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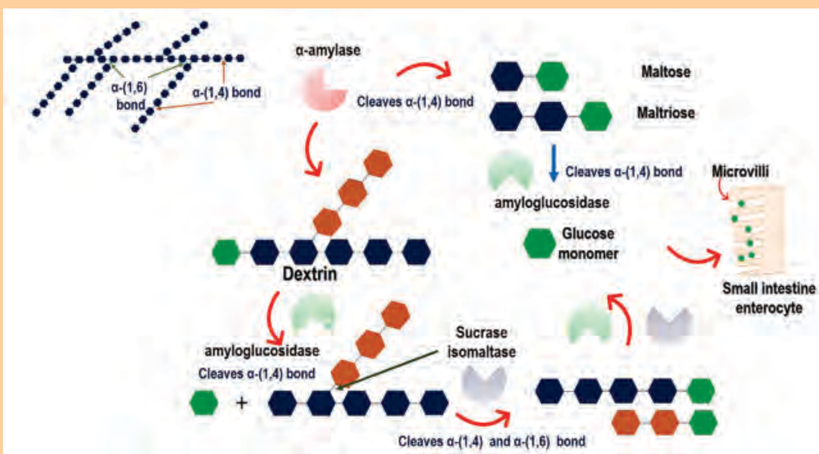

ICAR-National Rice Research Institute
Cuttack, Odisha, 753006

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Awadhesh Kumar, Milan Kumar Lal, Torit Baran Bagchi,
Rameswar Prasad Sah, Srigopal Sharma,
M. J. Baig, Amaresh Kumar Nayak

भाकृअनुप
ICAR

ICAR-National Rice Research Institute
Cuttack, Odisha-753006, India

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FOREWORD

Diabetes belongs to one of the largest global health crises of this century. Diabetes is a chronic disease that occurs either when the pancreas does not produce enough insulin or when the body cannot effectively use the insulin it produces. Insulin is a hormone that regulates blood sugar level. Hyperglycaemia, or raised blood sugar, is a common effect of uncontrolled diabetes and over time leads to serious damage to many of the body's systems, especially the nerves and blood vessels.

In India, there are estimated 77 million people above the age of 18 years are suffering from diabetes (type 2) and nearly 25 million are pre-diabetics (at a higher risk of developing diabetes in near future). More than 50% of people are unaware of their diabetic status which leads to health complications if not detected and treated early.

The glycemic index of rice is considered high (more than 60) which can be attributed to various factors including its fiber, lipid, and protein contents and the presence of resistant starch. Another important factor is the amylose-amylopectin ratio, with several studies indicated that high amylose content results in a lower Glycemic index. In the present compilation "**Glycemic index of Rice: Role in Diabetics**" describes the impact of rice starch digestibility on its glycemic index value. Here, the authors discussed different aspects of starch digestibility in rice grain along with biochemical indicators to identify low starch digestibility rice. Authors also discussed the type of resistant starch based identification of low starch digestibility rice where one can select low glycemic index rice based on different types of resistant starch. Further, authors describes in detail about the various facts related to starch digestibility and emphasized upon the possible strategies to modify starch digestibility in rice.

AK Nayak

Director, ICAR-NRRI, Cuttack

PREFACE

Recent studies indicate that dietary fibre rich wholegrain foods exhibit low starch digestibility. Hence, resistant starch content could be an important biochemical marker for slow starch digestibility and hence of low glycemic index and glycemic load. Rice is a starch rich grain. People consuming milled rice as a staple diet and leading sedentary life are likely to develop type-II diabetes in the long run. With rise in the number of diabetics worldwide, one possible approach is to develop rice based low GI foods with high RS content rice, as these show slow starch digestibility and hence would cause only slow rise in postprandial glucose level. In addition to amylose, the linear chains of amylopectin also influence starch digestibility. Starch debranching enzyme pullulanase action releases a mixture of linear amylose-like chains that facilitate retrogradation of starch and synthesis of type-3 resistant starch resulting in reduced starch digestibility. Besides mechanical processing, modern technologies like CRISPR have been used to increase amylose and resistant starch (type 5 and type 3) content in rice making it more suitable for diabetics. Phytic acid chelates Ca^{++} ions required by intestinal alpha amylase and hence lowers starch digestibility.

Present study reveals the inherent mechanism of starch digestibility and measurement of glycemic index. We discuss about the rice genotypes with different level of their glycemic index and resistant starch. This information is valuable for the large segment of world population, who consume rice as the staple food.

We thank all the Scientist of Crop Physiology and Biochemistry Division, ICAR-NRRI, Cuttack and others who provided support and valuable information to enrich this research bulletin.

CONTENTS

Introduction

Rice being a major staple food is a source of calories and nutrients for a large number of people, especially the poor who have limited access to a varied diet. People leading sedentary life and consuming the dietary fiber deficient milled rice are likely to be prone to develop type-II diabetes in the long run (Lal et al., 2021). The International Diabetes Federation has predicted that the number of diabetics may rise to 629 million by 2045. The starch digestibility of a food is the main determinant of the postprandial blood glucose level. Based on rate of digestibility, starch is categorized into three types : rapidly digestible starch (RDS) or high caloric starch (digested within 20 min); slowly digestible starch (SDS) or intermediate caloric starch (digested within 120 min) and, the non-digestible or non-caloric or resistant starch (RS) that remains undigested even after 120 min. Kumar et al., 2018 reported that rice grains with more than 2% RS exhibit lower Glycemic index (GI) values (60 or <60). Thus, low GI and glycemic load (GL) values and high RS content of a food are important biochemical indicators of low starch digestibility in the gastrointestinal tract. Thus, development of cost-effective rice-based foods with low GI/GL and high RS could be one of the effective measures to control the growing number of diabetics. Glycemic index is the ranking of carbohydrate food based on glycemic response and defined as the ratio of the incremental area under the glucose response curve after the standard amount of glucose from the test food relative to that of control food (white bread or glucose) is consumed (Venn and Green, 2007). Further, postprandial blood response is not only influenced by GI but also by the amount of carbohydrate taken per serving. Glycemic load is function of GI and related to the amount of carbohydrate consumed. The GL is defined as the average GI of individual food multiplied by the carbohydrate (%) present in the individual food consumed. The GL represents the equivalent glycemic impact of 1 g carbohydrate from white bread (reference food) and calculated by the formula [GL = (GI × amount of available carbohydrate)/100]. Thus, higher is the GL of food, higher is the response of postprandial blood glucose (Salari-Moghaddam et al., 2019). Therefore, both GI and GL values taken together are important indicators of starch digestibility that suggest how quickly and in what amounts one serving of a food contributes to blood glucose level.

