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Unlocking the potential of resistant starches from underutilized tropical fruits as substrates for fermentation into short-chain fatty acids

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ABSTRACT

Resistant starches (RS) are non-digestible, low molecular weight polysaccharides that, when consumed, act as prebiotics and provide multiple physiological benefits. Colonic fermentation of RS can yield short-chain fatty acids (SCFAs), which have therapeutic potential against metabolic disorders such as diabetes, obesity, overweight, and hypertension. Underutilized fruits have shown remarkable potential as sources of RS that can be fermented into SCFAs. This review explores the possibility of various underutilized tropical fruits as sources of RS and their prospective uses in producing SCFAs. The factors influencing the yield of SCFAs and the pathways and mechanisms of colonic fermentation are also assessed. The physiological benefits of RS-derived SCFAs are also reviewed. Exploiting the under-utilized fruit starches in the production of SCFAs will add value to natural resources and offer various physiological benefits to protect consumers' health.

1. Introduction

The modern era of optimal nutrition has seen advances in food processing technology as well as the discovery of novel nutrients due to customer demand for high-quality products with health-promoting properties (Amiri et al., 2021; Khaneghah, 2021). Efforts in food research are focused on formulating starch-based foods with low glycemic index via resistance to enzymatic hydrolysis and are, thus, of physiological importance. Of interest are foods formulated from starches that can impede or resist enzymatic hydrolysis to glucose (Quintero-Castaño et al., 2020). Food starches can be classified as rapidly digestible starch (RDS), slowly digestible starch (SDS), or resistant starch (RS), depending on how quickly it hydrolyzes in the small intestine (Englyst & Cummings, 1986; Englyst et al., 1987; Lehmann et al., 2002; Englyst et al., 2018). RS passes undigested to the large intestine, fermented by the bacteria to produce short-chain fatty acids (SCFAs). Some of the typical sources of RS are semi-ripe bananas, raw potatoes, whole grains, seeds, nuts, legumes, and cooked-then-cooled foods (Miao et al., 2015; Dobranowski & Stintzi, 2021).

Resistant starch, as a non-digestible starch, can promote the growth

of bacteria in the colon, functioning as a prebiotic (Pandey et al., 2015). A modern health trend that employs RS as a functional fiber and nutraceutical for colon health is consuming foods high in RS (Jaiturong et al., 2020). SCFAs, also known as volatile fatty acids (VFAs) such as acetate, propionate, and butyrate, are produced by bacterial fermentation and are essential for intestinal integrity and health (Dronamraju et al., 2009). SCFAs are used as an energy source by bacteria and intestinal epithelium, which lowers harmful bacteria and facilitates the body's complete absorption of food, resulting in rapid growth and good health (Tsen et al., 2004). They also maintain normal serum lipid-cholesterol levels and further influence the immune system and the absorption of minerals like calcium and iron (Scholz-Ahrens et al., 2007; Whisner & Castillo, 2018; Bojarczuk et al., 2022). The findings of recent studies suggest the therapeutic significance of SCFAs in treating neurological disorders. Preclinical research supports the therapeutic benefits of SCFAs as modulators of several inflammatory and metabolic processes in addition to colonic function (Tang et al., 2022). Fruits have long been valued for their micronutrients, natural sugars, organic acids, and other high-value phytochemicals such as antioxidants and phenolics (Arias et al., 2022). However, research has shown that fruits also contain

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a lot of starch, particularly when raw (Kringel et al., 2020). Numerous investigations conducted on certain fruits, such as bananas, mangoes, and kiwis (Wang et al., 2023), have demonstrated that fruit starches possess unique physicochemical, structural, and functional characteristics, which establish them as intriguing sources of starch (Kringel et al., 2020). The abundance of resistant starch, which has prominent physiological benefits, is the peculiar characteristic of fruit starches (Ribeiro et al., 2022). Fruits are generally produced worldwide; however, even with their high starch potential, some fruits in various regions of the world still need to be properly exploited (Chacha et al., 2021; Okigbo et al., 2021). These fruits may have substantial food and industrial potential if their value chains are thoroughly investigated and comprehended (Mudau et al., 2022). Therefore, exploring the starch content of these fruits, primarily the resistant starch, is essential for supporting their value-addition as well as potentially identifying native starches with suitable qualities for use in the food sector (Silva et al., 2022)This review primarily aims to explore the prebiotic potential of RS, derived from underutilized tropical fruits, as a substrate for the production of SCFAs during intestinal fermentation. In addition, the pathways of fermentation and physiological benefits of RS-derived SCFAs are reviewed.

2. Resistant starch and dietary fiber

Complex carbohydrates (polysaccharides) have gained increasing attention in recent decades as a key component of many dietetic and functional foods. In particular, non-digestible carbohydrates, such as resistant starches (RS) and dietary fiber (DF), are the focus of extensive research due to their bifidogenic and prebiotic potential (Schulz & Slavin, 2021). According to several studies, RS and DF are valued as low glycemic index (GI) foods. Their consumption is linked to reducing the incidence and/or managing cardiovascular disorders, diabetes, obesity, and colon cancer that pose a serious threat to human health (Dega & Barbhai, 2023; Dupuis et al., 2014; Matsuda et al., 2016; Wen et al., 2022). Since they are not broken down by gastrointestinal enzymes, the majority of these indigestible carbohydrates ferments and decompose in the large intestine as a result of bacterial activity. Therefore, these functional components benefit the host by selectively promoting the growth and/or activity of colonic bacteria and thus producing highvalue microbial metabolites with multiple physiological functions (Cerqueira et al., 2019; Dayib et al., 2020; Wen et al., 2022). The rate of fermentation, the subsequent metabolites (ca. SCFAs) yield and profile and the composition of gut microbiota depend on the physico-chemical characteristics of RS and DF (Wang et al., 2019; Wen et al., 2022). The micro-morphology, the degree of structural order (crystallinity type), and molecular size are crucial factors in influencing the metabolite responses microbial composition, and physiological functions (Sun et al., 2020; Wen et al., 2022). Hence, understanding these high-value carbohydrate components' chemistry, structural features, and food distribution sources is essential for developing functional foods and predicting their potential physiological benefits.

Resistant Starch: Starch is the main polysaccharide stored in different parts of plants such as fruits, seeds, grains, roots, tubers, stem core, and rhizomes (Farooq et al., 2021; Zhang & Zhai, 2020). Due to its affordability and widespread availability in various plant sources, starch serves as a vital energy source and makes up the majority of the carbohydrates in the human diet (Singh et al., 2023; Quintero-Castaño et al., 2020). World over, starch is conventionally produced from corn (64 %), potatoes (6 %), wheat (6 %), cassava and sweet potatoes. Presently, there is growing interest in investigating starches from unconventional sources such as fruits, cereals, pseudo cereals, legumes and nuts following United Nations SDG 2.4, which describes "sustainable food production and resilient agriculture practices" (Makroo et al., 2021). Based on their digestibility, starch can be classified as rapidly digestible starch (RDS), slowly digestible starch (SDS), and resistant starch (RS). RDS is the amount of starch that is broken down by enzymes in the upper small

intestine and absorbed into the bloodstream within 20 min of digestion. These are primarily found in many cooked and processed foods, such as breakfast cereals, processed breads, French fries, potato chips, etc. SDS is primarily found in fibrous plants and whole foods such as fruits, vegetables, grains, legumes, and tubers. It can be completely broken down in 20 to 120 min (Englyst & Cummings, 1986; Miao et al., 2015).

