten kinetics (i.e. the rate is directly proportional to the enzyme concentration).

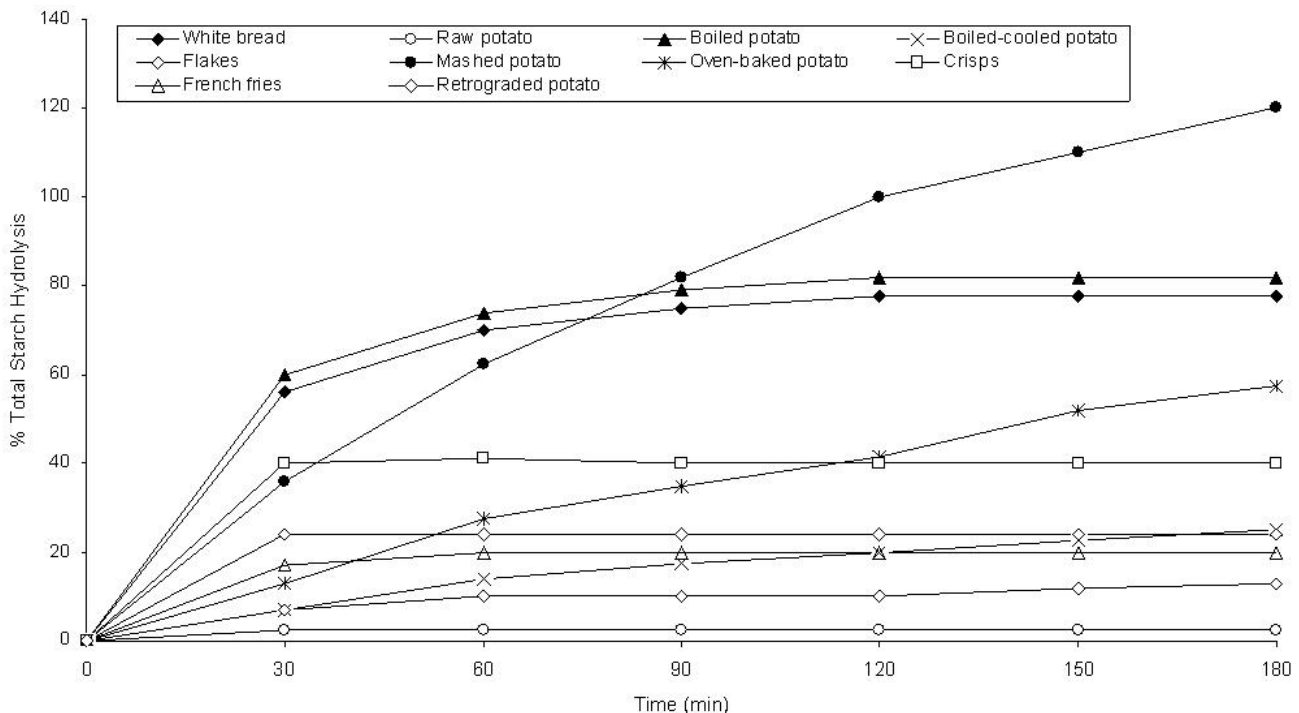


Fig. 4 Percentage of *in vitro* total starch hydrolysis in cooked potatoes in comparison with white bread as a reference food. Reprinted from García-Alonso, Goñi I (2000) Effect of processing on potato starch: *In vitro* availability and glycaemic index. *Nahrung* 44, 19-22, with kind permission of Wiley-VCH Verlag GmbH & Co. KGaA and authors, ©2000.

Table 1 Total, resistant (RS) and digestible (DS) starch content in potato samples processed in different ways. Results are mean \pm SD (on dry matter) of 4 assays. Reprinted and adapted from Garcia-Alonso A, Goñi I (2000) Effect of processing on potato starch: In vitro availability and glycaemic index. *Nahrung* 44, 19-22, with kind permission of Wiley-VCH Verlag GmbH & Co. KGaA and authors, ©2000.

Potato	Total starch (%)	Resistant starch	Digestible starch (%) ¹	Moisture (%)
Raw	79.36 \pm 5.75 d	69.05 \pm 1.76 h	10.31	81.25
Boiled	79.36 \pm 5.75 d	1.18 \pm 0.09 a	78.18	81.25
Boiled and cooled	75.18 \pm 2.94 cd	4.63 \pm 0.99 e	70.55	79.43
Raw flakes	71.97 \pm 1.10 c	2.80 \pm 0.21 cd	68.57	8.59
Mashed	71.97 \pm 1.10 c	2.08 \pm 0.18 bc	69.89	86.23
Oven-baked	65.91 \pm 3.23 b	3.70 \pm 0.84 d	62.20	79.63
French-fries	59.34 \pm 6.31 a	6.64 \pm 0.63 f	52.70	17.69
Crisps	65.42 \pm 1.45 b	3.27 \pm 0.79 d	65.15	2.57
Retrograded	79.36 \pm 5.75 d	10.38 \pm 0.08 g	68.98	4.32

¹Digestible starch is the difference between total and resistant starch. Different letters in a column denote significant differences ($P < 0.05$).