Recently, it was reported that besides amylose content (AC), the percentage of linear chains of amylopectin also influences starch digestibility (Krishnan et al., 2020a). The debranching enzyme pullulanase (PUL) cleaves α-1,6- glycosidic bonds in amylopectin. It also plays a crucial role in starch synthesis. Increased PUL activity releases a mixture of linear polyglucose molecules of various chain lengths which facilitate starch retrogradation and hence formation of type 3 RS, which lowers starch digestibility. With increased interest in lowering the rate of starch digestibility of rice, addition of food condiments and mechanical treatments have been in use to attain this goal. Over the past few years, CRISPR-Cas9 (Clustered Regularly Interspaced Short Palindromic Repeats with Cas9 protein) has revolutionized the area of genome engineering and emerges as novel technique for genome editing. These modern technologies (including genome editing and speed breeding) have helped modify and increase the RS content, especially the type 5 (amylose-lipid complex) and type 3 (retrograded starch) in rice making it more suitable for consumption by the diabetics (Ma et al., 2015). The development of high AC rice using CRISPR may help to develop nutritionally superior crops for people in general and the diabetics in particular. Phytic acid (PA) content of grains is another indicator of low starch digestibility, as it chelates Ca^{++} ions required by alpha (α) amylase and hence reduces digestibility of starch. Recently, Kumar et al., (2020a) identified some high PA rice showing lower α-amylase activity and consequently slower in starch digestibility (*in vitro*). Therefore, PA could affect starch digestibility either through binding with proteinaceous digestive enzymes and/or by combining with proteins linked with starch (Fig. 1).

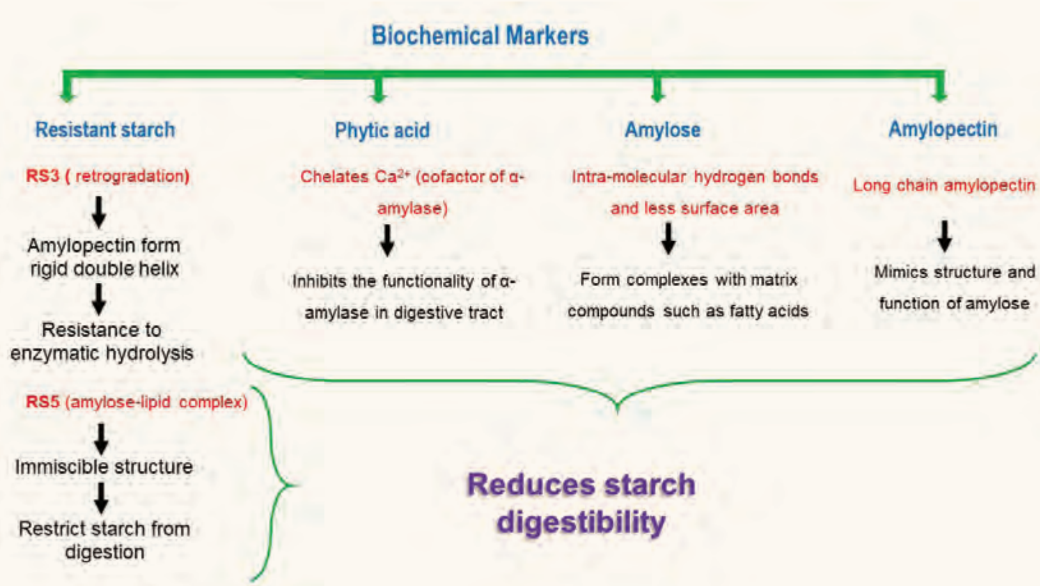

Fig. 1: Types of biochemical markers and their mechanism of lowering starch digestibility.

2. The constituents of starchy crops and their physical characteristics

2.1 Amylopectin and Amylose

Starch consists of amylopectin and amylose. Generally, starchy grains contain 70-80% amylopectin and 18-33% amylose. The two polymers vary in structure, molecular weight, chain length and degree of polymerization (DP: number of glucose units in a polysaccharide molecule). Amylose, though described as a linear, low molecular weight molecule has some

(< 1%) α-1,6 branch points in addition to the α-1 4-glycosidic linkages. Amylopectin is high molecular weight molecule with large number of α-1,6 branch points in addition to the α-1, 4-glycosidic linkages (Cornejo-Ramírez et al., 2018). Branched segments of amylopectin are classified as large (A), long (B1), mid length (B2), short (B3) and (B4) based on chain length. The DP of amylopectin (4700-18000) and amylose (570-8025) vary widely. Amylopectin with low molecular weight and long branched chains promotes the formation of helical amylose-lipids complexes (Kong et al., 2015). In waxy rice, AC is less than 5%, whereas in common rice it ranges from very low (5%-12%), lower (12%-20%), intermediate (20%-25%) to high (25%-33%) level. The *indica* rice vary widely in AC than the *japonica* subspecies, which generally have low to intermediate AC.

2.2. Starch granule size

The morphology (shape and size) of native starch granules varies widely among crops. Rice starch granule is polygonal and small (3-8 mm) (Toutounji et al., 2019). The specific surface area (total surface area/ unit volume) of rice starch is high, which allows high interaction between starch and the hydrolytic enzymes resulting in enhanced digestibility. Among cereals, rice has the smallest starch granules that is supposed to support high digestibility rate (Dhital et al., 2014). Starchy cereals including rice have naturally occurring superficial pores linked to internal channels resulting in an 'inside out' pattern of digestibility, which has a greater rate of hydrolysis in comparison to potato and high amylose maize starches which have an 'outside in' pattern (Gallant et al., 1992). A comparison of the rice starch sedimentation fractions revealed the presence of surface pores with interior channels which had prominent effect on the rate and extent of digestibility than the apparent surface area represented by granule size. The AC of starch and the amylopectin chain length affect the granular size distribution and functional characteristics (Chang et al., 2014). The particle size and form of rice also affects its rate of digestion, blood glucose level and hence the GI value.

2.3. Crystallinity

Granular starch is semi-crystalline, as it contains alternating crystalline and amorphous zones. Amylose and amylopectin are highly intermingled throughout the starch granule. The crystalline lamellae has double helices of amylopectin while the amorphous lamellae has branched segments of amylopectin and amylose. The degree of crystallinity ranges from 20% - 40% among crops (Fasahat et al., 2014). The crystalline polymorphs are differentiated based on the number of glucose units in amylopectin chains as: i) A-type (23-29 glucose units) ii) B-type (30-44 units) iii) C-type (combination of A and B type) and, iv) V-type (complex formed with lipids). A-type packing which is mainly present in cereal starches is denser than the B-type arrangement of high amylose maize and potato starch. A-type starch of wheat and rice can shift to B form if the branching enzyme activity is inhibited (Toutounji et al., 2019). The *in vitro* starch digestibility of cooked milled rice could be reduced by genetically switching crystalline polymorph from A to B or C-type (Butardo et al., 2011). Shi and Gao, (2011) treated cooked rice starch with PUL and found a combination of B- and V-type starch which was resistant to hydrolysis by α-amylase. Various physiochemical factors like chain length of amylopectin, AC, lipid content, amylose-lipid complexes and starch granule size affect crystallinity of starch. The variation between the starch granules also influences the degree of crystallinity. It is because the AC is higher in the A-type starch granules than that in the B- type, which results in lesser crystallinity in the starch granules (Singh et al., 2010). Industrial procedures like milling alters crystallinity by physical disruption of starch granules converting the crystalline amylopectin molecules to amorphous form with the formation of few low molecular weight fragments, which influences starch digestibility rate (Chi et al., 2021).