On the other hand, the RS is a type of starch resistant to enzymatic digestion in the small intestine and cannot be broken down within 120 min. Starch resistance is based on its structure; starch comprises two glucose polymers: amylose and amylopectin. Amylose is primarily a linear molecule consisting of α -1, 4-linked glucose units, as compared to the branched structure of amylopectin, which additionally contains α -1, 6 linkages. The proportion of these two components and their organization within a starch granule significantly affects the starch's digestibility. These structural characteristics tend to vary among botanical sources. Other structural features include granule size, relative crystallinity, amylose content, and amylopectin chain length. Granule size plays a pivotal role in enzymatic digestion, as smaller granules provide a larger surface area for enzyme interaction, thus enhancing the rate of digestion. The length of amylopectin side chains influences starch digestibility, with longer chains slowing down the process. Additionally, a higher proportion of crystallinity correlates with a faster digestibility rate (RDS; Cornejo-Ramírez et al., 2018; Ramadoss et al., 2019; Gebre et al., 2024).

The functional properties of RS are mainly determined by the arrangement of starch granules and the molecular structural composition of amylose and amylopectin as well as the source of plant foods (Wen et al., 2022). Common dietary sources of RS include grains, legumes, tubers, and some processed foods such as whole-grain bread and pasta (Chen et al., 2024). The type and content of RS varies among various natural and processed foods. It is important to understand that many real-world foods might have a mixture of RS types. Moreover, the amount of RS in various foods may be greatly influenced by variables, including storage conditions, food processing techniques, and the presence of other dietary ingredients (Zhang et al., 2021; Walsh et al., 2022). Based on the physicochemical characteristics and the sources, RS can be classified into five categories such as:

Resistant starch Type 1 (RS1): RS1 is physically inaccessible starch protected by physical barriers, such as plant cell walls and food matrix (Kraithong et al., 2022). Granules of this physically embedded starch are mostly encapsulated within plant cell wall components and protein encasements. These cell wall components give physical protection to the granules rendering them intact against enzymatic digestion (Wang et al., 2023). This type of RS is commonly found in the cell walls of whole grains or partially milled seeds, legumes, and pasta.

Resistant starch Type 2 (RS2): This is typically granular starch (e.g., potatoes, unripe banana, Hylon®VII); usually ungelatinized amylose starch granules with a complex crystalline structure found in raw potato and green bananas. Banana starch stands out as one of the primary sources of RS2. Studies have shown the remarkable resistance of native raw banana starch to enzymatic hydrolysis; up to 84 % of ingested starch remains intact until reaching the terminal ileum (Kaur et al., 2020; Yongliang et al., 2014). This has made banana flour of interest, especially as a functional ingredient. Efforts to enhance the utilization of bananas economically have led to the production of banana starch from unripe fruits, offering a novel strategy to incorporate this versatile ingredient into various innovative products (Kembabazi et al., 2018; Li, Chou, et al., 2020).

Much as resistance in many starches is attributed to amylose, amylopectin chains have also been shown to influence the formation of slowly digestible structures upon retrogradation. This feature is unique to banana starch (Martinez et al., 2018; Yee et al., 2021). Amylopectin chains, as classified based on the internal chain composition of the macromolecules, are: Type 1 is devoid of long internal chains and has a large distribution of short internal chains. In contrast, Type 4 has many long chains and few short chains. These chains are more prone to retrogradation and increase formation of SDS. Banana amylopectin falls into this category (Bertoft, 2017; Yee et al., 2021). Investigations into the fermentability of banana starch have demonstrated its potential as a substrate for colonic fermentation, as evidenced by various parameters evaluated using rat inoculum (Langkilde et al., 2002). In vitro studies have shown that banana starch undergoes significant fermentation in the colon, producing SCFAs such as acetate, butyrate, and propionate (Marta et al., 2022). This fermentation process emphasizes the physiological significance of banana starch as a source of fermentable substrates that contribute to gut health and overall well-being.

Resistant Starch Type 3 (RS3): This is a retrograded starch (e.g., retrograded starch, Novelose®330), characterized by the recrystallization of gelatinized amylose and amylopectin. When some foods are cooked and subsequently cooled, RS3 is produced. As a result of the cooling process, the starch molecules realign and recrystallize, making them even more resistant to enzymatic degradation (Chen et al., 2024). The retrogradation process results in the formation of two subtypes of RS3: RS3a, formed predominantly from retrograded amylose, and RS3b, formed from retrograded amylopectin (Yee et al., 2021). Typically, breadfruit (Artocarpus altilis) starch has emerged as a potential source of starch which, when modified, can yield RS3. Various processing techniques involving the disruption of starch granules, and enzymatic debranching, ultimately yield RS3 content of up to 54.59 % in breadfruit (Mohd Noor et al., 2020). Breadfruit has thus shown potential as a valuable source of RS3, offering both nutritional benefits and functional versatility in a variety of food formulations (Huang et al., 2020)

Resistant starch Type 4 (RS4): This is chemically modified starch generated by several different methods, including the addition of ester cross-links between starch molecules, the addition of chemical constituent groups, or acid hydrolysis and heat treatment. Resistant starch Type 5 (RS5) is an amylose-lipid complex, for example, stearic acid-complexed high amylose starch.

Other than resistant starch, there are other fermentable components in foods, including fruits, such as cell walls, polysaccharides, and dietary fiber. The cell wall of plant foods is a structural framework comprised of cellulose, hemicellulose, and pectin fibers. Cellulose forms fibrils, reinforced by hemicellulose and further strengthened by pectin, resulting in a complex, interwoven three-dimensional architecture. Cellulose, composed of simple glucose molecules linked in a β (1–4) arrangement, contrasts with the structural diversity of hemicellulose and pectin. Pectin, for instance, may exist as linear chains of monomers (homogalacturonan) or molecules with side chains comprising various compounds (rhamnogalacturonans), undergoing esterification and sugar decoration like xylogalacturonan. This intricate fiber structure not only provides support but also encapsulates various nutrients within the plant vacuole, including storage carbohydrates. Among these are fructans, dietary fibers with a fructose backbone, and starch. Starch is stored in granules, such as those found in fruits like (unripe) bananas (Gomes-Ruffi et al., 2009; Puhlmann & de Vos, 2022; Khorasaniha et al., 2023).