Table 2 Effect of various processing methods and storage temperatures on starch digestibility in potato (*Solanum tuberosum*) flour. RDS and SDS, respectively, represent rapidly digestible starch and slowly digestible starch. Reprinted and adapted from Niba LL (2003) Processing effects on susceptibility of starch to digestion in some dietary starch sources. *International Journal of Food Sciences and Nutrition* 54, 97-109, with kind permission of Taylor & Francis and the author, ©2003.

Digestibility (g/100 g)	Raw	Autoclaved	Microwaved	Parboiled	Stored at ambient temperature (10 days)			Stored frozen (10 days)		
					Autoclaved	Microwaved	Parboiled	Autoclaved	Microwaved	Parboiled
RDS	3.04 a	13.6 cd	8.44 abc	16.0 cd	10.7 bc	5.64 ab	7.96 abc	17.5 d	4.60 ab	15.9 cd
SDS	15.9 ab	14.6 a	14.2 a	23.4 bc	25.3 cd	12.2 a	13.6 a	33.8 e	17.0 ab	32.6 de
Total starch	43.1 abc	44.7 abc	39.0 abc	54.2 c	36.1 ab	32.3 a	47.0 abc	36.7 ab	31.3 a	51.9 bc

Means within a row with different letters are significantly different ($P < 0.05$).

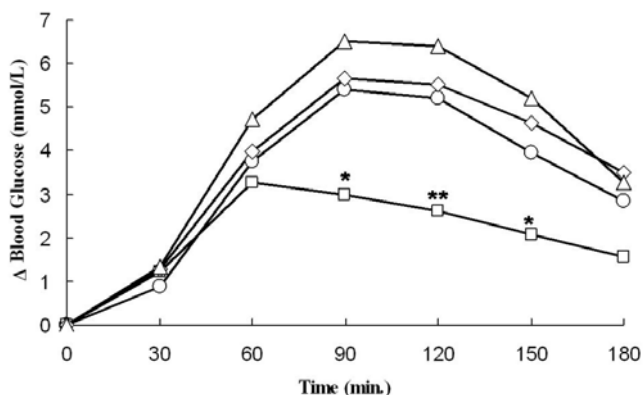


Fig. 5 Blood glucose rise above baseline after white bread O—O; hard toasted bread Δ—Δ; pizza ◇—◇; and potato dumplings □—□; * $P < 0.05$, ** $P < 0.01$ potato dumplings versus white bread. Reprinted from Riccardi G, Clemente G, Giacco R (2003) Glycemic index of local foods and diets: the Mediterranean experience. *Nutrition Reviews* 61, S56-S60, with kind permission of International Life Sciences Institute and authors, ©2003.

However, different processing techniques may affect the level of RS yielded as well as the glycemic index (GI). Garcia-Alonso and Goñi (2000) measured changes observed in the digestible and indigestible starch fractions and in the kinetics of digestion in potatoes processed in different ways (Fig. 4). In general, processed potato has high levels of digestible starch (Table 1), although the values may decrease with the time of storage. Boiled or mashed potato (instant potato) showed the highest rates of digestion similar to those of white bread. In general, modern methods of processing affect the rate of digestion and subsequent blood glucose profile. Thus, instant potato, which is prepared under repeated wetting and drying may promote higher GI than conventionally cooked potato, which generally involves less physical disruption and only moderate heat (Brand *et al.* 1985). On the other hand, potato dumplings, a typical potato and wheat food, used as a substitute for pasta has been described to promote reduced plasma glucose as compared to white bread, hard toasted bread, pizza (Fig. 5, Riccardi *et al.* 2003) or boiled potatoes (Parillo *et al.* 1985).

Frying potatoes in hot oil decreases the rate of starch hydrolysis, with home cooked (French fries) showing lower

values than crisps (Garcia-Alonso and Goñi 2000) or boiled potatoes (Leeman *et al.* 2008). Goñi *et al.* (1997) established a relationship between thickness and the RS content of fried potatoes ($RS = 2.24 + 0.54 \times (\text{thickness, mm})$), the levels of RS being higher in thicker French fries.

Usually, processed starchy foods undergo a period of storage between cooking and consumption. During this period, the amylose and amylopectin molecules of gelatinized starches can re-associate to form a gel (Miles *et al.* 1985). Gel formation is a dynamic process, because crystallinity within the gel increases with time. This crystallinity is referred to as retrogradation and can be detected by X-ray diffraction as a B-type pattern. Retrogradation may take from several hours, in the case of high amylose starches, to several days, in the case of high amylopectin starches (Annisson and Topping 1994). By repeating the heating and cooling cycles, retrogradation can be increased extending crystalline regions of α -glucan. Enzymatic treatment of retrograded starch with α -amylases breaks down non-retrograded starch, leaving a fraction that is enzymatically indigestible that has been called RS (Russell *et al.* 1989). The result is a reduction in the amount of the RDS and an increase in the amount of the SDS and the RS (Table 2, Fig. 4).