3. Biosynthesis of starch

Starch biosynthesis requires coordinated action of four types of enzymes namely, i) ADP-glucose pyrophosphorylase (AGPase) ii) starch synthase (SS) iii) starch branching enzymes (SBE) and, iv) de-branching enzymes (DBE). In amyloplasts, glucose 1-phosphate (Glc-1-P) and ATP react to form ADP-Glc and pyrophosphate (PPi) in the presence of AGPase. Starch synthase (further classified into granule bound starch synthase or GBSS and soluble starch synthase or SSS) catalyzes elongation of pre-existing linear glucose chains. In rice, GBSSI has two isoforms (GBSSI and GBSSII) required for synthesis and elongation of amylose chains and the super-long glucan chains in amylopectin (Vrinten and Nakamura, 2000). GBSSI mainly participates in the biosynthesis of storage starch in endosperm, while GBSSII catalyzes synthesis of non-storage starch in leaves. The SSS is mainly responsible for synthesis of amylopectin. In rice, SSS isoforms are grouped into 4 types, namely SSI, SSII (SSIIa, SSIIb and SSIIc), SSIII (SSIIIa and SSIIIb) and SSIV (SSIVa and SSIVb) (Fujita et al., 2006). The expression level of SSI is higher compared to that of SSIII in developing rice endosperms. SSIIb is expressed during early stages of grain filling in rice, while SSIIa is expressed during the mid-later stage. Bao, 2018 reported that SSIIIa and SSIVa were predominantly expressed in rice endosperm whereas SSIIIa and SSIVb were expressed mainly in leaves. In rice, three types of isoamylase (ISA1, ISA2 and ISA3) and one PUL gene is present. ISA1 and ISA2 are mainly expressed in seed endosperm but scarcely in leaves. ISA3 is expressed prominently in leaf but only slightly in endosperm; whereas PUL activity is low in leaf as compared to seed (Ohdan et al., 2010). In rice, PUL maintains a relatively higher expression level throughout kernel development and peaks in the mid to later stages (Jeon et al., 2010).

The AC in rice is regulated by *waxy (Wx)* gene which codes for GBSS protein. Five alleles (Wx^a, Wx^b, Wx^{in}, Wx^{op} and *wx*) are found at *Wx* locus that encodes GBSS (Larkin and Park, 1999). The *Indica* and *japonica* rice varieties carry different alleles of Wx^a and Wx^b, respectively which differ from each other in AC. Wx^b having a G to T mutation the first intron at the 5′ splicing site, leads to decreased splicing efficiency (Larkin and Park, 1999). Consequently, The Wx^b allele expresses lower level of waxy gene as compared to Wx^a allele which results in low amount of AC in the rice germplasm (Mikami et al., 2000). Fitzgerald et al., (2011) found strong correlation among AC, *Wx* gene and GI in traditional and modulated Asian rice cultivars indicating that amylose is the key constituent of grain that influences the GI value. In rice, the formation of RS 5 with polyglucan chains of hydrophobic nature imparts resistance to enzymatic hydrolysis and reduces the GI value of rice (Fig. 1) (Fuentes-Zaragoza et al., 2011). Amylose-lipid complexes are organized into a partially ordered structure called V-type crystalline lattice (Farooq et al., 2018). Both, amylose and RS negatively influence GI value. Therefore, it is necessary to characterize rice varieties with high AC and high RS content (Prasad et al., 2018).

Amylopectin biosynthesis needs fine coordination between SSs, SBEs and DBEs. The isoforms SSI, SSIIa and SBEIIb are required for the development of short segments of amylopectin (A and B1 chains), whereas the SSIIIa and SBEI are needed for the formation of long and intermediate chains (B2 and B3) of amylopectin . Amylose content alone cannot be a determinant of RS content in rice (Shu et al., 2007). Kong et al., (2015) reported that the linear chains of amylopectin affect starch digestibility and thus the GI of starchy crops. PUL activity was detected throughout the developing stages of rice grain (Li et al., 2009). Increased PUL activity released a mixture of oligosaccharides of various chain lengths, mainly from amylopectin that in turns facilitated starch retrogradation forming type 3 RS (Fig.1) (Krishnan et al., 2020a). This suggests that *PUL* gene plays an important role in RS formation in rice and needs to be taken into account to improve rice quality.

4. Properties of rice as a starchy crop

Starch is associated with small amounts of lipids (0.1-1.4%), protein (0.1 to 0.5%) and ash (0.1-0.3%) that influence its physical and end-use quality (Waterschoot et al., 2015). The amylose free starches have minimal lipid content, as a positive correlation exists between the two. The formation of amylose-lipid complexes decreases swelling and leaching of carbohydrates when starch is heated in excess water (Waterschoot et al., 2015). Phosphate monoesters in potato starch have great significance for its swelling capacity, as the negatively charged phosphate groups repel the adjacent amylopectin chains allowing fast hydration and granule enlargement (Singh et al., 2003). The phosphorous in cereal starches is mostly present as phospholipids (Waterschoot et al., 2015).

4.1 Nutritional value of brown and milled rice

Rice grain with 80% carbohydrates and 7% protein on dry wet basis is a valuable source of dietary energy and essential nutrients, though it lacks cholesterol and vitamins A, D and C. There is uneven scattering of nutrients and bioactive components in rice kernel. The bran layer is rich in vitamins, minerals, phytochemicals and dietary fibre. Milling removes thin layer of bran, husk and embryo from paddy grains leaving starchy endosperm or milled rice, (MR), which contains 70-80% starch, 7-10% protein and 1% lipid and thus forms the main source of nutrition (Yang et al., 2019). The dehusked or brown rice (BR) and MR are similar in energy value but the former is nutritionally superior as most minerals, vitamin B, γ-oryzanols, GABA (gamma-aminobutyric acid), tocopherols, tocotrienols, β-sitosterol, carotenoids, anthocyanins, proanthocyanidins, and other phenolic compounds are lost during bran (8-10%) removal (Carcea, 2021). Presence of high amount of lipid (1.9 %) in BR leads to excessive lipid oxidation and shorter shelf life. It is richer in RS and oligosaccharides that are fermented and used by gut microbiota and contribute to health**.** Thus, despite being a healthy food and potential source of several bioactive compounds, BR which is associated with reduced risk of non-communicable diseases like type-II diabetes and cardiovascular diseases, is not as popular as MR with consumers due to its shorter shelf life and variable sensory properties (Carcea, 2021).