Dietary fibers Dietary fiber comprises a wide array of structurally and chemically diverse polymers, composed of various sugar molecules including glucose, xylose, mannose, galactose, arabinose, and rhamnose (Zdunek et al., 2021). These polymers are interconnected through glycosidic bonds, which may follow specific or random patterns, resulting in either linear or branched structures. Importantly, these bonds resist digestion by human endogenous enzymes, rendering dietary fiber valuable for its physiological properties. For instance, pectin, exemplified by its complex structure known as rhamnogalacturonans, exhibits extensive branching with diverse side chains composed of different monomers (Feng et al., 2023; Li et al., 2021; Louis et al., 2021). Dietary fibers contribute to the structure and storage reserves of plant foods and fundamentally impact human health, partly by involving the intestinal microbiota, notably in the colon (Puhlmann & de Vos, 2022).

based polysaccharides; however, fruits and vegetables are also becoming recognized as significant sources of these components. It is now well known that fruits and vegetable and their by-products are a rich source of micronutrients, including vitamins, minerals, and polysaccharides such as dietary fiber and starch. Moreover, fruits are highly valued for their contributions to dietary health, particularly as sources of resistant starch (RS), polysaccharides, and dietary fiber (Wallace et al., 2020). The polysaccharides content in fruits is noteworthy as these components play a crucial role in the overall health benefits associated with fruit consumption. The contents and types of RS in various fruits vary significantly, with bananas being one of the most notable sources. Research indicates that some banana cultivars exhibit high levels of RS, attributed to factors like granule size, crystallinity, and amylose content (Leonel et al., 2021). The nutraceutical potential of green banana flour, which is rich in RS, has been highlighted in studies demonstrating its positive effects on metabolic markers in diabetic models (Munir et al., 2024). Typically, unripe banana flour contains a high content of RS (up to 68 % w/w), along with other bioactive compounds such as phenolics, phytosterols and β -carotene thereby, it can be used as a novel functional ingredient in the prevention of non-communicable diseases (Dibakoane et al., 2022; Ho & Wong, 2016). Dietary fiber, another critical component of fruits, works synergistically with RS to promote gut health and regulate blood sugar levels (Cui et al., 2019). However, more research is needed to explore the specific mechanisms by which these components exert their beneficial effects, as well as the potential for utilizing novel sources of underutilized fruit starches in functional food applications. In this regard, analyzing the potential of underutilized tropical plant seed sources as a novel supply of starch can be related to the sustainable use of natural resources.

2.1. Underutilized tropical fruits

Underutilized fruits (UFs) are referred to as fruit types that experience a meagre utilization capacity and are less economically valuable than more well-known varieties (Chacha et al., 2021). A large number of under-utilized fruits are domesticated, eaten across countries, and are distributed all over the world's diverse agro-climatic regions (Williams & Haq, 2002). Because they are excellent sources of both macro and micronutrients, dietary intake of these fruits has demonstrated significant potential in mitigating hunger, especially in regions like Africa by providing nutrition for the local communities (Okigbo et al., 2021; Okigbo et al., 2021; Chacha et al., 2021). The nutritional, folk medicinal and functional food benefits of numerous under-utilized fruits have been emphasized in recent studies due to their high nutrient density and nutraceutical potential (Okigbo et al., 2021; Okigbo et al., 2021; Chacha et al., 2021).

As the demand for functional foods and nutraceuticals rises in the current era of optimal nutrition, it would be advantageous to expand the pool of available food sources by making use of the abundance of underutilized fruits that have a rich profile of high-value phytochemicals (Okigbo et al., 2021). Given this, under-utilized fruits have the potential to significantly contribute to the health and well-being of the communities by offering a substantial quantity of sustainable raw materials for the production of food products that have physiological benefits (Donno & Turrini, 2020). Moreover, by exploring the potential of under-utilized fruits for value-addition, small-scale farmers and rural communities can improve their household incomes, food security, and nutritional status (Okigbo et al., 2021; Chacha et al., 2021; Donno & Turrini, 2020). Thus, the valorization of such fruits for value-added products will boost their commercial competitiveness, which is essential to extending the availability of healthy foods in developing and underdeveloped nations. Not only do most underutilized fruits have tremendous nutritional and medicinal potential, but they also can produce significant amounts of starch, most of which is resistant starch. Being a rich source of resistant starches, these fruits' resistance to enzymatic breakdown could be attributed to their high dietary fiber and amylose content (Chacha et al.,

2021).

The majority of tropical fruit production is estimated to come from emerging nations, mainly in Asia, the Amazon, and Africa (FAO, 2023). The countries in Southeast Asia and their neighbors, endowed with a climate conducive to many tropical plants, are the centers of origin of many fruit trees. Several less-known fruit species are found in these regions, which have significant potential for commercial exploitation as a sustainable source of starches.

2.2. Native fruits of the African region

The African continent harbors many native fruit species that are potent for food and nutritional security. These fruits can potentially play an important role in solving Africa's significant problems in rural development, hunger, malnutrition, and gender inequality (Nitcheu Ngemakwe et al., 2017). The native fruits of this region are rich in macro, micronutrients, and dietary phytochemicals, among other health benefits. Despite this and the existence of a vast and limitless niche utilization of these fruits in new product development (functional and medicinal products), they are primarily processed on a small scale for the production of a few food products (Nitcheu Ngemakwe et al., 2017) African Breadfruit, guava, and bananas have shown the potential to yield polysaccharides (starch), a possible substrate for fermentation into SCFAs. Their starch and resistant starch yields show promising potential as alternative starch sources.

2.2.1. African breadfruit (Treculia africana L.)

The African Breadfruit (Treculia africana) belongs to the Moraceae family, order Rosales and genus Treculia. It is a large evergreen tree in tropical and sub-tropical humid forests widely distributed in West, East, and Central Africa (Amujiri et al., 2018). The trees yield about 10 t/ha of fruit rich in macro and micronutrients (Jiménez-Escrig et al., 2001). Interestingly, its rich phytochemical content is responsible for its antioxidant, antimicrobial, and wound-healing properties (Ojimelukwe & Ugwuona, 2021). Further studies have revealed that a traditional diet based on African breadfruit can mitigate type II diabetes and obesity (Turi et al., 2015). African breadfruit has a starch content of 69 % (Oderinde et al., 2020), with 30 % amylose content, which is responsible for its resistant starch content. The amylose content is increased to 40 %upon modifications like annealing, thus increasing the resistant starch content. Despite this great potential as a food and medicinal fruit, it remains an underutilized fruit, receiving the least research attention among members of the mulberry family (Ojimelukwe & Ugwuona, 2021).

Other than its consumption as a fruit, breadfruit flour has shown the potential to partially substitute for wheat flour in composite flours used in many confectionaries, bread, pastry, and snack products (Ragone, 2014).