FERMENTATION OF POTATO RESISTANT STARCH

From the above references, it is clear that potato may be considered a main source of RS for the human large bowel, either by incomplete gelatinization of raw potato starch or by retrogradation. In Western countries, it has been estimated that the amount of resistant starch, as a potential substrate for bacteria, may range between 8-40 g/day, in comparison with the amount of non-starch polysaccharides (NSP) (8-18 g/day) or oligosaccharides (2-8 g/day) (Cummings and Englyst 1991). Of the typical starchy foods, the highest RS concentration is found in the legume grains (95-111 g/kg total starch basis, Liljeberg 2002), green bananas (527 g/kg, Langkilde *et al.* 2002) or commercially processed potato products (48-59 g/kg, Liljeberg 2002). Among the cereal products, intact rye grain bread, barley flakes or semolina porridge are identified as having RS levels in the high range (45-60 g/kg, Liljeberg 2002). Slightly lower values are observed in other cereal products (Englyst *et al.* 2003), such as breakfast cereals (33 g/kg), cornflakes (49 g/kg), bakery products and crackers (33 g/kg) and biscuits (32 g/kg). It is

generally accepted that as more starch is eaten, more enters the colon (Chapman *et al.* 1985), and it is thought that ~10% of dietary starch may escape digestion in the human small intestine (Topping and Clifton 2001).

Different studies have shown that RS is largely digested in the colon in most individuals. In a study by Cummings *et al.* (1996), RS was extensively digested in 27 of 34 diet periods of 15-days, but five subjects were unable to break down one or two of the RS sources. Fermentation of RS was associated with a significant increase of the stool wet weight by 1.6 g/d per g RS fed for potato, but this was significantly less than bran at 4.9 g/d per g NSP. RS consumption was also associated with a significant increase in the fecal excretion of N, short-chain fatty acids (SCFA) and NSP. The fermentation of RS in the colon may allow an increased microbial biomass throughout the colon, concomitantly with a higher excretion of N in feces and a lower excretion of urinary N. It is well known that bacteria inhabiting the colon of single-stomached animals obtain their energy mainly from dietary carbohydrates escaping foregut digestion. As fermentable carbohydrates decline in concentration along the length of the colon, bacteria switch to the degradation of proteinaceous material and bacteria autolysis (Gibson and Roberfroid 1995; Martínez-Puig *et al.* 2003).

SCFA (mainly acetic, propionic and butyric acids) are formed during microbial fermentation of carbohydrates in the colon. Starches have been shown to produce high proportions of butyric acid by *in vitro* fermentation with human faecal inocula (Casterline *et al.* 1997). Different *in vivo* trials have also shown an increased faecal excretion of butyrate in normal human subjects (Noakes *et al.* 1996) and animals (Henningson *et al.* 2003). It is accepted that RS from different sources and bran from wheat or oat, stimulate the formation of butyrate (Bach Knudsen *et al.* 1993), while xylans and pectin rich fractions (sugar-beet pulp) are all associated with a relatively low level of butyrate (Anguita *et al.* 2007). Among different sources of RS, only raw potato starch gave an increased faecal proportion of butyric acid (Cummings *et al.* 1996), which reflects that production of butyric acid and utilization of butyrate by the colonic mucosa may vary between sources of RS (Martin *et al.* 2000). Henningson *et al.* (2003) have also shown an increase in the proportion of butyric acid in the hindgut of rats with longer adaptation periods (42 *vs.* 13 days).

POTENTIAL HEALTH BENEFITS OF POTATO STARCH

There are well established beneficial effects of the dietary fiber, i.e. NSP and RS, on some major digestive and metabolic diseases in humans (Cummings *et al.* 1996). Different reports have described the influence of RS consumption on the prevention of digestive pathogens or diarrhea (Williams *et al.* 2001). For example, there is recent evidence that giving RS orally to human patients with cholera increases fecal SCFA concentration and shortens the duration of diarrhea (Ramakrishna *et al.* 2000). RS has also been associated with protective effects on chronic colonic diseases, including reduction of colon cancer risk and in the treatment of ulcerative colitis (Cassidy *et al.* 1994; Hylla *et al.* 1998; Topping and Clifton 2001; Champ 2004). The main mechanisms cited are the ability of RS to increase fecal bulk (Cummings *et al.* 1996), increase the molar ratio of butyrate in relation to other SCFA and dilute fecal bile acids (Van Munster and Nagengast 1993). Accordingly, raw potato starch may reduce indices associated with damage to epithelial cells, such as crypt cell proliferation and magnesium excretion, whereas it may increase mucin sulfation, which promotes epithelial protection (Nofrarias *et al.* 2007).

Increases in stool weight have a diluting effect on potential carcinogens and irritant compounds, and epidemiologic studies have shown a reduced risk of colon cancer under these circumstances (Cummings *et al.* 1992). However, due to its high fermentability, the contribution of RS to the bulk of digesta is low (Le Leu *et al.* 2002). It has

been reported that RS has mildly laxative properties, equivalent to the less effective forms of NSP, oligosaccharides or inulin (Gibson *et al.* 1995; Mortensen and Nielsen 1995). In contrast to NSP, the mode of action of RS in the colon is fermentation, bacterial growth and SCFA production; while NSP affect colonic function by fermentation and/or the water-holding capacity of unfermented polysaccharides structures (Adiotomre *et al.* 1990) and/or mechanical factors (Bardon and Fioramonti 1983).