5. Indicators of starch digestibility in rice

5.1. Glycemic index

Digestion of carbohydrate rich foods releases glucose into blood affecting the blood sugar and insulin levels. The concept of GI proposed by Jenkins et al., (1981) was mainly aimed at helping the diabetics to select appropriate food. The rate of starch digestion is positively related to GI value of food. The foods with GI value of 70 or more are called high GI foods, as they cause higher postprandial rise in blood glucose level compared to the medium GI (56-69) and low GI foods (less than 55). GI values of rice vary from 54 to 121 (Meera et al., 2019). Regular consumption of high GI foods is likely to increase the risk of type-II diabetes (Bhupathiraju et al., 2014) . Low GI rice is recommended for consumption by the diabetics as it may reduce the risk of cardiovascular diseases, type-II diabetes and metabolic syndrome (Meera et al., 2019). Factors such as granular size, milling degree, method of cooking, starch structure and the amount of food constituents (protein, dietary fibre, fat) also influence the glycemic response. Processing methods and combinations of rice with foods condiments alters GI value. Cooking changed the GI values of BR and MR from 96 and 83 to 64 and 93 respectively (Deepa et al., 2010). The GI values of rice also vary with AC, granule size, ratio of amylose/amylopectin, amylose-lipid complex, the extent of gelatinization and differential susceptibility to amylolytic enzymes (Deepa et al., 2010). Glycemic index is generally measured using *in vivo* methods. The GI values of test foods using white bread are roughly 1.4 times higher than those determined with glucose as the reference food (Goñi et al., 1997;). Recently, *in vitro* methods of GI determination that use either amylase or a combination of amylase and protease, have been preferred over the complicated *in vivo* methods due to high reproducibility and low cost of the former which suit analysis of large number of food samples (Lal et al., 2021). The *in vitro* method used provides quick and cost-effective yet reproducible indicative data that more or less reflect the *in vivo* glycemic potential of carbohydrate foods. Therefore, the *in vitro* method is suitable to rapidly screen and assess glycemic potential of staple carbohydrate foods like rice before *in vivo* testing which is more time-consuming and costly. In this study, the BR of 50 rice genotypes from different ecologies/traits were taken for measuring GI. The results indicated wide variation in GI ranging from 53 for Improved Lalat to 70 for Lunasuvarna (Kumar et al., 2020b) (Fig. 2).

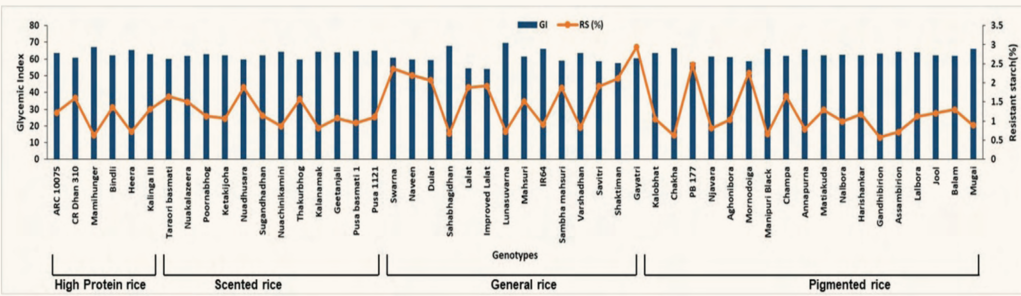

Fig. 2: Glycemic Index and resistant starch of different rice genotypes

5.2. Glycemic load

The postprandial blood sugar level is also influenced by the quantity and the type of carbohydrates present in the serving, which affects insulin release; this led to the concept of GL. GL is determined by multiplying the GI with total available carbohydrate present in one serving of food divided by 100 (Lal et al., 2021). Sethupathy et al., (2020) classified foods into low GL (less than or equal to 10), medium GL (10-20), and high GL (> 20) types. A high GI food can have low GL if taken in small quantity. Similarly, low GI foods may show high GL values when consumed in high quantity. The GL of a diet depends on the GL of all foods that form the diet. A diet high in fat and protein, though low in carbohydrates has low GL. Heterogeneity of foods can be used to construct a low GL diet, as high GL foods cause high postprandial blood glucose response (Salari-Moghaddam et al., 2019). Therefore, the long-term consumption of a diet rich in carbohydrates with high GL is shown to be associated with the risk of development of type II diabetes. Hence, both GL and GI are critical to judge the ability of a food to alter blood sugar level and to decide the diets for the diabetics (Lal et al., 2021).

5.3 Glycemic response of brown and milled rice

The amount and composition of starch affect the postprandial blood sugar response they evoke. Generally, rice is considered as high GI (64 to 93) food. The high amylose rice starch is relatively resistant to digestion in humans. Apart from amylose, processing methods such as parboiling, quick-cooking, milling, home cooking and cooling also affect starch digestibility (Hu et al., 2004). Boers et al., (2015) found that BR produced a lower postprandial glucose and insulin response than MR with identical cooking times, thus establishing the role of milling in enhancing GI. However, with increase in cooking time (which is high for BR), smaller and inconsistent differences in postprandial response were observed between BR and MR. Musa-Veloso et al., (2018) found the consumption of BR to be associated with significant reduction in blood glucose area under the curve (AUC) compared to MR. Thus, they concluded that BR significantly attenuates the postprandial blood glucose response.

6. Biochemical markers to identify rice with low starch digestibility

6.1. Resistant starch

The part of food starch that is not digested to glucose in the upper gastrointestinal tract and thus reaches the colon where it is fermented by microbiota to release short-chain fatty acids (mainly butyrate, which fuels the colorectal cells and microflora), acetate and propionate (which affect glucose and cholesterol metabolism in human) is known as RS (Li et al., 2020). In 1990, FAO listed RS as a dietary fibre for the prevention of type-II diabetes (Sha et al., 2012). Reports suggest that RS plays a crucial role in the reduction of postprandial blood glucose response which ultimately lowers the risk of obesity, insulin sensitivity, and increase

satiety thereby help to combat type II diabetes and chronic kidney diseases. Therefore, RS rich foods contribute to human health. RS is classified into five groups (Fig. 3): RS1