2.2.2. Guava (Psidium guajava L.)

Guava (Psidium guajava), a member of the family Myrtaceae, is a popular fruit widely cultivated in the tropical and subtropical regions of the world (Qin et al., 2017). It is also widely grown in East and Central Africa (Omayio et al., 2019). The fruit pulp weighs about 14.5 g and consists mainly of starch and non-digestible polysaccharides (Chiveu et al., 2016). Whereas guava has a low starch content estimated at 13 % (Abdullah & Chin, 2021), studies have shown that the guava pulp and peel fractions contain a high content of dietary fiber (48.55-49.42 %) and 2.62-7.79 % of extractable polyphenols (Jiménez-Escrig et al., 2001). The fruit has a great nutritional value and is good addition to the diet because of its high dietary fiber content. Guava polysaccharides fed to high-fat diet-induced obese mice induced growth of beneficial bacteria decreased inflammation-related bacteria accompanied by enhanced production of colonic SCFAs, especially butyric acid (Li et al., 2022). Thus, the pronounced effect of guava on the metabolic profile of high-fat diet-induced obese mice is via the gut microbiota pathway,

positioning guava starch as a source of prebiotics (Li et al., 2022). Despite this potential, guava must still be considered a minor fruit in the African cropping system and, thus, underutilized (Okigbo et al., 2021; Omayio et al., 2019). In other parts of the world, Studies have shown that guava is an economically significant fruit (Arévalo-Marín et al., 2021), with the highest production in India, China, Mexico, and Brazil (Altendorf, 2018; FAO, 2024).

2.2.3. Bananas (Musa spp.)

Banana (*Musa* spp.) is one of the world's major fruit crops belonging to the *Musaceae* family. Banana cultivar diversity comprises dessert types, like the Cavendish banana, and cooking types, like plantains; this diversity affects their commercialization (Hinge et al., 2022). The most traded cultivar is the Cavendish banana, which accounts for 50 million tonnes of estimated annual global production (FAO, 2023). Banana, also regarded as a non-true plantain, is a dual-purpose fruit grown in the East African Highlands. In Uganda, bananas are considered a primary staple food (FAOSTAT, 2018), contributing up to 30 % of daily caloric intake (FEWSNET, 2017).

Bananas are a significant household income-generating commodity, giving about US\$1244 annually to over 4 million smallholder households, ranking Uganda as the major banana producer in the East African Highland region (KILIMO, 2013; Marimo et al., 2019). Bananas have been shown to have over 90 % (dwb) total starch and 50 % resistant starch (Le Leu et al., 2007; Yang et al., 2022), with promising potential for being used in the formulation of functional foods (Muranga et al., 2010; Kembabazi et al., 2018). The bananas of this region have been shown to yield more resistant starch than other bananas because of their waxy nature (Gafuma, 2019). Despite this potential, these bananas are still considered an underutilized noncommercial cultivar (Anyasi et al., 2013; Okigbo et al., 2021).

2.3. Native fruits of the Asian region

Asia's most important commercially grown fruit crops are Mango, Banana, citrus, guava, grape, pineapple, papaya, litchi, and apple (Mitra et al., 2008). However, as the continent endures a high prevalence of malnutrition attributed to low dietary diversity (together with low production diversity), the utilization of promising neglected and underutilized species (NUS) that are nutrient-dense and locally available is timely (Li, Yadav, & Siddique, 2020)Moreover, these fruits are rich in macro and micronutrients. Jackfruit and Breadfruit have shown potential to yield abundant starch, a possible substrate for fermentation into SCFAs. Their starch and resistant starch yields show promising potential as alternative starch sources.

2.3.1. Jackfruit (Artocarpus heterophyllus L.)

Jackfruit belongs to the *Moraceae* family and is widely cultivated in Asia (Mitra et al., 2008). It has about 60–80 % seeds, a dry matter basis accounting for 8–15 % of fruit weight, positioning it as a cheap and sustainable carbohydrate source (Zhang et al., 2021). The fruit is eaten as a pulp; however, seeds, usually disposed of as waste, have shown potential as a starch source. Its seeds yield about 16–25 % starch (Zhang et al., 2016) and have an amylose content of about 22.10–38.34 % (Zhang et al., 2021), which makes them a potential source of resistant and slowly digestible starch. The seed flour has been used in the production of particular starch-based food in jackfruit-wheat flour composite in bakery products, extruded products, and traditional products, specifically in Asian countries (Suzihaque et al., 2022; Waghmare et al., 2019). In addition, jackfruit by-products have been used to enhance protein content and dietary fiber in meat analogs (Hamid et al., 2020).

Further research is essential to expand the potential usage of jackfruit, which has not yet reached its full potential despite its commercial value and significant role in ensuring food security (Li et al., 2022; Mitra et al., 2008; Zhang et al., 2021).

2.3.2. Bread fruit (Artocarpus altilis)

Breadfruit (Artocarpus Altilis) belongs to the family of Moracea, native to Malaysia and now grown all over the tropics (Wang et al., 2011). Along with a related species known as breadnut (Artocarpus camansi), breadfruit has long been used as a staple diet in the Pacific islands and is now widely available and utilized across the tropics. The fruit is an underutilized but highly nutritive crop containing complex carbohydrates and low in fat (Mehta et al., 2023). Breadfruit flour has been shown to contain over 70 % starch, which has been modified to give about 50 % resistant starch type 3 (Mohd Noor et al., 2020; Turi et al., 2015). The nutritional, functional, technological and physicochemical properties of breadfruit have been shown to positively influence the production of healthier food products using breadfruit flour and starch, such as meat analogs, prebiotic beverages and carbohydrate staples (Mehta et al., 2023). The nutritional composition of breadfruit flour suggests that it has the potential to mitigate type II diabetes and obesity in Oceania and elsewhere in the tropics where breadfruit is grown, probably due to the high amylose content (Turi et al., 2015). Furthermore, the high fiber content of breadfruit can help lower bad cholesterol and triglycerides, which lowers the risk of heart disease. It has been suggested that breadfruit protects the body from heart attacks and heart disease (Olaove & Ade-Omowave, 2011). Even though it is a staple crop high in carbohydrates and therefore a priority crop in reducing hunger and ensuring food security, it still needs to be used more, with particular focus paid to its large-scale commercial cultivation (Deivanai & Bhore, 2010; Mausio et al., 2020).

2.4. Native fruits of the Amazon region

The Amazon rainforest is the largest continuous tropical rainforest. It has a significant reserve of biological diversity, indicating a high potential for use by humanity, including as a new food alternative (Silva et al., 2022). Amazon's great fruitful diversity favors the search for innovative raw materials, enabling them to be explored as alternative sources of ingredients for the industry.

With the tremendous vegetative diversity in the Amazon, there is the possibility of alternative sources for the supply of starch, in which raw materials destined for disposal can be used and, consequently, added value (Arévalo-Marín et al., 2021). Peach palm and St. Hill have shown the potential to yield starch, a possible substrate for fermentation into SCFAs. Its starch yield and resistant starch show promising potential as alternative starch sources.