A reduction in digesta cytotoxicity could also be explained by the reduction of secondary bile acids formation (Van Munster *et al.* 1994; Hylla *et al.* 1998) or protein fermentation which is known to produce toxic end-products (Lin and Visek 1991; Goovers *et al.* 1999). Raw potato starch provides a large amount of RS available for colon fermentation, which is known to reduce protein fermentation (Martínez-Puig *et al.* 2003). However, there is no consensus on the ability of RS to reduce the luminal concentration of compounds that are damaging to the colonic mucosa, including fecal ammonia, phenols, and N-nitroso compounds (Kendall *et al.* 2004).

As described above, it is well known that the fermentation of RS produces large amounts of butyrate in the colon of humans and other single-stomach animals (Scheppach *et al.* 1988; van Munster *et al.* 1994; Noakes *et al.* 1998; Le Blay *et al.* 1999; Martínez-Puig *et al.* 2007). Butyrate, as the preferential colonocyte energy source (Roediger 1995), contributes to the maturation of colonic epithelium (Cherbuy *et al.* 1995) and to mucosal regeneration in the event of atrophy (Tappenden *et al.* 1997). By modulating proliferation, differentiation and apoptosis (Kruh *et al.* 1995; Luciano *et al.* 1996; Hass *et al.* 1997; Mentschel and Claus 2003; Nofrarias *et al.* 2007), butyrate assists in the maintenance of a normal cell phenotype and also in preventing the development of abnormal or neoplastic cell populations (Roediger and Millard 1995; Wachtershauser and Stein 2000; Topping and Clifton 2001). Apparently, the conditions in the colonic lumen, and particularly butyrate concentration, may have a major influence on colonic oncogenesis (Hill 1995). Epidemiological studies performed across 12 countries worldwide have shown an apparent relationship ($r = -0.70$, $P < 0.001$) between increased starch consumption and the diminished risk of colorectal cancer (Cassidy *et al.* 1994). However, the experimental evidence of a benefit of starch on colorectal cancer is not so strong. Data obtained from cancer patients in humans are inconclusive due to the absence of information of SCFA concentrations in the digestive tract. The evidence from animal experiments of RS feeding on colorectal carcinogenesis is limited and conflicting (Le Leu *et al.* 2003), because very diverse experimental protocols have been used. In rats exposed to carcinogens, Cassidy *et al.* (1997), but not Young *et al.* (1996), observed a reduction in the number of aberrant crypt foci in animals fed a diet containing potato starch. Criticisms of these experiments have referred to the feebleness of the animal models used, such as that derived from the coprophagic behavior of rats (Topping and Clifton 2001). Moreover, it may be important to consider the time required for intestinal microbiota to adapt to a chronic load of a fermentable substrate.

Some studies have indicated that the nature of fiber in the diet can also affect the composition, metabolism and function of the immune cells (Lim *et al.* 1997; Cavaglieri *et al.* 2000). These effects of fiber may be due to changes in the SCFA produced. Butyrate has also been shown to down-regulate the stimulatory function of blood-derived antigen-presenting cells (Bohmig *et al.* 1997), upregulate Kupffer cell PGE₂ production (Pérez *et al.* 1998) and inhibit B-lymphocyte function (Eftidiami *et al.* 1995) and Th1-type responses (Cavaglieri *et al.* 2003). These findings may explain the therapeutic effect of butyrate on inflammatory bowel disease, a pathological condition characterized by a chronic inflammation of the gut mucosa (Cavaglieri *et al.* 2003). Thus, recent studies in the pig model have found that feeding large quantities of raw potato starch reduces colonic

immune reactivity and also levels of blood leukocytes, including T lymphocytes and neutrophils which are increased as a result of inflammation or disease (Nofrarias *et al.* 2007).

The consumption of different types of starch has been shown to be beneficial in a variety of metabolic diseases, such as insulin resistance and diabetes (Higgins *et al.* 1996), plasma cholesterol and triglyceride concentrations (de Deckere *et al.* 1993), and chronic renal or hepatic disease (Younes *et al.* 1997). The amount and kind of ingested carbohydrate can modify ensuing plasma glucose and insulin responses, and raise the possibility that such dietary manipulation may have some therapeutic utility in patients with abnormal carbohydrate and lipid metabolism (Reaven 1979). In particular, RS intake, in substitution to digestible starch, seems to decrease postprandial glycemic and insulinemic responses, improve whole body insulin sensitivity, lower plasma cholesterol and triglyceride concentrations, increase satiety, and reduce fat storage (Higgins 2004). The potato, as a main source of RS in humans, could confer some of the above mentioned health benefits. However, the GI of potatoes is influenced by the variety (i.e. Russet brown potatoes have only a moderately high GI) and the method of cooking (Fernandes *et al.* 2005).