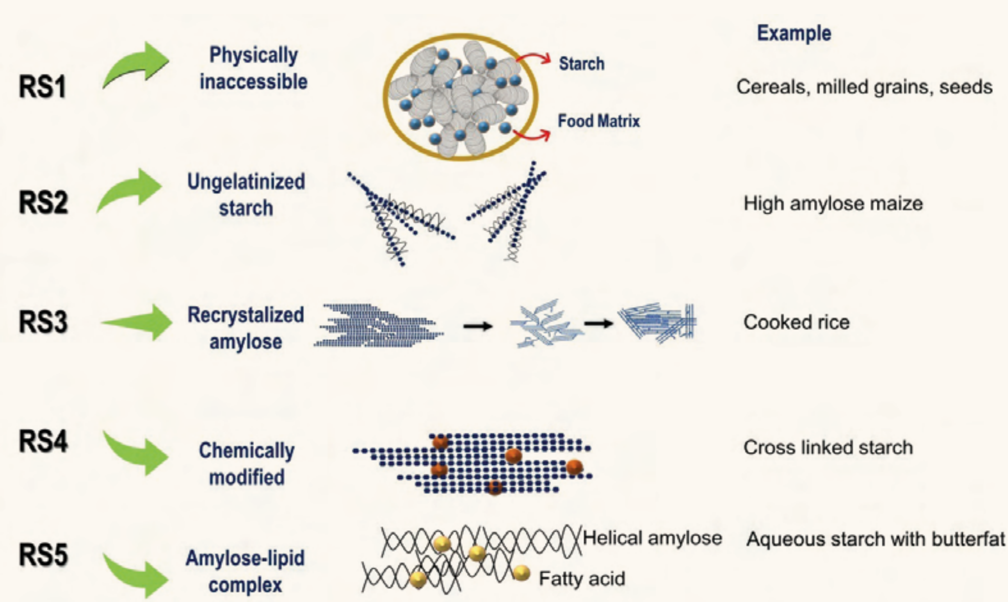

Fig 3. Types of resistant starch and there structure with examples.

is physically inaccessible starch present in undamaged food matrices of intact grains and whole-grain foods which are higher in RS compared to their processed counterparts (Yi et al., 2021). The RS2 is present in ungelatinized starch. Thus, products like popcorn that don't require gelatinization are a good source. The RS1 and RS2 are the most common types of RS, most of which can be converted to digestible starch during food processing. The RS3 is retrograded starch used mainly in food products and thus the major RS type for humans (Haralampu, 2000). RS4 is produced by chemical modification of starch (Ashwar et al., 2017). RS5 reported in rice is water immiscible amylose-lipid complex which restricts starch digestion (Kumar et al., 2018). It is found in both amorphous as well as crystalline amylose-lipid complexes and is formed at low as well as high temperatures (Hasjim et al., 2013).

Generally, cooked rice contains type 5 RS that inhibits starch granule expansion during cooking, rendering it resistant to hydrolytic enzymes (Fig. 4). Hence, increasing type 5 RS in rice is likely to render it suitable for diabetics and the calorie conscious persons. Zhou *et al.*, (2016) found a novel *indica* rice mutant (b10) through map based cloning that was high in type 5 RS. Further, the long amylopectin chains that mainly exist in intermediate and high amylose rice tend to form more rigid double helices; these are susceptible to retrogradation and resistant to enzymatic hydrolysis and thus could lead to more of type 3 RS in rice (Fig. 4) (Tuaño et al., 2021). Debranching enzymes (pullulanase, isoamylase) play important role in starch retrogradation through the formation of linear chain amylopectin. Demirkesen-Bicak et al., (2018) reported increased PUL activity in pulses in which a mixture of sugars of varied chain length

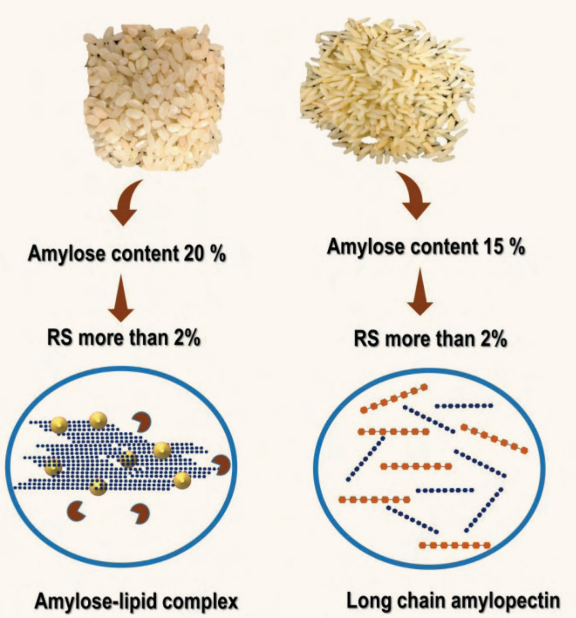

Fig. 4: Rice with different amylose content but same RS reduces starch digestibility by two mechanism. a) Formation of amylose-lipid immiscible structure prevent starch from digestive enzyme b) Linear long chain of amylopectin cause starch retrogradation which provide less surface area for digestive enzyme.

was released from the amylopectin molecules and augmented starch retrogradation and RS3 synthesis. Kumar et al., (2018) found negative correlation between RS content of rice and GI. Hence, high RS foods may suppress rise in blood sugar level. Naseer et al., (2021) found that rice with same AC differed in GI and GL values and surmised that besides AC and RS, other grain components like dietary fiber, protein and fat also affect glycemic response.

6.2. Phytic acid

Phosphorous is stored as PA in plant based foods and comprises 1-5% in cereals; it amounts to 65 to 73% of the total phosphorus in rice (Pereira et al., 2021). PA is stored in rice, barley and wheat in the outermost aleurone layer and bran. Kumar et al., (2020a) reported low starch digestibility in rice with intermediate to high PA content and proposed an inverse relationship between PA and blood glucose level/ GI values. Thus, high PA foods may help a healthy colon and prevent hyperglycemia in diabetics by reducing starch digestibility (Fig. 1). In fact, animal studies show reduction in blood glucose when PA is added to diet (Pereira et al., 2021). Kim et al., (2010) postulated that PA reduces starch digestion by binding to the salivary and pancreatic amylases through phosphate bonds or chelating Ca^{++} required by amylase. PA also binds to proteins and thus inhibits starch and glycogen hydrolysing enzymes (Kumar et al., 2021). Recent studies suggested that the food which is prepared by traditional method contain PA in moderate amount (0.72-1.05 g/100 g) that help to control type-II diabetes (Kumar et al., 2021). Moreover, the action of intestinal amylase activity was also reported to be reduced when Type-II diabetic rats fed the food supplemented with PA and inositol (Omoruyi et al., 2013). Rice is mainly consumed in the form of milled/polished/ white rice where the highest amount of PA is present in aleurone layer. After milling, major amount of PA is removed from outer layer of rice grain, still considerable amount of PA present in the endosperm which is capable for inhibiting starch digestibility (Kumar et al., 2017). Thus, hypoglycemic effect of PA might be attributed to reduced activity of intestinal amylase and consequently poor digestion and absorption of carbohydrates.