2.4.1. Peach palm (Bactris gasipaes Kunth)

Bactris gasipaes is a palm tree that was one of the first plants domesticated for logging by indigenous people in pre-Columbian times in southwestern Amazonia (Ferrari Felisberto et al., 2020). The peach palm fruit has 79 % starch, of which 12.40 % is amylose and 66.60 % amylopectin, presenting itself as an alternative for higher-scale starch production (de Melo Neto et al., 2017) and a possible source of resistant starch (Pires et al., 2021). The fruit is a rich source of bioactive compounds with significant antioxidant capacity and nutritional, both macro and micronutrient and functional properties (González-Jaramillo et al., 2022). Despite being an important food source and presenting opportunities for sustainable industrial production, its industrial potential is still poorly explored (Soares et al., 2022). Despite its widespread cultivation area, population, and genetic diversity, the species are at risk due to deforestation, neglect, and the climate crisis, yet with sustainable innovation, it has the potential to advance the sustainable development goals (SDGs González-Jaramillo et al., 2022). Fig. 1 depicts the images of some important underutilized fruits.

2.4.2. St. hill (Solanaceae) S. lycocarpum

Solanum lycocarpum St. Hill (*Solanaceae*) is a common fruit native to Brazilian Cerrado. Its fruits weigh from 400 g to 900 g and are consumed fresh or cooked in some regions (Pascoal et al., 2013). The abundance of



Fig. 1. Images of some important underutilized fruits. A: African Breadfruit, B: Peach palm, C: Cooking banana, D: jackfruit, E: guava: F: St. Hill. The structure of the large intestine shows where microbial fermentation of resistant starch occurs.

S. lycocarpum and its high fruit production have made it a desirable target for biotechnological exploitation. Of interest is its high content of starch (50–80 %), 10–30 % of which is resistant starch, thus making *S. lycocarpum* a hypoglycemic agent (Clerici et al., 2011; Pereira et al., 2020). It has further shown prebiotic potential by promoting acetate production in broth fermentation experiments using *Lactobacillus acidophilus* and *Lactobacillus casei* (Pereira et al., 2020). Despite this rich potential, St. Hill fruit and its processing wastes still need to be utilized for starch extraction, which can be used as a substrate to produce SCFAs. The RS potential for different underutilized fruits from three main production regions is depicted in Table 1.

Table 1

Underutilized fruits as potential sources of resistant starch.

Region of underutilization	Fruit	Resistant Starch (%)	Other fermentable components	Reference
Africa	African Breadfruit(<i>Treculia</i> <i>Africana</i> Decne)	8.2 RS2	Crude fiber (0.79 %)	Oderinde et al., 2020, Tan et al., 2014,
	Cooking Banana(Musa spp)	40–60 RS2	Not mentioned	Paramasivam et al., 2021, Yang et al., 2022, Olawoye et al., 2022
	Guava(Psidium guajava)	Not mentioned	Crude polysaccharide	Li et al., 2022
Asia	Breadfruit(Artocarpus altilis)	48 RS2 and 54 Retrograded starch (RS3)	Not mentioned	Otemuyiwa & Aina, 2021, Mohd Noor et al., 2020
	Jack fruit (Artocarpus heterophyllus)Lam	30–77 RS2	Seed starch extracted from fruit waste	Kittipongpatana & Kittipongpatana, 2015, Zhang et al., 2021, Lee et al., 2022
Amazon	Peach palm(Bactris gasipaes) Kunth	15–20 RS2	6.7 % dietary fiber and pectic polysaccharides	Pires et al., 2021, Ferrari Felisberto et al., 2020, Soares et al., 2022
	St. Hill (Solanaceae) <i>S. lycocarpum</i>	10–32 RS2	Not mentioned	Pascoal et al., 2013, Clerici et al., 2011

3. Fermentation mechanisms of starch form underutilized fruits

3.1. Colonic fermentation

The large intestine is the last part of the gastrointestinal tract (GIT) that trails after the small intestine and ends at the anus. It is also called the large bowel, where food waste is formed into feces, kept, and excreted; it comprises the colon, rectum, and anus. The colon is divided into the cecum, the ascending colon (travelling up), the transverse colon (travelling across to the left), the descending colon (travelling down), and the sigmoid colon (headed back across to the right). The caecum is the 'pocket' where most of the microbes are confined, while fermentation occurs in the ascending and transverse colon, with most SCFAs found in the ascending colon (Tan et al., 2014; Bazira, 2022).

The human colon is a habitat for over 3.8×10^{13} bacteria, predominantly composed of Bacteroidetes, Firmicutes, Proteobacteria, and Actinobacteria (Gill et al., 2006; Zhou, Ma, & Hu, 2021). This habitat is regulated by colonic anaerobic fermentation using available macronutrients; the fermentation rate, sites, and metabolite profile depend on the energy source of the microbes. Therefore, diet (in the long term or even a meal in the short term) influences microbiota diversity (Ratanpaul et al., 2023; Rose et al., 2010). These bacteria ferment RS and dietary fiber to specific SCFAs, mainly acetate, propionate, and butyrate (Yao et al., 2023). The structure of the large intestine showing the site for microbial fermentation is depicted in Fig. 2.

3.1.1. Pathways involved in colonic fermentation

Anaerobic fermentation is an essential function of the large colon

through which SCFAs are formed (Wang et al., 2019). While most (90–95 %) of SCFAs from carbohydrate sources are acetate, propionate, and butyrate, there are other smaller proportions of fatty acids, namely; valerate, hexanoate, and branched-chain fatty acids (BCFAs), such as isobutyrate and isovalerate which come from protein breakdown (Mortensen & Clausen, 1996; Wang et al., 2019). However, in situations of carbohydrate unavailability, protein fermentation rises, resulting in higher concentrations of potentially toxic products, such as ammonium (NH4⁺) ions whose chronic elevations are known to be harmful to gut health and are linked to the progress of colonic cancer (Le Leu et al., 2007; Grant et al., 2019). Up to (90–95 %) of SCFAs are absorbed by colonic epithelial cells, and only 5–10 % are excreted in the feces (Wu et al., 2018). The fermentation pathway leading to the formation of SCFAs in the colon is depicted in Fig. 3.

There are numerous pathways through which bacteria ferment sugar; upon phosphorylation, the sugar goes into either the glycolytic pathway, Entner–Doudoroff pathway, or the *Bifidobacterium* pathway, where it is transformed into pyruvate and, in some cases, pyruvate and acetyl-phosphate (Markowiak-Kopeć & Śliżewska, 2020). The Embden–Meyerhof–Parnassian (glycolytic) pathway is the main colonic catabolic pathway in enterobacteria, clostridia, homofermentative lactic acid bacteria, and propionibacteria. It produces only pyruvate as a partial oxidation product (Rauf et al., 2022). Regarding gluconate fermentation, *Zymomonas* and *Escherichia coli* use the Entner-Doudoroff pathway for alcoholic fermentation (Scotti, 2004). The *Bifidobacterium* and produces two acetate molecules and one lactate. The phosphoketolase pathway, which is common in heterofermentative lactic acid bacteria

Proximal colon has the highest concentration of SCFA; it is where most of fermentation of resistant starch occurs and absorption of SCFAs The fermentation of resistant starch begins in the Caecum, 'pocket', habitat for microbes

Fig. 2. Microbial fermentation of resistant starch into SCFAs in the colon (Li et al., 2021). The fermentation pathway leading to the formation of SCFAs in the colon.