In general terms, processed potato (boiled and mashed – instant-potatoes or French fries) contains higher levels of digestible starch and subsequently induce higher blood glucose profiles than traditional cooked potatoes or potato dumplings, and are comparable to white bread, pasta or pizza (Brand *et al.* 1985; Parillo *et al.* 1985; Garcia and Goñi 2000; Riccardi *et al.* 2003; Leeman *et al.* 2008). In diabetic subjects, the postprandial blood glucose response after raw potato was considerably slower and weaker compared to cooked potato (Vaaler *et al.* 1984). Individuals who wish to minimize dietary GI can be advised to precook potatoes and consume them cold or reheated (Fernandes *et al.* 2005).

Changes on glycemia and insulinemia promote changes on lipid metabolism. Diets with high GI increase lipogenesis in the adipose tissue in normal and to a lesser extent in diabetic rats (Kabir *et al.* 1998). Contrarily, diets rich in RS have reduced fatty acid synthase activity (Morand *et al.* 1994; Takase *et al.* 1994) and fat accretion on epididymal fat pads (de Deckere *et al.* 1993) in a rat model, and lipogenesis in adipose but not in muscular tissues (Martínez-Puig *et al.* 2006) in a pig model. Besides its effect on lipogenesis potato starch has a role on satiety. Some studies have demonstrated that potatoes in general (Kaplan and Greenwood 2002), and boiled or mashed potatoes but French fries in particular (Leeman *et al.* 2008), were more satiating than other carbohydrate sources. Moreover, the replacement of pregelatinized digestible starch with RS from raw potato starch resulted in the subjective sensations of satiety; differences in taste, visual appeal and texture may influence satiety (Raben *et al.* 1994). These properties make RS an attractive dietary target for the prevention of diseases associated with dyslipidemia and insulin resistance as well as the development of weight loss diets and dietary therapies for the treatment of Type 2 diabetes and coronary heart disease.