6.3. Amylose

Amylose polymers have smaller surface area and are richer in intra-molecular hydrogen bonds compared to amylopectin. They form complexes with matrix compounds such as fatty acids and hence are digested slowly and to a lesser extent due to reduced accessibility to α-amylase as compared to amylopectin (Fig. 1). Thus amylose rich starchy foods reduce the blood glucose response and cause slower emptying of digestive tract compared to low amylose foods (Frei et al., 2003). Rice starches having high AC are reported to have high RS content (Kumar et al., 2018). Zhu et al., (2011) suggested that amylose present in the amorphous lamella is hydrolysed by amylase and the re-association of hydrolysed molecules makes it resistant to further hydrolysis. Some studies have reported inverse relationship between AC and SDS and the rate of digestion (Chung et al., 2011; Kumar et al., 2018). It was proposed that amylose-lipid complexes prevent hydration and thus restrict the amylase from accessing starch granules (Cai et al., 2015).

6.4. Amylopectin

The tightly packed chains in amylopectin molecules form crystalline lamella of starch granules, making them poorly accessible to digestive enzymes in comparison to the amorphous portion resulting in slow starch digestibility (Singh et al., 2010). Lin et al., (2018) found that rice starches with similar amylopectin structure but with varied AC differed considerably in rate of digestibility. The reason might be the long chains of amylopectin which mimic the structure, as well as the function of amylose, and may add to the RS content lowering rice digestibility (Fig. 1). Other reports suggested that long glucan chains of amylose and long-chain amylopectin retrograde and re-associate faster and effectively than the shorter branch segments of amylopectin, rendering the cooked high AC cultivars more resistant to enzymatic digestion (Alhambra et al., 2019; Gallant et al., 1992).

The intermediate and high AC rice are more susceptible to retrogradation and resistant to enzymatic hydrolysis, as the long chains of amylopectin present in them tend to form compact double helices (Tuaño et al., 2021). Hence, factors other than AC, contribute to variation in GI in rice belonging to same amylose class. Zhu et al., (2011) found that long segments of amylopectin of intermediate AC rice starch withstand enzymatic hydrolysis, as they form more stable double helices structure, similar to amylose double helices that quickly retrograde. Researchers from The Philippines reported that *indica* rice with intermediate to high AC had higher percentage of long amylopectin chains than waxy and low AC rice varieties. This might explain the higher RS and lower GI values for cooked rice of IR64 and PSB Rc10 reported in this study compared to the lower RS and higher GI values of IMS2 and NSIC Rc160, in brown as well as milled rice (Paul et al., 2013).

7. Approaches to alter starch digestibility in rice

7.1. Chemical and mechanical approaches

Cross-linking and esterification within the starch molecules by citric acid significantly increases the RS content and reduces esterified starch to digestion in rice (Ye et al., 2019). Hung et al., (2016) found that the RS content of rice starches treated with acid was significantly higher (30.1%-39.0%) compared to native starches (6.3%-10.2%). Amylosucrase and β-amylase increases the RS content and reduced the hydrolysis of *in vitro* digestion in rice (Yi et al., 2021)._Pongjanta et al., (2008) found that rice treated with PUL (12 U/g) for 32 h under optimum conditions increases RS content sharply. Physical methods like heating, parboiling, retrogradation, cooking and soaking to modify foods are often used in food processing industry (Table 1). For example, rice noodles are the main extrusion products. Extrusion reduces the molecular weight of amylose and amylopectin. These short chain starch fractions form novel cross-links which are poorly digested resulting in reduced GI (Hou et al., 2010). Wang et al., (2018) found that heat moisture (< 30%) treated (HMT) rice starch consisted of 25% SDS and RS. Retrogradation caused by dual autoclaving or HMT combined with other methods like parboiling significantly increases RS content. Parboiling results in amylose-lipid complex formation that hinders *in vitro* rice digestion by enzymes. Sivakamasundari et al., (2020) reported that the degree of gelatinization of parboiled rice was directly proportional to RS content with reduction in GI value. Cheng et al., (2019) also reported lowering of GI by parboiling due to disruption in protein configuration which hindered enzymatic hydrolysis of starch. High AC (about 28%) brown rice soaked in citric acid (30-40 mg/mL) followed by cooking (121ºC, 30 min, 15 psi) and drying produced RS enriched rice (Kim et al., 2020). Retrogradation (i.e., recrystallization of amylose and amylopectin) by cold storage and subsequent reordering of starch molecules lowers starch digestibility rate and increased the RS content in cooked rice (Chiu and Stewart, 2013). Cooking of flours of 12 rice cultivars (AC: 15.84-17.18%) followed by cooling revealed that cultivars with higher levels of amylopectin with long, intermediate and short debranched linear chains had higher amount of SDS than RDS. Rice starch having very short linear chains of amylopectin had the highest amount of RDS (Benmoussa et al., 2007). Moderately gelatinized starches with higher crystallinity were more resistant to enzymatic digestion then retrograded rice samples. These studies indicate that starch digestibility in cooked rice can be reduced by retrogradation process, especially in cultivars with higher percentage of long and linear amylopectin fragments (Chung et al., 2006). Reed et al., (2013) concluded that stir-fried rice showed the highest RS content and the lowest starch hydrolysis rate among the various methods tested. Chiu & Stewart, (2013) found that type of cooking equipment (pressure cooker, rice cooker, conventional oven) had no effect on RS content of freshly prepared rice, though RS content was reduced in pressure cooked Jasmine rice. The RS content increased from 1.95% to 7.95% in pressure cooked (10 min) *japonica* rice. Further, The RS and SDS increased almost 3.5 times by HMT after or before parboiling (Cheng et al., 2019).

Table1: Different approaches for regulating starch digestibility in rice.

Approaches	Examples	Observations	References
Chemical	Citric acid	Increased SDS and RS contents	(Ye et al., 2019)
Enzymes	Amylosucrase	Increased RS content	(Yi et al., 2021)
	β-amylase	Increased RS content	(Yi et al., 2021)
	Pullulanase	Increased RS content	(Pongjanta et al., 2008)
Physical	Extrusion	Reduction in GI value	(Hou et al., 2010))
	HMT (<30%) in the rice flour	Increased SDS and RS content	(Wang et al., 2018)

	Parboiling	Enhanced RS fraction with reduced GI value	(Sivakamasundari et al., 2020)
	Heat treatment and drying	Increased RS content	(Kim et al., 2020)
	Retrogradation	Increased RS with lower starch digestibility	(Chiu and Stewart, 2013)
	Heat treatment followed by cooling	Higher amount of SDS than RDS	(Benmoussa et al., 2007)
	Stir-frying	Increased RS with lower starch hydrolysis	(Reed et al., 2013)
	Pressure cooking of Jasmine rice	Decreased RS content	(Chiu and Stewart, 2013)
	Pressure cooking of *japonica* rice for 10 min	Increased RS content from 1.95% to 7.95%	(Cheng et al., 2019)
Food condiments	Rice mixed with vegetables (Okra and Drumstick)	Slow down the release of blood glucose	(William et al., 1993)
	Rice mixed with cooking oils (palm oil, rice bran oil, sunflower oil, ghee)	Increased RS content with reduced GI	(Farooq et al., 2018; Krishnan et al., 2020b; Kumar et al., 2020)
	Rice mixed with pulses (pigeon pea)	Reduction in GI value	(Kumar et al., 2020)
Up-regulation of the genes related to AC	Incorporation of *Wxa* cDNA into null mutant of *japonica* rice	Higher AC (6-11%)	(Itoh et al., 2003)
	Site-directed mutagenesis for eight amino acids in *OsGBSSI*	Modulated AC	(Liu et al., 2014)
	Mutation in *GBSSI*	Increased RS content	(Gurunathan et al., 2019)
Down-regulation of the genes function using RNAi approach	Down regulation of starch synthase enzyme gene *SSI*	High Amylose content	(Lee et al., 2014)