Fig. 3. Pathway leading to the formation of SCFA in the colon (Scotti, 2004; Tran et al., 2020). In vitro fermentation batches of resistant starch into SCFAs using a colonic simulator and Biomass fermentation bioreactor.

and occasionally in *Bifidobacterium*, produces an extra acetyl-phosphate molecule (Louis et al., 2007). The chief product of this catabolism is SCFAs. Acetic acid is the most plentiful SCFA in the colon, accounting for more than half of the total SCFAs in feces (Scotti, 2004). Intestinal microorganisms produce acetic acid through two main pathways, the most commonly used being the fermentation of indigestible carbohydrates (Markowiak-Kopeć & Śliżewska, 2020). Some species of *Clostridium*, including *Fusobacterium nucleatum* and *Butyrivibrio fibrisolvens*, as well as *C. acetobutylicum*, *C. butyricum*, *C. pasteurianum*, and *C. perfringens*, are involved in butyric fermentation. For propionic fermentation, the primary substrates are glucose and lactate; their progression varies depending on the bacteria (Louis et al., 2007).

3.1.2. Effect of different substrates (resistant starch) on fermentability into SCFAs

Different RS sources have distinctive structures that affect the overall gut microbiota diversity (Deehan et al., 2020), i.e. the different bacterial taxa possess adaptations towards the respective substrates mainly due to their distinct crystalline and cross-linked structures (Zhou, Fu, et al., 2021). In addition, different starch modification methods (annealing and linearization) further affect its fermentation (Deehan et al., 2020). Studies on RS type 4 (RS4) have shown that only a few microbes possess the specialized adaptations needed to access and utilize the molecular structures of RS4 competitively (Xu et al., 2007). However, the same bacterial taxa (*B. adolescentis, R. bromii, and E. rectale*) are also able to selectively colonize resistant starch type 2 (RS2) granules (Leitch et al., 2007).

Eubacterium rectale and Bacteroides thetaiotaomicron have a restricted ability to ferment RS2 and RS3 compared to Bifidobacterium adolescentis and Ruminococcus bromii. In co-culture, however, R. bromii demonstrated exceptional in stimulating RS2 and RS3 fermentation by the other three bacterial species, even in a medium that does not permit the growth of R. bromii itself, thus proving that R. bromii has an essential role in the fermentation of RS3 in the human large intestine (Ze et al., 2012). Studies have further revealed that the comparative abundance of Bifidobacterium significantly rises with RS4; RS4 produces the highest levels of acetate, while RS2 produces the highest levels of propionate and butyrate. Megamonas and Prevotella are positively associated with the higher production of propionate and butyrate. Whereas all resistant starch types positively promote intestinal health, RS2 showed more abundant probiotic functions (Liang et al., 2021). However, more studies have shown that RS3 produces twice as much butyrate than RS2. In detail, fermentation of RS2 supports higher numbers of Bifidobacterium spp. RS3 samples stimulated the growth of Faecalibacterium spp.,

Eubacterium spp., and *Lachnospiraceace* better than the RS2 (Arcila & Rose, 2015; Plongbunjong et al., 2017; Zhou, Ma, & Hu, 2021).

Other factors that affect colonic fermentation are the particle size of the starch substrate and physicochemical characteristics, such as the water-holding capacity of the starch, pectin, and starch content (Yao et al., 2023). Starches are inherently insoluble and thus have poor functional properties (swelling power, solubility, and water absorption capacity). They must be modified physically and/or chemically to enhance their positive attributes. Water holding capacity has shown greater associations with microbial community changes, functional profiles, and fermentation outcomes (Yao et al., 2023)Thus, it may be concluded that modifying the water-holding capacity of some plantbased food components in diets could alter the microbiota and obtain desirable fermentation outcomes.

In addition, starch-lipid complexes in the starch substrate significantly raise the comparative abundance of some beneficial gut microbiota, such as *Roseburia* and *Prevotella* (Zhou, Fu, et al., 2021). Gut transit time is another aspect that affects colonic fermentation. Whereas gut transit time is primarily disregarded in many gut microbiome studies, there is growing evidence that whole gut transit time (WGTT), segmental transit time (SITT), or Colonic transit time (CTT) influences microbial composition (Procházková et al., 2023).

Variations in gut transit time have been linked to changes in fecal pH, fecal microbial load, and composition but, most importantly, with diet-microbe interactions and microbial metabolism, including shifts from saccharolytic to proteolytic fermentation (Procházková et al., 2023). Again, RS has been implicated in lowering gut transition time and increasing fecal bulk density (Topping & Clifton, 2001).

3.2. In vitro fermentation

Short-chain fatty acids have vast industrial applications in food, textile, cosmetics, detergents, and pharmaceutics, to mention but a few, thus positioning them as potential products for commercial industrial production (Sun et al., 2020). Several in vitro fermentation methods have been devised, namely static and dynamic batches, cells and ex-vivo models, and animal and human studies, to meet the SCFA's needs for the food and pharmaceutical industries (Luo et al., 2020). In vitro fermentation models offer exceptional advantages by closely simulating the microbial composition and action in the GIT and are thus commended replacements to in vivo studies. In addition to in vitro models being comparatively modest, they have no ethical restrictions and can be effectively controlled (Wang et al., 2019). In vitro models further allow for quantifiable measurements of metabolites formed by microbiota

after fermentation of specific substrates that may significantly impact the host's health (Wang et al., 2019). However, these models are limited by their failure to involve epithelial or immune cells, limiting their applicability to metabolite function studies in the colon (Wang et al., 2019). Fig. 4 depicts the in vitro fermentation batches of resistant starch into SCFAs using a colonic simulator and Biomass fermentation bioreactor.

To closely mimic physiological fermentation, conditions in the mouth, stomach, and small intestine are reproduced in vitro before simulating colonic fermentation through in vitro static batch fermentation models. These fermenters are generally closed anaerobic environments in sealed tubes or reactors with single bacterial strains or mixed cultures of gut microbiota from animals or humans (Wang et al., 2019). The cultures are usually from human or pig fecal inoculum. Pigs, being monogastric omnivores, tend to have almost similar colonic habitation of microbes to humans, dominated by Firmicutes and Bacteroidetes (Lancheros et al., 2020). Other than using fecal inoculum, microbes have been used to produce SCFAs from bio-based substrates; Saccharomyces cerevisiae has been used to ferment SCFAs from yeast extract, and Pseudomonas sp. has been used to produce isobutyric acid (Lang et al., 2014; Shi et al., 2019; Yu et al., 2016). However, the low vield and high feedstock cost limit their practical applications for largescale production (Yu et al., 2016).