REFERENCES

- Adiotomre J, Eastwood MA, Edwards CA, Brydon WG (1990) Dietary fibre: *in vitro* methods that anticipate nutrition and metabolic activity in humans. *The American Journal of Clinical Nutrition* **52**, 128-34
- Anguita M, Gasa J, Nofrarias M, Martín-Orúe SM, Pérez JF (2007) Effect of coarse ground corn, sugar beet pulp and wheat bran on voluntary intake and physicochemical characteristics of digesta of growing pigs. *Livestock Science* **107**, 182-191
- Annisson G, Topping DL (1994) Nutritional role of resistant starch: Chemical structure vs. physiological function. *Annual Review of Nutrition* **14**, 297-320
- Bach Knudsen KE, Jensen BB, Hansen I (1993) Digestion of polysaccharides and other major components in the small and large intestine of pigs fed diets consisting of oat fractions rich in β -D-glucan. *The British Journal of Nutrition* **70**, 537-556
- Baker AA, Miles MJ, Helbert W (2001) Internal structure of the starch granule revealed by AFM. *Carbohydrate Research* **30**, 249-256
- Bardon T, Fioramonti J (1983) Nature of the effects of bran on digestive transit time in pigs. *The British Journal of Nutrition* **50**, 685-690
- Bohmig GA, Krieger PM, Saemann MD, Wenhardt C, Pohanka E, Zlabinger GJ (1997) *n*-Butyrate downregulates the stimulatory function of peripheral blood-derived antigen-presenting cells: a potential mechanism for modulating T-cell responses by short-chain fatty acids. *Immunology* **92**, 234-243
- Brand JC, Nicholson P, Thorburn AW, Truswell AS (1985) Food processing and the glycaemic index. *The American Journal of Clinical Nutrition* **42**, 1192-1196
- Buléon A, Colonna P, Planchot V, Ball S (1998) Starch granules: structure and biosynthesis. *International Journal of Biological Macromolecules* **23**, 85-112
- Cassand P, Maziere S, Champ M, Meflah K, Bornet F, Narbonne JF (1997) Effects of resistant starch- and vitamin A-supplemented diets on the promotion of precursor lesions of colon cancer in rats. *Nutrition and Cancer* **27**, 53-59
- Cassidy A, Bingham SA, Cummings JH (1994) Starch intake and colorectal cancer risk: an international comparison. *The British Journal of Cancer* **69**, 937-942
- Casterline JLI, Oles CJ, Ku Y (1997) *In vitro* fermentation of various food fiber fractions. *Journal of Agricultural and Food Chemistry* **45**, 2463-2467
- Cavaglieri CR, Martins EF, Colleone VV, Rodrigues C, Vecchia MG, Curi R (2000) Fiber-rich diets alter rat intestinal leukocytes metabolism. *The Journal of Nutritional Biochemistry* **11**, 555-561
- Cavaglieri CR, Nishiyama A, Fernandes LC, Curi R, Miles EA, Calder PC (2003) Differential effects of short-chain fatty acids on proliferation and production of pro- and anti-inflammatory cytokines by cultured lymphocytes. *Livestock Science* **73**, 1683-1690
- Chapman RW, Sillery JK, Graham MM, Saunders DR (1985) Absorption of starch by healthy ileostomates: effect of transit time and of carbohydrate load. *The American Journal of Clinical Nutrition* **41**, 1244-1248
- Champ MM (2004) Physiological aspects of resistant starch and *in vivo* measurements. *Journal of AOAC International* **87**, 749-755
- Cherbuy C, Darcy-Vrillon B, Morel MT, Pegorier JP, Duec PH (1995) Effect of germfree state on the capacities of isolated rat colonocytes to metabolize butyrate, glucose, and glutamine. *Gastroenterology* **109**, 1890-1899
- Cummings JH, Englyst HN (1991) Measurement of starch fermentation in the human large intestine. *Canadian Journal of Physiology and Pharmacology* **69**, 121-129
- Cummings JH, Bingham SA, Heaton KW, Eastwood MA (1992) Fecal weight, colon cancer risk, and dietary intake of nonstarch polysaccharides (dietary fiber). *Gastroenterology* **103**, 1783-1789
- Cummings JH, Beatty ER, Kingman SM, Bingham SA, Englyst HN (1996) Digestion and physiological properties of resistant starch in the human large bowel. *The British Journal of Nutrition* **75**, 733-747
- de Deckere EA, Kloots WJ, van Amelsvoort JM (1993) Resistant starch decreases serum total cholesterol and triacylglycerol concentrations in rats. *The Journal of Nutrition* **123**, 2142-2151
- Englyst HN, Kingman SM, Cummings JH (1992) Classification and measurement of nutritionally important starch fractions. *European Journal of Clinical Nutrition* **46**, S33-S50
- Englyst KN, Vinoy S, Englyst HN, Lang V (2003) Glycaemic index of cereal products explained by their content of rapidly and slowly available glucose. *The British Journal of Nutrition* **89**, 329-340
- Eftimiadi C, Valente S, Mangiante S, Ferrarini M (1995) Butyric acid, a metabolic end product of anaerobic bacteria, inhibits B-lymphocyte function. *Minerva Stomatologica* **44**, 445-447
- Fernandes G, Velangi A, Wolever TM (2005) Glycemic index of potatoes commonly consumed in North America. *Journal of the American Dietetic Association* **105**, 557-562
- French D (1984) Organization of starch granules. In: Whistler RL, Bemiller JN, Pashall EF (Eds) *Starch: Chemistry and Technology*, Academic, New York, pp 183-245
- Gallant DJ, Bouchet B, Baldwin PM (1997) Microscopy of starch: evidence of a new level of granule organization. *Carbohydrate Polymers* **32**, 177-191
- García-Alonso A, Goñi I (2000) Effect of processing on potato starch: In vitro availability and glycaemic index. *Nahrung* **44**, 19-22
- Gérard C, Colonna P, Buléon A, Planchot V (2001) Amylolysis of maize mutant starches. *Journal of the Science of Food and Agriculture* **81**, 1281-1287
- Gernat C, Rodosta S, Damaschun G, Schierbaum F (1990) Supramolecular structure of legume starches revealed by X-ray scattering. *Starch-Stärke* **42**, 175-178
- Gibson GR, Roberfroid MB (1995) Dietary modulation of the human colonic microbiota: introducing the concept of prebiotics. *The Journal of Nutrition* **125**, 1401-1412
- Goñi I, García-Alonso A, Sauro-Calixto F (1997) Resistant starch in potatoes deep-fried in olive oil. *Food Chemistry* **59**, 269-272
- Hass R, Busche R, Luciano L, Reale E, Engelhardt WV (1997) Lack of butyrate is associated with induction of Bax and subsequent apoptosis in the proximal colon of guinea pig. *Gastroenterology* **112**, 875-881
- Henningson, AM, Margareta E, Nyman GL, Björck IM (2003) Influences of dietary adaptation and source of resistant starch on short-chain fatty acids in the hindgut of rats. *The British Journal of Nutrition* **89**, 319-327