	Down regulation of starch synthase enzyme genes *SSIIa* and *SSIIIa*	High RS content	(Zhang et al., 2011)
	Down regulation of starch branching enzyme genes *SBEI* and *SBEIIb*	High RS and amylose content	(Butardo et al., 2011; Zhu et al., 2012)
	Down regulation of starch branching enzyme gene *BEIIb*	High level of RS	(Wei et al., 2010; Butardo et al., 2011; Zhu et al., 2012)
Targeted mutagenesis of genes function using CRISPR-Cas9	Targeted mutagenesis of *Waxy (GBSSI)* gene	Low amylose starch	(Ma et al., 2015)
	Targeted mutagenesis of starch branching genes *SBEI* and *IIb*	Increased RS content up to 25% and 9.8% respectively, demonstrated the role of amylopectin structure in starch configuration and digestibility	(Sun et al., 2017)
	Targeted mutagenesis of starch branching gene *SBEIIb*	Increased RS and AC with reduced GI value	(Baysal at al., 2020, Wang et al., 2021)
	Targeted mutagenesis of starch debranching enzyme gene *ISA1*	Decreased total starch, AC and amylopectin content	(Shufen et al., 2019)
	Targeted mutagenesis of starch debranching enzyme gene *PUL*	Amylose content decreased by 18.70%	(Feng et al., 2019)

7.2. Addition of suitable food condiments

The food condiments consumed with cooked rice are likely to alter its GI value (Table 1). Addition of vegetables contributes extra dietary fibre that intermingles with starch of rice and enhances the RS content of mixed meal (Kang et al., 2018). Okra and drumstick slow down the release of glucose into blood; drumstick leaves help lower the postprandial hyperglycemia and hence are recommended for diabetics (William et al., 1993). Rice noodles with 10% okra helped lower the GI value. As vegetables also contain polyphenols, that may restrict enzymatic digestibility of starch, it is difficult to conclude if dietary fiber or polyphenols lower blood glucose level (Kang et al., 2018). Addition of lipids like palm oil to cooked rice is another approach to increase RS content, as starch-lipid complex shows reduced enzymatic starch hydrolysis (Farooq et al., 2018). The rice bran oil contained 72.6% of long chain unsaturated fatty acids with high capability to form complex with amylose of rice and contributed to high level of RS (Krishnan et al., 2020b). Addition of cooking oils (soybean oil, coconut oil, mustard oil, sunflower oil, clarified butter or *ghee*) to rice lowered the GI and increased the RS content. Among the above mentioned oils used, *ghee* when added during cooking, was found to be the best in lowering GI and increasing RS content compared to vegetable oils (Table 2) (Kumar et al., 2020b). Ai & Jane, (2018) reported that addition of protein-rich pulses interferes with the coalescence of starch molecules with the endogenous proteins in the matrix system resulting in increased resistance to starch digestion. The stearic hindrance caused by possible matting of starch granules with proteins involving disulfide bonds inhibits accessibility of the hydrolytic enzymes to starch. Kumar et al., (2020b) found maximum lowering of GI by pigeon pea in rice-pulse combinations compared to other pulses (Table 3).

Table 2: The GI and RS of rice-Oil combination

Rice variety	Oil types	GI (Mean±SD)	% Decrease in GI	RS (Mean±SD)	% Increase in RS
Shaktiman [a] GI: 57.5±1.00 RS: 2.107±0.01	[†]Ghee	55.3±0.92*	3.83	2.70±0.04**	28.30
	[†]Soybean	55.4±0.97*	3.65	2.60±0.07**	23.56
	Coconut	56.3±1.18	2.08	2.60±0.08**	23.40
	Mustard	57.4±1.17	0.17	2.40±0.03**	14.06
	Sunflower	56.9±0.99	1.02	2.50±0.04**	18.81
Hue [a] GI: 76.3±0.75 RS: 0.2±0.02	[†]Ghee	57.3±0.82**	24.90	1.13±0.05**	466.67
	[†]Soybean	57.9±1.12**	24.12	1.09±0.10**	448.33
	Coconut	58.9±0.86**	22.80	0.90±0.03**	350.00
	Mustard	59.5±1.07**	22.01	0.90±0.03**	351.67
	Sunflower	58.7±0.95**	22.94	0.79±0.04**	298.33
Kalashree [a] GI: 59.1±0.95 RS: 2.7±0.01	[†]Ghee	54.4±1.05*	7.96	3.19±0.04**	18.40
	[†]Soybean	54.6±1.26*	7.61	3.00±0.20*	11.11
	Coconut	56.7±1.12*	3.90	2.90±0.05*	7.41
	Mustard	58.9±0.95	0.34	2.80±0.04	3.70
	Sunflower	56.3±1.07*	4.57	2.90±0.06*	7.41

* &** Student's t-test for significant at *P* value 0.05 and 0.001 respectively

[a] Rice alone GI and RS values.

[†] Ghee and soybean oil resulted in maximum lowering effect of GI value compared with other cooking oils.

Table 3: The GI and RS of rice-pulses combination

Rice variety	Pulses	GI (Mean±SD)	% Decrease in GI	RS (Mean±SD)	% Increase in RS
Shaktiman [a] GI: 57.5±1.00 RS: 2.1±0.01	†Pigeon Pea	55.2±1.06*	4.00	2.50±0.07*	19.21
	Mung bean	56.2±1.10	2.26	2.3±0.04*	09.52
	Lentil	56.7±1.10	1.39	2.40±0.02*	14.44
	Pea	57.4±1.06	0.17	2.10±0.15	0.00
	Chickpea	57.0±0.82	0.86	2.60±0.01**	23.81
	Black Gram	57.1±1.18	0.53	2.20±0.20	4.76
	Soybean	57.1±0.90	0.70	2.59±0.04**	23.65
	Kidney bean	57.3±0.91	0.35	2.70±0.05**	28.73
Hue [a] GI: 76.3±0.75 RS: 0.2±0.02	†Pigeon Pea	59.1±1.06**	22.54	0.40±0.08*	101.67
	Mung bean	60.4±1.08**	20.83	0.39±0.02	98.33
	Lentil	60.4±0.90**	20.84	0.30±0.01	50.00
	Pea	65.0±0.95**	14.72	0.30±0.01	51.67
	Chickpea	60.8±1.15**	20.31	0.30±0.01	50.00
	Black Gram	64.8±1.12**	15.07	0.30±0.05	50.00
	Soybean	61.4±0.85**	19.53	0.40±0.01*	100.00
	Kidney bean	62.1±1.08**	18.61	0.40±0.02*	100.00
Kalashree [a] GI: 59.1±0.95 RS: 2.7±0.01	†Pigeon Pea	55.9±0.98*	5.41	3.10±0.60*	14.81
	Mung bean	57.2±1.09	3.21	3.0±0.10*	11.11
	Lentil	58.2±0.95	1.52	2.9±0.04*	07.53
	Pea	58.7±0.49	0.65	2.79±0.04	03.58
	Chickpea	57.3±1.03	2.88	2.89±0.06	07.28
	Black Gram	58.7±0.63	0.51	2.90±0.05*	07.41
	Soybean	58.4±0.90	1.18	3.0±0.10*	11.11
	Kidney bean	58.6±1.07	0.84	3.09±0.15*	14.69