In vitro, anaerobic fermentation faces a drawback of methanogenesis, which causes relatively low yield, making it expensive and unsustainable. Thus, more studies on the optimization of substrate concentration and inhibition of methanogenesis need to be done in addition to the economic feasibility (Simonetti et al., 2021). There is evidence that RS, compared to other non-starch polysaccharides, favors the production of SCFAs, especially butyrate (Zhou et al., 2013). Just as it is for microbial fermentation, starches from various botanical sources, when used as substrates in the bioreactor fermenters, are fermented differently and give varying yields of SCFAs (Singh et al., 2023). The differences in yield could also be attributed to the experimental method used, sample preparation, type, amount, and structure of RS, and feeding duration (Ferguson & Jones, 2000). Nevertheless, under tightly controlled experimental conditions, the starch's nature is vital in modulating bacterial fermentation and the amount and type of SCFA produced (Zhou et al., 2013). The utilization of different fermentation mechanisms and resistant starch sources to yield SCFAs is depicted in Table 2.

3.3. In vivo models

In vivo models of RS fermentation aid in understanding the complex interactions between RS and the gut microbiota, thus offering insights into its potential health benefits. These models involve use of animal subjects, such as rodents or pigs, which closely mimic human physiology and gastrointestinal processes (Domínguez-Oliva et al., 2023). By feeding these animals with diets containing specific types and amounts of RS, the effects of RS fermentation on gut microbial composition, metabolite production, and host physiology are monitored (Jha et al., 2019). In addition, parameters, including changes in SCFA concentrations, modulation of gut barrier function, and alterations in host metabolic parameters can be studied (Overby & Ferguson, 2021). Animals and human models have been used in different prebiotic studies, as shown in Tables 3 and 4. Wister male rats are commonly used as compared to females whose sex hormone changes may affect the studies (Quirós Cognuck et al., 2020). Crustacean models have recently been used (Tran et al., 2020). For human models, people of different ages, genders, or carrying various diseases can be selected to conduct the experiments, the experiments are generally conducted with a randomized, double-blind, placebo-controlled design (Deehan et al., 2020).

3.4. Physiological functions of short chain fatty acids (SCFAs)

Due to their physiological importance, SCFAs are being produced industrially using polysaccharide substrates, including resistant starch, non-starch polysaccharides, dietary fiber, sugar alcohols, and oligofructose yielding 95 % SCFAs (acetic acid, propionic acid, and butyric acid). Industrial production has further established optimal ratios (60:20:18, 60:25:10, or 60:25:15), which are effective at causing physiological importance (Tan et al., 2014; Wong et al., 2006). Industrial in vitro fermentation of polysaccharides has yielded synthetic SCFAs, which have been used in studies to exhibit their physiological importance further.



Fig. 4. In vitro fermentation of starch into SCFAs (Xiao et al., 2018; Luo et al., 2020). A. Fermentation using a colonic simulator, B. Biomass fermentation using a bioreactor.

Table 2

Fermentation of starch from various sources along with subsequent yield of SCFAs.

Type of fermentation	Inoculum	Type and source of starch	Microbe involved	SCFA content (%)	Reference
In vitro	Human fecal inocula	Resistant starch type5 (RS5)	Roseburia and Prevotella	Propionate (27), acetate (33)	Zhou, Ma, & Hu, 2021
		Saccharides, saccharide esters, fructooligosaccharides, starches, modified starches and non-starch polysaccharides	Not mentioned	Acetate (23), propionate (5), butyrate (16)	Ferguson & Jones, 2000
		Resistant starch type 2 (RS2) and type 3 (RS3)	Bifidobacterium spp.	RS2 (61:19:20) RS3 (54:10:36) Acetate: propionate: butyrate	Plongbunjong et al., 2017
		Tomato flour	Bifidobacterium and Clostridium	Acetate (65), propionate (22), and butyrate (13)	Coelho et al., 2023
		Peach palm fruits (Bactris gasipaes)	Not mentioned	Acetate (16.2), propionate (6.2), and butyrate (11.2)	Cantu-Jungles et al., 2017
	Simulated digestion	Grey mangrove (Avicennia marina (Forssk.) Vierh.	Megasphaera, Mistuokella, Prevotella, and Megamonas.	Acetate (80) and propionate (20)	Yuan et al., 2022
	Simulator of the human gut microbial ecosystem	A short-chain fructooligosaccharide	Bifidobacteria and Lactobacillus	Acetate (57), propionate (35), and butvrate (8)	Tiwari et al., 2021
	Pig fecal	Resistant starch from native purified starches	Not mentioned	Acetate (75), propionate	Giuberti et al., 2014
	Mixed human fecal and bacteria	dietary fiber and resistant starch (RS2- and RS3- resistant starches)	R. bromii	Not mentioned	Ze et al., 2012
	MRS broth	Solanum lycocarpum St. Hill starch	Lactobacillus acidophilus (LA5), Lactobacillus casei (LC01)	Acetate	Pereira et al. (2020)
In vivo	Placebo	Type-IV resistant starches (RS4s)	Eubacterium rectale, Oscillibacter spp, and Ruminococcaceae	Propionate (10) and butyrate (12)	Deehan et al., 2020
	Pig porcine large intestine	Fruit cell-wall matrix (mango) or a soluble cell- wall polymer (pectin),	Faecalibacterium prausnitzii (Pectin), and Lactobacillus mucosae (Mango)	Propionate (5), acetate (60), butyrate (10)	Grant et al., 2019
	Wister rat model	banana pulp flour	L. acidophilus, Bifidobacteria spp and E. coli	Not mentioned	Mahore & Shirolkar, 2018
	Mud crab (<i>Scylla</i> <i>paramamosain</i>), a crustacean model	Galactooligosaccharides (GOS) and resistant starch (RS)	GOS (Bacteroidetes), RS (Tenericutes)	Acetate (80), Propionate (15), and Butyrate (5)	Tran et al., 2020

SCFAs: Short chain fatty acids.

SCFAs have been shown to improve the integrity of the intestinal tight junction barrier in human intestinal Caco-2 cells, pro-resolving mediators due to their already-known role in the immune response modulation in COVID-19 patients. They have shown the ability to alleviate gut inflammation in murine colitis, have an anti-inflammatory effect on natural killer cells, have neuroprotective and neurodegenerative effects in the peripheral nervous system, and alleviate stressinduced brain-gut axis alterations (Grütera et al., 2022; Isayama et al., 2023; Jardou & Lawson, 2021; Lee et al., 2022; van de Wouw et al., 2018; Zaiatz-Bittencourt et al., 2023). The Physiological benefits of SCFAs derived from starches of different fruit sources are depicted in Table 3.