- Higgins JA, Brand Miller JC, Denyer GS (1996) Development of insulin resistance in the rat is dependent on the rate of glucose absorption from the diet. *The Journal of Nutrition* **126**, 596-602
- Hill MJ (1995) Bacterial fermentation of complex carbohydrate in the human colon. *European Journal of Cancer Prevention* **4**, 353-358
- Hizukuri S, Tabata S, Nikuni Z (1970) Studies on starch phosphate: Part 1. Estimation of glucose 6-phosphate residues in starch and the presence of tuber bound phosphate(s). *Starch-Stärke* **22**, 338-343
- Hizukuri S (1996) Starch: analytical aspects. In: Eliasson AC, Dekker M (Eds) *Carbohydrates in Food*, New York, EEUU, pp 347-429
- Hylla S, Gostner A, Dusel G, Anger H, Bartram HP, Christl SU, Kasper H, Scheppach W (1998) Effects of resistant starch on the colon in healthy volunteers: possible implications for cancer prevention. *The American Journal of Clinical Nutrition* **67**, 136-142
- Liu JM, Zhao SL (1990) Scanning electron microscopy study on gelatinization of starch granules in excess water. *Starch-Stärke* **42**, 362-366
- Kabir M, Rizkalla SW, Quignard-Boulangé A, Guerre-Millo M, Boillot J, Ardouin B, Luo J, Slama G (1998) A high glycemic index starch diet affects lipid storage-related enzymes in normal and to a lesser extent in diabetic rats. *The Journal of Nutrition* **128**, 1878-1883
- Kamasaka H, Uchida M, Kusaka K, Yoshikawa K, Yamamoto K, Okada S, Ichikawa T (1995) Inhibitory effect of phosphorylated oligosaccharides prepared from potato starch on the formation of calcium phosphate. *Bioscience, Biotechnology, and Biochemistry* **59**, 1412-1416
- Kaplan RJ, Greenwood CE (2002) Influence of dietary carbohydrates and glycaemic response on subjective appetite and food intake in healthy elderly persons. *International Journal of Food Sciences and Nutrition* **53**, 305-316
- Kendall CW, Emam A, Augustin LS, Jenkins DJ (2004) Resistant starches and health. *Journal of AOAC International* **87**, 769-774
- Kruh J, Defer N, Tichonky L (1995) Effects of butyrate on cell proliferation and gene expression. In: Cummings JH, Rombeau JL, Sakata T (Eds) *Physiological and Clinical Aspects of Short-Chain Fatty Acids*, Cambridge University Press, Cambridge, pp 275-288
- Langkilde AM, Champ M, Andersson H (2002) Effects of high-resistant-starch banana flour (RS(2)) on *in vitro* fermentation and the small-bowel excretion of energy, nutrients, and sterols: an ileostomy study. *The American Journal of Clinical Nutrition* **75**, 104-111
- Le Blay G, Michel C, Blottière HM, Cherbut C (1999) Enhancement of butyrate production in the rat caecocolonic tract by long-term ingestion of resistant potato starch. *The British Journal of Nutrition* **82**, 419-426
- Le Leu RK, Hu Y, Young GP (2002) Effects of resistant starch and nonstarch polysaccharides on colonic luminal environment and genotoxin-induced apoptosis in the rat. *Carcinogenesis* **23**, 713-719
- Leeman M, Ostman E, Björck I (2008) Glycaemic and satiating properties of potato products. *European Journal of Clinical Nutrition* **62**, 87-95
- Liljeberg EH (2002) Resistant starch content in a selection of starchy foods on the Swedish market. *European Journal of Clinical Nutrition* **56**, 500-505
- Lim BO, Yamada K, Nonaka M, Kuramoto Y, Hung P, Sugano M (1997) Dietary fibers modulate indices of intestinal immune function in rats. *The Journal of Nutrition* **127**, 663-667
- Luciano L, Groos S, Busche R, Von Engelhardt W, Reale E (2002) Massive apoptosis of colonocytes induced by butyrate deprivation overloads resident macrophages and promotes the recruitment of circulating monocytes. *Cell Tissue Research* **309**, 393-407
- Martin LJ, Dumon HJ, Lecanu G, Champ MM (2000) Potato and high-amylose maize starches are not equivalent producers of butyrate for the colonic mucosa. *The British Journal of Nutrition* **84**, 689-696
- Martínez-Puig D, Pérez JF, Castillo M, Andaluz A, Anguita M, Morales J, Gasa J (2003) Consumption of raw potato starch increases colon length and fecal excretion of purine bases in growing pigs. *The Journal of Nutrition* **133**, 134-139
- Martínez-Puig D, Mourot J, Ferchaud-Roucher V, Anguita M, García F, Krempf M, Pérez JF (2006) Consumption of resistant starch decreases lipogenesis in adipose tissues but not in muscular tissues of growing pigs. *Live-stock Science* **99**, 237-247
- Martínez-Puig D, Castillo M, Nofrarias M, Creus E, Pérez JF (2007) Long-term effects of feeding large amounts of resistant starch on the digestive tract: a study in pigs. *Journal of the Science of Food and Agriculture* **87**, 1991-1999
- Mentschel J, Claus R (2003) Increased butyrate formation in the pig colon by feeding raw potato starch leads to a reduction of colonocyte apoptosis and a shift to the stem cell compartment. *Metabolism* **52**, 1400-1405
- Miles MJ, Morris VJ, Orford PD, Ring SG (1985) The roles of amylose and amylopectin in the gelation and retrogradation of starch. *Carbohydrate Research* **135**, 271-281
- Moreau NM, Martin LJ, Toquet CS, Laboisse CL, Nguyen PG, Siliart BS, Dumon HJ, Champ MM (2003) Restoration of the integrity of rat caecocolonic mucosa by resistant starch, but not by fructo-oligosaccharides, in dextran sulfate sodium induced experimental colitis. *The British Journal of Nutrition* **90**, 75-85