* &** Student's t-test for significant at *P* value 0.05 and 0.001 respectively

[a] Rice alone GI and RS values.

† Pigeon pea resulted in maximum lowering effect of GI value compared with other pulses.

7.3. Modern approaches

Upregulating the genes related to the synthesis of high amylose starch through mutational breeding and targeted mutagenesis are newer approaches to increase the RS content in endosperm. Increasing the *GBSSI* expression leads to elongation of linear amylose chains, with enhanced AC and RS content in rice. Incorporation of *Wxa* cDNA into null mutant of *japonica* rice variety (wx) resulted in higher AC (6-11%) compared to the wild cultivar (Itoh *et al.,* 2003). Liu et al., (2014) reported that site-directed mutagenesis for eight amino acids in *OsGBSSI* affected starch binding capacity and modulated AC in rice. Kumar et al., (2018) reported a positive correlation between *GBSSI* expression and RS content in rice. Mutation within this gene is reported to increase the RS content (Gurunathan et al., 2019). Nevertheless, despite many modifications reported on *GBSSI* of cereals, significant increase in AC and RS content is yet to be achieved, which could be due to the limitation of GBSSI protein, availability of ADP-glucose and presence of physical space within the starch granules (Sestili *et al*., 2012). As high AC rice grains cook hard and are not preferred by consumers, other approaches are needed to increase RS content in rice.

Downregulating the expression of genes involved in amylopectin biosynthesis is yet another way to increase RS content, which is achievable with RNAi, TALEN and CRISPR methods (Table 1). Knockout of *SSI* gene through RNAi resulted in high AC (25%) rice (Lee et al., 2014). RNAi method simultaneously down regulated *SIIa* and *SIIIa* with increase in AC (66.7%) and intermediate amylopectin chain while reducing the long and short amylopectin chains. Thus, the high levels of RS and amylose are caused by higher percentage of long to medium type amylopectin chains (Zhang et al., 2011). Use of hairpin (hp) RNA with artificial microRNA mediated repression of *SBEIIb* resulted in high AC and RS and consequently lower GI value in rice, while suppression of *SBEI* did not alter AC (Butardo et al., 2011). The increase in amylose level was much higher in antisense RNAs transgenic lines of *SBEI* and *SBEIIb* indicating that simultaneous alteration of both genes can significantly increase AC in rice kernels.. RNAi mediated high amylose *SBEIIb* rice lines have been generated by several investigators (Ossowski et al., 2008; Warthmann et al., 2008).. RNAi mediated repression of both *SBEI* and *SBEIIb* caused dramatic increase in AC (from 27.2-64.8%) and RS (from 0-14.6%) (Zhu et al., 2012). Suppression of *BEIIb* by RNA silencing also resulted in higher RS2 content (Wei *et al*., 2010; Butardo *et al.,* 2011; Zhu *et al.,* 2012). However, the transgene expression was often incomplete and showed variation in different RNAi generated lines despite being time-consuming and costly procedures. Current genome editing technique like CRISPR/Cas9 precisely modify DNA sequences which offer great promise in harnessing plant genes for crop improvement. CRISPR/Cas9 system was used to modify *GBSSI* gene resulting in considerable lowering of AC from 14.6 to 2.6% in rice and a phenotype similar to the natural waxy mutants (Ma et al., 2015). First report on successful application of genome editing to enhance RS and AC was done in *japonica* cv. Kitaake (Sun et al., 2017). In this study, CRISPR/Cas9-mediated targeted mutagenesis on the first exon of *SBEI* and third exon of *SBEIIb* resulted in high-amylose rice with a significant increase in RS of 25.0% and 9.8 %, respectively. The ratio of amylose to amylopectin also increased significantly in the edited lines. Targeted mutagenesis through CRISPR/Cas9 method in *SBEIIb* and *SBEI* caused increase in the proportion of long chains in debranched amylopectin, with high RS and AC. Recently, Baysal et al., (2020) developed high RS and AC *japonica* rice by down regulating *SBEIIb* gene using CRISPR/Cas9 method. Wang et al., (2021) mutated the *OsSBEIIb* using CRISPR/Cas9 technique in *japonica* rice (TNG82) and obtained high RS and AC lines with low GI value. Shufen et al., (2019) edited *ISA1* gene in rice by CRISPR/Cas9 and reported a considerable lowering in total starch, AC and amylopectin content in the endosperm of the mutants. Feng et al., (2019) used CRISPR methodology to down regulate the starch debranching enzyme PUL located on chromosome 4 in rice and obtained a line T0-18 in which AC was reduced by 18.70% and the protein content increased by 22.02%. Thus, it can be hypothesized that higher expression of PUL has role in forming linear chains of amylopectin that leads to formation of retrograded type 3 RS.

Conclusion

The high amount of RS including the dietary fibre content reduces the starch digestibility rate and the consequent rise in blood glucose level. The structural variation in the RS types and their content in the food matrix has a huge potential to design food that will have a health

benefit. The amylose and lipid content and the percentage of unbranched long chains in amylopectin in a starchy food are important factors leading to RS formation. The enzyme pullulanase also plays a key role in RS formation. Starch digestibility can be regulated by mechanical (chemical, heat processing etc.) and modern molecular (CRISPR-Cas9, RNA-interference etc.) approaches. By targeting the biosynthetic pathway of starch could be a possible strategy to develop cultivars having high RS with low GI/ low starch digestibility.

The development of rice-based low GI food combinations with high RS may be a possible approach to help check the prevalence of type 2 diabetes in the rice-eating population.

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ICAR-National Rice Research Institute
Cuttack-753006, Odisha, India
(An ISO 9001:2015 Certified Institute)
Phone: 91-671-2367757, Fax: 91-671-2367663
E-mail: director.nrri@icar.gov.in | directorcrricuttack@gmail.com
Website: http://www.icar-nrri.in

@RiceICAR @RiceICAR @RiceICAR