Resistant starch which is a vital substrate for the fermentation into SCFAs, is known to have physiological importance: glucose tolerance, superior cellular sensitivity to insulin, and improved post-meal satiety (Bojarczuk et al., 2022). Resistant starch does this by modulating the intestinal microbiota, resisting complete digestion into dextrins, which are high glycemic index products, decreasing inflammation, and regulating the hypoglycemic-related enzymes (Liu et al., 2022). Dietary feeding of RS3 has exhibited effectiveness in the modulation of glucose and lipid profile in serum and in suppressing oxidative stress in rats under diabetic and high-fat diet conditions (Reddy et al., 2017). Fiber (essentially plant polysaccharide molecules) has further exhibited the potential to promote healthy fecal bulk during constipation and diarrhea (Qi & Tester, 2019). Whereas it is commonly known that dietary fiber promotes defecation, on the contrary, it regulates the luminal volume of fecal matter in health and disease. This effect is mainly linked to soluble fibers that modulate the fecal solid to water volume and water retention/absorption/loss from the body through the fecal matter (Qi & Tester, 2019).

A few recent pediatric research have demonstrated the beneficial

effect of dietary fibers and/or different fiber blends on constipation, abdominal pain, and irritable bowel syndrome (Salvatore et al., 2023). Animal studies have shown that RS can effectively decrease adiposity and weight gain in obesity-prone and obesity-resistant rats due to reduced energy intake, deviations in gut hormones, and extensive bowel carbohydrate fermentation (Belobrajdic et al., 2012). In several subjects, RS further decreases hyperglycemic, hyperinsulinemic, and hyperlipidemic reactions by controlling gluconeogenesis, boosting glycogenesis, sustaining glucose and lipid homeostasis, and alleviating pancreatic dysfunction (Meenu & Xu, 2019). In addition, prebiotic treatment with RS instigated stable alpha and beta-diversity alongside altered fecal butyrate and calprotectin concentrations in patients with Parkinson's disease, prompting research into the effect of RS on the modification of the clinical course of Parkinson's disease (Becker et al., 2022)Resistant starch from underutilized fruits has the potential to ferment into SCFAs of physiological importance, as Table 3 shows.

Since SCFAs have shown therapeutic potential, especially against metabolic disorders, their fermentation ought to be made commercially sustainable, which calls for using even the underutilized RS sources as a substrate for industrial anaerobic fermentation and packaging of the SCFAs for use as drugs and or food supplementations. The industrial utilization of underutilized fruit starches aligns with the Sustainable Development Goal 2 (SDG2) of the 2030 Agenda, which aims to "end hunger, achieve food security and improved nutrition and promote sustainable agriculture". It is important to note that the steady progress in achieving this SDG over the last couple of decades was hampered by the persistently high numbers of hungry and those suffering from undernutrition and yet the emergence of obesity and diet-related noncommunicable diseases worldwide, which is a health paradox that requires urgent attention.

Physiolo Starch source Fruit source

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Physiologic	al benefits of SCFAs derived from starches of di	fferent sources.			
Starch source	Starch source	Type of starch	SCFA (%)	Physiological benefits	Reference
Fruit sources	Green Banana (<i>Musa</i> sp.)	Resistant starch (RS)	Acetate (36), propionate (38), butyrate (26)	attenuates non-alcoholic fat liver accumulation and increases short-chain fatty acids production in high-fat diet-induced obesity in mice	Rosado et al., 2020
	Green banana Biomass	Resistant starch type 2 (RS2)	Not mentioned	improves plasma low-density lipoprotein particle functionality in Type II diabetic patients	Lotfollahi et al., 2020
	Banana (<i>Musa acuminata, AAA</i> Group, 'Dwarf Cavendish')	Native banana starch (RS2)	The beneficial effect of RS is related to fermentation by microbiota in the colon and subsequently generates short- chain fatty acids (SCFAs).	Alleviates Type 2 diabetic mellitus	Arias-Córdova et al., 2021
	Green dwarf banana(Musa spp. AAA)	Green dwarf banana flour (RS2)	Butyrate (100)	Prevents intestinal inflammation in rat colitis	Scarminio et al., 2012
	Jackfruit	Polysaccharides	Propionate (100)	Alleviates obesity-modulating gut microbiota in high-fat diet-induced rats	Zhang et al., 2016
	Guava	Crude polysaccharides	Acetate (67), propionate (19), butyrate (20)	ameliorate high-fat diet-induced obesity in mice in reshaping gut microbiota	Li et al., 2022
	Fruit powders,32 g blueberry, 15 g dragon fruit, 27 g yacon, 19 g lemon, 17 g purple sweet potato, 25 g papaya)	Prebiotic fructooligosaccharides	Acetate, propionate, butyrate, isobutyrate, isovalerate, valerate	Relieves constipation	Shi et al., 2019
	Cerrado and Pantanal plants	fruit flours	Acetate (31), propionate (27), butyrate (42)	modulate gut microbiota imbalances, relevant in the post- COVID-19 era	Mauro et al., 2022
	Beetroot	Red beetroot concentrate	Acetate (47), propionate (13), butyrate (22), isobutyrate (7), isovalerate (3), valerate (8)	Modulation of gut microbiota in healthy human volunteers	Wang et al., 2023
	Banana (<i>Musa</i> AAB)	Resistant starch type 3 (RS3)	Not mentioned	Anti-diabetic effect on Wister rats	Reddy et al., 2017
SCFAs: Shor	rt chain fatty acids.				

4. Conclusion and future prospects

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Historically, rice, corn, cassava, and potato have been referred to as the conventional starch sources. However, with the increased urbanization and climate change, there is growing demand in tropical countries to utilize their native fruits as alternative starch sources. Due to their high RS content and abundance of starch, the profile and potential health benefits of starches from the fruits of various plants have been suggested, including peach palm (Bactris gasipaes) Kunth, African breadfruit (Treculia Africana Decne), breadfruit (Artocarpus altilis), jackfruit (Artocarpus heterophyllus) Lam, and green bananas (Musa Spp). Both in vitro and in vivo, it has been demonstrated that these starches can be used as substrates for microbial fermentation, producing physiologically important SCFAs, including acetate, propionate, and butyrate, that may be used therapeutically to treat metabolic diseases. SCFAs offer a versatile range of applications across different industries; in the food industry, they can be used to develop functional foods, natural preservatives, and flavor enhancers. In pharmaceutics, SCFAs have the potential for disease prevention and targeted drug delivery, while in agriculture, they contribute to sustainable agronomic practices, animal health, and bio-based material production. Further studies on the mechanisms through which SCFAs are therapeutically potent need to be investigated using modern technologies, including in vivo trials, molecular docking, clinical trials, and computational techniques. Furthermore, effective agricultural practices must be used to produce these natural fruits as a commodity and help the tropical countries that are their primary producer.

CRediT authorship contribution statement

Stellamaris Kembabazi: Writing - original draft, Methodology, Investigation, Formal analysis, Data curation. Martin Mutambuka: Writing - review & editing, Validation, Supervision, Methodology. Radhiah Shukri: Writing - review & editing, Validation, Supervision, Methodology. Farooq Anwar: Writing - review & editing, Validation, Supervision, Methodology. Norhasnida Zawawi: Writing - review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

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Data availability

Data will be made available on request.

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