- Morand C, Levrat MA, Besson C, Demingue C, Remesy C (1994) Effect of a diet rich in resistant starch on hepatic lipid metabolism in the rat. *The Journal of Nutritional Biochemistry* **5**, 138-144
- Mortensen FV, Nielsen H (1995) *In vivo* and *in vitro* effects of short-chain fatty acids on intestinal blood circulation. In: Cummings JH, Rombeau JL, Sakata T (Eds) *Physiological and Clinical Aspects of Short-Chain Fatty Acids*, Cambridge University Press, Cambridge, pp 391
- Niba LL (2003) Processing effects on susceptibility of starch to digestion in some dietary starch sources. *International Journal of Food Sciences and Nutrition* **54**, 97-109
- Noakes M, Clifton PM, Nestel PJ, Le Leu R, McIntosh G (1996) Effect of high-amylose starch and oat bran on metabolic variables and bowel function in subjects with hypertriglyceridemia. *The American Journal of Clinical Nutrition* **64**, 944-951
- Noda T, Takigawa S, Matsuura-Endo C, Suzuki T, Hashimoto N, Kottearachchi NS, Yamauchi H, Zaidul ISM (2008) Factors affecting the digestibility of raw and gelatinized potato starches. *Food Chemistry* **110**, 465-470
- Nofrarias M, Martínez-Puig D, Pujols J, Majó N, Pérez JF (2007) Long-term intake of resistant starch improves colonic mucosal integrity and reduces gut apoptosis and blood immune cells. *Nutrition* **23**, 861-870
- Parillo M, Giacco R, Riccardi G, Pacioni D, Rivellesse A (1985) Different glycaemic responses to pasta, bread and potatoes in diabetic patients. *Diabetic Medicine* **2**, 374-377
- Pérez R, Stevenson F, Johnson J, Morgan M, Erickson K, Hubbard NE, Morand L, Rudich S, Katznelson S, German JB (1998) Sodium butyrate upregulates Kupffer cell PGE2 production and modulates immune function. *The Journal of Surgical Research* **78**, 1-6
- Ramakrishna BS, Venkataraman S, Srinivasan P, Dash P, Young GP, Binder HJ (2000) Amylase-resistant starch plus oral rehydration solution for cholera. *The New England Journal of Medicine* **342**, 308-313
- Raben A, Tagliabue A, Christensen NJ, Madsen J, Holst JJ, Astrup A (1994) Resistant starch: the effect on postprandial glycemia, hormonal response, and satiety. *The American Journal of Clinical Nutrition* **60**, 544-551
- Reaven GM (1979) Effects of differences in amount and kind of dietary carbohydrate on plasma glucose and insulin responses in man. *The American Journal of Clinical Nutrition* **32**, 2568-2578
- Riccardi G, Clemente G, Giacco R (2003) Glycemic index of local foods and diets: the mediterranean experience. *Nutrition Reviews* **61**, S56-S60
- Robyt JF (1997) Polysaccharides I: Structure and Function. In: Cantor CR (Ed) *Essentials of Carbohydrate Chemistry*, Springer-Verlag, New York, USA, pp 157-227
- Roediger WE, Millard S (1995) Selective inhibition of fatty acid oxidation in colonocytes by ibuprofen: a cause of colitis? *Gut* **36**, 55-59
- Russell PL, Berry CS, Greenwell P (1989) Characterisation of resistant starch from wheat and maize. *Journal of Cereal Science* **9**, 1-15
- Scheppach W, Fabian C, Sachs M, Kasper H (1988) The effect of starch malabsorption on fecal short-chain fatty acid excretion in man. *Scandinavian Journal of Gastroenterology* **23**, 755-759
- Singh N, Isono N, Srichuwong S, Noda T, Nishinari K (2008) Structural, thermal and viscoelastic properties of potato starches. *Food Hydrocolloids* **22**, 979-988
- Tappenden KA, Thomson AB, Wild GE, McBurney MI (1997) Short-chain fatty acid-supplemented total parenteral nutrition enhances functional adaptation to intestinal resection in rats. *Gastroenterology* **112**, 792-802
- Tester RF, Karkalas J, Qi X (2004) Starch structure and digestibility enzyme-substrate relationship. *World's Poultry Science Journal* **60**, 186-195
- Topping DL, Clifton PM (2001) Short-chain fatty acids and human colonic function: Roles of resistant starch and nonstarch polysaccharides. *Physiological Reviews* **81**, 1031-1064
- van Munster IP, Tangerman A, Nagengast FM (1994) Effect of resistant starch on colonic fermentation, bile acid metabolism, and mucosal proliferation. *Digestive Diseases and Sciences* **9**, 834-842
- Wachtershauser A, Stein J (2000) Rationale for the luminal provision of butyrate in intestinal diseases. *European Journal of Nutrition* **39**, 164-171
- Williams BA, Verstegen MWA, Tamminga S (2001) Fermentation in the large intestine of single-stomached animals and its relationship to animal health. *Nutrition Research Reviews* **14**, 207-227
- Younes H, Remesy C, Behr S, Demigne C (1997) Fermentable carbohydrate exerts a urea-lowering effect in normal and nephrectomized rats. *The American Journal of Physiology* **272**, G515-G521
- Young GP, McIntyre A, Albert V, Folino M, Muir JG, Gibson PR (1996) Wheat bran suppresses potato starch-potentialized colorectal tumorigenesis at the aberrant crypt stage in a rat model. *Gastroenterology* **110**, 508-514
- Zhang G, Venkatchalam M, Hamaker BR (2006) Structural basis for the slow digestion property of native cereal starches. *Biomacromolecules* **7**, 3259-3266